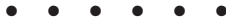


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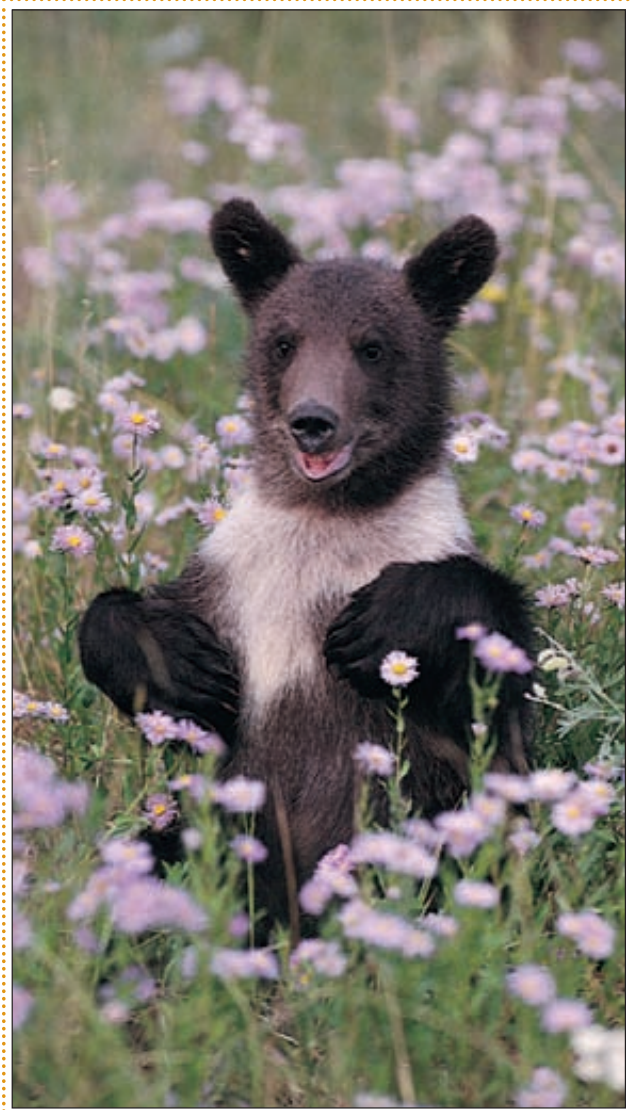
chapter twenty

Mammals

The Tell-Tale Hair

If Fuzzy Wuzzy, the bear that had no hair (according to the children's rhyme), was truly hairless, he could not have been a mammal or a bear. For hair is as much an unmistakable characteristic of mammals as feathers are of birds. If an animal has hair it is a mammal; if it lacks hair it must be something else. It is true that many aquatic mammals are nearly hairless (whales, for example) but hair can usually be found (with a bit of searching) at least in vestigial form somewhere on the body of an adult. Unlike feathers, which evolved from converted reptilian scales, mammalian hair is a completely new epidermal structure. Mammals use their hair for protection, for protective coloration and concealment, for waterproofing and buoyancy, and for behavioral signaling; they have turned hairs into sensitive vibrissae on their snouts and into prickly quills. Perhaps most important, mammals use their hair for thermal insulation, which allows them to enjoy the great advantages of homeothermy. Warm-blooded animals in most climates and at sunless times benefit from this natural and controllable protective insulation.

Hair, of course, is only one of several features that together characterize a mammal and help us to understand the mammalian evolutionary achievement. Among these are a highly developed placenta for feeding an embryo; mammary glands for nourishing the newborn; and a surpassingly advanced nervous system that far exceeds in performance that of any other animal group. It is doubtful, however, that even with this winning combination of adaptations, mammals could have triumphed as they have without their hair.



Juvenile grizzly bear.

Mammals, with their highly developed nervous system and numerous ingenious adaptations, occupy almost every environment on earth that supports life. Although not a large group (about 4600 species as compared with more than 9000 species of birds, approximately 24,600 species of fishes, and 800,000 species of insects), class Mammalia (mam-may'lee-a) (L. *mamma*, breast) is overall the most biologically differentiated group in the animal kingdom. Many potentialities that dwell more or less latently in other vertebrates are highly developed in mammals. Mammals are exceedingly diverse in size, shape, form, and function. They range in size from the recently discovered Kitti's hognosed bat, weighing only 1.5 g, to blue whales, exceeding 130 metric tons.

Yet, despite their adaptability and in some instances because of it, mammals have been influenced by humans more than any other group of animals. We have domesticated numerous mammals for food and clothing, as beasts of burden, and as pets. We use millions of mammals each year in biomedical research. We have introduced alien mammals into new habitats, occasionally with benign results but more frequently with unexpected disaster. Although history provides us with numerous warnings, we continue to overcrop valuable wild stocks of mammals. The whale industry has threatened itself with total collapse by exterminating its own resource—a classic example of self-destruction in the modern world, in which competing segments of an industry are intent only on reaping all they can today as though tomorrow's supply were of no concern whatever. In some cases destruction of a valuable mammalian resource has been deliberate, such as the officially sanctioned (and tragically successful) policy during the Indian wars of exterminating bison to drive the Plains Indians into starvation. Although commercial hunting has declined, the ever-increasing human population with accompanying destruction of wild habitats has harassed and disfigured the mammalian fauna.

We are becoming increasingly aware that our presence on this planet as the most powerful product of organic evolution makes us responsible for our natural environment. Since our welfare has been and continues to be closely related to that of the other mammals, it is clearly in our interest to preserve the natural environment of which all mammals, ourselves included, are a part. We need to remember that nature can do without humans but humans cannot exist without nature.

Origin and Evolution of Mammals

The evolutionary descent of mammals from their earliest amniote ancestors is perhaps the most fully documented transition in vertebrate history. From the fossil record, we can trace the derivation over 150 million years of endothermic, furry mammals from their small, ectothermic, hairless ancestors. The structure of the skull roof permits us to identify three major groups of amniotes that diverged in the Carboniferous period of the Paleozoic era, **synapsids**, **anapsids**, and **diapsids** (figure 20.1; see also p. 341). The synapsid group, which includes mammals and their ancestors, has a pair of openings in the

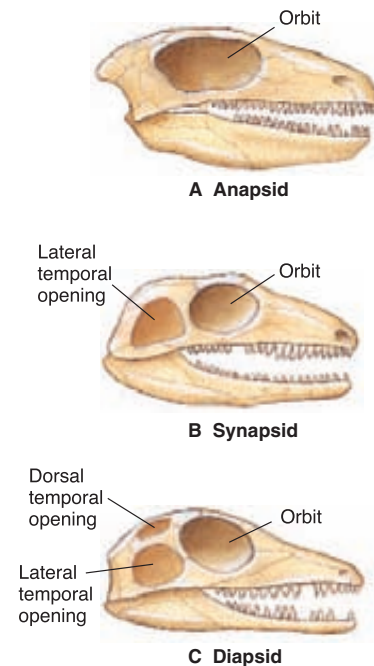


figure 20.1

Skulls of early amniotes, showing the pattern of temporal openings that distinguish the three groups.

skull roof for attachment of jaw muscles. Synapsids were the first amniote group to radiate widely into terrestrial habitats. The anapsid group is characterized by solid skulls and includes turtles and their ancestors (figure 20.1A and p. 346). Diapsids have two pairs of openings in their skull roof (Figure 20.1C; see also figure 18.2, p. 343) and this group contains dinosaurs, lizards, snakes, crocodilians, birds, and their ancestors.

The earliest synapsids radiated extensively into diverse herbivorous and carnivorous forms that are often collectively called **pelycosaurs** (figures 20.2 and 20.3). Pelycosaurs share a general outward resemblance to lizards, but this resemblance is misleading. Pelycosaurs are not closely related to lizards, which are diapsids, nor are they a monophyletic group. From one group of early carnivorous synapsids arose the **therapsids** (figure 20.3), the only synapsid group to survive beyond the Paleozoic. In therapsids we see for the first time an efficient erect gait with upright limbs positioned beneath the body. Since stability was reduced by raising the animal from the ground, the muscular coordination center of the brain, the cerebellum, assumed an expanded role. The therapsids radiated into numerous herbivorous and carnivorous forms but most disappeared during a great extinction at the end of the Permian.

Only the last therapsid subgroup to evolve, the **cynodonts**, survived to enter the Mesozoic. Cynodonts evolved several novel features including a high metabolic rate, which

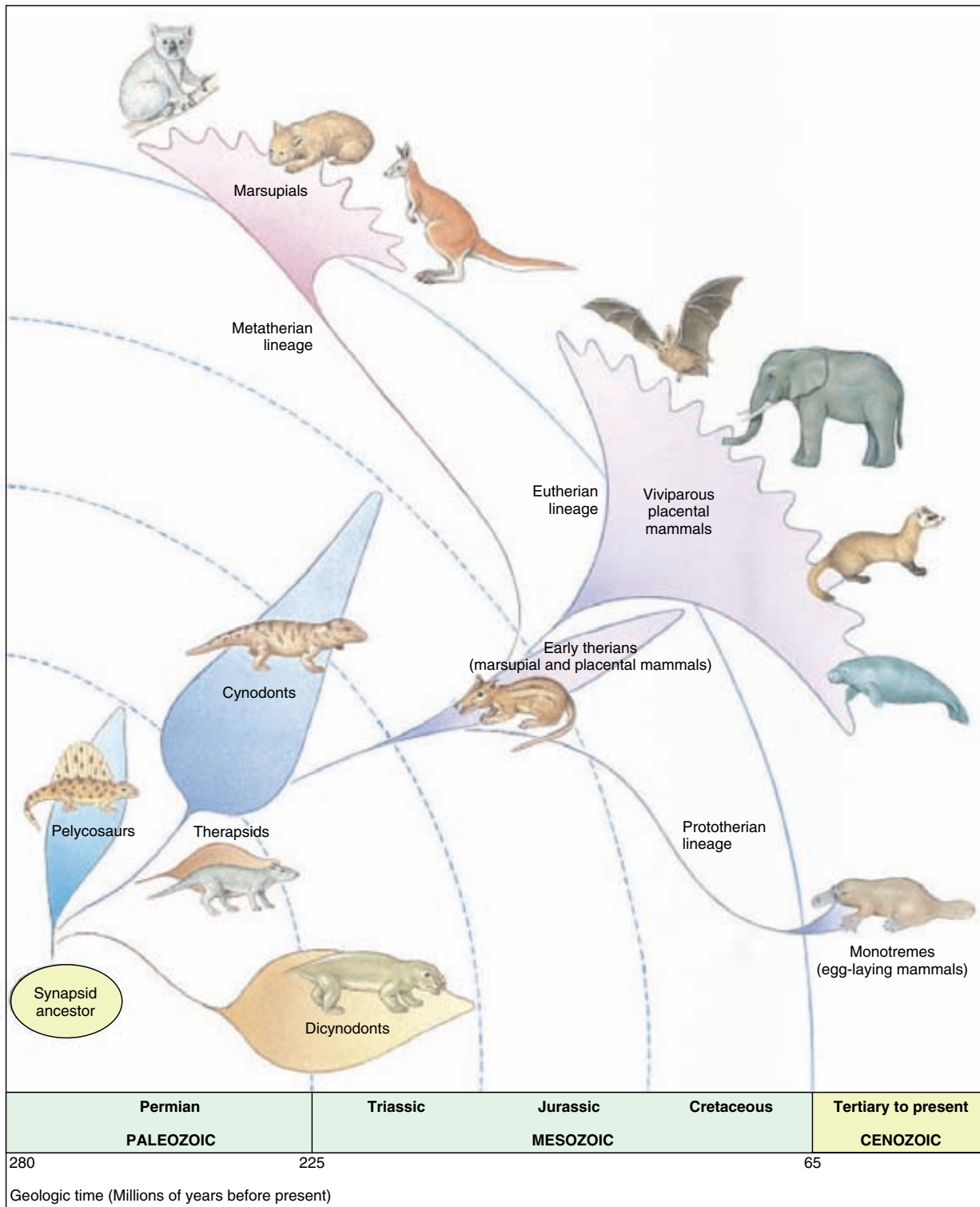


figure 20.2

Evolution of major groups of synapsids. The synapsid lineage, characterized by lateral temporal openings in the skull, began with pelycosaurs, early mammal-like amniotes of the Permian. Pelycosaurs radiated extensively and evolved changes in jaws, teeth, and body form that presaged several mammalian characteristics. These trends continued in their successors, the therapsids, especially in cynodonts. One lineage of cynodonts gave rise in the Triassic to therians (marsupial and placental mammals). Fossil evidence, as currently interpreted, indicates that all three groups of living mammals—monotremes, marsupials, and placentals—are derived from the same lineage. The great radiation of modern placental orders occurred during the Cretaceous and Tertiary periods.

