Chapter 34

The Origin and Evolution of Vertebrates

Lecture Outline

Overview: Half a Billion Years of Backbones

- In the early Cambrian period, 530 million years ago, a slender 3-cm-long animal, *Myllokunmingia fengjiaoa,* swam in the oceans.
  - This species was closely related to 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 over 150 million years, vertebrates were restricted to the oceans, but about 365 million years ago, the evolution of limbs in one lineage of vertebrates allowed them to colonize land.
  - On land, vertebrates diversified into amphibians, reptiles (including birds), and mammals.
- There are about 52,000 species of vertebrates, compared to 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 are members of the phylum Chordata, the chordates.
- Chordates are bilaterian animals belonging to the Deuterostomia clade.
  - Two goroups 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 key 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 embryonic and some adult chordates, 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 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 provides a firm but flexible structure against which muscles can work during swimming.
- In most vertebrates, the notochord remains as a remnant, surrounded by a more complex, jointed skeleton.
- In humans, the notochord is the gelatinous material of the disks between the vertebrae.

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 passing through the gut.
   - In many invertebrate chordates, pharyngeal slits function as suspension-feeding devices.
   - In vertebrates (with the exception of vertebrates that have limbs, the tetrapods), the slits and their supportive structures are 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.

- The most basal group of living chordates are bladelike animals called lancelets (Cephalochordata).
- 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 6 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 display chordate characteristics 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 is filtered from water, trapped by a mucous net, and 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.
- The tunicate larva appears to be highly derived.
    - Tunicates have 9 *Hox* genes, while all other chordates studied to date, including the early-diverging lancelets, share a set of 13 *Hox* genes.
    - The loss of 4 *Hox* genes indicates that the chordate body plan of a tunicate larva is built using a different set of genetic controls than other chordates.
- The anterior region of a tunicate is elongated and contains a heart and digestive system.
- Tunicates and lancelets may provide clues to the evolutionary origin of the vertebrate body plan.
    - 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.
- 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.

- 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.
  - Such genes likely arose in an early vertebrate and are unique to the vertebrate evolutionary lineage.

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 or more clusters of *Hox* genes; 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.

- Chinese fossils of early chordates have provided information about the origin of craniates.
  - The early chordates were 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* had a well-formed brain, eyes, muscular segments, and respiratory gills in its pharynx.
  - *Haikouella* lacked a skull and had no ear organ for maintaining balance.
- In other Cambrian rocks, paleontologists have found fossils of more advanced chordates, such as *Myllokunmingia*.
  - *Myllokunmingia*, with ear and eye capsules surrounded by a skull, is a true craniate.

Hagfishes (Myxini) are the most basal group of craniates.

- Hagfishes have a skull of cartilage, but lack jaws and vertebrae.
- Hagfishes swim in a snakelike fashion by using 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 30 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 (Petromyzontida) are the most basal lineage of living vertebrates.

- Like hagfishes, lampreys offer clues to early chordate evolution but also have acquired unique characteristics.
- About 35 species of lampreys inhabit marine and freshwater environments.
- Most lampreys are parasites that feed by clamping a round, jawless mouth onto a fish, use their rasping tongues to penetrate the skin of their prey, and 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.
- Most lampreys migrate to the sea or lakes as they mature into adults.
    - 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, they attain sexual maturity, reproduce, and die within a few days.
- The skeletons of lampreys are made of cartilage.
    - Unlike most vertebrate cartilage, 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 flexible sheath 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.
- Conodonts ranged in length from 3 to 30 cm.
- Conodonts probably hunted with their large eyes and impaled their prey on a set of anterior barbed hooks, made of *mineralized* tissues.
- The food 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 (like lampreys) an inner ear with two semicircular canals that provided a sense of balance.
    - Although they lacked jaws, they had a muscular pharynx to suck 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.
- 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, a adaptation that allowed these animals to become predators and scavengers.
- The bony armor of later jawless vertebrates was composed of small toothlike structures, suggesting that mineralization of the vertebrate body began in the mouth and later was incorporated into protective armor.
- In more derived vertebrates, the **endoskeleton** began to mineralize, starting with the skull.

