The wood bison (*Bison bison athabascae* Rhoads) in relation to hypotheses on the origin of the American bison (*Bison bison* Linnaeus)

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The late Pleistocene evolution of the genus *Bison* has been controversial, in particular, the origin of the American bison (*Bison bison* L). A review by Guthrie (1970) brought the present evidence on early bison in America *(Bison latifrons, B. antiquus)* under an ordered conception. Early American bison are probably descendants of an early wave of steppe wisent akin to *Bison priscus* that crossed Beringia from Siberia. The origin of the modern American bison, however, remained unsatisfactorily resolved (Geist 1971 a). There are three competing hypotheses to account for its origin:

1. American bisons arose from a late wave of steppe wisent *(Bison priscus)* that crossed into North America (Flerov 1965; Guthrie 1970)
2. American bisons arose from the very earliest immigrants of this genus through progressive reduction in horn and Body size and are thus the direct descendants of *Bison latifrons* and *B. antiquus* (Kurtén 1968)
3. American bisons are descendants of the last wave of bisons, a forest bison from Siberia akin to *Bison bonasus,* to cross into North America (Geist 1971 a). This makes the American bison a recent offshoot of a very primitive form.

In recent years, theoretical advances in our understanding of ungulate evolution, part of a greater theoretical advance in our understanding of the relationship between environment and social behaviour, have made it possible to arbitrate between these competing hypotheses. In particular, the publications by Geist (1971 a, b, 1974 a, b); Jarman (1973) and Estes (1974) are relevant. In addition, some data on wood bison *(Bison bison athabascae)* can be brought to bear on the problem.

The first hypothesis, that *Bison bison* arose from *Bison priscus,* can be regarded as most unlikely, as was pointed out earlier (Geist 1971 a). It requires an evolutionary gymnastics far beyond anything known or probable, entailing, for instance, selection against effective combat and display organs, as well as against efficient mastication. *Bison priscus* was a specialized form differing considerably in its coat characteristics from either *B. bonasus* or *B. bison bison* as the reconstruction from Paleolithic art showed (see Geist 1971 a, Fig. 7).

The second hypothesis, that *Bison bison* is a straight line descendant of the first wave of bisons to enter American, cannot be dismissed as yet. However, it predicts two testable propositions and will fall or stand by them.

a. It predicts that, barring differences in size or proportions due to allometric growth, the skulls of *Bison latifrons, B. antiquus, B. preoccidentalis,* and *B. bison* will not differ. The third hypothesis, however, states that the skulls of *B. latifrons* and *B. antiquus* are likely to differ qualitatively from those of *B. preoccidentalis, B. occidentalis* and *B. bison,* since *B. occidentalis,* plus its predecessor *B. preoccidentalis* are the dispersal form – a large-bodied phenotype – of the Siberian forest

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bison. Conversely, these large-bodied large-horned forms differ phenotypically from *Bison bison,* not genotypically, the latter being the phenotype adapted to exploit scarce resources at carrying capacity, following the colonization of American by these later primitive bisons (GEIST 1971 a). Thus, should the skulls of exceptionally large *Bison bison athabascae* or *bison* resemble those of *occidentalis,* not only in larger horn cores and proportions but also in the arrangement of skull plates, and should this differ from the earlier large-horned bisons, then the second hypothesis can be dismissed.

It must be said in favour of the second hypothesis that a size reduction after colonization has been noted in a number of Pleistocene mammals (see GEIST 1971 a). A difficulty proponents of the second hypothesis would have to explain is how the evolution of large horns can be reversed while simultaneously selecting for body dominance displays and concomitant display organs.

b. A second test of the second hypothesis is closely related to the first test: the hypothesis predicts that the tooth structure of early bisons *(B. latifrons* and *B. antiquus)* will be more primitive than that of *Bison bison,* not further advanced. If it is found that the early bisons did have relatively broader and longer, more hypsodont, molars, and/or the row of molars is relatively longer compared to the premolars than in *Bison bison,* then the second hypothesis is probably invalid, since it would imply that early American bisons experienced selection against effective mastication after having experienced selection for effective mastication. At present, relevant studies to negate the second hypothesis are outstanding.