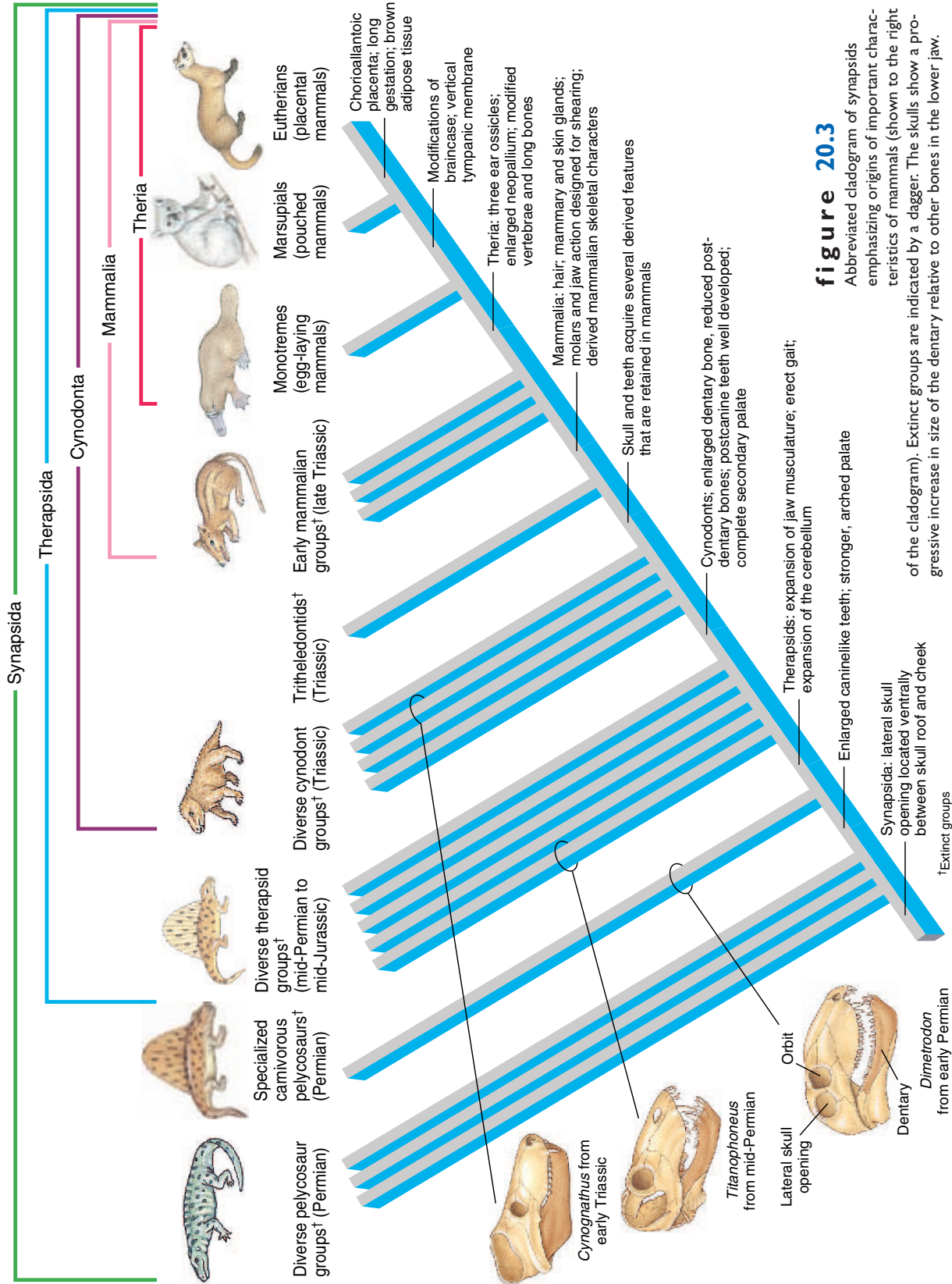


figure 20.3

Abbreviated cladogram of synapsids emphasizing origins of important characteristics of mammals (shown to the right of the cladogram). Extinct groups are indicated by a dagger. The skulls show a progressive increase in size of the dentary relative to other bones in the lower jaw.

Sources: T. S. Kemp, *Mammal-like reptiles and the origin of mammals*, 1982, Academic Press, NY; K. Gauthier, et al., "Amniote phylogeny and the importance of fossils" in *Cladistics*, 4:105–209, 1998; R. L. Carroll, *Vertebrate paleontology and evolution*, 1988, W. H. Freeman & Co., NY; F. H. Pough, et al., *Vertebrate life*, 3d ed., 1989, Macmillan Co., NY; and T. Rowe, "Phylogenetic systematics and the early history of mammals" in F. S. Szalay, et al., *Mammal phylogeny*, vol. 1, 1993, Springer-Verlag, NY.

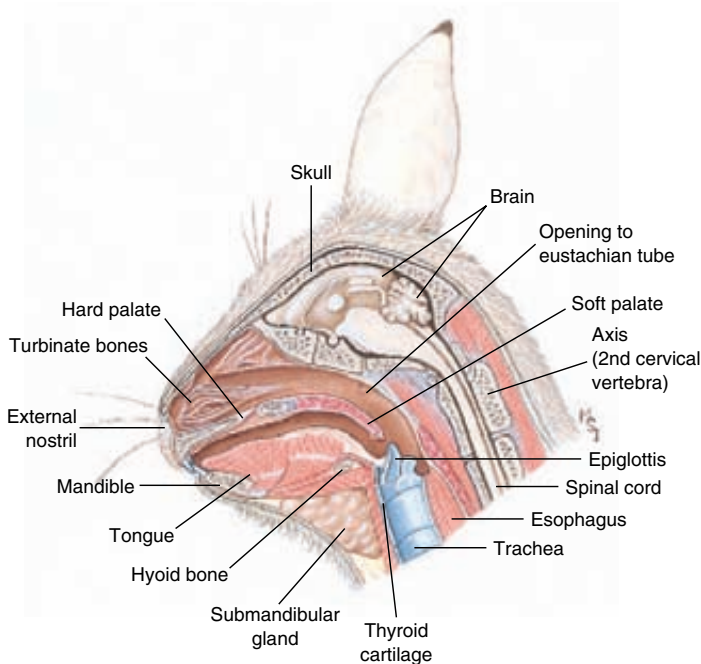


figure 20.4

Sagittal section through the head of a rabbit. Hard and soft palates together form the secondary palate, a roof that separates mouth and nasal cavities, and a characteristic of all mammals and some reptiles.

supported a more active life; increased jaw musculature, permitting a stronger bite; several skeletal changes, supporting greater agility; and a secondary bony palate (figure 20.4), enabling an animal to breathe while holding prey or chewing food. The secondary palate would be important to subsequent mammalian evolution by permitting young to breathe while suckling. Toward the end of the Triassic certain cynodont groups arose that closely resembled mammals, sharing with them several derived features of the skull and teeth.

Fishes, amphibians, most reptiles, and birds have a **primary palate**, which is the roof of the mouth cavity formed by ventral skull bones. In these vertebrates, there is no separation of nasal passages from the mouth cavity. In mammals and crocodylians nasal passages are completely separated from the mouth by development of a secondary bony roof, the **secondary palate**. Mammals extend the separation of oral and nasal cavities even farther backward by adding to this “hard palate” a fleshy soft palate; these structures are shown in figure 20.4.

The earliest mammals of the late Triassic period were small mouse- or shrew-sized animals with enlarged crania, jaws redesigned for shearing action, and a new type of dentition, called **diphyodont**, in which teeth are replaced only once

(deciduous and permanent teeth). This event contrasts with the primitive amniote pattern of continual tooth replacement throughout life. The earliest mammals were almost certainly endothermic, although their body temperature would have been rather lower than modern placental mammals. Hair was essential for insulation, and the presence of hair implies that sebaceous and sweat glands must have evolved at this time to lubricate the hair and promote heat loss. The fossil record is silent on the appearance of mammary glands, but they must have evolved before the end of the Triassic.

Oddly, early mammals of the mid-Triassic, having developed nearly all novel attributes of modern mammals, had to wait for another 150 million years before they could achieve their great diversity. While dinosaurs became diverse and abundant, all nonmammalian synapsid groups became extinct. But mammals survived, first as shrewlike, probably nocturnal, creatures. Then, beginning in the Cretaceous period, but especially during the Eocene epoch that began about 54 million years ago, modern mammals began to diversify rapidly. The great Cenozoic radiation of mammals is partly attributed to numerous habitats vacated by the extinction of many amniote groups at the end of the Cretaceous. Mammalian radiation was almost certainly promoted by the facts that mammals were agile, endothermic, intelligent, adaptable, and gave birth to living young, which they protected and nourished from their own milk supply, thus dispensing with vulnerable eggs laid in nests.

The class Mammalia includes 21 orders: one order containing monotremes, one order containing marsupials, and 19 orders of placentals. A complete classification is on pp. 401–403.

Structural and Functional Adaptations of Mammals

Integument and Its Derivatives

Mammalian skin and especially its modifications distinguish mammals as a group. As the interface between an animal and its environment, skin is strongly molded by an animal’s way of life. In general, skin is thicker in mammals than in other classes of vertebrates, although as in all vertebrates it is composed of **epidermis** and **dermis**. Among mammals the dermis becomes much thicker than the epidermis. The epidermis is thinner where it is well protected by hair, but in places that are subject to much contact and use, such as the palms or soles, its outer layers become thick and cornified with keratin.

Hair

Hair is especially characteristic of mammals, although humans are not very hairy creatures and, in whales, hair is reduced to only a few sensory bristles on their snout. A hair grows from a hair follicle that, although an epidermal structure, is sunk into the dermis of the skin (figure 20.5). A hair grows continuously

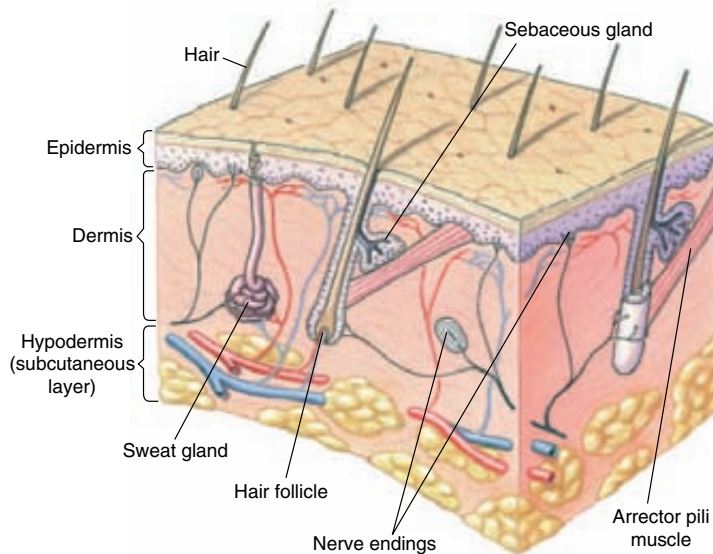


figure 20.5

Structure of human skin (epidermis and dermis) and hypodermis, showing hair and glands.

by rapid proliferation of cells in a follicle. As a hair shaft is pushed upward, new cells are carried away from their source of nourishment and die, turning into the same dense type of fibrous protein, called **keratin**, that constitutes nails, claws, hooves, and feathers.

