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## BISON EVOLUTION AND ZOOGEOGRAPHY IN NORTH AMERICA DURING THE PLEISTOCENE

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### ABSTRACT

*The fossil record and information about contemporary forms provide evidence that the evolutionary pattern of bison cannot be interpreted as either a unidirectional decrease in horn size or as a series of successive invasions to the New World from the Old. Rather, some species have persisted and remained relatively unchanged for long periods of time, while elsewhere other contemporaneous species were changing quite rapidly. Although the trends in the evolution of bison horn size have been remarkably regular, major reversals have taken place.*

*Bison arose in Eurasia and have had a much longer history there than in North America. In spite of this longer history in the Old World, bison have undergone greater evolutionary changes in North America. This can be explained by a different mode and intensity of competition in the New World.*

*The major points presented are the following: (1) The giant-horned *B. latifrons* was a New World product. (2) *B. priscus* (= *B. crassicornus*) appeared early as a holarctic northern species and remained in that niche until the late Wisconsin (Würm). (3) Most of the other bison species in the late Pleistocene were derived indirectly or directly from this widespread northern species. (4) Middle and Late Pleistocene bison can be placed into four species: *B. priscus*, which can be dated at least as far back as early mid-Pleistocene; *B. latifrons*, which extends back at least to late Illinoian (Riss) time (it is possible that *B. latifrons* gave rise to *B. antiquus*; if so the species *B. alleni* should be maintained); *B. antiquus*, which originated during the early to middle part of the Wisconsin (Würm) glaciation; and *B. bison*, which was a late Wisconsin product. (5) *B. latifrons* became extinct, at least over most of its range, in pre-Wisconsin time. *B. priscus* and *B. antiquus* became extinct in the late Wisconsin, and *B. bison* still exists in relict populations. (6) Two or more species of bison have not occurred sympatrically for extended periods of time. (7) Neither the "orthogenetic" nor the "wave" theory adequately accounts for the evolution of bison in North America; rather, the fossils can only be explained by a combination of invasions from Siberia and evolutionary changes that occurred in the new environment.*

## INTRODUCTION

PLEISTOCENE stratigraphers in North America have shown more than usual interest in the history of bison, presumably because some of the phylogenetic lines have undergone comparatively rapid evolution and these fossils may thus be used as sensitive stratigraphic indicators. Unfortunately, bison chronology has not been plotted with such precision that one can always key the fossil by the stratigraphic unit or the unit by the fossil, nor has there been complete agreement on the phylogenetic pattern. Bison evolution has been an area of heated controversy among many Pleistocene paleontologists and no doubt will continue to be for some time. In spite of, or perhaps because of, these disagreements, something of a synthesis is beginning to emerge. I have undertaken here the task of bringing this synthesis up to date. No doubt this version will undergo considerable refinement in the future and perhaps major revisions, as records of phylogenies become more complete and chronologies more refined.

In general, paleontological studies emphasizing stratigraphy are characterized by a tendency to subdivide taxa, for obvious utilitarian purposes. As interest shifts to the biology of the organism, taxa become more inclusive. This phenomenon can be attributed to the fact that the concepts of interpopulational and intrapopulational variation, both vertical and horizontal, were introduced into paleontology from biology, although these concepts suffered long from malnutrition, even there, under the burden of their typological predecessors. Since paleontology has been a subdiscipline of geology rather than biology, paleontologists have been, by tradition, taxonomic "splitters." The study of bison evolution in North America has been approached primarily from a geologist's viewpoint and interests. In this analysis, I have attempted to unite the varied interests of both geology and biology.

One of the main factors which has frustrated bison phylogenists is the nature of characters available for tracing evolutionary patterns. Bison post-cranial structures have differed little through time or spatially. With the exception of the horns, almost the same can be said of the skull. Flerov (1965) has illustrated several

cranial differences among living bison groups, but these character differences appear to be mainly adaptations to local environments. If bison had no horns, some paleontologists would consider placing all of the fossil and recent bison into one morphological species. This is the crux of the difficulty. Horns appear to be the most variable character among taxa, yet, used alone, horns have growth and variational characteristics which make mapping of phylogenies hazardous. Some of these difficulties have been reviewed elsewhere (Guthrie, 1966a). Horns show a tremendous variational lability. As well as having an additive ontogenetic growth pattern, they are responsive to changes in nutrition, hormonal imbalance, physical accidents, and the overall health of the animal. In addition to this great spatial intrapopulational and interpopulational variation, the fact that horns are important as a secondary sexual characteristic makes them very responsive to natural selection. Horn size and shape have undergone rapid changes, including apparent evolutionary regressions.

In using horns as a taxonomic character we are dealing with a quasi-indeterminate growth form; the concept of average size or shape borders on being meaningless, since all individuals of all species begin life with no horns at all and thereafter develop horns which vary in size and shape throughout ontogeny. Although techniques are available for use on characters exhibiting indeterminate growth patterns, these are as yet essentially inapplicable to bison because adequate samples of age structure, variation within and between age classes, sexual variation, and the nature and extent of interspecific variations for each of the groups being compared are not available. Thus, parameters such as *means* are of questionable value, except when taken in a general way. Also, one cannot expect the standardized variation parameters based on a normal distribution to be applicable.

During the late Pleistocene the bison of Eurasia were basically a northern genus. Bison apparently are a northern homologue of cattle, *Bos*, both phylogenetically and ecologically. Both genera have a long history in Eurasia that extends back to the early Pleistocene (Zeuner, 1945). Cattle and bison are so closely

related in their morphology that many postcranial skeletal elements are easily confused unless examined in detail (Olsen, 1960). The two are also very similar serologically (Stormont, Miller, and Suzuki, 1961). They have occupied the large-bovid grazing niche across Eurasia, *Bison* to the north and *Bos* in the south. In the far south other closely related large bovids, the buffalo, occupied a similar habitat. Intermediate zones between these three subhabitats existed and harbored both genera; thus bison co-existed with *Bos*, and *Bos* with buffalo (Zeuner, 1963). The chief osteological differences between these three bovid forms are in the horns. There are other major differences, such as the length of neural spines and the degree of orbital extension. The length of the neural spines is taxonomically distinct, but evolutionary studies have not, as yet, made use of this character. Unlike the cattle and buffalo, the orbits of bison protrude (telescope out) from the skull. This may be a compensation for the thick mass of wooly hair on the face of the bison (Guthrie, 1966b).

