CHAPTER

27

Mammalian Domestication

CHAPTER OUTLINE

History of Domestication

Animal and plant **domestication** allowed a cultural shift from small groups of nomadic hunter-gatherers to larger, more sedentary agrarian societies. In doing so, it played a critical role in the development of human civilization. Mammals in particular played an important and early role by providing a more reliable food source, along with clothing, transportation, protection, and perhaps companionship.

Domestication did not occur overnight, and each species likely had a unique economic application at first. For example, early domesticated dogs probably were used to help hunt game animals and to warn villagers of danger. Likewise, sheep, goats, cattle, and horses were all important sources of meat in the early stages of domestication. Only later did they provide additional economic benefits in the form of milk and wool production or as beasts of burden. Horses in particular played an important role in transportation and warfare. They were harnessed to chariots, yoked to carts for hauling people and trade goods, and eventually saddled and ridden over vast areas.

Domestication is generally a slow process whereby individuals from wild populations are bred for specific traits that are useful to humans. Such **selective breeding** over many generations alters the behavior, morphology, physiology, and/or reproduction of the animals. In some cases, the degree of domestication is subtle. Llamas (*Lama glama*) are raised commercially for wool. Water buffalo (*Bubalus bubalis*) are used to plow rice paddies and pull carts, and pandas (*Ailuropoda melanoleuca*) are bred by zoos. Despite captivity and some selective breeding, these species remain essentially indistinguishable from their wild counterparts. In contrast, the variation between domestic breeds of dogs and cattle far exceeds the variation observed in nature for the ancestral wild species. Over 800 breeds of cattle exist in the world today, and all are descended from aurochs, *Bos primigenius* (Fries & Ruvinsky 1999; **Fig. 27-1**).

Relatively few mammal species have been successfully domesticated, but those that have been played a significant role in shaping human culture (**Fig. 27-2**). Domestication requires species with adaptable diets, the ability to breed in captivity, and a predictable or even temperament. Additionally, social species tend to be easier to domesticate because they are better able to shift their social structure to include humans as dominant individuals (Diamond 1999). Not surprisingly, among the first animals to be domesticated were such herding animals as cattle, horses, sheep, and goats.

Today, humans not only have the ability to breed animals selectively for desirable traits, they can now genetically modify the animals' DNA. Using a suite of techniques collectively called **recombinant DNA technologies**, humans can alter the animal's **genome**. Genes can be deleted, or novel genes from other species can be added to create **transgenic organisms**. For example, in 2004, researchers inserted a gene from a nematode worm into pigs (Lai et al. 2004). The gene codes for an enzyme lacking in the pig genome that allows the transgenic pigs to transform the unhealthy omega-6 fatty acids they normal produce into healthy omega-3 fatty acids (similar to those found in fish oils). The goal was to produce pork products with a healthier fat content. Such genetic modification blurs the lines between species and creates ethical and ecological dilemmas for scientists and citizens alike.

Domesticated Mammals

Carnivora

Dogs

There is no consensus as to exactly when and how many times dogs were domesticated. What is clear is that domesticated dogs (*Canis lupus familiaris*), descended from wolves (*Canis lupus*), are the earliest domesticated mammals (Miklosi 2007; Serpell 1995; Vila et al. 1997; Wang & Tedford 2008).

Archaeological evidence, including co-burial of humans and dogs, and molecular studies of mitochondrial DNA from wolves and domestic dogs yield very different results. Until recently, the oldest archaeological evidence for

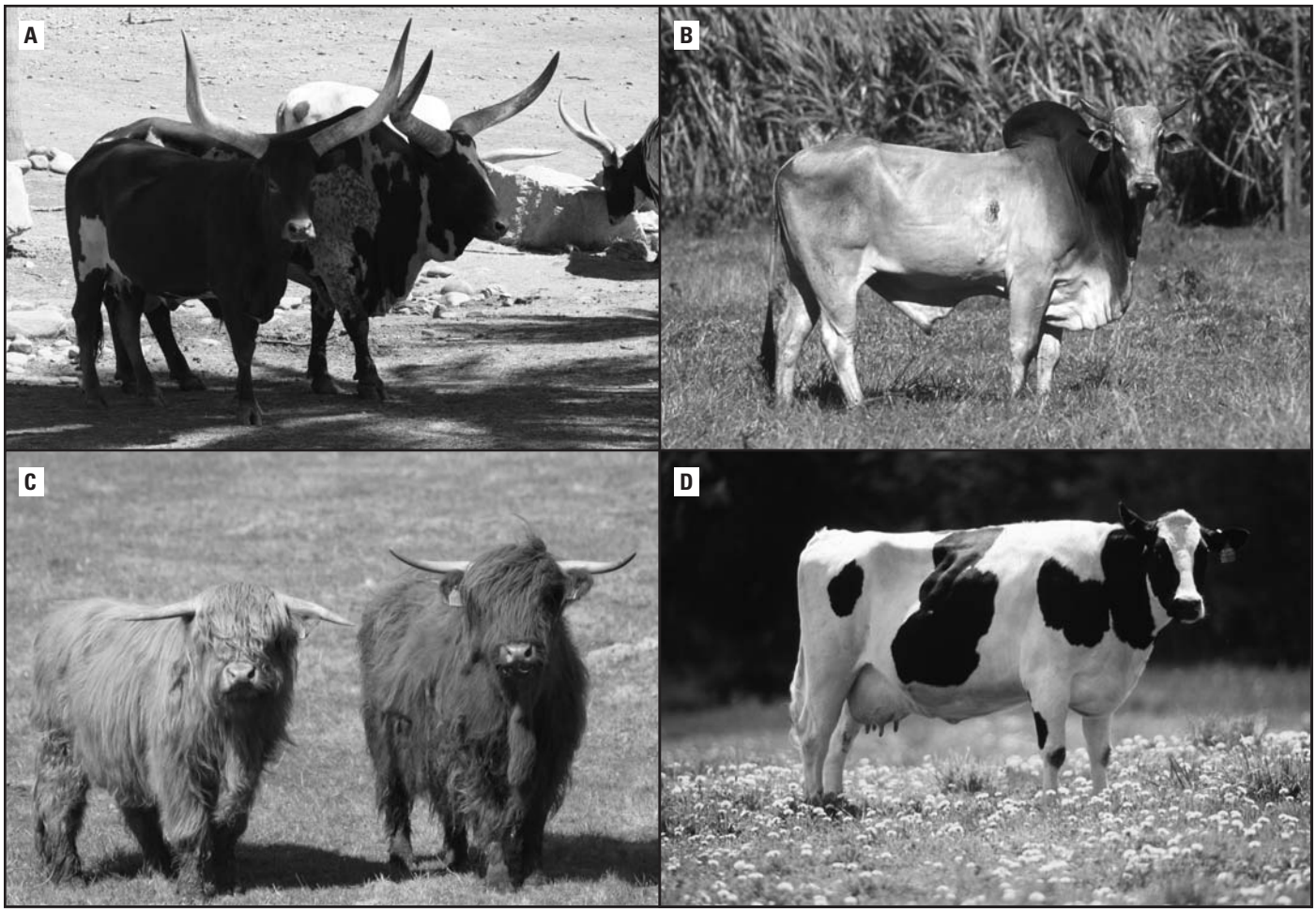

FIGURE 27-1 Phenotypic variation in domestic cattle breeds. (A) Ankole or Watusi cattle are an East African breed. They are used as currency, provide status, and are bred for massive horn size. (B) Humped cattle (zebuine cattle) are considered sacred animals by Hindus in India. (C) Highland cattle from Scotland have long, shaggy fur that provides insulation from cold. (D) Holstein cattle are a common dairy breed originally from the Netherlands. One Holstein cow is capable of producing over 8,000 liters of milk per year.

