BISON EVOLUTION AND MIGRATION

Robert E. Wrigley
Winnipeg, MB
robertwrigley@mts.net

Paintings by Dwayne Harty
dh@dwayneharty.com

This article, on the evolution and migration of ancient and modern bison from Eurasia and North America, was prepared to augment a major international travelling exhibit (125 canvasses, sketches, and bronzes) on bison by noted Saskatchewan wildlife artist and museum dioramist Dwayne Harty (studio currently in Jackson Hole, Wyoming). The exhibit opened at the Whyte Museum of the Canadian Rockies in Banff in October 2024. Dwayne has previously illustrated five of Robert's books, including *Mammals in North America: From Arctic Ocean to Tropical Rainforest*, *Manitoba's Big Cat; The Story of the Cougar in Manitoba* (with Robert Nero), *Large Mammals, Canadian Album Series, Volume 1-2*, and *Mammals in the Qu'Appelle Valley* (with David R.M. Hatch).

Introduction

Although we think of the Plains Bison as being the quintessential large mammal of North America, its ancestral lineage actually derives far away on another continent — Eurasia. A member of the cattle-sheep-antelope family Bovidae, the oldest-known bison-like animals were described in the genus *Leptobos*, at least eight species of which were distributed from the Iberian Peninsula to China 3.6 million years ago (late Pliocene). Resembling a modern steer, they weighed up to 500 kg and reached a shoulder height of 1.4 m. *Leptobos* gave rise to both the cattle genus *Bos* and *Bison*. The earliest bison was *Bison sivalensis* from the Indian subcontinent dated to 2.8 million years ago. Subsequent descendants included the Steppe Bison (*Bison priscus*) distributed from Europe to China and later to North America, and the mid-Pleistocene Woodland Bison (*Bison schoetensacki*) of Europe and Beringia (i.e., Bering Land Bridge).

From 240,000 to 195,000 years ago, the Steppe Bison (*Bison priscus*) gave rise to *Bison alaskensis* in Asia and the two species made their way across Beringia into Alaska. This was possible due to a drop in sea level of up to 120 m (394 ft) during glacial episodes, resulting in a 1600-km (994-mi)-wide tundra-steppe corridor. In time, both species spread all the way south through woodlands and plains to southern Mexico. A second wave of immigration of *Bison priscus* occurred into North America by the same route around 45,000 years ago. *Bison priscus* may also be the ancestor of the Wisent or European Bison (*Bison bonasus*), which survives to this day in Eurasia. Although there were many large-mammal exchanges across Beringia at various times, there is no compelling evidence that any bison species from North America emigrated to Eurasia. Remarkably, Beringia (including the unglaciated refugium in Alaska and Yukon) was occupied by several kinds of bison continuously for 300,000 years, while the rest of North America has supported bison for around 200,000 years. Given the dominant roles bison species have played within many of this continent's ecosystems, they and *Homo sapiens* represent the most successful natural mammalian dispersals into North America during the last couple of million years.

Great fluctuations in climate over the last three million years, multiple advances and retreats of glaciers, major shifts of vegetational composition and zones, and the presence of habitat refugia all convened to greatly influence the evolution and migration of bison lineages.

During the latter part of the Pleistocene Ice Age, *Bison priscus* and its descendants evolved into several other species in North America. Based on limited skeletal evidence (especially skull and horn cores), numerous species of bison have been described over the decades, however most of these are no longer recognized. The following six species are currently accepted, all of which have inhabited various landscapes from Alaska to Mexico (in successive, overlapping periods): *Bison priscus, B. alaskensis, B. latifrons, B. antiquus, B. occidentalis*, and most recently *Bison bison* — the modern species, which is the smallest in the bison lineage.

It is remarkable that the ancestor of the North American Plains Bison passed successfully through the mass extinction event that swept away most of the large mammals 12,000 to 10,000 years ago. This major loss of fauna was caused by rapid climate/vegetation changes and persistent hunting pressure from growing numbers of Paleoindians. Likely, massive herd sizes and their extensive distribution over the continent were factors in the species' survival up to the 1800s, when it then suffered mass slaughter by hunters with firearms.