Mammals characteristically have two kinds of hair forming their **pelage** (fur coat): (1) dense and soft **underhair** for insulation and (2) coarse and longer **guard hair** for protection against wear and to provide coloration. Underhair traps a layer of insulating air. In aquatic mammals, such as fur seals, otters, and beavers, it is so dense that it is almost impossible to wet. In water, guard hairs become wet and mat down, forming a protective blanket over the underhair (figure 20.6).

When a hair reaches a certain length, it stops growing. Normally it remains in its follicle until a new growth starts, whereupon it falls out. In most mammals there are periodic molts of the entire coat. In humans, hair is shed and replaced throughout life (although balding males confirm that replacement is not assured!).

A hair is more than a strand of keratin. It consists of three layers: the medulla or pith in the center of the hair, the cortex with pigment granules next to the medulla, and the outer cuticle composed of imbricated scales. The hair of different mammals shows a considerable range of structure. It may be deficient in cortex, such as the brittle hair of deer, or it may be deficient in medulla, such as the hollow, air-filled hairs of a wolverine. Hairs of rabbits and some others are scaled to interlock when pressed together. Curly hair, such as that of sheep, grows from curved follicles.



figure 20.6

American beaver, *Castor canadensis*, about to cut down an aspen tree. This second largest rodent (the South American capybara is larger) has a heavy waterproof pelage consisting of long, tough guard hairs overlying the thick, silky underhair so valued in the fur trade. Order Rodentia, family Castoridae.

In the simplest cases, such as foxes and seals, the coat is shed every summer. Most mammals have two annual molts, one in spring and one in fall. Summer coats are always much thinner than winter coats and in some mammals may be a different color. Several northern mustelid carnivores, for example, weasels, have white winter coats and brown-colored summer coats. It was once believed that the white inner pelage of arctic animals conserved body heat by reducing radiation loss; in fact, dark and white pelages radiate heat equally well. Winter white pelage of arctic animals is simply camouflage in a land of snow. The varying hare of North America has three annual molts: the white winter coat is replaced by a brownish gray summer coat, and this is replaced in autumn by a grayer coat, which is soon shed to reveal the winter white coat beneath (figure 20.7).

Outside the Arctic, most mammals wear somber colors that are protective. Often the species is marked with “salt-and-pepper” coloration or a disruptive pattern that helps make it inconspicuous in its natural surroundings. Examples are spots of leopards and fawns and stripes of tigers. Skunks advertise their presence with conspicuous warning coloration.

The hair of mammals has become modified to serve many purposes. Bristles of hogs, spines of porcupines and their kin, and vibrissae on the snouts of most mammals are examples. **Vibrissae**, commonly called “whiskers,” are really sensory hairs that provide a tactile sense to many mammals. The slightest movement of a vibrissa generates impulses in sensory nerve endings that travel to special sensory areas in the brain. Vibrissae are especially long in nocturnal and burrowing animals.

Porcupines, hedgehogs, echidnas, and a few other mammals have developed an effective and dangerous spiny armor. When cornered, the common North American porcupine

characteristics of mammals

1. **Body mostly covered with hair**, but reduced in some
2. **Integument with sweat, scent, sebaceous, and mammary glands**
3. Skull with **two occipital condyles** and **secondary bony palate**; middle ear with **three ossicles** (malleus, incus, stapes); **seven cervical vertebrae** (except some xenarthrans [edentates] and manatees); **pelvic bones fused**
4. Mouth with **diphyodont teeth** (milk, or deciduous, teeth replaced by a permanent set of teeth); teeth heterodont in most (varying in structure and function); lower jaw a **single enlarged bone (dentary)**
5. Movable eyelids and **fleshy external ears (pinnae)**
6. Four limbs (reduced or absent in some) adapted for many forms of locomotion
7. Circulatory system of a four-chambered heart, **persistent left aorta**, and **nonnucleated, biconcave red blood corpuscles**
8. Respiratory system of lungs with alveoli, and voice box (larynx); **secondary palate** (anterior bony palate and posterior continuation of soft tissue, the soft palate) separates air and food passages (figure 20.4); **muscular diaphragm** for air exchange separates thoracic and abdominal cavities
9. Excretory system of metanephros kidneys and ureters that usually open into a bladder
10. Brain highly developed, especially **neocerebrum**; 12 pairs of cranial nerves
11. Endothermic and homeothermic
12. Separate sexes
13. Internal fertilization; **embryos develop in a uterus** with **placental attachment** (placenta rudimentary in marsupials and absent in monotremes); **fetal membranes (amnion, chorion, allantois)**
14. Young nourished by **milk from mammary glands**



A



B

figure 20.7

Snowshoe, or varying, hare, *Lepus americanus* in **A**, brown summer coat and, **B**, white winter coat. In winter, extra hair growth on the hind feet broadens the animal's support in snow. Snowshoe hares are common residents of the taiga and are an important food for lynxes, foxes, and other carnivores. Population fluctuations of hares and their predators are closely related. Order Lagomorpha family Leporidae.



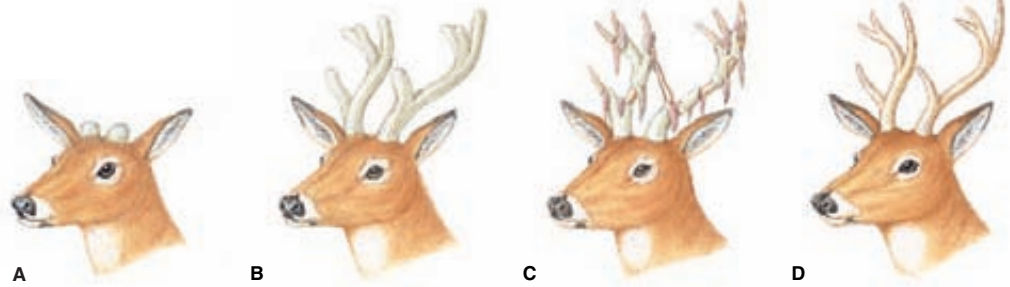
figure 20.8

Dogs are frequent victims of the porcupine's impressive armor. Unless removed (usually by a veterinarian) the quills will continue to work their way deeper in the flesh causing great distress and may lead to the victim's death.

turns its back toward its attacker and lashes out with its barbed tail. The lightly attached quills break off at their bases when they enter the skin and, aided by backward-pointing hooks on the tips, work deeply into tissues. Dogs are frequent victims (figure 20.8) but fishers, wolverines, and bobcats are able to flip the porcupine onto its back to expose vulnerable underparts.

figure 20.9

Annual growth of buck deer antlers. **A**, Antlers begin growth in late spring, stimulated by pituitary gonadotropins. **B**, The bone grows very rapidly until halted by a rapid rise in testosterone production by the testes. **C**, The skin (velvet) dies and sloughs off. **D**, Testosterone levels peak during the fall breeding season. The antlers are shed in January as testosterone levels subside.

**Horns and Antlers**

Three kinds of horns or hornlike structures are found in mammals. **True horns**, found in **ruminants** (for example, sheep and cattle), are sheaths of keratinized epidermis that embrace a core of bone arising from the skull. True horns are not normally shed, usually are not branched (although they may be greatly curved), grow continuously, and are found in both sexes. Horns may be absent from pronghorn antelope females but, if present, are shorter than those of the male.

Antlers of the deer family are branched and composed of solid bone when mature. During their annual growth, antlers develop beneath a covering of highly vascular soft skin called “**velvet**” (figure 20.9). When growth of antlers is complete just before the breeding season, the blood vessels constrict and the stag tears off the velvet by rubbing its antlers against trees. Antlers are shed after the breeding season. New buds appear a few months later to herald the next set of antlers. For several years each new pair of antlers is larger and more elaborate than the previous set. Annual growth of antlers places a strain on mineral metabolism, since during the growing season an older moose or elk must accumulate 50 or more pounds of calcium salts from its vegetable diet.

Rhinoceros horn is the third kind of hornlike structure. Hair-like keratinized filaments that arise from dermal papillae are cemented together to form these structures, which are not attached to the skull.

An escalating trade in rhinoceros products—especially rhinoceros horn—during the last three decades, is pushing Asian and African rhinos to the brink of extinction. Rhinoceros horn is valued in China as an agent for reducing fever, and for treating heart, liver, and skin diseases; and in North India as an aphrodisiac. Such supposed medicinal values are totally without pharmacological basis. The principal use of rhinoceros horns, however, is to fashion handles for daggers in the Middle East. Because of their phallic shape, rhinoceros horn daggers are traditional gifts at puberty rites. Between 1969 and 1977, horns from 8000 slaughtered rhinos were imported into North Yemen alone.

Glands

Of all vertebrates, mammals have the greatest variety of integumentary glands. Most fall into one of four classes: sweat, scent, sebaceous, and mammary. All are derivatives of epidermis.

Sweat glands are tubular, highly coiled glands that occur over much of the body surface in most mammals. They are not present in other vertebrates. There are two kinds of sweat glands: eccrine and apocrine (see figure 20.5). **Eccrine glands** secrete a watery fluid that, if evaporated on the skin’s surface, draws heat away from the skin and cools it. Eccrine glands occur in hairless regions, especially foot pads, in most mammals, although in horses and most primates they are scattered over the body. **Apocrine glands** are larger than eccrine glands and have longer and more convoluted ducts. Their secretory coil is in the dermis and extends deep into the hypodermis. They always open into a hair follicle or where a hair once was. Apocrine glands develop near sexual puberty and are restricted (in the human species) to the axillae (armpits), mons pubis, breasts, prepuce, scrotum, and external auditory canals. In contrast to the watery secretions of eccrine glands, apocrine secretions are milky fluids, whitish or yellow in color, that dry on skin to form a film. Apocrine glands are not involved in heat regulation. Their activity is correlated with certain aspects of the reproductive cycle.

Scent glands are present in nearly all mammals. Their location and functions vary greatly. They are used for communication with members of the same species, for marking territorial boundaries, for warning, or for defense. Scent-producing glands are located variously in orbital, metatarsal, and interdigital regions. The most odoriferous of all glands are those of skunks, which open by ducts into the anus; their secretions can be discharged forcefully for 2 to 3 m. During mating season many mammals produce strong scents for attracting the opposite sex. Humans also are endowed with scent glands. However civilization has taught us to dislike our own scent, a concern that has stimulated a lucrative deodorant industry to produce an endless output of soaps and odor-masking concoctions.

Sebaceous glands are intimately associated with hair follicles (see figure 20.5), although some are free and open directly onto the surface. The cellular lining of a gland is discharged in the secretory process and must be renewed for further secretion. These gland cells become distended with a fatty

accumulation, then die, and are expelled as a greasy mixture called **sebum** into the hair follicle. Called a “polite fat” because it does not turn rancid, it serves as a dressing to keep skin and hair pliable and glossy. Most mammals have sebaceous glands over their entire body; in humans they are most numerous in the scalp and on the face.

Mammary glands, which provide the name for mammals, are probably modified apocrine glands. Whatever their evolutionary origin, they occur on all female mammals and in a rudimentary form on all male mammals. They develop by the thickening of the epidermis to form a milk line along each side of the abdomen in the embryo. On certain parts of these lines mammae appear while intervening parts of the ridge disappear. Human female mammary glands begin to increase in size at puberty because of fat accumulation and reach their maximum development in approximately the twentieth year. Breasts (or mammae) undergo additional development during pregnancy. In other mammals the mammae are swollen only periodically when they are distended with milk during pregnancy and subsequent nursing of young.

Food and Feeding

Mammals exploit an enormous variety of food sources; some mammals require highly specialized diets, whereas others are opportunistic feeders that thrive on diversified diets. Food habits and physical structure are thus inextricably linked. A mammal’s adaptations for attack and defense and its specializations for finding, capturing, chewing, swallowing, and digesting food all determine a mammal’s shape and habits.

Teeth, perhaps more than any other single physical characteristic, reveal the life habit of a mammal (figure 20.10). All mammals have teeth (with few exceptions) and their modifications are correlated with what the mammal eats.