domestic dogs was two 13,000- to 17,000-year-old skulls from Eliseevichi I, a central Russian site including several mammoth-bone dwellings and carved figurines. These skulls have shorter and broader snouts than wolves and resemble a larger version of modern Siberian huskies (Sablin & Khlopachev 2002). More recently, Germonpré et al. (2009) reanalyzed a number of large canids from Upper Paleolithic sites in Belgium, Ukraine, and Russia. Using reference samples from 48 wolves and 53 modern dogs from 11 breeds, the researchers compared the cranial and dental characters from the canid skulls found at human Paleolithic sites with the reference skulls. Statistical analysis yielded six clusters, with canid skulls from Goyet cave in Belgium and two sites in Ukraine clearly separate from wolves; they are now classified as prehistoric dogs. Remarkably, radiocarbon dating placed the prehistoric dog skull from Goyet cave at approximately 31,700 years before the present.

DNA studies, however, place the divergence of dogs and wolves at either 100,000 to 140,000 years ago (Vilà et al. 1997) or between 15,000 and 40,000 years ago (Savolainen at al. 2002). These much older divergence dates have been criticized on a number of grounds. Nevertheless, genetic analyses (including ancient DNA from European canids living during the Last Glacial Maximum) do support multiple origins of dogs from wolves, probably in western Eurasia (Savolainen et al. 2002; Verginelli et al. 2005). Subsequently, prehistoric dogs spread rapidly throughout Europe, Africa, and Asia in the company of humans.

Ancient DNA from dog remains found in Alaska, Mexico, and South America suggest that New World dogs are derived from Old World gray wolves (Leonard et al. 2002). Thus, humans who crossed the Bering land bridge some 12,000 to 14,000 years ago brought dogs with them as they populated the New World (Leonard et al. 2002). A much more recent migration event brought dingoes (*Canis lupus dingo*) to Australia. Mitochondrial DNA evidence strongly suggests that Australian dingoes are derived from East Asian dogs brought to Australia during the expansion

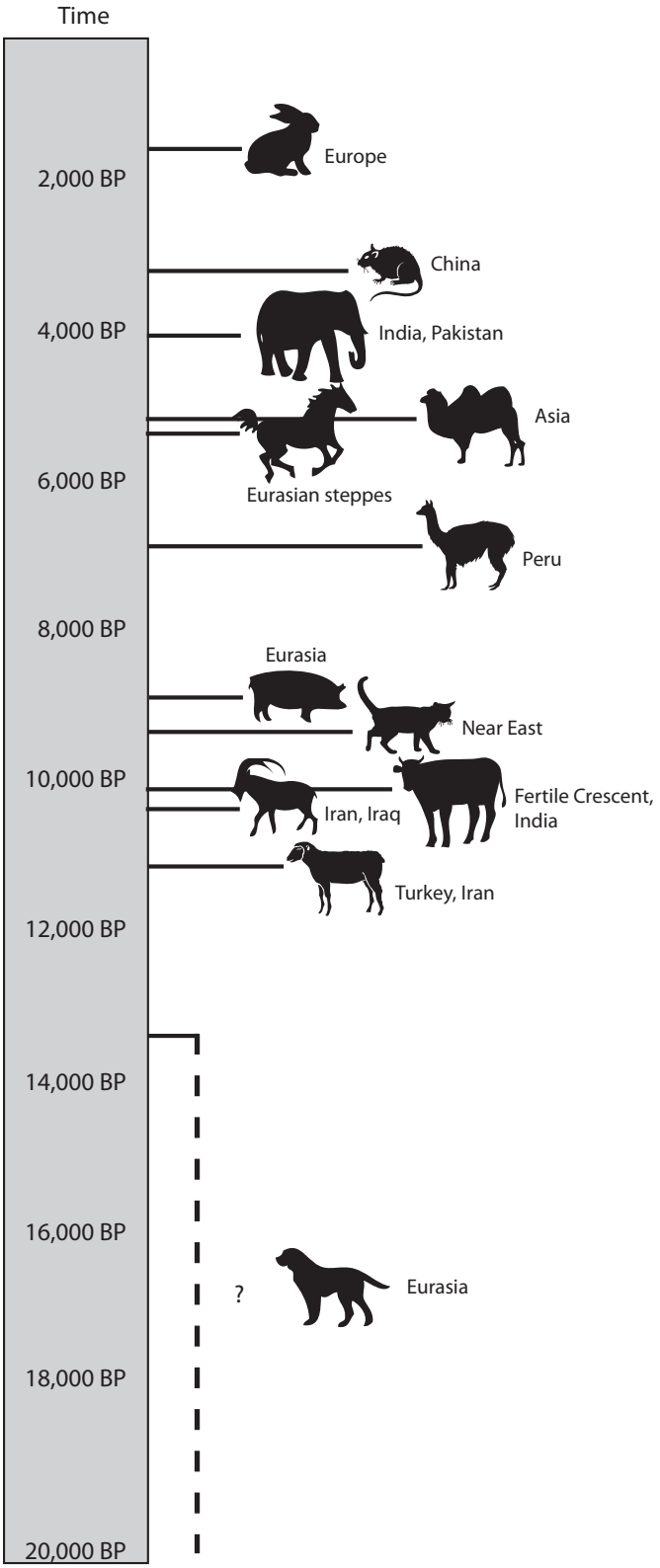

FIGURE 27-2 A time scale of mammalian domestication. Dog domestication is believed to have begun between 17,000 and 13,000 years before the present, but evidence from Goyet cave in Belgium suggests a much older origin (approximately 31,000 years ago). Several artiodactyls and cats were domesticated within a short period concomitant with domestication of cereal grains in the Middle East between 9,000 and 11,000 bp.

of Austronesian peoples approximately 5,000 years ago (Savolainen et al. 2004).

Although the timing and location of dog domestication are becoming clearer, the reasons for canid domestication remain murky and controversial. It is often assumed that humans intentionally domesticated dogs, but Morey (1994) argued that it may have been accidental. Paleolithic hunter-gatherers may have occasionally adopted wolf pups, and those that became submissive to humans were incorporated into the band as it moved in search of food. Unintentional selection for submissive behavior and a more omnivorous diet may have led to smaller body size and shorter, broader rostrums seen in early domestic dogs. As pointed out by Wang and Tedford (2008), canids were ideal candidates for domestication. They were "not too large and thus can be dominated by humans, and they are **mesocarnivorous** enough to be able to handle a variety of foods." In addition, their "submissive attitude toward humans probably also facilitated the training for other functions once dogs fully integrated themselves into human societies." Today, the American Kennel Club recognizes 157 breeds with another 58 breeds considered potential future breeds (**Fig. 27-3**).