Controversial relationships among bison species

Currently, there are many uncertainties regarding species status and lineage of bison species in both Eurasia and North America. Yet to be resolved are the following. Since 1849, the genus *Bison* has been widely recognized. However, an alternative view is that *Bison* should be reassigned as a subgenus under the genus *Bos* (Linnaeus 1758), indicative of Bison's close relationship to other wild cattle such as the Aurochs (*Bos primigenius*) and Yak (*Bos mutus*). There has been a long-standing debate over the genetic relationship of the European and North American bisons. A recent DNA analysis questioned the validity of recognizing the North American Plains and Wood Bisons as distinct subspecies (designated in 1897), although these two races differ physically, behaviorally and ecologically; other researchers even proposed separate ancestors. With ever-improving techniques for extracting and studying ancient DNA, relationships among extinct and current species of bison should become clearer.

Size difference between the sexes

All bison species are thought to have featured strong sexual dimorphism, meaning the size of the body (especially the head, shoulders and front legs) and horns of the bull were much larger than those of the cow. These traits likely evolved due to sexual selection by females, and to success in battles between mature bulls. The biggest, most powerful bull tended to be more successful in gathering and protecting a harem of cows, thereby providing improved mating opportunities.

Size differences among North American bison species

Inferring body size from horn, skull and postcranial traits, the largest to smallest species were: *Bison latifrons*, *B. alaskensis*, *B. priscus*, (possibly *B. schoetensacki*), *B. antiquus*, *B. occidentalis*, *B. bison athabascae*, and *B. bison bison*. In the late-Pleistocene, northern species in cool climates had larger body mass and longer legs, and occurred in small herds, while warm-adapted species were smaller, lived in grasslands, and gathered in large herds. It has been hypothesized that hunting pressure by Paleoindians was a significant selective force leading to dwarfing of the Plains Bison. Smaller individuals would attain reproductive age before larger ones, thereby providing an advantage in number of offspring produced over its lifetime.

Horns

Both sexes carry horns in all species of bison. A horn consists of a long, solid core of living bone covered in a thick sheath of extremely hard keratin (a polymer of fibrous structural proteins). This sheath extends many centimeters beyond the core tip. A bull's horn has a greater basal circumference, is bulkier, and curves less near the tip than a cow's. Horns are not shed like antlers, but grow from the animal's birth to maturity. Horn-core length in females of various species is 60 to 70 per cent that of a bull, and northern species tend to have longer horns than southern species. The horns of an old bull show multiple, rough expansion ridges at the base and significant wear at the tip, leaving only a stump and possibly a new horn tip exposed.

The horns serve as the main offensive and defense armature for intimidating and fighting off rivals and predators. Extinct species had to contend with powerful predators such as Dire Wolf, Sabertooth Cat, American Lion and Giant Short-faced Bear. Horns also come into play during display and combat between rutting bulls, and increase competitiveness with other large mammalian grazers and browsers. Horns in the Plains Bison extend laterally in a calf, and then progressively turn upward and inward with maturity. The horns help prevent head and eye injury during aggressive encounters by absorbing or deflecting strikes and hooks from a combatant. Constructed of very hard bone, the horn core and teeth are the most often found parts of a bison skeleton. Horn length, curvature, cross-section shape, and angle from the skull all vary among extinct and living species, and so play the major role in identification of fossil material.

Cave art

Aurochs, the Steppe Bison, and possibly a third species are featured prominently in the cave art of *Homo sapiens* in France and Spain (dated 38,500 to 12,000 years ago). More than 320 bison paintings have been recorded (around 21 per cent of all cave ornamentation), most in sufficient detail to identify the species. For example, the Chauvet-Pont d'Arc cave in Ardeche, France clearly portrays both the Steppe Bison (*Bison priscus*) and Wisent (*Bison bonasus*), radiocarbon dated at 38,500 and 36,300 years ago, respectively. Such attention demonstrates the importance of bison to the physical and spiritual life of these early people.

