# Chapter 34

# Vertebrates

## *Lecture Outline*

### Overview: Half a Billion Years of Backbones

- In the early Cambrian period, 540 million years ago, slender 3-cm-long animals swam in the oceans.
- These animals lacked armor and appendages, but they left behind a remarkable legacy.
- They were the ancestors of the **vertebrates**, one of the most successful groups of animals ever to swim, walk, slither, or fly.
- Vertebrates derive their name from vertebrae, the series of bones that make up the vertebral column, or backbone.
- For nearly 200 million years, vertebrates were restricted to the oceans, but about 360 million years ago, the evolution of limbs in one lineage of vertebrates set the stage for these vertebrates to colonize land.
    - On land, vertebrates diversified into amphibians, reptiles (including birds), and mammals.
- There are about 52,000 species of vertebrates, far fewer than the 1 million insect species on Earth.
- What vertebrates lack in species diversity, however, they make up for in *disparity*.
    - Plant-eating dinosaurs, at 40,000 kg, were the heaviest animals to walk on land.
    - The biggest animal that ever existed is the blue whale, at 100,000 kg.
    - A fish discovered in 2004 is only 8.4 mm long and has a mass roughly 100 billion times smaller than that of a blue whale.

### Concept 34.1 Chordates have a notochord and a dorsal, hollow nerve cord.

- Vertebrates belong to one of the two major phyla in the Deuterostomia, the **chordates**.
- Chordates are bilaterian animals belonging to the Deuterostomia clade.
    - Two phyla of invertebrate deuterostomes—the urochordates and the cephalochordates—are most closely related to the vertebrates.
    - Along with the hagfishes and the vertebrates, they make up the chordates.

#### *Four derived characters define the phylum Chordata.*

- Although chordates vary widely in appearance, all share the presence of four key characteristics at some point in their lifetime: a notochord; a dorsal, hollow nerve cord; pharyngeal slits or clefts; and a muscular, post-anal tail.

1. The **notochord**, present in all chordate embryos, is a longitudinal, flexible rod located between the digestive tube and the nerve cord.
   - The notochord is composed of large, fluid-filled cells encased in fairly stiff, fibrous tissue.
   - The notochord provides skeletal support throughout most of the length of a chordate.
   - In larvae or adults that retain the notochord, it also provides a firm but flexible structure against which muscles can work during swimming
   - In most vertebrates, the notochord remains only as a remnant, surrounded by a more complex, jointed skeleton.
   - For example, the notochord is the gelatinous material of the disks between the vertebrae in humans.
2. The dorsal, hollow nerve cord of a chordate embryo develops from a plate of ectoderm that rolls into a tube dorsal to the notochord.
   - Other animal phyla have solid nerve cords, usually located ventrally.
   - The nerve cord of the chordate embryo develops into the central nervous system: the brain and spinal cord.
3. The digestive tube of chordates extends from the mouth to the anus.
   - The region posterior to the mouth is the pharynx.
   - In all chordate embryos, a series of pouches separated by grooves forms along the sides of the pharynx.
   - In most chordates, these grooves (known as **pharyngeal clefts**) develop into **pharyngeal slits** that allow water that enters the mouth to exit without continuing through the entire digestive tract.
   - In many invertebrate chordates, the pharyngeal slits function as suspension-feeding devices.
   - In vertebrates (with the exception of vertebrates that have limbs, the **tetrapods**), the slits and the structures that support them have become modified for gas exchange and are known as gill slits.
   - In tetrapods, the pharyngeal clefts play an important role in the development of parts of the ear and other structures in the head and neck.
4. Most chordates have a muscular tail extending posterior to the anus.
   - In contrast, nonchordates have a digestive tract that extends nearly the whole length of the body.
   - The chordate tail contains skeletal elements and muscles, and provides propulsive force in many aquatic species.

### *Invertebrate chordates provide clues to the origin of vertebrates.*

- **Lancelets** (Cephalochordata) are bladelike in shape.
- The notochord, dorsal hollow nerve cord, numerous gill slits, and post-anal tail all persist in the adult stage.
- The larvae are suspension feeders, feeding on plankton in the water column.
- Adult lancelets are up to 5 cm long.
- Following metamorphosis, lancelets settle with their posterior end buried in the sand and their anterior end exposed for feeding.
- Cilia draw seawater into the lancelet’s mouth, where a net of mucus secreted across the pharyngeal slits removes tiny food particles as the water passes through the slits, and the trapped food enters the intestine.

- The pharynx and pharyngeal slits play a minor role in gas exchange, which occurs mainly across the external body surface.
- A lancelet frequently leaves its burrow to swim to a new location.
- Though feeble swimmers, their swimming mechanism resembles that of fishes through the coordinated contraction of serial muscle blocks.
    - Contractions of chevron-shaped muscles flex the notochord and produce lateral undulations that thrust the body forward.
    - The muscle segments develop from blocks of mesoderm, called *somites*, arranged serially along each side of the notochord of the embryo.
- Data from a series of recent molecular studies suggest that **tunicates** (Urochordata) are more closely related to other chordates than are lancelets.
- Tunicates most resemble chordates during their larval stage, which may last only a few minutes.
- The tunicate larva uses its tail muscles and notochord to swim through the water in search of a suitable substrate on which it can settle, guided by cues from light- and gravity-sensitive cells.
- Tunicates undergo a radical metamorphosis to form a sessile adult with few chordate characteristics.
    - Its tail and notochord are resorbed, its nervous system degenerates, and its organs rotate 90°.
- Tunicates are suspension feeders.
    - Seawater passes inside the animal via an incurrent siphon, through the pharyngeal gill slits, and into a ciliated chamber, the atrium.
    - Food filtered from the water is trapped by a mucous net and then passed by cilia to the esophagus.
    - Filtered water and feces exit through an anus that empties into an excurrent siphon.
- The degenerate adult stage of tunicates is a derived trait that evolved after the tunicate lineage branched off from other chordates.
- Even the tunicate larva appears to be highly derived.
- Studies of *Hox* gene expression suggest that the tunicate larva does not develop the posterior regions of its body axis.
- The anterior region of a tunicate is elongated and contains a heart and digestive system.
- Tunicates and lancelets may provide clues about the evolutionary origin of the vertebrate body plan.
- Tunicates display a number of chordate characteristics only as larvae, whereas lancelets retain those characteristics as adults.
    - The ancestral chordate may have looked something like a lancelet, with an anterior end with a mouth; a notochord; a dorsal, hollow nerve cord; pharyngeal slits; and a post-anal tail.
- The genome of tunicates has been completely sequenced and can be used to identify genes likely to have been present in early chordates.
    - Ancestral chordates likely had genes associated with vertebrate organs such as the heart and thyroid gland. Genes for these organs are found in tunicates and vertebrates but are absent from nonchordate invertebrates.
    - In contrast, tunicates lack many genes that in vertebrates are associated with the long-range transmission of nerve impulses. This result suggests that such genes arose in an early vertebrate and are unique to the vertebrate evolutionary lineage.

- Research on lancelets has revealed important clues about the evolution of the chordate brain.
  - Rather than a full-fledged brain, lancelets have only a slightly swollen tip on the anterior end of the dorsal nerve cord.
  - The *Hox* genes that organize major regions of the forebrain, midbrain, and hindbrain of vertebrates express themselves in a corresponding pattern in this small cluster of cells in the lancelet's nerve cord.
  - The vertebrate brain apparently is an elaboration of an ancestral structure similar to the lancelet's simple nerve cord tip.

## Concept 34.2 Craniates are chordates that have a head.

- After the evolution of the basic chordate body plan, the next major transition was the appearance of a head.
- Chordates with a head are known as **craniates.**
- The origin of a head—with a brain at the anterior end of the dorsal nerve cord, eyes and other sensory organs, and a skull—enabled chordates to coordinate more complex movement and feeding behaviors.

