THE FOSSIL BISON OF ALASKA AND PRELIMINARY REVISION OF THE GENUS

MORRIS F. SKINNER AND OVE C. KAISEN

BULLETIN
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MORRIS F. SKINNER AND OVE C. KAISEN
Frick Laboratory
The American Museum of Natural History

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INTRODUCTION

The present report deals with the study of the remarkable series of extinct Bison remains collected under the auspices of the Frick Laboratory, the American Museum of Natural History, and Alaska University during 14 consecutive seasons in connection with gold-mining operations in the vicinity of Fairbanks, Alaska. In the light of this study, a revision of the bison species, fossil and living, is attempted. The Alaskan collection embraces 178 male skulls and partial skulls, 1766 jaws, and a vast series of skeletal elements, including 4338 metapodials.

"Unfortunately, so far nothing is definitely known as to the American Tertiary forerunners of the far-flung Bovines of Quaternary time, those vast herds that stretched across the northern areas of both hemispheres—the British Isles, northern Europe, Asia and America. That in the history of the known forms many species were involved, and that there was a mingling from time to time of remote races and strains, well may be believed. The genus Bison appears suddenly and widespread in the Pleistocene accumulations of America. . . . As yet there seems to be no record of a Recent-sized Bison horn-core having been found in definite association with Superbison remains. . . . The pre-Pleistocene occurrences reported by Matthew and Cook (1909) of Bison species . . . and by Marsh (1877) . . . were evidently from the Pleistocene. . . . The Bison remains from the North American Quaternary for convenience may be divided on the character of the size of the horn-cores between Bison proper, in which the cores are of moderate dimensions, and the subgenus Superbison, in which they may greatly exceed in size those of Recent species . . . " (Frick, 1937, preliminary revision, pp. 567–568).

The present writers' studies point to the moderate-horned Bison and the large-horned "Superbison" forms of the Pleistocene as separable into six groups or subgenera; four of these (Bison, Simobison, Superbison, and Platycerobison) were common to both the Western and the Eastern Hemispheres, one (Gigantobison) apparently was confined to North America alone, and one (Parabison) to Eurasia.

The Alaskan collections present an excellent opportunity to study a series of largely contemporaneous remains from one general area, to attempt to determine the number of different forms present and the extent of individual variation in the four species recognized as present. The most typical of the Alaskan species is Bison (Superbison) crassicornis which makes up 87 per cent of the identifiable male skulls and crania. Large collections of Recent bison in the United States National Museum and the American Museum of Natural History have supplemented the study of the Pleistocene collection from Alaska.

Contrary to the popular belief, the bison population was not spreading in the period preceding the discovery of North America; in subsequent years, no effort was made to preserve the vast herds of bison—one of the most magnificent of North America's great mammals—until the last century, when timely conservation measures, initiated in both North America and Europe, fortunately averted the complete extermination of the bison by man.

Investigators must rely on early accounts and the occasional discovery of bison bones or crania to establish the former limits of the bison range in historic times. Fossil remains indicate a much more widespread distribution during the Pleistocene, as such remains have been encountered in Florida, along the Pacific coast, and in Lower California.

On the hypothesis that the habitat of the bison in Pleistocene times was circumpolar and that the group reached the New from the Old World by bridging the Bering Strait, it is natural to assume that similar species should be found in both the Old and the New Worlds. Casts of specimens from the Eastern Hemisphere have been examined which could not be separated from remains of the North American species.

Frick (1937, p. 568) saw the necessity for an intensive review of Bison when he wrote, "A careful reexamination of the named types, in the light of the more lately amassed Fairbanks evidence, is greatly to be desired." He divided the Quaternary forms according to size between the typical subgenus Bison and
the larger *Superbison*, listing the named species according to occurrence: (a) east, (b) west of the Mississippi, and (c) Alaska; a list of the Recent species and subspecies was appended. The rearrangement of the North American and Eurasian bison assemblage has been no small task, for the present literature is very extensive, as there are 32 named American and 33 named Eurasian *Bison* species and subspecies. In addition two new North American species and one new Eurasian subspecies are named. This revision recognizes as valid 12 North American and 15 Eurasian specific and subspecific names. Individual variation within the living and extinct bison has confused the relationships so that many synonymous forms have been described, based on individual and age variants of one or another of the here-recognized species.

On the basis of shapes of male horn-cores and skulls, the genus *Bison* is here divided into six subgenera. Both North America and Eurasia have members of the following subgenera: *B.* (*Bison*) (Hamilton Smith), typical subgenus, *B.* (*Superbison*) Frick, *B.* (*Simo-bison*) (Hay and Cook), and *B.* (*Platycerobison*), new subgenus. Examples of *B.* (*Gigantobison*), new subgenus, are known from North America, but are not conclusively proved to have existed in Eurasia. Species belonging to *B.* (*Parabison*), new subgenus, have so far been found only in Eurasia. It is possible that a seventh, unnamed, more primitive subgenus of *Bison* occurs in the late Pliocene deposits of China and the early Pleistocene of the Siwaliks; the present fragmental evidence is still inconclusive.

The concept of the time element during the Pleistocene has intentionally been generalized in this review. Each species of *Bison* flourished, perhaps, during some particular period, but the change from their onset to their decline was so gradual that it would be unwise to assign each species to a definite epoch. In general, the following terms are defined:

Recent to sub-Recent, period of time following the latter half of the Wisconsin
Very late Pleistocene to sub-Recent, inception to the middle of the Wisconsin
Late Pleistocene, middle of the Illinoian to inception of the Wisconsin
Middle Pleistocene, close of the Aftonian to the middle of the Illinoian

Early Pleistocene, close of the Pliocene to close of the Aftonian

In laying the groundwork for this review, methods of comparing the relative individual age of specimens have been developed. Although this system is used primarily for *Bison*, the principles involved may also be applied to other bovids that have similar tooth characters. The details of changing tooth pattern caused by wear are illustrated in the text, and in conjunction with this an original system of correlating age characters of skull and horn-core growth has also been worked out and illustrated.

The horn-cores of fossil bison seem to afford the best distinguishing criterion allowing for growth and age and individual variation. A consistent system of illustrating and measuring bison skulls and crania is proposed. It is hoped that the systems here illustrated may develop into a method whereby future students of bison may consider the specimens at hand from the same lines of approach. The methods of measurement are indicated in a key illustration (fig. 1C, p. 144).

**Acknowledgments**

The writers are particularly indebted to Mr. Childs Frick for the privilege of studying the Alaskan collections and for the constant encouragement and helpful suggestions given in the course of the work. To the several collectors of the Alaskan bison series under the direction of Dr. Charles E. Bunnell must go the credit for making this study possible. The initial collection was made in 1929 and 1930 by the late Mr. Peter C. Kaisen, a pioneer collector of the American Museum of Natural History and the father of the junior author. In the following years, work was carried on under the direction of Dr. Albert S. Wilkerson, 1931; Prof. Ray Hendrickson, 1932; Mr. John B. Dorsh, 1933–1936; and Mr. Otto Wm. Geist, 1937–1942. The cooperation of the United States Smelting, Refining, and Mining Company in the Alaskan excavations is gratefully acknowledged. The Eurasian literature has been translated by several individuals. Mrs. Margarethe Manschinger has translated German, French, and Dutch; Miss Francesca R. LaMonte, Italian; Dr. T. H. Cheng, Chinese; and Mrs. M. F. Skinner, Latin. Mrs. Skinner has also typed the manuscript and has aided in many
ways. Mr. Sydney E. Helprin has contributed editorial suggestions.

It has been necessary to have access to important bison collections and loans of specimens which were distributed in various institutions throughout the United States and Canada. For generous cooperation in this endeavor the writers are greatly indebted to the following individuals and institutions: Dr. Remington Kellogg, Dr. C. L. Gazin, and the late Mr. C. W. Gilmore, United States National Museum; Dr. T. H. Jackson, United States Biological Surveys; Dr. Claude Hibbard, University of Kansas; Mr. Bryan Patterson and Mr. James Quinn, Chicago Natural History Museum; Dr. C. O. Dunbar, Yale Peabody Museum; Dr. G. Dallas Hanna, California Academy of Sciences; Mr. J. LeRoy Kay, Carnegie Museum; Mr. George Sternberg, Fort Hays Kansas State Teachers College; Mr. R. M. Anderson, National Museum of Canada; Dr. C. Bertrand Schultz, University of Nebraska State Museum; Mr. Charles M. Cadwalader, Academy of Natural Sciences of Philadelphia; Dr. Alfred M. Bailey and Mr. H. C. Markman, Colorado Museum of Natural History; Dr. Emil W. Haury, University of Arizona; Dr. Chester Stock, California Institute of Technology; Dr. Harold E. Anthony and Dr. G. G. Simpson, the American Museum of Natural History.

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We are greatly indebted to all of those who have aided us in our efforts toward a lucid presentation of this revision; but for any errors in judgment or for deficiencies that may remain, we assume full responsibility.

**ABBREVIATIONS OF INSTITUTIONS CITED**

A.C.-F:A.M. See U.A.-F:A.M.

A.M.N.H. The American Museum of Natural History, Department of Geology and Paleontology

A.M.N.H:M. The American Museum of Natural History, Department of Mammals

A.N.S.P. Academy of Natural Sciences of Philadelphia

B.M. British Museum (Natural History)

C.A.S. California Academy of Sciences

C.M. Carnegie Museum, Pittsburgh

C.M.N.H. Colorado Museum of Natural History

C.N.H.M. Chicago Natural History Museum

F:A.M. Frick Collection American Mammals (The American Museum of Natural History)

F.H.K.S.C. Fort Hays, Kansas State Teachers College

I.P.A.S. Institut Paleozoologique de l'Académie des Sciences de l'URSS

K.U.M.V.P. Kansas University, Museum of Vertebrate Paleontology

M.P.M. Mark Provincial Collections, Germany

N.M.C. National Museum of Canada, Ottawa

S.N.H. Stuttgart Natural History Collections, Germany

T.A.M.C. Texas Agricultural Mechanical College, Mark Francis collection, College Station

U.A.-F:A.M. University of Alaska-Frick Collection American Mammals (The American Museum of Natural History). Formerly this collection designated as A.C.-F:A.M.

U.C.M.P. University of California, Museum of Paleontology

U.N.S.M. University of Nebraska State Museum

U.P. University of Pennsylvania

U.S.Bi.S. United States Biological Surveys Collections

U.S.N.M:M. United States National Museum, Division of Mammals

U.S.N.M:V.P. United States National Museum, Division of Vertebrate Paleontology

Y.P.M. Yale University, Peabody Museum of Vertebrate Paleontology
THE ALASKAN COLLECTION

The important Fairbanks collection consists of 180 complete and partial diagnostic male bison skulls listed and discussed in other parts of this paper. There are over 50 female skulls which are not listed or extensively discussed. In addition, the collection has a large number of isolated, less diagnostic mandibular rami and limbs which are useful in making a comparison between Pleistocene and living bison, although no specific allocation can be conclusively demonstrated. For this reason only summaries are presented.

SIZE RANGE AND SEX DETERMINATION
OF ISOLATED BISON METAPODIALS

The collection contains a total of 4838 mature and complete Bison metapodials, none of which were found in articulation with

### TABLE 1
SPECIMEN COUNT OF ALASKAN BISON METACARPI

<table>
<thead>
<tr>
<th>Size Range in 10-mm. Groups</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Right</td>
<td>Left</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Per cent of Total</td>
<td>Per cent of Total</td>
</tr>
<tr>
<td>240-250</td>
<td>6</td>
<td>7</td>
</tr>
<tr>
<td>230-240</td>
<td>72</td>
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<td>180-190</td>
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<td>none</td>
</tr>
<tr>
<td>Totals</td>
<td>909</td>
<td>831</td>
</tr>
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### TABLE 2
SPECIMEN COUNT OF ALASKAN BISON METATARSAL

<table>
<thead>
<tr>
<th>Size Range in 10-mm. Groups</th>
<th>Male</th>
<th>Female</th>
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<tr>
<td></td>
<td>Right</td>
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<td>Per cent of Total</td>
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<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Totals</td>
<td>655</td>
<td>655</td>
</tr>
</tbody>
</table>

Total male metapodials, 3050 Total female metapodials, 1788

Grand total male and female metapodials, 4838

134
TABLE 3
MEASUREMENTS (IN MILLIMETERS) AND INDICES OF SELECTED
SAMPLE OF MALE Bison Metacarpi

<table>
<thead>
<tr>
<th>U.A.-F: A.M. Number</th>
<th>Greatest Over-all Length</th>
<th>Transverse Diameters</th>
<th>Anterior-Posterior Diameter at Center</th>
<th>Indices (%)</th>
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<tr>
<td></td>
<td></td>
<td>Proximal End</td>
<td>Center of Shaft</td>
<td>Distal End</td>
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<tr>
<td>46816</td>
<td>248.5</td>
<td>90.0</td>
<td>54.2</td>
<td>95.2</td>
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<tr>
<td>46817</td>
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<td>91.2</td>
<td>59.8</td>
<td>92.7</td>
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<td>46818</td>
<td>243.3</td>
<td>97.5</td>
<td>59.8</td>
<td>98.2</td>
</tr>
<tr>
<td>46819</td>
<td>240.2</td>
<td>93.1</td>
<td>59.5</td>
<td>93.8</td>
</tr>
<tr>
<td>46820</td>
<td>238.0</td>
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<td>61.2</td>
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Sample Average: 218.7 86.0 56.4 88.5 35.8 25.7

Min. Max. (%) 76.7 74.5 71.8 78.0 76.5 74.2

Other limb elements. These can be separated sexually on the basis of the relative heaviness of shafts. The sexed metapodials have been separated into 10-millimeter size groups, and a representative male and female sample was selected. Tables 1-6 present a summary of these measurements. Although the skulls and horn-cores indicate that more than one species is represented, it is impossible to make specific separations of the metapodials. No distinctive characters could be found, and a similarity of body proportions for all the Alaskan species is indicated. The largest and smallest specimens are included in the representative tables. The observed minimum does not differ from the maximum over 29 per cent. A total of 1373 individuals are represented by the count of right metacarpi, as follows: male, 909; female, 464.

The functioning of the laws of chance is shown in the specimen count in tables 1 and 2, comparing the total number of right and left metapodials of the respective size groups collected over a period of 14 years.
TABLE 4
MEASUREMENTS (IN MILLIMETERS) AND INDICES OF SELECTED SAMPLE OF MALE Bison Metatarsi

<table>
<thead>
<tr>
<th>U.A.-F: A.M. Number</th>
<th>Greatest Over-all Length</th>
<th>Transverse Diameters</th>
<th>Anterior-Posterior Diameter at Center</th>
<th>Indices (%)</th>
</tr>
</thead>
<tbody>
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<td>Min./Max. (%)</td>
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TABLE 5
MEASUREMENTS (IN MILLIMETERS) AND INDICES OF SELECTED SAMPLE OF FEMALE Bison Metacarpi

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<th>Anterior-Posterior Diameter at Center</th>
<th>Indices (%)</th>
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### TABLE 5 (Continued)
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<th>Indices (%)</th>
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<td>Min. Max. (%)</td>
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### TABLE 6
**Measurements (in Millimeters) and Indices of Selected Sample of Female Bison Metatarsi**

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<th>Indices (%)</th>
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<td>80.7</td>
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Mortality Rate as Demonstrated by Isolated Rami

A total of 1766 complete and partial fossil Bison rami of both sexes and of all ages are available for study. Of this number, 1322 specimens can be allocated to an approximate individual age by tooth wear (p. 143). No specific separation seems possible, although the horn-cores suggest the existence of four species.

The age grouping of the rami (table 7) presents an idea of the mortality among these Pleistocene boids. Young specimens are living bison. Examples of these Pleistocene bison suggest an individual age of from 12 to 20 years (pl. 14, fig. 3C). Most specimens with very worn teeth approach an average age of 16 years.

The male bison acquires a mature horn-core length (but not diameter) at about the time the third molars come into wear (p. 146). The cores are first long and slender and later increase progressively in diameter with age. This has an outward effect on the appearance of the horn sheath which is loosened seasonally from its attachment to the skin.

<table>
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<tr>
<th>Stage of Wear</th>
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<th>Left</th>
<th>Totals</th>
<th>Per Cent of Totals</th>
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<td>257</td>
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<td>Totals</td>
<td>697</td>
<td>625</td>
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* Stage S-1 in the cattle seems to be between 3½ and 4 years (according to Chauveau; see also pp. 143–146).

Horn Sheath Growth and Wear

Mature skulls with horn sheaths and completely worn teeth (S-4) give an estimate of the years of life attained by the Alaskan fossil bison. The sheaths show seasonal growth rings resembling those observed on cattle and more easily destroyed before and after fossilization, and the death rate of young animals may be higher than indicated. The most hazardous time of a young bison's life is logically the first winter. The grouping shows that approximately 17 per cent of the individuals died during this period. Those that survived the second summer were apparently better fitted to withstand the following winter and acquired a dentition of early maturity, for which group a 4 per cent death rate is indicated. Among the remaining 79 per cent that acquired mature dentitions, 39 per cent died during maturity and 40 per cent in old age. (Pl. 13, figs. 4, 5.)

Abnormal Tooth Characters

Departures from normal tooth patterns in fossil bison rami were observed infrequently.
and in such a slight degree that they were considered of no specific or generic significance.

The most frequent departure from the normal in Pleistocene *Bison* is the presence of a metastylid on the metaconid of P4 and was observed 26 times in the collection. This is the normal condition in living bison (p. 140).

An additional external style was observed twice between the second lobe and the heel of the M3, and one other specimen had an extra style on both M4 and M3. Normally a style is present between the first and second lobes on the exterior side of the inferior molars and the interior side of the superior molars, and is the prime character used for age classification (p. 143).

Small external styles or pillars are sometimes present on the superior third molars. Whenever they were observed in skulls, the character was present in both maxillae. Otherwise the skulls differed in no other detail from the rest of the members of the species to which they were referred. For this reason, the character is not considered of generic importance, although it was the basis upon which Figgins established the genus "*Stelabison*" (p. 159, this paper). Styles were observed seven times on skulls, 17 times on maxillae, and 43 times among the several hundred isolated molars.

In nine examples small additional fossettes were observed on the crown patterns of the heels or third lobes of the lower third molars. Normally the molar possesses a fossette in the first and second lobes but not the heel.

Reentering folds in the enamel borders of the fossettes in superior molars of bovids are observed only in young and slightly worn dentitions. Examples have been found in the subgenera of *Bison, Superbison, Simobison,* and *Gigantobison.* Hay considered this character important in establishing *Bison* "*regius*" (this paper, p. 207). Reentering folds in the fossettes of molars may be a character that occasionally appears in all *Bison.* For example, the normal molar pattern of yak has a prominent reentering fold on the posterior side of the posterior fossette, while that of *Bos* or domestic cattle has a prominent reentering fold on the posterior side of the posterior fossette and, in addition, the anterior fossette has reentering folds on both the anterior and posterior sides. The reentering folds in the fosette borders of bovid molars follow fairly consistent generic patterns, but even these characters overlap each other in large population samples and should therefore be used with caution.

The third lobe or heel on the M3 shows a considerable amount of variation in size but is always present in *Bison.* In some of the other artiodactyls (American pronghorn), this heel is normally present but is sometimes missing.

**Difference Between Earlier Pleistocene and Living Bison Dentition**

Observations of the opened rami of *Bison* disclose that P4 is the last tooth to form from the germ stage, and likewise to erupt in the dental series. The M4 slightly precedes the P4 (see pls. 12, 13).

In most cases, taken as a group the P4 in Pleistocene *Bison* has several distinctive differences from that of living *Bison.* Some of the characters must be observed in unworn teeth and would, as a rule, be of no value in worn specimens. In general, the Recent *Bison* P4's are tending to become more molariform. The rami of living *Bison* disclose a small, median, labial root on the P4 that is nearly lacking in earlier forms. The root is located between the anterior and posterior prongs of the main roots, and is present in about 90 per cent of living *Bison* but is lacking in over 95 per cent of earlier forms. A median root is present on the dP4 of both Pleistocene and living *Bison.*

In Recent *Bison* the crown of an unworn P4 shows that the metaconid extends above the opposing protoconid. In earlier Pleistocene *Bison* the metaconid is lower than the protoconid. The base of the metaconid is more enlarged and posteriorly extended in living *Bison* than in the earlier forms. The lingual fold between the entoconid and metaconid is prominently open to the base of the tooth in early forms. In living *Bison* the posterior expansion of the metaconid has resulted in a shortening of the depth of the lingual fold, which is closed up about one-half to two-thirds the depth of the tooth and produces a deep posterior fossette on the P4, observed only in old age in the earlier *Bison,*
at which time a very shallow fossette may occur on the crown pattern.

The expansion of the metaconid has been accentuated by the presence of a metastylid in living *Bison* and is almost universal, but this character was observed on only 26 teeth of the entire Alaskan collection. The presence or lack of a metastylid on the metaconid is a distinguishing character between living and late Pleistocene *Bison* but is not absolute (p. 139).

The pronounced similarity in *Bison* teeth has defied the present attempt to establish useful characters that would permit specific or even subgeneric separations based on tooth characters alone. Large population samples suggest tendencies but show no clear-cut differences. Isolated examples of various *Bison* species appear to have tooth characters that would aid in making specific determinations. These characters, however, soon intergrade when a large population sample is examined. Actual size might be considered useful, but could not be relied on. Unless a complete dental series is present, it is often very difficult to determine the differences between *Bos taurus* (domestic bovid), *Bos grunniens* (yak), and *Bison*.

**Pathological Rami**

Pathological conditions in the bone of the horizontal ramus were observed only 41 times in the 1766 specimens. This amounts to 2.5 per cent. The main sources of infection were around the alveolar sockets of the teeth. In occasional specimens, the ramus appeared to have been broken and healed. In some, deposits of diseased bone were observed in affected parts and in others, abscesses or bad teeth had caused the bone to be eaten away from infected areas.