The symbolic bison

For many Indigenous peoples of North America, the Plains Bison has for millennia been honoured in ceremonies for its great spiritual value, and recognized as the very symbol of respect for creation and life. It offered all parts of its body to provide humans with food, shelter, clothing, fuel, tools, weapons, and ornaments. In more recent times, images of bison have appeared in countless official and unofficial capacities (emblems, seals, flags, certificates, money, team names). As examples, it was selected for the Great Seal of Manitoba in 1870, and for the badge and motto of the Royal Canadian Mounted Police (NWMP likely in 1877). It adorned several stamps of the United States Postal Service (e.g., 1898 Trans-Mississippi Exposition 4 cent orange), the $10 USA Lewis and Clark banknote of 1901, and the USA nickel from 1913-1938. In 1916, the National Bison Legacy Act named the Bison as the United States Official National Mammal, chosen to represent the spirit of the nation. Subsequently, the Plains Bison was chosen as the State Mammal for Kansas (1955), Oklahoma (1972) and Wyoming (1985), and as the Official Mammal Emblem of Manitoba (2014). The Wisent is the unofficial symbol of Belarus, representing nobleness, power and persistence.

Aurochs or ancient cattle *(Bos primigenius)*

The Aurochs (*Bos primigenius*) evolved from a species of *Leptobos* (as did the genus *Bison*) around 1.3 million years ago in Asia. The oldest fossils are known from 0.8 million years ago from India and northern Africa. It spread into Europe by 230,000 years ago, where it is believed to have interbred with the Steppe Bison (*Bison priscus*) 120,000 years ago. The European Bison (*Bison bonasus*) contains 10 per cent of Aurochs DNA, evidence of this ancient relationship. The Aurochs' massive body differed in shape from modern breeds of cattle, with longer legs, larger head,

Aurochs Bos primigenius

sideways/forward-directed horns, and with well-developed shoulder and neck musculature. The skull was also longer and narrower than bison. Males were much larger than females. It ranged in steppe, open forests and wetlands from Finland and North Africa to Siberia and Korea. Occurring contemporarily with the woodland dwelling (i.e., browsing) Wisent (*Bison bonasus*), it has been suggested that the Aurochs (a grazer) became extinct, while the Wisent survived, because the former depended more on grassland habitat, which was usurped by humans for agriculture. Both species were subjected to heavy hunting pressure for millennia by humans.

Four subspecies of Aurochs have been described from Eurasia, India, Greece and Africa. This is the bull that is so beautifully portrayed in colourful Paleolithic cave paintings in France and Spain, and later on Greek vases. Domestication occurred around 12,000 years ago (Neolithic Period) in the Middle East, leading to modern cattle breeds through selective breeding. Julius Caesar observed wild Aurochs in forests of Germania in 53 BCE, and specimens were captured or raised for combat as entertainment in Roman amphitheaters. The last surviving herd lived in a royal hunting ground in Poland, and with the poaching of the last breeding pair in 1627, the species was declared extinct, the result of over-hunting, habitat loss, and disease in the remnant herd. Projects have been proposed to 'recreate' the species using ancient DNA.

BULL SIZE (maxima):
· **WEIGHT** 1,500 kg (3,307 lb)
· **HEIGHT AT SHOULDER** 1.8 m (6 ft)
· **LENGTH OF HORN CORE** (outer curve) 1.2 m (3.9 ft)

Bison sivalensis

Bison sivalensis was the first in the bison lineage, believed to have evolved from a species of *Leptobos* around 3.4 million years ago (late Pliocene). Fossils have been found in India, Pakistan and China. There is speculation that it inhabited Beringia and then entered northwestern North America, but no fossil evidence has yet been uncovered. This species is pivotal because it was ancestral to both Eurasian and North American bison lineages. It gave rise to the Steppe Bison (*Bison priscus*) around 2 million years ago, which became widespread throughout both continents. *Bison sivalensis* inhabited grassland and open broadleaf forest, which were widespread across southern and eastern Asia. It coexisted with elephants, horses, and rhinoceros, all typical of open, arid habitats. It is thought to have closely resembled the Plains Bison in body size, but its horn cores were straight before curving, aligned away from the cranium.