Several studies (Larson, 1940; Szaniawski, 1960) have shown that *Bos* and *Bison* are predominately herb eaters, particularly of grass and grass-like plants, and differ little in their dietary preferences. Thus, during the middle and late Pleistocene *Bos* probably served as a biotic barrier to the expansion of *Bison* southward and *Bison* as a barrier to the northward expansion of *Bos*. However, in the highlands of Asia *Bos* gave rise to a cold-adapted form, the yak, which managed to penetrate into the far northern latitudes. This latter line, or a closely related form, crossed into North America and their remains are found in Alaska (Frick, 1937).

This entire group of large bovids probably began as an aural-crepuscular park feeder, eating in open grass clearings during twilight and dawn and then retreating to the protection of the forests to ruminate. Running in a northward cline, from the buffalo to cattle and then to bison, there is an increasing tendency to remain in the open areas throughout the day and to rely on flight or the protection of the herd, rather than seclusion, for safety.

Thus in Eurasia the grazing habitat was geographically partitioned between these three

forms. (It is not completely valid to treat all the buffalo and subtropical cattle as one ecological form; however, to go into more detail here is beyond the scope of our specific interest.) *Bison* did not expand to the south because of competitive exclusion, and likewise *Bos* was able to penetrate northward only in a single limited case. In the colonization of North America, however, no such limitations were placed on the southern extensions of *Bison*. The other two groups were not able to successfully colonize the New World, leaving bison as the only large bovid to compete with the native plains grazers. In this new environment the bison were free to undergo considerable range expansion and phylogenetic change. The various features of bison evolution are thus more dramatic in the New World, where it was able to invade the habitats of less efficient inhabitants. It is within this ecological setting that bison evolution is here re-examined.

#### THEORIES OF BISON EVOLUTION

Most of the taxonomic studies of fossil bison have been done on American forms, because, for reasons just noted, the greatest interspecific variation is found there. It is due to the apparent lesser degree of diversification in Eurasia, and perhaps to some degree to a different taxonomic orientation of paleontologists, that bison have not presented the same problems in Eurasia as they have in North America. Thus, concern with bison evolution has historically been heavily weighted in favor of Nearctic forms.

During the early history of Pleistocene paleontology in America it was not uncommon to give any horn core the status of a new species if it was slightly different from any other type that had been described; consequently, the literature abounds with forms such as *Bison regius*, *B. angularis*, *B. oliverhayi*, *B. rotundus*, *B. californicus*, *B. ferox*, *B. texanus*, *B. taylori*, *B. pacificus*, *B. sylvestris*, and *B. kansensis*, which have since been lost in the sea of synonymy.

Although fossil bison are referred to in the literature in hundreds of cases, there have been only two papers in the past several decades which have dealt in detail with bison evolution in North America. The first of these was a preliminary study by Schultz and Frankforter

(1946) and, a short time later, a more elaborate review by Skinner and Kaisen (1947). These two works have profoundly affected later concepts of bison evolution and Pleistocene stratigraphy as well.

Although Skinner and Kaisen speak of the chronologies in more general terms, they are in basic agreement with the major tenet of Schultz and Frankforter's work, which is, essentially, that the oldest bison in North America have the biggest horn cores, the later ones horn cores of medium size, and the latest ones small horn cores. Both state that this sequence of horn core diminution corresponds, respectively, to early mid-Pleistocene, late Pleistocene, and Holocene.

Although they are in agreement on the above point many major differences exist between the two works. Schultz and Frankforter conceived of the early large-horned invaders as becoming successively smaller horned in a gradation from *B. latifrons* to *B. bison* in one phylogenetic sequence. I will call this concept the *orthogenetic theory*. Almost at the opposite extreme, Skinner and Kaisen visualized little phylogenetic change in the North American forms. Instead, they explained the diversity as successive waves of migration from Eurasia. I will later refer to this as the *wave theory*.

According to Schultz and Frankforter the phylogeny follows the sequence, *B. latifrons*, *B. alleni*, *B. antiquus*, and *B. bison*. The primary character used is horn-core size. Skinner and Kaisen, as well as having a vertical (chronological) species differentiation, constructed a model of several species existing in a given place at one time. Also, in addition to size, they based their phylogenies on the degree of dorso-ventral horn compression and the degree of curvature or twisting. According to their model, the first wave of bison came over into North America via the Bering land bridge in the early or mid-Pleistocene. These species were *B. latifrons*, *B. chaneyi*, and *B. alleni*. The second wave, following the same route, consisted of *B. crassicornis*, *B. preoccidentalis*, *B. alaskensis*, and *B. geisti*. The very late Pleistocene saw the occurrence of two other new forms: *B. antiquus*, derived from *B. alleni* of the first migration, and *B. occidentalis*, an even later form derived from the Alaskan *B. preoccidentalis*. *B. occidentalis* then gave rise to *B. bison*

in recent times. Skinner and Kaisen thus accounted for the diversity of North American forms primarily by immigration from Eurasia in the middle to late Pleistocene followed by some degree of phylogenetic change in the very late Pleistocene and Recent.

In a more recent paper, Fuller and Bayrock (1965) interpret the late Wisconsin and recent bison phylogeny as a late branching of *B. bison occidentalis* from *B. crassicornis*, which in turn gave rise to *B. bonasus* and the two living subspecies of *B. bison*. According to their phylogeny, *B. bison occidentalis* and *B. crassicornis* lived contemporaneously with the form also found in the earlier Pleistocene, *B. latifrons*.

