Chapter 34

Vertebrates

Key Concepts

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

34.2 Craniates are chordates that have a head

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34.7 Mammals are amniotes that have hair and produce milk

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Framework

This chapter focuses on the phylogeny of chordates, introducing the derived characters that define the major clades. Fill in the cladogram of chordates on p. 269 as you work through this chapter. Fossil evidence and hypotheses about human ancestry are also described.

Chapter Review

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

The deuterostome clade of the animal kingdom includes the echinoderms and **chordates.** The chordates include two invertebrate groups—the urochordates and the cephalochordates, the hagfishes, and the **vertebrates,** which have a backbone, or vertebral column.

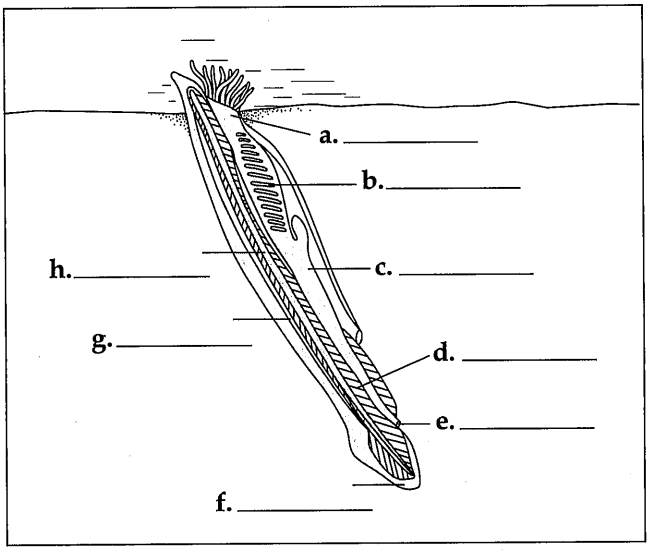
Derived Characters of Chordates Chordates have four distinguishing anatomical features, which may appear only during the embryonic stage: (1) a flexible rod called a **notochord** that provides skeletal support along the length of the animal; (2) a dorsal, hollow nerve cord that develops into the brain and spinal cord; (3) **pharyngeal clefts,** or grooves that may develop into **pharyngeal slits** that open from the pharynx to the outside and function in suspension feeding or are modified for gas exchange and other functions; and (4) a post-anal tail containing skeletal elements and muscles.

Tunicates **Tunicates** (subphylum Urochordata) belong to the deepest-branching lineage of chordates. The larval traits of notochord, nerve cord, and tail are lost in the adult animal. In this saclike, sessile animal, commonly called a sea squirt, water flows in the incurrent siphon, through pharyngeal slits where food is filtered by a mucous net, and out the excurrent siphon.

Lancelets **Lancelets** (subphylum Cephalochordata) are tiny marine animals that retain all four chordate characteristics into the adult stage. These suspension feeders burrow backward into the sand and filter food particles through a mucous net secreted across the pharyngeal slits. The lancelet swims by coordinated contractions of serial muscles that flex the notochord from side to side. Blocks of mesoderm, called **somites,** develop into these muscle segments.

■ INTERACTIVE QUESTION 34.1

What is the name for the animal shown in this diagram, and to which subphylum does it belong? Identify the labeled structures and indicate the four chordate characters.



Early Chordate Evolution An early hypothesis was that lancelets evolved by paedogenesis from a tunicate-like larva. Current evidence indicates that both the larval and degenerate adult stage of tunicates are derived traits. Studies have shown that several *Hox* genes are expressed in the vertebrate brain and in the anterior end of the lancelet dorsal nerve cord in the same anterior-to-posterior pattern.

34.2 Craniates are chordates that have a head

Derived Characteristics of Craniates The origin of a head with eyes and other sensory organs and a skull enclosing a brain was a major evolutionary transition seen in **craniates.**

Derived characters that distinguish craniates from other chordates include two clusters of *Hox* genes instead of only one, and a duplicated family of genes for signaling molecules and transcription factors. A group of embryonic cells called the **neural crest** is found along the margin of the embryonic folds that form the nerve cord. These cells migrate in the embryo and contribute to various craniate structures, including bones and cartilage of the cranium (skull). The pharyngeal clefts of craniates evolved into gill slits with muscles and nerves that facilitate sucking in food and water for gas exchange. Craniates have a higher metabolism, more extensive muscles, a heart with at least two chambers, red blood cells, hemoglobin, and kidneys.

The Origin of Craniates Newly discovered 530 million-year-old fossils (during the Cambrian explosion) appear to be transitional stages: an animal called *Haikouella,* which resembled lancelets, but with craniate characters such as eyes, mineralized toothlike structures, and a small but well-formed brain. Another fossil from this period, *Haikouichthys,* had a skull and is considered to be a true craniate.

Hagfishes Hagfishes, class Myxini, are the most primitive surviving craniate lineage. Their cartilaginous skeleton includes a skull and a notochord; they lack vertebrae and jaws. The marine hagfishes are mostly bottom-dwelling scavengers that produce slime to repulse predators and competing scavengers.

■ INTERACTIVE QUESTION 34.2

List the derived characters of craniates.