Cats

Like their wild ancestors, domestic cats are territorial, generally solitary, **hypercarnivorous**, and lack social hierarchies. Not surprisingly, modern cats are not strictly speaking fully domesticated; they retain their hunting instincts and their independence (Clutton-Brock 1999; Lipinski et al. 2007). Nevertheless, there are more than 82 million pet cats in the United States and an estimated 600 million domestic cats worldwide, making cats the most popular pet by a wide margin (AVMA 2007; Driscoll et al. 2009). How and when did cats begin their relationship with humans?

Recent DNA studies indicate that the modern felid radiation began 12 million years ago in South East Asia (Johnson et al. 2006). From their Miocene origins, eight major lineages of cats evolved. The *Panthera* lineage was first to emerge from a presumed *Pseudaelurus*-like ancestor in Asia (**Fig. 27-4**). This lineage gave rise to the large cats (lions, tigers, leopards, jaguars, and snow leopards). Approximately 1 million years later, a second Asian lineage split off forming the Southeast Asian bay cat lineage. During the Miocene, at a time when sea levels were considerably lower than they are today, one population of ancestral cats probably spread west to Africa across a land bridge between Africa and Arabia, and in Africa formed the caracal lineage. At roughly the same time, another group probably spread throughout Asia and into North America across the Bering land bridge to form the lynx, ocelot, and puma lineages in the New World. Ancestral lynx and puma species would later migrate back across the Bering land bridge to Asia approximately 6 to 7

million years ago and split again to form the leopard cat and domestic cat lineages (Johnson et al. 2006).

Three million years ago in Asia, several species of small cats in the genus *Felis* evolved, including the jungle cat, black-footed cat, desert cat, sand cat, and the wildcat (*Felis silvestris*). Of these, only *F. silvestris* was widely distributed across Europe, the Middle East, and Asia. In 2007, Driscoll et al. analyzed mitochondrial DNA from 979 cats from three continents, including wildcats, feral cats, sand cats, Chinese desert cats, and domestic cats. Their analysis revealed that domestic cats arose from a minimum of five female ancestors of Near Eastern wildcats (*Felis silvestris lybica*) in the Middle East. Their results also preclude European wildcats, southern African wildcats, and Asian wildcats as possible ancestors of modern domestic cats. However, mitochondrial DNA could not be used to estimate the timing of the split between Near Eastern wildcats and domestic cats.

Cat remains have been found in association with humans at several Neolithic sites. Ten-thousand-year-old cat figurines of stone and clay from Turkey, Syria, and Israel indicate that cats were important to these early cultures and suggest that domestication may have begun at that time; however, the oldest direct evidence of cats in association with human remains dates to 9,500 years ago in Cyprus (Vigne et al. 2004). More recent archaeological evidence of cat–human cohabitation exists at sites in Israel (9,000

FIGURE 27-3 Domestic dogs exhibit remarkable variation in size, pelage, and facial features. (A) Gray wolves are the ancestors of all domestic dog breeds. (B) An Afghan hound is a large, graceful breed with long, silky hair and a long snout. (C) Bloodhounds have floppy ears and loose skin and are bred for their ability to track the scent of humans. (D) Pugs are a "toy" breed with an extremely short rostrum.

years ago), Pakistan (4,000 years ago), and Egypt (3,600 years ago) and in Europe and China roughly 2,000 years ago (Driscoll et al. 2009).

The archaeological site in Cyprus includes the remains of an 8-month-old cat buried intact with those of an adult human. The island of Cyprus is an unusual place for such a find because wild cats never lived on Cyprus. This suggests that cats were brought to the island by humans perhaps to control mice, which also appear at these sites at the same time.

The house mouse (*Mus musculus*), a native of Asia, spread to the Middle East and eastern Mediterranean region about 14,000 years ago (Auffrey et al. 1990; Cucchi et al. 2005). At the same time, Neolithic peoples were beginning to domesticate cereal crops in the Fertile Crescent, a region of the Middle East comprising the valleys of the Tigris, Euphrates, and Jordan rivers (Brown et al. 2009). Plant cultivation provided humans with a more reliable food base that could be aggregated and stored. Cereal stores no doubt attracted mice. Near-Eastern wildcats probably were relatively common near human settlements and were probably tolerated because they exerted some control over mouse populations. Eventually, humans tamed wildcats, setting the stage for the appearance of more sociable domestic cats. Because cats were already well adapted to preying on rodents, artificial selection by humans was largely unnecessary. Thus, unlike dogs, cats retained many of the morphological and behavioral traits of their wild ancestors even as they spread along trade routes throughout Europe and Asia. Later, cats traveled on ships to the New World and arrived in Australia with Europeans in 1824 (Abbott 2002).

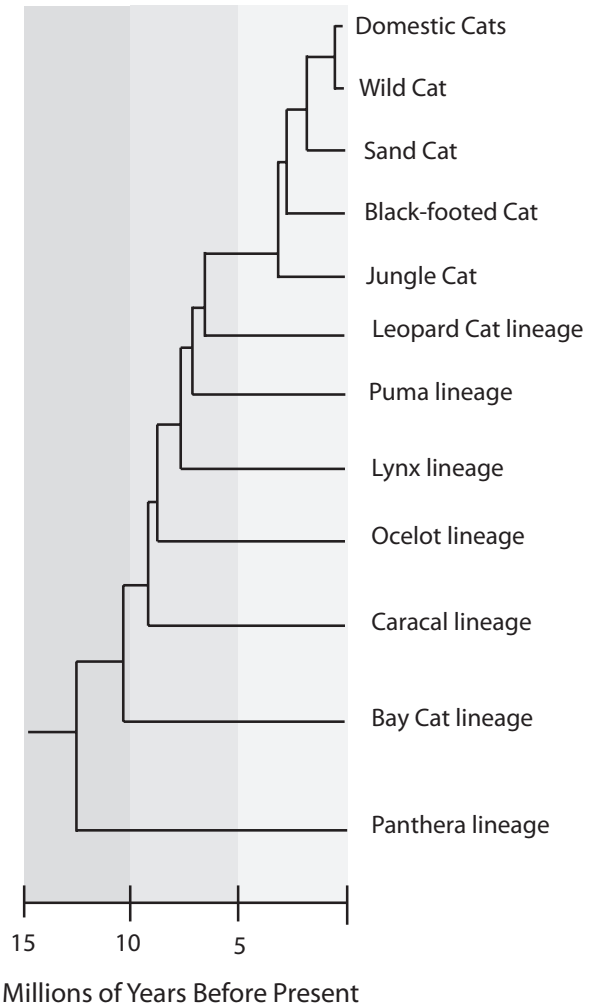

FIGURE 27-4 A phylogenetic history of the major living felid lineages based on the molecular data from O'Brien and Johnson 2005 and 2007.