Dalquest (1961) suggests a general picture similar to the pattern presented by Schultz and Frankforter (1946) and Skinner and Kaisen (1947), except that he follows Hibbard (1955a) in his later date of bison invasion into central North America. He indicates three major horn size groups. The first group, *B. latifrons*, *B. chaneyi*, and *B. alleni* were found during the Illinoian glacial and Sangamon interglacial. These giant-horned forms were replaced by the medium horned forms, *B. occidentalis* and *B. antiquus*, during the Wisconsin glacial, and these in turn were replaced by the modern *B. bison*. He does not indicate the source or origin of these species, but does imply that they do not represent a phylogenetic gradation.

Allen (1876) also proposed a type of orthogenetic theory of bison evolution when he stated that both the New World and Old World medium horned bison, *B. antiquus* and *B. priscus* developed from the large horned *B. latifrons*. The species *B. americanus* (*B. bison*) subsequently arose from *B. antiquus*, and in the other independent line *B. priscus* gave rise to *B. bonasus*.

The theory presented by Flerov and Zablotski (1961) pictures *B. latifrons* colonizing North America in the mid-Pleistocene and decreasing in horn size into the late Pleistocene as *B. antiquus*. Then there was a recolonization in the very late Pleistocene by *B. bison*, which replaced *B. antiquus*. In a later study Flerov (1967) proposed that the northern bison species, *B. priscus*, gave rise to both *B. bonasus* and *B. bison athabasca*. The latter he classified as *B. priscus athabasca*. He also suggested

that *B. alleni*, which came from *B. latifrons*, developed into *B. antiquus* (he reclassifies *B. antiquus* as *B. bison antiquus*). He thus proposed, like Allen (1876) and Schultz and Frankforter (1946), that the New World bison evolved in a gradation from *B. latifrons* through *B. antiquus* to *B. bison*. He differs from other authors by separating *B. bison bison* and *B. bison athabasca* (his *B. priscus athabasca*) into two different species with quite different origins.

Hillerud (1966) has followed the orthogenetic model of Schultz and Frankforter. He derived *B. bison* from *B. antiquus* and *B. antiquus* from *B. alleni*. The unique aspect of his theory is that he places *B. occidentalis* as a subspecies of *B. antiquus* and calls it *B. antiquus occidentalis*. This subspecies arose from *B. crassicornis*.

These are at present the major theories of bison evolution. Although they represent most of the possible permutations, there are some common threads that unite them, and they also contain numerous inconsistencies that can be resolved.

#### CRITIQUE OF THEORIES

Strangely enough, from the beginning there has been an unquestioned assumption by paleontologists concerned with bison evolution in North America that *B. latifrons*, the gigantic-horned form found in mid-Pleistocene deposits from the Great Plains, was an invader from Eurasia. This idea has persisted in spite of the fact that no comparably large horned forms have ever been found in Alaska or in Eurasia. A more tenable explanation is that *B. latifrons* was a New World product, evolving from an Eurasian immigrant with medium-sized horns, as Flerov (1967) has recently observed. Contrary to the concepts of bison evolution as a continual stage of horn reduction, the overall pattern of bison horn evolution in North America, as in Eurasia, is characterized by increasing size, followed by an irregular trend of size decrease. The bison of the early Pleistocene of Eurasia did not have extremely large horns (Fischer, 1963).

Although records from the Great Plains show a gradual decrease in horn size from mid-Pleistocene to the living bison (Schultz and Frankforter, 1946), this pattern is not commonly observed in other regions in the holarctic. The

general picture of decrease in horn size from very large horned forms is surely a correct interpretation, but the diverse faciations, migrations, and replacements seem to be more complex than the orthogenetic model indicates. The orthogenetic theory also fails to take into account the living Eurasian bison and the problem of its New World affinities, as well as the relationships of the now extinct northern *B. priscus* (= *B. crassicornis*). The close relationship of living Old World and New World bison indicate the necessity of finding a fairly recent common ancestor, which is most difficult to do within the orthogenetic theory. *B. priscus*, a species with medium-sized horns, occurred in Alaska and northern Eurasia and existed almost unchanged at least throughout the latter half of the Pleistocene and only became extinct (either by rapid evolution or elimination) as recently as the late Wisconsin.

Synonomizing the Alaskan *B. crassicornis* specimens with the Siberian and other Eurasian *B. priscus* seems appropriate since there is a morphological gradient across the Holarctic. Skinner and Kaisen (1947) recognized this continuum when they referred some of the Siberian specimens to *B. crassicornis*.

The phylogenetic pattern presented by the Alaskan fossils directly affects the plausibility of the wave theory with even more fatal consequences than it does the orthogenetic theory. The ubiquitous northern species, *Bison priscus* (= *B. crassicornis*), is present in Alaskan and Siberian deposits dating from Illinoian to late Wisconsin, and has been recorded in Pre-Illinoian sediments (Péwé and Hopkins, 1967). Even though thousands of medium-horned bison fossils have been found in northern Eurasia and in Alaska there is still good reason to believe that these represent just one species. If one considers all the factors that influence horn size, the variations within this series fall well within the range of variability of a comparable modern species. All other medium-horned species described from the latter half of the Pleistocene of Northern Eurasia and Alaska fall within the expected variation of this one species which, because of priority, should be referred to as *B. priscus*. Not unexpectedly, this synonymy fits into the general pattern found in northern ungulate communi-

ties which, apparently without exception, involve only one variable species per genus; for example, *Equus caballus*, *Alces alces*, *Rangifer tarandus*, *Ovibos moschatus*, *Saiga tatarica*, *Cervus elaphus* and *Elephas (Mammuthus) primigenius* were all monotypic species. Along with *B. priscus* these comprise almost the entirety of Illinoian- and Wisconsin-age ungulate assemblages throughout the northern part of the holarctic.

