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BISON bison. By Mary Meagher

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**Bison (Hamilton-Smith, 1827)**

*Bison* Hamilton-Smith, 1827:373. Type species *Bison bison* (Linnaeus, 1758). Proposed as subgenus, recognized as genus by Knight, 1849:408.

**CONTEXT AND CONTENT.** Order Artiodactyla, Family Bovidae, Tribe Bovini. The genus *Bison* includes two extant species, *B. bonasus*, the European bison or wisent, and *B. bison*, the late Holocene bison of North America.

**Bison bison** (Linnaeus, 1758)

*Bos bison* Linnaeus, 1758:72. Type locality earlier considered to be “Mexico” (Thomas, 1911); subsequently considered to be the “Quivira Region,” (central Kansas; Hershkovitz, 1957); redesignated as the Canadian River Valley of eastern New Mexico, United States (McDonald, 1981).

*Bison americanus* Brissos, 1762:56. Type locality America.

*Bison occidentalis* Lucas, 1898:678. Type locality Fort Yukon, Alaska.


*Bison jordan* (Linnaeus, 1758). Type locality Jordan, 1888:337. First use of present name combination.

**CONTEXT AND CONTENT.** Context as given above. Two subspecies are recognized (McDonald, 1981; Skinner and Kaisen, 1947). Synonymy for both subspecies follows Skinner and Kaisen (1947):

**B. b. athabascae** Rhoads, 1897:498. Type locality, within 50 miles southwest of Fort Resolution, Mackenzie District, Northwest Territories, Canada (*occidentalis* Lucas, *oregous* Bailey, and *hantingtoni* Figgins are synonyms).

**B. b. bison** (Linnaeus, 1758). Type locality America.

**DIAGNOSIS.** The following applies to the genus and species: horn cores in cross section at the base more or less triangular (males) or elliptical to circular (females), cores extend outward laterally from frontals forward of the occipital plane; parietals on or about the same plane as the frontals, parietal plane forming an obtuse angle with occipital plane; occipital broad; orbits tubular (more so in males), protruding anterolaterally; nasals broad, short, triangular; premaxilla triangular, nasal process of premaxilla not reaching nasals (Figs. 1 and 2). *B. b. bison* includes specimens dating 5,000 BP and less (McDonald, 1981; Wilson, 1975).

**GENERAL CHARACTERS.** The body is massive, tall but proportionately narrow in transverse profile (Fig. 3). Both massive- ness and height are accentuated by the shoulder hump formed by elongation of the neural processes of thoracic vertebrae and musculature of the shoulder and thoracic girdle. The hindquarters are lighter than the frontquaters; this disproportion is further accentuated by marked pelage differences between front and rear. Pelage is brown, long over the forehead, neck, hump, and frontquaters, short over the rear and tail. The tail is relatively short, with tufted tip. The head is large and carried low on the short, thick neck. Both sexes have short, black horns that curve upward and inward and taper to a circular, relatively sharp tip. Eyes are placed anterolaterally; ears are well buried in the long pelage of the head. The legs are relatively short and stout. Hooves are black with a nearly circular print.

Sexes are dimorphic with females similar to males but generally presenting a smaller, slighter appearance (Fig. 3). External measurements (in mm) for males and females, respectively (Hall, 1981; Meagher, 1973; Seton, 1929), are: total length, 3,040 to 3,800, 2,130 to 3,180; tail length, 330 to 910, 300 to 510; hindfoot, 580 to 680, 500 to 530; height at shoulder, 1,670 to 1,860, 1,520 to 1,570; body mass (in kg), 544 to 907, 318 to 545. Maximum recorded mass is 1,724 kg for a semidomestic bull (Hershkovitz, 1979). The hump structure is much larger and the neck is relatively stouter. They have longer pelage on the forehead, chin, ventral manne, and chaps of the forelegs, and a more pronounced line of demarcation between the longer hair of the forequarters and the shorter hair of flanks and rear.