### *Living craniates are distinguished from other chordates by a set of derived characters.*

- On the genetic level, craniates possess two clusters of *Hox* genes, whereas lancelets and chordates have only one.
- Other important families of genes that produce signaling molecules and transcription factors are also duplicated in craniates.
- This additional genetic complexity made a more complex morphology possible.
- In craniates, a group of embryonic cells called the **neural crest** forms near the dorsal margins of the closing neural tube.
  - Neural crest cells disperse throughout the body and contribute to the formation of various structures, such as teeth, some of the bones and cartilages of the skull, the dermis of the face, several types of neurons, and the sensory capsules of the eyes and other sense organs.
- In aquatic craniates, the pharyngeal clefts evolved into gill slits.
  - Unlike the pharyngeal slits of lancelets, which are used primarily for suspension feeding, gill slits are associated with muscles and nerves that allow water to be pumped through the slits.
  - This pumping facilitates gas exchange and may also suck in food.
- Craniates are more active than tunicates and lancelets and have a higher metabolism and a much more extensive muscular system.
  - Muscles lining their digestive tract aid digestion by moving food through the tract.
- Craniates have a heart with at least two chambers, red blood cells, and hemoglobin, as well as kidneys that remove waste products from the blood.

### *Cambrian fossils provide clues to craniate origins.*

- In China, several recent fossil finds of early chordates have provided information about the origin of craniates.
- The early chordates appear to be "missing links" that straddle the transition to craniates, formed during the Cambrian explosion 530 million years ago.

- The most primitive of these fossils is a 3-cm-long animal called *Haikouella.*
  - This animal resembles a lancelet and was probably a suspension feeder.
  - *Haikouella* also had a small but well-formed brain, eyes, and muscular segments.
  - It had hardened structures ("denticles") in the pharynx that may have functioned somewhat like teeth.
  - *Haikouella* did not have a skull, however.
- In other Cambrian rocks, paleontologists have found fossils of more advanced chordates, such as *Myllokunmingia*.
  - *Myllokunmingia* had a skull composed of cartilage and is the oldest known true craniate.
  - These fossils push craniate origins back to the Cambrian explosion.

***Hagfishes are the least derived craniate lineage.***

- Hagfishes have a skull of cartilage but lack jaws and vertebrae.
- Hagfishes swim in a snakelike fashion by using their segmental muscles to exert force against their notochord, which they retain in adulthood as a strong, flexible rod of cartilage.
- Hagfishes have a small brain, eyes, ears, and a nasal opening that connects with the pharynx. They have tooth-like formations made of keratin.
- All of the 30 or so species of hagfishes are marine scavengers, feeding on worms and sick or dead fish.
- Rows of slime glands along a hagfish's body produce large amounts of slime, perhaps to repulse other scavengers or deter a potential predator.

## Concept 34.3 Vertebrates are craniates that have a backbone.

- During the Cambrian period, a lineage of craniates evolved into vertebrates.
- With a more complex nervous system and a more elaborate skeleton, vertebrates became more efficient at two essential tasks: capturing food and avoiding being eaten.
- After vertebrates branched off from other craniates, they underwent another gene duplication, this one involving a group of transcription factor genes called the *Dlx* family.
- This additional genetic complexity was associated with innovations in vertebrate nervous systems and skeletons, including a more extensive skull and a backbone composed of vertebrae.
- In the majority of vertebrates, the vertebrae enclose the spinal cord and have taken over the mechanical roles of the notochord.
- Aquatic vertebrates also have a number of adaptations associated with faster swimming, including fins stiffened by fin rays and a more efficient gas exchange system in the gills.

***Lampreys represent the oldest living lineage of vertebrates.***

- Like hagfishes, lampreys offer clues to early chordate evolution but also have acquired unique characteristics.
- About 35 species of lampreys inhabit both marine and freshwater environments.
- Most lampreys are parasites that feed by clamping a round, jawless mouth onto a fish.
  - They use their rasping tongues to penetrate the skin of their prey and to ingest the fish's blood.

- Lampreys live as suspension-feeding larvae in streams for years before migrating to the sea or lakes as they mature into adults.
    - These larvae resemble lancelets and live partially buried in sediment.
    - The sea lamprey *(Petromyzon marinus)* has invaded the Great Lakes over the past 170 years, where it has devastated a number of fisheries.
- Some species of lampreys feed only as larvae.
    - After metamorphosis, these lampreys attain sexual maturity, reproduce, and die within a few days.
- The skeletons of lampreys are made of cartilage.
    - Unlike most vertebrate cartilage, however, lamprey cartilage contains no collagen. Instead, it is a stiff protein matrix.
- The notochord persists as the main axial skeleton in adult lampreys.
    - Lampreys also have a cartilaginous pipe surrounding the rodlike notochord.
    - Pairs of cartilaginous projections extend dorsally, partially enclosing the nerve cord.

### *Many vertebrate lineages emerged early.*

- **Conodonts** were slender, soft-bodied vertebrates with prominent eyes controlled by numerous muscles.
- At the anterior end of their mouth, conodonts had a set of barbed hooks made of mineralized dental tissues.
- Conodonts ranged in length from 3 to 30 cm.
- Conodonts probably hunted with their large eyes and impaled their prey on hooks.
- The food then passed to the pharynx, where a different set of dental elements crushed and sliced it.
- Conodonts were very abundant for more than 300 million years.
- Vertebrates with additional innovations emerged during the Ordovician, Silurian, and Devonian periods.
    - These vertebrates had paired fins and an inner ear with two semicircular canals that provided a sense of balance.
    - Although they lacked jaws, they had a muscular pharynx that may have sucked in detritus or bottom-dwelling organisms.
    - They were armored with mineralized bone that offered protection from predators.
    - These jawless, armored, swimming vertebrates went extinct by the end of the Devonian period.
- The vertebrate skeleton evolved initially as a structure of unmineralized cartilage.
- Its mineralization began only after lampreys diverged from other vertebrates.
- What initiated the process of mineralization in vertebrates? Mineralization may have been associated with the transition to new feeding mechanisms.
    - The earliest known mineralized structures in vertebrates were conodont dental elements.
    - The armor in later jawless vertebrates was derived from dental mineralization.
    - Thus, mineralization of the vertebrate body may have begun in the mouth.

- Only in more derived vertebrates did the endoskeleton begin to mineralize, starting with the skull.

## Concept 34.4 Gnathostomes are vertebrates that have jaws.

- The **gnathostomes** have true jaws, hinged structures that, especially with the help of teeth, enable vertebrates to grasp food firmly.
- Living gnathostomes are a diverse group that includes sharks and their relatives, ray-finned fishes, lobe-fins, amphibians, reptiles (including birds), and mammals.
- According to one hypothesis, gnathostome jaws evolved by modification of the skeletal rods that had previously supported the anterior pharyngeal gill slits.
- The remaining gill slits were no longer required for suspension feeding and remained as the major sites of respiratory gas exchange.

### *Gnathostomes share a number of derived characters.*

- Gnathostomes share other derived characters besides jaws.
- The common ancestors of all gnathostomes underwent an additional duplication of the *Hox* genes, so that the single cluster present in early chordates became four.
- Other gene clusters also duplicated, allowing further complexity in the development of gnathostome embryos.
- The gnathostome forebrain is enlarged, in association with enhanced senses of vision and smell.
- The lateral line system evolved as a row of microscopic organs sensitive to vibrations in the surrounding water.
- The common ancestor of living gnathostomes had a mineralized axial skeleton, a shoulder girdle, and two sets of paired appendages.
- Gnathostomes appeared in the fossil record in the mid-Ordovician period, about 470 million years ago, and steadily diversified.
- Gnathostome jaws and paired fins were major evolutionary breakthroughs.
  - Jaws, with the help of teeth, enable the animal to grip food items firmly and slice them up.
  - Paired fins, along with the tail, enable fishes to maneuver accurately while swimming.
  - With these adaptations, many fish species were active predators, allowing for the diversification of both lifestyles and nutrient sources.
- The earliest gnathostomes in the fossil record are an extinct lineage of armored vertebrates called placoderms.
  - Most placoderms were shorter than 1 m, although some giants were more than 10 m long.
- Another group of jawed vertebrates called acanthodians radiated in the Devonian period.
- Both placoderms and acanthodians disappeared by the end of the Devonian period, 360 million years ago.