The third hypothesis, that *B. bison* evolved from a *B. bonasus* form in eastern Siberia, has some support in the findings of extinct bisons in Siberia which were similar to the wisent or American wood bison. While FLEROV and ZABLOTSKI (1961) claim the former, FLEROV (1967) claims the latter. Regardless of this ambiguity, a wisent – like Siberian bison did exist until very late in the Pleistocene. The third hypothesis predicts on the basis of the "dispersal theory" (GEIST 1971 a, b) that forms most distant geographically from the parent form are also most divergent in social adaptations and ecological adaptations from the parent form. Conversely, those forms closest to the origin of radiation are most similar to the parent form, ecologically and morphologically. Therefore, the American bison closest to Siberia, the wood bison *(Bison bison athabascae)* ought to be less divergent from *Bison bonasus* than should the prairie bison *(Bison bison bison).* The predictions of the "dispersal theory", however, are more precise than this. Advanced in evolution means greater ecological specialization, and a greater investment in display organs and display, resulting in larger and more complex morphological display organs. The dispersal theory also predicts an increase in body size from primitive to advanced form, provided the populations compared have a similar energy budget. Since body size and proportions are strongly influenced by the availability of energy and nutrients for growth, and are thus very plastic phenotypically (see SHACKLETON 1973; SHACKLETON et al. 1975), we cannot use body size as a test criterion. The skulls of wood bison are normally larger than those of prairie bison, particularly if the latter came from high density populations (see SHACKLETON et al. 1975).

In ecological adaptations, it is predicted that the wood bison ought to be closer to *Bison bonasus* than the latter to the praire bison. Detailed studies of the ecology of pure wood and prairie bisons are not available, and little can be said beyond the obvious, that like the wisent (HEPTNER et al. 1961) the wood bison is closely associated with forests, be it in recent or in historic times. The prairie bison does have a "grazing" dentition compared to the "browsing" dentition of the wisent: FLEROV (1965) claims that the wood bison is intermediate in these characteristics. A critical study of the dentition and crania of wood and plains bisons of large