**DISTRIBUTION.** Bison formerly were widespread in North America from Alaska and western Canada across the United States and into northern Mexico (Fig. 4). Occupation of marginal areas may have been intermittent (McDonald, 1981). McDonald (1981) believes the maximum geographic distribution of *B. b. bison* occurred in the late prehistoric period because of the many historical accounts of bison presence near the margins of the indicated maximum range (Christman, 1971; Reed, 1955; Roe, 1970; Rostland, 1960). The distribution of *B. b. athabascae* and *B. b. jordan* extend well into Canada (McDonald, 1981). They apparently disappeared from Alaska before historic times but there are unfossilized specimens (Skinner and Kaisen, 1947).

**DIAGNOSIS.** Today bison occur as geographically isolated population units in parks, preserves, and other public lands, and on private ranches and small holdings throughout and external to the maximum known geographic distribution (Fig. 4). Major free-ranging populations occur in Canada (Mackenzie Sanctuary, Wood Buffalo National Park and adjacent Slave River lowlands) and the United States (Yellowstone National Park); a few smaller units also exist (Reynolds et al., 1982).

**FOSSIL RECORD.** Although the time and place of origin of the ancestors of *B. bison* are obscure, the earliest dated remains of the genus occur from the late Pleistocene of Central Asia, with possible early Pleistocene occurrences from northern India and northern China (McDonald, 1981). Bison seemingly were confined to temperate and upland east Asia until after the early Pleistocene. Thereafter they appeared in southeastern and central Europe, becoming relatively common as fossils and in later cave paintings throughout much of Europe. Bison reached northern Eurasia during the middle Pleistocene and spread across the Palearctic into Asia, but survived in northern Eurasia until the very late Pleistocene (McDonald, 1981). They first appeared in the fossil record south of Beringia in North America in early late Pleistocene faunas (Guthrie, 1980; McDonald, 1981). Most specimens of bison are known from the late Pleistocene of North America and higher latitude Eurasia, and the Holocene steppes and adjacent forests of Eurasia and North America (McDonald, 1981).

The evolutionary line leading to *B. bison* remains controversial although there seems to be general agreement on many elements. *Proleptobos* from the early Pleocene may be the ancestor of the
Bos-Bison group of Bovini (McDonald, 1981). Leptobos, appearing later in the Pliocene and widely distributed in central and southern Eurasia during both the Pliocene and Pleistocene, may be either a common ancestor (Guthrie, 1980; McDonald, 1981) or a closely related taxon (McDonald, 1981). B. sivalensis, the earliest known species and possible ancestor of later lineages of bison, dispersed northward into Siberia by the middle Pleistocene or earlier (McDonald, 1981). This species and another poorly known early form, B. paleosinensis, seem to have been small bodied, small horned, and more cattle-like compared to later bison, and were probably adapted to a woodland–parkland environment (Guthrie, 1980).

Early in the middle Pleistocene the so-called steppe bison, B. priscus appeared (Guthrie, 1980). This larger bodied, larger horned bison apparently was the dominant form during the rest of the Pleistocene and may be ancestral to the North American forms (Guthrie, 1980; Wilson, 1975).

By the late Illinoian to early Sangamon the large steppe bison seems to have spread into the grasslands of central North America where they became even larger, with enormous horn cores reaching 2 m tip to tip (Guthrie, 1980). This form, B. latifrons or B. priscus latifrons, occurred in much of unglaciated North America but seems to have been most common from Alberta to Texas along the east front of the Rocky Mountains and the intermontane basins. Guthrie
FIG. 3. Photographs of a fully mature male (top) during rut and female (bottom) bison showing contrast in head and horn shape. Photographs courtesy of A. Stephen Johnson.

FIG. 4. Map illustrating probable maximum distribution of B. bison during late prehistoric times with the north-south axis of the primary range coincident with the central North American grasslands. The maximum extent of the range of B. b. athabascae is not as well known as that of B. b. bison. Map is fig. 23 from McDonald (1981) courtesy of University of California Press (scale added).

(1980) and Wilson (1975) believed this line decreased in size during the Wisconsin, grading eventually into the smaller B. antiquus. About 13,000–12,000 BP, a gradual diminution in size of B. priscus seems to have occurred in the far north (Guthrie, 1980) leading to B. occidentalis (Guthrie, 1980; Wilson, 1975). At the end of the Wisconsin, this northern line of B. occidentalis may have reinvaded the grasslands of the Great Plains to contact and interbreed with the more southern line of B. antiquus (Wilson, 1975). At this time the two lines may have been similar in size although somewhat different in cranial and horn-core morphology (Guthrie, 1980). During the Holocene, North American bison seemingly continued to diminish in body size while at the same time increase in numbers (Guthrie, 1980).