Bison sivalensis

BULL SIZE (maxima):
· **WEIGHT** Unknown
· **LENGTH OF HORN CORE** 45 cm (18 in)

Bison palaeosinensis

Fossils of this species have been reported from sites in northern China dated 2.6 million years ago. It was characterized by dental characteristics and small size. It also evolved from ancient *Leptobos*, with the two species overlapping in time. This bison expanded its range into northern Russia, so it must have developed a dense coat and physiological adaptations to cold. It lived alongside mammoth, rhinoceros and horse. It has been proposed that populations of *Bison paleosinensis* gave rise to both the Steppe Bison (*Bison priscus*) and Menner's Bison (*Bison menneri*).

BULL SIZE (maxima):
· **WEIGHT** 1,000 kg (2,200 lb)
· **HEIGHT AT SHOULDER** 1.7 m (5.6 ft)
· **LENGTH OF HORN CORE** 41 cm (16 in)

Bison paleosinensis

Pleistocene Woodland Bison *(Bison schoetensacki)*

The Pleistocene Woodland Bison is known from 1.2 million to 50,000 (possibly 36,000) years ago with a distribution from the British Isles, France and Spain to southern Siberia. Fossil bones and dung (coprolites) have been recovered from more than 21 caves and excavated sites. Remarkably large numbers of this ancient Bison have been found at two sites in southern Spain. Additional fossils dated 700,000 years ago in Italy indicate that this species was the most heavily targeted prey of human hunters, since it was the only bison species in the region at the time. Other hunted species were rhinoceros, elephant, deer and bear. Cracked Bison bones revealed they had been gnawed on by hyaena. Formerly thought to have arisen from *Bison priscus*, recent genetic evidence indicates it is a related 'sister' species to the Wisent, to which it likely resembled closely. Its horn cores are shorter and heavier than *Bison priscus*. The Pleistocene Woodland Bison exhibited a high degree of sexual dimorphism, a common trait in bison lineages on both Eurasian and North America continents. Dental wear suggests its diet included both grasses and shrubs in open forests.

BULL SIZE (maxima):

· **WEIGHT** 1,000 kg (2,200 lb)
· **HEIGHT AT SHOULDER** 2 m (6.6 ft)

Menner's Bison *(Bison menneri)*

This early European bison was tall with long and slim legs, but was not heavily built. Its short horns had a backward and upward curvature. Based on the wear of its molars, it appears to have included a significant mixture of broad-leaved forest plants in its diet, in addition to grasses of open landscapes. It lived from 1.2 to 0.8 million years ago in a temperate-to-cooling boreal climate. It is known mainly from a major fossil site in Germany where numerous individuals perished in mud flows caused by catastrophic flood events, along with ancient hippopotamus and other species of large mammals. Crushing and gnaw marks on some of these bison bones indicate that the animal carcasses were devoured by hyaena (*Pachycrocuta brevirostris*). Cut marks and stone and bone tools demonstrate that early people included Menner's Bison in their diet. Fossils were also discovered in southern Russia with another early bison named *Eobison*. An ankle bone was dredged up from the North Sea (previously land) along with bones of mammoth, two-horned rhino, horse and hippopotamus, indicating that Menner's Bison was part of a rich large-mammal fauna around 800,000 years ago in Europe.

Bison menneri

BULL SIZE (maxima):

· **WEIGHT** 600 kg (1,323 lb)
· **HEIGHT AT SHOULDER** 2 m (6.6 ft)
· **LENGTH OF HORN CORE** 20 cm (8 in)

Steppe Bison *(Bison priscus)*

With fossils first found in northern China, this large-sized, long-legged species evolved from *Bison sivalensis* on the 'mammoth steppe' in Asia two million years ago (early Pleistocene). It spread throughout northern Eurasia (west to the British Isles) by 700,000 years ago. Numerous fossils of this bison have been dredged up from the southern part of the North Sea, which was formerly land. The Steppe Bison gave rise to the woodland-dwelling *Bison alaskensis*, and both species subsequently entered North America via the Bering Land Bridge around 230,000 to 200,000 years ago. Most fossils of *B. priscus* come from Alaska and the Yukon (more than 80 per cent of fossil mammal bones from Klondike gold mines are *B. priscus*), however a few have been recovered east to Manitoba and Iowa, and as far south as southern Mexico. It likely evolved into the Long-horned Bison (*Bison latifrons*) around 160,000 years ago.