Artificial selection resulting in over 40 cat breeds did not begin in earnest until the 1800s in Europe and was primarily based on aesthetic choices (Menotti-Raymond et al. 2008). Lipinski et al. (2007) used microsatellite DNA markers to trace the genetic relationships of cats and their presumed geographic origins. DNA from 1,100 cats of 22 breeds and 17 random-bred populations from 5 continents was analyzed. Included among the random-bred samples were feral cats and three subspecies of wildcat (*Felis silvestirs*) from Africa, Europe, and the Middle East. The genetic analyses clustered the breeds that are more closely related together. Their results confirm the Middle Eastern origin of domestic cats and suggest that there are four genetic clusters of domestic cats from Europe, the Mediterranean basin, East Africa, and Asia. North American breeds, which arrived with European colonists relatively recently, clustered with European cat breeds.

Modern domestic cats exhibit much phenotypic variation, but nowhere near the variation seen in dogs. Domestic cats retain the basic body plan of wildcats. As the widespread occurrence of **feral** house cats demonstrates, domestic cats can successfully revert to the wild state. Domestic cats are genetically similar to wildcats (*F. silvestris)* and may form fertile hybrids with these wild species (Oliveira et al. 2008). Today, the endangered European wildcat is restricted to fragmented populations across Europe and the Near East. In some of these isolated populations (e.g., in Portugal and Hungary), the genetic integrity of wildcats is increasingly threatened by interbreeding with feral domestic cats (Lecis et al. 2006).

One unintended consequence of cat domestication is the damage they cause to small mammal and song bird populations, especially in urban and suburban areas. In the United Kingdom, 986 domestic cats were responsible for killing 9,852 small mammals (68%), 3,391 birds (23%), and 730 reptiles and amphibians (5%) in a 5-month period (Woods et al. 2003). A similar pattern of predation occurs in North America, where Lepczyk et al. (2003) reported that each pet cat killed between 0.7 and 1.4 birds per week.

Feral cats are common in exurban areas in many parts of the US; 30 kilometers east of Norman, Oklahoma, a rural landowner trapped 16 cats on his property within three months in 2006. These feral or semi-feral animals likely compete with bobcats and other small wild predators. The presence of domestic cats alters bird nesting and foraging behaviors, and there is growing evidence that these indirect effects may be more important than those of predation alone (Preisser, et al. 2005).

Perissodactyla

Horses

Today there are over 300 breeds of domestic horses (*Equus caballus*) ranging in size from diminutive ponies standing only 1 meter high at the shoulders to massive draft horses such as Percherons and Clydesdales, which can reach shoulder heights over 2 meters. Horses are bred for a variety of purposes; draft horses pull heavy wagons, standardbreds and thoroughbreds for speed, and quarter horses for herding cattle. In 2005, the Food and Agriculture Organization estimated there were over 58 million horses, 40 million donkeys, and 12 million mules worldwide; 9.2 million of those horses reside in the United States (Global Livestock Production and Health Atlas, http://kids.fao.org/glipha/).

Historically, horses were used for food, transportation, and warfare. In many lesser-developed nations, the role donkeys, mules, and horses play in rural economies has changed little over time. Despite their importance in shaping human civilization, we are just beginning to understand the events that lead to the domestication of horses.

Wild horses first appear in Paleolithic cave art around 32,000 years ago (**Fig. 27-5**; Bahn 2007). These paintings depict big-headed horses with thick necks, dun coloration, and stiff manes similar to Przewalski's horse (*Equus caballus przewalskii*). These Ice Age horses were probably hunted for meat. Prehistoric horses, including the ancestor of modern domestic horses and Przewalski's horse, probably all belonged to a single species (*E. caballus*) that ranged widely across Europe, Asia, and North America (Weinstock et al. 2005). Mitochondrial DNA analyzed from modern and fossil horses (dating back to 53,000 years ago) reveal a single common ancestor with two clades (Weinstock et al. 2005). One clade was restricted to North America and became extinct at the end of the Pleistocene. The other group of horses, which was broadly distributed across northern North America, Asia, and Europe, gave rise to Przewalski's horse, the Tarpan (*E. c. ferus*), and the ancestors of domestic horses. The Tarpan became extinct in 1876.

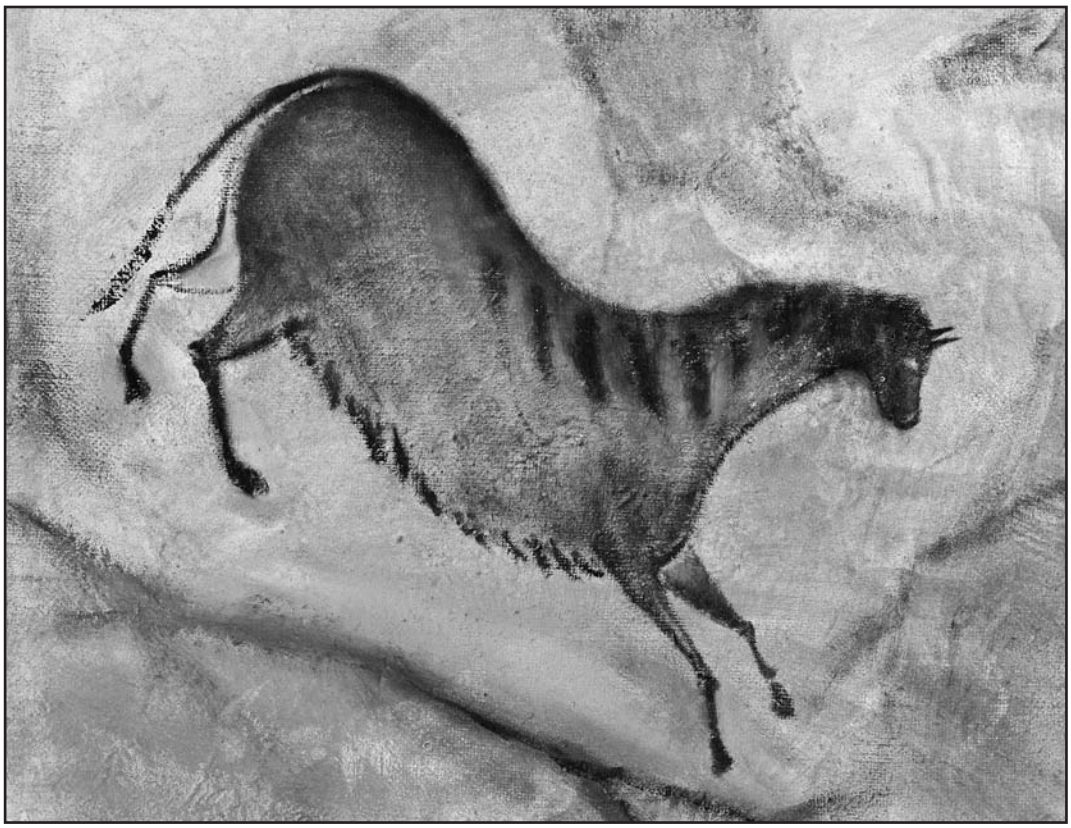

FIGURE 27-5 Drawing of a horse from Lascaux cave in southwestern France. These Paleolithic cave paintings depict the ancestors of modern domestic horses.