Guthrie (1980) pointed out that the rapid rate of bison evolution led to a bewildering assortment of taxonomic designations. The trend in recent years has been to synonymy (Guthrie, 1980; McDonald, 1981; Skinner and Kaisen, 1947; Wilson, 1975), but temporal and spatial trends seem to warrant subspecific status for resulting differences of form. In this view, then, the evolution of North American bison led to two Holocene species, the earlier B. priscus, and the extant B. bison, with their subspecies (Guthrie, 1980; Wilson, 1975).

FORM AND FUNCTION. The annual pelage molt begins late winter to early spring. Tattered patches of bleached winter hair may cling to the forequarters well into August. New growth is short, somewhat stiff, and nearly black. By late fall the winter coat of woolly underfur with overlying coarse guard hairs is essentially full grown. Head, underparts, flanks, and rear are dark brown, appearing black at a distance. The long woolly hair across the forequarters commonly lightens to bleached tan, most pronounced on older bulls. Usually there is a dark streak down the front of the hump, suggesting a mane, although the hair is scarcely longer than that over the shoulders.

Length of hair (in mm) has been estimated as follows: flanks and rear, 25; rump and hips, 50 to 90; shoulders and hump, 65 to 160; chaps, 150 to 190; and beard, 300 mm (Meagher, 1973; Soper, 1941). On bulls, the hair of the forehead may be 150 to

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210 mm, which may compact into a frizzy mat 100 to 130 mm thick at eye level (Lott, 1974). Peters and Slen (1964) found an average density of hair fibers per cm² at the midrib of bison calves to be about 2,900 for females and 2,182 for males. The winter pelage of bison showed a greater weight, density, and fineness of hair per unit area compared with that of three breeds of cattle (Peters and Slen, 1964). These pelage characteristics provide high hair per unit area compared with that of three breeds of cattle.

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Temperature apparently was exceeded at 100°C (Christopherson et al., 1979). When compared with cattle, digestibility coefficients for all nutrients in low quality (low protein, high fiber) diets were higher, as were the digestibilities of various native forages (Howley et al., 1981b). Rumen content lipids contained 4, 16, 17, 22, and 33%, respectively, of monoglycerides, triglycerides, sterols, phospholipids, and nonesterified fatty acids (Evans, 1964). Apparent digestibility in percent of a sedge hay diet was: dry matter, 51.3; crude protein, 38.3; crude fat, 64.2; neutral detergent fiber, 54.7; acid detergent fiber, 47.0; hemicellulose, 67.1; lignin, 25.2; and gross energy, 50.6 (Howley et al., 1981a). On this diet, bison showed an average daily gain in kg/day of 0.42 and 0.04 for summer and winter, respectively.

Bison have the ruminant digestive system with a four-compartment stomach consisting of the rumen, reticulum, omasum, and abomasum. Voluntary feed intake in kg kg body mass"/day" by bison was 0.009 on sedge and 0.011 on grass (Richmond et al., 1977).

During rumination a bolus may be chewed 38 to 70 times at a rate of about one chew/¡/ (Fischer, 1967). Pearson (1967) found that rumen microorganisms included eight species of ciliate protozoa and five morphological types of bacteria, with average total counts of 0.38 × 10^9/ml and 7.14 × 10^9/ml, respectively. Rumen content lipids contained 4, 16, 17, 22, and 33%, respectively, of monoglycerides, triglycerides, sterols, phospholipids, and nonesterified fatty acids (Evans, 1964). Apparent digestibility in percent of a sedge hay diet was: dry matter, 51.3; crude protein, 38.3; crude fat, 64.2; neutral detergent fiber, 54.7; acid detergent fiber, 47.0; hemicellulose, 67.1; lignin, 25.2; and gross energy, 50.6 (Howley et al., 1981a). On this diet, bison showed an average daily gain in kg/day of 0.42 and 0.04 for summer and winter, respectively. When compared with cattle, digestibility coefficients for all nutrients in low quality (low protein, high fiber) diets were higher, as were the digestibilities of various native forages (Howley et al., 1981b). Rumen ammonia concentrations and urinary urea levels appeared to be proportional to dietary N levels (Keith et al., 1981). Apparent absorption of N from the gastrointestinal tract was 3.50 g/100 g of dry matter; and the time of digests in feeding trials was 78.8 h (Schaefer et al., 1978).