Concept 34.4 Gnathostomes are vertebrates that have jaws

- The **gnathostomes** have true jaws, hinged structures that, with the help of teeth, enable vertebrates to grasp and slice food.
- Living gnathostomes are a diverse group that includes sharks and their relatives, ray-finned and lobe-finned fishes, 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 *Hox* genes, so that the single cluster present in early chordates became four.
    - The entire genome appears to have 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.
- Gnathostomes appeared in the fossil record in the mid-Ordovician period, about 450 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 swim efficiently after prey.
- 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 during the Silurian and Devonian periods (444 to 359 million years ago).
- Placoderms disappeared by 359 million years ago, while acanthodians became extinct about 70 million years later.
- New fossil discoveries suggest that 450 to 420 million years ago was a period of tumultuous evolutionary change.
- Gnathostomes that lived during this period had highly variable forms, and by 420 million years ago, they had diverged into the three lineages of jawed vertebrates that survive today: chondrichthyans, ray-finned fishes, and lobe-fins.

Sharks and rays have cartilaginous skeletons.

- The clade 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.
  - Bonelike tissues have been found in early chondrichthyans, such as the fin skeleton of a shark that lived in the Carboniferous period.
  - 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.
- Loss of bone in chondrichthyes is a derived condition, which emerged after they diverged from other gnathostomes.
- There are about 1000 species of living chondrichthyans, almost all in the subclass of sharks and rays, with a few dozen species in a second subclass of ratfishes or chimaeras.
- 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.
  - Paired pectoral and pelvic fins are important for maneuverability.
- Although some buoyancy is provided by low-density oils in the large liver, 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.
- The largest sharks and rays are suspension feeders that consume plankton.
- Most sharks are carnivores that swallow prey whole or use powerful jaws and sharp teeth to tear flesh from large animals.
  - 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 to 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 generated by the muscle contractions of nearby prey.
  - 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; they hatch outside the mother's body.
- **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 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 thrived for over 400 million years but are now severely threatened by overfishing.
  - Shark stocks in the northwest Atlantic have declined 75% over a 15-year period.

The clade Osteichthyes includes tetrapods and bony fishes.

- The vast majority of vertebrates (including tetrapods) belong to the clade Osteichthyes.
  - Aquatic osteichthyans are known informally as fishes.
- Nearly all living **osteichthyans** have an ossified endoskeleton with a hard matrix of calcium phosphate.
- Most 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 lungs that may have been used by early osteichthyans to breathe air to supplement gas exchange in the gills.
  - 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 ancient gnathostomes, fishes 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 fishes 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.
- Named for the bony rays that support their fins, the ray-finned fishes originated during the Silurian period (444 to 416 million years ago).

- Ray-finned fishes serve as a major source of protein for humans, who have harvested them for thousands of years.
- Industrial-scale fishing operations 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.
- **Lobe-fins** (Sarcopterygii) also originated in the Silurian period.
- 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 (416 to 359 million years ago), 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 east coast of South Africa.
    - Coelocanths were also found near the Comoros Islands in the western Indian Ocean.
    - Since 1999, coelacanths have been found along the eastern coast of Africa and 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 365 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.
  - Most living tetrapods do not have gills; 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.
- A recent discovery, *Tiktaalik,* has provided new details on how this process occurred.
- Like a fish, *Tiktaalik* had fins, gills, lungs, and a scaly body.
- *Tiktaalik* also had many characteristics that were not fish-like.
  - It had ribs to help it breathe air and support its body.
  - Its head and shoulders were not connected, allowing it to move its head on its neck.
  - The bones of *Tiktaalik*'s front fin have the same basic pattern found in all limbed animals: one bone (the humerus), followed by two bones (the radius and ulna), followed by a group of small bones that comprise the wrist.
  - *Tiktaalik* could not walk on land, but could prop itself up in water on its fins.
- *Tiktaalik* and other fossil discoveries allow paleontologists to reconstruct how fins became progressively more limb-like over time, culminating in the appearance of the first tetrapods 365 million years ago.
  - Most early tetrapods were tied to the water, just like modern amphibians.

Salamanders, frogs, and caecilians are living amphibians.

- **Amphibians** (class Amphibia) are represented by about 6,150 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.

- Paedomorphosis is common among aquatic salamanders. The axolotl retains larval features even when it is sexually mature.

- 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 sticky tongues attached to the front of the mouth.
  - Anurans may avoid predation by secreting distasteful or poisonous mucus from skin glands.
  - Many poisonous species are brightly colored to warn off predators.
- 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.
- *Amphibian* means “both ways of life,” 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, which swim by undulating their tails.
  - During metamorphosis, the tadpole develops legs, lungs, external eardrums, and a digestive system adapted to a carnivorous diet.
  - The lateral line and the gills disappear as the adult frog becomes a terrestrial hunter.
- Many amphibians do not live a dual aquatic and terrestrial life.
  - There are strictly aquatic and 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 vocalize to 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 30 years, zoologists have been documenting a rapid and alarming decline in amphibian populations throughout the world.
    - Since 1980, at least 9 amphibian species have become extinct and more than 100 other species may have been lost.
    - Possible causes include habitat loss, a disease-causing chytrid fungus, climate change, and pollution.