As mammals evolved during the Mesozoic, major changes occurred in teeth and jaws. Unlike the uniform **homodont** dentition of reptiles, mammalian teeth became differentiated to perform specialized functions such as cutting, seizing, gnawing, tearing, grinding, and chewing. Teeth differentiated in this manner are called **heterodont**. Mammalian dentition is differentiated into four types: **incisors**, with simple crowns and sharp edges, used mainly for snipping or biting; **canines**, with long conical crowns, specialized for piercing; **premolars**, with compressed crowns and one or two cusps, suited for shearing and slicing; and **molars**, with large bodies and variable cusp arrangement, used for crushing and grinding. The primitive tooth formula, which expresses the number of each tooth type in one-half of the upper and lower jaw, was I 3/3, C 1/1, PM 4/4, M 3/3. Members of order Insectivora, some omnivores, and carnivores come closest to this primitive pattern (figure 20.10).

Most mammals grow just two sets of teeth: a temporary set, called **deciduous**, or **milk**, teeth, which is replaced by a permanent set when the skull has grown large enough to accommodate a full set. Only incisors, canines, and premolars are deciduous; molars are never replaced and a single permanent set must last a lifetime.

Feeding Specializations

The feeding, or trophic, apparatus of a mammal—teeth and jaws, tongue, and alimentary canal—are adapted to its particular feeding habits. Mammals are customarily divided among four basic trophic categories—insectivores, carnivores, omnivores, and herbivores—but many other feeding specializations have evolved in mammals, as in other living organisms, and feeding habits of many mammals defy exact classification. Principal feeding specializations of mammals are shown in figure 20.10.

Insectivores are small mammals, such as shrews, moles, anteaters, and bats, that feed on a variety of small invertebrates, such as worms and grubs, as well as insects. The insectivorous category is not a sharply distinguished one because carnivores and omnivores often include insects in their diets.

Herbivorous mammals that feed on grasses and other vegetation form two main groups: (1) **browsers** and **grazers**, such as ungulates (hooved mammals including horses, deer, antelope, cattle, sheep, and goats); and (2) **gnawers**, such as rodents, and rabbits and hares. In herbivores, canines are absent or reduced in size, whereas molars, which are adapted for grinding, are broad and usually high-crowned. Rodents have chisel-sharp incisors that grow throughout life and must be worn away to keep pace with their continual growth (figure 20.10).

Herbivorous mammals have interesting adaptations for dealing with their fibrous diet of plant food. **Cellulose**, the structural carbohydrate of plants, is composed of long chains of glucose units linked by chemical bonds that few enzymes can attack. No vertebrates synthesize cellulose-splitting enzymes. Instead, herbivorous vertebrates harbor anaerobic bacteria and protozoa in large fermentation chambers in their gut. These microorganisms break down and metabolize cellulose, releasing a variety of fatty acids, sugars, and starches that the host animal can absorb and use.

Some herbivores, such as horses, zebras, rabbits, hares, elephants, and many rodents, have a gut with a spacious side-pocket, or diverticulum, called a **cecum**, which serves as a fermentation chamber and absorptive area. Hares, rabbits, and some rodents often eat their fecal pellets (**coprophagy**), giving food a second pass through the fermenting action of intestinal microorganisms.

Ruminants (cattle, bison, buffalo, goats, antelopes, sheep, deer, giraffes, and okapis) have a huge **four-chambered stomach** (figure 20.11). As a ruminant feeds, grass passes down the esophagus to the **rumen**, where it is broken down by bacteria and protozoa and then formed into small balls of cud. At its leisure the ruminant returns a cud to its mouth where the cud is deliberately chewed at length to crush the fiber. Swallowed again, the food returns to the rumen where the cellulolytic bacteria and protozoa continue fermentation. The pulp passes to the **reticulum**, then to the **omasum**, where water, soluble food, and microbial products are absorbed. The remainder proceeds to the **abomasum** (“true” acid stomach), where proteolytic enzymes are secreted and normal digestion occurs.

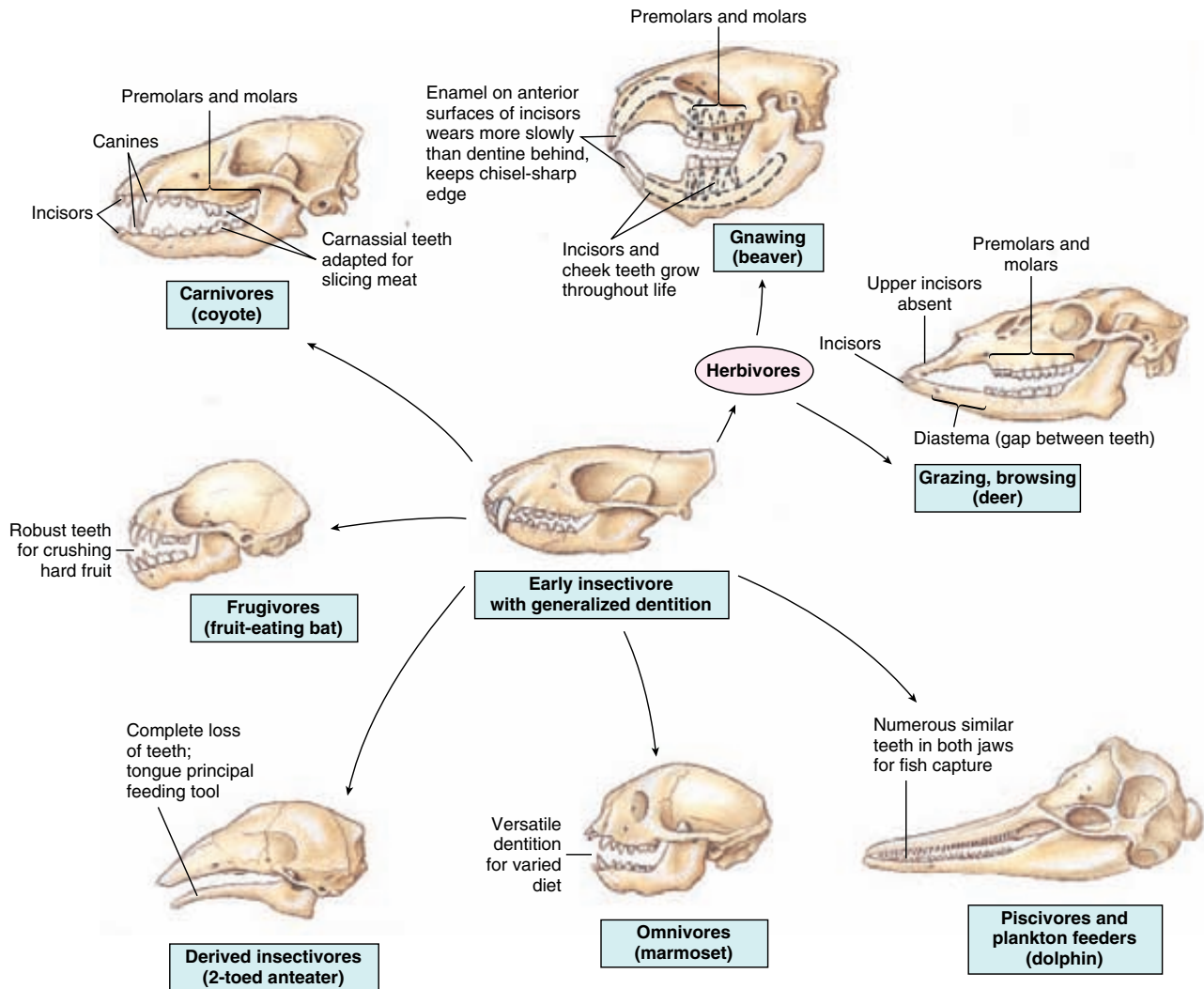


figure 20.10

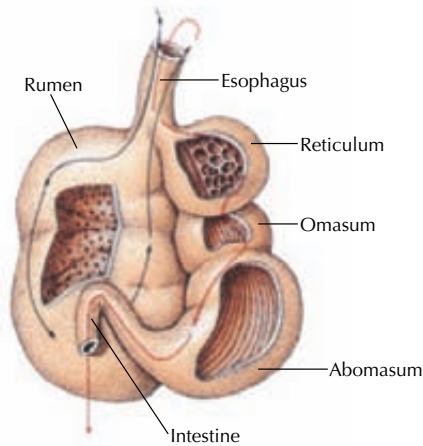
Feeding specializations of major trophic groups of eutherian mammals. Early eutherians were insectivores; all other types are descended from them.

Herbivores generally have large, long digestive tracts and must eat a considerable amount of plant food to survive. A large African elephant weighing 6 tons must consume 135 to 150 kg (300 to 400 pounds) of rough fodder each day to obtain sufficient nourishment for life.

Carnivorous mammals feed mainly on herbivores. This group includes foxes, dogs, weasels, wolverines, fishers, cats, lions, and tigers. Carnivores are well-equipped with biting and piercing teeth and powerful clawed limbs for killing their prey. Since their protein diet is more easily digested than is the woody food of herbivores, their digestive tract is shorter and the cecum small or absent. Carnivores organize their feeding into discrete meals rather than feeding continuously (as do most herbivores) and therefore have much more leisure time for play and exploration (figure 20.12).

Note that the terms “insectivores” and “carnivores” have two different uses in mammals: to describe diet and to denote specific taxonomic orders of mammals. For example, not all carnivores belong to the order Carnivora (many marsupials, pinnipeds, cetaceans, and all insectivores are carnivorous) and not all members of the order Carnivora are carnivorous. Many are opportunistic feeders and some, such as pandas, are strict vegetarians.

Omnivorous mammals use both plants and animals for food. Examples are pigs, raccoons, rats, bears, and most primates (including humans). Many carnivorous forms also eat fruits, berries, and grasses when hard pressed. Foxes, which

**figure 20.11**

Ruminant's stomach. Food passes first to the rumen (sometimes through the reticulum) and then is returned to the mouth for chewing (chewing the “cud,” or rumination) (black arrow). After reswallowing, food returns to the rumen or passes directly to reticulum, omasum, and abomasum for final digestion (red arrow).

**figure 20.12**

Lionesses, *Panthera leo*, eating a wildebeest. Lions stalk prey and then charge suddenly to surprise the victim. They lack stamina for a long chase. Lions gorge themselves with the kill, then sleep and rest for periods as long as one week before eating again. Order Carnivora, family Felidae.

usually feed on mice, small rodents, and birds, eat frozen apples, beechnuts, and corn when their normal food sources are scarce.

Migration

Migration is a much more difficult undertaking for mammals than for birds. Not surprisingly, few mammals make regular seasonal migrations, preferring instead to center their activities in a defined and limited home range. Nevertheless, there are

some striking examples of mammalian migrations. More migrators are found in North America than on any other continent.

An example is the barren-ground caribou of Canada and Alaska, which undertakes direct and purposeful mass migrations spanning 160 to 1100 km (100 to 700 miles) twice annually (figure 20.13). From winter ranges in boreal forests (taiga), they migrate rapidly in late winter and spring to calving ranges on the barren grounds (tundra). Calves are born in mid-June. As summer progresses, caribou are increasingly harassed by warble and nostril flies that bore into their flesh, by mosquitoes that drink their blood (estimated at a liter per caribou each week during the height of the mosquito season), and by wolves that prey on their calves. They move southward in July and August, feeding little along the way. In September they reach the taiga and feed there almost continuously on low ground vegetation. Mating (rut) occurs in October.

Caribou have suffered a drastic decline in numbers since the nineteenth century when there were several million of them. By 1958 less than 200,000 remained in Canada. Their decline has been attributed to several factors, including habitat alteration from exploration and development in the north, but especially to excessive hunting. For example the western arctic herd in Alaska exceeded 250,000 caribou in 1970. Following five years of heavy unregulated hunting, a 1976 census revealed only about 65,000 animals left. After restricting hunting, the herd had increased to 140,000 by 1980 and 160,000 in 1997. However, the proposed scheme to open the Arctic National Wildlife Refuge to petroleum development threatens this recovery.

