22

Mammals:
Synapsid Amniotes

Hair, mammary glands, and specialized teeth—these are some of the hallmark traits that evolved in synapsid amniotes during the Mesozoic era. Two spotted hyenas (Crocuta crocuta) are shown here defending their kill from a vulture (lower left). Hyenas are opportunistic feeders, acting as predators and scavengers.

22.1 Evolutionary Perspective

Learning Outcomes

1. Describe the characteristics of the members of the class Mammalia.
2. Assess the importance of two mass-extinction events in the evolution of modern mammals.

The fossil record that documents the origin of the mammals from ancient reptilian ancestors is very complete and relatively uncontroversial. It is being used to test, and has confirmed, many macroevolutionary theories (see chapter 4). The beginning of the Tertiary period, about 70 mya, was the start of the "age of mammals." It coincided with the extinction of many reptilian lineages, which led to the adaptive radiation of the mammals. Tracing the roots of the mammals, however, requires returning to the Carboniferous period 320 mya, when the synapsid branch of the amniote lineage diverged from the reptilian branch of this lineage. The fossil record is conclusive—the synapsid lineage was the first amniote lineage to diversify, beginning about 320 mya (see figure 20.3). Synapsids quickly became very diverse and widespread. They were the dominant, large-bodied animals on the earth for more than 100 million years, through the remaining Carboniferous and Permian periods.

Mammalian characteristics evolved gradually over a period of 200 million years (figure 22.1). Most of what we know about early synapsids is based on skeletal characteristics. Other mammalian features like hair, mammary glands, and endothermy do not preserve well in the fossil record. Early synapsids had a sprawling gait and were probably ectothermic. The large sails on some, like Dimetrodon (figure 22.2a), probably helped these synapsids raise body temperature after a cool night. These sails are also an evidence that early synapsids lacked hair. Early synapsids were probably also egg-layers (they were oviparous). Some were herbivores; others showed skeletal adaptations reflecting increased effectiveness as predators.

The anterior teeth of the upper jaw were large and were separated from the posterior teeth by a gap that accommodated the enlarged anterior teeth of the lower jaw when the jaw closed. The palate was arched, which strengthened the upper jaw and allowed air to pass over prey held in the mouth.

By the middle of the Permian period, other successful synapsids had arisen. They were a diverse group known as the therapsids. Some were predators, and others were herbivores. In the predatory therapsids, teeth were concentrated at the front of the mouth and enlarged for holding and tearing prey. The posterior teeth were reduced in size and number. The jaws of some therapsids were elongate...
CHAPTER TWENTY-TWO

FIGURE 22.1

Class Mammalia. The decline of the ruling reptiles about 70 mya permitted mammals to radiate into diurnal habitats previously occupied by dinosaurs and other reptiles. Hair, endothermy, and mammary glands characterize mammals. The lowland gorilla (Gorilla gorilla graueri, order Primates) is shown here.

and generated a large biting force when snapped closed. The teeth of the herbivorous therapsids were also mammal-like. Some had a large space, called the diastema, separating the anterior and the posterior teeth. The posterior teeth had ridges (cusps) and cutting edges that were probably used to shred plant material. Unlike other synapsids, therapsids held hindlimbs directly beneath the body and moved them parallel to the long axis of the body. Changes in the size and shape of the ribs suggest the separation of the trunk into thoracic and abdominal regions and a breathing mechanism similar to that of mammals.

About 240 mya, most of the very successful therapsids were wiped out during a major extinction event at the Permian–Triassic boundary—possibly as a result of huge Siberian volcanic events. Only a few cynodont therapsids, including Cynognathus (see figure 22.2b), survived this extinction event. By this time, however, the reptilian (diapsid) amniote lineage had also emerged (see figure 20.3). The archosaurs (dinosaurs, crocodiles, and eventually the birds) also survived this extinction event, and these reptiles became the dominant large animals on terrestrial landscapes through the Mesozoic era, which ended about 65 mya. Cynodonts became increasingly smaller (ranging in size from a mouse to a domestic cat), probably nocturnal, and more mammal-like. The smaller size and development of hair and endothermy were probably selected for as these mammal precursors exploited niches not occupied by much larger dinosaurs and smaller diurnal (day-active [L. diurnalis, daily]) reptiles living at the same time. Other mammalian characteristics evolved during the Jurassic period. Teeth became highly specialized to facilitate rapid food processing. There were changes in the structure of the middle ear and regions of the brain devoted to hearing and olfaction. The fact that most mammals lack color vision also reinforces the idea that these early mammals were nocturnal.

The first "true mammals" were present in the Jurassic period. (What constitutes a "true mammal" is debated and not really an important distinction for most taxonomists.) The oldest preserved hair is found in fossils about 160 million years old. During the Mesozoic era, mammal populations were relatively diverse, with over 300 genera present, but they were not particularly abundant. New molecular and fossil data suggest that ecologically diverse representatives of all 18 extant mammalian orders were present in the late Mesozoic era.

About 65 mya another mass extinction occurred—probably associated with asteroid impact in what is now Central America. Dinosaurs, many ancient birds, and many other taxa became extinct, but at least some early mammals survived this second mass extinction event of synapsid history. This Cretaceous–Tertiary extinction allowed surviving mammals to
continue the diversification that began in the Mesozoic era and expand into niches formerly occupied by the dinosaurs. The Tertiary period became the "age of mammals."

**Section Review 22.1**

Mammals are characterized by the presence of mammary glands; hair; a diaphragm; three middle-ear ossicles; sweat, sebaceous, and scent glands; a four-chambered heart; and a large cerebral cortex. They evolved in the synapsid amniote lineage, which has been traced back about 320 million years. The ancestors of modern mammals survived two mass-extinction events, 240 and 65 mya. The demise of the dinosaurs in the last extinction event allowed surviving mammals to diversify into niches formerly occupied by the dinosaurs. The beginning of the Tertiary period marks the beginning of the "age of mammals."

**In what ways did the demise of the dinosaurs present evolutionary opportunities for mammals? What evidence of their early evolution is seen in modern mammals?**

**22.2 Diversity of Mammals**

**Learning Outcome**

1. Explain the role of continental movements in influencing mammalian evolution.

Hair, mammary glands, specialized teeth, three middle-ear ossicles, endothermy, and other characteristics listed in table 22.1 characterize the members of the class Mammalia (mah-ma'le-ah) (L. mamma, breast). There are about 5,400 species of mammals that range in size from the bumblebee bat (3 to 4 cm in length, 2 g) to the blue whale (more than 30 m in length, 180 metric tons). They are the dominant large terrestrial animals on all continents of the earth, and some have extended their habitats into the oceans and the air.

There are two lineages of living mammals (figure 22.3). The subclass Prototheria (Gr. protos, first + therion, wild beast) contains the surviving infraclass Ornithodelphia (Gr. ornis, bird + delphia, birthplace), commonly called the monotremes (Gr. monos, one + trena, opening). These names refer to the fact that monotremes, unlike other mammals, possess a cloaca...
**TABLE 22.1**