34.3 Vertebrates are craniates that have a backbone

Derived Characters of Vertebrates The gene duplication involving the *Dlx* family of transcription factor genes was associated with nervous system innovations and the more extensive skull and backbone of vertebrates. In most vertebrates, the vertebrae enclose the spinal cord. The dorsal, ventral, and anal fins supported by fin rays of aquatic vertebrates provided thrust and steering control for swimming.

Lampreys The jawless lampreys of class Cephalaspidomorphi represent the oldest lineage of vertebrates. Lampreys are suspension feeders as larvae and blood-sucking parasites as adults. The notochord is the main axial skeleton and is surrounded by a cartilaginous pipe with pairs of projections that partially enclose the nerve cord.

Fossils of Early Vertebrates **Conodants** were soft-bodied vertebrates with prominent eyes and barbed, mineralized hooks in their mouth, and dental elements in the pharynx for processing food. Conodonts appeared in the late Cambrian and were abundant for more than 300 million years.

During the Ordovician, Silurian, and Devonian periods, vertebrates with paired fins and an inner ear with semicircular canals emerged. These animals lacked jaws but had a muscular pharynx and were armored with mineralized bone. This paraphyletic group of diverse armored jawless vertebrates, previously called "ostracoderms," disappeared by the end of the Devonian period.

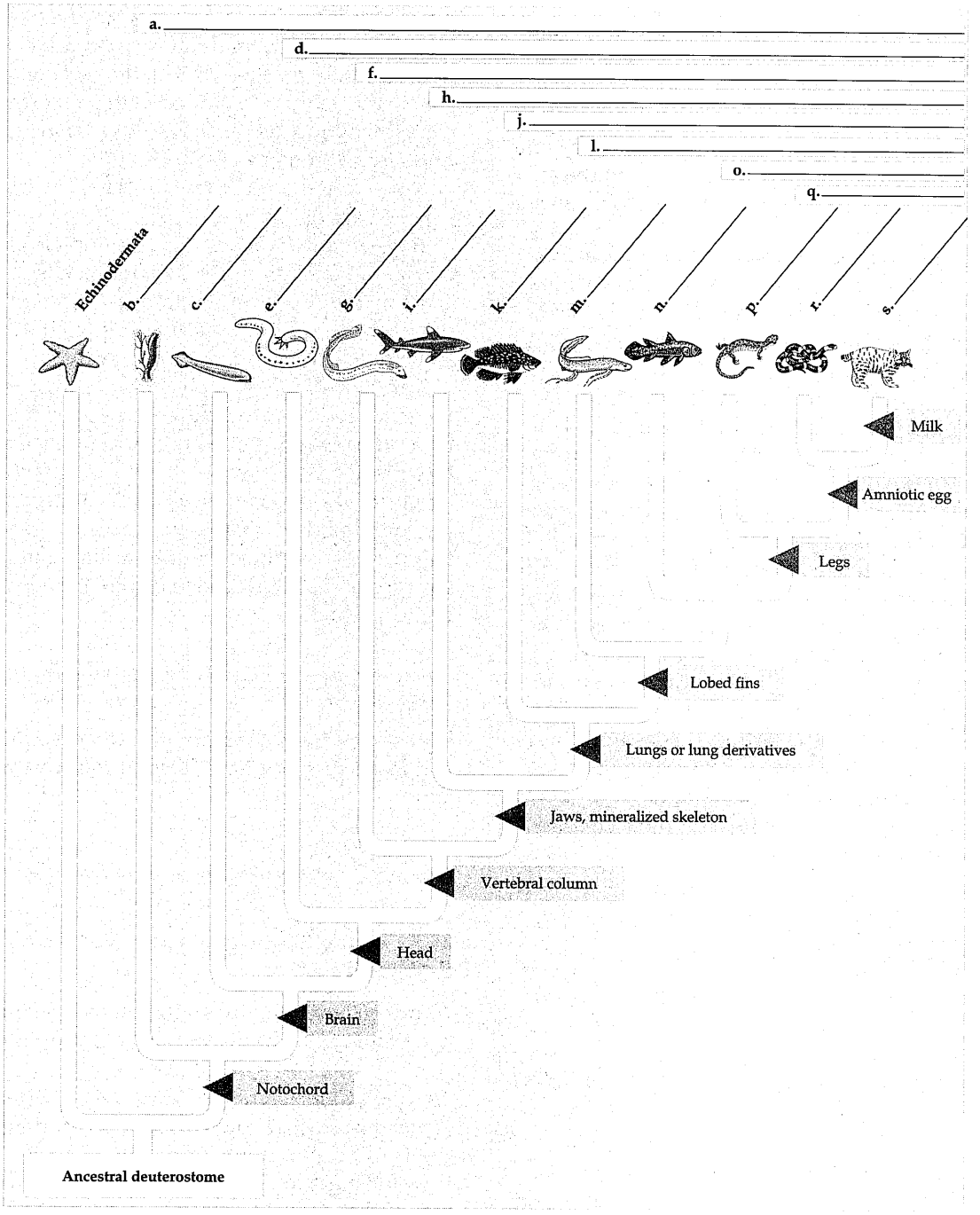
Origins of Bone and Teeth One hypothesis for mineralization in vertebrates is that it is associated with the switch from suspension-feeding to scavenging and predation. The earliest known mineralized structures are conodont dental elements. The armor of jawless vertebrates was derived from dental mineralization.