Of the wild horses, only Przewalski's horse survives today; it became extinct in the wild in the 1960s (but have been reintroduced to the Mongolian steppes from captive stocks in recent years). Przewalski's horse has two more chromosomes than domestic horses, and mitochondrial DNA data suggest that they are not the ancestors of modern domestic horses (Jansen et al. 2002). The wild subspecies of *Equus* that was the direct ancestor of modern domestic horses did not survive to historic times. The DNA evidence also reveals that horses were domesticated independently several times (Jansen et al. 2002; Lau et al. 2009). Recent sequencing of the complete horse genome will likely improve our understanding of their domestication in the future (Wade et al. 2009).

Horses were probably domesticated at least 5,500 to 5,000 years ago on the Eurasian steppes (Outram et al. 2009). Among the most important archaeological sites are Dereivka in Ukrainie and Botai in Kazakhstan (Brown & Anthony 1998; Outram et al. 2009). The Botai people were hunter–foragers that lived in settlements of 50 to over 100 pit houses (Olsen 2003). Garbage piles associated with these small villages contain thousands of animal bones, the majority of which are from horses. Some archaeologists have suggested that the Botai hunted on horseback, but others maintain that they hunted wild horses on foot. Bits, placed in the horse's mouth and used by a rider to control its mount, can create wear facets on the horse's premolars. Such wear facets occur on the premolars of several horses from Botai. Evidence for horse husbandry at these sites also includes pottery containing traces of horse milk, mats of horse dung, and evidence of corrals (Outram et al. 2009). Thus, the accumulated evidence from these sites strongly suggests that horses were originally domesticated for meat, for riding, and for producing milk.

Other, as yet undiscovered, sites of early horse domestication may exist at other localities, but it is clear that the use of horses for transportation, food, and warfare spread rapidly across Eurasia. Approximately 4,000 years ago horses were used to pull chariots, as evidenced by the co-burial of horses and chariots at several sites in southern Russia and Kazakhstan (Anthony & Vinogradov 1995). Five hundred years later, horse-drawn chariots appear around the eastern Mediterranean and within 1,000 years in China. Eventually, mounted cavalry replaced chariot warfare. No other domesticated animal played such an important role in human warfare. Mounted Hun warriors extended their empire into Europe around 370 ad. Beginning in the 13th century, the Mongol cavalry invaded eastern Europe. In North America, the plains Indian tribes used horses (brought to the Western Hemisphere by Europeans) as mounts when defending their lands from the westward expansion of settlers.

Donkey

The donkey or ass (*Equus asinus asinus*) is a domesticated subspecies of African wild ass (*E. a. africanus*; Grubb 2005). The Asiatic wild ass or onager (*Equus hemionus*) and the kiang (*Equus kiang*) are closely related wild species. Asses were first domesticated between 6,000 and 5,000 years ago in northeastern Africa as pack animals (Beja-Pereira et al. 2004; Rossel et al. 2008). Approximately 1,000 years later, donkeys had reached the Middle East. Donkeys (also called burros) were brought to the western hemisphere by conquistadors in the 1500s. Although smaller than horses, asses can carry loads weighing up to a third of their own body weight (**Fig. 27-6**). The estimated 40 million donkeys alive today continue to serve as "beasts of burden," as well as a source of milk and meat.

Artiodactyla

A number of artiodactyls have been domesticated including cattle, sheep, goats, pigs, camels, and llamas. The Fertile Crescent of the Near East (a region encompassing much of modern-day Israel, Jordan, Lebanon, Syria, southeastern Turkey, Iraq, and southwestern Iran) is the center of artiodactyl domestication, for it was here that cattle, sheep, goats, and pigs were tamed and domesticated along with grains such as wheat, oats, and barley. Domestication of both grains and mammals allowed humans to develop more settled agricultural societies, leading to the formation of the first city-states and the spread of human societies across the globe.

Cattle

Since their domestication by Neolithic peoples, cattle have been bred for milk, meat, hides, transportation, wealth, and sport (e.g., bull fighting and bull riding). Living domestic cattle have no surviving wild ancestors. They share a common ancestor with a species of wild oxen called aurochs (*Bos primigenius*); wild aurochs, depicted in cave paintings, were massive animals, weighing approximately 1,000 kilograms and standing 2 meters at the top of the shoulder (van Vuure 2002). Until a few hundred years ago, wild aurochs roamed Europe, Asia, and North Africa; the last surviving auroch was killed in Poland in 1627 (van Vuure 2005). Genomic data and archaeological evidence indicate that wild aurochs were domesticated approximately 10,000 years ago in the Fertile Crescent (Achilli et al. 2008, 2009; Edwards et al. 2007). The cattle resulting from this domestication event are referred to as taurine cattle (*Bos taurus*). A second center of cattle domestication took place in what is now Pakistan and India, resulting in humped animals called zebuine cattle (*Bos indicus*; Achilli et al. 2008). Mitochondrial genome data also suggest that

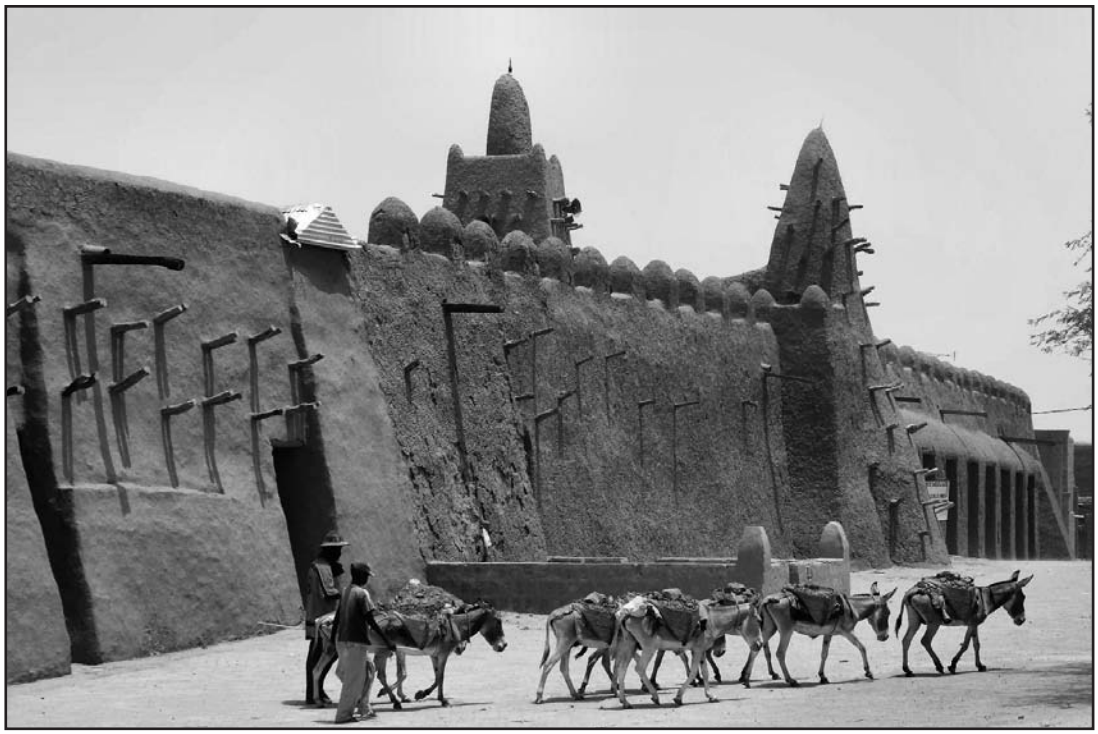

FIGURE 27-6 A group of donkeys (*Equus asinus*) carry rubble from a construction site in Timbuktu, Mali.