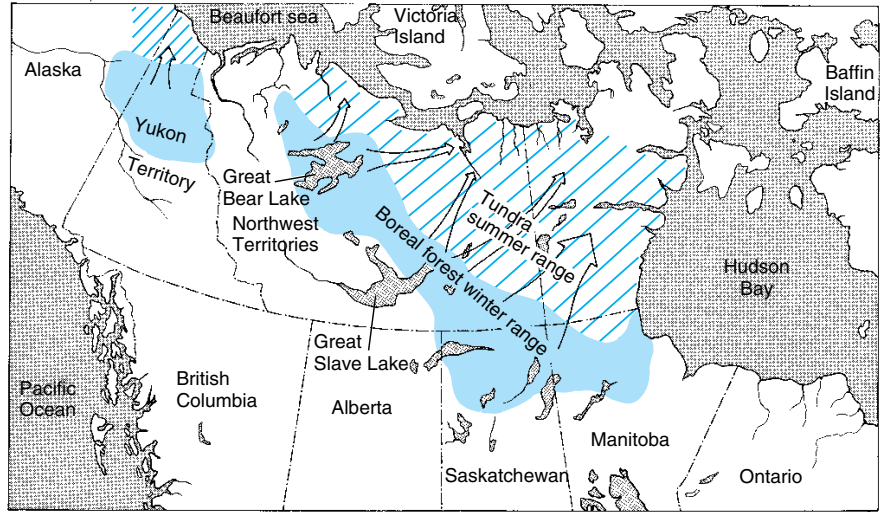
Plains bison, before deliberate near extinction by humans, made huge circular migrations to separate summer and winter ranges.

The longest mammalian migrations are made by oceanic seals and whales. One of the most remarkable migrations is that of fur seals, which breed on the Pribilof Islands approximately 300 km (185 miles) off the coast of Alaska and north of the Aleutian Islands. From wintering grounds off southern California females journey as much as 2800 km (1740 miles) across open ocean, arriving in spring at the Pribilofs where they congregate in enormous numbers (figure 20.14). Young are born within a few hours or days after arrival of the cows. Then bulls, having already arrived and established territories, collect harems of cows, which they guard with vigilance. After the calves have been nursed for approximately three months, cows and juveniles leave for their long migration southward. Bulls do not follow but remain in the Gulf of Alaska during winter.

Although we might expect bats, the only winged mammals, to use their gift of flight to migrate, few of them do. Most spend winters in hibernation. Four species of American bats that migrate spend their summers in northern or western states and their winters in the southern United States or Mexico.



A



B

figure 20.13

Barren-ground caribou, *Rangifer tarandus*, of Canada and Alaska. **A**, Adult male caribou in autumn pelage and antlers in velvet. **B**, Summer and winter ranges of some major caribou herds in Canada and Alaska (other herds not shown occur on Baffin Island and in western and central Alaska). The principal spring migration routes are indicated by arrows; routes vary considerably from year to year. The same species is known as reindeer in Europe. Order Artiodactyla, family Cervidae.

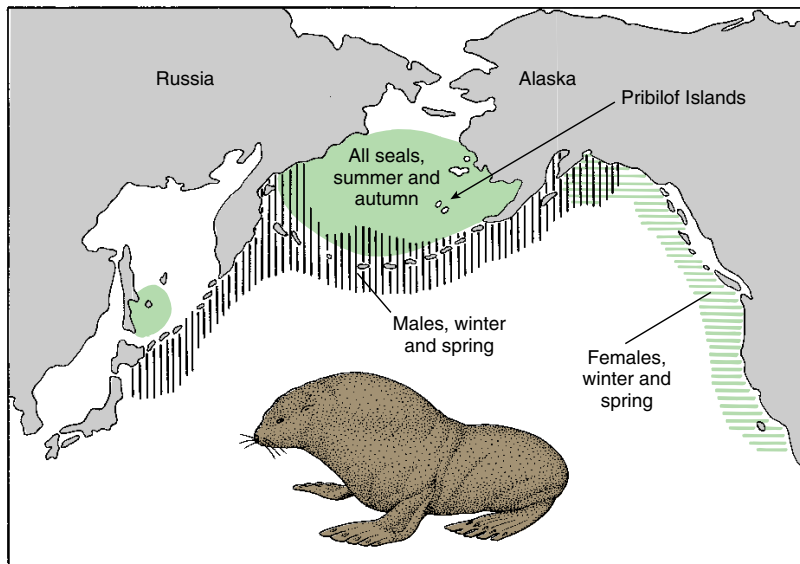


figure 20.14

Annual migrations of fur seals, showing the separate wintering grounds of males and females. Both males and females of the large Pribilof population migrate in early summer to the Pribilof Islands, where females give birth to their pups and then mate with males. Order Carnivora, family Otariidae.

Flight and Echolocation

Mammals have not exploited the skies to the same extent that they have terrestrial and aquatic environments. However, many mammals scamper about in trees with amazing agility; some can glide from tree to tree, and one group, bats, is capable of full flight. Gliding and flying evolved independently in several

groups of mammals, including marsupials, rodents, flying lemurs, and bats. Anyone who has watched a gibbon perform in a zoo realizes there is something akin to flight in this primate, too. Among arboreal squirrels, all of which are nimble acrobats, by far the most efficient are flying squirrels (figure 20.15). These forms actually glide rather than fly, using the gliding skin that extends from the sides of the body.



figure 20.15

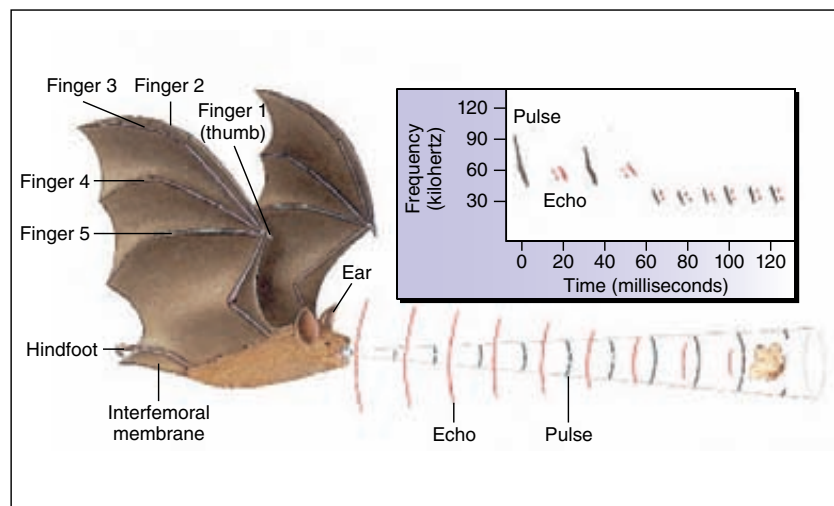
Flying squirrel, *Glaucomys sabrinus*, making a landing. Area of undersurface is nearly trebled when gliding skin is spread. Glides of 40 to 50 m are possible. Good maneuverability during flight is achieved by adjusting the position of the gliding skin with special muscles. Flying squirrels are nocturnal and have superb night vision. Order Rodentia, family Sciuridae.

Bats are nocturnal and thus hold a niche unoccupied by most birds. Their achievement is attributed to two features: flight and capacity to navigate by echolocation. Together these adaptations enable bats to fly and avoid obstacles in absolute darkness, to locate and catch insects with precision, and to find their way deep into caves (a habitat largely ignored by both mammals and birds) where they sleep during the daytime hours.

When in flight, bats emit short pulses 5 to 10 milliseconds in duration in a narrow directed beam from the mouth or nose (figure 20.16). Each pulse is frequency modulated; that is, it is highest at the beginning, up to 100,000 hertz (Hz, cycles per second), and sweeps down to perhaps 30,000 Hz at the end. Sounds of this frequency are ultrasonic to human ears, which have an upper limit of about 20,000 Hz. When bats are

figure 20.16

Echolocation of an insect by the little brown bat *Myotis lucifugus*. Frequency modulated pulses are directed in a narrow beam from the bat's mouth. As the bat nears its prey, it emits shorter, lower signals at a faster rate. Order Chiroptera.



searching for prey, they produce about 10 pulses per second. If prey is detected, the rate increases rapidly up to 200 pulses per second in the final phase of approach and capture. Pulses are spaced so that the echo of each is received before the next pulse is emitted, an adaptation that prevents jamming. Since transmission-to-reception time decreases as a bat approaches an object, the bat can increase pulse frequency to obtain more information about the object. Pulse length is also shortened as it nears an object. It is interesting that some prey of bats, certain nocturnal moths for example, have evolved ultrasonic detectors used to detect and avoid approaching bats.

The external ears of bats are large, like hearing trumpets, and shaped variously in different species. Less is known about the inner ear of bats, but it obviously is capable of receiving the ultrasonic sounds emitted. Biologists believe bat navigation is so refined that a bat builds a mental image of its surroundings from echo scanning that approaches the resolution of a visual image from eyes of diurnal animals.

For reasons not fully understood, all bats are nocturnal, even fruit-eating bats that use vision and olfaction instead of echolocation to find their food. The tropics and subtropics have many kinds of bats, including the famed vampire bat. Vampire bats are provided with razor-sharp incisors used to shave away the epidermis of their prey, exposing underlying capillaries. After infusing an anticoagulant to keep blood flowing, the bat laps up its meal and stores it in a specially modified stomach.

Reproduction

Most mammals have definite mating seasons, usually in winter or spring and timed to coincide with the most favorable time of year for rearing young after birth. Many male mammals are capable of fertile copulation at any time, but female mating function is restricted to a time during a periodic cycle, known as the **estrous cycle**. Females only copulate with males during a relatively brief period known as **estrus**, or heat (figure 20.17).

**figure 20.17**

African lions *Panthera leo* mating. Lions breed at any season, although predominantly in spring and summer. During the short period a female is receptive, she may mate repeatedly. Three or four cubs are born after gestation of 100 days. Once the mother introduces cubs into the pride, they are treated with affection by both adult males and females. Cubs go through an 18- to 24-month apprenticeship learning how to hunt and then are frequently driven from the pride to manage themselves. Order Carnivora, family Felidae.

There are three different patterns of reproduction in mammals. One pattern is represented by egg-laying (oviparous) mammals, the **monotremes**. The duck-billed platypus has one breeding season each year. Ovulated eggs, usually two, are fertilized in the oviduct. As they continue down the oviduct, various glands add albumin and then a thin, leathery shell to each egg. When laid, eggs are about the size of a robin's egg. A platypus lays its eggs in a burrow nest where they are incubated for about 12 days. After hatching, the young suck milk from the fur of the mother around openings of her mammary glands. Thus in monotremes there is no gestation (period of pregnancy) and developing embryos draw on nutrients stored in their eggs, much as do the embryos of reptiles and birds. But in common with all other mammals, monotremes rear their young on milk.

Marsupials are pouched, viviparous mammals that exhibit a second pattern of reproduction. Although only eutherians are called “placental mammals,” marsupials do have a primitive type of yolk sac placenta. An embryo (blastocyst) of a marsupial is at first encapsulated by shell membranes and floats free for several days in uterine fluid. After “hatching” from the shell membranes, the embryo does not implant, or “take root” in the uterus as it would in eutherians, but it does erode a shallow depression in the uterine wall in which it lies and absorbs nutrient secretions from the mucosa by way of the vascularized yolk sac. Gestation (the intrauterine period of development) is brief in marsupials, and therefore all marsupials give birth to tiny young that are effectively still embryos, both anatomically and physiologically (figure 20.18). However,

**figure 20.18**

Opossums, *Didelphis marsupialis*, 15 days old, fastened to teats in mother's pouch. When born after a gestation period of only 12 days, they are the size of honey bees. They remain attached to the nipples for 50 to 60 days. Order Marsupialia, family Didelphidae.