### *Sharks and rays have cartilaginous skeletons.*

- Chondrichthyes (sharks, rays, and their relatives) includes some of the biggest and most successful vertebrate predators in the oceans.
- **Chondrichthyans** have relatively flexible endoskeletons of cartilage rather than bone.

- In most species, parts of the skeleton are impregnated by calcium.

- Conodonts and armored, jawless fishes show that mineralization of the vertebrate skeleton had begun before the chondrichthyan lineage branched off from other vertebrates.
  - Traces of bone can be found in living chondrichthyes—in their scales, at the base of their teeth, and (in some sharks) in a thin layer on the surface of their vertebrae.
  - Bonelike tissues have been found in early chondrichthyans, such as the fin skeleton of a shark that lived in the Carboniferous period.
  - The loss of bone in chondrichthyes is a derived condition, which emerged after they diverged from other gnathostomes.
- There are about 750 extant species of chondrichthyans, almost all in the subclass of sharks and rays, with a few dozen species in a second subclass of chimaeras or ratfishes.
- The streamlined bodies of most sharks enable them to be swift, but not maneuverable, swimmers.
- Powerful axial muscles power undulations of the body and caudal fin to drive the fish forward, and the dorsal fins provide stabilization.
- Although some buoyancy is provided by low-density oils in the large liver, the flow of water over the pectoral and pelvic fins also provides lift to keep the animal suspended in the water column.
  - Sharks and rays are more dense than water and sink if they stop swimming.
  - Continuous swimming ensures that water flows into the mouth and out through the gills.
  - Some sharks and many skates and rays spend much time resting on the seafloor, using the muscles of their jaws and pharynx to pump water over the gills.
- Most sharks are carnivores that swallow their prey whole or use their powerful jaws and sharp teeth to tear flesh from animals too large to swallow.
  - The largest sharks and rays are suspension feeders that consume plankton.
  - Sharks have several rows of teeth that gradually move to the front of the mouth as old teeth are lost.
  - Within the intestine of a shark is a **spiral valve,** a corkscrew-shaped ridge that increases surface area and prolongs the passage of food along the short digestive tract.
- Acute senses are adaptations that go along with the active, carnivorous lifestyle of sharks.
  - Sharks have sharp vision but cannot distinguish colors.
  - Their acute olfactory sense (smelling) occurs in a pair of dead-end nostrils that do not function in breathing.
  - Sharks can detect electrical fields, including those generated by the muscle contractions of nearby prey, through patches of specialized skin pores.
  - The lateral line system, a row of microscopic organs sensitive to pressure changes, can detect low-frequency vibrations.
  - In sharks, the whole body transmits sound to the hearing organs of the inner ear.
- Shark eggs are fertilized internally. Males transfer sperm via claspers on their pelvic fins to the reproductive tract of the female.
- **Oviparous** sharks encase their eggs in protective cases and lay them outside the mother's body.
  - The eggs hatch months later as juveniles.
- **Ovoviviparous** sharks retain fertilized eggs in the oviduct.
  - The embryo completes development in the uterus, nourished by the egg yolk.

- A few sharks are **viviparous**. The young develop within the uterus, obtaining nutrients through a yolk sac placenta, by absorbing a nutritious fluid produced by the uterus or by eating other eggs.
- Rays are closely related to sharks, but they have adopted a very different lifestyle.
  - Most rays are flattened bottom-dwellers that crush molluscs and crustaceans in their jaws.
  - The enlarged pectoral fins of rays are used like wings to propel the animal through the water.
  - The tail of many rays is whiplike and may bear venomous barbs for defense against threats.
- Chondrichthyans have changed little in more than 300 million years.
- Now chondrichthyans are severely threatened by overfishing.
  - In 2003, researchers reported that shark stocks in the northwest Atlantic had declined 75% in 15 years.

***The clade Osteichthyes includes tetrapods and bony fishes.***

- The vast majority of vertebrates belong to a clade of gnathostomes called the Osteichthyes (meaning "bony fish").
- Systematists today include tetrapods with bony fish in Osteichthyes, which otherwise would be paraphyletic.
- Nearly all living **osteichthyans** have an ossified (bony) endoskeleton with a hard matrix of calcium phosphate.
  - It is not clear when the shift to a bony skeleton took place during gnathostome evolution.
  - It is possible that the common ancestor of both chondrichthyans and osteichthyans was already highly ossified and that chondrichthyans subsequently lost much of this bone.
- Bony fishes breathe by drawing water over four or five pairs of gills located in chambers covered by a protective flap, the **operculum**.
- Water is drawn into the mouth, through the pharynx, and out between the gills by movements of the operculum and muscles surrounding the gill chambers.
- Most fishes have an internal, air-filled sac, the **swim bladder**.
  - The swim bladder evolved from balloon-like lungs that may have been used by early osteichthyans to breathe air when dissolved oxygen levels were low in stagnant, shallow waters.
  - Swim bladders evolved from lungs in some lineages.
- Movement of gases from the blood to the swim bladder increases buoyancy, making the animal rise; a transfer of gases back to the blood causes the animal to sink.
- The skin of bony fishes is often covered with flattened bony scales that differ in structure from the tooth-like scales of sharks.
  - Glands in the skin secrete mucus that reduces drag in swimming.
- Like sharks, aquatic osteichthyes have a lateral line system, which is evident as a row of tiny pits in the skin on either side of the body.
- The reproduction of aquatic osteichthyes varies.
  - Most species are oviparous, reproducing by external fertilization after the female sheds large numbers of small eggs.
  - Internal fertilization and birthing characterize other species.
- Nearly all aquatic osteichthyans belong to the **ray-finned fishes** (Actinopterygii).
  - This group has more than 27,000 species, including bass, trout, perch, tuna, and herring.

    - The fins are supported by long, flexible rays and are modified for maneuvering, defense, and other functions.
- Ray-finned fishes likely evolved in fresh water and then spread to the seas during their long history.
    - Many species of ray-finned fishes returned to fresh water at some point in their evolution.
    - Some ray-finned fishes, such as salmon, make a round-trip from fresh water to seawater and back to fresh water during their life cycle.
- Ray-finned fishes serve as a major source of protein for humans, who have harvested them for tens of thousands of years.
- Recently, industrial-scale fishing operations appear to have driven some of the world's biggest fisheries to collapse.
    - In the 1990s, the catch of cod *(Gadus morhua)* in the northwest Atlantic plummeted to only 5% of its historic maximum, nearly halting cod fishing there.
    - Despite ongoing heavy restrictions on the fishery, populations of this economically important fish have yet to recover to sustainable levels.
- Ray-finned fishes also face other pressures from humans, such as the diversion of rivers by dams.
    - Changing water flow patterns hamper the fishes' ability to obtain food and interfere with migratory pathways and spawning grounds.
- Ray-finned fishes evolved during the Devonian period, along with the **lobe-fins** (Sarcopterygii).
- The key derived character in lobe-fins is rod-shaped bones surrounded by a thick layer of muscle in their pectoral and pelvic fins.
- During the Devonian, many lobe-fins lived in brackish waters, such as in coastal wetlands.
- Many Devonian lobe-fins were gigantic predators, bottom-dwellers that may have used their paired, muscular fins to "walk" along the bottom.
- By the end of the Devonian period, lobe-fin diversity was dwindling. Today, only three lineages survive.
- One lineage, the coelacanths (Actinistia), thought to have become extinct 75 million years ago, has been rediscovered in the Indian Ocean.
    - In 1938, fishermen caught a living coelacanth off the Comoros Islands in the western Indian Ocean.
    - In 1999, a second population was identified in the eastern Indian Ocean, near Indonesia. The Indonesian population may represent a second species.
- The second lineage of living lobe-fins, the lungfishes (Dipnoi), live in the Southern Hemisphere.
    - Six species of lungfishes, in three genera, generally inhabit stagnant ponds and swamps.
    - They gulp air into lungs connected to the pharynx.
    - Lungfishes also have gills, which are the main organs for gas exchange in Australian lungfishes.
    - When ponds shrink during the dry season, some lungfishes can burrow into the mud and aestivate.
- The third lineage of lobe-fins that survives today is far more diverse than coelacanths or lungfishes.
    - During the mid-Devonian, these vertebrates adapted to life on land and gave rise to vertebrates with limbs and feet, called tetrapods, a lineage that includes humans.