The pathological specimens were segregated as to age, by tooth wear (this paper, p. 143). The great majority of pathological cases occurred in old age, as follows:

---

**TABLE 8**

Distribution and Occurrence of Male *Bison* Skulls and Horn-Cores in Alaskan Localities

<table>
<thead>
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<th>Collecting Localities</th>
<th><em>Bison</em></th>
<th></th>
<th></th>
<th>Totals</th>
<th>Per Cent</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>(Super-<em>Bison</em>)</td>
<td>(Bison) preoccidentals</td>
<td>(Platycerobison)</td>
<td>Number</td>
<td>Per Cent</td>
</tr>
<tr>
<td></td>
<td>crassi-cornis</td>
<td>alaskensis</td>
<td>geisti</td>
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<td>Cleary Creek</td>
<td>53</td>
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<td>Goldstream Creek</td>
<td>43</td>
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<td>Fairbanks area</td>
<td>17</td>
<td>2</td>
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<td>—</td>
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<td>—</td>
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<td>9</td>
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<td>Engineer Creek</td>
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<td>—</td>
<td>9</td>
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<tr>
<td>Cripple Creek</td>
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<td>1</td>
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<td>Little Eldorado Creek</td>
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<td>4</td>
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<td>17 miles N. of Fairbanks</td>
<td>3</td>
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<td>—</td>
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</tr>
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<td>—</td>
<td>—</td>
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<td>Pedro Creek</td>
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<td>—</td>
<td>—</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>Moose Creek</td>
<td>1</td>
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<tr>
<td>Lillian Creek</td>
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<td>—</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>Seward Peninsula at Candel</td>
<td>1</td>
<td>—</td>
<td>—</td>
<td>—</td>
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*(Eschscholtz Bay)*
Tables 1 and 2 not only demonstrate the functioning of the laws of chance, but also tabulate a collection large enough to demonstrate nearly normal biological population curves of quantitative zoology. In table 1, 75 per cent of the male Bison metacarpi occur in the 210–230-mm. size range, while 78 per cent of the female metacarpi occur in the 200–220-mm. size range. In table 2, 69 per cent of the male Bison metatarsi occur in the 260–280-mm. size range, and 67 per cent of the female metatarsi occur in the 250–270-mm. size group. The distribution for the metatarsi, however, indicates a wider range of variation. Both tables present the expected smaller size of the female Bison.

In tables 3 to 6 inclusive, the selected samples of Bison metapodials do not represent a population distribution about a size norm, but demonstrate the sexual differences of proportion in the metapodials by the use of the indices and the actual physical size.
METHODS

SYNONYM, REFERENCES, AND TERMS USED

The style of synonymy adopted in this report has been designed to focus attention on (1) the type of the here-recognized species and its literature, (2) the types and literature of species here considered synonymous, and (3) the literature dealing with other referred specimens which have been assigned to the species under consideration. This style of treatment may eliminate much of the difficulty in distinguishing between types and referred specimens.

Admittedly a species is founded on or anchored to a type specimen, but it is well known that types are often not average individuals of the species. For this reason, the concept of each Bison species is not based entirely on the type but on all of the available specimens that are referable to the respective species here recognized. Types are considered important control specimens from which the basic characters of the species may be observed. Every available holotype has been carefully examined and studied before being considered valid or synonymous.

The practice has been followed of placing the name of the original author of a genus or species in parentheses whenever the generic or specific names have been altered in spelling or classification. Such practice aids in indicating that the author's original designation has been retained but the usage or spelling has been altered.

Interpretation of term usages is as follows:

Type: A general term for type specimens of various ranks
Genotype or Genotypic Species: The species upon which the genus is based
Subgenotype or Subgenotypic Species: The species upon which the subgenus is based
Holotype: A single specimen used by the original author as the "type" in the original description of his species
Syntypic Series: Two or more specimens used in establishing a species for which no holotype was designated by the original author
Syntype: Any one specimen of the above syntypic series
Lectotype: One of the syntypic specimens selected by the first reviser as "type" of a species based on a syntypic series. This specimen can never be the holotype but has an equivalent value
Paratype: Specimens other than the holotype used by the original author of the species as a basis for his diagnosis
Plastotype: A cast of the holotype, checked for accuracy
Neotype: A specimen selected to replace the holotype in case all of the type material used in the original specific diagnosis has been lost
Specific Member or Members: As used in conjunction with the genus or subgenus, implies one of the included species as a population, not as individuals within a species

DEFINITIONS OF HORN-CORE INDICES

Indices are a means of expressing the proportionate relationship of various anatomical parts and serve to eliminate deceiving impressions of physical size and shape (horn-core curvature). Conversely, specimens may have similar indices and still differ greatly. For this reason, all factors must be considered.

INDEX

1. Horn-core curvature:

Previously used to indicate the relative amount of horn-core curvature, but is not absolute because of the variety of core shapes assumed by Bison. It is derived from the following measurements and reduces all curved horn-cores to a relative proportion regardless of shape.

Horn-core length on lower curve (4)\[4\] \times 100
Distance, core tip to upper base at burr (5) = index of curvature

2. Horn-core compression or roundness:

Indicates the relative amount of dorsoventral horn-core compression. As the index approaches 100, the core roundness is emphasized; whenever the index exceeds 100, which occasionally occurs,

1 Numbers in parentheses refer to designation on figure 1C, key to cranial measurements.
the anteroposterior compression of the core is emphasized.

Vertical diameter of core at base (6) \times 100
Transverse diameter of core at base (12) \times 100
= index of compression

3. Horn-core proportion:
   Indicates the relative slenderness or stubbiness of the horn-core in relation to the basal circumference. The cores start to be proportionately long when the index exceeds 100.

Horn-core length on upper curve, tip to burr (3)
Circumference of core at base (7)
\times 100 = index of proportion

4. Horn-core length:
   Indicates the relative length of the horn-core in relation to the frontal width of the skull.

Length of horn-core on upper curve, tip to burr (3)
Width of cranium between horn-cores and orbits (14)
\times 100 = index of length

5. Tooth-row proportion:
   Indicates the relative length of the tooth row to the length of the skull. It bears a direct ratio to the individual age of the animal. The tooth row shortens with age and the skull is somewhat lengthened after the M3 has erupted. Therefore, the index should be used only when the individual age of the animal is also considered, and should be compared with similarly aged individuals.

Alveolar length, P2 - M4 (19)
Basilar length of skull (F - P) \times 100 = index of tooth-row proportion

COMPARATIVE VIEWS AND SCALES USED IN TEXT
AND CRANIAL MEASUREMENTS

In this publication, all views of skulls and horn-cores are at an approximate scale of 1/10, lateral views of rami at \frac{1}{4}, and occlusal views of dentitions at \frac{1}{2}.

It is highly important that all views for comparative work on bison skulls, crania, and horn-cores be taken with the camera lens and specimens in a standard position. A slight change in the angle of the view makes a considerable change in the apparent direction of the horn-core. Photographs seldom show true horn-core dimensions, since the cores are generally at oblique angles to the focal plane.

All specific descriptions pertaining to horn-core compression, directional trend, and other physical skull characters are based on placing the skull in a horizontal plane, as in figure 1B.

As illustrated in figure 1C, all points of measurements used in this report are set forth in an idealized diagram of a bison skull. An approach to solving the language barrier has been attempted by the use of applying key numbers to each measurement as set forth in the caption of figure 1C. An international understanding of bison must be accomplished before completely solving all bison relationships.

A SYSTEM OF WEAR CLASSIFICATION FOR THE
TEETH OF BISON

It was found necessary to develop a uniform system of individual age classification in Bison before attempting a segregation of cranial characters. The system, here illustrated in plates 8 to 13, is quite simple since Bison molars 1 to 3 erupt in a progressive order as the animal becomes mature. Molars of Bison and other related bovids have a small style located between the anterior and posterior lobes of the molars, on the lingual side of the superior teeth and the buccal side of the inferior teeth, which appears on the crown surface in the tooth pattern as a small enamel circle or loop depending on the wear of the tooth. Tooth wear is the same in the superior and inferior dentitions of the individual. The stages of tooth wear are illustrated in the plates and here described in detail.

SUPERIOR DENTITION
IMMATURITY (I-S)
Plate 8, figures 1C, 2C, 3C, 4C
Deciduous P4-P4 in use; a small, prominent style present on dP4; by the time this style
becomes worn, $M^1$ has started to erupt; before $dP^2-dP^3$ are shed, $M^1$ has erupted and is in wear, $M^2$ is erupting, and the germ of $M^3$ is still forming.

**EARLY ADOLESCENCE (A–S)**

Plate 8, figure 5C

Deciduous $P^2$ shed; $M^1$ and $M^2$ erupted and in wear; the style of $M^1$ has not become worn; $M^2$ is worn only on the anterior lobe of the crown; $M^3$ is just starting to erupt from the maxilla.

**LATE ADOLESCENCE (S-1) (SEE P. 138)**

Plate 9, figures 1C, 2C

Deciduous $P^4$ shed; $P^2–P^4$ present and becoming worn; style of $M^3$ starting to wear; $M^3$ worn on crown but style not worn; crown of $M^4$ worn off until style is well developed on pattern. At close of this stage $M^2$ style becomes worn; top of $M^2$ style is still 20 to 50 mm. below crown of tooth which is in wear.

**EARLY MATURITY (S-2)**

Plate 9, figure 3C

Style of $M^2$ becomes worn; by close of this stage the fossettes of $M^1$ have become smaller,

and the fold of the enamel of its style has started to shrink at the base of the tooth.

**FULL MATURITY (S-3)**

Plate 9, figure 4C

Style of $M^2$ becomes worn. At the close of this stage, the anterior and posterior prongs of the roots of $P^2–M^2$ are exposed above the alveolar border of the maxilla and the fossettes in $M^1$ are nearly worn away. The fossettes of $M^2$ are smaller, and the loop of the enamel fold of the style of $M^1$ has disappeared into the enamel border of the root. The style of $M^3$ has become a small loop or outfolding of enamel between the posterior and anterior lobes of $M^2$.

**OLD AGE (S-4)**

Plate 10, figures 1C, 2C

Fossettes of $P^2–P^4$ are disappearing; fossettes of $M^3$ and $M^2$ getting small or worn away. This stage of wear does not show characters which could be studied. Styles of both $M^1$ and $M^2$ may be lacking. Styles of $M^2$ very small towards close of stage. It is noted that this is the only stage in which the fossettes start to disappear in the molar teeth of *Bison*.

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**FIG. 1 (OPPOSITE PAGE).** A–B. Position of bison skulls and horn-cores in relation to camera lens as photographed for this report. A. Posterior views taken at right angles to the occipital plane; lateral views with camera at right angles to the median plane of skull and lens centered on middle of orbit. B. Dorsal views taken at right angles to frontal-nasal plane and camera lens centered on frontals at the level of horn-cores. Palatal views taken with camera at right angles to palate and centered on dental series.

C. Key to cranial measurements:

1. Spread of horn-cores, tip to tip.
2. Greatest spread of cores on outside curve.
3. Core length on upper curve, tip to burr.
4. Core length on lower curve, tip to burr.
5. Length, tip of core to upper base at burr.
6. Vertical diameter of horn-core at right angle to longitudinal axis.
7. Circumference of horn-core at right angle to longitudinal axis.
8. Greatest width at auditory openings.
10. Depth, occipital crest to top of foramen magnum.
11. Depth, occipital crest to lower border of foramen magnum.
12. Transverse diameter of core at right angle to longitudinal axis.
14. Width of cranium between horn-cores and orbits.
15. Greatest postorbital width.
16. Angerian orbital width at notch.
17. Width of skull at masseteric processes above $M^1$.
18. Rostral width at maxillary-premaxillary suture.
20. $M^3–M^2$, alveolar length.
21. O–P. Length, over all, occipital crest to tip of premaxilla.
22. F–P. Length, basilar, foramen magnum to tip of premaxilla.
23. O–T. Length, occipital crest to tip of nasals.
25. M–P. Length, beyond $P^3$ to tip of premaxilla.
27. Angle of posterior divergence of horn-core.
28. Angle of proximal horn-core depression.
INFERIOR DENTITION

IMMATURITY (I-S)
Plate 12, figures 1, 1A, 2, 2A, 3, 3A, 4, 4A

Milk premolars dP₂-dP₄ present. During this stage, the germs of the permanent molars M₁-M₃ are forming in a progressive order. At the close of this stage, germs of P₃-P₄ are forming. By the time dP₃ is shed, the germs of the molars are nearly formed, M₁ and M₂ are in use, and the germ of M₃ is erupting.

EARLY ADOLESCENCE (A-S)
Plate 12, figures 5, 5A

Deciduous P₄ is still retained, and permanent P₂ and P₃ are erupting. At the close of this stage, the style of M₁ is always worn, but never the style of M₂; M₃ has started to wear on the anterior lobe.

LATE ADOLESCENCE (S-1)
Plate 13, figures 1, 1A

Most desirable for study; the style of M₁ worn, the style of M₂ unworn, the milk incisors and canines replaced by permanent incisors and canines, and the heel of M₃ starting to wear. This stage of wear continues until style of M₂ becomes worn.

EARLY MATURITY (S-2)
Plate 13, figures 2, 2A

The style of M₂ becomes worn. By the close of this stage, P₂-P₄ are well worn and M₁ has been worn away from one-third to one-half its original length. The heel of M₃ is now in full wear.

FULL MATURITY (S-3)
Plate 13, figures 3, 3A

The style of M₃ becomes worn; the crowns of P₃-M₂ are now well worn. At the close of this stage, the anterior and posterior prongs of the roots of P₂-M₁ are exposed above the bone of the horizontal ramus. The style of M₁ has begun to disappear, and the styles of M₂ and M₃ form large enamel loops between the anterior and posterior lobes.

OLD AGE (S-4)
Plate 13, figures 4, 4A, 5, 5A

All the teeth are greatly worn, and the fossettes of M₁ have started to disappear from the base of the tooth. The folds of the styles are indistinct. The teeth are worn to the prongs of the roots which have become filled with dentine.

ANALYSIS OF MALE CRANIAL CHARACTERS CORRELATED WITH TOOTH WEAR OR INDIVIDUAL AGE

To aid in judging the maturity of each specimen, it was found that characters of bone growth in the cranium and horn-cores could be correlated with individual age as evidenced by tooth wear in the series of Recent Bison skulls. These characters are summarized in conjunction with the various stages of tooth wear. The horn-cores approach mature length, but not circumference, at the time the M₄ is erupting. (For change in sheath appearance, see p. 138.)

IMMATURE SKULLS
Plate 8, figures 1-4

<table>
<thead>
<tr>
<th>Tooth Wear (I-S)</th>
<th>Skull shape</th>
</tr>
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<tr>
<td>dP₂-dP₄ in wear</td>
<td>Skull small, one-half the length of adult; frontals and supraoccipital bones un fused; supraorbital foramen in open groove; orbits not prominently protruding; horn-cores have begun growth from frontals on a horizontal plane posterior to the orbits</td>
</tr>
<tr>
<td>M₁ erupted</td>
<td>Skull enlarging to three-fifths the length of adult; frontals and supraoccipital bones un fused; supraorbital foramen in a deepening groove; orbits not prominently protruding; horn-cores have started to elongate but are not curved or large in circumference</td>
</tr>
<tr>
<td>dP₂-dP₄ in wear</td>
<td>Skull enlarging three-fourths to four-fifths the length of adult; frontals and supraoccipitals still un fused; supraorbital foramen in a deep groove; orbits show signs of protuberance and becoming tubular; horn-cores have elongated to about adult length but are slender and have</td>
</tr>
<tr>
<td>M₁ and M₂ erupted</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Plate 12, figures 1, 1A</th>
<th>Plate 13, figures 2, 2A</th>
<th>Plate 13, figures 3, 3A</th>
<th>Plate 13, figures 4, 4A, 5, 5A</th>
</tr>
</thead>
<tbody>
<tr>
<td>Milk premolars dP₂-dP₄ present</td>
<td>Deciduous P₄ still retained, and permanent P₂ and P₃ are erupting.</td>
<td>Early maturity (S-2)</td>
<td>Old age (S-4)</td>
</tr>
<tr>
<td>IMMATURITY (I-S)</td>
<td>EARLY ADOLESCENCE (A-S)</td>
<td>EARLY MATURITY (S-2)</td>
<td>OLD AGE (S-4)</td>
</tr>
<tr>
<td>Plate 12, figures 5, 5A</td>
<td>Plate 13, figures 3, 3A</td>
<td>Plate 13, figures 1, 1A</td>
<td>Plate 13, figures 4, 4A, 5, 5A</td>
</tr>
<tr>
<td>Deciduous P₄ is still retained, and permanent P₂ and P₃ are erupting. At the close of this stage, the style of M₁ is always worn, but never the style of M₂; M₃ has started to wear on the anterior lobe.</td>
<td>The style of M₂ becomes worn. By the close of this stage, P₂-P₄ are well worn and M₁ has been worn away from one-third to one-half its original length. The heel of M₃ is now in full wear.</td>
<td>The style of M₃ becomes worn; the crowns of P₃-M₂ are now well worn. At the close of this stage, the anterior and posterior prongs of the roots of P₂-M₁ are exposed above the bone of the horizontal ramus. The style of M₁ has begun to disappear, and the styles of M₂ and M₃ form large enamel loops between the anterior and posterior lobes.</td>
<td>All the teeth are greatly worn, and the fossettes of M₁ have started to disappear from the base of the tooth. The folds of the styles are indistinct. The teeth are worn to the prongs of the roots which have become filled with dentine.</td>
</tr>
</tbody>
</table>
Tooth Wear

**Tooth Wear (A-S)**

- dP² shed
- dP² and dP⁴ retained
- P² and M⁴ erupting

**Tooth Wear (S-1)**

- dP²–dP⁴ shed
- P²–P⁴ slightly worn
- M¹ style beginning wear
- M³ still unworn on posterior half

**Tooth Wear (S-2)**

- M¹ style worn
- M² style worn to well worn
- M³ style unworn

**Tooth Wear (S-3)**

- M¹ style ½–¾ worn
- M² style well worn
- M³ style worn to well worn

**Tooth Wear (S-4)**

- M¹ style and fossettes gone
- M² fossettes and style well worn or missing
- M³ style well worn

**SKULLS IN EARLY MATURITY**

Plate 9, figure 3

Skull mature length; frontal and supraoccipital sutures unfused during first part of this stage, but are nearly fused before its close; orbits tubular to prominently so; cores still larger in circumference, basal burrs and longitudinal ridges becoming more prominent; groove containing supraorbital foramen more enclosed; frontal, lacrimal, and nasal sutures unfused

**FULLY MATURE SKULLS**

Plate 9, figure 4, plate 10, figure 1

Skull mature length; frontal and supraoccipital sutures fused in majority of cases; orbits protruding and tubular; cores have distinct burrs and longitudinal ridges; circumference of core nearly static, mature length but not circumference acquired in youth; groove containing supraorbital foramen well enclosed; frontal, lacrimal, and nasal sutures starting to fuse. (The late fusing of these three sutures indicates a continued growth of the bones of the cranium until this stage of life has been reached in Bison. This may be the reason for the predominant occurrence of Bison cranium in the fossil condition, since the skull would tend to part along this line of weakness.)

**SKULLS IN OLD AGE**

Plate 10, figure 2

Frontal and supraoccipital sutures well fused; orbits tubular and protruding; cores have developed distinct longitudinal ridges and burrs; circumference of cores static; groove containing supraorbital foramen well enclosed; frontal, lacrimal, and nasal sutures becoming progressively fused with age

**SEXUAL DIFFERENCES**

In so far as can be determined, all recognized North American Bison species are founded on male examples. Age and growth changes of skulls of living bison are illustrated in plates 8 to 10 (males), and plate 11 (females).
Average male skulls are more massive overall, with heavier, more tubular orbits, frontal and occipital sutures fused earlier in life, and have heavier horn-cores with larger basal burrs than average female skulls.

The average *B. (B.) bison* female skull has a 9 per cent smaller basilar length, 26 per cent smaller spread of horn-cores, 40 per cent smaller length of horn-cores on upper curve, 37 per cent smaller circumference of horn-cores, 36 per cent smaller transverse diameter of horn-cores, and 18 per cent smaller width of cranium between horn-cores and orbits than the average male skull.
REVISED, PART 1, BISON OF NORTH AMERICA

The formal taxonomic treatment of the known Bison species of North America and Eurasia is divided into two parts. The arrangement is based on conclusions drawn from the Alaskan collection in conjunction with numerous Recent and fossil Bison specimens from other institutions.

LISTING OF NORTH AMERICAN BISON BY SUBGENERA

The North American Bison are here divided into one living and four extinct subgenera which embrace one living species and one subspecies, and nine extinct species and one subspecies. The extinct subgenus Parabison and a primitive unnamed subgenus, both of which occur in Eurasia, are unknown.

FAMILY BOVIDAE Gray, 1821
SUBFAMILY BOVINAE Gill, 1872
GENUS BISON (Hamilton Smith, 1827)

A. SUBGENUS BISON
3 species, 1 subspecies, 9 synonyms
Late Pleistocene and Recent.
Horn-cores moderate to small sized, subcircular in cross section and posteriorly twisted.

1. B. (Bison) bison bison (Linnaeus, 1758)
Genotype, Recent plains bison.
Northern Mexico, United States, and southern Canada. Not native to Alaska.
Spread of horn-cores, 465–662 mm.

SYNONYMS
B. sylvestris Hay, 1915
B. americanus pennsylvanicus Shoemaker, 1915
B. b. septemtrionalis Figgins, 1933

1A. B. (Bison) bison athabascae Rhoads, 1897
Recent woodland or mountain bison.
Rocky Mountains of United States, northwestern Canada. Alaskan occurrence new.
Spread of horn-cores, 585–735 mm.

SYNONYMS
B. bison oregonus Bailey, 1932
B. bison haningtoni Figgins, 1933

2. B. (Bison) occidentalis Lucas, 1898
Very late Pleistocene and sub-Recent.
From Alaska through central United States to Texas.
Spread of horn-cores, 670–875 mm.