A second wave of *Bison priscus* immigration occurred about 45,000 years ago, and may have given rise to *Bison antiquus*, as revealed by molecular studies. Many fossils from Beringia initially described as *Bison crassicornis* may in fact be hybrids between *Bison priscus* and *Bison antiquus*. The greatest distribution and numbers of *Bison priscus* occurred from 90,000 to 10,000 years ago, with the southern plains population separated from the northwestern population in Beringia by the Wisconsin Glacier. The last Eurasian herd became extinct 8,700 years ago in a steppe-forest refugium in southeastern Siberia, and frozen mummies have been discovered there thawing out of the permafrost. The latest North American fossils were discovered in North Dakota dated 8,000 years ago, and in Alaska and Whitehorse, Yukon, dated 5,400 years ago. The rapidly changing climate and habitats at the end of the last glaciation resulted in the species' optimal cold-steppe habitat being replaced by boreal forest and tundra. Its restriction into islands of remaining habitat probably resulted in small isolated herds becoming inbred and highly vulnerable to human hunters. This is a bison species depicted dramatically in the cave art of France and Spain.

BULL SIZE (maxima):

· **WEIGHT** 1,200 kg (2,645 lb)
· **HEIGHT AT SHOULDER** 2.2 m (7.2 ft)
· **LENGTH OF HORN CORE** 50 cm (20 in)

Bison priscus

Bison alaskensis

Bison alaskensis evolved in eastern Asia from *Bison priscus* (or possibly *Bison sivalensis*), and entered North America via Beringia around 230,000 to 200,000 years ago. Well-preserved fossils have been recovered from sediments in the Yukon (dated 40,000 years ago), and in southeastern Idaho (26,000 years ago). Interestingly, it occurred around the same time in Idaho with three other species of bison (*B. priscus*, *B. latifrons* and *B. antiquus*). It had slender horns intermediate is size between the long-horned *B. latifrons* and shorter-horned *B. priscus*. It inhabited cool woodland and forest in Alaska and the Yukon, but also spread south to coastal California, and in the plains to central Mexico. Likely it reached its greatest populations numbers and distribution during the last interglacial period about 125,000 years ago, when woodland was widespread in North America. This species apparently became extinct at the end of the Wisconsinan glacial maximum, around 20,000 years ago.

BULL SIZE (maxima):

- **POSSIBLE WEIGHT** 1,200 kg (2,645 lb)
- **LENGTH OF HORN CORE** 80 cm (32 in)

Extinct Long-Horned Bison (Bison latifrons)

This is the first species of bison to have evolved in North America, derived about 160,000 years ago from the Eurasian immigrant Steppe Bison (*Bison priscus*). Inhabiting grassland, woodlands and forests, it ranged over most of the United States, including the Great Plains, Florida and coastal California, and south to the Mexican State of Oaxaca. It likely extended north into south-central Canada as well. Most fossils come from the central plains states from South Dakota to Texas. The least known of North America's bison species, *Bison latifrons* is thought to have lived in family groups, not congregating into immense herds. It was a massive animal, up to 50 per cent larger than the Plains Bison. In fact, it was the largest species and had the longest horns of any member of the cattle family Bovidae. Consequently, it was not built for running long distances or agile movement. Most notable were the pair of elongated upward- and sideways-sweeping horns. Taking into account the extra length of the horn sheath beyond the end of the core, a horn of the bull could have attained a length of 1.1 m (3.6 ft). The tip-to-tip width span of the horns may have reached an astonishing 2.3 m (7.6 ft). This great set of weapons would have been important in defending against large predators like the Giant Short-faced Bear, Sabertooth Cat, American Lion and Dire Wolf, as well as intimidating other large forage competitors such as camels, mammoths, giant deer, horses and muskox.