Droppings are similar to those of cattle. On succulent feed, a flat mass of 30 cm diameter is common; with drier feed a more rounded, layered mass forms (Murie, 1954). Defecation rates of approximately once per h were observed in bulls (Herrig and Haugen, 1969).

The mean brain weight for four subadult males and two mature females was 458 g. Mean forebrain measurements (in mm) were: length, 114.3; width, 93.3; height, 64.1. Mean cerebellum measurements were: length, 44.8; height, 38.7 (Harper and Masner, 1976). In 4.5-year-old bison the mean chest height for males (n = 95) was 677 ± 3.3 mm and for females (n = 23) was 643 ± 7.0 mm; the mean foot load, in g/cm², was 884 ± 8.02 and 67.4 ± 4.97 for males and females, respectively (Telfer and Kelsall, 1979). These authors suggested that males might cope more successfully with increased snow depth, but that females might have a greater advantage when walking on hard or dense snow. The musculature of the neck and shoulders allows bison to forage by swinging the head from side to side to clear feeding areas. Mixed groups regularly foraged in snows of up to 70 cm deep (Hartigan et al., 1982). McHugh (1958) observed some bison to forage at 1,200 mm.

ONTOGENY AND REPRODUCTION. A few precocious female bison first conceive as yearlings but sexual maturity most commonly occurs at 2 to 4 years of age (Fuller, 1962; Halloran, 1968; Meagher, 1973). Sexual maturity in males is similar. A few show sperm in the epididymis as yearlings; by age 3 most males are sexually mature (Fuller, 1962; Shult, 1972). Although Halloran (1968) found that 2-year-old males might perform effectively as sires in the absence of older males, bulls usually do not breed cows until age 6 (Herrig and Haugen, 1969; Lott, 1981; McHugh, 1958).

The breeding season may extend from late June or early July through September (McHugh, 1958; Meagher, 1973; Shult, 1972). Although Halloran (1968) found that 2-year-old males might perform effectively as sires in the absence of older males, bulls usually do not breed cows until age 6 (Herrig and Haugen, 1969; Lott, 1981; McHugh, 1958).

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recorded in most herds, usually later in summer (Fuller, 1962; Lott and Galland, 1985; McHugh, 1958; Meagher, 1973).

Bull calves twice as large as cow calves are rare (Engelhard, 1970; Fuller, 1962; Halloran, 1968, Haugen, 1974; McHugh, 1958; Roe, 1970). At birth, the calf may weigh 15 to 25 kg (Rutberg, 1984). The fetal sex ratio usually favors males (Fuller, 1962; Haugen, 1974; McHugh, 1958; Meagher, 1973).

Calves are precocious; average times for 10 calves to first stand and first nurse were 10.9 min and 32.2 min, respectively (Lott and Galland, 1985). They may try to graze by 5 days of age (Shult, 1972) and will drink water after the first week (Engelhard, 1970; Shult, 1972). Engelhard (1970) noted a 1-month-old calf with partly digested grass in the abomasum; calves orphaned at 7 to 8 weeks of age have survived (Shult, 1972). Cows nurse their calves for at least 7 to 8 months (McHugh, 1958), but most calves apparently are weaned by the end of the first year (Halloran, 1968; McHugh, 1958; Roe, 1970; Van Vuren, 1984).

Age of physical maturity in bison apparently differs between the sexes. Bulls appear to attain near-maximum mass by age 5 or 6 with small increments thereafter (McHugh, 1958). Average mass of 237 known-age bulls suggests that maximum was reached at age 10 to 12; similar data for cows suggests that maximum size might be attained by 3 years of age (Halloran, 1968). Horn development provides a rough estimate of maturity for bulls; mature curve and thickness was attained by 7 to 8 years (Fuller, 1959). Cows attain full curvature by 3 to 5 years of age (McHugh, 1958).