**Classification of Living Mammals**

<table>
<thead>
<tr>
<th>Class Mammalia (mah-ma'le-ah)</th>
<th>Mammary glands; hair; diaphragm; three middle-ear ossicles; heterodont dentition; sweat, sebaceous, and scent glands; four-chambered heart; large cerebral cortex.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subclass Prototheria (pro-to-ther'e-ah)</td>
<td>Oviparous; cloaca present.</td>
</tr>
<tr>
<td>Infraclass Ornithodelphia (or-ne-tho-del'fe-ah)</td>
<td>Technical characteristics of the skull distinguish members of this infraclass. Monotremes.</td>
</tr>
<tr>
<td>Subclass Theria (ther'e-ah)</td>
<td>Technical characteristics of the skull distinguish members of this subclass.</td>
</tr>
<tr>
<td>Infraclass Metatheria (me-tah-ther'e-ah)</td>
<td>Viviparous; primitive placenta; young are born early and often are carried in a marsupial pouch on the female's belly. Marsupials.</td>
</tr>
<tr>
<td>Infraclass Eutheria (u-ther'e-ah)*</td>
<td>Complex placenta; young develop to advanced stage prior to birth. Placentals.</td>
</tr>
<tr>
<td>Superorder Afrotheria (af-ro-th'er'e-ah)</td>
<td></td>
</tr>
<tr>
<td>Order Proboscidea (pro-bosh-sid'e-ah)</td>
<td>Long, muscular proboscis (trunk) with one or two finger-like processes at the tip; short skull with the second incisor on each side of the upper jaw modified into tusks; six cheek teeth are present in each half of each jaw; teeth erupt (grow into place) in sequence from front to rear, so that one tooth in each jaw is functional. African and Indian elephants.</td>
</tr>
<tr>
<td>Order Sirenia (si-re-ne-ah)</td>
<td>Large, aquatic herbivores that weigh in excess of 600 kg; nearly hairless, with thick, wrinkled skin; heavy skeleton; forelimbs are flipped-like, and hindlimb is vestigial; horizontal tail fluke is present; horizontally oriented diaphragm; teeth lack enamel. Manatees (coastal rivers of the Americas and Africa), dugongs (western Pacific and Indian Oceans).</td>
</tr>
<tr>
<td>Superorder Xenarthra (ze-nar-thra)</td>
<td>(This name is also used as the order name.)</td>
</tr>
<tr>
<td>Order Xenarthra (ze-nar-thra)</td>
<td>Incisors and canines absent; cheek teeth, when present, lack enamel; braincase is long and cylindrical; hindfoot is four toed; forefoot has two or three prominent toes with large claws; limbs are specialized for climbing or digging; xenarthrous lumbar vertebrae. Anteaters, tree sloths, armadillos.</td>
</tr>
<tr>
<td>Superorder Laurasiatheria (lo-rat'sha-ther'e-ah)</td>
<td></td>
</tr>
<tr>
<td>Order Eulipotyphla (u-li-po-tif'lah)</td>
<td>Small mammals with long, narrow mobile snouts. Feed on insects and earthworms. Formerly, these animals were included in an order, Insectivora, that included a variety of additional taxa, including tenrecs and golden moles. Insectivora was found to be polyphyletic. Tenrecs and golden moles are now separated into the order Afrosoricida, which is within the superorder Afrotheria. Hedgehogs, true moles, shrews.</td>
</tr>
<tr>
<td>Order Chiroptera (ki-rop'ter-ah)</td>
<td>Cosmopolitan, but especially abundant in the tropics; bones of the arm and hand are elongate and slender; flight membranes extend from the body, between digits of forelimbs, to the hindlimbs; most are insectivorous, but some are fruit eaters, fish eaters, and blood feeders; second-largest mammalian order. Bats.</td>
</tr>
<tr>
<td>Order Carnivora (kar-niv'o-ra)</td>
<td>Predatory mammals; usually have a highly developed sense of smell and a large braincase; premolars and molars modified into carnivassal apparatus; three pairs of upper and lower incisors usually present, and canines are well developed. Dogs, cats, bears, raccoons, minks, sea lions, seals, walruses, otters.</td>
</tr>
<tr>
<td>Order Perissodactyla (pe-ris'so-dak'ti-lah)</td>
<td>Hoofed; axis of support passes through the third digit. Skull usually elongate; large molars and premolars; primarily grazers. (The Artiodactyla also have hoofs. Artiodactyls and perissodactyls are, therefore, called ungulates) (L. ungula, hoof). Odd-toed ungulates: horses, rhinoceroses, zebras, tapirs.</td>
</tr>
<tr>
<td>Order Artiodactyla (ar-te-o-dak'ti-lah)</td>
<td>Hoofed; axis of support passes through third and fourth digits; digits one, two, and five reduced or lost; primarily grazing and browsing animals (pigs are an obvious exception). Even-toed ungulates: pigs, hippopotamuses, camels, antelope, deer, sheep, giraffes, cattle.</td>
</tr>
<tr>
<td>Order Cetacea (se-ta'she-ah)</td>
<td>Streamlined, nearly hairless, and insulated by thick layers of fat (blubber); no sebaceous glands; forelimbs modified into paddlelike flippers for swimming; hindlimbs reduced and not visible externally; tail fins (flukes) flattened horizontally; external nares (blowhole) on top of skull. Toothed whales (beaked whales, narwhals, sperm whales, dolphins, porpoises, killer whales); toothless, filter-feeding baleen whales (right whales, gray whales, blue whales, and humpback whales).</td>
</tr>
<tr>
<td>Order Lagomorpha (lag'o-mor'fah)</td>
<td>Two pairs of upper incisors; one pair of lower incisors; incisors are ever-growing and slowly worn down by feeding on vegetation. Rabbits, pikas.</td>
</tr>
<tr>
<td>Order Rodentia (ro-den'te-ah)</td>
<td>Largest mammalian order; upper and lower jaws bear a single pair of ever-growing incisors. Squirrels, chipmunks, rats, mice, beavers, porcupines, woodchucks, lemmings.</td>
</tr>
<tr>
<td>Order Primates (pri-ma'tez)</td>
<td>Adaptations of primates reflect adaptations for increased agility in arboreal (tree-dwelling) habitats; omnivorous diets; specialized teeth; grasping digits; freely movable limbs; nails on digits; reduced nasal cavity; enlarged stereoscopic eyes and cerebral hemispheres. Lemurs (Madagascar and the Comoro Islands), tarsiers (jungles of Sumatra and the East Indies), monkeys, gibbons, great apes (apes and humans).</td>
</tr>
</tbody>
</table>

*Selected eutherian orders are described.*
and are oviparous. Recall that a cloaca is a common opening for excretory, reproductive, and digestive products and was found in all other vertebrates, including the reptilian amniote lineage. The six species of monotremes are found in Australia and New Guinea (figure 22.4).

The subclass Theria diverged into two infraclasses by the late Cretaceous period. The infraclass Metatheria (Gr. meta, after) contains the marsupial mammals. They are viviparous but have very short gestation periods. A protective pouch, called the marsupium, covers the female mammary glands. The young crawl into the marsupium after birth, where they feed and complete development. The oldest marsupial fossils are found in 125-million-year-old deposits in China. About 250 species of marsupials live in the Australian region and the Americas (figure 22.4c; see also figure 22.17).

The other therian infraclass, Eutheria (Gr. eu, true), contains the placental mammals. They are usually born at an advanced stage of development, having been nourished within the uterus. Exchanges between maternal and fetal circulatory systems occur by diffusion across an organ called the placenta, which is composed of both maternal and fetal tissue. Over 4,000 species of eutherians are classified into 18 orders (figures 22.5 and 22.6; see also figures 22.11 through 22.17).

Some of the 18 eutherian orders are listed in table 22.1. Recent molecular data, along with traditional morphological studies, have resulted in the description of four eutherian clades, shown in table 22.1 as superorders. The evolution of these four clades was strongly influenced by geological events. Between 250 and 100 mya, the earth's landmasses were combined into a single landmass called Pangaea. About 100 mya, a southern supercontinent that consisted of Africa, South America, and Antarctica broke away from a northern supercontinent (Laurasia) that consisted of North America, Europe, and Asia. These continental movements isolated the ancestors of the southern placental mammals, listed in table 22.1 as afrotherians and xenarthans, from other ancestral groups on Laurasia. Later continental movements, such as the separation of South America from Africa, the rejoining of Africa with Europe and Asia, and the joining of North and South America, further isolated, or united, groups of mammals. One current hypothesis on the relationships between these superorders is shown in figure 22.3. Evolutionary relationships among the orders within the four major clades is controversial.

**SECTION REVIEW 22.2**

Mammals are characterized by hair, mammary glands, specialized teeth, three middle-ear ossicles, and endothermy. The evolution of mammals was strongly influenced by continental movements that separated a single landmass, Pangaea, first...
into southern and northern supercontinents and later into the continents of North America, Europe, and Asia. These and other movements isolated groups of mammals, resulting in four clades. Placental mammals are further divided into 18 orders.

**How are biogeographic events important influences on mammalian evolution?**

### 22.3 Evolutionary Pressures

**Learning Outcomes**

1. Justify the statement that "easily recognizable mammalian characters are epidermal in origin."
2. Compare the usefulness of the study of tooth structure by a mammalogist, an ornithologist, and a herpetologist.
3. Compare the function of menstrual cycles in female primates to estrus cycles in other female mammals.

Mammals are naturally distributed on all continents except Antarctica, and they live in all oceans. This section discusses the many adaptations that have accompanied their adaptive radiation.

**External Structure and Locomotion**

The skin of a mammal, like that of other vertebrates, consists of epidermal and dermal layers. It protects from mechanical injury, invasion by microorganisms, and the sun's ultraviolet light. Skin is also important in temperature regulation, sensory perception, excretion, and water regulation (see figure 23.9).