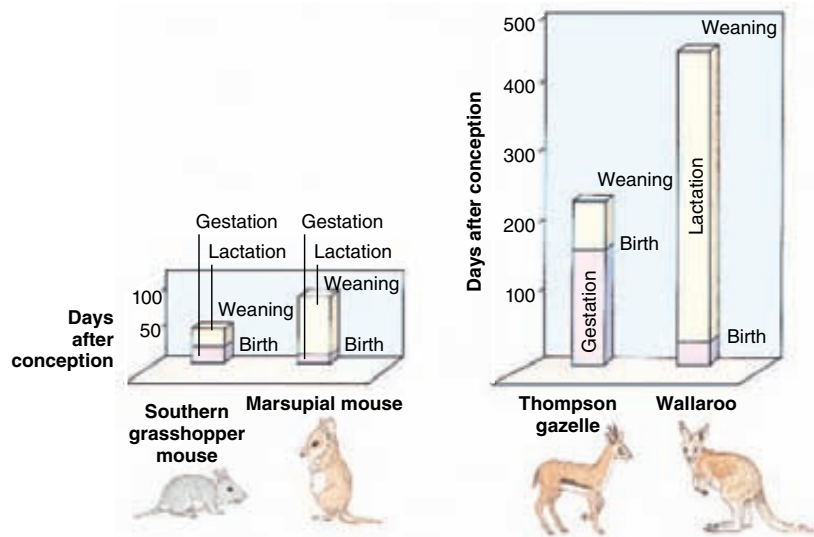
early birth is followed by a prolonged interval of lactation and parental care (figure 20.19).

The third pattern of reproduction is that of viviparous **placental mammals**, eutherians. In placentals, the reproductive investment is in prolonged gestation, unlike marsupials in which the reproductive investment is in prolonged lactation (figure 20.19). Embryos remain in the uterus, nourished by food supplied through a chorioallantoic type of placenta, an intimate connection between mother and young. Length of gestation is longer in placentals than marsupials, and in large mammals it is much longer. For example, mice have a gestation period of 21 days; rabbits and hares, 30 to 36 days; cats and dogs, 60 days; cattle, 280 days; and elephants, 22 months (the longest). But there are important exceptions (nature seldom offers perfect correlations). Baleen whales, the largest mammals, carry their young for only 12 months, while bats, no larger than mice, have gestation periods of 4 to 5 months. The condition of the young at birth also varies. An antelope bears its young well furred, eyes open, and able to run about. Newborn mice, however, are blind, naked, and helpless. We all know how long it takes a human baby to gain its footing. Human growth is in fact slower than that of any other mammal, and this is one of the distinctive attributes that sets us apart from other mammals.

A curious phenomenon that lengthens the gestation period of many mammals is delayed implantation. The blastocyst remains dormant while its implantation in the uterine wall is postponed for periods of a few weeks to several months. For many mammals (for example, bears, seals, weasels, badgers, bats, and many deer) delayed implantation is a device for extending gestation so that the young are born at a time of year that is best for their survival.

figure 20.19

Comparison of gestation and lactation periods between matched pairs of ecologically similar species of marsupial and placental mammals. The graph shows that marsupials have shorter intervals of gestation and much longer intervals of lactation than in similar species of placentals.



Mammalian Populations

A population of animals includes all members of a species that share a particular space and potentially interbreed. All mammals (like other organisms) live in ecological communities, each composed of numerous populations of different animal and plant species. Each species is affected by the activities of other species and by other changes, especially climatic, that occur. Thus populations are always changing in size. Populations of small mammals are lowest before breeding season and greatest just after addition of new members. Beyond these expected changes in population size, mammalian populations may fluctuate from other causes.

The renowned fecundity of meadow mice, and the effect of removing natural predators from rodent populations, is felicitously expressed in this excerpt from Thornton Burgess’s “Portrait of a Meadow Mouse:”

He’s fecund to the nth degree
 In fact this really seems to be
 His one and only honest claim
 To anything approaching fame.
 In just twelve months, should all survive,
 A million mice would be alive—
 His progeny. And this, ‘tis clear,
 Is quite a record for a year.
 Quite unsuspected, night and day
 They eat the grass that would be hay.
 On any meadow, in a year,
 The loss is several tons, I fear.
 Yet man, with prejudice for guide,
 The checks that nature doth provide
 Destroys. The meadow mouse survives
 And on stupidity he thrives.

Irregular fluctuations are commonly produced by variations in climate, such as unusually cold, hot, or dry weather, or by natural catastrophes, such as fires, hailstorms, and hurricanes. These are **density-independent** causes because they affect a population whether it is crowded or dispersed. However, the most spectacular fluctuations are **density dependent**; that is, they correlate with population crowding. These extreme limits to growth are discussed in Chapter 2 (p. 39).

Cycles of abundance are common among many rodent species. One of the best known examples is the mass migrations of Scandinavian and arctic North American lemmings following population peaks. Lemmings (figure 20.20) breed all year, although more in summer than in winter. The gestation period is only 21 days; young born at the beginning of summer are weaned in 14 days and are capable of reproducing by the end of summer. At the peak of their population density, having devastated vegetation by tunneling and grazing, lemmings begin long, mass migrations to find new undamaged habitats for food and space. They swim across streams and small lakes as they go but cannot distinguish these from large lakes, rivers, and the sea, in which they drown. Since lemmings are the main



figure 20.20

Collared lemming, *Dicrostonyx* sp., a small rodent of the far north. Populations of lemmings fluctuate widely. Order Rodentia, family Muridae.

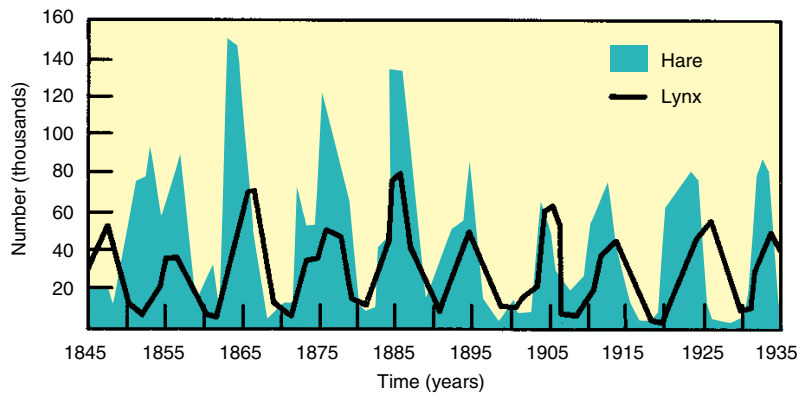


figure 20.21

Changes in population size of varying hare and lynx in Canada as indicated by pelts received by the Hudson's Bay Company. The abundance of lynx (predator) follows that of the hare (prey).

diet of many carnivorous mammals and birds, any change in lemming population density affects all their predators as well.

Varying hares (snowshoe rabbits) of North America show 10-year cycles in abundance. The well-known fecundity of rabbits enables them to produce litters of three or four young as many as five times per year. The density may increase to 4000 hares competing for food in each square mile of northern forest. Predators (owls, minks, foxes, and especially lynxes) also increase (figure 20.21). Then the population crashes precipitously for reasons that have long been a puzzle to scientists. Rabbits die in great numbers, not from lack of food or from an epidemic disease (as was once believed) but evidently from some density-dependent psychogenic cause. As crowding increases, hares become more aggressive, show signs of fear and defense, and stop breeding. The entire population reveals symptoms of pituitary-adrenal gland exhaustion, an endocrine imbalance called “shock disease,” which results in death. These dramatic crashes are not well understood. Whatever the causes, population crashes that follow superabundance, although harsh, permit vegetation to recover, providing survivors with a much better chance for successful breeding.

In his book *The Arctic* (1974. Montreal, Infacor, Ltd.), Canadian naturalist Fred Bruemmer describes the growth of lemming populations in arctic Canada: “After a population crash one sees few signs of lemmings; there may be only one to every 10 acres. The next year, they are evidently numerous; their runways snake beneath the tundra vegetation, and frequent piles of rice-sized droppings indicate the lemmings fare well. The third year one sees them everywhere. The fourth year, usually the peak year of their cycle, the populations explode. Now more than 150 lemmings may inhabit each acre of land and they honeycomb it with as many as 4000 burrows. Males meet frequently and fight instantly. Males pursue females and mate after a brief but ardent courtship. Everywhere one hears the squeak and chitter of the excited, irritable, crowded animals. At such times they may spill over the land in manic migrations.”

Human Evolution

Darwin devoted an entire book, *The Descent of Man and Selection in Relation to Sex*, largely to human evolution. The idea that humans shared common descent with apes and other animals was repugnant to the Victorian world, which responded with predictable outrage (figure 1.16, p. 17). When Darwin's views were first debated, few human fossils had been unearthed, but the current accumulation of fossil evidence has strongly vindicated Darwin's belief that humans descended from primate ancestors. All primates share certain significant characteristics: grasping fingers on all four limbs, flat fingernails instead of claws, and forward-pointing eyes with binocular vision and excellent depth perception. The following synopsis will highlight probable relationships among major primate groups.

The earliest primate was probably a small, nocturnal animal similar in appearance to tree shrews. This ancestral primate stock split into two major lineages, one of which gave rise to **prosimians**, which include lemurs, tarsiers (figure 20.22), and lorises, and the other to **simians**, which include monkeys (figure 20.23) and apes (figure 20.24). Prosimians and many simians are arboreal (tree-dwellers), which is probably the ancestral lifestyle for both groups. Arboreality probably selected for

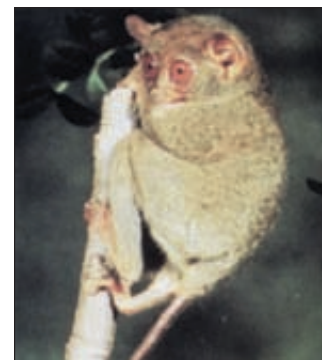


figure 20.22

A prosimian, the Mindanao tarsier, *Tarsius syrichta carbonarius* of Mindanao Island in the Philippines.



figure 20.23

Monkeys. **A**, Red-howler monkeys, an example of New World monkeys. **B**, The olive baboon, an example of Old World monkeys.

increased intelligence. Flexible limbs are essential for active animals moving through trees. Grasping hands and feet, in contrast to the clawed feet of squirrels and other rodents, enable primates to grip limbs, hang from branches, seize food and manipulate it, and, most significantly, use tools. Highly developed sense organs, especially good vision, and proper coordination of limb and finger muscles are essential for an active arboreal life. Of course, sense organs are no better than the brain processing sensory information. Precise timing, judgment of distance, and alertness require a large cerebral cortex.

The earliest simian fossils appeared in Africa some 40 million years ago. Many of these primates became day-active rather than nocturnal, making vision the dominant special sense, now enhanced by color vision. We recognize three major simian groups whose precise phylogenetic relationships are unknown. These are (1) New World monkeys of South America (ceboids),



figure 20.24

The gorilla, order Primates, family Hominidae, an anthropoid ape.

including howler monkeys (see figure 20.23A), spider monkeys, and tamarins; (2) the Old World monkeys (cercopithecoids), including baboons (see figure 20.23B), mandrills, and colobus monkeys; and (3) anthropoid apes (figure 20.24). In addition to their geographic separation, Old World monkeys differ from New World monkeys in lacking a grasping tail while having close-set nostrils, better opposable, grasping thumbs, and more advanced teeth. Apes first appear in 25-million-year-old fossils. At this time woodland savannas were arising in Africa, Europe, and North America. Perhaps motivated by the greater abundance of food on the ground, these apes left the trees and became largely terrestrial. Because of the benefits of standing upright (better view of predators, freeing of hands for using tools, defense, caring for young, and gathering food), emerging hominids gradually evolved upright posture.

Evidence of the earliest hominids of this period is sparse. Not until about 4.4-million years ago, after a lengthy fossil gap, do the first “near humans” appear in the fossil record. One was *Australopithecus afarensis*, a short, bipedal hominid with a face and brain size resembling those of a chimpanzee. Numerous fossils of this species have now been unearthed, the most celebrated of which was the 40% complete skeleton of a female discovered in 1974 by Donald Johanson and named “Lucy” (figures 20.25 and 20.26).