Females may be seasonally polyestrous, with a cycle of approximately 3 weeks (Fuller, 1962). Estrus may last 9 to 28 h (Haugen, 1974).

Average longevity in bison has not been documented. Fuller (1959, 1962) placed the onset of old age at 12 to 15 years. In the wild, a few bison apparently survive more than 20 years (Meagher, 1973); records of a few known-age cows of 40+ years were cited by McHugh (1958).

ECOLOGY. An estimated 30 million bison inhabited North America about the time the modern man arrived (McHugh, 1972). Subsequently, bison were exterminated over a wide area. Various writers have chronicled this exploitation (Dary, 1974; Haines, 1970; McHugh, 1958; Roe, 1970). By 1903, a known 1,644 bison existed (Garrettson, 1938), mostly in zoos and privately owned herds. They survived near extermination as a wild species in two areas: Wood Buffalo National Park, Canada (Soper, 1941), and Yellowstone National Park, Wyoming (Meagher, 1973). Through establishment of additional public preserves and privately owned herds, bison numbered an estimated 75,000 in 1983 (Jennings and Hubbrin, 1983).

Prehistoric distribution occurred primarily on the central grasslands and northern parklands of North America, but habitats used ranged from semidesert to boreal forest where suitable grazing was available (McDonald, 1981). Bison are grazers at all seasons, with winter grazing usually more limited by snow cover than by availability of water, and grazed steeper slopes than cattle (Van Vuren, 1979). Bison and pronghorn showed spatial overlap but quite different food habits (McCullough, 1980; Wydeven and Dahloren, 1985). The existence of prairie dog (Cynomys sp.) towns apparently facilitated bison habitat selection for a shortgrass successional state in a mixed-grass community (Coppock et al., 1983). Among four species of ungulates on a shortgrass pasture, bison were the least selective and ingested the lowest quality forage (Rice et al., 1974; Schwartz and Ellis, 1981). In montane habitat in winter, bison appeared more restricted than elk (Cervus elaphus) to highly productive wet meadows where they ate snow while obtaining a large amount of food (Houston, 1982). In boreal forest—aspen—meadows of Elk Island National Park, elk and bison in winter overlapped most in habitat use but least in food habits; the reverse was true in summer (Telfer and Cairns, 1979). Telfer and Kelsall (1984) developed a morphological index in combination with behavioral information to evaluate snow-coping ability of eight species of ungulates; bison ranked below all but pronghorn (Antilocapra americana).

Use of forested areas appears limited except occasionally for shade, for escape from insects and other disturbances (Fuller, 1962; Meagher, 1973; Soper, 1941), and for shelter during severe winter storms (Fuller, 1962; Soper, 1941). Foraging in more open forest may be relatively frequent (Fuller, 1962; Soper, 1941) or incidental (Meagher, 1973). Extensive forests were traversed between open foraging areas and on seasonal migrations (Fuller, 1962; McHugh, 1958; Roe, 1970; Van Vuren, 1983).

Most free-ranging bison appear to be seasonally migratory; movements are directional and also altitudinal in some regions (McHugh, 1958; Meagher, 1973; Soper, 1941; Van Vuren, 1983). They moved distances of about 14 to 40 km in montane habitat (McHugh, 1958), and as much as about 240 km in boreal forest-parkland habitat (Soper, 1941). Travel was usually along well-defined travel routes in montane areas from elevations of 1,828 to 3,049 m (Meagher, 1973). In boreal forest—parkland movements, bison were more fan-like from winter to summer ranges (Soper, 1941). Apparent influences on seasonal migrations included supply and accessibility of forage (Soper, 1941), spring weather conditions and temperatures, and fall snow storms at higher elevations (Meagher, 1973).