SYNONYMS
B. kansensis McClung, 1905
B. texanus Hay and Cook, 1928
Stelabison occidentalis, Figgins, 1933
Stelabison occidentalis francisi Figgins, 1933

3. B. (Bison) preoccidentalis, new species
Late Pleistocene.
Known only from Alaska.
Spread of horn-cores, 740–925 mm.

B. SUBGENUS SIMOBISON (Hay and Cook, 1930)
2 species, 1 subspecies, and 6 synonyms
Early middle Pleistocene to sub-Recent.
Horn-cores large to small sized, extending from skull at approximately right angles.

1. B. (Simobison) antiquus antiquus
Leidy, 1852
Very late Pleistocene and sub-Recent.
Central and southern North America.
Alaskan occurrence unknown.
Spread of horn-cores, 816–975 mm.

SYNONYMS
B. californicus Rhoads, 1897
B. pacificus Hay, 1927
1A. B. (Simobison) antiquus figginsi
(Hay and Cook, 1928)
Subgenotype, very late Pleistocene or sub-Recent.
New Mexico, Texas, and Nebraska. Alaskan occurrence unknown.
Spread of horn-cores, 780–980 mm.

SYNONYMS
B. taylori Hay and Cook, 1928
B. oliverhayi Figgins, 1933
Stelabison occidentalis taylori, Figgins, 1933
B. antiquus barbouri Schultz and Frankforter, 1946
2. B. (Simobison) allenii (Marsh, 1877)
Middle and ? Late Pleistocene.
Western and central North America, unknown from Alaska.
Spread of horn-cores, 1100–1338 mm.

SYNONYM
B. willistoni Martin, 1924

C. SUBGENUS SUPPERBISON FICcK, 1937
1 species
Late Pleistocene.
Horn-cores large to moderate sized, proportionately long.

1. B. (Supperbison) crassicornis
(Richardson, 1854)
Subgenotypic species, late Pleistocene.
Known only from the headwaters of the Yukon and Alaska.
Spread of horn-cores, 765–1322 mm.

D. PLATYCEROBISON, NEW SUBGENUS
3 species
Early middle to ? late Pleistocene.
Horn-cores large to moderate sized, dorso-ventrally flattened.

1. B. (Platycerobison) chaneyi
(Cook, 1928)
Subgenotypic species, middle Pleistocene.
Known only from Texas, ? Nebraska.
Spread of horn-cores, 1071 mm.

2. B. (Platycerobison) geisti,
new species
Late Pleistocene.
Known only from Alaska and ? northern Canada.
Spread of horn-cores, 810 mm.

3. B. (Platycerobison) alaskensis
(Rhoads, 1897)
Late Pleistocene.
Known only from Alaska.
Spread of horn-cores, 1115 mm.

E. GIGANTOBISON, NEW SUBGENUS
1 species and 6 synonyms
Early middle to ? late Pleistocene.
Horn-cores extremely large, subcircular in cross section.

1. B. (Gigantobison) latifrons
(Harlan, 1825)
Subgenotypic species, middle Pleistocene.
Central southern North America, unknown from Alaska.
Spread of horn-cores, 1422–2129 mm.

SYNONYMS
B. ferox Marsh, 1877
B. crampianus Cope, 1894
B. arisonica Blake, 1898
B. regius Hay, 1913
B. angularis Figgins, 1933
B. rotundus Figgins, 1933

SUMMARY OF MALE HORN-CORE AND CRANIAL CHARACTERS OF BISON SUBGENERA AND HERE-RECOGNIZED SPECIES OF NORTH AMERICA (SEE TABLE 25, P. 244)

A. BISON (BISON) (HAMILTON SMITH, 1827)
Horn-cores moderately large to small, circular in cross section, proportionately moderate to short, extending from skull in posterior direction with respect to the longitudinal axis, not strongly depressed, with tips having a distinct posterior twist.

1. Bison (Bison) bison (Linnaeus, 1758)
Genotype and subgenotype Plains race

1A. Bison (Bison) bison athabascae Rhoads, 1897
Mountain or woodland race

Smallest of bison. Horn-cores small in size; length on upper curve seldom exceeding basal circumference or cranial width, subcircular in basal cross section, posteriorly directed with respect to longitudinal axis of skull; distal tips posteriorly twisted and pointed; superior longitudinal groove weak or missing; tips tending to be most posteriorly directed of Bison, seldom rising high above plane of frontals and seldom strongly depressed, curvature varying from nearly straight to recurved; frontals flat to arched; cranium moderate

Same general characters as above species, except horn-cores tend to be larger and stubbier with a broader cranium and larger skull
2. Bison (Bison) occidentalis
Lucas, 1898

Horn-cores moderate in size; length on upper curve may be slightly greater or less than basal circumference or cranial width, subcircular in basal cross section, posteriorly directed with respect to longitudinal axis of skull; distal tips posteriorly twisted and pointed; superior longitudinal groove slightly indicated or missing; cores rising well above plane of frontals in a regular backward upsweep, curvature moderate to strong; frontals flat to slightly arched; cranium moderate

3. Bison (Bison) preoccidentalis, new species

Horn-cores moderately large; length on upper curve equal to, or exceeding, either basal circumference or cranial width, subcircular in basal cross section, posteriorly directed with respect to longitudinal axis of skull; distal tips slender, posteriorly twisted and pointed; superior longitudinal groove moderately indicated; rising well above plane of frontals in a uniform backward upsweep, posterior to occipital plane; curvature moderate; frontals tend to be flat; cranium moderate

B. BISON (SIMOBISON) (Hay and Cook, 1930)

Horn-cores large to moderate, circular to slightly compressed in cross section, proportionately long to short, extending from skull at nearly right angles to the longitudinal axis, usually depressed before swinging up on tips.

1. Bison (Simobison) antiquus
antiquus (Leidy, 1852)

Horn-cores moderate in size; length on upper curve seldom exceeding basal circumference or cranial width, subcircular in cross section, extending from skull at almost right angles to longitudinal axis of skull; proximally cores are depressed and swing straight up on tips with little or no posterior twist; distal tips tend to be stubby and heavy, seldom rising far above plane of frontals or extending posterior to occipital plane of skull; superior longitudinal groove is sometimes indicated; frontals tend to be arched; cranium broad

1A. Bison (Simobison) antiquus figginisi (Hay and Cook, 1928)

Subgenotype

About same general characters as above, except horn-cores tend to be slightly longer and more posteriorly directed but not rising far above plane of frontals. (All known specimens have undergone much crushing, and may or may not be subspecific to B. (S.) antiquus)

2. Bison (Simobison) alleni
(Marsh, 1877)

Horn-cores moderate to quite large; length on upper curve equal to, or strongly exceeding, basal circumference or cranial width; cores vary from subcircular to moderately dorsoventrally compressed in cross section, directed in a very moderate posterior direction with respect to longitudinal axis of skull and but slightly posterior to occipital plane; distal tips not posteriorly twisted, but are heavy and blunt with strong to moderate superior longitudinal grooves; cores moderate to strongly depressed and curved, rising slightly above plane of frontals; frontals tend to be slightly arched; cranium broad

C. BISON (SUPERBISON) FRICK, 1937

(See specific characters below.)

1. Bison (Superbison) crassicornis (Richardson, 1854)

Subgenotype

Horn-cores moderately large to large; length on upper curve equal to, or exceeding, either basal circumference or cranial width, subcircular in basal cross section, posteriorly directed from slight to moderate with respect to longitudinal axis of skull; distal tips occasionally have slight posterior twist, being pointed to slightly blunt and heavy with moderate to weak superior longitudinal grooves; cores vary from strongly depressed and rising but slightly above frontals with slight curvature and backward upsweep to cores with no depression, rising high above frontals with strong curvature and uniform backward upsweep; cores may extend backward to slightly ahead of, or well beyond, the occipital plane; frontals strongly arched to flat; cranium moderate to broad
Horn-cores large to moderate, distinctly flattened dorsoventrally in cross section, proportionally long to moderate, more posteriorly placed on frontals, extending from skull in slight posterior direction with respect to longitudinal axis; cores proximally depressed, rising high above frontals, tips not posteriorly twisted or directed.

1. *Bison* (*Platycerobison*) *chaneyi* (Cook, 1928) Subgenotype
   
   **Horn-cores quite large;** length on upper curve strongly exceeding either basal circumference or cranial width; **cores dorsoventrally compressed** in cross section, directed in a very slight posterior direction, slightly behind occipital plane with respect to longitudinal axis of skull; **distal tips not posteriorly directed or twisted, being heavy and blunt with strong superior longitudinal groove;** cores slightly depressed and rising high above the plane of frontals; frontals flat; cranium broad; cores more posteriorly placed than in most species

2. *Bison* (*Platycerobison*) *geisii*, new species
   
   About same general over-all characters as above but smaller; horn-cores moderate, length on upper curve equal to, or exceeding, basal circumference or cranial width, **dorsoventrally compressed in cross section**, directed more posteriorly and a little more strongly depressed and sharply curved than *chaneyi*; **distal tips not posteriorly directed and are blunt with moderate superior longitudinal grooves,** rising high above frontals; frontals tend to be slightly arched; cranium moderate

3. *Bison* (*Platycerobison*) *alaskanus* (Rhoads, 1897)
   
   **Horn-cores moderate but tend to be large;** length on upper curve equal to, or exceeding, either basal circumference or cranial width, **dorsoventrally compressed in cross section**, directed in a moderate posterior direction with respect to the longitudinal axis of the skull; **distal tips not posteriorly twisted, being heavy and blunt with a moderate superior longitudinal groove;** cores moderately depressed and rising well above the plane of frontals and extending slightly posterior to the occipital plane; frontals tend to be flat; cranial width moderately broad

E. BISON (*Gigantobison*), NEW SUBGENUS

(See specific characters below.)

1. *Bison* (*Gigantobison*) *latifrons* (Harlan, 1825) Subgenotype
   
   **Horn-cores extremely large;** length on upper curve greatly exceeding basal circumference or cranial width, **cores subcircular in cross section,** directed in slight to moderate posterior direction with respect to longitudinal axis of skull, extending posterior to occipital plane; **distal tips not posteriorly twisted, with heavy tapering tips and a moderately developed superior longitudinal groove;** cores not strongly depressed, slight to strongly curved in a uniform manner, rising well above the frontals; frontals tend to be flat to slightly arched; cranium broad. *The largest of all North American Bison*

SUMMARY OF NORTH AMERICAN TYPES AND BEST FIGURED SPECIMENS

The types of many of the *Bison* species of North America are horn-cores or partial skulls. Fortunately, all seem to have been male individuals. Fossil species undoubtedly have the same sexual differences observed in living bison (p. 147, pls. 10, 11.) Examples of the fossil Alaskan females (pl. 23) show approximately the same marked sexual differences. (See detailed lists of specimens for figure references except for figures in this paper.)
### Types

<table>
<thead>
<tr>
<th>Types</th>
<th>Figured Specimens Types or Referred</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. BISON (BISON)</td>
<td>See Allen, 1876</td>
</tr>
<tr>
<td></td>
<td>This paper, pls. 8-11</td>
</tr>
<tr>
<td></td>
<td>Referred: See Hay, 1913b, p. 170, K.U.M.V.P. No. 3190; Hay, 1924, U.S.N.M.: V.P. No. 10452. This paper, plastotype, pl.14, figs. 2, 2A, 2B</td>
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<tr>
<td></td>
<td>Holotype: This paper, pl. 14, figs. 3, 3A, 3B, 3C</td>
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<tr>
<td>B. BISON (SIMOBISON)</td>
<td>Referred: Skulls. See Lucas, 1899a, A.N.S.P. No. 297; Hay, 1913b, p. 166; Chandler, 1916 (several figures of male and female). This paper, pl. 15. Holotype and referred specimens</td>
</tr>
<tr>
<td></td>
<td>Referred: Complete skull. See Hay and Cook, 1928, C.M.N.H. No. 1236. (Formerly holotype of B. “taylori” but provisionally referred to figginsi)</td>
</tr>
<tr>
<td>C. BISON (SUPERBISON)</td>
<td>Referred: Complete skulls and crania. See Frick, 1937, figs. 57 and (in part) 58. This paper, pls. 17–23. Lectotype after Richardson, pl. 18, fig. 1, pl. 19, fig. 1</td>
</tr>
<tr>
<td>D. BISON (PLATYCEOBISON)</td>
<td>Holotype: No complete skull known. Plastotype: This paper, pl. 24, figs. 1, 1A, 1B</td>
</tr>
<tr>
<td></td>
<td>Holotype: No complete skull known. This paper, pl. 25, figs. 2, 2A, 2B</td>
</tr>
<tr>
<td></td>
<td>Holotype: No complete skull known. This paper, pl. 24, figs. 3, 3A, 3B</td>
</tr>
<tr>
<td>E. BISON (GIGANTOBISON)</td>
<td>Referred: Complete skull. See VanderHoof, 1942, U.C.M.P. No. 4067. This paper, holotype and referred specimens, pl. 26, holotype, figs. 1, 1A</td>
</tr>
</tbody>
</table>

### BISON DISTRIBUTION

The three distribution maps on pages 154, 156, 158 present the complex distribution of *Bison* in North America, and are arranged in such a manner as to show both the geographic and time elements. The distribution is based entirely on identifiable male skulls, horn-cores, and, in the case of living *Bison*, historic records. Specific identification cannot be ac-
MAP 1. Middle to late Pleistocene distribution of extinct species of the subgenera B. (Gigantobison), B. (Platycerobison), B. (Simobison), B. (Superbison), and B. (Bison). Symbols indicate location of one or more specimens. Based on male horn-cores.
accomplished for distribution with the present evidence on the basis of limbs or dentitions. The limbs and dentitions of the large B. (Gigantobison) latifrons, B. (Simobison) allenii, and B. (Platycerobison) chaneyi can probably be distinguished from all species of the typical subgenus Bison, but not from one another.

MIDDLE TO LATE PLEISTOCENE

Map 1 shows the distribution of Bison species during the middle to late Pleistocene, in which the occurrences divide between the large southern and the smaller northern species. The southern species, B. (Gigantobison) latifrons, B. (Simobison) allenii, and B. (Platycerobison) chaneyi, appear to be the first arrivals in North America from their Old World sources of origin. They probably become established in Alaska and northern Canada during an interglacial epoch in the latter part of the early Pleistocene, before they were isolated from Siberia by recurrent cold or glacial conditions. As a result, a segment of the Eurasian bovid population was isolated from Eurasia and forced southward out of Alaska, leaving no evidence as yet discovered of their passage. This first migration probably did not take place rapidly, but by middle Pleistocene the southern half of North America was populated by three distinct subgenera of Bison which never returned to the northern regions when the cold abated.

The best traveler seemed to be B. (Gigantobison) latifrons, for remains of this giant form have been found from coast to coast and southward into Mexico. There is also some suggestion that latifrons was able to survive until late Pleistocene in Florida. B. (Platycerobison) chaneyi is extremely rare, known from one specimen in Texas. The smallest of these great migrants, B. (Simobison) allenii, ranged over most of western North America and must have been better suited to survive the environmental changes of the Pleistocene, for this species has all the necessary attributes to be the progenitor of B. (Simobison) antiquus antiquus which lived on the plains of North America until very late Pleistocene.

The second migration of Bison (northern species), consisting of B. (Superbison) crassicornis, B. (Bison) preoccidentalis, B. (Platycerobison) alaskensis, and B. (Platycerobison) geisti, reached North America in the following interglacial epoch after the first migration (southern species) had been forced to the south. The faunal composition of the second migration reflects a change caused by the earlier Pleistocene isolation since specimens of the subgenera Gigantobison and Simobison are not represented, while those of the subgenera Superbison and Bison occur for the first time in North America. The subgenus Platycerobison is represented in both migratory faunas by different species.

On the basis of occurrence, crassicornis was predominant and preoccidentalis was next, while alaskensis and geisti were extremely rare. They probably arrived from Eurasia during the start of the late Pleistocene, spreading over Alaska and most of the Yukon River drainage where their remains are now found. Evidently the last Eurasian migrants did not extend their range southward in North America, for they are not recorded from the Great Plains. This does not imply that these northern and southern species of Bison lived at completely different times, but it does appear that the populations were geographically isolated and never lived on contemporaneous ranges during late Pleistocene.

Only a small segment of the second migration was able to withstand the changing conditions of another period of glaciation, probably the Wisconsin. This species appears to have been B. (Bison) preoccidentalis, whose descendants seem to be B. (Bison) occidentalis which later populated the North American plains.

VERY LATE PLEISTOCENE AND SUB-RECENT

Map 2 shows a concept of the extinct Bison distribution in very late Pleistocene and sub-Recent times. From the foregoing discussion, it seems that the two parental stocks, B. (Simobison) allenii and B. (Bison) preoccidentalis, are the respective ancestors of the extinct species B. (Simobison) antiquus and B. (Bison) occidentalis.

As a result of the first migration, B. (Simobison) antiquus developed and became well established on the plains of North America. A later climatic change presumably forced B. (Bison) occidentalis, the only surviving descendant of the second migration, southward from Alaska, the exact time of which remains to be established, but it was probably
MAP 2. Very late Pleistocene and sub-Recent distribution of extinct species of the subgenera *B. (Bison)* and *B. (Simobison)* based on male horn-cores. Symbols indicate location of one or more specimens.
before or during Wisconsin times. Unlike *antiquus*, which seems to have been confined to the southern portions of North America, *occidentalis* not only spread out over the central plains of North America but followed the retreat of ice and returning favorable climatic conditions back into the northern regions, to give rise to the last survivors of these Eurasian emigrants to North America, or the races *B. (B.) bison bison* and *B. (B.) bison athabascae*.

Evidently *antiquus* and *occidentalis* lived contemporaneously, sharing part of a common range during very late Pleistocene, but probably did not interbreed, for no specimens are known that display intermediate characters. No reasons are set forth here in an attempt to explain why *antiquus*, the first species to develop and establish itself in North America, became extinct while the later arrival, *occidentalis*, gradually developed into the living plains and woodland races of *B. (B.) bison*.

It may be noted, in comparing maps 2 and 3, that *antiquus* was able to extend its range along the west coast and farther southward into Mexico than either *occidentalis* or *bison* but did not move northward. Since *antiquus* evidently populated certain geographic localities never invaded by plains *Bison* or *occidentalis*, the extinction of *antiquus* cannot be attributed to competition or inbreeding with other species. Other explanations must be brought forward for the complete extinction of the geographically isolated west coast *antiquus* population.

The plotted occurrences of *occidentalis* and *antiquus* on map 2, based on distributional records, as presently known, lack continuity. Knowledge of these extinct forms is dependent on the chance discoveries as a result of the activities of man. Only the probable range is suggested here.

**Recent**

Map 3 shows that the distribution of living *Bison* on a historic and prehistoric basis is even more extensive than the wide-ranging *antiquus*. The historic distribution, which is based mainly on the records of Allen (1876) and Hornaday (1889), is indicated by the dot and dash outline, and the prehistoric range, which is based on identifiable horn-cores, is shown by the dotted outline. Crosses indicate definite occurrences of one or more known examples of the larger mountain or woodland race, *B. (B.) b. athabascae*.

The evidence does not warrant recognition of more than two races of Recent *Bison*. This conclusion is based on a population concept which does not permit the existence of races having no taxonomic differences other than geographic distribution.

Evidence is still to be desired concerning the distribution of *B. (B.) bison* south of the Rio Grande, considered the type locality, for it was here that *Bison* was first seen and reported by the Spaniards. The eastern coastal regions lack records of *Bison* horn-core remains, although certain dentitions would indicate the presence of the genus in prehistoric times beyond the here-indicated range.

The subgenus *B. (Parabison)* seems to have been confined to Eurasia and does not enter into the understanding of North American bison distribution.

**Genus [and Subgenus] Bison** (Hamilton Smith, 1827)

1. References for genus:


*Bos (Bison)* Hamilton Smith, 1827, in Cuvier, Georges, The animal kingdom, with additional descriptions of all the species hitherto named, and of many not before noticed, by Edward Griffith and others, vol. 5, p. 373.


**Genotype:** *Bos bison* Linnaeus, 1758.

**Generic Characters**

*(Based on Male Skulls)*

Horn-cores small to very large; subcircular to dorsoventrally compressed in cross section; may be directed at right angles, but usually in a moderate, posterior direction with respect to the longitudinal axis of the skull; may be strongly depressed and not rising above the plane of the frontals, or rising from the fron-
MAP 3. Recent distribution of *B. (Bison) bison bison* and *B. (Bison) bison athabascae* based on historical accounts and prehistorical horn-core occurrences. Symbols indicate location of one or more *athabascae* specimens.
tals in a backward upsweep with no depression; distal tips may be heavy and blunt or slender and pointed, with or without a posterior twist or a superior longitudinal groove; base of cores tending to rise from the frontal bones behind center between the orbits and occipital; forehead short, varying from moderate to broad; muzzle narrowed; nasals pointed and not extended so far forward as tips of premaxillae; external nasal openings made up by premaxillae, maxillae, and nasals; premaxillae bones not reaching nasals, orbits tubular and formed by the frontal, lacrimal, and malar bones.

Molars with a style or fold of enamel between the anterior and posterior lobes.

Both sexes horned, but male horn-cores larger and heavier with more pronounced basal burrs, orbits more tubular, skull larger, more massive, and limbs larger and more heavily proportioned than in females.

**GENERIC DISCUSSION**

The genus *Bison* is founded upon the typical species *Bos bison* Linnaeus which populated the Great Plains of North America. In 1827, Hamilton Smith considered the species distinct enough from *Bos* to separate it subgenerically. In 1849 Knight elevated Smith’s subgenus to generic rank. In 1937, Frick considered certain large *Bison* species to be subgenerically distinct and erected the subgenus *Superbison*. In so doing he automatically created the typical subgenus *Bison*. He had used the name “super-bison” as a descriptive adjective in 1930 when referring to remains of *B. (S.) crassicornis*, the subgenotypic species, but the formal taxonomic treatment was not presented until 1937.