Hair is a keratinized derivative of the epidermis of the skin and is uniquely mammalian. It is seated in an invagination of the epidermis called a hair follicle. A coat of hair, called pelage, usually consists of two kinds of hair. Long guard hairs protect a dense coat of shorter, insulating underhairs.

Because hair is composed largely of dead cells, it must be periodically molted. In some mammals (e.g., humans), molting occurs gradually and may not be noticed. In others, hair loss occurs rapidly and may result in altered pelage characteristics. In the fall, many mammals acquire a thick coat of insulating underhair, and the pelage color may change. For example, the Arctic fox takes on a white or cream color with its autumn molt, which helps conceal the fox in a snowy environment. With its spring molt, the Arctic fox acquires a gray and yellow pelage (see figure 22.6).

Hair is also important for the sense of touch. Mechanical displacement of a hair stimulates nerve cells associated with the hair root. Guard hairs may sometimes be modified into thick-shafted hairs called vibrissae. Vibrissae occur around the legs, nose, mouth, and eyes of many mammals. Their roots are richly innervated and very sensitive to displacement.

Air spaces in the hair shaft and air trapped between hair and the skin provide an effective insulating layer. A band of smooth muscle, called the arrector pili muscle, runs between the hair follicle and the lower epidermis. When the muscle contracts, the hair stands upright, increasing the amount of air trapped in the pelage and improving its insulating properties. Arrector pili muscles are under the control of the autonomic nervous system, which also controls a mammal's "fight-or-flight" response. In threatening situations, the hair (especially on the neck and tail) stands on end and may give the perception of increased size and strength.

Hair color depends on the amount of pigment (melanin) deposited in it and the quantity of air in the hair shaft. The pelage of most mammals is dark above and lighter underneath. This pattern makes them less conspicuous under most
FIGURE 22.6
Order Carnivora. An Arctic fox (*Vulpes lagopus*) with its winter pelage. With its spring molt, the Arctic fox acquires a gray-and-yellow-colored coat.

Conditions. Some mammals advertise their defenses using aposematic (warning) coloration. The contrasting markings of a skunk are a familiar example.

Pelage is reduced in large mammals from hot climates (e.g., elephants and hippopotamuses) and in some aquatic mammals (e.g., whales) that often have fatty insulation. A few mammals (e.g., naked mole rats) have almost no pelage (see box figure 28.1).

Claws are present in all amniote classes. They are used for locomotion and offensive and defensive behavior. Claws form from accumulations of keratin that cover the terminal phalanx (bone) of the digits. In some mammals, they are specialized to form nails or hooves (figure 22.7).

Glands develop from the epidermis of the skin. Sebaceous (oil) glands are associated with hair follicles, and their oily secretion lubricates and waterproofs the skin and hair. Most mammals also possess sudoriferous (sweat) glands. Small sudoriferous glands (eccrine glands) release watery secretions used in evaporative cooling. Larger sudoriferous glands (apocrine glands) secrete a mixture of salt, urea, and water, which microorganisms on the skin convert to odorous products.

Scent or musk glands are around the face, feet, or anus of many mammals. These glands secrete pheromones, which may be involved with defense, species and sex recognition, and territorial behavior.

Mammary glands are functional in female mammals and are present, but nonfunctional, in males. The milk that mammary glands secrete contains water, carbohydrates (especially the sugar lactose), fat, protein, minerals, and antibodies. Mammary glands are probably derived evolutionarily from apocrine glands and usually contain substantial fatty deposits.

Monotremes have mammary glands that lack nipples. The glands discharge milk into depressions on the belly, where the young lap it up. In other mammals, mammary glands open
Mammary Glands. Mammary glands are specialized to secrete milk following the birth of young. (a) In humans, many ducts lead from the glands to a nipple. Parts of the duct system are enlarged to store milk. Suckling by an infant initiates a hormonal response that causes the mammary glands to release milk. (b) Some mammals (e.g., cattle) have teats that form by the extension of a collar of skin around the opening of mammary ducts. Milk collects in a large cistern prior to its release. The number of nipples or teats varies with the number of young produced.

via nipples or teats, and the young suckle for their nourishment (figure 22.8).

The Skull and Teeth

The skulls of mammals show important modifications of the reptilian pattern. One feature that zoologists use to distinguish reptilian from mammalian skulls is the method of jaw articulation. In reptiles, the jaw articulates at two small bones at the rear of the jaw. In mammals, these bones have moved into the middle ear, and along with the stapes, form the middle-ear ossicles. A single bone of the lower jaw articulates the mammalian jaw.

A secondary palate evolved twice in vertebrates—in the archosaur lineage (see figure 20.3) and in the synapsid lineage. In some therapsids, small, shelflike extensions of bone (the hard palate) partially separated the nasal and oral passages (see figure 20.11). In mammals, the secondary palate extends posteriorly by a fold of skin, called the soft palate, which almost completely separates the nasal passages from the mouth cavity. Unlike other vertebrates that swallow food whole or in small pieces, some mammals chew their food. The more extensive secondary palate allows mammals to breathe while chewing. Breathing needs to stop only briefly during swallowing (figure 22.9).

The structure and arrangement of teeth are important indicators of mammalian lifestyles. In reptiles, the teeth are uniformly conical, a condition referred to as homodont. In mammals, the teeth are often specialized for different functions, a condition called heterodont. Recall that in reptiles other than archosaurus, teeth were acrodont and attached along the top or inside of the jaw. In mammals (as well as crocodylians) teeth are thecodont. That is, teeth are set into sockets of the jaw. Most mammals have two sets of teeth during their lives. The first teeth emerge before or shortly after birth and are called deciduous or milk teeth. These teeth are
lost, and permanent teeth replace them. This single replacement of teeth is called the \textit{diphyodont} condition. (Recall that most reptiles have polyphodont teeth.)

Adult mammals have up to four kinds of teeth. Incisors are the most anterior teeth in the jaw. They are usually chisel-like and used for gnawing or nipping. Canines are often long, stout, and conical. They are usually used for catching, killing, and tearing prey. Canines and incisors have single roots. Premolars are positioned next to canines, and have one or two roots and truncated surfaces for chewing. Molars have broad chewing surfaces and two (upper molars) or three (lower molars) roots.

Mammalian species have characteristic numbers of each kind of adult tooth. Zoologists use a \textit{dental formula} to characterize taxa. It is an expression of the number of teeth of each kind in one-half of the upper and lower jaws. The teeth of the upper jaw are listed above those of the lower jaw and in the following order: incisors, canine, premolars, and molars. For example:

\begin{center}
\begin{tabular}{l|l}
\textbf{Human} & \textbf{Beaver} \\
\hline
2 & 1 & 2 & 3 & 1 & 0 & 1 & 3 \\
2 & 1 & 2 & 3 & 1 & 0 & 1 & 3 \\
\end{tabular}
\end{center}

Mammalian teeth (dentition) may be specialized for particular diets. In some mammals, the dentition is reduced, sometimes to the point of having no teeth. For example, armadillos and the giant anteater (order Edentata) feed on termites and ants, and their teeth are reduced.

Some mammals (e.g., humans, order Primates; and pigs, order Artiodactyla) are omnivorous; they feed on a variety of plant and animal materials. They have anterior teeth with sharp ripping and piercing surfaces, and posterior teeth with flattened grinding surfaces for rupturing plant cell walls (figure 22.10a).
How Do We Know about the Evolution of Mammary Glands?

Why do we think mammary glands are related to apocrine skin glands? Much of the evidence comes from similar developmental patterns and secretions of the two kinds of glands. Like mammary glands, some apocrine glands secrete lipids and other complex organic molecules.

Lactation may have evolved well before mammals were present. Even though there is no fossil record that traces the evolution of mammary glands, information from the study of changes in bones, teeth, and skin suggests that mammary glands may have been functioning in nonmammalian synapsids. Rather than having glands with a nipple, early synapsids probably had a mammary area similar to that found in monotremes. Monotreme young suck milk from mammary hairs following hatching. A similar function may have occurred in early synapsids, but other observations suggest another possible function. Monotreme eggs are covered with a moist, sticky secretion of unknown origin. It is possible that this secretion is produced by mammary glands and protects the eggs from desiccation. Hairs that develop in association with apocrine glands, distributed over a wide area, would help apply this secretion to a batch of eggs. (Hair is shed from the nipple area of mammals other than monotremes.) These hypotheses need testing but, if they are true, the two hallmark mammalian characters—hair and mammary glands—first arose in synapsid reptiles for functions other than their primary use in modern mammals. More often than not, evolution does not reinvent—it recycles.