In smaller preserves, bison may have individual but overlapping home ranges. On Santa Catalina Island, 16 bison cows had average home ranges of 36.1 km², ranging from 26.9 to 70.5 km² (Lott and Minta, 1983a); in the Henry Mountains, Utah, six cows had average home ranges of 52 km² (Van Vuren, 1983). Factors which appeared to influence home-range size were plant productivity (Lott and Minta, 1983a; Van Vuren, 1983), environmental homogeneity, and the presence of large ungulates on a shortgrass pasture, bison were the least selective and ingested the lowest quality forage (Rice et al., 1974; Schwartz and Ellis, 1981). Daily movements of bison herds between foraging sites in summer are usual (McHugh, 1958). These averaged 3.2 km in a montane valley (McHugh, 1958) and 2.8 km in coastal scrub-grassland on Santa Catalina Island (Lott and Minta, 1983a). In a shrub-steppe habitat the average stay in one area was about 80 days (Lott and Minta, 1983a; Van Vuren, 1983). Apparent influences on summer range movements are seasonal vegetation changes, interspersal and size of forage sites, the rut, and the presence of biting insects in large numbers (Meagher, 1973). Size of preserve and availability of water may be additional influences (McHugh, 1985).

Population structures for free-ranging herds of Wood Buffalo National Park, Henry Mountains (Utah), and Yellowstone National Park, respectively, were: calves, 16, 21, and 22%; yearlings, 9, 13, and 17%; 2- and 3-year olds, 15, no data, and 16%; cows, 39, 36, and 28%; and bulls, 21, 30, and 16% (Fuller, 1960; Meagher, 1973; Van Vuren, 1979). Productivity for females 2.5 years and older was 53, 60, and 52%, respectively. A sub-population with a relatively younger age structure showed productivity of 76% (Fuller, 1962). The proportion of calves in mixed herds in shrub-steppe was 18 to 20% for 10 calves. The number of males may be more usual in a population undergoing increase (Meagher, 1973). Population composition of calves may be consistent during the first year of life (Meagher, 1973), or may decline June to December at about 2% per month (Fuller, 1962). Recruitment may occur as yearlings (Fuller, 1962) or after the second year (Meagher, 1973). In all these of the foregoing populations, adult males appeared to outnum-
Mortality in most herds is man-caused through commercial and sport harvest, or subsistence hunting. The wolf (Canis lupus) is apparently a predator of free-ranging bison. McHugh (1958) reported 65% of the winter diet of wolves in Wood Buffalo National Park, but wolves did not appear to have a negative impact on the bison population (Fuller, 1962). However, wolf and human predation may be additive. On the Slave River lowlands a severe winter storm apparently triggered a 50% decline in bison numbers from 1,900 to 1,250; bison declined further to about 750 (Reynolds et al., 1982). Bison separated from herds appeared to be the primary targets of attack (Haynes, 1982).

Periodically, severe winter weather is the primary mortality agent in Yellowstone National Park; winterkill to some degree occurs every year with differential mortality among age and sex classes (Meagher, 1973). Unusually severe spring storms may cause both high calf mortality and increase adult mortality (Meagher, 1976). Winterkill also occurs frequently in and adjacent to Wood Buffalo National Park (Reynolds et al., 1982). Accidents are usually insignificant but several thousand bison have drowned in single occurrences (Reynolds et al., 1982).

At least 31 endoparasites have been reported from bison, mostly from captive herds where confinement may enhance occurrence. Efects in wild bison appear insignificant; 2 of 26 species of nematodes were reported from free-ranging herds: the lungworm, Dictyocaulus sp., and the coelomic worm, Setaria sp. (Reynolds et al., 1982).

Anthrax outbreaks cause sporadic but appreciable mortality in northern bison. Tuberculosis may affect as much as 50% of the bison in Wood Buffalo National Park but effects of the disease on the population remain obscure. Brucellosis occurs at varying rates, sometimes more than 50% (Reynolds et al., 1982); it may cause abortions but does not appear to prevent population increases (Reynolds et al., 1982). Brucellosis occurs at varying rates, sometimes more than 50% (Reynolds et al., 1982); it may cause abortions but does not appear to prevent population increases (Reynolds et al., 1982).

Behavior. Bison are gregarious, forming herds according to sex, age, season, foraging conditions, and habitat. Females of all ages, calves, most males 2 to 3 years old, and one to a few older males form mixed (sometimes called cow) groups throughout the year (Fuller, 1960; McHugh, 1958). Older males join these groups in increasing numbers as rut approaches (McHugh, 1958), but are apparently not reported from free-ranging herds: the lungworm, Dictyocaulus sp., and the coelomic worm, Setaria sp. (Reynolds et al., 1982).

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