■ INTERACTIVE QUESTION 34.3

List the derived characters of vertebrates.

■ INTERACTIVE QUESTION 34.4

This cladogram shows the major clades of chordates with some of the derived characters that define them. As you work through this chapter, fill in the eight large clades across the top and representative animals of each group.



34.4 Gnathostomes are vertebrates that have jaws

Derived Characters of Gnathostomes The hinged jaws of **gnathostomes** may have evolved from the skeletal rods of the anterior pharyngeal slits, with the remaining gill slits functioning in gas exchange.

Other derived characters of gnathostomes include an addition duplication of *Hox* genes, duplication of other gene clusters, an enlarged forebrain associated with enhanced senses of smell and vision, a pressure-sensing **lateral line system,** and a mineralized endoskeleton.

Fossil Gnathostomes Beginning in the mid-Ordovician period, about 470 mya, gnathostomes became increasingly diverse. Their paired fins, tail, and hinged jaws facilitated a predatory lifestyle. The earliest gnathostomes were the armored **placoderms. Acanthodians** radiated during the Devonian period and were related to the ancestors of osteichthyans (ray-finned fishes and lobe-fins).

Chondrichthyans (Sharks, Rays, and Their Relatives) The sharks, rays, and their relatives of class Chondrichthyes have a skeleton made predominantly of cartilage. The cartilaginous skeleton of **chondrichthyans** appears to be a derived condition.

The largest subclass consists of sharks and rays. Sharks swim using powerful muscles in their caudal fin. The paired pectoral and pelvic fins provide lift. Swimming maintains buoyancy and moves water past their gills. Although most sharks are carnivores, the largest sharks and rays are suspension feeders on plankton.

Sharks have keen senses: sharp vision, nostrils, and skin regions in the head that can detect electric fields generated by muscle contractions of nearby animals. The shark's body transmits sound waves to the inner ear.

Following internal fertilization, **oviparous** species of sharks lay eggs that hatch outside the mother; **ovoviviparous** species retain the fertilized eggs until they hatch; and, in the few **viviparous** species, developing young are nourished by a yolk sac placenta until born.

Rays, which propel themselves with their enlarged pectoral fins, are primarily bottom dwellers that feed on mollusks and crustaceans.

■ INTERACTIVE QUESTION 34.5

a. List the derived characters of gnathostomes.

b. What is the function of the **spiral valve** in a shark's intestine?

c. What is a **cloaca?**

Ray-Finned Fishes and Lobe-Fins Nearly all vertebrates belong to a clade of gnathostomes called Osteichthyes, which historically included only the "bony fishes" but now includes the tetrapods. Almost all living **osteichthyans** have an ossified endoskeleton with a hard calcium phosphate matrix.

Aquatic osteichthyans (informally called fishes) move water through the mouth and out between the gills by the contraction of muscles in the gill chambers and movement of the protective bony flap called the **operculum.** Most aquatic osteichthyans also have a **swim bladder,** an air sac that controls buoyancy. It appears that lungs arose first as a supplement to gas exchange in the gills, and later evolved into swim bladders in some lineages. The flattened, bony scales that cover the skin of some aquatic osteichthyans are coated with mucus to reduce drag. They have a lateral line system similar to that of sharks.

Most aquatic osteichthyans have external fertilization and are oviparous.

Ray-finned fishes (class Actinopterygii) probably originated in fresh water during the Devonian period. They include most of the familiar modern fish, many of which spread to the seas during their evolution and some of which returned to fresh water.

The **lobe-fins** (Sarcopterygii), known mainly from the fossil record, have paired muscular fins supported by a series of rod-shaped bones that may have enabled these lobe-fins to "walk." Only three lobe-fin lineages survive: Two populations of coelacanths (class Actinistia) found in deep marine waters, three genera of lungfishes (class Dipnoi) found in stagnant ponds and swamps in the Southern Hemisphere, and the tetrapods found on land.

■ INTERACTIVE QUESTION 34.6

Go back to the cladogram in Interactive Question 34.4 and make sure you have filled in the information up to letter *n*.

34.5 Tetrapods are gnathostomes that have limbs and feet

About 360 million years ago, the fins of some lobe-fins evolved into the limbs and feet of tetrapods.

Derived Characters of Tetrapods **Tetrapods** have limbs that support their weight on land and feet with digits. The pelvic girdle is fused to the backbone, transferring forces generated by the hind legs to the rest of the body. Pharyngeal clefts formed during development give rise to parts of the ears, glands, and other structures.

The Origin of Tetrapods During the Devonian, a wide range of lobe-fins had evolved, probably using their stout fins to crawl through shallow waters and supplementing their gas exchange with their lungs. In one lineage, the fins became more limb-like while the rest of the body retained adaptations for the water. A diversity of tetrapods emerged during the Carboniferous period, most of which probably remained tied to the water. Many newly discovered fossils from 400 to 350 million years ago document the origin of tetrapods.