There are two species, *B. alleni* and *B. chaneyi*, recognized from post-*B. latifrons* and pre-*B. antiquus* sediments in the great plains. Most paleontologists who have worked recently with bison assume that one of these was a degenerate (in horn size) descendant of the *B. latifrons* line, or that both were. Although there is support for this assumption, there is also some evidence to the contrary. Actually, the published distinction between *B. alleni* and *B. chaneyi* is so nebulous that the two are operationally inseparable (Dalquest, 1957). Moreover, all the horn measurements referred to in the literature as being diagnostic of *B. alleni* (and/or *B. chaneyi*) show considerable overlap with the large samples of *B. priscus* from Alaska. The means of the measurements of these characters are obviously not the same for *B. alleni* and *B. priscus*, but on face value they are not different enough to give the former "species" a taxonomic distinction above that of a chronological or geographical subspecies. Some of the Alaskan *B. priscus* have even been referred to *B. alleni* (Hay, 1913). The chief difference between *B. priscus* and those specimens now referred to as *B. alleni* is not in the horn cores but in the cranium. The crania of the *B. alleni* specimens are more like *B. latifrons*, i.e., large and robust with less protruding orbits. However, the published indices of horn length of *B. alleni* are almost half those of *B. latifrons* with no overlap (Skinner and Kaisen, 1947; Brophy, 1965). Compared to *B. priscus* (= *B. crassicornis*), on the other hand, *B. alleni* shows considerable overlap in every index of horn size or shape (Brophy, 1965). Thus, one is confronted with the decision of either thinking of the *B. alleni* line as a continuation of *B. latifrons* that has converged upon the *B. priscus* horn characters, or as a side branch of the *B. priscus* line that has converged on the *B. lati-*

*frons* type of crania. The evidence is still inconclusive. Since there is such a great size discrepancy between the adult male horn cores of *B. alleni* and *B. latifrons*, however, it would appear that the specimens referred to as *B. alleni* came from the *B. priscus* line and replaced *B. latifrons*, acquiring in the process some of the characteristics of the displaced species. Orbital protrusion and skull size may well be directly related to the particular demands of the immediate environment (Guthrie, 1966b). However, the hiatus between *B. alleni* and *B. latifrons* may simply be due to incompleteness of the fossil record.

The fossils now considered to be *B. alleni* would have had to undergo few changes from *B. priscus* ancestors, in fact so few that specific recognition for the former is difficult to justify. This phylogenetic scheme would account for the several specimens far to the south of Alaska which are referred to as *B. priscus* (= *B. crassicornis*) (Romer, 1951; Fuller and Bayrock, 1965).

There is little argument that *B. antiquus* descended from the line represented by the specimens that have been referred to as *B. alleni* or *B. chaneyi*. On this point most agree, since there seems to be a gradation, through time, into *B. antiquus*.

Both Skinner and Kaisen (1947) and Schultz and Frankforter (1946) have interpreted *B. bison* as a species of North American origin. This poses some difficulty in accounting for the origin of the Eurasian *B. bonasus*, which, because of its morphological similarity and ability to interbreed freely with *B. bison*, has been considered distinct by some only at the subspecific level or at least as a closely related species. If one classified *B. bonasus* as a completely separate line the difficulty still remains because of the fossil remains, *B. bison athabasca* (= *B. occidentalis* = *B. bison occidentalis* = *B. priscus diminutus*), found in northern Asia (Flerov, 1967).

Fuller and Bayrock (1965) attack the problem by suggesting that *B. bonasus*, *B. bison athabasca* and *B. bison bison* branched from *B. bison occidentalis* at approximately the same time [less than 8,000 years Before Present (= B.P.)]. Their interpretation could only be possible if they classified some Asiatic forms as *B. bison occidentalis*, and pushed their date for the

branching back earlier. It is difficult to postulate that *B. bison* of North America gave rise to *B. bonasus* of Eurasia at such a late date, because the land bridge between the two continents was probably not available then for large ungulate interchange (Hopkins, 1959).

If one assumes that the New World *B. bison* could not have given rise to the Old World *B. bonasus* then there are two alternative positions to choose between. The first alternative is to postulate a Eurasian origin for *B. bison* (Flerov and Zablotzki, 1961). There is a good fossil sequence in Northern Russia from a medium-horned form (*B. priscus*) to smaller-horned form (*B. bison occidentalis*). The *B. bison* in North America would then be considered a post-glacial immigrant. Skinner and Kaisen (1947) essentially had *B. bison* colonizing North America from Eurasia, except they called the immigrants *B. preoccidentalis* and *B. occidentalis*.

Fossils of small-horned bison are found in late Wisconsin and post-glacial deposits of northeastern Siberia and central Alaska. (These have been variously called *B. priscus diminutus*, *B. priscus athabascaae*, *B. occidentalis*, and *B. bison athabascaae*.) This is the route the invaders would have had to take, and at the right time for colonization through the Cordilleran Corridor. The early *B. bison* forms were slightly larger in horn size than living subspecies. This size reduction seems to have taken place concurrently in all modern forms, both in Eurasia and North America. There is an unresolved minor sub-argument within this Old World origin theory as to whether *B. bison occidentalis* arose from *B. priscus* in Alaska as it did in Siberia, or replaced the Alaskan *B. priscus* after the latter had become extinct. Since the large mammals of Alaska were really a part of the Siberian community, the first alternative seems more plausible.

The future validity of either form of the Old World origin theory of *B. bison*, as in the case of the next alternative, will depend upon the accumulation of more material and dates from the critical area of Alaska and Siberia. Although the explanation invoking a Eurasian origin is made unappealing by the late date required for such an extensive North American invasion, it

has considerably more appeal after the other alternative is evaluated.

To take the second position, that *B. bison* originated in North America, one must contend that the living North American bison and the living and extinct Eurasian small-horned bison evolved independently. Continental correlations and cross comparisons of the origins and chronologies of the small-horned bison prove to be no encumbrance to this theory, although a more basic problem does develop: As was pointed out above, one must explain the morphological similarities between the Eurasian and North American bison. This general type of problem could be entitled *Coon's Dilemma*, as it has appeared elsewhere in another context (Coon, 1963). The dilemma originates from the general doubt about the existence of *polyphyletic species* (without hybridization). If one is to support rigorously the extreme orthogenetic theory, it means that starting from a large-horned form, the North American *B. bison bison*, the living Eurasian *B. bison bonasus* (= *B. bonasus*) and the extinct *B. bison occidentalis* of Siberia, originated independently through a long succession of reductions in horn core size which resulted in subspecies which, as some contend, are not sufficiently distinct to warrant the status of separate morphological species. The less orthodox supporter of the orthogenetic theory may indicate a later separation than the mid-Pleistocene. However, one escapes the dilemma only when he grades into the preceding alternative, which specifies a common ancestor of Eurasian, or perhaps amphiberengian, origin (*B. bison occidentalis*) from which came both the Eurasian and North American small-horned bison during late Wisconsin times.