European cattle are descended from those originating in the Fertile Crescent, but probably interbred with wild aurochs on a few occasions in the past (Achilli et al. 2008, Edwards et al. 2007).

The origins of African cattle are more enigmatic. They may be descended from taurine cattle brought to northern Africa from the Fertile Crescent, or they may represent a third domestication event from wild North African aurochs populations (Bradley et al. 1996). In any case, genetic studies of 50 African cattle breeds across the African continent reveal that domesticated taurine cattle spread west and south from northern Africa, eventually reaching the African Cape. Later, European taurine cattle and Asian zebuine cattle were brought to the continent where they interbred with African breeds (Hanotte et al. 2002). Tracing the story of African cattle has not been easy. Nevertheless, genetic evidence suggests that zebuine cattle were probably brought to East Africa aboard trading ships from India via Arabia. The spread of zebuine genes through interbreeding with African cattle yielded a number of uniquely African breeds (Fig. 27-1A). The humped cattle of Africa are well adapted to hot, dry conditions. In addition, they carry genes resistant to rinderpest, a cattle disease that devastated African taurine cattle (and many wild ungulates) herds in the late 1800s (Bradley 2003; Hanotte et al. 2002).

Modern cattle have been bred for increased milk production, muscle mass, coat coloration, and in the case of fighting bulls, aggression. Today, most North American and European breeds can trace their ancestry back to the 19th century. Intense artificial selection for economically important traits has resulted in uniformity in breed appearance and genetics. In contrast, African breeds exhibit more genetic and physical variation in part because African cattle are also used as a source of wealth and because "Africans breed their herds without the obsession for uniformity that has emerged in the West" (Bradley 2003).

An interesting side note in the story of cattle breeding took place in the 1920s in Germany. The Heck brothers attempted to recreate aurochs from domestic cattle via a process known as back breeding. Back breeding entails crossing domestic cattle breeds that retain phenotypic traits (and presumably genes) similar to aurochs and selecting in their offspring for those traits over several generations. The resulting "Heck cattle" resemble drawings of wild aurochs (**Fig. 27-7**), but phenotypic similarity does not guarantee genetic or behavioral similarity (van Vuure 2005).

Pigs

Wild boars (*Sus scrofa*), the ancestors of domestic pigs, were hunted across much of Europe and Asia by early humans. Around 9,000 years ago wild boars were independently domesticated at least seven times (Larson et al., 2005). Although archaeological evidence suggests pigs were first domesticated in Turkey and separately in China, the

FIGURE 27-7 Heck cattle were bred in Germany in the 1920s in an attempt to re-create aurochs through a selection process called back-crossing. This male stands 1.6 meters tall at the shoulder.

mitochondrial DNA data point to separate domestication events in Central Europe, Italy, India, Southeast Asia, and the southeastern Asian islands (Larsen et al., 2005). Additional analysis of ancient DNA from pigs and boars in Europe reveals that Neolithic farmers from the Near East brought domestic pigs with them as they spread across Europe (Larsen et al. 2007). By 6,000 years ago, pigs of Near Eastern origin were present in central France. At the same time, European wild boars were also being domesticated in Europe and later completely replaced the pigs of Near Eastern ancestry. Using similar data, Larsen et al. (2007b) traced the dispersal of humans and their pigs in Asia. Contradicting long-held views of human colonization, the pig DNA data suggest that early human colonists from mainland Southeast Asia brought their domestic pigs with them as they traveled between Southeast Asian islands before reaching New Guinea and later landing on Hawaii and French Polynesia; therefore, the so-called wild pigs of New Guinea are most likely feral descendants of domestic pigs introduced by these early colonists.

Sheep and Goats

Domestic sheep (*Ovis aries*) are most likely descended from the wild mouflon (*Ovis aries orientalis*) of Europe and Asia (**Fig. 27-8**). Sheep were domesticated approximately 11,000 years ago in Turkey and western Iran (Hiendleder et al. 1998). Mitochondrial DNA evidence suggests that there were at least three domestication events for sheep and ruled out the urial (*O. a. vignei*) and the argali (*O. ammon*) as potential ancestors of domestic sheep (Pedrosa et al. 2005).

Sheep were originally used for meat, milk, and hides. Harvesting sheep's wool or fleece probably did not begin until 8,000 years ago. During the Bronze Age, sheep's wool was plucked by hand and woven into cloth. Later, probably during the Iron Age, herders used shears to remove the wool (Barber 1992). Because wool was a renewable resource of relatively high value, shepherds raised large flocks, which were also used as barter.

Goats (*Capra hircus*) were first domesticated in Turkey and the Zagros Mountains of Iran and Iraq roughly 10,500 to 9,500 years ago (Naderi et al. 2008; Zedar & Hesse 2000). The ancestor of domestic goats is widely believed to be the bezoar (*C. h. aegagrus*). Neolithic farmers probably kept goats primarily for meat and milk; however, their hides served as water and wine skins, and their dung was burned for fuel.

Camels and Other Artiodactyls

The origins of camel domestication are poorly known (Köhler-Rollefson 1993). Today there are two species

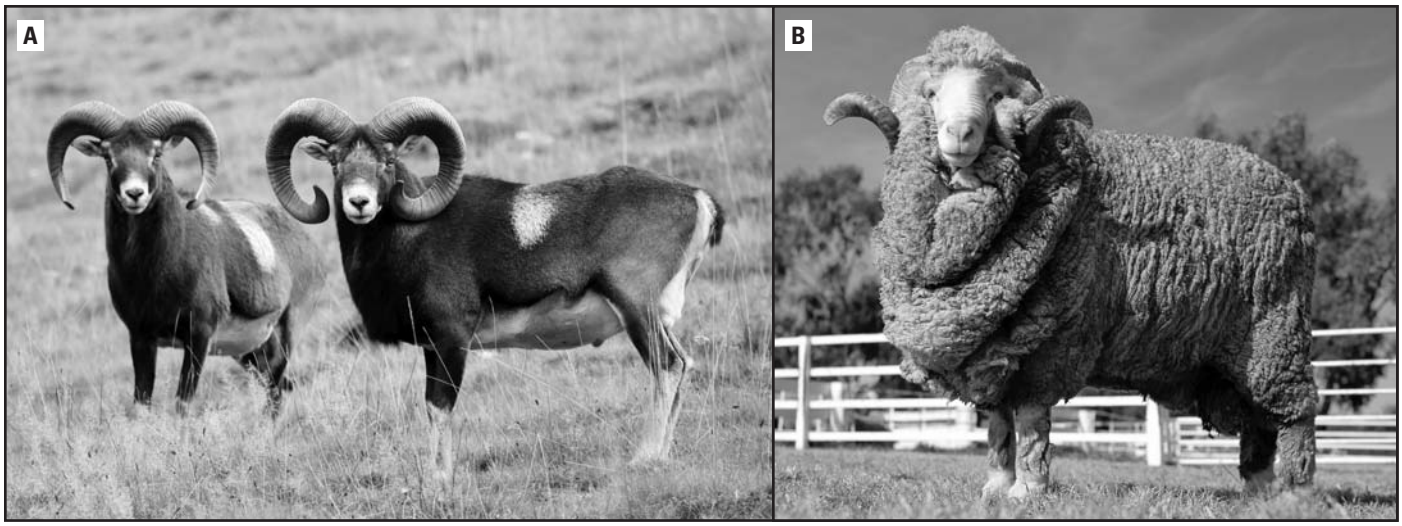

FIGURE 27-8 (A) The mouflon (*Ovis aries orientalis*) is believed to be the ancestor of domestic sheep. (B) Merino sheep are prized for the fine wool they produce.