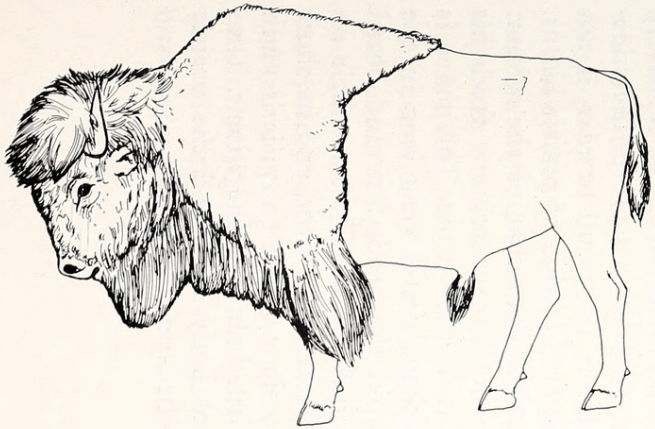

Fig. 1 a

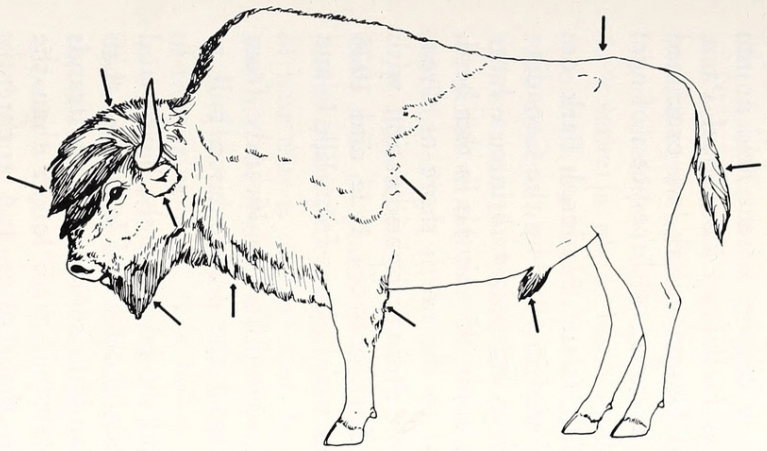

Fig. 1 b

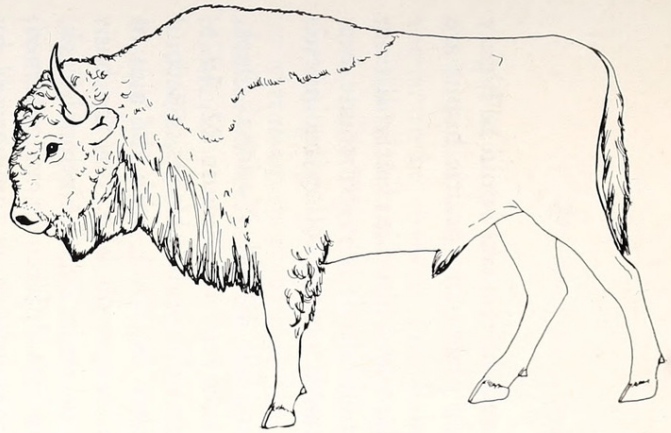

Fig. 1 c

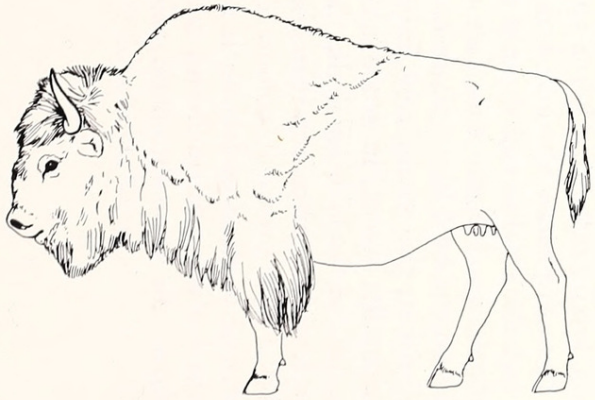

Fig. 2 a

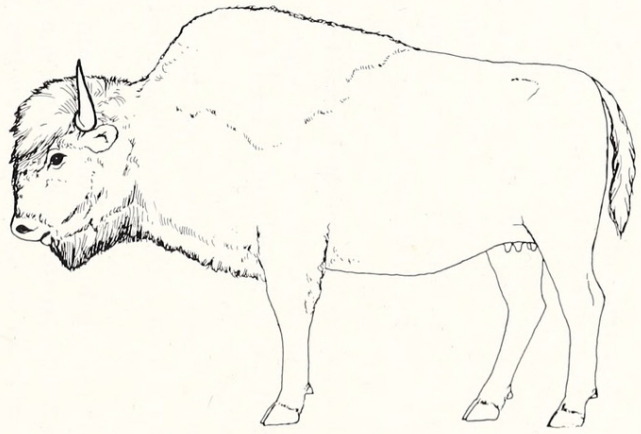

Fig. 2 b

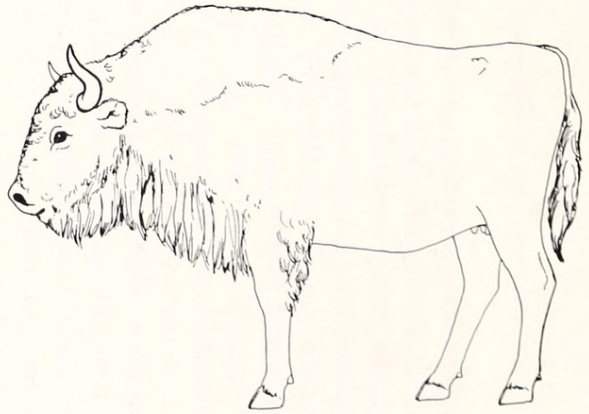

Fig. 2 c

Fig. 1 (above). A comparison of the bulls in the genus *Bison.* a = *Bison bison bison,* the prairie bison; b = *Bison bison athabascae*, the wood bison; c = *Bison bonasus*, the wisent. The arrows point to features on the wood bison in which it differs from the prairie bison and wisent. (Further description in text). — *Fig. 2 (below).* A comparison of the females in the genus *Bison:* a = prairie bison; b = the wood bison; c = the wisent

samples with the aim of detecting ecologically determined differences would be highly desirable. Differences in ecological adaptations between plains and prairie bisons are at present not adequately established.

In its morphological social adaptations, however, the wood bison is clearly distinct from the prairie bison. As predicted by the third hypothesis, it is intermediate between the wisent and prairie bison. We base this statement on the following investigation.