Amphibians **Amphibians** (class Amphibia) include salamanders (order Urodela), frogs (order Anura), and caecilians (order Apoda).

Salamanders, which may be aquatic or terrestrial, move with a lateral bending of the body. Frogs are more specialized for moving on land, using their powerful hind legs for hopping. Protective adaptations of frogs include camouflage coloring and distasteful or poisonous skin mucus that may be advertised by bright coloration. Tropical caecilians are burrowing, legless, nearly blind, wormlike animals.

Many frogs undergo a metamorphosis from a tadpole—the aquatic, herbivorous larval form with gills, a lateral line system, and a finned tail—to the carnivorous, terrestrial adult form with legs and lungs. Some amphibians are exclusively aquatic or terrestrial. Amphibians are most abundant in damp habitats, since some of their gas exchange occurs across their moist skin or mouth.

Fertilization is generally external. Oviparous species lay their eggs in aquatic or moist environments. Some species show varying amounts of parental care. During breeding season, some frogs communicate with vocalizations. Some species migrate to specific breeding sites, using various forms of communication and navigation.

■ INTERACTIVE QUESTION 34.7

a. What are the three lineages of lobe-fins?

b. Describe *Acanthostega*, a Devonian relative of tetrapods.

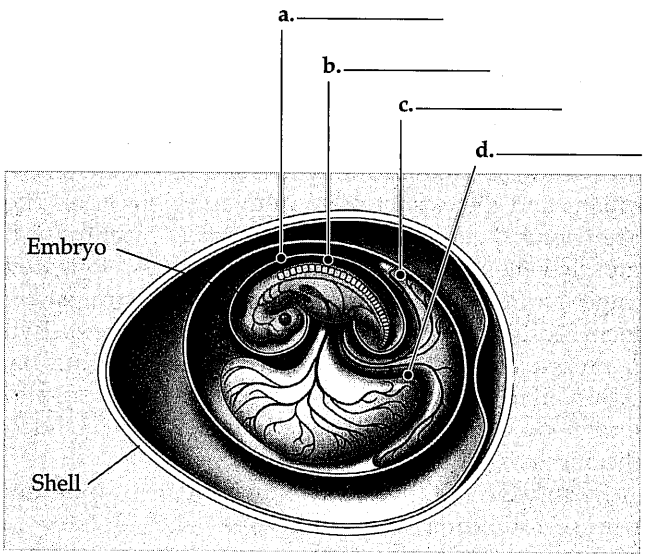
34.6 Amniotes are tetrapods that have a terrestrially adapted egg

Amniotes include reptiles (and birds) and mammals.

Derived Characters of Amniotes The amniotic egg contains **extraembryonic membranes** that are involved in gas exchange, waste storage, and transfer of nutrients to the embryo. The amnion encases the embryo in fluid. Most reptiles and some mammals have shelled amniotic eggs. The shells of bird eggs are calcareous; those of nonbird reptiles are leathery and flexible. Most mammals retain the embryo within the mother. Other terrestrial adaptations of the amniotes include a waterproof skin and increased use of the rib cage to ventilate the lungs.

■ INTERACTIVE QUESTION 34.8

Identify the four extraembryonic membranes in this sketch of an amniotic egg. What are the functions of these membranes?



a.

b.

c.

d.

Early Amniotes The most recent common ancestor of living amphibians and amniotes lived in the Carboniferous period, about 340 mya. Early amniotes lived in drier environments than earlier tetrapods. They included herbivores and predators.

Reptiles The **reptile** clade includes a number of extinct groups (such as dinosaurs), and tuatara, lizards, snakes, turtles, crocodilians, and birds. We must infer the derived characters that distinguished early reptiles from other tetrapods. The skin of reptiles is covered with keratinized, waterproof scales. Lungs are the vehicle for gas exchange. Most species lay shelled

amniotic eggs, and fertilization is internal. Some species are viviparous, in which case the extraembryonic membranes form a placenta.

Many reptiles are **ectothermic.** They absorb external heat rather than generating their own, although they may regulate their body temperature through behavioral adaptations. Birds are **endothermic,** warming their bodies with metabolic heat.

The oldest reptilian fossils date from the end of the Carboniferous period, 300 million years ago. The first major branch to emerge was the **parareptiles,** large herbivores with dermal plates on their skin. The relationship of turtles to parareptiles remains controversial.

The **diapsids** diversified next. Their most obvious derived character is a pair of holes on each side of the skull. The two main lineages of the diapsids are the **lepidosaurs,** which include tuatara, lizards, and snakes (and a number of now extinct huge marine reptiles) and the **archosaurs,** which produced the crocodilians and the extinct pterosaurs and dinosaurs. The **pterosaurs** had wings formed from a vascularized, muscled membrane stretched between an elongated finger and the hind leg. The highly diverse **dinosaurs** included the largest animals ever to live on land. Two main branches of dinosaurs were the herbivorous ornithischians and the saurischians, which gave rise to long-necked giants and the **theropods,** which included the ancestors of birds.

Scientists continue to debate whether dinosaurs were ectothermic or endothermic. The ancestor of birds was certainly endothermic. Evidence indicates that many dinosaurs were active; agile; and, in some species, social. At the end of the Cretaceous, all dinosaurs (except birds) became extinct.