## Concept 34.5 Tetrapods are gnathostomes that have limbs.

- One of the most significant events in vertebrate history took place 360 million years ago, when the fins of some lobe-fins evolved into tetrapod limbs and feet.
- The most significant characteristic of **tetrapods** is four limbs, which allow them to support their weight on land.
- The feet of tetrapods have digits that enable them to transmit muscle-generated forces to the ground when they walk.
- Life on land brought numerous additional changes to the tetrapod body plan.
    - The head is separated from the body by a neck that originally had one vertebra (the atlas) on which the skull could move up and down.
    - The second vertebra, the axis, allowed the head to swing from side to side.
    - The bones of the pelvic girdle (to which the hind legs are attached) became fused to the backbone, permitting forces generated by the hind legs against the ground to be transferred to the rest of the body.
    - Living tetrapods do not have gill slits; during embryonic development, the pharyngeal clefts instead give rise to parts of the ears, glands, and other structures.

### *Tetrapods arose on Devonian coastal wetlands.*

- The Devonian coastal wetlands were home to a wide range of lobe-fins. Those that entered shallow, oxygen-poor water could use their lungs to breathe air.
- Some species likely used their stout fins to move across the muddy bottom.
- At the water's edge, leg-like appendages were probably better equipment than fins for paddling and crawling through the dense vegetation in shallow water.
- The tetrapod body plan was thus a modification of a preexisting body plan.
- In one lineage of lobe-fins, the fins became progressively more limb-like, while the rest of the body retained adaptations for aquatic life.
    - For example, fossils of *Acanthostega* from 365 million years ago had bony gill supports and rays in its tail to support propulsion in water, but it also had fully formed legs, ankles, and digits. Its pectoral and pelvic girdles and vertebrae were too weak to carry its body on land, however.
    - *Acanthostega* may have slithered out of the water from time to time, but it was primarily aquatic.
- A great diversity of tetrapods emerged during the Carboniferous period.
- Judging from the morphology and location of the fossils, most of these early tetrapods remained tied to water.

### *Salamanders, frogs, and caecilians are living amphibians.*

- **Amphibians** (class Amphibia) are represented by about 6,159 species of salamanders (order Urodela, "tailed ones"), frogs (order Anura, "tail-less ones"), and caecilians (order Apoda, "legless ones").
- Some of the 550 species of urodeles are entirely aquatic, but others live on land as adults or throughout life.

- On land, most salamanders walk with a side-to-side bending of the body inherited from early terrestrial tetrapods.

- The 5,420 species of anurans are more specialized than urodeles for moving on land.
  - Adult frogs use powerful legs to hop along the terrain.
  - Frogs nab insects by flicking out their sticky tongues, which are attached to the front of the mouth.
  - Anurans may be camouflaged or secrete a distasteful, even poisonous, mucus from their skin glands.
  - Many poisonous species are brightly colored, perhaps to warn predators who associate the coloration with danger.
- Apodans, the caecilians (about 170 species), are legless and nearly blind.
  - The reduction of legs evolved secondarily from a legged ancestor.
  - Superficially resembling earthworms, most species burrow in moist forest soil in the tropics.
  - A few South American species live in freshwater ponds and streams.
- *Amphibian* means "two lives," a reference to the metamorphosis of many frogs from an aquatic stage, the tadpole, to the terrestrial adult.
  - Tadpoles are usually aquatic herbivores with gills and a lateral line system, and they swim by undulating their tails.
  - During metamorphosis, the tadpole develops legs, the lateral line disappears, and lungs replace gills.
  - Adult frogs are carnivorous hunters.
- Many amphibians do not live a dualistic—aquatic and terrestrial—life.
  - There are some strictly aquatic and some strictly terrestrial frogs, salamanders, and caecilians.
  - The larvae of salamanders and caecilians look like adults; both are carnivorous.
- Most amphibians retain close ties to water and are most abundant in damp habitats.
- Those amphibians that are adapted to drier habitats spend much of their time in burrows or under moist leaves where the humidity is higher.
- Most amphibians rely heavily on their moist skin to carry out gas exchange with the environment.
  - Some terrestrial species lack lungs entirely and breathe exclusively through their skin and oral cavity.
- Most amphibian species have external fertilization, shedding their eggs in ponds or swamps or at least in moist environments.
  - Amphibian eggs lack a shell and dehydrate quickly in dry air.
  - Some species lay vast numbers of eggs in temporary pools where mortality is high.
  - Others display various types of parental care and lay relatively few eggs.
  - In some species, males or females may house eggs on their back, in their mouth, or even in their stomach.
  - Some species are ovoviviparous or viviparous, retaining the developing eggs in the female reproductive tract until released as juveniles.
- Many amphibians display complex and diverse social behavior, especially during the breeding season.

- Many male frogs fill the air with their mating calls as they defend breeding territories or attract females.
- In some terrestrial species, migrations to specific breeding sites may involve vocal communication, celestial navigation, or chemical signaling.

- For the past 25 years, zoologists have been documenting a rapid and alarming decline in amphibian populations throughout the world.
  - A 2004 study indicates that since 1980, at least nine amphibian species have become extinct.
  - An additional 113 species have not been seen since that time and are considered "possibly extinct."
- Causes that have been proposed include habitat degradation, the spread of a pathogen (a chytrid fungus), climate change, and pollution.

## Concept 34.6 Amniotes are tetrapods that have a terrestrially adapted egg.

- The **amniote** clade consists of the mammals and reptiles (including birds).
- The evolution of amniotes from an amphibian ancestor involved new adaptations for life on land.
- The **amniotic egg** is the major derived character of the clade.
- Inside the shell of the amniotic egg are several *extraembryonic membranes* that function in gas exchange, waste storage, and the transfer of stored nutrients to the embryo.
  - The amniotic egg is named for one of these membranes, the amnion, which encloses a fluid-filled "private pond" that bathes the embryo and acts as a hydraulic shock absorber.
- The amniotic eggs enabled terrestrial vertebrates to complete their life cycles entirely on land.
  - In contrast to the shell-less eggs of amphibians, the amniotic eggs of most amniotes have a shell that retains water and can be laid in a dry place.
  - The calcareous shells of bird eggs are inflexible, whereas the leathery eggs of many reptiles are flexible.
  - The shell significantly slows dehydration of the egg in air.
  - Most mammals have dispensed with the shell. The embryo avoids desiccation by developing within the mother.

### *Amniotes are well adapted to life on land.*

- Amniotes acquired other key adaptations to terrestrial life, including less permeable skin and increasing use of the rib cage to ventilate the lungs.
- The most recent common ancestor of living amphibians and amniotes lived about 370 million years ago.
  - No fossils of amniotic eggs have been found from that time.
- Early amniotes lived in drier environments than did earlier tetrapods.
- Some early amniotes were herbivores, with grinding teeth. Others were large and predatory.
- The **reptile** clade includes tuatara, lizards, snakes, turtles, crocodilians, and birds, as well as extinct groups such as dinosaurs.
- All of the living reptile lineages are highly derived, and none can serve as a straightforward model for the earliest reptiles that lived some 320 million years ago.