Wood bison and prairie bison were compared in Elk Island National Park, Alberta, on two separate occasions. Following the discovery on August 22, 1975, that the wood bison differed in diagnostic features from the prairie bisons, a second trip was made to Elk Island National Park on October 24, 1975, with the aim of examining the animals critically and recording their images on film. On the basis of this film record, as well as pictures of plains bison taken in Banff National Park, we compiled the ink sketches in Figs. 1 and 2 to show the differences we observed. We base our descriptions of wisent on published characteristics as summarized by GEIST (1971 a), as well as on observations we made on captive wisent held at the Alberta Game Farm, Edmonton, and those captive in Hellabrun Zoological Park, Munich, Germany. During our last trip of Elk Island National Park, we examined eighteen adult wood bisons, of which eight were bulls in excess of three years of age; we examined an undetermined number of prairie bisons.

It is crucial to note that the wood bisons of Elk Island National Park are offspring from a remnant herd of these animals discovered in 1957 by the Canadian Wildlife Service. In 1959, members of this herd were transplanted into a large enclosure in Elk Island National Park. There are now about 95 animals in this herd. A second herd of pure wood bison was transplanted to the north shore of Great Slave Lake to save this form of bison from extinction through hybridization with the plains bison liberated in Wood Bison National Park between 1925 and 1928 (MCHUGH 1972). Our descriptions are based purely on wood bisons from Elk Island National Park.

To a trained observer, the wood bison bull and cow differ significantly from those of prairie bison. The wood bison bull differs from the prairie bison bull as follows:

1. The hair on top of the head, between and behind the horns, in the beard, and the midventral line on the neck and nape is significantly shorter and less dense than in prairie bison bulls of equal age. In a few wood bison bulls some long thin strands of hair fell from the forehead over the eyes; these strands were longer than the corresponding strands in plains bison bulls. Due to the shorter and apparently thinner display hair on the head, the head in the wood bison appears to be relatively smaller than in prairie bison, the horns appear longer, and the ears protrude noticeably further from the head. The beard of the wood bison, be it bull or cow, is not only shorter, but also smaller and sharply pointed compared to that of prairie bisons. The beard of the wood bison is in fact not much larger than that of the wisent. Moreover, the wisent bull has a short but distinct ventral mane running from his beard to the brisket; the wisent cow has a rather long ventral mane. This mane is very short, virtually absent, in wood bison bulls, although it is very long in the prairie bison. In the wood bison bull, the long hair on the head, face and beard appears to be less dark in colour than that of the prairie bison. The same hair on the wisent bull is light brown in colour. The colour of the lower neck, and its short ventral hair fringe in the wood bison is of the same colour as the body; it is much darker than the body in prairie bisons, while it is a little lighter in the wisent. Thus the wisent shows the least chromatic enhancement of body hair, and the prairie bison the most.

2. The wood bison lacks the long "chaps" or "pants" on the front legs that typify the bulls and cows of prairie bisons. The upper parts of the front legs of wood bisons appear to be covered with hair of much the same length and colour as the hair on the flanks. In the prairie bisons, however, the upper front legs grow very long, very dark, hair. Together with the long hairs on the neck, beard and head, the pants on the front legs give the prairie bison a "massive" appearance in the front quarters; by virtue of short hair in the same regions, the wood bison appears "leggy". The absence of chaps is the most striking difference between wood bisons and plains bisons.

3. The "robe" found on the shoulders, hump and neck is noticeably smaller, shorter haired and darker (less contrasting with the dark hair on the back, flanks, ribs and belly) in the wood bison than in the prairie bison. Therefore the wood bison's hump appears more compressed than that of the prairie bison when viewed from the front. In the prairie bison bull, this robe tends to be goldcoloured, contrasting sharply in colour with the dark brown body hair and the black head, nape and chap hair. It is also distinctly set off in the plains bison by virtue of its longer hair, and runs into the long hair on the front legs. In the wood bison, the robe does not extend onto the front legs but gradually diminishes, due to shortening hair onto the lower shoulder region; the robe is bisected into two halves by a mid-dorsal line of dark hair; in plains bison bulls, this division is absent or rare. In wood bison, the colour of the robe is a reddish-brown, rather than golden. In the prairie bison, the robe appears to close over the neck and back. In the wisent, the robe is only a little lighter than the body; it extends downward from the mid-dorsal line far less than in either wood or plains bisons, and fuses into body hair quite high up on the shoulder (Fig. 1 c).