Concept 34.6 Amniotes are tetrapods that have a terrestrially adapted egg

- Mammals and reptiles (including birds) belong to the clade of **amniotes**.
- During their evolution, amniotes acquired 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 the amnion, which encloses a fluid-filled “private pond” that bathes the embryo and acts as a hydraulic shock absorber.
    - Other membranes in the egg function in gas exchange, the transfer of stored nutrients to the embryo, and waste storage.
- The amniotic egg 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 350 million years ago. No fossils of amniotic eggs have been found from that time.
- The earliest amniotes lived in warm, moist environments.
- Some early amniotes were small and predatory, with sharp teeth and long jaws.
    - Later groups included herbivores, with grinding teeth.
- The **reptile** clade includes tuatara, lizards, snakes, turtles, crocodilians, and birds, as well as extinct groups such as plesiosaurs and ichthyosaurs.
- Reptiles have several derived characters that distinguish them from other tetrapods.
    - 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.

- Many 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.

- The oldest reptilian fossils date back to the late Carboniferous period.
- The first major group of reptiles to emerge was the **parareptiles**, large, stocky, quadrupedal herbivores.
  - Some parareptiles had dermal plates on their skin for defense against predators.
  - Parareptiles died out 200 million years ago, at the end of the Triassic period.
- As parareptiles dwindled, another ancient clade of reptiles, the **diapsids**, diversified.
  - One derived character of diapsids is a pair of holes on each side of the skull, behind the eye socket, through which jaw muscles pass.
- The diapsids are composed of two main lineages: lepidosaurs and archosaurs.
  - The **lepidosaurs** include lizards, snakes, and tuataras, as well as extinct marine reptiles such as 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 digit on the forelimb.
  - 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, eating insects, marine fishes, and filter-feeding small marine animals.
  - 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: mostly herbivorous ornithischians and saurischians, which included long-necked herbivores and 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.

- In the warm Mesozoic climate, behavioral adaptations and low surface-to-volume ratios may have been sufficient for terrestrial dinosaurs to maintain a suitable body 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 and fast moving.
  - Dinosaurs' limb structure allowed them to walk and run more efficiently than could earlier tetrapods, which had a sprawling gait.
  - Fossilized footprints and other evidence suggest that some species were social, living and traveling in groups.
  - 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 were abundant 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 include about 7,900 species of 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, reaching a length of 3 m.
  - The Komodo dragon hunts deer and other large prey, delivering venom with its bite.
- Snakes are legless lepidosaurs that evolved from lizards with legs.
  - 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 grip 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 snakes to swallow prey larger than their own diameter.
- 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.
  - Most of the 307 known species of turtles have a hard protective shell.
- In 2008, the oldest known fossil on the turtle lineage, from 220 million years ago, was found.
  - This fossil had a complete lower shell but an incomplete upper shell, suggesting that turtles may have acquired fully developed shells in stages.
  - The location of this fossil also suggested that turtles may have originated in shallow marine waters.
  - It is also possible that turtles originated on land and that the incomplete upper shell of this fossil may have been a specialized adaptation for an aquatic lifestyle.
- 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.
- The largest living turtles, the leatherbacks, can weigh more than 1,500 kg and feed on jellies.
  - Leatherbacks and other sea turtles are endangered by being caught in fishing nets and 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 are aquatic, breathing air through upturned nostrils.
  - Crocodilians are confined to the tropics and subtropics.

Birds evolved as feathered dinosaurs.

- There are about 100,000 species of birds.
- Birds are archosaurs with many derived features that are adaptive for flight.
- Among weight-saving modifications is the loss of organs.
  - Birds lack a urinary bladder and females have only one ovary.
  - The gonads of both females and males are small, except during the breeding season.
  - 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 b-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 large pectoral muscles, anchored to a keel on the sternum.