Since the discovery of Lucy new finds of even older hominid fossils have extended our knowledge of human ancestry. In 1994 the sands of Ethiopia yielded teeth and bone fragments of the most ancient hominid yet discovered, *Ardipithecus ramidus*, dated at 4.4 million years old. *Ardipithecus ramidus*, a mosaic of primitive apelike and derived hominid traits, appears



figure 20.25

Lucy (*Australopithecus afarensis*), the most nearly complete skeleton of an early hominid ever found. Lucy is dated at 2.9 million years old. A nearly complete skull of *A. afarensis* was discovered in 1994.

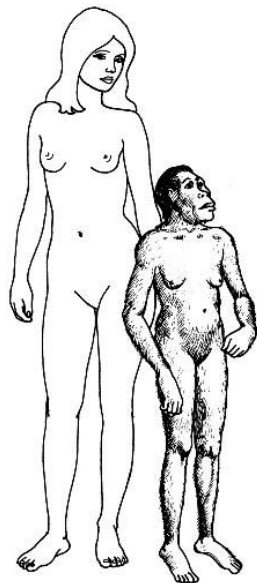


figure 20.26

A reconstruction of the appearance of Lucy (right) compared with a modern human (left).

to be ancestral to the australopithecine species. In 1995 *Australopithecus anamensis* was discovered in the Rift Valley of Kenya. Many researchers agree that this species, which may have been bipedal, is an intermediate between *A. ramidus* and *A. afarensis* (Lucy). *Ardipithecus anamensis* lived between 4.2 and 3.9 million years ago.

Between 3 and 4 million years ago two quite separate hominid lines emerged that coexisted for at least 2 million years. One lineage was *Homo*, our own genus. The other was a bipedal australopithecine lineage. *Australopithecus africanus*, which lived between 2.8 and 2.3 million years ago, had a more

humanlike face than *A. afarensis* and a brain size about one-third as large as that of modern humans. A different line of large and robust australopithecines included *Paranthropus robustus* (figure 20.27), which probably approached the size of a gorilla. The “robust” australopithecines were heavy jawed with skull crests and large back molars, perhaps for eating roots and tubers. They are a side branch in hominid evolution and not part of our own lineage. In 1998 *Australopithecus garhi*, dated at 2.5 million years old, was discovered in Ethiopia. This most recent fossil appears to be a descendant of *A. afarensis* and thus a possible candidate for an ancestor for *Homo*. Although researchers are deeply divided over who the first members of *Homo* were, and indeed how to define the genus *Homo*, it is generally agreed that at least three species of *Homo* shared the African landscape with australopithecines. One of these was *Homo habilis* (figure 20.27), a fully erect hominid, more lightly built and larger brained than the australopithecines. *Homo habilis* unquestionably used stone and bone tools. This species appeared about 2 million years ago and survived for perhaps 500,000 years.

About 1.5 million years ago *Homo erectus* appeared, a large hominid standing 150 to 170 cm (5 to 5.5 feet) tall, with a low but distinct forehead and strong brow ridges. The brain capacity was around 1000 cc, intermediate between the brain capacity of *Homo habilis* and modern humans (figure 20.27). *Homo erectus* was a social species living in tribes of 20 to 50 individuals. *Homo erectus* had a successful and complex culture and became widespread throughout the tropical and temperate Old World.

After the disappearance of *Homo erectus* about 300,000 years ago, subsequent human evolution and establishment of *Homo sapiens* (“wise man”) threaded a complex course. From among the many early subcultures of *Homo sapiens*, Neanderthals emerged about 130,000 years ago. With a brain capacity well within the range of modern humans, Neanderthals were proficient hunters and tool users. They dominated the Old World in the late Pleistocene epoch. About 30,000 years

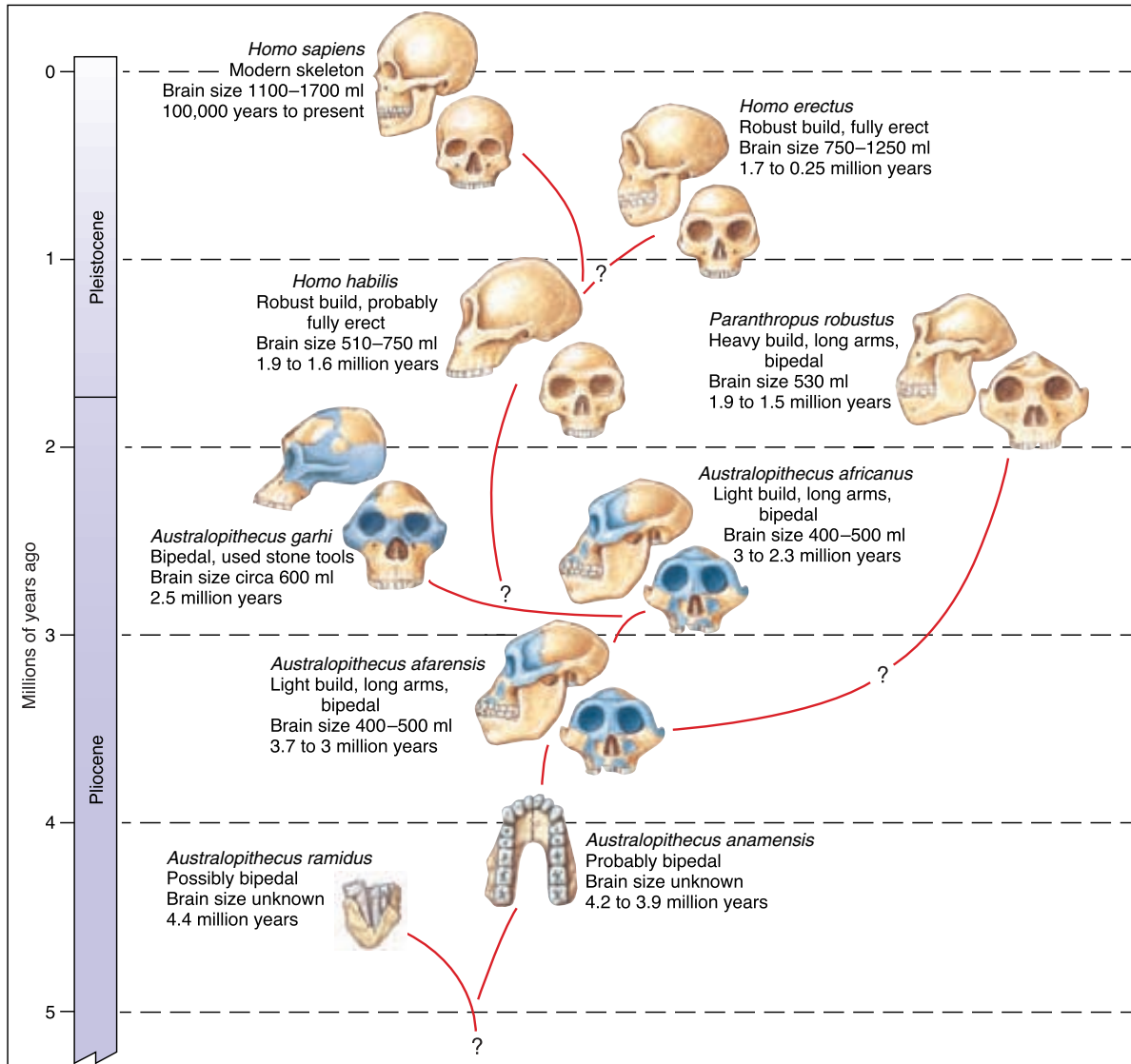


figure 20.27

Hominid skulls, showing several of the best-known hominid lines preceding modern humans (*Homo sapiens*).

ago the Neanderthals were replaced and quite possibly exterminated by modern humans, tall people with a culture very different from that of Neanderthals. Implement crafting developed rapidly, and human culture became enriched with aesthetics, artistry, and sophisticated language.

Biologically, *Homo sapiens* is a product of the same processes that have directed the evolution of every organism from the time of life's origin. Mutation, isolation, genetic drift, and natural selection have operated for us as they have for other animals. Yet we have what no other animal has, a non-

genetic cultural evolution that provides a constant feedback between past and future experience. Our symbolic languages, capacities for conceptual thought, knowledge of our history, and abilities to manipulate our environment emerge from this nongenetic cultural endowment. Finally, we owe much of our cultural and intellectual achievements to our arboreal ancestry which bequeathed us with binocular vision, superb visuotactile discrimination, and manipulative skills in use of our hands. If horses (with one toe instead of five fingers) had human mental capacity, could they have accomplished what humans have?

classification of living mammalian orders¹

All modern mammals are placed in two subclasses, Prototheria, containing the monotremes, and Theria, containing marsupials and placentals. Of the 19 recognized placental orders, seven of the small orders are omitted from this classification.

Class Mammalia

Subclass Prototheria (pro´to-thir´ee-a) (Gr. *prōtos*, first, + *thēr*; wild animal). Cretaceous and early Cenozoic mammals. Extinct except for egg-laying monotremes.

Infraclass Ornithodelphia (or´ni-tho-del´fee-a) (Gr. *ornis*, bird, + *delphys*, womb). Monotreme mammals.

Order Monotremata (mon´o-tre´ma-tah) (Gr. *monos*, single, + *trēma*, hole): **egg-laying (oviparous) mammals: duck-billed platypus, spiny anteater.** Three species in this order from Australia, Tasmania, and New Guinea; most noted member of order is the duck-billed platypus (*Ornithorhynchus anatinus*); spiny anteater, or echidna (*Tachyglossus*), has a long, narrow snout adapted for feeding on ants, its chief food.

Subclass Theria (thir´ee-a) (Gr. *thēr*; wild animal). Marsupial and placental mammals.

Infraclass Metatheria (met´a-thir´e-a) (Gr. *meta*, after, + *thēr*; wild animal). Marsupial mammals.

Order Marsupialia (mar-su´pe-ay´le-a) (Gr. *marsypion*, little pouch): **viviparous pouched mammals: opossums, kangaroos, koalas, Tasmanian wolves, wombats, bandicoots, numbats, and others.** Mammals characterized by an abdominal pouch, **marsupium**, in which they rear their young; young nourished via a yolk-sac placenta; mostly Australian with representatives in the Americas; 260 species.

Infraclass Eutheria (yu-thir´e-a) (Gr. *eu*, true, + *thēr*; wild animal). Viviparous placental mammals.

Order Insectivora (in-sec-tiv´o-ra) (L. *insectum*, an insect, + *vorare*, to devour): **insect-eating mammals: shrews** (figure 20.28), **hedgehogs, tenrecs, moles.** Small, sharp-snouted animals with primitive characters that feed principally on insects; 419 species.

Order Chiroptera (ky-rop´ter-a) (Gr. *cheir*; hand, + *pteron*, wing): **bats.** Flying mammals with forelimbs modified into wings; use of echolocation by most bats; most nocturnal; second largest

mammalian order, exceeded in species numbers only by order Rodentia; 925 species.

Order Primates (pry-may´teez) (L. *prima*, first): **prosimians, monkeys, apes, humans.** First in the animal kingdom in brain development with especially large cerebral hemispheres; mostly arboreal, apparently derived from insectivores with retention of many primitive characteristics; five digits (usually provided with flat nails) on both forelimbs and hindlimbs; group singularly lacking in claws, scales, horns, and hooves; two suborders; 233 species.

Suborder Strepsirhini (strep´suh-ry-nee) (Gr. *strepsō*, to turn, twist, + *rhinos*, nose): **lemurs, aye-ayes, lorises, pottos, bush babies.** Seven families of arboreal primates, formerly called prosimians, concentrated on Madagascar, but with species in Africa, Southeast Asia, and Malay peninsula. With comma-shaped nostrils, long nonprehensile tail, and second toe provided with a claw; 47 species.