Mammals that eat plant material often have flat, grinding posterior teeth and incisors, and sometimes have canines modified for nipping plant matter (e.g., horses, order Perissodactyla; deer, order Artiodactyla) or gnawing (e.g., rabbits, order Lagomorpha; beavers, order Rodentia) (figure 22.10b and c). In rodents, the incisors grow throughout life. Although most mammals have enamel covering the entire tooth, rodents have enamel only on the front surfaces of their incisors. The teeth are kept sharp by slower wear in front than in back. A gap called the diastema separates the anterior food-procuring teeth from the posterior grinding teeth. The diastema results from an elongation of the snout that allows the anterior teeth to reach close to the ground or into narrow openings to procure food. The posterior teeth have a high, exposed surface (crown) and continuous growth, which allows these teeth to withstand years of grinding tough vegetation.

Predatory mammals use canines and incisors for catching, killing, and tearing prey. In members of the order Carnivora (e.g., coyotes, dogs, and cats), the fourth upper premolars and first lower molars form a scissorlike shearing surface, called the carnassial apparatus, that is used for cutting flesh from prey (figure 22.10d).

The Vertebral Column and Appendicular Skeleton

The vertebral column of mammals is divided into five regions. As with reptiles and birds, the first two cervical vertebrae are the atlas and axis. Five other cervical vertebrae usually follow. Even the giraffe and the whale have seven neck vertebrae, which are greatly elongated or compressed, respectively. In contrast, tree sloths have either six or nine cervical vertebrae, and the manatee has six cervical vertebrae.

The trunk is divided into thoracic and lumbar regions, as is the case for birds. In mammals, the division is correlated with their method of breathing. The thoracic region contains the ribs. Most ribs connect to the thoracic vertebrae and to the sternum via costal cartilages. Other ribs attach only to the thoracic vertebrae or to other ribs through cartilages. All ribs protect the heart and lungs. The articulation between the thoracic vertebrae provides the flexibility needed in turning, climbing, and lying on the side to suckle young. Lumbar vertebrae have interlocking processes that give support, but little freedom of movement.

The appendicular skeleton of mammals rotates under the body so that the appendages are usually directly beneath the body. Joints usually limit the movement of appendages to a single anteroposterior plane, causing the tips of the appendages to move in long arcs. The bones of the pelvic girdle are fused in the adult, a condition that is advantageous for locomotion but presents problems during the birth of offspring. In a pregnant female, the ventral joint between the halves of the pelvis—the pubic symphysis—loosens before birth, allowing the pelvis to spread during birth.

Muscles

Because the appendages are directly beneath the bodies of most mammals, the skeleton bears the weight of the body. Muscle mass is concentrated in the upper appendages and
girdles. Many running mammals (e.g., deer, order Artiodactyla) have little muscle in their lower leg that would slow leg movement. Instead, tendons run from muscles high in the leg to cause movement at the lower joints.

**Nutrition and the Digestive System**

The digestive tract of mammals is similar to that of other vertebrates but has many specializations for different feeding habits. Some specializations of teeth have already been described.

The feeding habits of mammals are difficult to generalize. Feeding habits reflect the ecological specializations that have evolved. For example, most members of the order Carnivora feed on animal flesh and are therefore carnivores. Other members of the order, such as bears, feed on a variety of plant and animal products and are omnivores. Some carnivorous mammals are specialized for feeding on arthropods or soft-bodied invertebrates, and are often referred to (rather loosely) as insectivores. These include animals in the orders Eulipotyphla (e.g., shrews), Chiroptera (bats), and Edentata (anteaters) (see figure 22.5a). Herbivores such as deer (order Artiodactyla) and zebras (order Perissodactyla) (figure 22.11) feed mostly on vegetation, but their diet also includes invertebrates inadvertently ingested while feeding.

Specializations in the digestive tracts of most herbivores reflect the difficulty of digesting food rich in cellulose. Horses, rabbits, and many rodents have an enlarged cecum at the junction of the large and small intestines. A cecum is a fermentation pouch where microorganisms aid in cellulose digestion (see figure 27.10). Sheep, cattle, and deer are called ruminants (L. ruminare, to chew the cud). Their stomachs are modified into four chambers (see figure 27.9). The first three chambers are storage and fermentation chambers and contain microorganisms that synthesize a cellulose-digesting enzyme (cellulase). Gases that fermentation produces are periodically belched, and some plant matter (cud) is regurgitated and rechewed. Other microorganisms convert nitrogenous compounds in the food into new proteins.

**Circulation, Gas Exchange, and Temperature Regulation**

The hearts of birds and mammals are superficially similar. Both are four-chambered pumps that keep blood in the systemic and pulmonary circuits separate, and both evolved from the hearts of ancient tetrapodomorphs. Their similarities, however, are a result of adaptations to active lifestyles. The evolution of similar structures in different lineages is called convergent evolution. The mammalian heart evolved from the synapsid lineage, whereas the avian heart evolved within the diapsid archosaur lineage (figure 22.12).

One of the most important adaptations in the circulatory system of eutherian mammals concerns the distribution of respiratory gases and nutrients in the fetus (figure 22.13a). Exchanges between maternal and fetal blood occur across the placenta. Although maternal and fetal blood vessels are intimately associated, no blood actually mixes. Nutrients, gases, and wastes simply diffuse between fetal and maternal blood supplies.

Blood entering the right atrium of the fetus is returning from the placenta and is highly oxygenated. Because fetal lungs are not inflated, resistance to blood flow through the pulmonary arteries is high. Therefore, most of the blood entering the right atrium bypasses the right ventricle and passes instead into the left atrium through a valved opening between the atria (the foramen ovale). Some blood from the right atrium, however, does enter the right ventricle and the pulmonary artery. Because of the resistance at the uninfated lungs, most of this blood is shunted to the aorta through a vessel connecting the aorta and the left pulmonary artery (the ductus arteriosus). At birth, the placenta is lost, and the lungs are inflated. Resistance to blood flow through the lungs is reduced, and blood flow to them increases. Flow through the ductus arteriosus decreases, and the vessel is gradually reduced to a ligament. Blood flow back to the left atrium from the lungs correspondingly increases, and the valve of the foramen ovale closes and gradually fuses with the tissue separating the right and left atria (figure 22.13b).

**Gas Exchange**

High metabolic rates require adaptations for efficient gas exchange. Most mammals have separate nasal and oral cavities and longer snouts, which provide an increased surface area for warming and moistening inspired air. Respiratory passageways are highly branched, and large surface areas exist for gas exchange. Mammalian lungs resemble a highly vascular sponge, rather than the saclike structures of amphibians and a few reptiles.

Mammalian lungs, like those of reptiles, inflate using a negative-pressure mechanism. Unlike reptiles and birds, however, mammals possess a muscular diaphragm that separates...
FIGURE 22.12
Possible Sequence in the Evolution of the Vertebrate Heart. (a) Diagrammatic representation of a bony fish heart. (b) In lungfish, partially divided atria and ventricles separate pulmonary and systemic circuits. This heart was probably similar to that in primitive amphibians and early amniotes. (c) The hearts of modern reptiles were derived from the pattern in (b). (d) The archosaur and (e) synapsid lineages resulted in completely separated, four-chambered hearts.

the thoracic and abdominal cavities. Inspiration results from contraction of the diaphragm and expansion of the rib cage, both of which decrease the intrathoracic pressure and allow air to enter the lungs. Expiration is normally by elastic recoil of the lungs and relaxation of inspiratory muscles, which decreases the volume of the thoracic cavity. The contraction of other thoracic and abdominal muscles can produce forceful exhalation.

Temperature Regulation
Mammals are widely distributed over the earth, and some face harsh environmental temperatures. Nearly all face temperatures that require them to dissipate excess heat at some times and to conserve and generate heat at other times.

The heat-producing mechanisms of mammals are divided into two categories. Shivering thermogenesis is muscular activity that generates large amounts of heat but little movement. Nonshivering thermogenesis involves heat production by general cellular metabolism and the metabolism of special fat deposits called brown fat. Chapter 28 discusses these heat-generating processes in more detail.