- Reptiles have several adaptations for terrestrial life not generally found in amphibians.
- Scales containing the protein keratin waterproof the skin of reptiles, preventing abrasion and dehydration in dry air.
- Most reptiles lay shelled amniotic eggs on land.
    - Fertilization occurs internally, before the shell is secreted as the egg passes through the female's reproductive tract.
    - Some species of lizards and snakes are viviparous, with their extraembryonic membranes forming a placenta that enables the embryo to obtain nutrients from its mother.
- Nonbird reptiles are sometimes labeled "cold-blooded" because they do not use their metabolism extensively to control body temperature.
- Most regulate their body temperature behaviorally by basking in the sun when cool and seeking shade when hot.
- Because they absorb external heat rather than generating much of their own, nonbird reptiles are more appropriately called **ectotherms**.
- One advantage of this strategy is that an ectothermic reptile can survive on fewer than 10% of the calories required by a mammal of equivalent size.
- The reptile clade is not entirely ectothermic. Birds are **endothermic**, capable of keeping the body warm through metabolism.

*Reptiles have diversified considerably since they arose 310 million years ago.*

- The oldest reptilian fossils date back to the late Carboniferous period, about 310 million years ago.
- The first major group of reptiles to emerge was the **parareptiles**, large, stocky, quadrupedal herbivores.
    - Some parareptiles had dermal plates on their skin, which may have provided defense against predators.
    - Parareptiles died out 200 million years ago, at the end of the Triassic period.
- As parareptiles were dwindling, an equally ancient clade of reptiles, the **diapsids**, was diversifying.
    - The most obvious derived character of diapsids is a pair of holes on each side of the skull, behind the eye socket.
    - The diapsids are composed of two main lineages: lepidosaurs and archosaurs.
    - The **lepidosaurs** include lizards, snakes, and tuataras.
        - This lineage also produced a number of marine reptiles, including plesiosaurs and ichthyosaurs.
    - The **archosaurs** include crocodilians and the extinct pterosaurs and dinosaurs.
- **Pterosaurs**, which originated in the late Triassic, were the first tetrapods to exhibit flapping flight.
    - The pterosaur wing is formed from a collagen-strengthened membrane that stretched between the hind leg and a very long finger.
    - Well-preserved fossils show the presence of muscles, blood vessels, and nerves in the wing membrane, suggesting that pterosaurs could dynamically adjust their membranes to assist their flight.
    - The pterosaurs ranged from sparrow-sized to the largest, with a wingspan of nearly 11 m.

- Pterosaurs converged on many of the ecological roles later taken by birds; some were insect-eaters, others grabbed fish out of the ocean, and still others filtered small animals through thousands of fine needle-like teeth.
    - By the end of the Cretaceous period, 65 million years ago, pterosaurs had become extinct.
- **Dinosaurs** were an extremely diverse group, varying in body shape, size, and habitat.
    - There were two main dinosaur lineages: the ornithischians, which were mostly herbivorous, and the saurischians, which included both long-necked, giant herbivores and bipedal, carnivorous **theropods**.
    - Theropods included the famous *Tyrannosaurus rex* as well as the ancestors of birds.
- There is continuing debate about whether dinosaurs were **endothermic**, capable of keeping their body warm through metabolism.
- Some experts dispute the claim that dinosaurs were endothermic.
    - In the warm, consistent Mesozoic climate, behavioral adaptations may have been sufficient for terrestrial dinosaurs to maintain a suitable body temperature.
    - Also, the low surface-to-volume ratios of dinosaurs would have reduced the effects of daily fluctuations in air temperature on the animal's internal temperature.
- Some anatomical evidence supports the hypothesis that at least some dinosaurs were endotherms.
    - Paleontologists have found fossils of dinosaurs in both Antarctica and the Arctic, although the climate in those areas was milder during the Mesozoic than it is today.
    - The dinosaur that gave rise to birds was *certainly* endothermic, like all birds.
- There is increasing evidence that many dinosaurs were agile, fast moving, and, in some species, social.
    - Paleontologists have discovered signs of nest-building, brooding, and parental care among dinosaurs.
- By the end of the Cretaceous, all dinosaurs (except birds) became extinct.
    - It is uncertain whether dinosaur populations were declining before they were finished off by an asteroid or comet impact.
- Lepidosaurs are represented by two living lineages: tuatara and squamates.
- The tuatara includes two species of lizard-like reptiles found on only 30 islands off the coast of New Zealand.
    - Tuatara relatives lived at least 220 million years ago, when they thrived on every continent well into the Cretaceous period.
    - When humans arrived in New Zealand 750 years ago, the rats that came with them devoured tuatara eggs, eliminating the reptiles on the main islands.
- The squamates are lizards and snakes.
- Lizards are the most numerous and diverse reptiles (apart from birds) alive today.
    - Most lizards are relatively small, but they range in length from 16 mm to 3 m.
    - The Komodo dragon of Indonesia is the world's largest lizard.
        - The Komodo dragon hunts deer and other large prey, delivering bacteria with its bite. As its wounded prey weakens from the infection, the lizard slowly stalks it.
- Snakes are legless lepidosaurs that evolved from lizards closely related to the Komodo dragon.
    - Some species of snakes retain vestigial pelvic and limb bones as evidence of their ancestry.

- Despite their lack of legs, snakes move well on land, producing waves of lateral bending that pass from head to tail.
- Force exerted by the bends against solid objects pushes the snake forward.
- Snakes can also move by gripping the ground with their belly scales at several points along the body, while the scales at intervening points are lifted slightly off the ground and pulled forward.
- Snakes are carnivorous, and a number of adaptations aid them in hunting and eating prey.
- Snakes have acute chemical sensors and are sensitive to ground vibrations.
- The flicking tongue fans odors toward olfactory organs on the roof of the mouth.
- Heat-detecting organs of pit vipers, including rattlesnakes, enable these night hunters to locate warm animals.
- Some poisonous snakes inject their venom through a pair of sharp, hollow or grooved teeth.
- Loosely articulated jaws enable most snakes to swallow prey larger than the diameter of the snake itself.

- Turtles are the most distinctive group of reptiles alive today.
  - All turtles have a boxlike shell made up of upper and lower shields that are fused to the vertebrae, clavicles, and ribs.
- The earliest fossils of turtles are 220 million years old, with fully developed shells.
  - In the absence of transitional fossils, clues to the origin of the turtle shell have been sought in molecular data.
  - These data suggest that turtles are closely related to crocodiles and other Triassic archosaurs—organisms that had bony plates along their backbones and sometimes over their bodies.
  - These plates may have become more elaborate in the ancestors of turtles, over time resulting in a shell.
  - The earliest turtles could not retract their head into their shell, but mechanisms for doing so evolved independently in two separate branches of turtles.
- Turtles live in a variety of environments, from deserts to ponds to the sea.
  - Sea turtles have a reduced shell and enlarged forelimbs that function as flippers.
  - This radiation has produced the largest living turtles, the leatherbacks, which can weigh more than 1,500 kg.
  - Feeding on jellies, the leatherbacks dive as deep as 60 m.
  - Leatherbacks and other sea turtles are endangered by fishing boats that accidentally catch them in their nets, as well as by the human development of the beaches where the turtles lay their eggs.
- Crocodiles and alligators (crocodilians) are among the largest living reptiles.
  - The earliest members of this lineage were small terrestrial quadrupeds with long, slender legs.
  - Some Mesozoic crocodilians grew as long as 12 m and may have attacked dinosaurs and other prey at the water's edge.
  - Modern crocodilians spend most of their time in water, breathing air through upturned nostrils.
  - Crocodilians are confined to the tropics and subtropics.