The lizardlike tuatara represent one lineage of lepidosaurs, surviving only on islands off New Zealand. The other living lineage of lepidosaurs are the squamates. Lizards are the most numerous and diverse reptiles (aside from birds). Snakes are limbless, although some species have vestigial pelvic and limb bones. Snakes are carnivorous, with adaptations for locating (heat-detecting and olfactory organs), killing (sharp teeth, sometimes that inject toxins), and swallowing (loosely articulated jaws and elastic skin) their prey.

The earliest turtle fossils, from 220 mya, already had fully developed shells, so the origin of the turtle shell has not been established. This protective, usually hard shell has an upper and lower shield fused to the vertebrae, clavicles, and ribs.

Crocodiles and alligators, collectively called crocodilians, belong to an archosaur lineage. Living in warm regions, they are adapted to aquatic habitats.

■ INTERACTIVE QUESTION 34.9

The two main lineages of diapsids are archosaurs and lepidosaurs. List several representatives, both living and extinct, of these two lineages.

Birds Birds are archosaurs, whose reptilian features have been modified as they adapted to flight. Many of the derived characters of birds are adaptations that reduce weight: only one ovary, honeycombed bones, and lack of teeth.

Feathers made of β-keratin are extremely light and strong, and shape the wing into an airfoil. Large pectoral muscles attached to a keel on the sternum flap the aerodynamic wings. The evolution of strong flying ability enhanced hunting, foraging, escape from predators, and migration to favorable habitats.

Birds are endothermic; feathers and a fat layer in some species help retain metabolic heat. The four-chambered heart and efficient respiratory system facilitate a high metabolic rate.

Birds have excellent vision. Their relatively large brains permit detailed visual processing and motor coordination. Birds display complex behaviors, particularly in courtship rituals and parenting. Eggs are brooded during development by the female and/or male bird.

Cladistic analysis indicates that birds are theropods. Feathered, but flightless theropod fossils have recently been found in Chinese sediments. Several species had feathers with vanes, others had filamentous feathers. Functions of early feathers may have been insulation and courtship displays.

Flight may have evolved as ground-running dinosaurs used feathers to gain extra lift or as tree-climbing dinosaurs used feathers to glide.

Feathered theropods had evolved into birds by 150 million years ago. *Archaeopteryx,* the oldest bird known, had feathered wings with clawed digits, teeth, and a long tail. Fossils from the Cretaceous period show a gradual loss of dinosaur features and acquisition of bird innovations.

The clade Neornithes, which includes the 28 orders of living birds, appeared about 65 million years ago. Most birds can fly. Flightless birds, collectively called **ratites,** such as the ostrich, kiwi, and emu, lack a keeled breastbone and enlarged pectoral muscles. The general body form of many flying birds is similar. The beak has assumed a great variety of shapes associated with different diets. Foot structure also shows variation.

■ INTERACTIVE QUESTION 34.10

List several adaptations for flight found in birds.

34.7 Mammals are amniotes that have hair and produce milk

Derived Characters of Mammals **Mammals** are the other amniote lineage. Their derived characters include mammary glands, which produce milk to nourish the young, and hair, which (along with a layer of fat under the skin) helps to insulate these endothermic animals. Active metabolism is provided for by an efficient respiratory system that uses a diaphragm to help ventilate the lungs and a circulatory system with a four-chambered heart.

Mammals generally have large brains and many are capable of learning. Extended parental care of the young provides time to learn survival skills.

Mammalian teeth come in a diverse assortment of shapes and sizes that are specialized for eating a variety of foods.

Early Evolution of Mammals Mammals are part of the amniote group known as **synapsids,** distinguished by the temporal fenestra, a hole behind each eye socket. During the evolution of mammals from nonmammalian synapsids, the jaw was remodeled, with a stronger, single-bone lower jaw and the incorporation of two jaw bones into the middle ear. Synapsids were the dominant tetrapods during a time in the Permian period, but many became extinct at the end of that period. Mammal-like synapsids emerged 200 million years ago at the end of the Triassic.

The first true mammals arose and diversified during the Jurassic period. The still small Mesozoic mammals, which were probably nocturnal and insectivorous, coexisted with dinosaurs. Mammals underwent an extensive radiation in the wake of the Cretaceous extinctions. There are three major lineages of mammals today.

Monotremes The platypus and echidnas (spiny anteaters) are the only extant **monotremes,** egg-laying mammals. Although egg-laying is a primitive character for amniotes, monotremes have hair and produce milk for their young. Monotremes may have diverged from other mammals about 200 mya.

Marsupials **Marsupials,** including opossums, kangaroos, and koalas, share derived characters with eutherians including a higher metabolic rate, nipples that provide milk, and giving birth to live young. The embryo develops in the uterus. A **placenta,** formed from the uterine lining and extraembryonic membranes of the embryo, nourishes the developing embryo. A marsupial is born very early in development and completes its embryonic development in a maternal pouch called a marsupium.

Australian marsupials have radiated and filled the niches occupied by eutherian mammals in other parts of the world. After the breakup of Pangaea, South America and Australia became island continents where marsupials diversified in isolation from eutherians. Eutherians reached South America in several migrations, whereas Australia has remained isolated since about 65 mya.