- Flight provides many benefits.
  - Flight enhances hunting and scavenging; enables many birds to catch flying insects, an abundant, highly nutritious food resource; provides a ready escape from earthbound predators, and 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.
  - Birds have color vision and excellent eyesight.
- Birds generally display very complex behaviors.
  - During the breeding season, they may 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 birds belong to a group of bipedal saurischian dinosaurs called **theropods**.
- Since the late 1990s, Chinese paleontologists have 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 display.
- 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.
- *Archaeopteryx*, found in a German limestone quarry, is the earliest known bird.
  - It lived about 150 million years ago, during the late Jurassic period.
  - *Archaeopteryx* had feathered wings but retained ancestral characteristics such as clawed forelimbs, teeth, and a long tail.
  - *Archaeopteryx* flew well at high speeds, but could not take off from a standing position.

- Fossils of later Cretaceous birds show a gradual loss of 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 the **ratites**, which lack a sternal keel and have small pectoral muscles, are flightless.
  - 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 mean that all flying birds share a similar general form.
  - The beak of birds has taken on a great variety of shapes suited to different diets.
  - Foot structure also shows considerable variation, as 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.
- Like birds, mammals 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 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.
- Fossil evidence shows that the jaw was remodeled over 100 million years 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.
  - This evolutionary change is reflected in changes that occur during development. As a mammalian embryo grows, the posterior region of its jaw—which in a reptile forms the

articular bone—can be observed to detach from the jaw and migrate to the ear, where it forms the malleus.

- Synapsids evolved into large herbivores and carnivores during the Permian period.
- Mammal-like synapsids emerged by the end of the Triassic, 251-200 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 (200-145 million years ago).
- Early mammals diversified into a number of lineages, most less than 1 m in size.
    - 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 a few species of opossum are found in North America.
- Invasions of placental mammals from North America affected the marsupial fauna of South America 3 million years ago, when the continents were connected by the Isthmus of Panama.
- Compared to marsupials, **eutherians** (placental mammals) have longer pregnancies.
    - Young eutherians complete embryonic development within the uterus, joined to the mother by the placenta.

- The placentas of eutherians 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 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 living 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 clade, but consist of two groups, New and Old World monkeys.
- Both groups originated in Africa or Asia.
  - New World monkeys colonized South America about 25 million years ago.
- 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 live in bands held together by social behavior.

- In addition to monkeys, anthropoids include apes such as *Hylobates* (gibbons), *Pongo* (orangutans), *Gorilla* (gorillas), *Pan* (chimpanzees and bonobos), and *Homo* (humans).
  - Apes diverged 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, 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

- Our own species, *Homo sapiens,* is about 200,000 years old.
- Humans are distinguished from apes by 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, artistic expression, and the manufacture and use of complex tools.
  - Humans have reduced jawbones and jaw muscles and a shorter digestive tract.
- Although 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.
  - These genes turn other genes on and off and may account for many differences between humans and chimpanzees.
- Such genomic differences and the 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.
- 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.
- What evidence points to an increasingly bipedal stance?
  - 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.
- The pelvis, leg bones, and foot of the 4.4-million-year-old *Ardipithecus ramidus* also suggest that early hominins were increasingly bipedal**.**

- The brains of early hominin remained small: about 300-450 cm^3, compared with an average of 1,300 cm^3 for *Homo sapiens.*
- Early hominins were small in stature, with relatively large teeth and a protruding jaw.
- It is important to avoid two common misconceptions in considering early hominins:
  1. Our ancestors were not chimpanzees and did not evolve from chimpanzees.
  - Chimpanzees represent the tip of a separate branch of evolution and 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*.
  - Many splinter groups traveled down other evolutionary paths.
  - At times, several different hominin species coexisted, differing 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.
  - Many of these hominin belong to a paraphyletic group called australopiths, whose phylogeny remains unresolved on many points.
- The first australopith, *Australopithecus africanus*, lived between 3 and 2.4 million years ago.
  - *A. africanus* walked fully erect and had human-like hands and teeth.
  - Its brain 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, "Lucy," was described as a new species, *A. afarensis.*
  - Fossils found in the early 1990s show that *A. afarensis* existed as a species for at least 1 million years.
- *A. afarensis* was 1 meter tall and had a brain the size of a chimpanzee's, a long lower jaw, and long arms for arboreal locomotion.
  - The pelvis, skull bones, and fossil tracks showed that *A. afarensis* walked bipedally.
- Two lineages appeared after *A. afarensis*: "robust" australopiths with sturdy skulls, powerful jaws, and teeth for grinding hard, tough foods; and "gracile" australopiths with lighter jaws.
- Why did hominins become bipedal?
  - Our anthropoid ancestors of 30–35 million years ago were tree-dwellers.
  - Ten million years ago, the forests of Africa and Asia contracted as the climate became drier. The result was an increasingly 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 selection favored adaptations for moving over open ground more efficiently.
  - All early hominins show indications of bipedalism, but they lived in forests and open woodlands, not savanna.