### *Birds evolved as feathered dinosaurs.*

- Almost every part of a typical bird's anatomy is modified in some way to reduce weight and enhance flight.
- One adaptation to reduce weight is the absence of some organs.
  - For instance, birds lack a urinary bladder and females have only one ovary.
  - The gonads of both females and males are usually small, except during the breeding season, when they increase in size.
  - Modern birds are toothless and grind their food in a muscular gizzard near the stomach.
- A bird's most obvious adaptations for flight are its wings and feathers.
  - Feathers are made of β-keratin, a protein similar to the keratin of reptile scales.
  - The shape and arrangement of feathers form wings into airfoils.
  - Power for flapping the wings comes from contractions of the pectoral muscles, anchored to a keel on the sternum.
- The evolution of flight required a radical alteration in body form but provides many benefits.
  - Flight enhances hunting and scavenging.
  - Flight enables many birds to catch flying insects, an abundant, highly nutritious food resource.
  - Flight provides a ready escape from earthbound predators.
  - It enables many birds to migrate great distances to exploit different food resources and seasonal breeding areas.
- Flying requires a great expenditure of energy with an active metabolism.
  - Birds are endothermic, using their own metabolic heat to maintain a constant body temperature.
  - Feathers and, in some species, a layer of fat provide insulation.
- Efficient respiratory and circulatory systems with a four-chambered heart keep birds' tissues well supplied with oxygen and nutrients.
  - The lungs have tiny tubes leading to and from elastic air sacs that improve airflow and oxygen uptake.
- Birds have acute vision and fine muscle control, supported by well-developed visual and motor areas of the brain.
  - The large brains of birds (proportionately larger than those of nonbird reptiles or amphibians) support very complex behavior.
- During the breeding season, birds engage in elaborate courtship rituals.
- These rituals culminate in copulation, contact between the mates' vents, the openings to their cloacae.
- After eggs are laid, the avian embryo is kept warm through brooding by the mother, father, or both, depending on the species.
- Cladistic analyses of fossilized skeletons support the hypothesis that the closest reptilian ancestors of birds were **theropods**.
- In the late 1990s, Chinese paleontologists unearthed a treasure trove of feathered theropods that are shedding light on bird origins.
  - Several species of dinosaurs closely related to birds had feathers with vanes, and a wider range of species had filamentous feathers.

- These fossils suggest that feathers evolved long before powered flight, possibly for insulation, camouflage, or courtship.

- Theropods may have evolved powered flight by one of three possible routes.
  1. Small ground-running dinosaurs chasing prey or evading predation may have used feathers to gain extra lift as they jumped into the air.
  2. Small dinosaurs could have gained traction as they ran up hills by flapping their feathered forelimbs—a behavior seen in some birds today.
  3. Dinosaurs could have glided from trees, aided by feathers.
- The most famous Mesozoic bird is *Archaeopteryx*, known from fossils from a German limestone quarry.
  - This ancient bird lived about 150 million years ago, during the late Jurassic period.
  - *Archaeopteryx* had feathered wings but retained primitive characteristics such as clawed forelimbs, teeth, and a long tail containing vertebrae.
  - Without its feathers, *Archaeopteryx* would probably be classified as a theropod dinosaur.
  - Its skeletal anatomy indicates that *Archaeopteryx* was a weak flyer, perhaps a tree-dwelling glider.
- Fossils of later birds from the Cretaceous period show a gradual loss of certain ancestral dinosaur features, such as teeth and clawed forelimbs, as well as the acquisition of innovations that are shared by all birds today, including a short tail covered by a fan of feathers.
- Neornithes, the clade that includes 28 orders of living birds, arose before the Cretaceous-Paleogene boundary, 65.5 million years ago.
- Most birds can fly, but Neornithes includes a few flightless birds, the **ratites**, which lack both a breastbone and large pectoral muscles.
  - The ratites include the ostrich, kiwi, cassowary, and emu.
- The penguins make up the flightless order Sphenisciformes.
  - Penguins have powerful pectoral muscles, which they use in swimming.
  - As they swim, penguins flap their flipper-like wings in a manner that resembles the flight stroke of a more typical bird.
- The demands of flight have rendered the general form of all flying birds similar.
  - The beak of birds is very adaptable, taking on a great variety of shapes suited to different diets.
  - Foot structure, too, shows considerable variation.
  - Various birds use their feet for perching on branches, grasping food, defense, swimming or walking, and even courtship.

## Concept 34.7 Mammals are amniotes that have hair and produce milk.

- There are more than 5,300 living species of mammals.
- **Mammals** (class Mammalia) have a number of derived traits.
- All mammalian mothers have mammary glands to nourish their babies with milk, a balanced diet rich in fats, sugars, proteins, minerals, and vitamins.
- All mammals have hair and a layer of fat under the skin that retain metabolic heat, contributing to endothermy in mammals.

- Endothermy is supported by an active metabolism, made possible by efficient respiration and circulation.
- Other adaptations include a muscular diaphragm and a four-chambered heart.
- Mammals generally have larger brains than other vertebrates of equivalent size.
    - Many species are capable of learning.
    - The relatively long period of parental care extends the time for offspring to learn important survival skills by observing their parents.
- Feeding adaptations of the jaws and teeth are other important mammalian traits.
    - Unlike the uniform conical teeth of most reptiles, the teeth of mammals come in a variety of shapes and sizes adapted for processing many kinds of foods.

***Mammals belong to a group of amniotes known as synapsids.***

- **Synapsids** have a temporal fenestra behind the eye socket on each side of the skull.
- Early nonmammalian synapsids lacked hair, had a sprawling gait, and laid eggs.
- Fossil evidence shows that the jaw was remodeled as mammalian features arose gradually in synapsid lineages.
    - Two of the bones that formerly made up the jaw joint were incorporated into the mammalian middle ear.
- Synapsids evolved into large herbivores and carnivores during the Permian period.
- Mammal-like synapsids emerged by the end of the Triassic, 200 million years ago.
    - These animals were not mammals, but they were small and likely hairy, fed on insects at night, and had a higher metabolism that other synapsids. They probably laid eggs.
- The first true mammals arose in the Jurassic period.
- Early mammals diversified into a number of lineages, most about the size of a shrew.
    - One possible explanation for their small size is that dinosaurs already occupied the ecological niches of large-bodied animals.
- By the early Cretaceous, the three major lineages of living mammals emerged: monotremes (egg-laying mammals), marsupials (mammals with a pouch), and eutherians (placental mammals).
- After the extinction of large dinosaurs, pterosaurs, and marine reptiles during the late Cretaceous period, mammals underwent an adaptive radiation, giving rise to large predators and herbivores as well as flying and aquatic species.
- **Monotremes**—the platypuses and the echidnas—are the only living mammals that lay eggs.
    - The reptile-like egg contains enough yolk to nourish the developing embryo.
    - Monotremes have hair, and females produce milk in specialized glands.
    - After hatching, the baby sucks milk from the mother's fur because she lacks nipples.
- **Marsupials** include opossums, kangaroos, and koalas.
- In contrast to monotremes, marsupials (as well as eutherians) have a higher metabolic rate, have nipples that produce milk, and give birth to live young.
- The marsupial embryo develops inside the uterus of the female's reproductive tract. The lining of the uterus and the extraembryonic membranes that arise from the embryo form a **placenta**, a structure in which nutrients diffuse into the embryo from the mother's blood.