Bison latifrons reached its greatest numbers during an interglacial period from 130,000 to 115,000 years ago. Both *B. latifrons* and *B. antiquus* fossils have been found in gravel deposits in south Texas dated at 13,000 years ago, and it appears they both went extinct shortly after this date. Excessive hunting pressure by Paleoindians, changing climate, and vegetational shifts are believed to have caused the demise of both species.

BULL SIZE (maxima):

- **WEIGHT** 2,100 kg (4,630 lb)
- **HEIGHT AT SHOULDER** 2.5 m (8.2 ft)
- **LENGTH OF HORN CORE** 1.1 m (3.6 ft)
- **TIP-TO-TIP WIDTH OF HORNS** 2.3 m (7.6 ft)

Extinct Ancient Bison (*Bison antiquus*)

Bison antiquus evolved from *Bison latifrons* by 60,000 years ago in the American Southwest. It was the most widely distributed North America bison species, spreading northward to Alaska,

Bison latifrons

Bison antiquus

Northwest Territories, central Alberta and Manitoba south to Florida, Mexico and Nicaragua. It averaged about 25 per cent heavier than the modern Plains Bison, and had horns that stood out at right angles to the head. This species lived in grasslands with patches of woodland and shrubland, from lowlands to mountains. Its generalist diet consisted more of broad-leaved plants than grasses, as evidenced by lighter wear on the teeth (grasses are more abrasive). The great abundance of fossils (500 individuals at one Nebraska archeological site dated at 10,000 years ago) suggests it reached high numbers on the plains 18,000 years ago. This species was a member of the rich North American megafauna that perished from climate change, vegetational-zone shifts, and mounting hunting pressure by Paleoindians. It became 'extinct' by 10,000 years ago, leaving a population to evolve into the Western Bison, *Bison occidentalis*.

Fossils of this giant species are known from 47 fossil sites. More than 300 individuals (many young) have been recovered so far from the famous La Brea Tar Pits in Los Angeles, and age profiles indicate that this species migrated past here during the same two-month period for many generations. There is evidence that *Bison antiquus* and all megafauna died out in this region of California by 12,900 years ago from a combination of rapid cooling followed by a warming phase, which resulted in drought, habitat changes, and major fires. Following the extinction of other megafauna, Paleoindians of the Clovis and Folsom cultures focused on hunting this bison, which contributed to the species' demise. A fluted projectile point and butchering evidence were found with 13 fossil *Bison antiquus* skeletons at a site in western Kansas (dated 10,400 years ago).

BULL SIZE (maxima):

- **WEIGHT** 1,580 kg (3,483 lb)
- **HEIGHT AT SHOULDER** 2.3 m (7.5 ft)
- **LENGTH OF HORN CORE** 40 cm (15.8 in)

Extinct Western Bison *(Bison occidentalis)*

This chronospecies lived on the North American plains for the relatively short period from 13,000 to 4,270 years ago, reaching its highest populations around 8,000 years ago. It descended from *Bison antiquus* and transitioned rapidly into the smaller Plains Bison. This decrease in size is thought to have been caused by increasing global temperature following the end of the Pleistocene Ice Age. Some researchers prefer to recognize it as a subspecies of *Bison antiquus*. The thinner, and upward/rearward extension of the horn core distinguished it from its predecessor. The large herds of this species supported a rapid population increase and spread of Paleoindians across North America. It was subjected to heavy hunting pressure from 11,000 to 9500 years ago. There is a record in Nebraska of *B. occidentalis* skeletal remains associated with an arrow point. Most specimens have been reported from the Great Plains, but records occur from Alaska to northwestern Ontario and south to Florida and southern Mexico.