The phenomenon of range extension outward from the Great Plains, even in recent times (Roe, 1951), by *B. bison* argues for the Eurasiatic invasion theory of the species' origin. The fact that *B. bison* apparently failed to penetrate the eastern and western mountain ranges which bound North America, or at most, did so only to a very limited degree, also suggests a late arrival. *B. antiquus*, however, which according to some theories gave rise to *B. bison*, was able to establish itself on the west coast where it did not grade into *B. bison* phylogenetically, but became extinct without being replaced.

Flerov and Zablotski (1961) have argued that the differences between the two North American subspecies can be explained by the interbreeding of the early *B. bison* immigrants with the native species *B. antiquus*. Since this occurred on the more southern boundary the result of these hybridizations was *B. bison bison*. They contended that the forms to the north, *B. bison athabasca*, did not have occasion to interbreed with *B. antiquus*, and consequently remained more similar to *B. bonasus*. Some interbreeding could have been possible between *B. bison* and *B. antiquus*; however, the difference between the modern subspecies can also be explained by direct adaptation. Elsewhere, Flerov (1967), in order to explain the differences between living bison groups, has suggested that *B. bonasus* (= *B. bison bonasus*) and *B. bison athabasca* arose from *B. priscus* and that *B. bison* arose from *B. antiquus*. The differences between *B. bison bison* and the other living representatives of the genus need not be due to such separate phylogenetic histories, however; rather, they can be explained easily by a moderate rate of adaptation to the environment each occupies. Flerov (1965) reviews these adaptations in detail. Schultz and Frankforter (1946) and later Hillerud (1966) have visualized *B. antiquus antiquus* giving rise to the modern *B. bison bison*. The evidence against this position is derived from the fact that replacement of the former by the latter is rather abrupt (Wendorf, 1961). Dalquest (1961) has even reported an instance of the two species occurring contemporaneously at the same locality. Published radiocarbon dates from the *occidentalis* and *athabasca* material indicate a post-glacial occurrence in North America throughout the Wisconsin glaciation. Actually, no dates on *occidentalis* have ever been established that would pre-date man's arrival into the New World. Hillerud also courts *Coon's Dilemma* when he says that his *B. antiquus occidentalis* was derived from *B. crassicornis* (= *B. priscus*) while *B. antiquus antiquus* came from the *B. allenii* line.

Thus far I have discussed mainly the controversies involved in tracing phylogenies. There is also the problem of vertical separation of species. Unlike the real questions of "where did species X originate and how long ago did

the existing species Z separate from the existing species Y?," the decision as to how many species one phylogenetic line has included is, in a sense, rather arbitrary. The source of the difficulty is that our taxonomic conceptualizations and nomenclature are geared to one slice of time or a very incomplete phylogenetic sample. When we begin to get numerous specimens from transitional periods the system must incorporate, or at least tolerate, the idea of a "process" or "continuum." Bison horn evolution has been comparatively rapid and horns changed at a time most likely to be well-documented. The combination of these two factors has resulted in the problem of where to delimit the species in one phylogenetic sequence. For example, if *B. bison* came from the larger-horned *B. priscus*, are the intermediates to be given separate specific rank? Rather than attempt to manage the many difficulties that would result in too many separations, I feel that it is more prudent to label, as species, the forms which represent ends of continuums that were relatively stable for extended periods but to consider the intermediates simply as transitional stages. Yet, one can retain the subspecific designation for the utilitarian purposes of Pleistocene stratigraphers in such sequences as *B. bison occidentalis* → *B. bison athabasca* → *B. bison bison*.

#### SYNTHESIS

The following discussion presents a more or less reconstituted theory of bison evolution and zoogeography in North America that embodies parts of several theories as well as some new features.

Looking first to Eurasia, we see smaller-horned bison (Fisher, 1963), sometimes called *B. schoetensacki*, becoming larger-horned in the early to mid-Pleistocene, at which time they are called *B. priscus*. During this time the species became widespread with many local variants. Other similar bovids were present, and characteristic distributional patterns arose as ecological separations became more mature. Buffalo occupied the southern-most part of Eurasia, particularly the humid southeast. The true cattle specialized in exploiting the temperate climatic belt, while bison became associated with the irregularly expanding northern environment.



This species of bison, *B. priscus*, is found in deposits dating from early to late Pleistocene throughout most of northern Eurasia and in middle Pleistocene deposits from Alaska. *B. priscus* seems to have flourished in the northern niche. If the thousands of fossil ungulate remains removed from the Alaskan late Pleistocene muck deposits are used as an index, one can only conclude that bison must have been the dominant ungulate in this northern habitat (Guthrie, 1968).

The major expansion of bison into the interior of North America appears to have taken place in late Yarmouth or Illinoian. The presence of bison is used as an indicator of Nearctic Rancholabrean mammalian faunas (see Repenning 1967, for an excellent review of the Palearctic-Nearctic mammalian dispersal). There is evidence that *B. priscus* did reach Alaska in Kansan times, but as Repenning points out, the concept of a North American Rancholabrean fauna is really not applicable to Alaskan faunas since Alaska was more a part of Asia than North America during the glaciations. When the *B. priscus* in Alaska extended their range southward to the central part of the North American continent (Figs. 1 and 2) they found a large complex ungulate community, but apparently not one competitive enough to prevent their colonization. In Eurasia, bison were subject to

keen competition on their southern periphery by a closely related species. They met with no similar species in North America. The native grazing community in North America had been dominated chiefly by horses, *Equus*, a genus with which bison had sympatrically evolved and competed in Eurasia. In their new habitat, this line of bison increased considerably in body and horn size, as is common in many ungulate species during the early phases of the exploitation of a more suitable habitat.