- A marsupial is born very early in development and, in most species, completes its embryonic development while nursing within a maternal pouch, the marsupium.
  - In most species, the tiny offspring climbs from the exit of the female's reproductive tract to the marsupium.
- Marsupials existed worldwide throughout the Mesozoic era but now are restricted to Australia and the Americas.
  - In Australia, marsupials have radiated and, through convergent evolution, have evolved to fill niches occupied by eutherian mammals in other parts of the world.
  - Australia's isolation facilitated the diversification and survival of its marsupial fauna.
  - Today, only three families of marsupials live outside the Australian region, and only one species, the opossum, is found in North America.
- While the marsupial mammals diversified throughout the Tertiary in South America and Australia, the placental mammals began an adaptive radiation on the northern continents.
- Invasions of placental mammals from North America affected the marsupial fauna of South America about 12 million years ago and then again about 3 million years ago when the continents were connected by the Isthmus of Panama.
- This mammalian biogeography is an example of the interplay between biological and geologic evolution.
- Compared to marsupials, **eutherians** (placental mammals) have longer pregnancies.
  - Young eutherians complete their embryonic development within the uterus, joined to the mother by the placenta.
  - Eutherians are commonly called placental mammals because their placentas are more complex than those of marsupials and provide a more intimate and long-lasting association between mother and young.
- The major groups of living eutherians are thought to have diverged in a burst of evolutionary change.
- The timing of this burst is uncertain: It is dated to 100 million years ago by molecular data and 60 million years ago by morphological data.

### *Primate evolution provides a context for understanding human origins.*

- The mammalian order Primates includes lemurs, tarsiers, monkeys, and apes (including humans).
- Primates have a number of derived characters.
  - Most primates have hands and feet adapted for grasping.
  - Primates have flat nails on their digits, rather than narrow claws, and have skin ridges on their fingers.
  - Compared with other mammals, primates have large brains and short jaws. Their eyes are forward-looking.
  - Primates also have relatively well-developed parental care and relatively complex social behavior.
- The earliest primates were tree dwellers, shaped by natural selection for arboreal life.
  - The grasping hands and feet of primates are adaptations for hanging on to tree branches.
- All modern primates, except humans, have a big toe that is widely separated from the other toes, allowing them to grasp with their toes.

- The thumb is relatively mobile and separate from the fingers in all primates, but a fully **opposable thumb** is found in only monkeys and apes.
- The unique dexterity of humans, aided by distinctive bone structure at the thumb base, represents descent with modification from ancestral hands adapted for life in the trees.
- Other primate features also originated as adaptations for tree dwelling.
  - The overlapping fields of vision of the two eyes enhance depth perception, an obvious advantage when brachiating.
  - Excellent hand-eye coordination is also important for arboreal maneuvering.
- Primates are divided into three main groups: the lemurs of Madagascar and the lorises and pottos of Southeast Asia; the tarsiers, which live in Southeast Asia; and the **anthropoids**, which include monkeys and apes and are found worldwide.
  - Lemurs, lorises, and pottos probably resemble early arboreal primates.
- The oldest known anthropoid fossils, from about 45 million years ago, support the hypothesis that tarsiers are more closely related to anthropoids than to the lemur group.
- Monkeys do not constitute a monophyletic group.
- The first monkeys probably evolved in the Old World (Africa and Asia).
- By the Oligocene, monkeys were established in the New World (South America).
- Old World and New World monkeys underwent separate adaptive radiations.
  - All New World monkeys are arboreal, but Old World monkeys include both arboreal and ground-dwelling species.
  - Most monkeys in both groups are diurnal and usually live in bands held together by social behavior.
- In addition to monkeys, anthropoids include: *Hylobates* (gibbons), *Pongo* (orangutans), *Gorilla* (gorillas), *Pan* (chimpanzees and bonobos), and *Homo* (humans).
- Modern apes evolved from Old World monkeys about 20–25 million years ago and are confined exclusively to the tropical regions of the Old World.
- With the exception of gibbons, modern apes are larger than monkeys, with relatively long arms and short legs and no tails.
- Only gibbons and orangutans are primarily arboreal.
- Social organization varies among the apes, with gorillas and chimpanzees being highly social.
- Apes have larger brains than monkeys, and their behavior is more flexible.

## **Concept 34.8 Humans are mammals that have a large brain and bipedal locomotion.**

- In the continuity of life spanning more than 3.5 billion years, humans and apes have shared ancestry for all but the past few million years.
- Our own species, *Homo sapiens,* is about 200,000 years old.
- Human evolution is marked by the evolution of a number of derived characters.
  - Humans stand upright and walk on two legs.
  - Humans have a much larger brain than apes and are capable of language, symbolic thought, and complex tool use.
  - Humans have reduced jawbones and jaw muscles and a shorter digestive tract.

- Human and chimpanzee genomes are 99% identical.
- A disparity of 1% translates into a large number of differences in a genome that contains 3 billion base pairs.
    - Recent studies have found that humans and chimpanzees differ in the expression of 19 regulatory genes.
    - Such genomic differences—and whatever derived phenotypic characters they code for—separate humans from other *living* apes.
- Many of the derived characters in humans first emerged in our ancestors, long before our own species appeared.
- **Paleoanthropology** is the study of human origins and evolution.
- Paleoanthropologists have found fossils of 20 species of extinct species that are more closely related to humans than to chimpanzees. These species are known as **hominins.**
- The oldest hominin is *Sahelanthropus tchandensis*, which lived 6–7 million years ago.
- *Sahelanthropus* and other early hominins shared some of the derived characters of humans.
    - They had reduced canine teeth and relatively flat faces.
    - They were more upright and bipedal than other apes.
    - The foramen magnum, the hole at the base of the skull through which the spinal cord exits, is located directly underneath the skull in early hominins and humans.
    - This derived position allows humans—and early hominins—to hold their heads directly over their bodies.
    - Leg bones of *Australopithecus anamensis*, a hominin that lived 4.5–4 million years ago, show that early hominins were increasingly bipedal.
- While early hominins were becoming bipedal, their brains remained small—about 400–450 $cm^3$ in volume.
- Early hominins were small in stature, with relatively large teeth and a protruding lower jaw.
- It is important to avoid two common misconceptions in considering early hominins:
    1. Our ancestors were not chimpanzees or any other modern apes.
        - Chimpanzees represent the tip of a separate branch of evolution, and they acquired derived characters of their own after they diverged from their common ancestor with humans.
    2. Human evolution did not occur as a ladder with a series of steps leading directly from an ancestral ape to *H. sapiens*.
        - If human evolution is a parade, then many splinter groups traveled down dead ends.
        - At times, several different hominin species coexisted. These species differed in skull shape, body size, and diet.
        - Human phylogeny is more like a multibranched bush, with our species at the tip of the only surviving twig.
- Hominin diversity increased dramatically between 4 and 2 million years ago.
- The various pre-*Homo* hominins are classified in the genus *Australopithecus* ("southern ape") and are known as australopiths.
    - Their phylogeny remains unresolved on many points. As a group, they are almost certainly paraphyletic.
    - *Australopithecus anamensis* links the australopiths to older hominins such as *Ardipithecus ramidus*.