The genus *Bison* is here divided into six subgenera on the basis of a combination of physical characters displayed in male horn-cores. It is felt that the subgeneric divisions here used will gather the numerous *Bison* species into phyletic groups that will demonstrate continuous tendencies of horn-core change in conjunction with the time element. The subgenotypic species are as follows: *B. (Bison) bison*, type of the genus and subgenus; *B. (Simobison) antiquus* [figginsi]1; *B. (Platy...
A. Bison (Bison) (Hamilton Smith, 1827)

Subgeneric Characters
(Based on Male Skulls)

Subgenotype: Bos bison Linnaeus, 1758.

Horn-cores moderate to small in size, never so large as in Gigantobison but earlier forms approach Superbison in size; circular in cross section; proportionately moderate to short, length on upper curve exceeds basal circumference and cranial width between horn-cores and orbits in the late Pleistocene species and seldom exceeds this proportion in Recent forms; skulls moderate in size; cranium moderate in width, not so broad as in Simobison; orbits tubular; frontals flat to arched; cores extend from skull in a stronger posterior direction than in Simobison and Platycerobison which are less posteriorly directed; core tips have a pronounced posterior twist that is weakly seen in Superbison and occasionally suggested in Simobison, Platycerobison, and Gigantobison. Living forms smallest of the known Bison. Premolars + tend to be more molariform in living species than in earlier species and Superbison.

Discussion

Under the present arrangement, the species still remaining in the typical subgenus Bison are confined to the late Pleistocene and Recent, and have small horn-cores when compared to Superbison and Gigantobison.

Two of the species are extinct. The presumably earliest and largest extinct species, B. (Bison) preoccidentalis, new species, is found in the faunal assemblages of the late Pleistocene deposits around Fairbanks and Eschscholtz Bay, Alaska, but has not been found in the more southern portion of North America. As discussed on page 171, preoccidentalis apparently gave rise to the smaller of the extinct species, B. (Bison) occidentalis, which also has been found in Alaska but not from deposits producing preoccidentalis. B. (B.) occidentalis appears to have been the true ancestor of the living plains and woodland races of bison inhabiting North America when discovered by white man. Plate 14 illustrates these contentions.

Bison (B.) occidentalis has frequently been confused with B. (Simobison) antiquus, since
both forms have been found in association with early man. Another phyletic line of *Bison* arrived in North America in an earlier Pleistocene migration, as *B. (Simobison) alleni* and *antiquus* represents the terminal species of this line before its extinction in North America.

To suggest why *antiquus* became extinct, and *occidentalis* did not, would be too conjectural. It does appear, however, that the two species lived contemporaneously for a period of time on the central plains of North America in the very late Pleistocene.

Since evidence suggests that the first arrival of members of the typical subgenus *B. (Bison)* reached North America during the late Pleistocene, it is to be expected that close relatives occurred in the Old World faunas. Such a species is known from Siberia. The holotype, found in 1906 on the Lena River, was called *Bison primivius* by Hilzheimer in 1909. If one can judge from the type figure and the size, this species is closely related to, if not synchronous with, *B. (Bison) occidentalis*.

1. **Bison (Bison) bison bison** (Linnaeus, 1758)

   **Living Plains Bison of North America**

   Type locality considered to be Mexico

   Plates 8, 9, 11

   1. References for the typical subgenus, species, and subspecies:

   *Bos bison* LINNAEUS, 1758, Systema naturae, ed. 10, vol. 1, p. 72.

   *Bos americanus* Gmelin, 1788, Systema naturae, vol. 1, p. 204.

   *Bos (Bison) americanus*, HAMILTON SMITH, 1827, in Cuvier, Georges, The animal kingdom, with additional descriptions of all the species hitherto named, and of many not before noticed, by Edward Griffith and others, vol. 5, p. 374.


   *Bison bison* (Linnaeus), JORDAN, 1888, Manual of the vertebrate animals of the northern United States, p. 337.

   *Bison bison bison*, the typical subspecies automatically came into being when *B. (Bison) sylvestris* (1947, p. 567) split the genus and established the subgenus *Superbison*. (Art. 9, International Rules of Zoological Nomenclature.)

   2. References for the holotype of *Bison sylvestris*

   *Hay, 1915:*


   3. References for the name *B. americanus pennsylvanicus* Shoemaker, 1915:

   *Bison americanus pennsylvanicus* SHOEMAKER, 1915, A Pennsylvania bison hunt, pp. 9, 16, 17.


   4. References for the holotype of *B. b. septemtrionalis*

   *Figgins, 1933:*


   **Specific Characters**

   **(Based on Male Skulls)**

   Horn-cores small in size, smallest of *Bison*; core length on upper curve seldom exceeds basal circumference or cranial width between horn-cores and orbits, subcircular in basal cross section; posteriorly directed with respect to longitudinal axis of skull and extending posterior to occipital plane; distal tips posteriorly twisted and pointed, superior longitudinal groove weak or missing, tips tend to be most posteriorly directed of *Bison*, seldom rising high above the plane of the frontals and seldom strongly depressed, curvature varying from nearly straight to recurved.

   Largest horn-cores as large as in *B. (Bison) athabascae* and nearly as large as in the small variants of *B. (Bison) occidentalis*, but never so large as in *B. (Bison) preoccidentalis* or shaped as in *B. (Simobison) antiquus*; general core shape much like that of *B. (B.) occidentalis* but smaller.

   Frontals vary from flat to arched; orbits tend to be tubular; facial region tends to be slender and somewhat shorter than in occiden-
Male skulls larger and more massive with longer, better developed horn-cores and basal burrs than female; basal longitudinal grooves of core surface better developed, and orbits tend to be more tubular in old males than in females.

Premolars, 4 tend to be more molariform than in earlier forms. Superior and inferior molars have a median style or enamel fold between the anterior and posterior lobes that disappear in a progressive order with age (see p. 143).

Discussion

The well-known plains bison is the last surviving bovid of the Pliocene migrations from the Old World and probably developed from the extinct species B. (Bison) occidentalis, for it has none of the horn-core attributes of B. (Simobison) antiquus antiquus (pls. 14, 15).

The literature, both scientific and historic,

**TABLE 10**

**Summary of Male Skull Measurements and Indices of B. (Bison) bison bison**

(Measurements in millimeters, figure 1C for key; indices in per cent, page 142.)

<table>
<thead>
<tr>
<th>Key No.</th>
<th>No. of Measurements</th>
<th>Summary</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td>Min.</td>
</tr>
<tr>
<td>1</td>
<td>Spread of horn-cores, tip to tip</td>
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</tr>
<tr>
<td>2</td>
<td>Greatest spread of cores on outside curve</td>
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</tr>
<tr>
<td>3</td>
<td>Core length on upper curve, tip to burr</td>
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<td>4</td>
<td>Length of core on lower curve, tip to burr</td>
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<td>Length, tip of core to upper base at burr</td>
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<tr>
<td>12</td>
<td>Transverse diameter of core</td>
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<td>Vertical diameter of core</td>
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<td>7</td>
<td>Circumference of core at base</td>
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<td>14</td>
<td>Width of cranium between cores and orbits</td>
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<td>Greatest postorbital width</td>
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<td>Width of skull at masseteric processes at M1</td>
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<td>8</td>
<td>Greatest width at auditory openings</td>
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<td>9</td>
<td>Width of condyles</td>
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<td>O-T</td>
<td>Occipital crest to tip of nasals</td>
<td>30</td>
</tr>
<tr>
<td>O-N</td>
<td>Occipital crest to tip of nasal-frontal suture</td>
<td>30</td>
</tr>
<tr>
<td>11</td>
<td>Depth, occipital crest to lower border foramen magnum</td>
<td>29</td>
</tr>
<tr>
<td>F-P</td>
<td>Basilar length of skull</td>
<td>43</td>
</tr>
<tr>
<td>O-P</td>
<td>Over-all length of skull</td>
<td>29</td>
</tr>
<tr>
<td>19</td>
<td>P3-M3 alveolar length</td>
<td>30</td>
</tr>
<tr>
<td>20</td>
<td>M1-M2 alveolar length</td>
<td>30</td>
</tr>
<tr>
<td>M-P</td>
<td>Median length of premaxilla beyond P3</td>
<td>30</td>
</tr>
<tr>
<td>18</td>
<td>Rostral width at maxillary-premaxillary suture</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>Index of horn-core curvature</td>
<td>44</td>
</tr>
<tr>
<td></td>
<td>Index of horn-core compression</td>
<td>44</td>
</tr>
<tr>
<td></td>
<td>Index of horn-core proportion</td>
<td>44</td>
</tr>
<tr>
<td></td>
<td>Index of horn-core length</td>
<td>44</td>
</tr>
</tbody>
</table>
of the last of these wild bison. The American Museum of Natural History also has an extensive collection that has formed the basis for a concept of the specific range of variation found in this race. Both of these large collections were obtained in Montana and can be considered as one population sample.

The summary of male horn-core and skull size variation presented in table 10 represents the observed range of this population. The measurements of all immature individuals not having M\(^4\) in wear were eliminated; a specific concept based on a mature male population is presented.

The specific concept has been highly important in making possible an understanding of the complicated Bison relationships. Population samples obtained from other areas of the Great Plains would no doubt produce small average differences that could not be considered racially significant. These samples from geographic localities differ insignificantly, but the living populations will differ in direct proportion to the time element of paleo-populations, until they have changed sufficiently to be considered another species, such as B. (Bison) occidentalis. The population sample of occidentalis is larger in horn-core size than that of B. (Bison) bison and perhaps should be considered a paleo-race of the living B. (Bison) bison.

One other species and two subspecies have been proposed which are considered synonymous with the plains bison as discussed under the following headings.

**Bison "sylvestris"** HAY, 1915

The holotype of B. "sylvestris" is a young individual of Bison. No other specimen of record has been referred to this species which is here considered a Bison specimen of indeterminate specific allocation owing to its extreme youth.

**The Name Bison americanus "pennsylvanicus"** SHOE MAKER, 1915

This race of Bison must be considered invalid for its description is based on hearsay. Shoemaker (1915, pp. 11, 12, 16) described this hypothetical race\(^1\) in a semipopular discussion on the extermination of Bison in Pennsylvania. No specimen has been produced to demonstrate subspecific distinctness. Shoemaker (1944, pp. 15–21) later disclosed the possibility of obtaining a skin of bison supposedly killed in Pennsylvania, and of several locations in which bison cranial material might be found, but still gave no further data on his subspecies, which was not mentioned by name in this later article.

**Bison bison "septemtrionalis"**

FIGGINS, 1933

The average difference of horn-cores of a northern and southern Bison population was set forth as the reason for proposing B. b. "septemtrionalis" as a northern subspecies. B. bison bison was retained for the southern population. There is a complete overlap in size and had these samples been larger, the average difference between the populations would have been less.

A comparison of the summary of male specimens from northern Montana (the proposed range of "septemtrionalis") with Figgins' northern population sample should show similar size averages. This, however, is not the case, for the northern population (this paper, table 10) is quite in agreement with Figgins' southern, and neither is considered significantly different.

Figgins listed only in a generalized way where he obtained his sample of the northern population, but indicates that some of the specimens were deeply buried and partly fossilized. If this is the case, B. b. "septemtrionalis" may represent a paleo-population which would be expected to differ slightly but which is not ancient enough to differ racially.

It is difficult to distinguish the larger members of a B. (Bison) bison bison population from most members of B. (Bison) bison athabascae and the smallest observed fossil variants of B. (Bison) occidentalis which immediately preceded the living species in geological time. It hardly seems advisable to add further confusion to Bison nomenclature by including other subspecies based on slight size differences and having no other taxonomic distinction.

---

TABLE 11
SUMMARY OF MALE SKULL MEASUREMENTS AND INDICES OF B. (Bison)
bison athabascae (True Forms)
(Measurements in millimeters, figure 1C for key; indices in per cent, page 142.)

<table>
<thead>
<tr>
<th>Key No.</th>
<th>No. of Measurements</th>
<th>Summary</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Min.</td>
<td>Av.</td>
</tr>
<tr>
<td>1</td>
<td>585</td>
<td>665</td>
</tr>
<tr>
<td>2</td>
<td>645</td>
<td>683</td>
</tr>
<tr>
<td>3</td>
<td>155</td>
<td>216</td>
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<tr>
<td>4</td>
<td>190</td>
<td>255</td>
</tr>
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<td>5</td>
<td>150</td>
<td>189</td>
</tr>
<tr>
<td>6</td>
<td>81</td>
<td>92</td>
</tr>
<tr>
<td>7</td>
<td>72</td>
<td>85</td>
</tr>
<tr>
<td>8</td>
<td>230</td>
<td>271</td>
</tr>
<tr>
<td>9</td>
<td>272</td>
<td>288</td>
</tr>
<tr>
<td>10</td>
<td>326</td>
<td>355</td>
</tr>
<tr>
<td>11</td>
<td>179</td>
<td>195</td>
</tr>
<tr>
<td>12</td>
<td>185</td>
<td>263</td>
</tr>
<tr>
<td>13</td>
<td>113</td>
<td>130</td>
</tr>
<tr>
<td>14</td>
<td>447</td>
<td>477</td>
</tr>
<tr>
<td>15</td>
<td>248</td>
<td>286</td>
</tr>
<tr>
<td>16</td>
<td>140</td>
<td>149</td>
</tr>
<tr>
<td>F-P</td>
<td>525</td>
<td>537</td>
</tr>
<tr>
<td>O-P</td>
<td>560</td>
<td>573</td>
</tr>
<tr>
<td>19</td>
<td>143</td>
<td>148</td>
</tr>
<tr>
<td>20</td>
<td>92</td>
<td>92</td>
</tr>
<tr>
<td>21</td>
<td>151</td>
<td>160</td>
</tr>
<tr>
<td>22</td>
<td>108</td>
<td>121</td>
</tr>
</tbody>
</table>

1. References for here-referred specimens of B. (B.) b. athabascae:


5. References concerning *B. (B.) b. athabascae*:


**Subspecific Characters**

*(Based on Male Skulls)*

Same general over-all characters as plains race, except horn-cores larger and more robust, with a broader cranium and larger skull.

**Discussion**

This race was known as woodland or mountain bison previous to its being named by Rhoads. Considerable data referring to the large bison in the vicinity of Great Slave Lake and the Yukon Territory have been published in the accounts of northern exploration, although no accounts have referred to white men's seeing bison in Alaska. The credit for the actual proof of the existence of woodland bison ranging into Alaska shortly preceding historic exploration must go to Charles Sheldon who brought back two skulls from his northern trek in 1906 and presented them to the United States National Museum. One skull has never been described. The other skull, although completely unfossilized, has been described as *B. occidentalis* by Osgood and Hay. Another specimen from St. Michael, Alaska, figured by Allen (1876, pl. 4) as *B. antiquus*, referred by Lucas (1899a, p. 758) to *B. occidentalis*, and later transferred to *Superbison* by Frick (1937, p. 591) is in complete agreement with other *B. (Bison)* *bison athabascae* specimens. Definite examples of the existence of large woodland bison in Alaska are shown on the distribution map (p. 158), Alaska is considered a part of the range previously covered by this race until Recent times. Their extermination in Alaska cannot be blamed on ruthless hunting, and no attempt is made to account for their withdrawal southeast towards the Great Slave Lake district.

Enumerated in the lists are Alaskan specimens that do not differ materially from the few available unquestionable *athabascae* specimens from the Great Slave Lake and northern Alberta collected before the introduction of plains bison into their native range in 1924.

Although the population sample of true *athabascae* skulls is too small to present a comprehensive understanding of the amount of variation possible within this mountain or woodland race, several important facts are brought out. The largest members of *athabascae* can be separated from the smaller individuals of *occidentalis* only with difficulty, or on the basis of fossilization. The horn-core size of the smaller members of the *athabascae* population is in complete agreement with that of the average- to large-sized portion of the plains bison, and presents an intergrading population between the living and fossil forms. This suggests that *athabascae* is the more primitive race of living bison.

In the more southern portions of North America, particularly the Rocky Mountains, early writings of explorations often refer to the immense size of mountain bison and their solitary habits. The woodland or northern bison may have acquired their mountain habitat by extending their range southward down the Rocky Mountains until they reached the mountains of Colorado, Wyoming, Utah, and Oregon. The mountain or northern bison has been variously described.

*Bison bison* "haningtoni" Figgins, 1933

Figgins (1933, p. 30) called the woodland bison *B. b. "haningtoni,"* and presented a set of measurements for their horn-cores that was much larger than that for the plains
bison. He compared his mountain bison with the plains form and apparently did not consider seriously the possibility of the Colorado mountain bison's belonging to the woodland forms of the north, from which it differs but little in size.

*Bison bison "oregonus"* Bailey, 1932

Bailey (1932, p. 48) described a subspecies *B. b. "oregonus."* The specimens were found in the dried bottom of Malheur Lake in the southeastern part of Oregon. This locality is but slightly beyond the recorded historical limits of the bison range, as shown by Allen (1876, see map) and Hornaday (1889, see map). As disclosed by Merriam (1926, pp. 211–214), Indian legends tell of bison migrations into this general district, not from the east but from the north down the inter-montane valleys. Since Bailey's race is extinct, it is not necessary to consider hair coloration or life habits, but only to compare his holotype with the observed ranges of variation in the known specimens of *athabascae.* Here again is a record of the larger northern bison's following down the Rocky Mountain ranges and valleys where, in this case, they spread out into the now arid region around Lake Malheur from the nearby mountains. The entire Lake Malheur collection was measured and studied. It presents a population whose average size was larger than that of the plains race, precluding the chance that part of the plains race migrated across the mountains and spread out into Oregon.

The skull size of specimens of native wild bison from Yellowstone Park in the United States National Museum suggests that it approximates the skull size of *athabascae* of the north. These bison have never been considered other than a part of the plains race, but they may possibly represent *athabascae.* Little factual knowledge exists concerning the natural isolating mechanisms that kept *athabascae* from interbreeding with the plains race when their ranges bordered on each other. This seems to be the case, for Rhoads (1897, p. 497), in his original description, quotes a letter from Mr. H. I. Moberly describing some of their habits, indicating that these isolating mechanisms did function.

The true, pure-blooded woodland bison may be considered extinct as a result of the repopulation of their last wild range by the introduction of the plains bison in 1924. In selecting a population sample for the summary, specimens that might be the offspring of this cross breeding have been avoided.

Sixty-two male and female specimens are here recorded.

---

**ALBERTA, MACKENZIE, AND YUKON PROVINCES, CANADA**

**Holotype**

<table>
<thead>
<tr>
<th>Mounted specimen</th>
<th>N.M.C. 299</th>
<th>Collected in March, 1892, by Indians within 50 miles southwest of Fort Resolution, Great Slave Lake. Obtained by Warburton Pike in same year and presented to National Museum of Canada, Ottawa</th>
</tr>
</thead>
</table>

**Referred**

<table>
<thead>
<tr>
<th>Skull</th>
<th>N.M.C. 625</th>
<th>From near Athabaska Lake, 1898</th>
</tr>
</thead>
<tbody>
<tr>
<td>Skull</td>
<td>4538</td>
<td>From near Fort Smith, 1921</td>
</tr>
<tr>
<td>Skull, skin, and skeleton of old male</td>
<td>8755</td>
<td>From Wood Buffalo Park, Sept., 1927; collected by R. M. Anderson. Young plains bison from the Wainwright herd were introduced two years before this date and had not reached maturity</td>
</tr>
<tr>
<td>Skull, skin, and skeleton of adult cow</td>
<td>10405</td>
<td>From Wood Buffalo Park, March, 1928</td>
</tr>
<tr>
<td>Skull, skin, and skeleton</td>
<td>Univ. Saskatchewan Coll.</td>
<td>From Wood Buffalo Park, Sept., 1927</td>
</tr>
<tr>
<td>Region</td>
<td>Description</td>
<td>Collection Numbers</td>
</tr>
<tr>
<td>--------</td>
<td>-------------</td>
<td>--------------------</td>
</tr>
<tr>
<td>Alberta</td>
<td>Skull with skeleton; tooth wear (S-3)</td>
<td>A.M.N.H: M. 73615, 123053</td>
</tr>
<tr>
<td></td>
<td>Cranium with sheaths</td>
<td>123053</td>
</tr>
<tr>
<td></td>
<td>Skull and skeleton</td>
<td>U.S.N.M: M. 172689</td>
</tr>
<tr>
<td></td>
<td>Cranium, partial and badly weathered</td>
<td>U.S.Bi.S. 177630</td>
</tr>
<tr>
<td></td>
<td>Partial cranium with complete left core</td>
<td>177631</td>
</tr>
<tr>
<td></td>
<td>Cranium with horn-cores, unfossilized</td>
<td>U.S.N.M: V.P. 5513</td>
</tr>
<tr>
<td></td>
<td>Cranium with cores and or- bits</td>
<td>16861</td>
</tr>
<tr>
<td></td>
<td>Complete skull, tooth wear (S-3); completely un-weathered</td>
<td>U.S.Bi.S. 223292</td>
</tr>
<tr>
<td></td>
<td>Cranium with horn-cores, unfossilized</td>
<td>C.A.S. Coll.</td>
</tr>
<tr>
<td></td>
<td>Complete skull, well-worn teeth (S-4)</td>
<td>U.S.Bi.S. 168816</td>
</tr>
<tr>
<td></td>
<td>Seven crania, all of which have weathered surfaces</td>
<td>U.S.N.M: M. 120507, 120508, 120509, 120510, 120511, 120512, 221089</td>
</tr>
<tr>
<td></td>
<td>Adult male, mounted specimen</td>
<td>C.M.N.H. 2</td>
</tr>
<tr>
<td></td>
<td>Skull of adult male</td>
<td>1369</td>
</tr>
<tr>
<td></td>
<td>Cranium</td>
<td>U.S.N.M: M. 14442</td>
</tr>
<tr>
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<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Male skull (S-4) and skeleton U.S.Bi.S. From Malheur Lake; collected by George M. Benson, Nov., 1931
250145
Holotype of B. b. "oregonus"

Five male skulls:
- Skull, young 249844 From Malheur Lake
- Skull, S-3 249895 From Malheur Lake
- Skull, S-3 250092 From Malheur Lake
- Skull, S-2 249842 From Malheur Lake
- Skull, S-3 250090 From Malheur Lake

Twelve female skulls:
- Skull, S-1 250093 From Malheur Lake
- Skull, S-3 250089 From Malheur Lake
- Skull, S-2 250091 From Malheur Lake
- Skull, S-3 249849 From Malheur Lake
- Skull, S-2 249843 From Malheur Lake
- Skull, no teeth 249848 From Malheur Lake
- Skull, S-3 249841 From Malheur Lake
- Skull, S-3 249850 From Malheur Lake
- Skull, S-2 249845 From Malheur Lake
- Skull, S-3 249847 From Malheur Lake
- Skull, S-3 250095 From Malheur Lake

Posterior male cranium and orbits 246529 From Izee, Grant County; collected by Stanley Jewett, 1925.