4. The penis sheath tuft of wood bison bulls appears to be shorter and thinner than that of plains bison bulls, barely longer than that of the wisent bull. In the plains bison (but not in the wood bison) the penis sheath tuft appears to be formed of hair that is darker than the body hair. The penis tuft is subject to wear in snow and may be missing by springtime.

5. The tail of the wood bison appears to be longer and heavierhaired than that of the plains bison. It is, however, noticeably shorter than that of the wisent.

6. The contour of the back from the top of the hump to the root of the tail is a descending line in the prairie bison, but not in the wood bison, and particularly in the wisent. In the latter, the pelvis is relatively larger than in the plains bison and appears a little "cattlelike". The dorsal line descends from the top of the hump to the lumbar regions and then becomes a horizontal line whose contour is interrupted by the pelvis protruding dorsally. In the wisent, this protrusion is quite pronounced, which in turn causes the back line to rise from the rear of the lumbar region to the dorsal point of the pelvis and then continues level to the root of the tail.

The relatively small pelvis of the plains bison is shared by a number of advanced Ice-Age ungulates, particularly the mammoth. In the lineages of a number of other ungulates, we find not only a shift of proportions enhancing the front quarters, but also a ridiculous relationship of the enlarging hornlike organs or display organs in the front and a shortening tail in the rear (see GEIST 1971 b). The relatively smaller hindquarters of prairie bison are – following the predictions of the dispersal theory – a combat adaptation; they permit greater mobility in evading attacks by an opponent and speedier turns for counterattack.

From our comparisons during the course of sketching body outlines of bisons, we predict that the wood bison will be found to be relatively taller in the hindquarters than the prairie bison; the development of the hindquarters in the wood bison is intermediate between that of the wisent and the prairie bison.

7. In view of the fact that the wood bison is intermediate between wisent and prairie bison in pelage characteristics, we suspect from the sighting of wood bison calves in dark pelage by August 22, 1975, that wood bison calves lose their juvenile coat earlier than do prairie bison calves. Unfortunately hair shedding is subject to considerable phenotypic variation and is a function of the quality of the environment (see GEIST 1971 a). We urge that the following hypothesis be disproven: that the juvenile pelage of wood bison is intermediate in its characteristics between that of wisent (which does not have a light-coloured juvenile pelage, HEPTNER et al. 1961) and that of the prairie bison.

In summary, the display organs of the prairie bison bull differ from those of the wood bison bull by virtue of longer hair length (except on the front, between the eyes) and colour contrast: those of the wood bison bull are enhanced in hair length and colour over those of the wisent, excepting the shorter ventral neck mane of the wood bison bull. We find a shortening of the tail concomitant with enhancement of display organs in the front of the animal, a correlation noted repeatedly in ungulates (GEIST 1971 a), as well as a decrease in the relative size of the pelvis and height of the hips. The wood bison bull is thus quite intermediate between the wisent and plains bison bull in the development of display organs, albeit he is closer to the prairie bison in external appearance than to the geographically more distant European forest wisent.

The females of wood and prairie bisons also differ substantially. The wood bison cows are less sexually dimorphic than those of prairie bisons; wood bison cows are noticeably closer in body size, horn structure, pelage characteristics and body proportions to bulls, than is the case for prairie bisons. The cows of prairie bisons in Elk Island National Park and Banff National Park appeared somewhat "wisentlike" by virtue of their cattlelike horn form and horn orientation, and long ventral neck mane. Wood bison cow females had horns shaped more similarly to those of bulls; they also have relatively and absolutely thicker horns than plains bison females. In hair coat they were darker than plains bison females; we did not notice that wood bison bulls were darker than plains bison bulls, although they had a somewhat darker robe. In plains bison females the ventral neck mane appears to be longer than that of bulls, and is more distinctly set off, very much as one sees in wisent. In wood bison cows, we did not note this difference; like the bulls, they had virtually no midventral neck mane. Wood bison cows were on the whole more difficult to identify as cows than is the case for plains bison or for wisent.