- *Ardipithecus* could switch to upright walking but was well suited for climbing trees.
- Australopiths 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 began to walk 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, while 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 from our genus*, Homo,* include those of *Homo habilis*.
  - These fossils range in age from 2.4 to 1.6 million years old.
  - *Homo habilis* had a shorter jaw and larger brain (about 600–750 cm^3) than australopiths.
  - Sharp stone tools were found with these fossils.
- Fossils from 1.9–1.5 million years ago are recognized as a distinct species, *Homo ergaster*.
  - *H. ergaster* had a larger brain than *H. habilis* (over 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 *H. ergaster* did not climb trees.
  - This species lived in arid environments and was associated with sophisticated tool use.
  - Its reduced teeth suggest that it might have been able to cook or mash its food.
- Specimens of early *Homo* show reduced sexual dimorphism.
  - Male gorillas and orangutans weigh about twice as much as females of their species, while chimpanzees and bonobos males are about 1.35 times as heavy as females.
- In *A. afarensis*, males were 1.5 times as heavy as females.
  - In early *Homo*, 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, in order to provide long-term biparental care of babies.
- *Homo erectus* originated in Africa and was the first hominin 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.
  - Fossil evidence suggests *H. erectus* became extinct about 200,000 years ago, although one group may have persisted on Java until 50,000 years ago.
- *Homo neaderthalensis* were living in Europe by 350,000 years ago. They later spread to the Near East, Central Asia, and southern Siberia.

- Neanderthals had brains as large as those of modern humans, buried their dead, and made hunting tools from stone and wood.
- Neanderthals apparently went extinct about 28,000 years ago.
- Further genetic analyses and fossil discoveries will be needed to resolve the ongoing debate over the extent of genetic exchange between the two species.

- Researchers in Ethiopia found the oldest members of our species, 195,000 and 160,000-year-old fossils of *Homo sapiens*.
  - These early humans were slender and lacked prominent brow ridges.
- DNA analysis suggests that all living humans have ancestors that originated as *H. sapiens* in Africa.
  - This is supported by analysis of mitochondrial DNA and Y chromosomes from members of various human populations.
- The oldest fossils of *H. sapiens* outside Africa are from the Middle East and date back about 115,000 years.
  - 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 is about 15,000 years ago.
- In 2004, researchers reported an astonishing find: the skeletons of adult hominin from 18,000 years ago, representing a previously unknown species, *Homo floresiensis.*
  - Discovered in a limestone cave on the Indonesian island of Flores, the individuals were much shorter and had a much smaller brain volume than *H. sapiens*.
  - The skeletons also display many derived traits, including skull thickness and proportions and teeth shape, suggesting it is descended from the larger *H. erectus*.
- Other scientists argue that the fossil was from a small *H. sapiens* who had a deformed, miniature brain, a condition called microcephaly.
  - A 2007 study found that the wrist bones of the Flores fossils are similar in shape to those of nonhuman apes and early hominins, but different from those of Neanderthals and *H. sapiens.*
  - This suggests that the Flores fossils represent a species whose lineage branched off before the origin of the clade that includes Neanderthals and humans.
- A later study comparing the foot bones of the Flores fossils to those of other hominins also concluded that *H. floresiensis* arose before *H. sapiens*.
  - *H. floresiensis* may have descended from a hominin that lived before *H. erectus*.
- One explanation for the apparent shrinkage of *H. floresiensis* is that isolation on the island may have resulted in selection for greatly reduced size.
  - Reduction in size is well studied in other dwarf mammalian species that are endemic to islands, including primitive pygmy elephants found near the Flores fossils.
- On islands, the brains of dwarf fossil hippos were proportionally smaller than their bodies.
  - The mammalian brain uses large amounts of energy, and a possible explanation is that smaller brains resulted from selection for reduced energy consumption.).
  - The researchers found that the brain size of *H. floresiensis* closely matched that predicted for a dwarf hominin of its body size.

- Compelling questions include how *H. floresiensis* originated and whether they ever encountered *H. sapiens,* which also lived in Indonesia 18,000 years ago.
- 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.
- Neanderthals also made complex tools and showed a capacity for symbolic thought.
    - As a result, the suggestion that Neanderthals were driven to extinction by competition with *H. sapiens* is questioned by some scientists.