CANADA

From Wood Buffalo Park, Alberta, but collected over four years after the introduction of the plains bison; therefore, the purity of the stock is questioned in the following specimens:

Skull N.M.C. Collected by J. Dewey Soper, 1932, Blind Bull Lake
11435
11436 Cabin 7, Murdock Creek
12091 Cabin 7, Murdock Creek

Skull with sheaths A.M.N.H:M. From Alberta; collected by G. G. Goodwin, 1934
86950

Skull, skin, and skeleton, mature 98953 From Salt Lick, Five Acre Wallow; collected by G. G. Goodwin, 1934

Skin and skeleton of young female 98954 From plains, Seven Mile Camp; collected by G. G. Goodwin, 1934

Skin and skeleton of young male 98955 From same locality as above
Skin and skeleton of very young male 98956 From same locality as above
Skin and skeleton of young female 98957 From same locality as above
Skin and skeleton of young female 98958 From same locality as above
Skin and skull of young female 98959 From same locality as above

Skull, skin, and skeleton of mature male 130171 From Wood Buffalo Park on Salt River, Alberta; collected by M. Dempsey through G. G. Goodwin, 1936

Skull, skin, and skeleton 98228 Collected by G. G. Goodwin, 10 miles from Slave River, 1935

Skull 98229 From same locality as above

Complete skull, tooth wear (S-3) U.S.Bi.S. From near Government Hay Camp, 1936–1937
263390

Complete skull 263389 From same locality as above
2. *Bison (Bison) occidentalis* Lucas, 1898

From the Late Pleistocene and sub-Recent deposits of Alaska and through central United States to Texas

Plate 14, figures 2, 2A, 2B

**TOTAL AVAILABLE SPECIMENS:** 18

1. References for the holotype:


2. References for the holotype of *Bison kansenensis* McCLUNG, 1904:


3. References for the holotype of *Bison texanus* Hay and Cook, 1928:


4. References for the holotype of *Stelabison occidentalis* (Lucas), Figgins, 1933:

*Stelabison occidentalis*, Figgins, 1933, Proc. Colorado Mus. Nat. Hist., vol. 12, no. 4, pp. 17–19. (Figgins cited *B. occidentalis* as the genotype of "Stelabison," but used a referred specimen of *B. (S.) crassicornis*, pl. 1, figs. 1, 2, to illustrate his genus.)


5. References for the indeterminate holotype of *Stelabison occidentalis francisi* Figgins, 1933:

*Stelabison occidentalis francisi* Figgins, 1933, Proc. Colorado Mus. Nat. Hist., vol. 12, no. 4, pp. 17–19, pl. 2, figs. 1, 2. (Holotype of this subspecies is a specifically indeterminate M of *Bison.*)


6. References for here-referred specimens of *B. (B.) occidentalis*:


*Bison antiquus taylori* (Hay and Cook), BARBOUR AND SCHULTZ (in part), 1936, Bull. Nebraska State Mus., vol. 1, no. 45, pp. 434, 435, fig. 204 (Scottsbluff Bison Quarry form, first called *B. occidentalis* by Schultz, 1934, but later changed).


**SPECIFIC CHARACTERS**

**(BASED ON MALE SKULLS)**

The outstanding characters of this important species were well defined by Lucas (1899b, p. 17) as "Horn cores of moderate size, although much larger than in the existing species; circumference at base equal to or slightly greater than length along upper curve; sub-cylindrical in section and regularly curved upward and backward."

To this description can be added: core length on upper curve may be slightly greater or less than cranial width between horn-cores and orbits; cores posteriorly directed with respect to longitudinal axis of skull; distal tips posteriorly twisted and pointed, with superior longitudinal groove but slightly indicated or missing; cores seldom more than
moderately depressed, rising well above the plane of the frontals in a uniform backward upsweep; curvature moderate to strong; frontals vary from flat to slightly arched; cranium moderate.

The skull of B. (Bison) occidentalis closely resembles that of B. (B.) b. bison, but tends to resemble that of B. (Bison) antiquus. In strong contrast to antiquus, the horn-cores of occidentalis are posteriorly directed and twisted on the tips with respect to the longitudinal axis of the skull, extending well above the frontal plane and posterior to the occipital, while those of antiquus are directed at almost right angles to the skull and are strongly depressed before curving upward with very little backward twist to the tips, which seldom rise far above the plane of the frontals or extend posterior to the occipital.

**TABLE 12**

**Summary of Male Skull Measurements and Indices of B. (Bison) occidentalis and Measurements of Holotype (U.S.N.M: V.P. No. 4157)**

(Measurements in millimeters, figure 1C for key; indices in per cent, page 142.)

<table>
<thead>
<tr>
<th>Key No.</th>
<th>Holo-etype</th>
<th>No. of Measurements</th>
<th>Summary</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Spread of horn-cores, tip to tip</td>
<td>706 13</td>
<td>Min. 767 Av. 875</td>
</tr>
<tr>
<td>2</td>
<td>Greatest spread of cores on outside curve</td>
<td>764 8</td>
<td>735 782 892</td>
</tr>
<tr>
<td>3</td>
<td>Core length on upper curve, tip to burr</td>
<td>293 12</td>
<td>222 279 330</td>
</tr>
<tr>
<td>4</td>
<td>Length of core on lower curve, tip to burr</td>
<td>365 12</td>
<td>275 340 405</td>
</tr>
<tr>
<td>5</td>
<td>Length of tip of core to upper base at burr</td>
<td>247 11</td>
<td>210 243 290</td>
</tr>
<tr>
<td>6</td>
<td>Transverse diameter of core</td>
<td>102 16</td>
<td>85 98 114</td>
</tr>
<tr>
<td>7</td>
<td>Vertical diameter of core</td>
<td>95 16</td>
<td>76 91 100</td>
</tr>
<tr>
<td>8</td>
<td>Circumference of base at base</td>
<td>300 16</td>
<td>253 290 336</td>
</tr>
<tr>
<td>9</td>
<td>Width of cranium between cores and orbits</td>
<td>297 12</td>
<td>277 299 340</td>
</tr>
<tr>
<td>10</td>
<td>Greatest postorbital width</td>
<td>360 8</td>
<td>328 351 400</td>
</tr>
<tr>
<td>11</td>
<td>Width of skull at masseteric processes at M¹</td>
<td>— 5</td>
<td>169 187 204</td>
</tr>
<tr>
<td>12</td>
<td>Greatest width at auditory openings</td>
<td>280 9</td>
<td>259 275 307</td>
</tr>
<tr>
<td>13</td>
<td>Width of condyles</td>
<td>129 8</td>
<td>124 131 147</td>
</tr>
<tr>
<td>O-T</td>
<td>Occipital crest to tip of nasals</td>
<td>— 5</td>
<td>471 493 543</td>
</tr>
<tr>
<td>O-N</td>
<td>Occipital crest to tip of nasal-frontal suture</td>
<td>267 8</td>
<td>229 259 273</td>
</tr>
<tr>
<td>14</td>
<td>Depth, occipital crest to lower border foramen magnum</td>
<td>177 6</td>
<td>136 158 177</td>
</tr>
<tr>
<td>F-P</td>
<td>Basilar length of skull</td>
<td>— 6</td>
<td>467 516 582</td>
</tr>
<tr>
<td>O-P</td>
<td>Over-all length of skull</td>
<td>— 6</td>
<td>505 573 630</td>
</tr>
<tr>
<td>19</td>
<td>P¹-M¹ alveolar length</td>
<td>— 6</td>
<td>137 147 160</td>
</tr>
<tr>
<td>20</td>
<td>M¹-P² alveolar length</td>
<td>— 5</td>
<td>84 91 102</td>
</tr>
<tr>
<td>M-P</td>
<td>Median length of premaxilla beyond P²</td>
<td>— 5</td>
<td>143 153 168</td>
</tr>
<tr>
<td>18</td>
<td>Rostral width at maxillary-premaxillary suture</td>
<td>— 6</td>
<td>102 115 125</td>
</tr>
</tbody>
</table>

Index of horn-core curvature: 148 11 121 140 169
Index of horn-core compression: 93 16 86 93 104
Index of horn-core proportion: 98 12 85 97 110
Index of horn-core length: 99 9 88 95 112

be larger and proportionately similar with a tendency for a longer, narrower facial region and larger horn-cores, and does not tend to be so broad as in B. (Simobison) a. antiquus. In strong contrast to antiquus, the horn-cores of occidentalis are posteriorly directed and twisted on the tips with respect to the longitudinal axis of the skull, extending (pls. 14, 15). The cores, compared to those of B. (B.) prooccidentalis, new species, are smaller in size and proportion, more curved, have a stronger posterior twist of the tips. There is a proportionately similar but smaller skull. The skull of occidentalis, compared with that of B. (B.) athabascae, is slightly larger but proportionately similar in all details, ex-
cept for the horn-cores which are dimensionally and proportionately larger. The smallest individual variants of an *occidentalis* population cannot easily be separated from the largest plains bison and the moderate- to large-sized *athabascae*. (See tables 10, 11, 12.)

**DISCUSSION**

Although *B. (Bison) occidentalis* has distinctive characters of horn-core shape, directional trends, and cranial proportions that readily distinguish it from other *Bison*, it has been frequently confused with *B. (Simobison) antiquus*. Although, theoretically, *occidentalis* was confined to the northern and *antiquus* to the southern regions of North America—a theory based upon the absence, so far, of remains of true *occidentalis* in Mexico and of true *antiquus* in the far north—more recent studies indicate that during the late Pleistocene the two species ranged contemporaneously on the Great Plains (see maps 1 and 2, pp. 154, 156).

The common range of *occidentalis* and *antiquus* was the plains of central North America. Some specimens of *occidentalis* found in Nebraska, Kansas, and Texas have been incorrectly referred to *B. antiquus* "taylori." If the characters of the holotypes of *occidentalis*, *antiquus*, and "taylori" are well observed, their contemporaneous existence is evident.

It appears that *occidentalis* was a later arrival on the plains of North America than *antiquus*, but was the successful surviving species that gave rise to the recent plains bison. The range of variation is now well enough known to show that the smaller individual variants of *occidentalis* are nearly inseparable from some of the larger individuals of plains and woodland bison, both of which have horn-core characters in common with *occidentalis* and not *antiquus*.

In the type area of Alaska it was thought that *occidentalis* existed contemporaneously with *B. (Suberbison) crassicornis*. This study does not substantiate this belief in its entirety.

In the great collection from Fairbanks, it was found necessary to consider the *occidentalis*-like form that lived contemporaneously with *B. (S.) crassicornis* as a separate species. The new species *B. (B.) preoccidentalis* differs as much from *occidentalis* as does the Recent *Bison* (pl. 14). It appears that the Alaskan deposits that yielded the holotype of *occidentalis* are not so early in age as the deposits around Fairbanks which contain *preoccidentalis*. Geologic data substantiating this assumption are still lacking, although biological differences are evident.

The new species *B. (B.) preoccidentalis* has all the physical requirements to be the only *Bison* that can be considered the progenitor of *occidentalis*, which was in turn the progenitor of *B. (B.) b. bison* and *B. (B.) b. athabascae*.

The species *occidentalis* and *antiquus* are especially interesting, for evidences of early man, or the Folsom and Yuma cultures, in the form of artifacts have been found in association with both. Three skeletons of *occidentalis* having artifacts in association are now mounted, two in the Nebraska State Museum and one in the University of Kansas Museum.

*Bison "texanus"* **HAY AND COOK, 1928**

All skull proportions of the holotype of this species are in agreement with the ranges of variation observed in specimens of *occidentalis*, with the exception of the horn-core which has a curvature index of 169. Hay and Cook, (1928, p. 33) considered this of specific importance and for this reason made a new species. This difference does not seem to be great enough to be considered of specific importance in view of the observed range of variation in horn curvature, in which young males tend to have a higher curvature than the older, more mature animals. The holotype of "*texanus*" is just mature, with an early (S-3) tooth wear. In *occidentalis*, the range of curvature index in the small population sample is 121–148 with the exception of the holotype of "*texanus*." In the closely related, living plains bison, the curvature index ranges from 120–182, and in the large *crassicornis* collection, the curvature index ranges from 109–153.

*Bison "kansensis"* **McCLUNG, 1904**

The holotype of *B. "kansensis"* consists of a posterior portion of the cranium with one partial horn-core. The median suture of the frontal is not strongly fused, indicating a young animal. When McClung described this
specimen, he had no access to the extensive data now available and considered the characters of individual variability evidenced in his specimen to be of specific importance. Later discovery of a second complete skull from the same locality disclosed that McClung's holotype was inseparable from the second specimen which had all the affinities of occidentalis and represents the smaller extreme of a population. Both specimens were fossilized, the most complete of which is here figured (pl. 16). Hay, in 1924, properly considered both of these specimens B. occidentalis. Paradoxically, one of the largest variants of referred B. occidentalis specimens is mounted in the University of Kansas and has been figured in numerous papers.

Eighteen male specimens with horn-cores, unless otherwise stated, are here recorded:

ALASKA

**Holotype**

Cranium with complete right horn-core and partial left core

U.S.N.M.:V.P. 4157 From near Fort Yukon; collected by Sir John Richardson

Figured by Lucas, 1899a, pl. 65; by Hay, 1913, vol. 46 (1914), pl. 9, figs. 3, 4; 1914, vol. 23, pl. 39, figs. 2, 3

(Plasototype made in 1945 and checked against the holotype)

Plasototype, this paper, pl. 14, figs. 2, 2A, 2B

**Refereed**

Right horn-core

U.S.N.M.:V.P. 2325 From Tatlo River; collected by W. H. Dall

MINNESOTA

**Refereed**

Four skulls and other associated material:

Mature skull, lacking part of nasals and teeth

U.S.N.M.:V.P. 10541

Nearly complete skull; tooth wear (S-4)

10542

Cranium and horn-cores

10545

Partial skull, top of cranium, and one horn-core, complete

10546

IOWA

**Refereed**

Left horn-core and portion of cranium of young male

U.S.N.M.:V.P. 2349 From Webster City, Hamilton County; collected by Charles Aldrich, 1878, “on a gravel bar in the Boone River”

Figured by Hay, 1914, pl. 40, figs. 3, 4

NEBRASKA

**Refereed**

Skull and composite skeleton

U.N.S.M. 1-21-11-31 From 8 miles southeast of Grand Island, Hall County; collected by F. G. Meserve, 1923, and C. B. Schultz, 1931

Complete skull; tooth wear (S-3)

1-16-7-29 From 24 miles southeast of Broken Bow, Custer County; collected by F. Crabill and C. B. Schultz, 1929

Posterior cranium of young male

No number From Logan Creek, 4 miles east of Wayne, Wayne County; collected by Knox Jones, Aug. 7, 1943
SKINNER AND KAISEN: FOSSIL BISON

Complete skull and composite skeleton
Male skull, lacking nasals
Complete female skull

Posterior portion of skull and partial right horn-core of young male
Complete skull lacking premolars; tooth wear (S-4)
Skull and mounted skeleton

KANSAS
REFERRED

K.U.M.V.P. 388 From 3 miles northeast of North Lawrence and 1½ miles north of the Kaw River in Leavenworth County; collected by C. H. Sternberg Figured by McClung, 1905, fig. 10 Holotype of B. "kansensis"

K.U.M.V.P. 2827 From 3 miles northeast of North Lawrence and 1½ miles north of the Kaw River in Leavenworth County; collected by L. D. Read, 1903 This paper, pl. 16, figs. 4, 4A

Skull and mounted skeleton

TEXAS
REFERRED

F: A.M. 23347 From 9 miles west of Silverton; collected by A. F. Johnson, 1929 Frick, 1937, p. 587, questionably referred this specimen to B. "Simobison figginsi"

C.M.N.H. 629 From near Michies, Dawson County Holotype of B. "taylori"

631 From same locality as above

CALIFORNIA
TENTATIVELY REFERRED

U.S.N.M: V.P. 11158 From the mouth of Tin Cup Creek; collected by Homer E. Sargent, 1924 (This suggests that occidentalis may have reached California)

1 Barbour and Schultz considered this specimen to be representative of the group of individuals collected from the above site and now have on exhibit a mounted skeleton with this skull attached. They referred the material to B. antiquus "taylori." Circumstances did not permit the authors to examine all of the associated material, except that on exhibition, which can be said to be typical of Bison occidentalis.
3. **Bison (Bison) preoccidentalis**, new species

From Late Pleistocene deposits near Fairbanks and Kotzebue Sound, Alaska

Plate 14, figures 3, 3A, 3B, 3C

**TOTAL AVAILABLE SPECIMENS: 19**


**SPECIFIC CHARACTERS**

(Based on Male Skulls)

Horn-cores greater in size, proportionately longer and more slender, tending to be straighter and more uniformly curved for entire length than in other species of the subgenus *Bison*, slightly depressed from one-third to one-fourth dorsal length below plane of frontals before swinging upward in moderate posterior direction with uniform backward upsweep, extending posteriorly beyond

---

**TABLE 13**


(Measurements in millimeters, figure 1C for key; indices in per cent, page 142.)

<table>
<thead>
<tr>
<th>Key No.</th>
<th>Description</th>
<th>Holo-type</th>
<th>No. of Measurements</th>
<th>Min.</th>
<th>Av.</th>
<th>Max.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Spread of horn-cores, tip to tip</td>
<td>875</td>
<td>18</td>
<td>740</td>
<td>842</td>
<td>925</td>
</tr>
<tr>
<td>2</td>
<td>Spread of horns with sheaths, tip to tip</td>
<td>625</td>
<td>8</td>
<td>485</td>
<td>632</td>
<td>786</td>
</tr>
<tr>
<td>3</td>
<td>Greatest spread of cores on outside curve</td>
<td>898</td>
<td>17</td>
<td>792</td>
<td>861</td>
<td>958</td>
</tr>
<tr>
<td>4</td>
<td>Greatest spread of horns with sheaths</td>
<td>964</td>
<td>8</td>
<td>829</td>
<td>912</td>
<td>1005</td>
</tr>
<tr>
<td>5</td>
<td>Sheath length on upper curve</td>
<td>540</td>
<td>15</td>
<td>410</td>
<td>478</td>
<td>540</td>
</tr>
<tr>
<td>6</td>
<td>Core length on upper curve, tip to burr</td>
<td>395</td>
<td>32</td>
<td>315</td>
<td>364</td>
<td>415</td>
</tr>
<tr>
<td>7</td>
<td>Difference between sheaths and core length</td>
<td>145</td>
<td>15</td>
<td>50</td>
<td>100</td>
<td>160</td>
</tr>
<tr>
<td>8</td>
<td>Core length on lower curve, tip to burr</td>
<td>435</td>
<td>32</td>
<td>370</td>
<td>414</td>
<td>464</td>
</tr>
<tr>
<td>9</td>
<td>Length, tip of core to upper base at burr</td>
<td>355</td>
<td>32</td>
<td>300</td>
<td>332</td>
<td>365</td>
</tr>
<tr>
<td>10</td>
<td>Transverse diameter of core</td>
<td>104</td>
<td>34</td>
<td>99</td>
<td>108</td>
<td>128</td>
</tr>
<tr>
<td>11</td>
<td>Vertical diameter of core</td>
<td>91</td>
<td>34</td>
<td>88</td>
<td>97</td>
<td>107</td>
</tr>
<tr>
<td>12</td>
<td>Circumference of core at base</td>
<td>302</td>
<td>34</td>
<td>295</td>
<td>320</td>
<td>361</td>
</tr>
<tr>
<td>13</td>
<td>Width of cranium between cores and orbits</td>
<td>269</td>
<td>18</td>
<td>250</td>
<td>284</td>
<td>305</td>
</tr>
<tr>
<td>14</td>
<td>Greatest postorbital width</td>
<td>325</td>
<td>16</td>
<td>321</td>
<td>342</td>
<td>368</td>
</tr>
<tr>
<td>15</td>
<td>Width of skull at mastectomy processes</td>
<td>184</td>
<td>9</td>
<td>179</td>
<td>184</td>
<td>196</td>
</tr>
<tr>
<td>16</td>
<td>Greatest width at auditory openings</td>
<td>283</td>
<td>16</td>
<td>268</td>
<td>284</td>
<td>302</td>
</tr>
<tr>
<td>17</td>
<td>Width of condyles</td>
<td>138</td>
<td>18</td>
<td>130</td>
<td>139</td>
<td>148</td>
</tr>
<tr>
<td>18</td>
<td>Occipital crest to tip of nasals</td>
<td>502</td>
<td>4</td>
<td>480</td>
<td>496</td>
<td>514</td>
</tr>
<tr>
<td>19</td>
<td>Occipital crest to nasal-frontal suture</td>
<td>281</td>
<td>16</td>
<td>253</td>
<td>274</td>
<td>297</td>
</tr>
<tr>
<td>20</td>
<td>Occipital crest to lower border foramen magnum</td>
<td>161</td>
<td>18</td>
<td>153</td>
<td>160</td>
<td>175</td>
</tr>
<tr>
<td>21</td>
<td>Basilar length of skull</td>
<td>543</td>
<td>7</td>
<td>526</td>
<td>539</td>
<td>547</td>
</tr>
<tr>
<td>22</td>
<td>Over-all length of skull</td>
<td>604</td>
<td>7</td>
<td>577</td>
<td>599</td>
<td>629</td>
</tr>
<tr>
<td>23</td>
<td>P³-M³ alveolar length</td>
<td>148</td>
<td>15</td>
<td>147</td>
<td>152</td>
<td>158</td>
</tr>
<tr>
<td>24</td>
<td>M₁-M³ alveolar length</td>
<td>93</td>
<td>15</td>
<td>91</td>
<td>94</td>
<td>97</td>
</tr>
<tr>
<td>25</td>
<td>Median length of premaxilla beyond P³</td>
<td>160</td>
<td>7</td>
<td>147</td>
<td>155</td>
<td>165</td>
</tr>
<tr>
<td>26</td>
<td>Rostral width at maxillary-premaxillary suture</td>
<td>121</td>
<td>7</td>
<td>108</td>
<td>117</td>
<td>124</td>
</tr>
<tr>
<td></td>
<td>Index of core curvature</td>
<td>123</td>
<td>32</td>
<td>112</td>
<td>126</td>
<td>134</td>
</tr>
<tr>
<td></td>
<td>Index of core compression</td>
<td>87</td>
<td>18</td>
<td>83</td>
<td>90</td>
<td>94</td>
</tr>
<tr>
<td></td>
<td>Index of core proportion</td>
<td>131</td>
<td>18</td>
<td>100</td>
<td>113</td>
<td>131</td>
</tr>
<tr>
<td></td>
<td>Index of core length</td>
<td>147</td>
<td>18</td>
<td>110</td>
<td>128</td>
<td>152</td>
</tr>
</tbody>
</table>
a plane produced by occiput and condyles; tips posteriorly twisted but not so strongly as in type of B. (B.) occidentalis; cores more posteriorly curved than in Superbison or Platycerobison; core length on upper curve equal to or exceeding basal circumference and cranial width between horn-cores and orbits as opposed to other B. (Bison) species; cores subcircular in cross section.