Eutherians (Placental Mammals) **Eutherians** complete development attached to a placenta within the maternal uterus. Eutherians and marsupials may have diverged about 180 million years ago.

Molecular systematics is helping to establish the phylogeny of eutherian orders, although there is still no consensus. There appear to be at least four main clades. One clade evolved in Africa and includes the elephants, manatees, hyraxes, and aardvarks. A second clade radiated in South America and includes the sloths, anteaters, and armadillos. The third and largest clade includes the lagomorphs (rabbits), rodents, and primates. The fourth diverse clade includes many groups: the bats, shrews and moles, carnivores, the hoofed herbivores, and the cetaceans (dolphins and whales).

Primates include the lemurs, tarsiers, monkeys, and apes (including humans). Derived characters include grasping hands and feet, and flat nails on their digits. Compared to other mammals, primates have a large brain, short jaws, forward-looking eyes with overlapping visual fields that enhance depth perception, and exhibit complex social behavior and extensive parental care. Many of these traits were shaped by natural selection in the tree-dwelling early primates. All primates, except humans, have a wide separation between the big toe and the other toes, allowing them to grasp branches with their feet. The anthropoids have an **opposable thumb,** which functions in a grasping "power grip" in monkeys and apes, but is adapted for precise manipulation in humans.

There are three main groups of living primates: the lemurs, lorises, and pottos; the tarsiers; and the anthropoids. The lemurs, lorises, and pottos probably resemble early arboreal primates. The **anthropoids** include monkeys and hominoids. The oldest known anthropoid fossils are 45 million years old and point to tarsiers as the closest relative. Monkeys appeared in the New World during the Oligocene, after first evolving in the Old World. New World monkeys are strictly arboreal. Most monkeys in both groups are diurnal and live in social bands.

The **hominoids,** primates informally called apes, include gibbons, orangutans, gorillas, chimpanzees and bonobos, and humans. Hominoids diverged from Old World monkeys about 20–25 million years ago. Nonhuman hominoids live in the Old World tropics. Living hominoids, with the exception of gibbons, are larger than monkeys. All living hominoids have relatively long arms, short legs, and no tails. Hominoids have a larger brain and their behavior is more flexible than that of other primates. Gorillas and chimpanzees are highly social.

■ INTERACTIVE QUESTION 34.11

a. List the derived characteristics of mammals.

b. Go back to the cladogram in Interactive Question 34.4 and make sure you have filled in all the information.

34.8 Humans are bipedal hominoids with a large brain

Derived Characters of Humans The species *Homo sapiens* is about 160,000 years old. Characters that distinguish humans from other hominoids are upright stance and bipedal locomotion, larger brain with the capacity for language and symbolic thought, and the manufacture and use of complex tools. Humans also have reduced jaws and a shorter digestive tract.

The Earliest Hominids **Paleoanthropology** is the study of human origins. Approximately 20 extinct species of **hominids,** species that are more closely related to humans than to chimpanzees, have been identified. The oldest of these lived about 7–6 million years ago. These early hominids shared some derived characters of humans, such as reduced canine teeth, relatively flat faces, and upright stance, as indicated by the location of the foramen magnum underneath the skull. Different human features have evolved at different rates, known as **mosaic evolution.** Thus, for example, bipedalism evolved before an enlarged brain developed.

These early hominids and chimpanzees represent divergent branches from a common, anthropoid ancestor. Human evolution has not occurred within an unbranched hominid line; there have been times when several different human species coexisted.

Australopiths Hominid diversity increased between 4 and 2 million years ago, and many of the hominids from this period are called australopiths, although their phylogeny is unresolved. The name came from the 1924 discovery of *Australopithecus africanus.* It appears that *A. africanus* lived between 3 and 2.4 million years ago and was an upright hominid, with human-like hands and teeth but a small brain.

In 1974, a 3.24-million-year-old *Australopithecus* skeleton was discovered in the Afar region of Ethiopia. "Lucy" and similar fossils have been designated *Australopithecus afarensis,* a species that appears to have existed for about 1 million years. Although bipedal, *A. afarensis* had a brain size similar to that of a chimpanzee, an apelike skull with a long lower jaw, and long arms.

Another lineage from that time was the "robust" australopiths, such as *Paranthropus boisei,* which had sturdy skulls with powerful jaws and teeth.

Bipedalism About 20 million years ago, the Himalayan range rose, the climate became drier, and the forests of Africa and Asia contracted, presenting an increased savannah habitat that may have influenced anthropoid evolution. But all recently discovered fossils of early hominids show signs of bipedalism, and these hominids lived in mixed forests and open woodlands, leading to the hypothesis that bipedalism was an adaptation for reaching low-hanging fruit on trees. About 1.9 million years ago hominids that lived in more arid environments began to walk long distances on two legs.

Tool Use The first evidence of tool use are 2.5-million-year-old cuts on animal bones, suggesting that hominids used stone tools. *Australopithecus garhi,* whose fossils were found nearby, had a relatively small brain.