This giant-horned species, *B. latifrons*, persisted at least during a glacial age and part of an interglacial, then became extinct. During its existence *B. latifrons* must have affected the evolutionary patterns of the native grazers — increasing their capacity to offer more effective competition even though their numbers may have been reduced in the process. Although it is difficult to support on a quantitative basis because of the lack of population studies, the percent of *Equus* fossils in North America seems to decline in the late Pleistocene. The expansion of bison may have been responsible for this decline. If so, this type of replacement is consistent with the general pattern, beginning in the mid-Tertiary of artiodactyl increase at the expense of the perissodactyls.

Radical increases and decreases in horn size

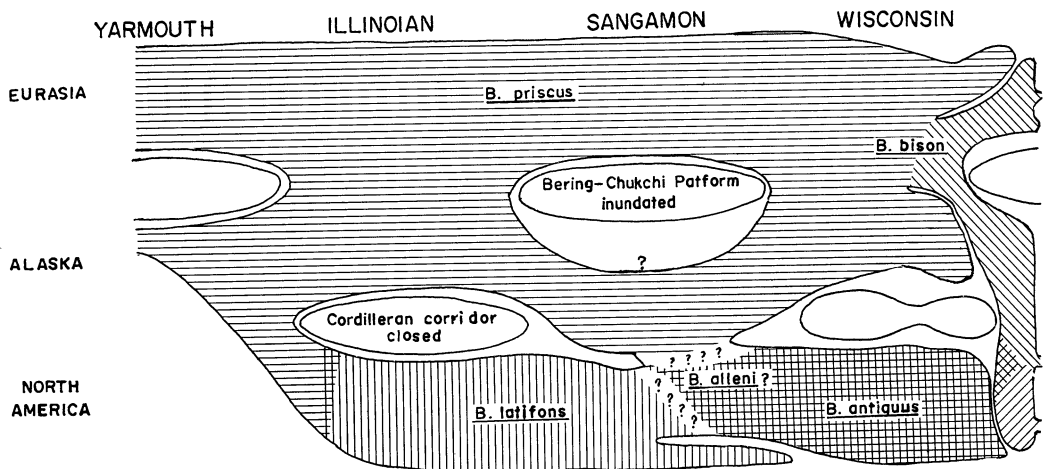


FIG. 1. THE RELATIONSHIP BETWEEN THE BISON OF EURASIA, ALASKA (ACTUALLY THE AMPHIBERINGIAN REGION), AND CENTRAL NORTH AMERICA

The periodic isolation of Eurasia and Alaska is due to flooding of the Bering-Chukchi Platform during Interglacials; the isolation of Alaska from the rest of North America during the glacials is a result of the continental ice sheet. *B. Bison* is illustrated here as having an Amphiberingian origin.

such as are found in the *B. latifrons* line have long presented an unsolvable problem to paleontologists. However, recent studies on the biology of horns and horn-like organs (Geist, 1966a) have given us a much better foundation to understand evolutionary changes in horns. Geist has shown that there is an intimate relationship between horn size and the nature of the intraspecific aggression patterns. Like several other bovids, the bison use a semi-broadside stance (fronto-lateral display) when confronting other members of the species in an intimidating manner. Unlike the short-haired cattle groups which use only the dewlaps (skin hanging from the neck) and elongated neural spines in the lumbar area such as in the gaur (*Bos gaurus*) to present a more massive image, the bison have, in addition, a thick woolly mat of hair covering the forequarters and head, which performs much the same function. The evolutionary "choice" of using thick fur in addition to skeletal changes for display functions was perhaps a product of the genus' long history in the north where thick fur would not be much of a detriment, and might even be an asset to survival.

But as was proposed above, in colonizing North America the bison could move far into the south, an area that was equivalent to the *Bos* niche in Eurasia. In the south the heavy coat of hair used for display was probably reduced, as I indicated in an earlier study of bison orbital protrusion (Guthrie, 1966b), which is directly correlated with the amount of facial hair. Geist (1966b) also has shown that in several ungulate groups (sheep are the classic example) the extent of body display paraphernalia is inversely correlated with horn size. He found that large horns, in addition to their role as weapons, are also used for display, replacing such structures as manes and ruffs. The two lines of evidence are: (1) an indication of hair reduction in *B. latifrons*, and (2) large horns in known cases always being used as display organs. These suggest that *B. latifrons* shifted emphasis from body wool to horns for display. The shifting of the display organs toward the head is a trend Geist found in a number of artiodactyl lines and is generally accompanied by a more frontal display posture. The rudiments of this trend can be seen in short-horned bison (Fuller, 1960). Geist (1966b)

mentions that the increased use of horns as display organs in sheep seems to be correlated with the colonization of new habitats which have not yet been exploited.

Such may also have been the case with *B. latifrons*. The increased supply of nutrients increased the survival of the larger individuals and those with larger horns, allowing them to contribute more to future generations (it is the larger-horned males which do most of the breeding in a population which uses horns as a means of social ranking). Increased intrapopulation competition between ungulates generally results in a heritable decrease in individual size (Foster, 1965). By the same mechanism, but perhaps independently, a lowered nutritional level tends to result in a genetic decrease in horn or antler size. The reverse also presumably holds, i.e., an increase in the mean horn size requires an increase in available nutrition. Some of these forces will have to be considered if we are to understand the evolutionary causes of horn change in bison. The theory of bison horn evolution presented in this paper is illustrated in Fig. 3.

Unlike the conditions when *B. latifrons* arrived, future bison in the Great Plains were never again to experience a situation which enabled them to reach this large size, and were, moreover, to undergo a general trend in horn reduction into recent times. It is probable that before its extinction *B. latifrons* also underwent some horn reduction at least over part of its range. The chronological distribution of *B. latifrons* is still in question, although convincing arguments have been presented (Hibbard, 1955a; Green, 1962) for an Illinoian and Sangamon age in the midwest. There is a possibility that *B. latifrons* may have existed into early Wisconsin as relic populations in restricted refugia (e.g., Savage, 1950).