Frontals vary from flat to slightly arched; orbits prominently tubular and anteriorly directed; nasals moderately long; occipital region of skull uniformly rounded and well developed. Skull tends to be slightly narrower in proportion, averaging 7 per cent narrower than in B. (B.) b. bison and B. (B.) occidentalis and 13 per cent narrower than in B. (Simobison) a. antiquus. General over-all characters of skull similar to those in B. (B.) b. bison but larger. Dental characters similar to those of B. (Bison) bison with possible exception of slightly less molariform P4.

Horn sheaths extend from 50 to 160 mm. beyond tips of horn-cores, are recurved with tips directed inward and tending to be blunted; surface of sheaths indicates seasonal growth rings.

**DISCUSSION**

The holotype of B. (Bison) *preoccidentalis* (U.A.-F: A.M. No. 46885) and 17 other referred skulls and crania from the vicinity of Fairbanks present a fair sample of the range of individual variation. As the name implies, it appears that this species of Bison was the progenitor of B. (Bison) *occidentalis*, the type of which was also found in Alaska near Fort Yukon, but probably in later sediments. Species found in association with *preoccidentalis* are B. (Superbison) *crassicornis*, B. (Platycerobison) *alaskensis*, and B. (Platycerobison) *geisiti*, new species.

The deposits in the vicinity of Eschscholtz Bay, which is the type locality for B. (Superbison) *crassicornis*, have also yielded specimens of *preoccidentalis*.

This species, in particular, suggests that much remains to be known concerning the exact geological succession of Bison species. The fauna from the vicinity of Fairbanks probably represents only one phase of the Pleistocene. The possibility remains that collections from other localities in Alaska may eventually produce a later Pleistocene fauna containing true *occidentalis* specimens like the few isolated examples known. No Alaskan faunas are known which have produced the geologically earlier Bison found in the more southern portions of North America, such as B. (Platycerobison) *chaneyi*, B. (Simobison) *allenii*, and B. (Gigantobison) *latifrons*. These largest and presumably earliest forms of Bison may have passed through Alaska on their migratory trek from the Old World. The only other possible explanation of the extremely large Bison forms in the New World is the postulation of a theory that part of the Bison species were undergoing a progressive enlargement of their horn-cores while the other part underwent a retrogressive horn-core development.

Nineteen specimens, with horn-cores unless otherwise stated, are here recorded:

**ALASKA**

**HOLOTYPE**

Complete male skull with sheaths, P2–P4 alv., M1–M3; tooth wear (S–4)  
U.A.-F: A.M. 46885  
From near Fairbanks, on upper Cleary Creek; collected by Otto Wm. Geist, 1937  
This paper, pl. 14, figs. 3, 3A, 3B, 3C

**REFERRED**

From near Fairbanks; collected by Peter C. Kaisen, 1929–1930; Albert S. Wilmerson, 1931; Ray Henricksen, 1932; John B. Dorsh, 1933–1936; Otto Wm. Geist, 1937–1942

Cranium with partial orbits, sheaths attached  
U.A.-F: A.M. 30595  
From Cleary Creek, 1931  
Figured by Frick, 1937
BISON (SIMOBISON) (Hay and Cook, 1930)

References for the subgenus:


Subgenotype: Bison figginsi Hay and Cook, 1928.

Subgeneric Characters
(Based on Male Skulls)

Cores range from large to small in size, never approaching those of B. (Gigantobison), and extend from the skull at nearly right angles to the median line as distinct from B. (Bison) and B. (Superbison), tending to be proximally depressed with upcurved tips that are not posteriorly twisted as in B. (Bison). The cores are subcircular in basal cross section, as a rule, with the earlier species of this subgenus showing a tendency towards dorso-ventral compression although not so prominently as in B. (Platycerobison). The core tips have strong superior longitudinal grooves tending to be less prominent in the later forms. The tips of the cores seldom rise far above the plane of the frontals, owing to the directional trend and proximal depression as opposed to the more elevated tips of the other Bison subgenera. The cranium tends to be broad as opposed to B. (Bison). Premolars 4 of the later forms tend to be more complicated than in B. (Superbison).

Discussion

Some of the characters attributed by Hay and Cook to Simobison may not be applicable to the subgenus, as here discussed.

Examination of the specific holotype, the only known specimen, revealed that generic distinction may have been founded on distorted characters caused by crushing and the method of restoration. The occipital region and the horn-cores of the type skull were dorsoventrally crushed during fossilization. The directional trend of the cores, with respect to the longitudinal axis of the skull, is at right angles as in B. (Simobison) a. antiquus.

Although this specimen was thought to be one individual, there is some question concerning the association of the skull and man-
dible that has important bearing on the generic characters. Hay and Cook (1930, p. 24, pl. 7, figs. 1, 2) stated: “The nasal bones were not found and a considerable part of the maxilla in front of the orbits was in a decayed condition; also the greater part of the pre-maxilla is missing. However, that the face is little or not at all shortened, is assured by the fact that when the lower jaws are articulated in position this naturally fixes rather definitely the length of the missing premaxil-iae.” There is no indication that the jaws used for restoration were articulated with the skull on discovery. Note the amount of the anterior portion of the skull stated to be missing, yet the name given implies a “snub-nosed Bison.”

It should be noted that the mandible associated with the skull is of a different tooth wear. The dP4 has not been shed, and the heel of M3 is not in wear, indicating a young animal. The skull has shed the dP4, indicating a more mature individual.

If an older skull was restored with a younger mandible, an apparent forward shifting of the orbits and shortening of the face would be produced. This may account for the generic character given this distinction. A study of the growth of bison rami disclosed that the symphysis still elongates after the dP4 has been shed, and the ascending ramus and condyles are extended in a more posterior position with respect to the M3.

Since the species to which the holotype of Simobison belongs is in a group of subgenerically distinct Bison, this name must be used, since it has priority over all other generic or subgeneric names applied to this group of species.

1. Bison (Simobison) antiquus antiquus
   (Leidy, 1852)

From the very late Pleistocene and sub-Recent deposits of Kentucky, Indiana, Colorado, New Mexico, Texas, California, Oregon, Washington, Mexico including Lower California

Plate 15, holotype and referred skulls

TOTAL AVAILABLE SPECIMENS: 14 MALES

1. References for the holotype:


Bos priscus, Lydekker, 1898, Wild oxen, sheep, and goats of all lands, p. 61.

2. References for the holotype of B. californicus Rhoads, 1897:


3. References for the holotype of B. pacificus Hay, 1927:


4. References for here-referred specimens:


Bison latifrons (Harlan), Condon, 1902, The two islands, p. 153, pl. 29.
TABLE 14
SUMMARY OF MALE SKULL MEASUREMENTS AND INDICES OF B. (Simobison) antiquus antiquus AND MEASUREMENTS OF HOLOTYPE (A.N.S.P. No. 12990)
(Measurements in millimeters, figure 1C for key; indices in per cent, page 142.)

<table>
<thead>
<tr>
<th>Key No.</th>
<th>Description</th>
<th>Holotype</th>
<th>No. of Measurements</th>
<th>Summary</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Spread of horn-cores, tip to tip</td>
<td>—</td>
<td>10</td>
<td>816 881 975</td>
</tr>
<tr>
<td>3</td>
<td>Core length on upper curve, tip to burr</td>
<td>(283)</td>
<td>13</td>
<td>220 281 344</td>
</tr>
<tr>
<td>4</td>
<td>Length of core on lower curve, tip to burr</td>
<td>(360)</td>
<td>10</td>
<td>280 336 395</td>
</tr>
<tr>
<td>5</td>
<td>Length, tip of core to upper base at burr</td>
<td>(245)</td>
<td>8</td>
<td>197 245 280</td>
</tr>
<tr>
<td>12</td>
<td>Transverse diameter of core</td>
<td>122</td>
<td>13</td>
<td>92 107 122</td>
</tr>
<tr>
<td>6</td>
<td>Vertical diameter of core</td>
<td>102</td>
<td>14</td>
<td>90 98 108</td>
</tr>
<tr>
<td>7</td>
<td>Circumference of core at base</td>
<td>358</td>
<td>14</td>
<td>290 320 358</td>
</tr>
<tr>
<td>14</td>
<td>Width of cranium between cores and orbits</td>
<td>—</td>
<td>12</td>
<td>292 319 337</td>
</tr>
<tr>
<td>15</td>
<td>Greatest postorbital width</td>
<td>—</td>
<td>2</td>
<td>346 353 360</td>
</tr>
<tr>
<td>17</td>
<td>Width of skull at massecetic processes at M1</td>
<td>—</td>
<td>4</td>
<td>188 205 218</td>
</tr>
<tr>
<td>18</td>
<td>Length, occipital crest to tip of nasals</td>
<td>—</td>
<td>4</td>
<td>482 510 527</td>
</tr>
<tr>
<td>19</td>
<td>Length, occipital crest to tip of nasal-frontal suture</td>
<td>—</td>
<td>11</td>
<td>240 295 350</td>
</tr>
<tr>
<td>20</td>
<td>Basilar length of skull</td>
<td>—</td>
<td>3</td>
<td>520 545 560</td>
</tr>
</tbody>
</table>

| Index of horn-core curvature | (147) | 8 | 128 138 147 |
| Index of horn-core compression | 84 | 13 | 83 93 108 |
| Index of horn-core proportion | (79) | 12 | 68 88 100 |
| Index of horn-core length | — | 10 | 66 89 114 |


SPECIFIC CHARACTERS
(BASED ON MALE SKULLS)

Horn-cores moderate in size, length on upper curve seldom exceeding basal circumference or cranial width between horn-cores and orbits, subcircular in basal cross section, extending from the skull at nearly right angles to the longitudinal axis of the skull; proximally, cores are depressed and swing up on tips with little or no posterior twist; distally, tips tend to be stubby and heavy, seldom rising high above the plane of the frontals or extending posterior to the occipital plane of the skull; a superior longitudinal groove is sometimes indicated and is not to be confused with the basal longitudinal grooves common to all mature male bison horn-cores.

Frontals tend to be arched and the cranium broad; orbits tubular; teeth have a suggested tendency to be more complicated than in most Bison.

SUBSPECIFIC CHARACTERS

The holotype of B. (Simobison) a. antiquus has slightly larger, stubbier, and less posteriorly directed horn-cores than those of B. (Simobison) antiquus figginsi, and for this reason antiquus and figginsi are provisionally considered subspecifically distinct. Larger population samples may eventually prove the subspecific distinction to be superficial.

DISCUSSION

Bison (Simobison) a. antiquus is readily recognized by the characteristic set and shape of the horn-cores and the broad forehead, making it distinct from B. (Bison)
occidentalis with which it is most frequently confused (p. 170). The discovery of, and extensive writings about, the subspecies B. antiquus "taylori" have nearly superseded the recognition of antiquus specimens found in the Southwest.

Distribution based on identifiable horn-cores and not dentitions indicates that antiquus ranged over the central portion of North America, down into Mexico, including Lower California. It has not yet been observed in Alaska. On the basis of discoveries, the South-west and Pacific coastal regions seem to have been the center of this species population. The holotype was found in the Big Bone Lick of Kentucky, indicating, as well, an eastern range (map 2, p. 156).

The evidence points to the belief that antiquus developed on the North American plains from one of the first migrants of the Old World, B. (Simobison) alleni (p. 155). Since antiquus was the last survivor of this phyletic line, it is assumed that it was living here at the time the surviving species of the second Old World migration, B. (Bison) occidentalis, reached the antiquus range from the northern regions. This probably occurred during Wisconsin times. Why occidentalis survived and gave rise to the living plains bison, while antiquus became extinct, is a matter for conjecture. This hypothesis can hardly be rejected, however, for the plains bison has all the horn-core attributes of occidentalis and none of antiquus (pls. 14, 15).

Two synonymous species of antiquus recorded in the literature are here discussed in the chronological order in which they appear.

Bison "californicus" Rhoads, 1897

This species was based on a cranium found in the Pilarcitos Valley, near San Francisco. Lucas, 1899, pointed out that this specimen is referable to antiquus; moreover, this specimen seems to be typical of the species antiquus. It is in the Academy of Natural Sciences of Philadelphia with the holotype of antiquus, making direct comparison possible. (Pl. 15, figs. 4, 4A.)

Bison "pacificus" Hay, 1927

This species was founded on a horn-core in the California Academy of Sciences. The specific description by Hay was based on a photograph and measurements sent him from California. The size and index of horn-core curvature were considered sufficient reason for proposing a new name. The index of horn-core curvature has proved to be highly variable in living plains bison, however, ranging from 120-182. The size of "pacificus" is quite comparable to other antiquus specimens.

Dr. G. Dallas Hanna of the California Academy of Sciences has kindly forwarded new photographs and other information which indicate that this specimen is referable to antiquus. There is no record of other specimens referred to "pacificus."

Fourteen male specimens [of B. (Simobison) antiquus antiquus], with horn-cores unless otherwise stated, are here recorded:

KENTUCKY

Holotype

Fragment of frontal with right horn-core lacking tip

A.N.S.P. 12990

From Big Bone Lick; Jefferson Collection
Figured by Leidy, 1852c, pl. 2, fig. 1; by Lucas, 1899, vol. 8, pl. 8; 1899, vol. 21, pls. 67, 68; by Hay, 1913, vol. 46 (1914), text fig. 1
This paper, pl. 15, figs. 1, 1A

INDIANA

Referred

Partial skull with horn-cores, lacking teeth and premaxilla

Earlham College Coll.

From near Vincennes, Knox County; collected by Bower, 1896
Figured by Middleton and Moore, 1899, p. 179; by Hay, 1912, figs. 50, 51; 1913, vol. 46 (1914), figs. 2, 3; 1914, vol. 23, figs. 100, 101
COLORADO

**REFERRED**

Complete horn-core
- **C.M.N.H. 1642**
- From Arikaree River, Yuma County; collected by W. T. Bennett, 1935

Partial skull with one maxilla, lacking tips of cores and condyles
- **U.S.N.M.:V.P. 16800**
- From 28 miles north of Fort Collins, Larimer County; collected by F. H. Roberts, Jr., for the Smithsonian Institution, 1935

NEW MEXICO

**REFERRED**

Cranium with horn-cores and partial orbits
- **U.S.N.M.:V.P. 13683**
- From Lea County; collected by J. G. Braecklein

Partial skull
- **A.N.S.P. 10226**
- From Clovis; collected by J. E. Howard

TENNESSEE

**REFERRED**

Complete skull
- **U.N.S.M. 1-8-8-39**
- From Lipscomb County; collected by Nebraska State Museum party

CALIFORNIA

**REFERRED**

Cranium with complete horn-cores
- **A.N.S.P. 297**
- From Pilarcitos Valley, near San Francisco, San Mateo County; collected by Calvin and Wilfred Brown, about 1867

Complete and partial skulls as listed by Chandler, 1916
- **U.C.M.P. 7952**
- Figured by Chandler, 1916

Partial horn-core
- **C.A.S. 8523**
- From near bed rock of Centennial Mine, Klamath River, Siskiyou County, 1888

OREGON

**REFERRED**

Cranium with partial left horn-core
- **Oregon Agr. School, Corvallis**
- From above the falls in the Willamette River, near Oregon City, Clackamas County, 1923

Cranium with horn-cores
- **Univ. Oregon**
- From 5 or 6 miles east of The Dalles, Wasco County

WASHINGTON

**REFERRED**

Right horn-core broken off at burl, with part of left horn-core
- **U.S.N.M.:V.P. 8523**
- Wallula, Walla Walla County; collected by R. C. Fulkerson, 1916
MEXICO

Partial skull, crushed, with P2-P4 F:A.M. 42885

From Baja, Lower California; collected by Howard S. Gentry, 1939

This paper, pl. 15, figs. 5, 5A, 5B, rev.

1A. Bison (Simobison) antiquus figginsi1

(Hay and Cook, 1928)

Late Pleistocene and sub-Recent deposits of New Mexico, Texas, and Nebraska

(See Hay and Cook for figures)

1. References for the holotype:

2. References for the holotype of Bison taylori Hay and Cook, 1928:
   Bison taylori Hay and Cook, 1928, Proc. Colorado Mus. Nat. Hist., vol. 8, no. 2, pt. 1, p. 33; 1930, ibid., vol. 9, no. 2, p. 26, pl. 8, figs. 1, 2, pl. 9, figs. 2, 3 (the holotype is figured on pl. 9, not pl. 10 as indicated in the report). Barbour

1 As first revisers, the writers have the responsibility for fixing the name of this subspecies. It cannot be demonstrated beyond all doubt that the name figginsi and "taylori" are synonymous. The name figginsi has paragraph priority over "taylori," but the International Rules of Zoological Nomenclature (Article 28, recommendation c) only recommend that paragraph priority be followed, "other things being equal"; no passage in the Rules states that line, page, or paragraph priority must be followed. It would therefore be possible to suppress figginsi in favor of "taylori," and there would be considerable justification in such a procedure, for the holotype of figginsi is crushed and restored on the basis of the length of an immature associated ramus. However, to avoid undue confusion, figginsi has been chosen as the valid name, inasmuch as further material may eventually be found at or near the type figginsi site which may demonstrate that the two forms are synonymous. In any case, the name Simobison is available under the Rules as a valid subgenus since it is the first generic (or subgeneric) name to be proposed for members of this species group. To recognize the name "taylori" as the valid name would introduce uncalled-for complications. It should be pointed out that the genotype would still remain unchanged as Bison figginsi Hay and Cook, even if figginsi was placed as a synonym of "taylori."
DISCUSSION

The type of *figginsi* does not appear to be specifically distinct from *B. (Simobison) antiquus* but might be considered a subspecies of *antiquus* since the only pronounced difference is in slightly longer and more posteriorly directed horn-cores.

As pointed out in footnote 1, page 181, no differences of specific value exist between "taylori" and *figginsi*, but taxonomic procedure makes it expedient to recognize the priority of *figginsi*. In this case a genus and species were first represented by one specimen now considered subspecific to *antiquus*. Therefore, this single specimen, a skull (C.M.N.H. No. 574), stands for the type of the subspecies. When the distorted characters caused by crushing are eliminated from *figginsi*, part of the subgeneric characters are very evident. The horn-cores extend from the skull at about right angles and are not upcurved; the skull has a very broad forehead, as in *B. (Simobison) antiquus* and *B. (Simobison) alleni*. In "taylori" specimens, here considered synonyms of *figginsi*, the horn-cores tend to be slightly longer and more posteriorly directed than in *antiquus*.

*B. "taylori" Hay and Cook, 1928*

This synonymous subspecies of *B. (Simobison) antiquus figginsi* has been popularly accepted, primarily because the holotype was found in association with artifacts of the well-known Folsom man and was one of the first generally accepted discoveries of fossil bison and man. Owing to widespread use of the name in anthropological and paleontological works, the specific name *Bison "taylori"* nearly superseded the recognition of all other true *B. (Simobison) antiquus figginsi* specimens found in the Southwest. Barbour and Schultz (1936, p. 435) stated "that *B. taylori* and *B. antiquus* are two very closely related species. Perhaps it would be best to retain the name *taylori* only as a variety since *antiquus* has priority."

Figgins (1933, p. 20) made *B. "taylori"* a subspecies of his genus "Stelabison," calling it "Stelabison occidentalis taylori" since the holotype has small external styles on the molars. As discussed on page 159, these characters are not believed to be of generic importance.

When *B. "taylori"* was placed in the genus "Stelabison" the rest of the *Bison* material from the Folsom Bison Quarry was left open to redescription. For this reason, Figgins named a specimen from the same quarry *B. "oliverhayi".*

*B. "oliverhayi" Figgins, 1933*

After studying and measuring the holotypes of *B. "oliverhayi"* and *B. "taylori,"* it appears that their differences were only those to be expected in individual variants of one population. The characters of "taylori" differ from "oliverhayi" only in the presence of small external pillars on the M² (not considered generically important). Since "taylori" and "oliverhayi" are synonymous, "oliverhayi" can also be considered a member of the subspecies *figginsi*.