***Early* Homo** Larger-brained fossils dating from 2.4 to 1.6 million years old are the first to be placed in the genus *Homo.* Sometimes found with sharp stone tools, *Homo habilis,* or "handy man," had some derived hominid characters. Fossils from 1.9 to 1.6 years ago are recognized by a number of paleoanthropologists as the species *Homo ergaster,* which had a larger brain, long legs and hip joints adapted for long-distance walking, relatively short and straight fingers, and more sophisticated stone tools.

The sexual dimorphism of size difference between the sexes was also less in early *Homo* than that in *Australopithecus afarensis,* a trend that continued in humans, with males now only about 1.2 times the weight of females. In living hominoids, reduced sexual dimorphism is associated with more pair-bonding. Thus, *H. ergaster* may have engaged in pair-bonding, perhaps associated with long-term biparental care of babies.

Some paleoanthropologists still consider *H. ergaster* to be early members of *Homo erectus,* the first hominid

to migrate out of Africa. The oldest fossils of hominids outside of Africa date back 1.8 million years. Most paleoanthropologists conclude that *H. erectus* became extinct around 200,000 years ago.

Neanderthals The Neanderthals appear to be descendants of *Homo heidelbergensis*, which originated about 600,000 years ago in Africa. Neanderthals lived in Europe from about 200,000 to 30,000 years ago. They had large brains and made tools from stone and wood. Comparisons of DNA from four Neanderthal fossils with DNA of living humans show that Neanderthals form a clade, while Europeans are more closely related to Africans and Asians.

Homo sapiens Evidence indicates that the ancestors of humans originated in Africa. The oldest known fossils of *H. sapiens* date from 160,000 years ago. These early humans lacked heavy brow ridges and were more slender than other hominids. DNA comparisons show that Europeans and Asians share a relatively recent common ancestor, with many African lineages branching off earlier. Comparisons of mitochondrial DNA and Y chromosomes of various populations support a common African ancestor of all *Homo sapiens*.

The oldest fossils outside Africa date back about 50,000 years. Y chromosome studies suggest that one wave of humans first spread into Asia, then to Europe and Australia. The date of arrival in the New World may be 15,000 years ago. The rapid expansion of our species may be tied to the evolution of human cognition. Symbolic thought may have emerged along with human language, enabling the construction of new tools and the ability to teach others to build them.

The gene *FOXP2* has been identified as essential for human language. Comparisons with homologous genes in other mammals indicate that the gene underwent intense natural selection within the past 200,000 years.

■ INTERACTIVE QUESTION 34.12

List some of the derived characters of humans.

Word Roots

arch- = ancient (*archosaurs:* the reptilian group that includes crocodiles, alligators, dinosaurs, and birds)
cephalo- = head (*cephalochordates:* a chordate without a backbone, represented by lancelets)
aktin- = a ray; **-pterygi** = a fin (*Actinopterygii:* the class of ray-finned fishes)
crani- = the skull (*craniata:* the chordate clade that possess a cranium)
crocodil- = a crocodile (*Crocodilia:* the reptile group that includes crocodiles and alligators)
di- = two (*diapsids:* a group of amniotes distinguished by a pair of holes on each side of the skull)
dino- = terrible; **-saur** = lizard (*dinosaurs:* an extremely diverse group of ancient reptiles varying in body shape, size, and habitat)
endo- = inner; **-therm** = heat (*endotherm:* an animal that uses metabolic energy to maintain a constant body temperature, such as a bird or mammal)
eu- = good (*eutherians:* placental mammals; those whose young complete their embryonic development within the uterus, joined to the mother by the placenta)
extra- = outside, more (*extraembryonic membranes:* four membranes that support the developing embryo in reptiles and mammals)
gnantho- = the jaw; **-stoma** = the mouth (*gnathostomes:* the vertebrate clade that possesses jaws)
homin- = man (*hominid:* a term that refers to mammals that are more closely related to humans than to any other living species)
lepido- = a scale (*lepidosaurs:* the reptilian group that includes lizards, snakes, and tuatara)
marsupi- = a bag, pouch (*marsupial:* a mammal, such as a koala, kangaroo, or opossum, whose young complete their embryonic development inside a maternal pouch called the marsupium)
mono- = one (*monotremes:* an egg-laying mammal, represented by the platypus and echidna)
neuro- = nerve (*neural crest:* a band of cells along the border where the neural tube pinches off from the ectoderm)
noto- = the back; **-chord** = a string (*notochord:* a longitudinal, flexible rod formed from dorsal mesoderm and located between the gut and the nerve cord in all chordate embryos)
opercul- = a covering, lid (*operculum:* a protective flap that covers the gills of fishes)
osteo- = bone; **-ichthy** = fish (*Osteichthyans:* the vertebrate clade that includes the ray-finned fishes and lobe-fins)
ostraco- = a shell; **-derm** = skin (*ostracoderm:* an extinct paraphyletic group of armored fish-like vertebrates)
ovi- = an egg; **-parous** = bearing (*oviparous:* referring to a type of development in which young hatch from eggs laid outside the mother's body)
paedo- = a child; **-genic** = producing (*paedogenesis:* the precocious development of sexual maturity in a larva)