The bison of California provide examples of extinction both by, and without, interspecific competition. If Savage (1950) is correct in saying that *B. latifrons* existed during the Wisconsin glaciation in California, it indicates that the extinction of *B. latifrons* in other areas was due to competition. *B. antiquus* was able to invade the west coast during the Wisconsin, and probably resulted in the demise of the *B. lati-*

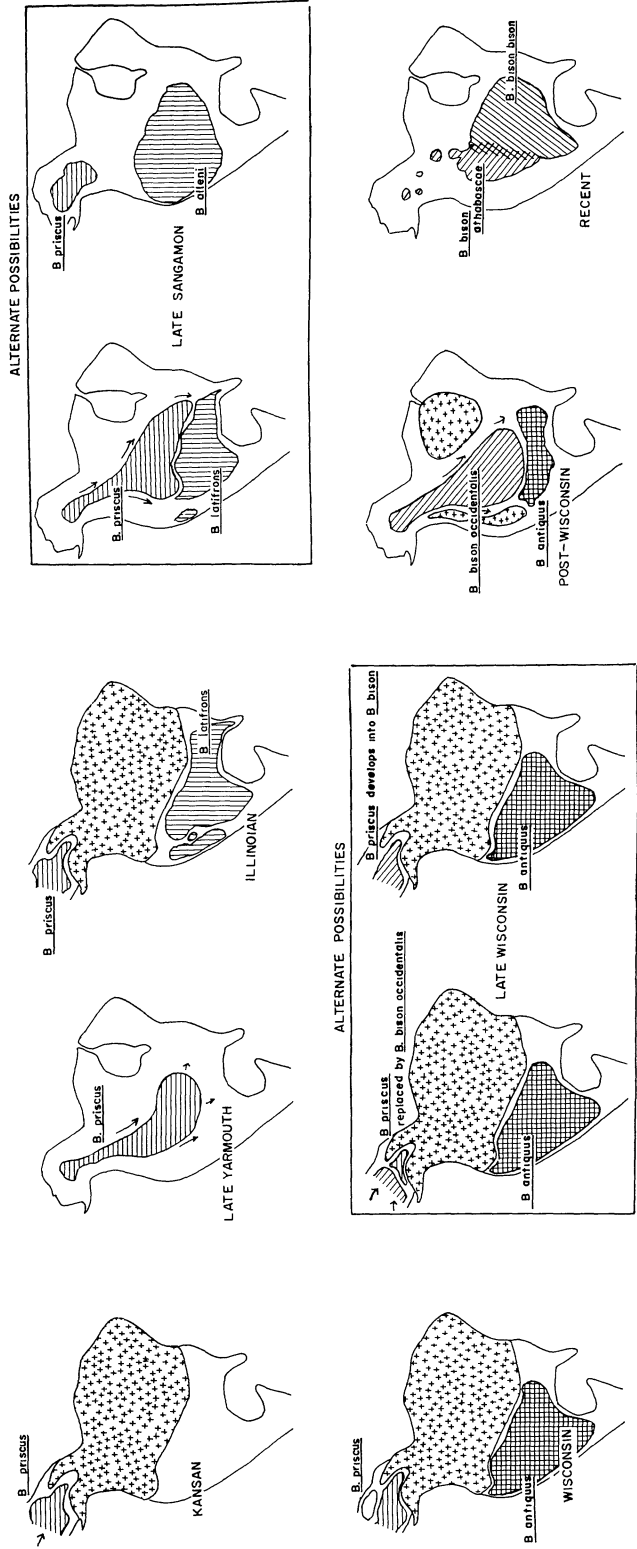


FIG. 2. DIAGRAMMATIC SEQUENCE OF BISON EVOLUTION IN NORTH AMERICA

The scattered checks represent continental glaciation. Note that one species, *B. priscus*, persists in the Amphiberian Region through most of the mid and late Pleistocene, while there is much variety in the Great Plains during this time. Although there are several features still open to question, the data seem particularly incomplete in two cases. These are presented as alternate possibilities.

*frons* there. West of the Rocky Mountains *B. antiquus* also eventually became extinct, apparently without other bison being present.

It is probable that the demise of *B. latifrons* in the great plains came about when confronted with the reinvasion of the northern *B. priscus* during an interglacial or interstadial; either that, or an evolutionary change of *B. latifrons* into *B. alleni* took place. Thus, one would expect to find somewhat smaller-horned forms both predating and postdating *B. latifrons*. If *B. priscus* replaced *B. latifrons*, it apparently underwent a small increase in horn size (although it may be difficult to separate these from the earlier intermediates between *B. priscus* and *B. latifrons*). Quite a few of those specimens that have been placed in the species *B. alleni* or *B. chaneyi* may have been representatives of the *B. priscus* invaders that underwent a slight increase in horn size, or *B. latifrons* could have evolved rapidly into a smaller-horned form. If the latter alternative is correct, *B. alleni* should be retained as a species. The Wisconsin age representative of this line was rather different from its ancestors because of its smaller horns, and is given the name *B. antiquus*. It is this species that the late Paleoindians used as the mainstay of their hunting economy. *Bison antiquus* became extinct at the close of the Wisconsin glaciation. The fossils with the most recent radiocarbon dates are between 8–9,000 years B.P. (Wendorf, 1961).

Before, or shortly after, man's invasion of the new world — while *B. antiquus* was the dominant member of the great plains grazing ungulate community — a small-horned form was differentiating from *B. priscus* in Eurasia and possibly Alaska. Flerov and Zablotski (1961) have contended that *B. priscus* in Alaska and Siberia developed into *B. bison* (*B. bison occidentalis*) directly. Although there is moderately good evidence of this transition in Siberia, the exact placement of the Alaskan fossils in time is only beginning. One adult male *B. priscus* (= *B. crassicornis*) from Alaska was dated by radiocarbon as about 31,400 (i.e., 29,585–33,440) years B.P. and a female at 11,950 ± 135 years B.P. (Péwé, 1965). Another adult male horn core was dated (Guthrie, unpubl.) at greater than 39,900 years B.P. (I-2246).