(**Fig. 27-9**). Domestic and feral dromedary camels (*Camelus dromedarius*) live in the Middle East, in East Africa, in the Sahel, across Saharan Africa, and as introduced populations in Australia, but these one-humped camels are extinct in the wild (Grubb 2005b). The Bactrian camel (*Camelus bactrianus*) is a two-humped species with shorter legs and long shaggy fur. They are adapted for the cold, high-altitude deserts of Mongolia and China, where an estimated 1,000 wild Bactrian camels survive today. The two species are genetically similar, and some scholars have suggested that dromedary camels were domesticated from Bactrian camel ancestors (Köhler-Rollefson 1993). Others believe the two species were independently domesticated. Archaeological evidence currently supports the latter hypothesis. Camel bones and Arabian stone stelae depicting one-humped camels date to approximately 4,700 years ago along the Abu Dhabi coast (Frifelt 1975). Turkmenistan and Iran may be the center of domestication of the Bactrian camel. At a site in Iran dating roughly 5,200 years ago, archaeologists found clay vessels containing camel dung and cloth woven from a combination of camel and sheep hair (Compagnoni & Tosi 1978).

Domesticated camels provide milk, hides, and in the case of Bactrian camels, wool, but camels were probably domesticated primarily as beasts of burden. They can carry heavy loads over long distances and can go without water or food for several days. Between 4,000 and 3,500 years ago, domesticated camels spread out of the Near East. Camel-mounted tribes (e.g., Ishmaelites) expanded their empires out of Arabia into the Middle East beginning around 3,000

FIGURE 27-9 (A) A camel herder leads a group of domestic dromedary camels (*Camelus dromedarius*) across the dunes in the Sahara. (B) A Bactrian camel (*Camelus bactrianus*) in Mongolia.

years ago and dramatically altered the history of that region (Bulliet 1975; Köhler-Rollefson 1993).

Domestication of the South American camelids likely took place some 7,000 to 6,000 years ago on the Peruvian puna (high-altitude grasslands) of the Andes (Wheeler 1995). The guanaco (*Lama glama*) and vicuña (*Vicugna vicugna*) were domesticated to form llamas and alpacas, respectively (**Fig. 27-10**; Grubb 2005b). From high-altitude domestication centers in Peru, domestication spread to lower elevations in Peru, northern Chile, and Ecuador (Wing 1986). By approximately 1,000 years ago, llamas had been domesticated across much of the central Andes. The Incas probably raised alpacas for their extremely fine wool, but llamas were probably used as pack animals. Pack trains of llamas attended Incan armies as they expanded their empires north to Colombia and south to central Chile in the late 1400s (Wheeler et al. 1995). After the Spanish conquest of the Americas, llamas were used by the colonizers to haul silver and gold ore from Andean mines.

A number of other artiodactyls have been tamed or domesticated to varying degrees, including water buffalo (*Bubalus bubalis*, **Fig. 27-11A**), reindeer (*Rangifer tarandus*), yak (*Bos grunniens*, Fig. 27-11B), banteng (*Bos javanicus*), and gaur (*Bos frontalis*). For example, wild yaks were probably first domesticated in the Qinghai-Tibetan Plateau some time between 10,000 and 5,000 years ago (Guo et al. 2006). Similarly, beginning in the late Bronze Age, several northern Eurasian cultures began herding and breeding reindeer. Genetic analyses reveal that reindeer were probably domesticated independently in northern Russia and Fennoscandia (Roed et al. 2008).

Other Mammals

For centuries, elephants have been used for carrying heavy loads, as mounts in warfare, and for entertainment in circuses. They were first captured, tamed, and put to work in the Indus Valley of Pakistan and India approximately 4,000 years ago (Prothero & Schoch 2003). Initially, elephants may have been used primarily for carrying heavy loads but soon became important in warfare. War elephants were used by the Punjabi, Babylonian, and Persian armies. During this period, the ranks of the elephant corps consisted exclusively of Asian elephants (*Elephas maximus*). Only later, after sources of Asian elephants were cut off, did North African armies attempt to domesticate African elephants (*Loxodonta africana*). During the Punic Wars, Carthaginian armies used African war elephants against the Romans. In the most famous example, Hannibal marched an army of warriors and war elephants across the Alps, coming within three miles of Rome in 216 bc (Prevas 2001). Eventually, the use of war elephants as a military tactic became obsolete because infantry learned how to cause the massive animals to panic and run, trampling their own soldiers in the process.

Today, elephants are employed in timber harvesting in the jungles of Laos (Lao People's Democratic Republic) and Thailand (**Fig. 27-12**). Work elephants are typically captured in the wild, rather than bred in captivity, and trained (often harshly) to obey the mahout (master). Elephants are also exhibited in zoos and circuses and increasingly used as mounts in ecotourism safaris in Asia and Africa.

Rodents are not typically thought of as domesticated animals, but there are hundreds of laboratory strains of mice, rats, and hamsters used in medical and scientific research today. Laboratory mice and rats are model organisms for human disease in part because virtually all the estimated 23,700 mouse genes have human counterparts (Mouse Genome Sequencing Consortium 2002).

The history of mouse breeding dates back to approximately 3,100 years ago when the Chinese bred mice for

FIGURE 27-10 (A) A domesticated Bolivian llama and (B) a wild Patagonian guanaco (*Lama glama*).