- The first australopith, *Australopithecus africanus*, was discovered in 1924 in a quarry in South Africa.
    - *A. africanus* lived between 3 and 2.4 million years ago.
    - From skeletons, it has become clear that *A. africanus* walked fully erect and had human-like hands and teeth.
    - However, the brain of *A. africanus* was only about one-third the size of a modern human's brain.
- In 1974, a new fossil, about 40% complete, was discovered in the Afar region of Ethiopia.
    - This 3.2-million-year-old fossil, nicknamed "Lucy," was described as a new species, *A. afarensis*.
    - Fossils discovered in the early 1990s show that *A. afarensis* existed as a species for at least 1 million years.
    - *A. afarensis* had a brain the size of a chimpanzee's, a long lower jaw, and longer arms (for some level of arboreal locomotion).
    - However, the pelvis, skull bones, and fossil tracks showed that *A. afarensis* walked bipedally.
- Two lineages appeared after *A. afarensis*: the "robust" australopiths with sturdy skulls and powerful jaws and teeth for grinding and chewing hard, tough foods; and the "gracile" australopiths with lighter feeding equipment adapted for softer foods.
- Combining evidence from the earliest hominins with the fossil record of australopiths makes it possible to ask questions and consider hypotheses about trends in hominin evolution.
- Why did hominins become bipedal?
    - Our anthropoid ancestors of 30–35 million years ago were tree-dwellers.
    - Ten million years ago, the forests contracted as the climate became drier. The result was an large savanna with few trees.
    - For decades, paleontologists thought that bipedalism was an adaptation to life on the savanna.
    - According to one hypothesis, tree-dwelling hominins could no longer move through the canopy, so natural selection favored adaptations that made moving over open ground more efficient.
    - All early hominins show indications of bipedalism, but they lived in forests and open woodlands, not savanna.
    - Australopiths seem to have had various locomotor styles, and some species spent more time on the ground than others.
    - About 1.9 million years ago, hominins living in arid environments walked long distances on two legs.
- When and why did tool use arise in the human lineage?
    - The manufacture and use of complex tools are derived human characters.
    - Apes are capable of sophisticated tool use.
    - Orangutans can fashion probes from sticks for retrieving insects from their nests.
    - Chimps use rocks to smash open food and put leaves on their feet to walk over thorns.
    - The oldest generally accepted evidence of tool use is 2.5-million-year-old cut marks on animal bones found in Ethiopia.
    - The australopith fossils near the site had relatively small brains.
    - If these hominins, *Australopithecus garhi,* made the stone tools used on the bones, that suggests that stone tool use originated before the evolution of large hominin brains.

- The earliest fossils that anthropologists place in our genus, *Homo*, are classified as *Homo habilis*.
  - These fossils range in age from 2.4 to 1.5 million years old.
  - This species had a shorter jaw and larger brain (about 600–750 $cm^3$) than australopiths.
  - In some cases, anthropologists have found sharp stone tools with these fossils, indicating that some hominins had started to use their brains and hands to fashion tools.
- Fossils from 1.9–1.6 million years ago are recognized as a distinct species, *Homo ergaster*.
  - *H. ergaster* had a larger brain than *H. habilis* (more than 900 $cm^3$) as well as long, slender legs with hip joints well adapted for long-distance walking.
  - The fingers were relatively short and straight, suggesting that *H. ergaster* did not climb trees like earlier hominins.
  - This species lived in more arid environments and was associated with more sophisticated tool use.
  - Its reduced teeth suggest that it might have been able to cook or mash its food before eating it.
- Specimens of early *Homo* show reduced sexual dimorphism.
  - Male gorillas and orangutans weigh about twice as much as females of their species.
  - In chimpanzees and bonobos, males are only about 1.35 times as heavy as females, on average.
  - In *A. afarensis*, males were 1.5 times as heavy as females.
  - In early *Homo*, however, sexual dimorphism was significantly reduced, and this trend continued through our own species: Human males average about 1.2 times the weight of females.
  - Sexual dimorphism is reduced in pair-bonding species.
  - Male and female *H. ergaster* may have engaged in more pair-bonding than earlier hominins, perhaps in order to provide long-term biparental care of babies.
- Some paleontologists still think that *H. ergaster* were merely early specimens of *Homo erectus*.
- *H. erectus* was the first hominin species to migrate out of Africa, colonizing Asia and Europe.
  - The oldest fossils of hominins outside Africa, dating back 1.8 million years, were discovered in 2000 in the former Soviet Republic of Georgia.
  - *H. erectus* eventually migrated as far as the Indonesian archipelago.
  - *H. erectus* became extinct sometime after 200,000 years ago.
- In Europe, Neanderthals arose from an earlier species, *Homo heidelbergensis,* which arose in Africa about 600,000 years ago and spread to Europe.
- The term *Neanderthal* is now used for humans who lived throughout Europe 200,000–30,000 years ago.
  - Neanderthals lived in Europe and the Near East by 200,000 years ago but never spread outside that region.
  - Fossilized skulls indicate that Neanderthals had brains as large as those of modern humans.
  - Neanderthals made hunting tools from stone and wood.
  - Neanderthals apparently went extinct about 28,000 years ago.
- Preliminary results from a 2006 study that compared Neanderthal and human nuclear DNA are consistent with limited gene flow between the two species.

- Some researchers argue that evidence of gene flow can be found in fossils that show a mixture of *H. sapiens* and Neanderthal characteristics.
- Further genetic analyses and fossil discoveries are needed to resolve the ongoing debate over the extent of genetic exchange between the two species.

- In 2003, researchers in Ethiopia found 195,000- and 160,000-year-old fossils of *H. sapiens*, the oldest members of our species.
  - These early humans were slender and lacked brow ridges.
- DNA analysis indicates that all living humans are more closely related to one another than to Neanderthals.
- Other studies on human DNA show that Europeans and Asians share a relatively recent common ancestor and that many African lineages branched off more ancient positions on the human family tree.
- These findings strongly suggest that all living humans have ancestors that originated as *H. sapiens* in Africa, which is further supported by analyses of mitochondrial DNA and Y chromosomes from members of various human populations.
- The oldest fossils of *H. sapiens* outside Africa date back about 115,000 years, from the Middle East.
- Studies of the human Y chromosome suggest that humans spread beyond Africa in one or more waves, first into Asia and then to Europe and Australia.
- The oldest generally accepted evidence of the first arrival of humans in the New World puts that date at 15,000 years ago.
- In 2004, researchers reported an astonishing find: the skeleton of an adult hominin dating from just 18,000 years ago and representing a previously unknown species, which they named *Homo floresiensis.*
  - Discovered in a limestone cave on the Indonesian island of Flores, the individual was much shorter and had a much smaller brain volume than *H. sapiens.*
  - The skeleton also displays many derived traits, including skull thickness and proportions and teeth shape, suggesting it is descended from the larger *H. erectus.*
- Other scientists, however, are not convinced that the Flores fossils represent a new hominin. They argue that the fossil was from a small *H. sapiens* who had a deformed, miniature brain, a condition called microcephaly.
- Scientists are seeking new information to resolve the debate over the Flores fossils.
  - If further evidence supports the designation of *H. floresiensis* as a new hominin, one explanation for this species' apparent "shrinkage" is that isolation on the island may have resulted in selection for greatly reduced size.
  - Compelling questions include how *H. floresiensis* originated and whether they ever encountered *H. sapiens,* which coexisted in Indonesia during the late Pleistocene.
- Although Neanderthals and other hominins were able to produce sophisticated tools, they showed little creativity and not much capability for symbolic thought.
- Researchers have found evidence of more sophisticated thought as *H. sapiens* evolved.
  - In 2002, researchers reported the discovery in South Africa of 77,000-year-old art—geometric markings made on pieces of ochre.
  - In 2004, archaeologists working in southern and eastern Africa found 75,000-year-old ostrich eggs and snail shells with holes neatly drilled through them.

    - By 36,000 years ago, humans were producing spectacular cave paintings.
- Both symbolic thought and human language may have increased the survival and reproductive fitness of humans by allowing them to construct new tools and teach others how to build them.
- Long-range trade for scarce resources also became possible.
- As the population in Africa rose, population pressures may have driven humans to migrate into Asia and then Europe.
- Neanderthals may have been driven to extinction by the combined stresses of the last ice age and competition from newly arrived humans.
- Clues to the cognitive transformation of humans can be found in the human genome.
- A gene known as *FOXP2* was identified in 2001 as essential for human language.
    - People who inherit mutated versions of the gene suffer from a range of language impediments and have reduced activity in Broca's area in the brain.
- In 2002, geneticists compared the *FOXP2* gene in humans with the homologous gene in other mammals.
- The researchers concluded that the gene experienced intense natural selection after the ancestors of humans and chimpanzees diverged.
    - By comparing mutations in flanking regions of the gene, the researchers estimated that this bout of natural selection occurred within the past 200,000 years.
- The evolutionary change in *FOXP2* may be the first genetic clue as to how our own species came to play its unique role in the world.