Heat production is effective in thermoregulation because mammals are insulated by their pelage and/or fat deposits. Fat deposits are also sources of energy to sustain high metabolic rates.
Mammals without a pelage can conserve heat by allowing the temperature of surface tissues to drop. A walrus in cold, arctic waters has a surface temperature near 0°C; however, a few centimeters below the skin surface, body temperatures are about 35°C. Upon emerging from the icy water, the walrus quickly warms its skin by increasing peripheral blood flow. Most tissues cannot tolerate such rapid and extreme temperature fluctuations. Further investigations are likely to reveal some unique biochemical characteristics of these skin tissues.

Even though most of the body of an arctic mammal is unusually well insulated, appendages often have thin coverings of fur as an adaptation to changing thermoregulatory needs. Even in winter, an active mammal sometimes produces more heat than is required to maintain body temperature. Patches of poorly insulated skin allow excess heat to be dissipated. During periods of inactivity or extreme cold, however, arctic mammals must reduce heat loss from these exposed areas, often by assuming heat-conserving postures. Mammals sleeping in cold environments conserve heat by tucking poorly insulated appendages and their faces under well-insulated body parts.

Countercurrent heat-exchange systems may help regulate heat loss from exposed areas (figure 22.14). Arteries passing peripherally through the core of an appendage are surrounded by veins that carry blood back toward the body. When blood returns to the body through these veins, heat transfers from arterial blood to venous blood and returns to the body rather than being lost to the environment. When excess heat is produced, blood is shunted away from the countercurrent veins toward peripheral vessels, and excess heat is radiated to the environment.
Winter Sleep and Hibernation Mammals react in various ways to environmental extremes. Caribou migrate to avoid extremes of temperature, and wildebeest migrate to avoid seasonal droughts. Other mammals retreat to burrows under the snow, where they become less active but are still relatively alert and easily aroused—a condition called winter sleep. For example, bears and raccoons retreat to dens in winter. Their body temperatures and metabolic rates decrease somewhat, but they do not necessarily remain inactive all winter.

Hibernation is a period of winter inactivity in which the hypothalamus of the brain slows the metabolic, heart, and respiratory rates. True hibernators include the monotremes (echidna and duck-billed platypus) and many members of the Insectivora (e.g., moles and shrews), Rodentia (e.g., chipmunks and woodchucks), and Chiroptera (bats). In preparation for hibernation, mammals usually accumulate large quantities of body fat. After a hibernating mammal retreats to a burrow or a nest, the hypothalamus sets the body’s thermostat to about 2°C. The respiratory rate of a hibernating ground squirrel falls from 100 to 200 breaths per minute to about four breaths per minute. The heart rate falls from 200 to 300 beats per minute to about 20 beats per minute. During hibernation, a mammal may lose a third to half of its body weight. Arousal from hibernation occurs by metabolic heating, frequently using brown fat deposits (see figure 28.7), and it takes several hours to raise body temperature to near 37°C. As described in chapter 6, winter sleep and hibernation are forms of controlled hypothermia (lowered body temperature) and are different forms of the same set of physiological processes. They differ by the extent to which body temperature falls and the duration of hypothermic condition.

Nervous and Sensory Functions The basic structure of the vertebrate nervous system is retained in mammals. The development of complex nervous and sensory functions goes hand-in-hand with active lifestyles and is most evident in the enlargement of the cerebral hemispheres and the cerebellum of mammals. Most integrative functions shift to the enlarged cerebral cortex (neocortex; see figure 24.12).

In mammals, the sense of touch is well developed. Receptors are associated with the bases of hair follicles and are stimulated when a hair is displaced.

Olfaction was apparently an important sense in early mammals, because fossil skull fragments show elongate snouts, which would have contained olfactory epithelium. Cranial casts of fossil skulls show enlarged olfactory regions.
Olfaction is still an important sense for many mammals. Mammals can perceive olfactory stimuli over long distances during either the day or night to locate food, recognize members of the same species, and avoid predators.

Auditory senses were similarly important to early mammals. More recent adaptations include an ear flap (the pinna) and the external ear canal leading to the tympanum that directs sound to the middle ear. The middle ear contains three ear ossicles that conduct vibrations to the inner ear. The sensory patch of the inner ear that contains the sound receptors is long and coiled and is called the cochlea. This structure provides more surface area for receptor cells and gives mammals greater sensitivity to pitch and volume than is present in reptiles. Cranial casts of early mammals show well-developed auditory regions.

Vision is an important sense in many mammals, and eye structure is similar to that described for other vertebrates. Accommodation occurs by changing the shape of the lens (see figure 24.29). Color vision is less well developed in mammals than in reptiles and birds. Rods dominate the retinas of most mammals, which supports the hypothesis that early mammals were nocturnal. Primates, squirrels, and a few other mammals have well-developed color vision.

**Excretion and Osmoregulation**

Mammals, like all amniotes, have a metanephric kidney. Unlike reptiles and birds, which excrete mainly uric acid, mammals excrete urea. Urea is less toxic than ammonia and does not require large quantities of water in its excretion. Unlike uric acid, however, urea is highly water soluble and cannot be excreted in a semisolid form; thus, some water is lost. Excretion in mammals is always a major route for water loss.

In the nephron of the kidney, fluids and small solutes are filtered from the blood through the walls of a group of capillary-like vessels, called the glomerulus. The remainder of the nephron consists of tubules that reabsorb water and essential solutes and secrete particular ions into the filtrate.

The primary adaptation of the mammalian nephron is a portion of the tubule system called the loop of the nephron. The transport processes in this loop and the remainder of the tubule system allow mammals to produce urine that is more concentrated than blood. For example, beavers produce urine that is twice as concentrated as blood, while Australian hopping mice produce urine that is 22 times more concentrated than blood. This accomplishes the same function that nasal and orbital salt glands do in reptiles and birds.

Water loss varies greatly, depending on activity, physiological state, and environmental temperature. Water is lost in urine and feces, in evaporation from sweat glands and respiratory surfaces, and during nursing. Mammals in very dry environments have many behavioral and physiological mechanisms to reduce water loss. The kangaroo rat, named for its habit of hopping on large hind legs, is capable of extreme water conservation (figure 22.15). It is native to the southwestern deserts of the United States and Mexico, and it survives without drinking water. Its feces are almost dry, and its nocturnal habits reduce evaporative water loss. Condensation as warm air in the respiratory passages encounters the cooler nasal passages minimizes respiratory water loss. A low-protein diet, which reduces urea production, minimizes excretory water loss. The nearly dry seeds that the kangaroo rat eats are rich sources of carbohydrates and fats. Metabolic oxidation of carbohydrates produces water as a by-product.
Behavior

Mammals have complex behaviors that enhance survival. Visual cues are often used in communication. The bristled fur, arched back, and open mouth of a cat communicate a clear message to curious dogs or other potential threats. A tail-wagging display of a dog has a similarly clear message. A wolf defeated in a fight with other wolves lies on its back and exposes its vulnerable throat and belly. Similar displays may allow a male already recognized as being subordinate to another male to avoid conflict within a social group.

Pheromones are used to recognize members of the same species, members of the opposite sex, and the reproductive state of a member of the opposite sex. Pheromones may also induce sexual behavior, help establish and recognize territories, and ward off predators. The young of many mammalian species recognize their parents, and parents recognize their young, by smell. Bull elk smell the rumps of females during the breeding season to recognize those in their brief receptive period. They also urinate on their own bellies and underhair to advertise their reproductive status to females and other males. Male mammals urinate on objects in the environment to establish territories and to allow females to become accustomed to their odors. Rabbits and rodents spray urine on a member of the opposite sex to inform the second individual of the first's readiness to mate. Skunks use chemicals to ward off predators.

Auditory communication is also important in the lives of mammals. Herd animals stay together and remain calm as long as familiar sounds (e.g., bellowing, hooves walking over dry grasses and twigs, and rumblings from ruminating stomachs) are uninterrupted. Unfamiliar sounds may trigger alarm and flight.

Vocalizations and tactile communication are important in primate social interactions. Tactile communication ranges from precopulatory "nosing" that occurs in many mammals to grooming. Grooming helps maintain a healthy skin and pelage, but also reinforces important social relationships within primate groups.

Territoriality

Many mammals mark and defend certain areas from intrusion by other members of the same species. When cats rub their faces and necks on humans or on furniture, the behavior is often interpreted as affection. Cats, however, are really staking claim to their territory, using odors from facial scent glands. Some territorial behavior attracts females to, and excludes other males from, favorable sites for mating and rearing young.