BULL SIZE (maxima):

- **WEIGHT** 1,000 kg (2,200 lb)
- **HEIGHT AT SHOULDER** 1.8 m (6 ft)
- **LENGTH OF HORN CORE** 41 cm (16 in)

North American Plains Bison *(Bison bison bison)*

Originating from the *Bison antiquus*–*B. occidentalis* lineage as recently as 5,100 years ago (an arbitrary delineation) on the northern Great Plains, the Plains Bison

Bison occidentalis

spread over most of North America, from southern Canada to Mexico, the Rocky Mountains to the Mississippi River. Small herds ranged as far east as Ontario, New York, North Carolina and Florida by 2,610 years ago. It was considered a 'Keystone Species,' meaning it played a major role in the functioning of ecosystems, including river valleys, prairies and plains, sagebrush and desert scrub, aspen parkland, and coniferous woodland. This nomadic species' diet is focussed on grasses. The Plains Bison is relatively small compared to its ancestors, with short and highly curved horns. There appears to be a correlation between decrease in body size and warming air temperature (due to metabolic factors and food resources). It has been estimated that average size of the Plains Bison may continue to decrease in the future by 41 kg (88.2 lb) for each degree increase in global temperature.

The Plains Bison successfully adapted to great climatic fluctuations, ecological changes, and heavy hunting pressure from Indigenous tribes of the plains. Suspected to have attained its highest population numbers around 2,500 years ago, early historical estimates exceed 30 million. Although this figure is unreliable, there is no doubt that the Plains Bison was the most-abundant large mammal in North America at the end of the Pleistocene Ice Age. Through over a century of wanton slaughter by people with firearms (especially from 1860 to 1880, mainly for hides but also Indigenous genocide), the herds collapsed to only 541 individuals in the United States, where it was declared extinct in the wild in 1883, and in Canada in 1888.

From a breeding stock of less than 100 founders, currently more than 500,000 Bison (including hybrids with cattle) now exist in reserves and private herds in both countries. These consist of 50 conservation herds, such as national and state parks (42 in USA, eight in Canada) totalling almost 21,000. Ranchers raise over half a million commercially for meat and hides. However, the species remains 'ecologically extinct' in Nature, since it is no longer free-ranging, it has lost its natural role over traditional landscapes, and herd size, range and predation are managed. The largest semi-wild herd of Bison in the USA consists of around 5,700 in Greater Yellowstone National Park area (once down to 23 individuals), where it has existed continuously since prehistoric times. This managed population has been designated as Threatened by the U.S. Fish and Wildlife Service. The species is listed as Threatened in Canada (COSEWIC). The Plains Bison now occupies less than one per cent of its original range from Canada to Mexico. While cross-breeding Bison with cattle has occurred frequently in the past, many herds have culled cattle genes, so the current level of cattle DNA in most Bison is low (0.6-1.8 per cent).

BULL SIZE (maxima):

- **WEIGHT** 1,270 kg (2,800 lb)
- **HEIGHT AT SHOULDER** 1.8 m (6 ft)
- **LENGTH OF HORN CORE** 31 cm (12 in)
- **LENGTH OF HORN SHEATH** 46 cm (18 in)

North American Wood Bison *(Bison bison athabascae)*

Evolving from *Bison antiquus* around 5,000 years ago, the Wood Bison occupied a vast boreal region from Alaska, Yukon and British Columbia east to Alberta and Saskatchewan. From an original estimated 170,000 individuals, only 250 survived the slaughter following the arrival of Europeans. In recent years, populations have varied from 7,000 to 10,000 (most carrying genes of Plains Bison), occurring in nine areas (with 16 conservation herds) located from Alaska, Yukon and British Columbia to Manitoba, with the largest herd in Wood Buffalo National Park (established 1922) in northeastern Alberta and adjacent Northwest Territories. Populations in Manitoba and Siberia were introduced outside the native range. The Manitoba herd was shipped into the Interlake Region in 1984, and offspring were released in 1991. The first of three shipments of Bison to Siberia was released in 2006. The Wood Bison now occupies less than one per cent of its original range. Protected since 1891 in Canada, it was designated Endangered in 1978 (COSEWIC), and since 2013 as Special Concern. The U.S. Fish and Wildlife Service has downlisted the species from Endangered to Threatened.