Our present understanding of the evolution of sexual dimorphism in ungulates (GEIST 1974 a) suggests that the wood bison evolved under conditions in which both sexes were more closely associated spatially during the course of the year than was the case for either the plains bison or the European wisent. The same inference can be reached from an ecological consideration of the areas inhabited by wood bison. The argument runs as follows: despite some differences in habitat preference and food habits, the natural history of *Bison bonasus* and *Bison bison* is remarkably similar (HEPTNER et al. 1961; FULLER 1960, 1962; MCHUGH 1972; MEAGHER 1973). Cows tended to segregate from bulls and form larger herds than bulls outside the rutting season. Grouping into cohesive units is a means of reducing predation, particularly by wolves. Since cows formed larger herds than did bulls, they also reduced the forage resources more quickly, and consequently had to move more frequently as a unit. Since cow herds were large, they required larger areas of concentrated pasture than did the smaller bull herds. Thus bulls, by virtue of forming smaller groups, could exploit smaller and more dispersed areas of forage resources than could cows. This was, in turn, aided by fewer costly movements between areas of forage resources. Consequently, it is logical within the above exploitation syndrome

that single bulls tend to do the least movements, probably because they occupy small areas that supply their forage needs year round. The antipredator strategy of the bulls lies in grouping, larger body size and, presumably, competence in facing down wolves, and reduced conspicuousness by staying in areas of low population density. The greatest segregation of sexes could, of course, be achieved in areas of continuous grasslike vegetation, such as in the prairie, where consequently the largest and most mobile herds formed as a means of minimizing predation. However, in regions with scattered small patches of forage, such as meadows in forested country alongside streams, in regions where snowfall impeded mobility and extracted a high cost of movement, only small groups of bisons could form during winter. Now the antipredation strategy of the cow must shift from flight and the security of the herd, to facing predators much as the larger bulls in their small groups would be doing. Moreover, the more marginal the habitat, the more likely bulls and cows would come together on the same meadows during winter. Therefore cows would have to compete more frequently against at least young bulls for resources, and it would be to their advantage to look like bulls so that predators could not readily identify them as the smaller-bodied sex. These conditions would select for malelike appearance of females, as would a third condition: large aggressive cows could reduce harassment from sexual approaches of young bulls, and thus save energy from maintenance for reproduction. The larger the patches of habitat the lower and less cumbersome the snow, the shorter the winter and the higher the productivity of the land the more likely the evolution of sexual dimorphism in bison and the better the ecological segregation of the sexes, with the bulls exploiting the smaller areas of habitat often peripheral to the female ranges. One can also predict from the foregoing well-developed submissive behaviour in the bison, since predation is heavier on individuals away from herds than in herds; complex submissive behaviour has been described by LOTT (1974) for the plains bison. In open country, where bulls can see each other, we expect very intense competition by males for females during the rut, and, consequently, relatively intense selection for effective combat and displays. Therefore the rut of the plains bison ought to be a far more showy, noisy affair than that of the wisent or the wood bison. Again this appears to be the case, as judged from the descriptions of LOTT (1974) and MCHUGH (1972) for bison and HEPTNER et al. (1961) for wisent; for wood bison there are no observations.

It may be noted that the surviving bisons of Yellowstone National Park, according to MEAGHER (1973) are hybrids of native wood bisons and introduced plains bisons. The view that wood bison lived in Yellowstone is based on old crania with horn cores larger than those found in skulls of plains bisons, as well as on the words of early travellers that the mountain bisons were darker than the plains variety. It must be noted that large horn cores and skulls are typical of individuals which have suffered little shortage of energy and nutrients during growth, and could thus be a phenotypic expression of plains bison genes (see GEIST 1971 b; SHACKLETON 1973; SHACKLETON et al. 1975). The external appearance of Yellowstone bisons as revealed by photographs in MEAGHER (1973) is that of prairie bisons, except for a small or missing penis tuft in bulls. A picture of two cows taken in 1894 in Hayden Valley identifies them as plains bison by virtue of long chaps, long ventral neck mane, a full beard and forward-angled horns. It is therefore likely that wood bison of northern Canada differ in external appearance from the mountain bison living formerly under somewhat similar marginal conditions in Yellowstone Park.