Male California sea lions (Zalophus californianus) establish territories on shorelines where females come to give birth to young. For about two weeks, males engage in vocalizations, displays, and sometimes serious fighting to stake claim to favorable territories (figure 22.16). Older, dominant bulls are usually most successful in establishing territories, and young bulls generally swim and feed just offshore. When they arrive at the beaches, females select a site for giving birth. Selection of the birth site also selects the bull that will father next year's offspring. Mating occurs approximately two weeks after the birth of the previous year's offspring.

FIGURE 22.16
Order Carnivora. California sea lions (Zalophus californianus) on a rookery at Monterey, California. The adult male in the foreground is vocalizing and posturing.

Development is arrested for the three months during which the recently born young do most of their nursing. This mechanism is called embryonic diapause. Thus, even though actual development takes about nine months, the female carries the embryo and fetus for a period of one year.

Reproduction and Development

In no other group of animals has viviparity developed to the extent it has in mammals. Mammalian viviparity requires a large expenditure of energy on the part of the female during development and on the part of one or both parents caring for young after they are born. Viviparity is advantageous because females are not necessarily tied to a single nest site but can roam or migrate to find food or a proper climate. Viviparity is accompanied by the evolution of a portion of the reproductive tract where the young are nourished and develop. In viviparous mammals, the oviducts are modified into one or two uteri (sing., uterus).

Reproductive Cycles

Most mammals have a definite time or times during the year in which ova (eggs) mature and are capable of being fertilized. Reproduction usually occurs when climatic conditions and resource characteristics favor successful development. Mammals living in environments with few seasonal changes and those that exert considerable control over immediate environmental conditions (e.g., humans) may reproduce at any time of the year. However, they are still tied to physiological cycles of the female that determine when ova can be fertilized.

Most female mammals undergo an estrus (Gr. oistros, a vehement desire) cycle, which includes a time during which the female is behaviorally and physiologically receptive to the male. During the estrus cycle, hormonal changes stimulate the maturation of ova in the ovary and induce ovulation (release of one or more mature ova from an ovarian follicle).
**Wildlife Alert**

The Southern (California) Sea Otter (*Enhydra lutris nereis*)

**Vital Statistics**

- **Classification:** Phylum Chordata, class Mammalia, order Carnivora
- **Range:** Southern California coast
- **Habitat:** Kelp beds in near-shore waters
- **Number remaining:** 2,000
- **Status:** Threatened

**Natural History and Ecological Status**

Sea otters (*Enhydra lutris*) are divided into three subspecies based upon the morphological and molecular characteristics. Their historic range includes most of the northern Pacific rim from Hokkaido, Japan, to Baja California (box figure 22.1). Prior to the 1700s, the sea otter population probably numbered between 150,000 and 300,000 individuals. Of the three subspecies, the southern (California) sea otter (*E. lutris nereis*) has been in the greatest danger of extinction.

Sea otters are the smallest marine mammals (box figure 22.2). Mature males average 29 kg and mature females average 20 kg. They feed on molluscs, sea urchins, and crabs. They use shells and rocks to pry their prey from the substrate and to crack shells and tests of their food items. Unlike other marine mammals, they have no blubber for insulation from cold water. Their very thick fur, with about 150,000 hairs per cm², is their insulation. (The human head has about 42,000 hairs per cm².) Sea otters are considered a keystone predator. By preying on a variety of kelp herbivores, they enhance the productivity of kelp beds and increase the diversity of the kelp ecosystem. (The kelp ecosystem is one of the most diverse ecosystems in temperate regions of the earth.)

Southern sea otters have faced, and continue to face, pressures that threaten their survival. In the 1700s, they were hunted extensively for their thick fur. They are sensitive to contaminants in the ecosystem. Poisons such as pesticides, PCBs, and tributyltin (a component of antifouling agents used on boat hulls) accumulate in their tissues and weaken the animals. When oil from tanker spills becomes trapped in an otter’s thick fur, it destroys its insulating qualities and quickly kills the otter. Today the leading cause of sea otter mortality is disease. All of these pressures devastated southern sea otter populations. Historically, there were about 150,000 to 300,000 southern sea otters along their range, which extended along what is now the California coast. In the early 1900s, they were thought to be extinct until a small group of otters was observed on California’s Big Sur coast.

Southern sea otters are now protected by the International Convention for the Preservation and Protection of Fur Seals, the Marine Mammal Protection Act, and the Endangered Species Act. This protection and other recovery efforts have protected the otters and sheltered other species in the kelp ecosystem. Since 1995, the population has fluctuated between 2,000 and 3,000 animals.

A few mammals (e.g., rabbits, ferrets, and mink) are induced ovulators; coitus (copulation) induces ovulation.

Hormones also mediate changes in the uterus and vagina. As the ova are maturing, the inner lining of the uterus proliferates and becomes more vascular in preparation for receiving developing embryos. External swelling in the vaginal area and increased glandular discharge accompany the proliferation of vaginal mucosa. During this time, males show heightened interest in females, and females are receptive to males. If fertilization does not occur, the changes in the uterus and vagina are reversed until the next cycle begins. No bleeding or sloughing of uterine lining usually occurs.

Many mammals are monestrus and have only a single yearly estrus cycle that is sharply seasonal. Wild dogs, bears,
and sea lions are monestrous; domestic dogs are diestrous. Other mammals are polyestrous. Rats and mice have estrus cycles that repeat every four to six days.

The menstrual cycle of female humans, apes, and monkeys is similar to the estrus cycle in that it results in a periodic proliferation of the inner lining of the uterus and correlates with the maturation of an ovum. If fertilization does not occur before the end of the cycle, menses—the sloughing of the uterine lining—occurs. Chapter 29 describes human menstrual and ovarian cycles.

Fertilization usually occurs in the upper third of the oviduct within hours of copulation. In a few mammals, fertilization may be delayed. In some bats, for example, coitus occurs in autumn, but fertilization is delayed until spring. Females of some species in the uterus for periods in excess of two months. This delayed fertilization is apparently an adaptation to winter dormancy. Fertilization can occur immediately after females emerge from dormancy rather than waiting until males attain their breeding state.

In many other mammals, fertilization occurs right after coitus, but development is arrested after the first week or two. This embryonic diapause, which was described previously for sea lions, also occurs in some bats, bears, martens, and marsupials. The adaptive significance of embryonic diapause varies with species. In the sea lion, embryonic diapause allows the mother to give birth and mate within a short interval, but not have her resources drained by both nursing and pregnancy. It also allows young to be born at a time when resources favor their survival. In some bats, fertilization occurs in the fall before hibernation, but birth is delayed until resources become abundant in the spring.

**Modes of Development**

Monotremes are oviparous. The ovaries release ova with large quantities of yolk. After fertilization, shell glands in the oviduct deposit a shell around the ovum, forming an egg. Female echidnas incubate eggs in a ventral pouch. Platypus eggs are laid in their burrows.

In marsupials, embryos are initially enclosed by extraembryonic membranes and float in uterine fluid. After emerging from extraembryonic membranes, most nourishment for the fetus comes from "uterine milk" that uterine cells secrete. Some nutrients diffuse from maternal blood into a highly vascular yolk sac that makes contact with the uterus. This connection in marsupials is called a choriovitelline (yolk sac) placenta. This period of development is very brief. The marsupial gestation period (the length of time young develop within the female reproductive tract) varies between 8 and 40 days in different species. The gestation period is short because of marsupials' inability to sustain the production of hormones that maintain the uterine lining. After birth, tiny young crawl into the marsupium and attach to a nipple, where they suckle for an additional 60 to 270 days (figure 22.17).

In eutherian mammals, the embryo implants deeply into the uterine wall. Embryonic and uterine tissues grow rapidly and become highly folded and vascular, forming a chorioallantoic placenta. Although maternal and fetal blood do not mix, nutrients, gases, and wastes diffuse between the two bloodstreams. Gestation periods of eutherian mammals vary from 20 days (some rodents) to 19 months (the African elephant). Following birth, the placenta and other tissues that surrounded the fetus in the uterus are expelled as "afterbirth." The newborns of many species (e.g., humans) are helpless at birth (altricial); others (e.g., deer and horses) can walk and run shortly after birth (preocial).