Compared to the huge numbers and long-distance seasonal migrations of the Plains Bison, the Wood Bison occurs in small scattered herds which move short distances during the seasons. Most travel less than 20 km, although a wandering mature bull may move over 100 km. Wood Bison average larger than the Plains Bison, the shoulder hump is less rounded, and there is less pelage on the head and forequarters. It gallops less, and there are fewer battles between males during the rutting period. It is well adapted to extremely cold conditions, inhabiting lowland meadows interspersed with boreal coniferous forest and aspen parkland, where it feeds on grasses, sedges, rushes, lichens, and the leaves and bark of shrubs and small trees. It copes well even in deep snow, pushing out feeding craters with its huge head. It holds its head higher than the Plains Bison, enabling it to routinely browse on higher vegetation. Likely the Wood Bison interbred routinely with the Plains Bison in contact zones where parkland-boreal forest graded into grassland-steppe.

BULL SIZE (maxima):

- **WEIGHT** 1,180 kg (2,601 lb)
- **HEIGHT AT SHOULDER** 2 m (6.6 ft)
- **LENGTH OF HORN CORE** 33 cm (13 in)

Bison bonasus

Wisent or European Bison *(Bison bonasus)*

There is still controversy over when the Wisent first appeared in the European fossil record. Genetic analysis dates its evolution from an unknown ancestor by 395,000 years ago, while other researchers suggest 60,000 years ago. It no doubt lived alongside the ancient Steppe Bison (*Bison priscus*), which has been proposed as its direct ancestor, or possibly arose through hybridization of Steppe Bison and the Aurochs 120,000 years ago. Recent genetic research suggests it may have descended from the Pleistocene Woodland Bison (*Bison schoetensacki*) around 12,000 years ago. The Wisent became widely distributed in Europe, from the British Isles and Scandinavian Peninsula to Italy, by 9,500 years ago, inhabiting both dense and open deciduous forest, open coniferous forest, and forest-steppe. Wisent-like paintings appear in cave art in France dated around 17,000 years ago. Certain Middle East artifacts from the third millennium BCE, Mesopotamia, accurately portray Wisent, so herds appear to have been present there for a period. The Roman naturalist Pliny The Elder first described the Wisent as "iubatos bisontes" in volume III of his *Naturalis Historia* (AD 77). "There are reports of a wild animal in Paeonia [region of modern Kosovo and North Macedonia] called the bonasus, which has the mane of a horse, but in all other aspects resembles a bull; its horns are curved back."

Following extinction of most prehistoric megafauna in Europe, this species became the largest land mammal over this vast region. *Bison bonasus* is taller, has longer legs, longer horns and tail, is less hairy, and less tamable than the American Bison. Its horns point more forward compared to sideways and upwards of the Plains Bison's. Two subspecies have been described: the Carpathian Wisent (*B.b. hungarorum*) of the broadleaf forests on the Carpathian Mountains, Moldova and Transylvania (extinct 1852), and the Caucasian Wisent (*B.b. caucasicus*) of the highland steppes in the Caucasus Mountains of eastern Europe (extinct 1927).

Although extinct in the wild, this species barely survived in captivity with 54 individuals, but only 12 individuals were involved in restoration efforts in zoos. Consequently, genetic variability is precariously low. Recovery efforts began in 1929 at a breeding facility in Bialowieza, Poland. In a remarkable conservation success story, the total number of Wisent has now increased to over 9,200, including 7,000 in 45 free-ranging herds, the largest in Belarus, Poland and Russia. Herds of various sizes are now found in 24 countries from the United Kingdom to Russia. The IUCN listed this species as Endangered in 1996, but with growing populations it has been downlisted to Near Threatened. More than 30 zoos worldwide maintain small herds and most participate in a European Bison Pedigree Book for historic and breeding purposes. As well, the European Association of Zoos and Aquariums (EAZA) operates a studbook program (EEP) for 450 captive Wisent in 77 participating institutions. In North America, the only recent zoo herd was in the Assiniboine Park Zoo in Winnipeg, which was acquired from a 1955 importation from European zoos by the Smithsonian National Zoological Park, Washington, D.C.

BULL SIZE (maxima):

- **WEIGHT** 2,025 kg (4,465 lb)
- **HEIGHT AT SHOULDER** 2.1 m (6.8 ft)
- **LENGTH OF HORN CORE** 65 cm (25.6 in)

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