paleo- = ancient; **anthrop-** = man; **-ology** = the science of (*paleoanthropology:* the study of human origins and evolution)
placo- = a plate (*placoderm:* a member of an extinct group of gnathostomes that had jaws and were enclosed in a tough, outer armor)
ptero- = a wing (*pterosaurs:* winged reptiles that lived during the time of dinosaurs)
ratit- = flat-bottomed (*ratites:* the group of flightless birds)
soma- = body (*somites:* blocks of mesoderm that give rise to muscle segments in chordates)
syn- = together (*synapsids:* an amniote group distinguished by a single hole behind each eye socket)
tetra- = four; **-podi** = foot (*tetrapod:* a terrestrial lobe-fin, possessing two pairs of limbs, such as amphibians, reptiles, and mammals)
tunic- = a covering (*tunicates:* members of the subphylum Urochordata)
uro- = tail (*urochordate:* a chordate without a backbone, commonly called a tunicate)
uro- = (note) tail; **-del** = visible (*Urodela:* the order of salamanders that includes amphibians with tails)
vivi- = alive (*ovoviviparous:* referring to a type of development in which young hatch from eggs that are retained in the mother's uterus)

Structure Your Knowledge

1. Review the cladogram on page 269. Make note of the derived characters that define each clade.
2. Describe several examples from vertebrate evolution that illustrate the common evolutionary theme that new adaptations usually evolve from preexisting structures.
3. How did various vertebrate groups meet the challenges of a terrestrial habitat?

Test Your Knowledge

FILL IN THE BLANKS

_____ 1. chordate subphylum of sessile, suspension-feeding marine animals

_____ 2. chordate subphylum that includes lancelets

_____ 3. blocks of mesoderm along notochord that develop into muscles

_____ 4. clade of jawed vertebrates

_____ 5. flap over the gills of bony fishes

_____ 6. adaptation that allows reptiles to reproduce on land

_____ 7. egg-laying mammals

_____ 8. structure that helps mammals ventilate their lungs

_____ 9. group of primates that includes monkeys, apes, and humans

_____ 10. genus in which the fossil Lucy is placed

MULTIPLE CHOICE: *Choose the one best answer.*

1. Pharyngeal slits appear to have functioned first as
   a. suspension-feeding devices.
   b. gill slits for respiration.
   c. components of the jaw.
   d. portions of the inner ear.
   e. mouth openings.
2. Which of the following is *not* a derived character of craniates?
   a. cranium or skull
   b. neural crest in embryonic development
   c. a mineralized endoskeleton
   d. heart with at least two chambers
   e. cephalization with sensory organs
3. Which of these represents the oldest lineage of vertebrates?
   a. caecilians
   b. sharks and rays
   c. lancelet
   d. hagfishes
   e. lampreys
4. Which of the following is in the lobe-fin clade?
   a. lampreys
   b. sharks and rays
   c. ray-finned fishes
   d. hagfishes
   e. tetrapods
5. Which of the following is not in the same lineage as the others?
   a. lizards
   b. birds
   c. dinosaurs
   d. crocodilians
   e. pterosaurs

6. Which of the following is *incorrectly* paired with its gas exchange mechanism?
   a. amphibians—skin and lungs
   b. lungfishes—gills and lungs
   c. reptiles—lungs
   d. bony fishes—swim bladder
   e. mammals—lungs with diaphragm to ventilate
7. Nonbird reptiles have lower caloric needs than do mammals of comparable size because they
   a. are ectotherms.
   b. have waterproof scales.
   c. have a longer digestive tract and obtain more nutrients from their food.
   d. move by bending their vertebral column back and forth.
   e. have a more efficient respiratory system.
8. Which of the following best describes the earliest mammals?
   a. large, herbivorous
   b. large, carnivorous
   c. small, insectivorous
   d. small, herbivorous
   e. small, carnivorous
9. Oviparity is a reproductive strategy that
   a. allows mammals to bear well-developed young.
   b. is used by both reptiles and some sharks.
   c. is necessary for vertebrates to reproduce on land.
   d. is a necessity for all flying vertebrates.
   e. protects the embryo inside the mother and uses the food resources of the egg.
10. In Australia, marsupials fill the niches that eutherians (placental mammals) fill in other parts of the world because
    a. they are better adapted and have outcompeted eutherians.
    b. their offspring complete their development attached to a nipple in a marsupium.
    c. they originated in Australia.
    d. they evolved from monotremes that migrated to Australia about 65 million years ago.
    e. after Pangaea broke up, they diversified in isolation from eutherians.
11. Which of the following is closely associated with language development?
    a. four clusters of *Hox* genes
    b. gene duplication involving *Dlx* genes
    c. reduced sexual dimorphism and postnatal care
    d. *FOXP2* gene
    e. shorter hinged jaws and a hole in the skull behind each eye socket through which jaw muscles pass
12. In accordance with the model of mosaic evolution,
    a. biogeography explains the adaptive radiation of many groups.
    b. erect posture preceded the enlargement of the brain in human evolution.
    c. modern humans evolved in parallel in different parts of the world, laying the groundwork for geographic differences more than a million years ago.
    d. modern humans first evolved in Africa and later dispersed to other regions.
    e. the rapid expansion of *H. sapiens* may be tied to the evolution of human cognition, including symbolic thought, language, and complex tool construction.