*Bison antiquus "barbouri" Schultz and Frankforter, 1946*

The holotype of "barbouri" has all the basic physical characters of the *Bison (Simobison) antiquus figginsi* population as just discussed. The very slight difference in actual size and the time element are not great enough to warrant subspecific distinction. A large sample of a *figginsi* population would certainly include individuals as large as the holotype of "barbouri."

The exact horizon of "barbouri" was reported as the "Citellus" soil zone between Loveland and Peorian loesses, Late Pleistocene. Other examples of the *figginsi* population have been reported from the late Pleistocene of Texas and New Mexico. These examples could have lived in a contemporaneous time period with "barbouri." This cannot be settled, however, as the late Pleistocene deposits of Nebraska and the Southwest are separated and are not of continuous stratigraphic extent.

Nine specimens of *B. (Simobison) a. figginsi* are here recorded:
### Texas

**Holotype**
- C.M.N.H. 574
- From Lone Wolf Creek, near town of Colorado, Mitchell County
- Figured by Hay and Cook, 1930

**Referred**
- Reported by E. H. Sellards; preliminary report by Grayson Mead at 1945 Geological Society of America convention
- Figures indicate presence of *taylori* or *figginsi* forms

#### New Mexico

**Referred**
- C.M.N.H. 1236
- From 11 miles west of Folsom (Folsom Bison Quarry)
- Figured by Hay and Cook, 1930; by Figgins, 1933
- Holotype of *taylori*
- From Folsom Bison Quarry
- Figured by Figgins, 1933
- Holotype of *oliverhayi*
- From Folsom Bison Quarry
- Figured by Hay and Cook, 1930
- From Folsom Bison Quarry

#### Nebraska

**Referred**
- U.N.S.M. 30310
- From west side of "Devils Gap" southwest of Gothenburg, Dawson County
- Holotype of *antiquus "barbouri"*

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### References

2. *Bison (Simobison) alleni* (Marsh, 1877)

From Middle Pleistocene deposits of Kansas, Idaho, California, and the late Pleistocene of Nevada

**Total Available Specimens:** 14 males

1. References for the holotype:

2. References for the holotype of *B. willistoni*
   - Martin, 1924:

3. References for here-referred specimens:
   - (Two crania measured and figured.)
   - *Bison aff. occidentalis* Lucas, Simpson, 1933, Amer. Mus. Novitates, no. 667, p. 6, fig. 3.
TABLE 15

<table>
<thead>
<tr>
<th>Key No.</th>
<th>Holotype</th>
<th>No. of Measurements</th>
<th>Summary</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Spread of horn-cores, tip to tip</td>
<td>—</td>
<td>1100</td>
</tr>
<tr>
<td>3</td>
<td>Core length on upper curve, tip to burr</td>
<td>640</td>
<td>10</td>
</tr>
<tr>
<td>4</td>
<td>Length of core on lower curve, tip to burr</td>
<td>740</td>
<td>10</td>
</tr>
<tr>
<td>5</td>
<td>Length, tip of core to upper base at burr</td>
<td>540</td>
<td>9</td>
</tr>
<tr>
<td>12</td>
<td>Transverse diameter of core</td>
<td>143</td>
<td>10</td>
</tr>
<tr>
<td>6</td>
<td>Vertical diameter of core</td>
<td>117</td>
<td>10</td>
</tr>
<tr>
<td>7</td>
<td>Circumference of core at base</td>
<td>417</td>
<td>11</td>
</tr>
<tr>
<td>14</td>
<td>Width of cranium between cores and orbits</td>
<td>—</td>
<td>5</td>
</tr>
<tr>
<td>15</td>
<td>Greatest postorbital width</td>
<td>—</td>
<td>4</td>
</tr>
<tr>
<td>17</td>
<td>Width of skull at masseteric processes at M₁</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>8</td>
<td>Greatest width at auditory openings</td>
<td>—</td>
<td>4</td>
</tr>
<tr>
<td>9</td>
<td>Width of condyles</td>
<td>—</td>
<td>4</td>
</tr>
<tr>
<td>O-T</td>
<td>Occipital crest to tip of nasals</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>O-N</td>
<td>Occipital crest to nasal-frontal suture</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>11</td>
<td>Occipital crest to lower border foramen magnum</td>
<td>—</td>
<td>2</td>
</tr>
<tr>
<td>F-P</td>
<td>Basilar length of skull</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>19</td>
<td>P²-M³ alveolar length</td>
<td>—</td>
<td>2</td>
</tr>
<tr>
<td>M-P</td>
<td>Median length of premaxilla beyond P²</td>
<td>—</td>
<td>2</td>
</tr>
<tr>
<td>18</td>
<td>Rostral width at maxillary-premaxillary suture</td>
<td>—</td>
<td>2</td>
</tr>
<tr>
<td>Index of core curvature</td>
<td>137</td>
<td>9</td>
<td>121</td>
</tr>
<tr>
<td>Index of core compression</td>
<td>82</td>
<td>10</td>
<td>72</td>
</tr>
<tr>
<td>Index of core proportion</td>
<td>153</td>
<td>10</td>
<td>100</td>
</tr>
<tr>
<td>Index of core length</td>
<td>—</td>
<td>4</td>
<td>114</td>
</tr>
</tbody>
</table>


**Specific Characters**

*(Based on Male Skulls)*

Horn-cores vary from moderate to large in size, always larger than in *B. (Bison)* species, large forms equalling *B. (Platycerobison) chaneyi* but never so large as *B. (Gigantobison) latifrons*. Cores tend to be heavy and blunt tipped as in *chaneyi* and unlike the large, tapering, tipped cores of *latifrons*. Contrary to their appearance, the cores are proportionately long and slender, varying from one to one and a half times longer than their basal circumference or the cranial width and are more regularly curved than those of *chaneyi*. Some of the larger variants of *B. (Super-bison)* *crassicornis* bear a superficial resemblance to this species but do not have so stout a core or blunt a tip; proximally, cores are heavy and strongly depressed one-half to one-third their dorsal length below the plane of the frontals, the tips rising slightly above it; distally, the cores are not posteriorly twisted as in *B. (Bison)*. On the distal tips, a prominent superior longitudinal groove is present which seems to be better developed in *allenii*, *chaneyi*, *latifrons*, and *B. (Platy-cerobison) alaskensis* than in other *Bison*. This groove is not to be confused with the basal longitudinal grooves resulting from individual age which are present on almost all mature male bison horn-cores. Cores extend in a very moderate posterior direction in respect to the median axis of the skull and slightly posterior to the occipital plane. No specimens with sheaths are known.
Frontals tend to be broad and slightly arched; orbits tend to be tubular and forwardly directed; nasals strong and wide; occipital region rounded and well developed; skull tends to be proportionately broad with respect to the basilar length, similar to, but larger than, that of B. (Simobison) antiquus and proportionately broader and larger than in most specimens of B. (Superbison) crassicornis or B. (Bison) occidentalis.

Discussion

The holotype of B. (Simobison) alleni, described by Marsh (1877, p. 252) and later figured by Lucas (1899a, p. 765, pls. 77, 78), is a well-preserved, nearly complete horn-core (see plastotype, pl. 16, figs. 1, 1A). The geologic age of alleni was originally considered to be Pliocene. Subsequent discoveries of other specimens referred to this species have all been considered to be early to middle Pleistocene.

This species is not represented in the Alaskan fauna, although Gilmore (1908, p. 33, pl. 11) and Hay (1913b, pp. 182–192, figs. 7–9, pl. 15, fig. 3, pl. 16, figs. 1, 2, pl. 17, figs. 1, 2; 1914, p. 326, fig. 103, pl. 41) have referred specimens of B. (Superbison) crassicornis to it. These referred specimens were carefully studied and measured and are clearly referable to crassicornis and not to alleni.

The principal occurrences of alleni indicate that this species was distributed in the central and western part of North America, principally in Kansas, Idaho, California, and Nevada. This does not imply that alleni did not inhabit the eastern portion of North America, since individual occurrences are still quite rare.

Certain referred specimens in the alleni collections might be considered subspecific because of slight geographic or geologic differences.

Martin's species B. "willistoni" is here considered an example of one of the smaller variants to be expected in a large series of alleni. Although smaller than the holotype of alleni, it has similarities of core characters when compared with it.

Several specimens of alleni have been found in the vicinity of American Falls, Idaho, and appear to represent a geographic or geologic variant slightly larger than the holotype. Insufficient data make it impossible to do more than suggest that these differences are equivalent to a variety.

The smallest observed variant of this species was found near Las Vegas, Nevada, and may represent either individual variation or a geological variety. It suggests the same tendency towards retrogressive horn-core growth as observed in other species of Bison.

The best-known referred example of alleni is a nearly complete uncrushed skull in the collection of the Fort Hays Kansas State Teachers College (pl. 16, figs. 2, 2A). Many of the characters previously unknown are disclosed by this specimen from which some of the specific inferences are made.

This species was one of the middle Pleistocene bovid emigrants from the Old World that left no record of its passage through Alaska, probably living contemporaneously for a time in North America with B. (Gigantobison) latifrons and B. (Platycerobison) chaneyi. Evidence suggests that the descendants of alleni were subjected to the same process of retrogressive horn-core growth observed in the line of retrogression in B. (Bison) precoccidentalis, B. (B.) occidentalis, and B. (B.) bison (pl. 14). In the case of alleni, the descendants appear to be the species B. (Simobison) antiquus which has many of the retrogressed attributes of alleni (compare pls. 15, 16).

Fourteen specimens are here recorded:

KANSAS

Holotype

(? Right horn-core, nearly complete
Plastotype made in 1944 and checked against the holotype) Y.P.M. 911
From Blue River, Manhattan
Figured by Lucas, 1899a, pls. 77, 78
This paper, pl. 16, figs. 1, 1A
Left horn-core, broken off at burr  
K.U.M.V.P. 390  
From near Garden City on south side of Arkansas River, Finney County; collected by A. F. Osbun, 1909  
Figured by Martin, 1924, pl. 26, fig. 1, pl. 27, figs. 3, 3a  
Holotype of "B. willistoni"

Skull, nearly complete  
F.H.K.S.C. 40  
From 3 miles northwest of Lenora, Norton County; collected by George F. Stemnberg and Dale H. Hendrick, 1939

Cranium with complete left and partial right horn-core, associated ramus with M1–M3  
K.U.M.V.P. 4634  
From 7½ miles northeast of Newton, Harvey County; collected by Kenneth Scott, 1939  
Figured by Hibbard, 1939, pl. 5, figs. 20, 21, 22

Cranium with both horn-cores  
K.U.M.V.P. 4927  
From banks of Fall River near Fredonia, Wilson County; collected by Fred Stroud  
Figured by Hibbard, 1939, pl. 5, fig. 79

Crushed skull, lacking left horn-core, orbit and maxilla  
A.M.N.H. 30052  
From northwest of Las Vegas, Clark County; collected by Fenley Hunter and A. C. Silberling, 1933  
Figured by Simpson, 1933, fig. 3

Partial skull with horn-cores and right dentition  
30051  
From same locality as above; sent to National Museum of Canada in 1936

Cranium with horn-cores and partial orbits  
Stanford Univ. Collection  
From 9 miles above American Falls, Power County; collected by C. W. Green, 1894  
Figured by Lucas, 1899a, pls. 79, 80

Cranium with partial right core, lacking left core  
U.S.N.M.:V.P. 13692  
From American Falls; collected by J. W. Gidley, 1929

Partial right horn-core, tip missing  
13693  
From same locality as above

Two partial horn-cores lacking distal tips  
5318  
From Minidoka, Minidoka County; collected by F. C. Horn, 1905; referred by O. P. Hay, 1927

Cranium with horn-cores  
Rupert High School  
From a gravel pit near Rupert, Minidoka County, as reported by Hay, 1927, p. 127

Horn-core and fragment of skull  
Rupert High School  
From same locality as above

Partial posterior cranium and two associated horn-cores  
C.A.S. 2412  
From Buhne's Point, Humboldt Bay, Humboldt County; collected by H. G. Guthridge, 1920  
Figured by Hay, 1927, fig. 2

C. BISON (SUPERBISON) FRICK, 1937

References for the subgenus:


SUBGENOTYPE: Bison crassicornis Richardson, 1854.
Subgeneric Characters
(Based on Male Skulls)

The same characters as those of the subgenotypic species, *Bison (Superbison) crassicornis* (Richardson).

Discussion

The name “super-bison” was first used by Frick (1930, pp. 71, 75, 78) in 1930, but was not given its subgeneric rank as *Superbison* until 1937. Frick clearly indicated that he considered *B. (Superbison) crassicornis* the subgenotypic species, as it is here designated. This species is common from the deposits in the vicinity of Fairbanks, Alaska, and appears to have existed in Eurasia as well.

Frick (1937, p. 567) stated: “The *Bison* remains from the North American Quaternary for convenience may be divided on the character of the size of the horn-cores between *Bison* proper, in which the cores are of moderate dimensions, and the subgenus *Superbison*, in which they may greatly exceed in size those of Recent species.” *Superbison* in these pages is restricted to one of the large horned types found in the Alaskan collection (p. 159).

A cast of a specimen from the Royal Museum of Belgium in Brussels sent to Yale in 1872 and bearing a Yale accession number, 1544, is identifiable with *crassicornis*. No other direct comparison has been possible concerning other European specimens which are believed to belong to this species (p. 232).

1. *Bison (Superbison) crassicornis*

Richardson, 1854

Late Pleistocene deposits of Alaska and Yukon Territory

Plates 17–23

Total available specimens: 184

1. References for the lectotype:


*Bos priscus* Bojanus, Lydekker, 1898, Wild oxen, sheep, and goats of all lands, p. 61 (Richardson’s specimen 1-A).


2. References for here-referred specimens of *B. (S.) crassicornis*:


*Bison priscus* Richardson, 1852–1854, Zoology of the voyage of H.M.S. “Herald,” pp. 33–39, 139, pl. 6, figs. 5, 6, pl. 7, fig. 1, pl. 10, fig. 1, pl. 13, fig. 3 of female core.


*Bos priscus* Bojanus, Lydekker, 1898, Wild
TABLE 16
SUMMARY OF MALE SKULL MEASUREMENTS AND INDICES OF B. (Superbison) crassicornis AND MEASUREMENTS OF LECTOTYPE (B.M. 1-A)*
(Measurements in millimeters, figure 1C for key; indices in per cent, page 142.)

<table>
<thead>
<tr>
<th>No.</th>
<th>Key</th>
<th>Lectotype</th>
<th>No. of Measurements</th>
<th>Summary</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Spread of horn-cores, tip to tip</td>
<td>—</td>
<td>118</td>
<td>765</td>
</tr>
<tr>
<td>2</td>
<td>Greatest spread of cores on outside curve</td>
<td>—</td>
<td>108</td>
<td>790</td>
</tr>
<tr>
<td>3</td>
<td>Sheath length on upper curve</td>
<td>—</td>
<td>68</td>
<td>410</td>
</tr>
<tr>
<td>4</td>
<td>Core length on upper curve, tip to Burr</td>
<td>—</td>
<td>208</td>
<td>295</td>
</tr>
<tr>
<td>5</td>
<td>Difference between sheaths and core length</td>
<td>—</td>
<td>64</td>
<td>45</td>
</tr>
<tr>
<td>6</td>
<td>Length of core on lower curve, tip to Burr</td>
<td>—</td>
<td>207</td>
<td>310</td>
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<tr>
<td>7</td>
<td>Length, tip of core to upper base at Burr</td>
<td>—</td>
<td>207</td>
<td>280</td>
</tr>
<tr>
<td>8</td>
<td>Transverse diameter of core</td>
<td>109</td>
<td>291</td>
<td>90</td>
</tr>
<tr>
<td>9</td>
<td>Vertical diameter of core</td>
<td>95</td>
<td>291</td>
<td>82</td>
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<td>10</td>
<td>Circumference of core at base</td>
<td>320</td>
<td>286</td>
<td>272</td>
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<td>11</td>
<td>Width of cranium between cores and orbits</td>
<td>293</td>
<td>156</td>
<td>255</td>
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<td>12</td>
<td>Greatest postorbital width</td>
<td>—</td>
<td>110</td>
<td>307</td>
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<tr>
<td>13</td>
<td>Width of skull at masseteric processes at M1</td>
<td>—</td>
<td>21</td>
<td>177</td>
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<tr>
<td>14</td>
<td>Greatest width at auditory openings</td>
<td>275</td>
<td>131</td>
<td>250</td>
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<tr>
<td>15</td>
<td>Width of condyles</td>
<td>145</td>
<td>150</td>
<td>115</td>
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<td>16</td>
<td>Occipital crest to tip of nasals</td>
<td>10</td>
<td>473</td>
<td>491</td>
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<tr>
<td>17</td>
<td>Occipital crest to naso-frontal suture</td>
<td>246</td>
<td>107</td>
<td>235</td>
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<tr>
<td>18</td>
<td>Depth, occipital crest to lower border foramen magnum</td>
<td>158</td>
<td>153</td>
<td>141</td>
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<tr>
<td>19</td>
<td>Basilar length of skull</td>
<td>—</td>
<td>8</td>
<td>487</td>
</tr>
<tr>
<td>20</td>
<td>Over-all length of skull</td>
<td>—</td>
<td>8</td>
<td>558</td>
</tr>
<tr>
<td>21</td>
<td>P4-M3 alveolar length</td>
<td>—</td>
<td>37</td>
<td>131</td>
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<tr>
<td>22</td>
<td>M1-M4 alveolar length</td>
<td>—</td>
<td>30</td>
<td>72</td>
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<tr>
<td>23</td>
<td>Median length of premaxilla beyond P3</td>
<td>—</td>
<td>8</td>
<td>137</td>
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<tr>
<td>24</td>
<td>Rostral width at maxillary-premaxillary suture</td>
<td>—</td>
<td>7</td>
<td>112</td>
</tr>
</tbody>
</table>

* After Richardson or estimated from his figures.

oxen, sheep, and goats of all lands, p. 64 (No. 24589).


_Stelabison occidentalis_, Figgins, 1933, Proc. Colorado Mus. Nat. Hist., vol. 12, no. 4, p. 18, pl. 1, figs. 1, 2 (A.M.N.H. No. 13721 cited as standing for the type of _Stelabison occidentalis_).


Specific Characters
(Based on Male Skulls)

Horn-cores range moderately large to large; length on upper curve equal to or exceeding either basal core circumference or cranial width between horn-cores and orbits; cores subcircular in cross section and posteriorly directed from slight to moderate with respect to the longitudinal axis of skull; distal tips occasionally have weak posterior twist, being pointed to blunt and heavy with a moderate to small superior longitudinal groove; cores vary from strongly depressed and rising but little above the frontals with a low curvature to cores with no depression, rising high above the frontals, having a strong curvature and uniform backward upswEEP and may extend backward to a little ahead of, or well beyond, the occipital plane; frontals strongly arched to flat; cranium moderate to broad; orbits tubular and forwardly directed.

Cores and skulls of B. (Superbison) crassicornis always smaller than those of B. (Gigantobison), B. (Platycerobison) chaneyi, and B. (Simobison) alleni, but larger than those of B. (Platycerobison) geisti and all species of the subgenus Bison, except preoccidentalis; equal to B. (Platycerobison) alaskensis but not dorsoventrally compressed as in Platycerobison. Although the cores of crassicornis are variable in the degree of posterior direction, they do not extend so straight out from the skull as in B. (Simobison) nor are they so posteriorly directed or twisted on the tips as in B. (Bison). The cranium of crassicornis does not tend to be so broad proportionately as that of Simobison, but is more as in B. (Bison).

The sheaths extend from 45 to 275 mm. beyond the tips of the horn-cores, are recurved and inwardly directed. The surfaces of the sheaths indicate seasonal growth rings. The premolars † tend to be less molariform in crassicornis than in all the later species of B. (Bison) and B. (Simobison).

Discussion

Bison (Superbison) crassicornis was found on a syntypic series of two specimens, a partial skull and a horn-core. It is problematical which specimen Richardson intended for the “type.” As the first reviser of this syntypic series, Rhoads (1897, pp. 489, 490) selected for the lectotype the partial skull B.M. No. 1-A as the “type” of crassicornis but referred it to B. antiquus. He referred the remaining syntype, a partial horn-core, No. 91 of Richardson’s syntypic series, to his species alaskensis.

The lectotype of the species was found in the region of Eschscholtz Bay, Alaska, and is now deposited in the British Museum. Although the specimen was not available for study, it is so well figured that it can readily be placed in the Alaskan collection (pl. 18, fig. 1, pl. 19, fig. 1, after Richardson). The distal ends of both horn-cores are missing but enough remains to indicate size and directional trends. The specimen is of a near average individual of the crassicornis population.

The horn-core size and shape of crassicornis are extremely variable. The cores may be comparatively straight, extending from the skull in a very moderate posterior direction as in the lectotype, or they may be comparatively straight, strongly depressed in one extreme, or sharply curved with virtually no depression in the other. The cores are almost universally subcircular in cross section. Individuals could be selected from this large population sample that differ radically from each other in some details. Had these individuals been found singly without intergrading members, there would be a strong tendency to recognize them as specific or subspecific varieties. This collection, however, is extensive enough to show all the intergrading possibilities in such a population.

Although the size and shape variation in living plains bison is not so spectacular because of its comparative smallness, the actual proportionate change is similar to that of crassicornis. On the basis of these observed differences in crassicornis and B. (Bison) bison, many other specimens of Bison which have been described at one time or another as new species are here placed in synonymy with the first described species to which they appear to belong, since they represent only segments of specific populations.

In the case of crassicornis, the literature indicates the diversity of opinion concerning the identification of specimens referable to this species. Nevertheless, no synonymous species has been described in North America
for specimens referable to *crassicornis*. The situation, however, is quite different in
Europe where *crassicornis* has not been recognized, but virtually all of the varying seg-
ments of the *crassicornis*-like population have been described as distinct species or as sub-
species of the loosely defined *Bison priscus*.