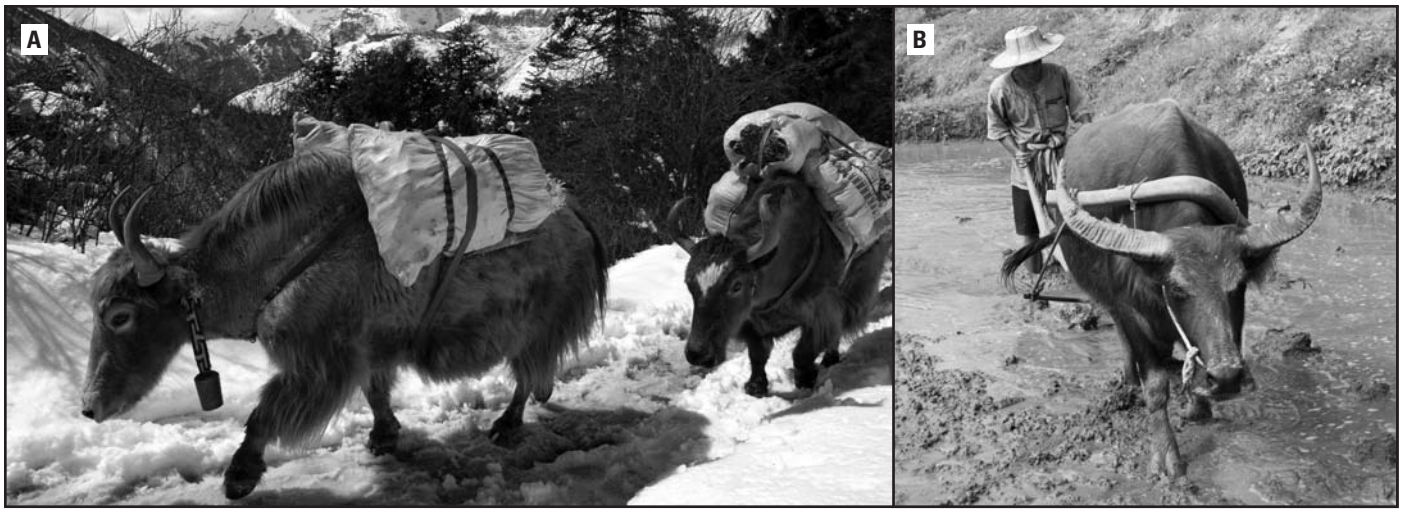

FIGURE 27-11 (A) A group of domesticated yaks (*Bos grunniens*) in Nepal. (B) A water buffalo (*Bubalus bubalis*) plows a rice paddy in Southeast Asia.

unusual pelage colors (Beck et al. 2000). The hobby spread to Japan and by the 19th century to Europe (Silver 1995). Most of the inbred strains of mice in use today trace their ancestry to William Castle's mouse genetics laboratory at Harvard and a mouse breeder in Massachusetts (Eisen 2005). Laboratory mice are derived from house mouse subspecies, typically *Mus musculus domesticus* and *Mus musculus musculus*, with some contributions from Asian *M. m. castaneus* (Wade et al. 2002). Most laboratory strains are highly inbred (e.g., resulting from crosses between siblings), making individuals within the strain nearly genetically identical. Among inbred strains used for medical research are nude mice (**Fig. 27-13**), which lack an immune response, transgenic mice containing foreign genes (e.g., oncogenes used in the study of cancer), and knockout mice that have had one gene inactivated to study the consequences of the gene deficiency (e.g., "mighty mice" lack the myostatin gene and exhibit increased muscle mass).

FIGURE 27-12 An Asian elephant (*Elephas maximus*) working at a logging camp in India.

FIGURE 27-13 Nude mice (*Mus musculus*) have a mutation in the *FOXN1* gene that causes them to lack a thymus gland. The result is that these mice lack an immune response and are useful for studying AIDS, cancer, and immunodeficiencies.

Limits of Domestication

Despite the obvious advantages of domesticating animals for food, clothing, work, and other benefits, relatively few mammal species have been successfully domesticated. Some species are more tractable than others; social species are more susceptible to domestication than solitary ones. Selective breeding for specific traits by humans over many generations may result in the domestication of even solitary species. In a classic example, breeding experiments on Russian silver fox (*Vulpes vulpes*) conducted in the 1950s by Russian scientists resulted in tame foxes that have many behavioral and physical traits of domestic dogs (floppy ears, curled tails, spotted pelage, and behaviors such as tail wagging; Trut 1999). In contrast, efforts to domesticate some social species such as the zebra have largely failed (Hayes 1893) because zebras are aggressive toward one another and do not appear to follow a single leader.

Selective breeding for behavioral and physical traits rather than for survival can lead to unintended consequences. Domesticated species often lack the genetic variation of their wild ancestors, making them susceptible to disease. Several dog breeds, for example, appear prone to genetic problems. A related consequence of domestication and the resulting close association between humans and their domestic animals has been the transfer of diseases to humans. Such **zoonotic diseases** (diseases transferred from animals to humans are called zoonoses) are discussed in Chapter 28 (online).

SUMMARY

Animal and plant domestication played a critical role in the development of human civilization. Mammals in particular provided reliable food sources, clothing, transportation, protection, and perhaps companionship. Domestication is generally a slow process whereby wild individuals are bred for specific traits useful to humans. Over many generations, such breeding alters the behavior, morphology, physiology, and/or reproduction of the animals. Relatively few mammal species have been successfully domesticated because the process requires species with adaptable diets, the ability to breed in captivity, a predictable or even temperament, and usually some degree of social structure. Not surprisingly, among the first animals to be domesticated were pack- or herd-forming animals. Among the Carnivora, dogs were the earliest domesticated mammals. Domesticated dogs are descended from wolves beginning perhaps 30,000 years before present.

In contrast, modern domestic cats exhibit few of the social traits believed to be important for domestication. Domestic cats arose from a minimum of five female ancestors of Near Eastern wildcats in the Middle East. Cats may have been tolerated in human settlements because they exerted some control over mouse populations.

Wild horses appear in Paleolithic cave art around 32,000 years ago and were probably hunted for meat. Horses were probably domesticated much later, approximately 5,500 to 5,000 years ago on the Eurasian steppes. Historically, horses were used for food, transportation, and warfare. At roughly the same time, African wild asses were domesticated in northeastern Africa and used primarily as pack animals.

The Fertile Crescent of the Near East is the center of artiodactyl domestication; cattle, sheep, goats, and pigs were domesticated there along with grains such as wheat, oats, and barley, setting the stage for the development of the first city-states. Living domestic cattle have no surviving wild ancestors. They share a common ancestor with the massive wild aurochs, depicted in cave paintings. These wild ancestors were probably domesticated 10,000 years ago. Today, cattle are bred for increased milk production, muscle mass, coat coloration, and in the case of fighting bulls, aggression. Around 9,000 years ago, wild boars were independently domesticated at least seven times in Europe and Asia. Domestic sheep most likely descended from the wild mouflon of Europe and Asia approximately 11,000 years ago in Turkey and western Iran. The origins of camel domestication are poorly known. One-humped dromedary camels were likely domesticated approximately 4,700 years ago along the Abu Dhabi coast of the Arabian peninsula; domestication of the Bactrian camel took place in Turkmenistan and Iran. Domestication of the South American lamine camelids

(llamas and alpacas) likely took place 7,000 to 6,000 years ago on the Peruvian puna of the Andes.

A number of other mammals have been domesticated. For example, there are hundreds of laboratory strains of mice, rats, and hamsters used in scientific and medical research today (although rodents are not typically thought of as domesticated animals). For centuries, elephants have been used for carrying heavy loads, as mounts in warfare, and for entertainment in circuses. They were first domesticated in the Indus Valley of Pakistan and India approximately 4,000 years ago.

Despite the obvious advantages of domesticating animals, selective breeding for behavioral and physical traits rather than for survival can lead to unintended consequences. Domesticated species lack genetic variation, making them susceptible to disease, and their close association with humans allows the transfer of some diseases to humans (zoonotic diseases).

KEY TERMS

Ancient DNA
Domestication
Feral
Genome
Hypercarnivorous
Mesocarnivorous
Recombinant DNA technology
Selective breeding
Transgenic organisms
Zoonotic disease

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