**Section Review 22.3**

The skin of a mammal is protective and is responsible for many mammalian characteristics. Epidermal derivatives of
the skin include hair, claws, and glands (including mammary glands). Hair functions in the sense of touch, as insulation, and in communication. Unlike other amniotes, the teeth of mammals are specialized for different functions, and tooth structure is used by zoologists to characterize mammalian taxa. Mammals possess four-chambered hearts and separate pulmonary and systemic circuits. Circulation through the placenta provides the fetus with nutrients and promotes gas exchange. Mammals excrete primarily urea and have a long loop of the nephron to help conserve water. Mammals rely on behaviors, pheromones, sound, and the sense of touch for communication with other animals. Monotremes are oviparous. Other mammals are viviparous. Most female mammals undergo estrus, which is a time when females are receptive to males. Primate females undergo menstrual cycles, which involve the preparation of the uterus to receive the fertilized egg. Following fertilization, gestation periods may last from eight days (some marsupials) to 19 months (African elephant).

**What modifications of the general circulatory pattern of adult mammals are found in fetal mammals? What do these modifications accomplish?**

### 22.4 Human Evolution

**Learning Outcomes**

1. Explain the global conditions that influenced the evolution of bipedal locomotion in early apes in Africa.
2. Describe a sequence of hominins and time frames that are important in understanding events of human evolution.
3. Describe the role of cultural evolution in the development of human societies.

Before modern theories of evolution appeared, questions about our origins absorbed human thought and fueled the fires of debate. Today paleontologists hunt fossil remains, paleoecologists study environmental constraints placed on early humans, molecular biologists study the genetic sequences of primates, cytologists study the chromosome composition of primates, taphonomists study the way that bones and artifacts become buried, and ethologists study the behavior of social primates. All of these fields have supplied a wealth of information that helps us understand phylogeny within the primate lineage. As you will see in the this section, there are many exciting questions regarding our origins remaining to be answered.

### Who Are the Primates?

Primates arose in the late Cretaceous period about 65 mya. Ancestral species were probably insectivores that ran along tree branches and across the ground. Arboreal (tree-dwelling) habits and a shift to diurnal (daytime) activity favored color vision as the primary means for locating food and negotiating uncertain footing. The eyes of most mammals are on the sides of their heads, but the eyes of primates are on the front of the head. This location provides an overlapping field of view for each eye and improved depth perception. Other primate characteristics that can be traced to arboreal origins include a center of gravity that is shifted over hindlimbs, nails that protect the ends of long digits, sensitive foot and hand pads that are used in exploring arboreal environments, and friction ridges that aid in clinging to tree branches. The medial digits of the hands, and usually also the feet, are opposable to allow the hand and foot to close around a branch or other object.

Primates are divided into two suborders (table 22.2). One includes lemurs, the aye-aye, and bush babies. The other includes tarsiers, New and Old World monkeys, gibbons, the gorilla, chimpanzees, the orangutan, and humans (figure 22.18). The latter four are all apes and members of one family, Hominidae. Until recently humans were classified in a family separate from the gorilla, chimpanzees, and the...
Primates. (a) Lemurs are found only on the island of Madagascar, off the eastern coast of Africa. Their eyes are partially directed toward the front, allowing some binocular vision. They have longer hindlimbs than forelimbs and somewhat elongated digits. A black lemur (*Eulemur macaco macaco*) is shown here. (b) Old World monkeys are found in Africa, Asia, Japan, and the Philippines. They use their tails as a balancing aid, but they are not prehensile (grasping). A red shanked douc langur (*Pygathrix nemaeus nemaeus*) is shown here. (c) New World monkeys are found in Central and South America. They have prehensile tails. A red howler monkey (*Alouatta seniculus*) is shown here. (d) Gorillas (*Gorilla gorilla*), along with chimpanzees, orangutans, and humans, belong to the family Hominidae.
orangutan. DNA and chromosome analysis, however, reveals that chimpanzees and humans are as similar to each other as many sister species. (That is, they are as similar as different species within the same genus.) The classification system in table 22.2 keeps the chimps and humans in different genera, but in the same subfamily (Homininae) and tribe (Hominini). The term "hominin" is used to refer to the chimpanzees and members of this human lineage. (Hominini is sometimes defined to exclude chimpanzees and refer only to modern humans and our human ancestors. When it is used in the more inclusive sense to include chimpanzees and humans, the subtribe Panina designates the chimpanzee lineage and the subtribe Hominina designates the human lineage.)

**Evolution of Hominins**

The first apes appeared about 25 mya. The fossil record that could document the evolution of the ape lineage to a point of common ancestry of humans and chimpanzees is quite fragmentary. Molecular evidence suggests that divergence between apes and hominins occurred between 6 and 10 mya, but this evidence cannot help us visualize what this common ancestor looked like. We must avoid the temptation to visualize living chimpanzees as models for ancestors of the human lineage as the chimpanzee lineage has surely undergone many changes over the time frame that encompasses the human lineage. Unfortunately, changes within the chimpanzee lineage are poorly documented.

Ape evolution was strongly influenced by geography and climate. Continental drift had isolated Asian and African apes. Africa was largely tropical at the time. Climate and geography changed, however, and these changes probably supplied the pressures that fostered evolutionary change. About 20 mya, global temperatures turned sharply cooler. Temperate regions expanded, and seasons became more pronounced. Geological uplift created highlands and dry belts across eastern Africa. Between 5 and 7 mya, global temperatures fell further. The continuous tropical forests of Africa began breaking into a mosaic of forest and vast savannah. Under these circumstances, African apes acquired adaptations that allowed them to move from arboreal habitats to exploit grains, tubers, and dead grazing animals. An upright posture and bipedal locomotion, hallmark characteristics that distinguish the hominins, promoted exploitation of these resources. Earliest hominins were probably not strictly arboreal or ground dwelling, but would have come out of the trees to forage and used trees as refugia. It is very possible that bipedal locomotion evolved in more than one lineage in the bush-like hominin phylogeny. A few of the host of skeletal adaptations that give paleontologists clues to bipedal locomotion are described next.

Bipedal locomotion required adaptations for balancing and adaptations that permit the weight of the body to be supported by two, rather than four, appendages. In humans, the vertebral column is curved in a manner that brings the center of gravity more in line with the axis of support (figure 22.19). In addition, the vertebrae that make up the vertebral column become larger from the neck to the pelvis as the force of compression increases. Another important skeletal change associated with bipedalism involves a reduction in the size of spinous processes on neck vertebrae. This change is associated with reduced neck musculature required by the positioning of the head on top of the vertebral column, rather than being held horizontally at the end of the column.

Bipedal locomotion is also reflected in the structure of appendages. Unlike the knuckle walking and brachiation of apes, the shorter human forelimbs are not used in bipedal locomotion. The pelvis is short and wide, which transmits weight directly to the legs, maintains the size of the birth canal, and provides surfaces for the attachment of leg muscles. The femur of humans is angled at the knee toward the axis of the body (see figure 22.19). Angling the femur places feet under the center of gravity while walking, which results in a smooth stride compared to the "waddle" of other apes.

Although not necessarily directly associated with bipedal locomotion, changes in the skull also accompanied human evolution. The face of humans is less protruding than that of other apes. This change accompanies the expansion of the anterior portion of the skull in association with the enlargement of the brain. Other skull changes include a reduction in the size of jaws, teeth, and the bones that contribute to the ridges above the eyes (supraorbital ridges). The foramen magnum, the opening of the skull for the exit of the spinal cord, is shifted anteriorly in humans. This positioning results in the skull being balanced on top of the vertebral column rather than protruding forward as the skull does in nonhuman apes.

**Earliest Hominins**

Early hominin evolution occurred between 7 and 5 mya. Recent important discoveries reveal a very bush-like hominin phylogeny that includes multiple species, some of which were contemporaries who lived in relatively close proximity. *Sabelanthropus tchadensis* fossils date to between 6 and 7 mya and show a mixture of ape and hominin features. This species was undoubtedly not a part of the lineage leading to *Homo*, but it has the distinction of being the fossil dating closest to the chimp/human divergence (table 22.3 and figure 22.20). The next oldest hominin fossil is that of *Ardipithecus ramidus*, which has been dated to 5.8 million years. *A. ramidus* shows a mosaic of hominin/ancient ape characteristics, which suggest that this species combined tree climbing with walking on all four limbs—but supporting its weight on the palms of the hand rather than on the knuckles. It also had an anterior position of the foramen magnum and foot-bone structure that suggests intermittent bipedal locomotion or a short term upright stance, for example, when using hands for holding or carrying objects.