The Asiatic or “amphiberingian” origin of the North American *B. bison* must have taken place in the late Wisconsin. With the opening of the Cordilleran Corridor which followed soon afterward, this small-horned species moved southward into North America and there replaced the dominant *B. antiquus*. Folsom points of the same character are found with remains of *B. antiquus* and *B. bison*, with only a short interval separating the two (Wendorf, 1961). The replacement of *B. priscus* in Europe and *B. antiquus* (and perhaps the Alaskan *B. priscus*) in North America by the present species may have been an active biotic replacement, in which case the contender eliminated the occupant through direct competition, or by a more passive replacement, in which the indigenous form became extinct and the niche was immediately reoccupied by the new form, or perhaps even a replacement pattern involving both types.

The fact that *B. antiquus* became extinct in areas such as California where *B. bison* has never been able to invade, suggests that the replacement in the Great Plains involved the invasion of a vacated niche rather than the direct competitive elimination by an invading species. However, according to the various dates listed in the journal, *Radiocarbon*, over the past 15 years it appears that there was some temporal overlap between *B. antiquus* and *B. bison* (see Hester, 1967, for review). This overlap does not necessarily negate the concept of the reoccupation of a vacated niche.

It is doubtful that, within the genus *Bison*, sufficient specialization has taken place to allow a stabilized sympatric distribution of two or more species for any great length of time. The fossil record essentially supports this idea. The contradictory evidence may represent transitional situations where one species is in process of replacing another (see Hibbard, 1955b, for possible example); or they may be situations in which species with different chronologies occur in one heterogeneous reworked deposit and are described as contemporaneous, as appears to be the case in the instance of *B. latifrons*, *B. crassicornis*, and *B. bison occidentalis* horn cores found in a single gravel terrace in Alberta, Canada (Fuller and Bayrock, 1965).

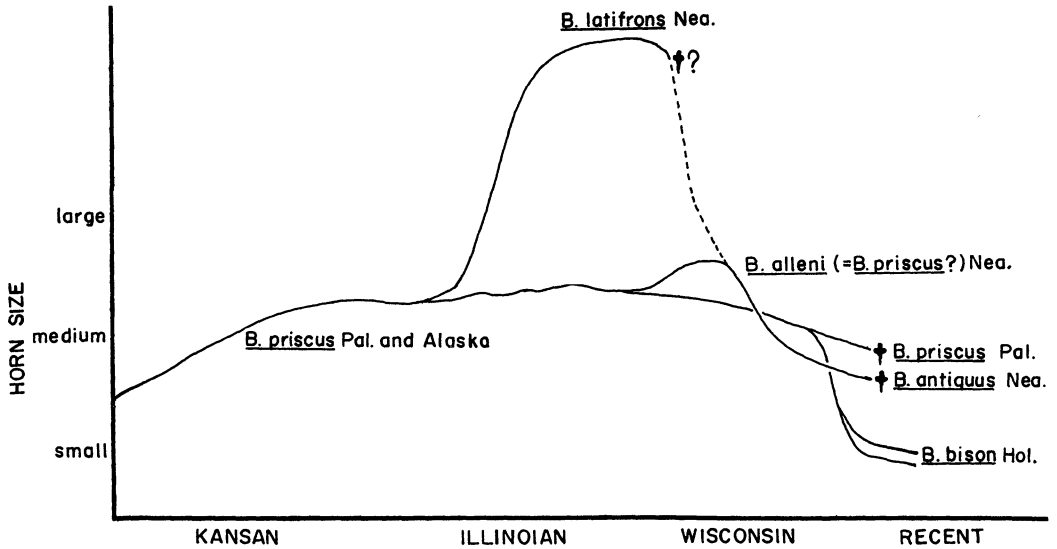


FIG. 3. AN ILLUSTRATION OF THE CHANGE IN BISON HORN SIZE DURING THE LATTER HALF OF THE PLEISTOCENE

At this time only the general features can be presented, and even these must be considered as only a preliminary outline. Nea = Nearctic, Pal. = Palearctic, Hol = Holarctic.

The usual condition of apparent sympatry, however, is the situation where one species is taxonomically partitioned into several. The previously discussed studies of fossil Alaskan bison serve as an excellent example.

If the extinction of many of the plains ungulates and their predators can be traced to the cultural development of the big-game hunting societies, as some have suggested (Martin, 1958), man may have worked inadvertently with *B. bison* to eliminate the other larger-horned bison species. As man reduced the numbers of the larger bison (*B. antiquus* and *B. priscus*), the smaller form, which was adapted to the mode and magnitude of predation pressure exerted by Paleolithic (and/or Paleoindian) cultures, took over the vacated niche. The fact that *B. bison* not only survived this time of widespread extinction, but extended its range and established itself as a dominant grazer over large areas in both northern continents, supports this idea. The replacement theories, of course, still apply even if *B. priscus* and *B. antiquus* became extinct by forces other than man's predation.

Both the recent Eurasian and American bison have undergone horn reduction from the late

Wisconsin ancestral species, *B. bison occidentalis*. The two subspecies, *B. bison bonasus* and *B. bison athabasca*, seem to be more closely related to *B. bison occidentalis* than does *B. bison bison* (Flerov, 1965). However, *B. bison bison* has become farther removed from its earlier habitat. It has become more of a resident of the open plains than the other subspecies, which are park-woodland or savanna inhabitants.

Although there are several characters other than overall horn size which change in the phylogeny of bison, the main feature of bison evolution is the quite extreme changes in their horns (Fig. 3). There are certainly many factors that regulate horn shape and size, some of which we know moderately well; however, we know much less about their interaction. The evolutionary mechanics of secondary sex-ornamentation offer many intriguing problems. These characters are generally among the more labile ones, both ontogenetically and phylogenetically, with a great deal of feedback between the two. An animal nutritionist, or behaviorist, or morphologist concerned with horn variations is just as handicapped without an historical perspective as a paleontologist is without

the knowledge of the factors affecting intrapopulational variation. Understanding of horn variations and their phylogenetic change must be a product of interdisciplinary cooperation.

It will be some time before our knowledge of bison evolution will be resolved to the point that most investigators will agree on the major features. Bison evolution will continue to be vigorously studied for a long time to come, but gradually a general image is beginning to form, albeit still a blurred one.

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