Suborder Haplorhini (hap´lo-ry-nee) (Gr. *haploos*, single, simple + *rhinos*, nose): **tarsiers, marmosets, New and Old World monkeys, gibbons, gorilla, chimpanzees, orangutans, humans.** Six families, four of which were formerly called Anthropoidea. Haplorhine primates have dry, hairy noses, ringed nostrils, and differences in uterine anatomy, placental development, and skull morphology that distinguish them from strepsirhine primates; 186 species.



figure 20.28

Shorttail shrew, *Blarina brevicauda*, eating a grasshopper. This tiny but fierce mammal, with a prodigious appetite for insects, mice, snails, and worms, spends most of its time underground and so is seldom seen by humans. Shrews are believed to resemble the insectivorous ancestors of placental mammals. Order Insectivora, family Soricidae.

¹Based on Nowak, R.M. 1991. Walker's Mammals of the world, ed. 5. Baltimore, The Johns Hopkins University Press.

Order Xenarthra (ze-nar´thra) (Gr. *xenos*, intrusive, + *arthron*, joint) (formerly Edentata [L. *edentatus*, toothless]): **anteaters, armadillos, sloths**. Either toothless (anteaters) or with simple peglike teeth (sloths and armadillos); restricted to South and Central America with the nine-banded armadillo in the southern United States; 29 species.

Order Lagomorpha (lag´o-mor´fa) (Gr. *lagos*, hare; + *morphē*, form): **rabbits, hares, pikas** (figure 20.29). Dentition resembling that of rodents but with four upper incisors rather than two as in rodents; 80 species.

Order Rodentia (ro-den´che-a) (L. *rodere*, to gnaw): **gnawing mammals: squirrels** (figure 20.30), **rats, woodchucks**. Most numerous of all mammals both in numbers and species; dentition with two upper and two lower chisel-like incisors that grow continually and are adapted for gnawing; 1935 species.

Order Cetacea (see-tay´she-a) (L. *cetus*, whale): **whales** (figure 20.31), dolphins, porpoises. Anterior limbs of cetaceans modified into broad flippers; posterior limbs absent; nostrils represented by a single or double blowhole on top of the head; teeth, when present, all alike and lacking enamel; hair limited to a few hairs on muzzle, no skin glands except mammary and those of eye; no external ear; 78 species.



figure 20.29

A pika, *Ochotona princeps*, atop a rockslide in Alaska. This little rat-sized mammal does not hibernate but prepares for winter by storing dried grasses beneath boulders. Order Lagomorpha.



figure 20.30

Eastern gray squirrel, *Sciurus carolinensis*. This common resident of Eastern towns and hardwood forests serves as an important reforestation agent by planting numerous nuts that sprout into trees. Order Rodentia, family Sciuridae.



figure 20.31

Humpback whale, *Megaptera novaeangliae*, breaching. Among the most acrobatic of whales, humpbacks appear to breach to stun fish schools or to communicate information to other herd members. Order Cetacea, family Balaenopteridae.



figure 20.32

Grizzly bear, *Ursus horribilis*, of Alaska. Grizzlies, once common in the lower 48 states, are now confined largely to northern wilderness areas. Order Carnivora, family Ursidae.

Order Carnivora (car-niv´o-ra) (L. *caro*, flesh, + *vorare*, to devour): **flesh-eating mammals: dogs, wolves, cats, bears** (figure 20.32), **weasels, seals, sea lions, walruses**. All with predatory habits (except giant pandas); teeth

especially adapted for tearing flesh; in most, canines used for killing prey; worldwide except in Australian and Antarctic regions; 280 species.

Order Proboscidea (pro´ba-sid´e-a) (Gr. *proboskis*, elephant’s trunk, from *pro*, before, + *boskein*, to feed): **proboscis mammals: elephants**. Living land animals, have two upper incisors elongated as tusks, and molar teeth are well developed; two extant species: Indian elephant, with relatively small ears, and African elephant, with large ears.

Order Perissodactyla (pe-ris´so-dak´ti-la) (Gr. *perissos*, odd, + *dactylos*, toe): **odd-toed hoofed mammals: horses, asses, zebras, tapirs, rhinoceroses**. Mammals with an odd number (one or three) of toes and with well-developed hooves (figure 20.33); all herbivorous; both Perissodactyla and Artiodactyla often called ungulates, or hoofed mammals, with teeth adapted for chewing; 18 species.

Order Artiodactyla (ar´te-o-dak´ti-la) (Gr. *artios*, even, + *daktylos*, toe): **even-toed hoofed mammals: swine, camels, deer and their allies, hippopotamuses, antelopes, cattle, sheep, goats**. Each toe sheathed in a cornified hoof; most have two toes, although hippopotamuses and some others have four (figure 20.33); many, such as cattle, deer, and sheep, with horns or antlers; many are ruminants, that is, herbivores with partitioned stomachs; 217 species.

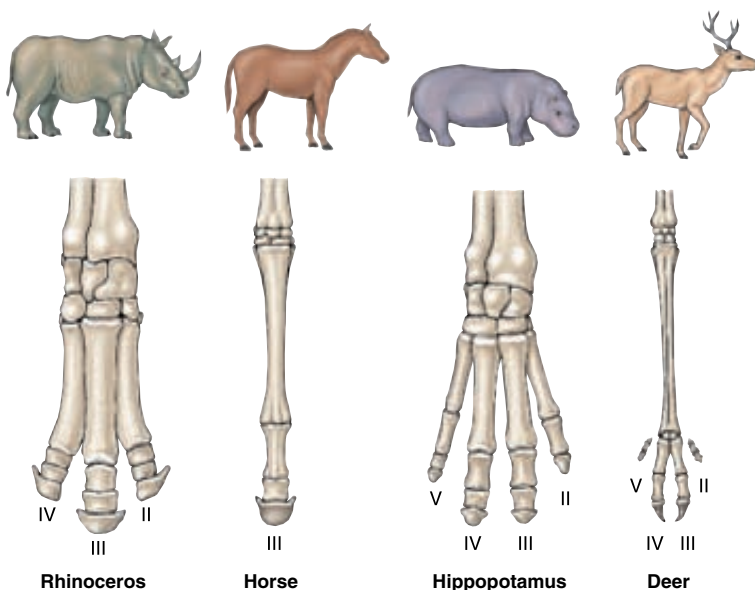


figure 20.33

Odd-toed and even-toed ungulates. Rhinoceroses and horses (order Perissodactyla) are odd-toed; hippopotamuses and deer (order Artiodactyla) are even-toed. Lighter, faster mammals run on only one or two toes.

summary

Mammals are endothermic and homeothermic vertebrates whose bodies are insulated by hair and who nurse their young with milk. The approximately 4600 species of mammals are descended from the synapsid lineage of amniotes that arose during the Carboniferous period of the Paleozoic era. Their evolution can be traced from pelycosaurs of the Permian period to therapsids of the late Permian and Triassic periods of the Mesozoic era. One group of therapsids, the cynodonts, gave rise during the Triassic to therians, the true mammals. Mammalian evolution was accompanied by the appearance of many important derived characteristics, among these enlarged brain with greater sensory integration, high metabolic rate, endothermy, and many changes in the skeleton that supported a more active life. Mammals diversified rapidly during the Tertiary period of the Cenozoic era.

Mammals are named for the glandular milk-secreting organs of females (rudimentary in males), a unique adaptation which, combined with prolonged parental care, buffers infants from demands of foraging for themselves and eases the transition to adulthood. Hair, the integumentary outgrowth that covers most mammals, serves variously for mechanical protection, thermal insulation, protective coloration, and waterproofing. Mammalian skin is rich in glands: sweat glands that function in evaporative cooling, scent glands used in social interactions, and sebaceous glands that secrete lubricating skin oil. All placental mammals have deciduous teeth that are replaced by permanent

teeth (diphyodont dentition). Four groups of teeth—incisors, canines, premolars, and molars—may be highly modified in different mammals for specialized feeding tasks, or they may be absent.

Food habits of mammals strongly influence their body form and physiology. Insectivores feed mainly on insects and other small invertebrates. Herbivorous mammals have special adaptations for harboring intestinal bacteria that break down cellulose of plant materials, and they have developed adaptations for detecting and escaping predators. Carnivorous mammals feed mainly on herbivores, have a simple digestive tract, and have developed adaptations for a predatory life. Omnivores feed on both plant and animal foods.

Some marine, terrestrial, and aerial mammals migrate; some migrations, such as those of fur seals and caribou, are extensive. Migrations are usually made toward favorable climatic and optimal food and calving conditions, or to bring the sexes together for mating.

Mammals with true flight, the bats, are mainly nocturnal and thus avoid direct competition with birds. Most employ ultrasonic echolocation to navigate and feed in darkness.

Living mammals with the most primitive characters are egg-laying monotremes of the Australian region. After hatching, young are nourished with their mother's milk. All other mammals are viviparous. Embryos of marsupials have brief gestation periods, are born underdeveloped, and complete their early growth in the mother's pouch, nourished

by milk. The remaining mammals are eutherians, mammals that develop an advanced placental attachment between mother and embryos through which embryos are nourished for a prolonged period.

Mammal populations fluctuate from both density-dependent and density-independent causes and some mammals, particularly rodents, may experience extreme cycles of abundance in population density. The unqualified success of mammals as a group cannot be attributed to greater organ system perfection, but rather to their impressive overall adaptability—the capacity to fit more perfectly in total organization to environmental conditions and thus exploit virtually every habitat on earth.

Darwinian evolutionary principles give us great insight into our own origins. Humans are primates, a mammalian group that descended from a shrewlike ancestor. The common ancestor of all modern primates was arboreal and had grasping fingers and forward-facing eyes capable of binocular vision. Primates radiated over the last 80 million years to form two major lines of descent: prosimians (lemurs, lorises, and tarsiers) and simians (monkeys, apes, and hominids).

Earliest hominids appeared about 4.4 million years ago; these were the australopithecines. These gave rise to, and coexisted with, *Homo habilis*, the first user of stone tools. *Homo erectus* appeared about 1.5 million years ago and was eventually replaced by *Homo sapiens* about 300,000 years ago.

review questions

1. Describe the evolution of mammals, tracing their synapsid lineage from early amniote ancestors to true mammals. How would you distinguish the skull of a synapsid from that of diapsid?
2. Describe structural and functional adaptations that appeared in early amniotes that foreshadowed the mammalian body plan. Which mammalian attributes do you think were especially important to successful radiation of mammals?
3. Hair is believed to have evolved in therapsids as an adaptation for insulation, but modern mammals have adapted hair for several other purposes. Describe these.
4. What is distinctive about each of the following: horns of ruminants, antlers of the deer, and horns of rhinos? Describe the growth cycle of antlers. What is velvet? Why is it called velvet?
5. Describe the location and principal function(s) of each of the following skin glands: sweat glands (eccrine and apocrine), scent glands, sebaceous glands, and mammary glands.
6. Define the terms “diphyodont” and “heterodont” and explain how both terms apply to mammalian dentition.
7. Describe the food habits of each of the following groups: insectivores, herbivores, carnivores, and omnivores. Give the common names of some mammals belonging to each group.
8. Most herbivorous mammals depend on cellulose as their main energy source, yet no mammal synthesizes cellulose-splitting enzymes. How are the digestive tracts of mammals specialized for symbiotic digestion of cellulose?
9. Describe the annual migrations of barren-ground caribou and fur seals.
10. Explain what is distinctive about the life habit and mode of navigation in bats.

- Describe and distinguish patterns of reproduction in monotremes, marsupials, and placental mammals. What aspects of mammalian reproduction are present in *all* mammals but in no other vertebrates?
- What is the difference between density-dependent and density-independent causes of fluctuations in size of mammalian populations?
- Describe the hare-lynx population cycle, considered a classic example of a prey-predator relationship (figure 20.21). From your examination of the cycle, formulate a hypothesis to explain the oscillations.
- What anatomical characteristics set primates apart from other mammals?
- What role does the fossil named “Lucy” play in reconstruction of human evolutionary history?
- In what ways do the genera *Australopithecus* and *Homo*, which coexisted for at least 2 million years, differ?
- When did the different species of *Homo* appear and how did they differ socially?
- What major attributes make the human position in animal evolution unique?

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See also general references on page 406.

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