Numerous fossils in the genus *Australopithecus* have been discovered since 1974. These fossils date to more than 4 million-years-old and provide strong evidence of bipedal locomotion. The discovery of a nearly complete *A. afarensis* in 1974 in East Africa is one of the most famous hominin
discoveries of all time (figure 22.21). Dubbed “Lucy,” this fossil, and others discovered since 1974 date between 3.9 and 3.0 mya and show pelvis and leg structure that leaves no doubt that this species was bipedal. Females were substantially shorter than males. Height varied between 107 and 152 cm. A. africanus existed between 3 and 2 mya. Its body and brain were slightly larger than those of A. afarensis. The shape of the jaw and sizes of the teeth are more similar to those of Homo than are those of A. afarensis. Most anthropologists believe that A. afarensis is a strong candidate as an ancestor of the Homo lineage—but that is not certain. If that is the case, A. afarensis probably represents a point of divergence between the Homo lineage and other australopithecines that were contemporaries of early Homo species.

Interestingly, a newly described hominin fossil (Burtele sp.) has been described from the same time as, and only 50 km distant from, A. afarensis fossils. Burtele shows fewer bipedal characteristics, for example, it had grasping big toes. One can imagine that as A. afarensis foraged for food on the ground, it may have looked into the trees at Burtele looking down at it.

**Homo**

The criteria for assigning fossils to the genus Homo divide paleontologists. There is, however, general acceptance of six Homo species. H. habilis is called “handy man” because of the evidence of primitive stone “toolkits” associated with these fossils. The brain size overlapped that of later australopithecines (the low end) and later species of Homo (the high end). Casts of their skulls indicate the presence of Broca’s area, which is essential for speech. H. habilis existed between 2.4 and 1.5 mya. H. erectus lived about 1.5 mya (between 1.8 million and 300,000 years ago). H. erectus spread widely from its African birthplace. Fossils have been uncovered in Africa, Europe, China (Peking Man), and Indonesia. Artifacts associated with their campsites indicate the use of more sophisticated stone tools, hunting, and fire. One site in China showed ash accumulations 6 m thick!
The following species were formerly included as subspecies of one species, *H. sapiens*. Taxonomic revisions have resulted in these former subspecies being elevated to species. *H. heidelbergensis* appeared about 500,000 years ago and was followed by *H. neanderthalensis*. The latter existed between 230,000 and 30,000 years ago. Neandertals lived mostly in cold climates, and their body proportions suggest a short (170 cm), solid physique. Their bones were thick and heavy and indicate powerful musculature. They were found throughout Europe and the Middle East and lived in caves and shelters made of wood. They used a diversity of tools made of stone, bone, antler, and ivory and observed burial rituals. *H. sapiens* arose in Africa 195,000 years ago. In addition to more sophisticated tools for making clothing, sculpting, engraving, and hunting, they produced fine artwork— including spectacular cave paintings like those at Lascaux, France (figure 22.22). Over the 200,000 years of our history, changes toward smaller molars and decreased robustness are evident. Fully modern humans were present about 30,000 years ago.

**Cultural Evolution—A Distinctively Human Process of Change**

Culture is a system of nongenetic behaviors, symbols, beliefs, institutions, and technology characteristic of a group that is transmitted through generations. Although a rudimentary
Human Evolution. This illustration shows the approximate time frames and plausible sequences in human evolution. Solid arrows show fairly certain pathways. Dashed arrows depict uncertain pathways. Colors depict various hominin pathways. Green pathways show the plausible evolutionary sequence leading to modern humans. Numerous species have been omitted and new fossils are being found on a regular basis. Hominin phylogeny is very bush-like. Bipedal adaptations probably arose independently in branches that did not lead to _H. sapiens_. The chimpanzee (_Pan troglodytes_) lineage is poorly documented and is not shown.

**FIGURE 22.20**

Australopithecus afarensis. This fossil, named "Lucy," was discovered in 1974. It dates between 3.9 and 3.0 mya and shows pelvis and leg structure that leaves no doubt that this species was bipedal.
Revolution is a reminder that biological evolution and cultural evolution do share a common feature—progress is not guaranteed by either. Finally, we are in the midst of another revolution—the "genetic revolution." We are only beginning to experience its influence. Only the advantage of a historical perspective will reveal its full impact.

**SECTION REVIEW 22.4**

Ancestral primates evolved from arboreal ancestors. The family Hominidae includes the hominin lineage, represented today by chimpanzees and humans. Global cooling about 20 mya resulted in the expansion of savannas in Africa. African apes moved from arboreal habitats to terrestrial habitats. Bipedal locomotion evolved as an adaptation for life in the savannah and at the forest edge. Early hominin evolution began about 7 mya. The genus *Homo* first appeared about 2.4 mya, and our species arose 195,000 years ago. Changing human cultures over the last 30,000 years have resulted in agricultural innovations, metallurgy, the Industrial Revolution, and a genetic revolution.

**How were the evolutionary events that occurred early in the human lineage different from the "evolutionary" events of the last 30,000 years?**

**SUMMARY**

22.1 *Evolutionary Perspective*

Mammalian characteristics evolved from the synapsid lineage over a period of about 200 million years. Mammals evolved from a group of synapsids called therapsids.

22.2 *Diversity of Mammals*

Modern mammals include the monotremes, marsupials, and placental mammals.

22.3 *Evolutionary Pressures*

Hair is uniquely mammalian. It functions in sensory perception, temperature regulation, and communication. Mammals have sebaceous, sudoriferous, scent, and mammary glands.

The teeth and digestive tracts of mammals are adapted for different feeding habits. Flat, grinding teeth and fermentation structures for digesting cellulose characterize herbivores. Predatory mammals have sharp teeth for killing and tearing prey. The mammalian heart has four chambers, and circulatory patterns are adapted for viviparous development. Mammals possess a diaphragm that alters intrathoracic pressure, which helps ventilate the lungs. Mammalian thermoregulation involves metabolic heat production, insulating pelage, and behavior. Mammals react to unfavorable environments by migration, winter sleep, and hibernation. The nervous system of mammals is similar to that of other vertebrates. Olfaction and hearing were important for early...
mammals. Vision, hearing, and smell are the dominant senses in many modern mammals. The nitrogenous waste of mammals is urea, and the kidney is adapted for excreting a concentrated urine. Mammals have complex behavior to enhance survival. Visual cues, pheromones, and auditory and tactile cues are important in mammalian communication. Most mammals have specific times during the year when reproduction occurs. Female mammals have estrus or menstrual cycles. Monotremes are oviparous. All other mammals nourish young by a placenta.

22.4 Human Evolution
Apes diverged from other primates about 25 mya. The human lineage is traced back about 7 million years to its divergence from that of chimpanzees. The fossil record indicates a very bush-like hominin phylogeny that leaves many unanswered questions.

CONCEPT REVIEW QUESTIONS
1. Members of this subclass include the monotremes, for example, the spiny anteater and the duck-billed platypus.
   a. Prototheria
   b. Theria
   c. Eutheria
   d. Metatheria
2. Placental mammals belong to the infraclass
   a. Prototheria
   b. Theria.
   c. Eutheria.
   d. Metatheria.
3. These glands are associated with hair follicles, and their oily secretion lubricates and waterproofs the skin and hair of mammals.
   a. Sebaceous glands
   b. Sudoriferous glands
   c. Musk glands
   d. Mammary glands
4. Mammals have teeth that are specialized for specific functions. This is called the _____ condition.
   a. homodont
   b. heterodont
   c. odontophore
5. Chimpanzees and humans are all members of the same primate lineage. Which one of the following is the LEAST inclusive shared lineage?
   a. Hominidae
   b. Haplorhini
   c. Hominini
   d. Homininae

ANALYSIS AND APPLICATION QUESTIONS
1. Why is tooth structure important in the study of mammals?
2. What does the evolution of secondary palates have in common with the evolution of completely separated, four-chambered hearts?
3. Why is classifying mammals by feeding habits not particularly useful to phylogenetic studies?
4. Under what circumstances is endothermy disadvantageous for a mammal?
5. What is induced ovulation? Why might it be adaptive for a mammal?
6. Do you think tool use selected for increased intelligence or increased intelligence (perhaps selected for by social behaviors) promoted tool use? Explain.

Enhance your study of this chapter with study tools and practice tests. Also ask your instructor about the resources available through Connect, including a media-rich eBook, interactive learning tools, and animations.