Our descriptions show that the wood bison of northern Canada is a form distinct in external appearance from the plains bison of the type found in northern Montana during pioneer times, and today are known as offspring of the Pablo herd (see MCHUGH 1958). The wood bison differs in external characteristics from

the prairie bison by at least as much as a black-tailed deer *(Odocoileus hemionus columbianus)* differs from a mule deer *(O. h. hemionus)* (see COWAN 1936), and differs more than does a Rocky Mountain bighorn *(Ovis canadensis canadensis)* differs from a desert bighorn *(O. c. nelsoni)*. Hybrids of wood bisons and plains bisons, as now found in Wood Bison National Park on the Athabaska delta, show primarily plains bison features in their pelage. It appears that plains bison features dominate over those of wood bison. One must recognize at this point, and applaud, the farsightedness both of the Canadian Wildlife Service and of the National and Historic Parks Branch in rescuing the wood bison, and ensuring that this form may live on removed from the threat of extinction.

Summary

The wood bison differs in pelage characteristics from the plains bison by virtue of somewhat less developed display hairs and relatively larger hindquarters; this form is thus intermediate between the European wisent and the American plains bison in external appearance.

The pelage characteristics of the wood bison coincide with the predictions of the "dispersal" theory (GEIST 1971 b), provided the assumption is made that the American bison evolved from a forest wisent and not from a steppe wisent. Predictions arising from competing hypotheses are discussed.

The females of wood bison are less sexually dimorphic than those of plains bison, a finding which is explained ultimately by one ecological difference between the two forms: the wood bisons occupy smaller and more scattered areas of grassland than do prairie bisons.

The external characteristics of wood bisons are not found in bisons from Yellowstone Park, as illustrated in photographs taken in Hayden Valley late in the 19th century.

The pelage characteristics of plains bison dominate in hybrids of wood bisons and plains bisons.

Zusammenfassung

Der Waldbüffel (Bison bison athabascae Rhoads) im Verhältnis zu Vorstellungen über den Ursprung Amerikanischer Bisons (Bison bison Linnaeus)

Der Waldbüffel unterscheidet sich vom Präriebüffel in Haartracht und Körperform. Die Haartracht des Waldbüffels ist etwas geringer entwickelt, und Hinterläufe sowie Keulen sind größer und höher. Somit kann der Waldbüffel in seiner äußeren Erscheinung zwischen Wisent und Präriebüffel eingeordnet werden. Die Haartracht des Waldbüffels stimmt mit den Aussagen einer Theorie überein, welche die Evolution von Großsäugern in Beziehung zu ihrer geographischen Verbreitung erklärt („dispersal theory", GEIST 1971 b). Hier muß vorausgesetzt werden, daß der amerikanische Büffel vom Waldwisent, nicht aber vom Steppenwisent abstammt. Die verschiedenen Hypothesen werden diskutiert.

Der Unterschied zwischen Waldbüffelkühen und -bullen ist geringer als bei Präriebüffeln. Unterschiede zwischen den beiden Unterarten können auf ökologische Unterschiede zurückgeführt werden. Waldbüffel bevorzugen kleinere Flecken von Grasland als Präriebüffel.

Die typischen Merkmale des Waldbüffels sind nicht an jenen Individuen aus dem Yellowstone National Park zu finden, die im späten 19. Jahrhundert in Hayden Valley photographiert wurden.

Bei Mischlingen von Wald- und Präriebüffeln dominiert die Haartracht des Präriebüffels.

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BUCHBESPRECHUNGEN

DENTON, D. A.; COGHLAN, J. P. (eds.): **Olfaction and Taste.** Vol. V. New York — San Francisco — London: Academic Press 1975. 460 pp., $ 22.50.

Seit erstmals 1962 in Stockholm finden alle drei Jahre internationale Symposien zum Thema Geruch und Geschmack (ISOT) statt. Die wissenschaftlichen Beiträge und Diskussionen erscheinen in Folgebänden. Vorliegend werden die Ergebnisse des 5. ISOT von 1974 in Melbourne wiedergegeben. Die Themenkreise sind: Physiologie von süßem, saurem, salzigem und bitterem Geschmack, Ontogenese von Geschmack und Geruch, Chemorezeption bei aquatischen Tieren und bei Insekten, Geruch allgemein; Geruch bei Vögeln, Geruch und Pheromone im tierischen Verhalten. Die Darlegungen an Wirbellosen und Wirbeltieren sind Ergebnisse aus verschiedenen zoologischen Disziplinen. Der interessierte Säugetierkundler kann dem Buch sicherlich manchen nützlichen Hinweis über den modernen Wissensstand an Ratte, Maus, Hamster, Kaninchen, Katze, Affen und Mensch entnehmen.

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