One hundred and eighty-six specimens, with horn-cores unless otherwise stated, are here
recorded:

### ALASKA

#### LECTOTYPE

<table>
<thead>
<tr>
<th>Partial skull, lacking nasals and one-half premaxilla, P4–M4 alv.</th>
<th>U.A.-F:A.M. 30653</th>
<th>From Goldstream, 1933</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cranium with sheaths</td>
<td>30524</td>
<td>From Fairbanks area, 1929</td>
</tr>
<tr>
<td>Cranium with sheaths, lacking one orbit</td>
<td>30619</td>
<td>Figured by Frick, 1930, vol. 30, no. 1, pp. 71, 75, lower right specimen</td>
</tr>
<tr>
<td>Cranium with partial orbits</td>
<td>46894</td>
<td>From Cripple Creek, 1941</td>
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<td>Cranium with partial orbits and sheaths</td>
<td>30601</td>
<td>From Goldstream, 1931</td>
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<tr>
<td>Cranium with partial orbits</td>
<td>46895</td>
<td>Figured by Frick, 1937, fig. 57</td>
</tr>
<tr>
<td>Cranium with partial orbits</td>
<td>30623</td>
<td>This paper, pl. 17, fig. 7, pl. 20, 2, pl. 21, fig. 5</td>
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<tr>
<td>Cranium with partial orbits</td>
<td>30638</td>
<td>From Ester Creek, 1942</td>
</tr>
<tr>
<td>Cranium, lacking orbits</td>
<td>30589</td>
<td>From Cleary Creek, 1932</td>
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<tr>
<td>Cranium with partial orbits</td>
<td>46896</td>
<td>From Goldstream, 1933</td>
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<tr>
<td>Cranium with partial cores and orbits</td>
<td>30593</td>
<td>From Fairbanks Creek, 1942</td>
</tr>
<tr>
<td>Cranium with one partial and one complete core, partial orbits</td>
<td>30645</td>
<td>From Cleary Creek, 1931</td>
</tr>
<tr>
<td>Partial cranium, lacking left core and orbits</td>
<td>30556</td>
<td>From Cleary Creek, 1933</td>
</tr>
<tr>
<td>Cranium with left partial core and orbit</td>
<td>30558</td>
<td>From Goldstream, 1930</td>
</tr>
<tr>
<td>Cranium with partial cores, lacking orbits</td>
<td>30628</td>
<td>From 17 miles north of Fairbanks, 1930</td>
</tr>
<tr>
<td>Cranium with one core, one partial core, no orbits</td>
<td>30615</td>
<td>From Fairbanks area, 1932</td>
</tr>
<tr>
<td>Cranium with partial cores, no orbits</td>
<td>30535</td>
<td>From Cleary Creek, 1931</td>
</tr>
<tr>
<td>Partial cranium with partial right core, lacks left side</td>
<td>30547</td>
<td>From Livengood Creek, 1930</td>
</tr>
<tr>
<td>Cranium with partial cores, lacking orbits</td>
<td>30588</td>
<td>From Cleary Creek, 1930</td>
</tr>
<tr>
<td>Cranium, lacking orbits</td>
<td>46897</td>
<td>From Goldstream, 1931</td>
</tr>
<tr>
<td>Cranium with partial cores, lacks orbits</td>
<td>30602</td>
<td>From Ester Creek, 1942</td>
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</table>

From Eschscholtz Bay; collected by Beechey on the voyage of H.M.S. "Blossom," 1825–1828

Figured by Buckland, 1831; by Richard-
son, 1852–1854

This paper, pl. 18, fig. 1, pl. 19, fig. 1
Cranium with partial cores, lacks orbits
Cranium with partial cores and orbits
Cranium with partial cores, lacks orbits
Cranium with partial cores and one partial orbit
Cranium with partial right core, lacking left core and orbit
Cranium with partial left core, lacking orbits
Complete skull, lacks right core tip, left core abnormally shaped and small, $P^2$-$M^3$ alv., $M^2$-$M^3$
Cranium with partial cores and orbits
Cranium with partial orbits
Cranium with sheaths and partial orbits
Cranium
Cranium with partial orbits
Cranium, lacking orbits
Cranium with partial left core, lacking orbits
Cranium with partial orbits
Cranium (immature) with partial orbits
Cranium with partial orbits
Cranium with partial cores and orbits
Cranium with sheaths and partial orbits
U.A.-F: A.M.
Skull with sheaths, lacking one-half premaxilla and nasals, $P^2$-$P^4$ alv., $P^4$, $M^2$ alv., $M^2$-$M^3$; also has mandible
Skull lacking nasals and premaxilla, $P^2$-$P^4$ alv., $M^2$-$M^3$, $M^3$ alv.
Complete skull with sheaths, $P^2$-$P^3$ alv., $P^4$-$M^3$
Cranium with sheaths and partial orbits
Cranium with left sheath and partial orbits
Partial cranium with one complete and one partial core, one partial orbit, lacks basicranium
Cranium with partial orbits
Cranium, lacking orbits
Partial cranium with one complete and one partial core, no orbits
Cranium with partial orbits
Cranium with left orbit
Cranium with one partial orbit
Cranium, lacking orbits
Cranium with partial orbits, lacking left core
Cranium with right orbit and partial left core

U.A.-F: A.M. 30566 From Cleary Creek, 1930
30654 From Goldstream, 1929
30515 From Goldstream, 1929
30539 From Cleary Creek, 1930
30536 From Livgood Creek, 1930
30534 From Livgood Creek, 1930
46898 From Engineer Creek, 1941
30603 From Cleary Creek, 1931
30594 From Chatham, 1931
30631 From Goldstream, 1933
This paper, pl. 17, fig. 1, pl. 18, fig. 3, pl. 19, fig. 3
30649 From upper Cleary Creek, 1934
30618 From Cleary Creek, 1932
This paper, pl. 18, fig. 2, pl. 19, fig. 2
30578 From Cleary Creek, 1931
30607 From Cleary Creek, 1931
46899 From Ester Creek, 1942
46900 From Ester Creek, 1942
46901 From Cleary Creek, 1931
This paper, pl. 21, fig. 1
30542 From Cleary Creek, 1930
C.M.N.H. 1368 From Fairbanks area, 1929
30560 From Fairbanks Creek, 1940
46901 From Fairbanks Creek, 1940
This paper, pl. 17, fig. 3, pl. 20, fig. 3, pl. 21, fig. 4, pl. 22, fig. 4
46902 From Goldstream, 1940
From Goldstream (banks near Fox), 1942
46903 From Goldstream, 1940
30512 From Cleary Creek, 1929
30580 From Gilmore Creek, 1931
46904 From Cripple Creek, 1942
30560 From Moose Creek, 1930
30654A From Fairbanks area
30617 From Cleary Creek, 1932
46906 From Engineer Creek, 1942
30582 From Cleary Creek, 1931
30635 From Goldstream, 1933
30571 From Cleary Creek, 1931
30613 From Cleary Creek, 1931
<table>
<thead>
<tr>
<th>U.A.-F:A.M.</th>
<th>Description</th>
<th>Location/Date</th>
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<tbody>
<tr>
<td>30533</td>
<td>Cranium with partial cores, lacking orbits</td>
<td>From Fairbanks area, 1929</td>
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<td>30528</td>
<td>Cranium with partial cores, lacking orbits</td>
<td>From Cleary Creek, 1930</td>
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<td>30544</td>
<td>Cranium with partial cores, lacking orbits</td>
<td>From Cleary Creek, 1930</td>
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<td>30550</td>
<td>Cranium with partial orbits</td>
<td>From Cleary Creek, 1930</td>
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<td>46907</td>
<td>Cranium with partial left core and partial orbits</td>
<td>From Goldstream (banks near Fox), 1940</td>
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<tr>
<td>30596</td>
<td>Cranium with partial left core and partial orbits</td>
<td>From Cleary Creek, 1931</td>
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<td>30612</td>
<td>Cranium with partial cores and orbits</td>
<td>From Cleary Creek, 1931</td>
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<td>30583</td>
<td>Cranium with partial left and fragment of right core, partial orbits</td>
<td>From Goldstream, 1931</td>
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<td>30587</td>
<td>Cranium lacking right core and partial orbits</td>
<td>From Ester Creek, 1942</td>
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<td>46908</td>
<td>Cranium with partial right core</td>
<td>From Ester Creek, 1942</td>
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<td>46909</td>
<td>Cranium with partial right core</td>
<td>From Cleary Creek, 1929</td>
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<td>30513</td>
<td>Cranium with partial orbits</td>
<td>From Cripple Creek, 1942</td>
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<td>46910</td>
<td>Cranium with partial cores, lacking orbits</td>
<td>From Goldstream, 1929</td>
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<td>30517</td>
<td>Cranium with partial right core and partial orbits</td>
<td>From Goldstream, 1931</td>
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<tr>
<td>46911</td>
<td>Skull, complete, with sheaths, P4–P4 alv., M1–M3, M4 alv.</td>
<td>Figured by Frick, 1937, fig. 57</td>
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<td>46912</td>
<td>Skull, complete, P4–P4 alv., P4–M3</td>
<td>From upper Cleary Creek (?), 1937</td>
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<td>Partial skull with sheaths, lacking palate and premaxilla</td>
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<td>Cranium with sheaths, cores, and orbits</td>
<td>From Cripple Creek, 1942</td>
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<td>30592</td>
<td>Cranium with sheaths, cores, and orbits</td>
<td>From Little Eldorado Creek, 1938</td>
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<td>30555</td>
<td>Cranium with sheaths and partial orbits</td>
<td>From upper Cleary Creek, 1937</td>
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<td>30632</td>
<td>Cranium with left sheath and partial orbits</td>
<td>From upper Cleary Creek, 1937</td>
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<tr>
<td>46915</td>
<td>Skull with sheaths, lacking nasals and premaxilla, P4 alv., P4–M3</td>
<td>From upper Cleary Creek, 1937</td>
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<td>46916</td>
<td>Skull with right sheath, lacking nasals and premaxilla, P4–P2 alv., P4–M3</td>
<td>From upper Cleary Creek, 1937</td>
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<td>46917</td>
<td>Skull with partial left core, lacking nasals and premaxilla, P4–P4 alv., M1–M3</td>
<td>From upper Cleary Creek, 1934</td>
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<td>30647</td>
<td>Skull, lacking right maxilla and premaxilla, P4–P4 alv., M1–M3</td>
<td>From second stripping area in Goldstream, 1937</td>
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<td>46918</td>
<td>Skull, lacking nasals and premaxilla, P4–M3 alv.</td>
<td>From Cleary Creek, 1934</td>
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<td>30650</td>
<td>Cranium with sheaths and partial orbits</td>
<td>From Cleary Creek, 1931</td>
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<td>30579</td>
<td>Cranium with sheaths and partial orbits</td>
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<td>30625</td>
<td>Cranium with sheaths and partial orbits</td>
<td>From Goldstream (banks near Fox), 1942</td>
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<td>46919</td>
<td>Cranium with sheaths and partial orbits</td>
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Cranium with left sheath and partial orbits
Cranium with partial orbits
Cranium with partial orbits
Cranium with partial orbits
Cranium with right sheath and partial orbits
Cranium with partial orbits
Cranium lacking orbits
Cranium with partial right core, lacking orbits
Cranium with partial orbits, lacking basicranium
Cranium lacking orbits
Cranium with partial left core and orbit, lacking right orbit
Cranium with partial cores and orbits
Cranium with right sheath and partial right orbit, lacking left side
Cranium with right sheath and partial right orbit, lacking left side
Cranium with partial orbits and fragment of left core
Cranium with fragment of left core, lacking orbits
Cranium with partial left core, lacking orbits
Cranium, lacking left side and orbits
Cranium with fragment of left core and partial orbits
Cranium with fragment of cores and partial orbits
Cranium with sheaths and partial orbits
Cranium with partial orbits
Cranium with partial orbits
Cranium with right sheath, partial left core and partial right orbit
Cranium with fragment of right core and partial orbits
Cranium with partial right core and partial orbits, lacking basicranium
Cranium with partial right core and partial orbits
Cranium with left sheath and partial left orbit, lacking right side
Cranium with fragment of cores and partial orbits
Partial cranium with left sheath, lacking right side
Skull with sheaths, lacking premaxilla and teeth
Skull, lacking premaxilla, P4-P4 alv., M1-M2
Skull, lacking left core, right nasal, and premaxilla, P4-M1 alv., M2-M3

From Goldstream, 1933
From Fairbanks area, 1932
From Cleary Creek, 1932
From Fairbanks Creek, 1942
From Ester Creek, 1942
From Cripple Creek, 1942
From Ester Creek, 1942
From Cleary Creek, 1929
From 17 miles north of Fairbanks, 1930
From Goldstream, 1933
From Cleary Creek, 1931
From Cleary Creek, 1932
From Goldstream, 1931
From Fairbanks area, 1930
From Fairbanks area, 1931
From Cleary Creek, 1931
From Goldstream, 1930
From Cleary Creek, 1930
From Goldstream Camp 21, 1930
From Fairbanks Creek, 1931
From Goldstream, 1930
From Cleary Creek, 1930
From Cleary Creek, 1931
From Engineer Creek, 1942
From Cleary Creek, 1930
From Cleary Creek, 1930
From Fairbanks area, 1930
From Fairbanks area, 1929
Figured by Frick, 1930, p. 75, bottom left
From Engineer Creek, 1939
From Little Eldorado Creek, 1938
Complete skull with sheaths, P²–P⁴ alv., M¹–M³ 46926
From Goldstream (banks at Fox), 1940
This paper, pl. 17, fig. 6, pl. 18, fig. 7, pl. 19, fig. 7, pl. 22, fig. 3

Cranium with sheaths 30523
From Goldstream, 1929
Figured by Frick, 1937, fig. 57
This paper, pl. 17, fig. 4, pl. 18, fig. 4, pl. 19, fig. 4

Cranium with partial orbits 30644
From Goldstream, 1933
From Seward Peninsula at Candle, 1941.
[Candle is near Eschscholtz Bay, the type area for B. (S.) crassicornis]

Cranium with right sheath and partial orbits 46927
From Goldstream, 1933

Skull with left sheath, lacking nasals and premaxilla, P²–M¹ alv., M²–M³ 30633
From Goldstream, 1929

Cranium with sheaths 30520
From Cripple Creek, 1940

Partial skull with sheaths, partial premaxilla, P²–M³, left ramus 46928
From Fairbanks Creek, 1940

Skull, lacking nasals and premaxilla, P² alv., P²–M³ 46929
From Engineer Creek, 1938

Skull, lacking nasals and premaxilla, P²–M¹ alv., M², M³ alv. 46930
From Goldstream at Fox, 1933

Skull, lacking nasals and premaxilla, P²–P⁴ alv., M¹–M³ 30640
From upper Cleary Creek, 1937

Skull, lacking nasals, premaxilla, and right horn-core, P²–P⁴ alv., P²–M³ 46931
From Chatham, 1932

Cranium with sheaths and partial orbits 30624
From Pedro Creek, 1929

Cranium with left sheath 30521
From Livengood, 1941

Cranium with right sheath and partial orbits 46932
From Fairbanks Creek, 1942

Cranium with partial orbits 46933
From Goldstream (banks near Fox), 1942

Cranium with one sheath and partial orbits 46934

Cranium with sheaths and partial orbits 30630
From Goldstream at Fox, 1933

Cranium with right sheath and partial orbits 46935
From Fairbanks Creek, 1940

Cranium with sheaths, lacking orbits 30626
From Fairbanks area, 1932

Cranium, lacking orbits 46936
From Fairbanks Creek, 1940

Cranium, lacking orbits 30545
From Cleary Creek, 1930

Cranium, lacking orbits 30654B
From lower Goldstream, 1939

Cranium, lacking orbits 30518
From Goldstream, 1929

Cranium, lacking left core and partial orbits 30654C
Figured by Frick, 1930, p. 75, second from bottom right

Cranium, lacking left core and partial orbits 30646
From upper Cleary Creek, 1934

Cranium, lacking left core and partial orbits 30604
From Fairbanks area, 1931

Cranium with partial cores and orbits 30598
From Fairbanks area, 1931

Cranium with partial cores and orbits 30610
From Cleary Creek, 1931

Cranium with partial core and partial orbits 30597
From Goldstream, 1931

Cranium with partial cores and orbits 46938
From Engineer Creek, 1942

Cranium with partial cores and orbits 30538
From Goldstream, 1930

Cranium with partial cores and orbits 30557
From 17 miles north of Fairbanks, 1930

Cranium with partial orbits 30514
From Goldstream, 1929, 1930

Cranium with partial orbits 30565
<table>
<thead>
<tr>
<th>Description</th>
<th>Museum</th>
<th>Catalog No.</th>
<th>Location/Details</th>
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<tbody>
<tr>
<td>Cranium with right sheath and partial orbits</td>
<td>U.A.-F:A.M.</td>
<td>30561</td>
<td>From Cleary Creek, 1930</td>
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<td>Cranium with partial orbits</td>
<td></td>
<td>30611</td>
<td>From Cleary Creek, 1931</td>
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<td>Cranium with partial orbits</td>
<td></td>
<td>30586</td>
<td>From Goldstream, 1931</td>
</tr>
<tr>
<td>Cranium with weathered cores and partial orbits</td>
<td></td>
<td>30636</td>
<td>From Goldstream, 1933</td>
</tr>
<tr>
<td>Cranium with partial left core and partial orbits</td>
<td></td>
<td>30616</td>
<td>From Goldstream, 1931</td>
</tr>
<tr>
<td>Cranium with partial left core and partial orbits</td>
<td></td>
<td>30516</td>
<td>From Goldstream, 1929</td>
</tr>
<tr>
<td>Cranium with partial cores and orbits</td>
<td>C.M.N.H.</td>
<td>30548</td>
<td>From Cleary Creek, 1930</td>
</tr>
<tr>
<td>Cranium with partial orbits, tips weathered</td>
<td>U.S.N.M.:V.P.</td>
<td>5726</td>
<td>From Little Minook Creek near Rampart; collected by C. W. Gilmore, 1907</td>
</tr>
<tr>
<td>Partial cranium, lacking tips</td>
<td></td>
<td>5727</td>
<td>From Little Minook Creek, 6 miles south-east of Rampart; collected by Bowen and Coole through C. W. Gilmore.</td>
</tr>
<tr>
<td>Cranium of young animal</td>
<td>B.M.</td>
<td>24589</td>
<td>From Eschscholtz Bay: collected by Kellett, 1845-1851</td>
</tr>
<tr>
<td>A cast of this specimen is in the United States National Museum</td>
<td>U.S.N.M.:V.P.</td>
<td>2078</td>
<td>Figured by Richardson, 1852-1854, as <em>Bison priscus?</em>, pl. 7, fig. 1, pl. 10, fig. 1; by Lucas, 1899a, pl. 76 (figure of cast, called <em>B. crassicornis</em>); by Hay, 1913b, pl. 13, figs. 2, 3 (figure of cast, as <em>B. occidentalis</em>), pp. 176, 177.</td>
</tr>
<tr>
<td>Left horn-core with sheath of female</td>
<td></td>
<td>Richardson 105</td>
<td>From Eschscholtz Bay, Kellett's collection, 1845-1851</td>
</tr>
<tr>
<td>Cranium with weathered cores</td>
<td>U.S.N.M.:V.P.</td>
<td>10607</td>
<td>Figured by Richardson, 1852-1854, as <em>Bison priscus?</em>, pl. 7, fig. 1, pl. 10, fig. 1; by Lucas, 1899a, pl. 76 (figure of cast, called <em>B. crassicornis</em>); by Hay, 1913b, pl. 13, figs. 2, 3 (figure of cast, as <em>B. occidentalis</em>), pp. 176, 177.</td>
</tr>
<tr>
<td>Cranium with horn-cores</td>
<td>U.S.N.M.:V.P.</td>
<td>5514</td>
<td>From Tolovana River</td>
</tr>
<tr>
<td>Cranium with sheaths, lacking orbits</td>
<td></td>
<td>2383</td>
<td>From Tanana River, 20 miles above mouth; collected by Charles Sheldon, 1906</td>
</tr>
<tr>
<td>Complete skull with sheaths and mandible, also articulated cervicals, tooth wear (S-3)</td>
<td></td>
<td>7706</td>
<td>Figured by Hay, 1913b, pl. 11, figs. 1, 2 (as <em>B. occidentalis</em>)</td>
</tr>
<tr>
<td>Complete skull with sheaths and mandible, also articulated cervicals, tooth wear (S-3)</td>
<td></td>
<td></td>
<td>From Little Minook Creek, 8 miles south-east of Rampart; collected by McLain and Ballou</td>
</tr>
<tr>
<td>Cranium, lacking orbits</td>
<td></td>
<td>11980</td>
<td>From Hunter Creek just below mouth of Dawson Creek about 6 miles southeast of Rampart; collected by James Nelson, 1912</td>
</tr>
<tr>
<td>Partial cranium, with core surfaces weathered</td>
<td>Formerly U.P.</td>
<td>13752</td>
<td>Figured by Hay, 1913b, text figs. 7, 8, 9 (as <em>B. alleni</em>), pl. 16, 17; by Hay, 1914, text fig. 103, pl. 41, figs. 1, 2 (as <em>B. alleni</em>)</td>
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<td></td>
<td>Figured by Hay, 1913b, text figs. 7, 8, 9 (as <em>B. alleni</em>), pl. 16, 17; by Hay, 1914, text fig. 103, pl. 41, figs. 1, 2 (as <em>B. alleni</em>)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>From Kotzebue Sound; collected by H. B. Collins, 1929</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>From tundra behind Point Barrow; collected by Stewart Gulin (see Rhoads, 1897)</td>
</tr>
</tbody>
</table>

SKINNER AND KAISEN: FOSSIL BISON 195
<table>
<thead>
<tr>
<th>Specimen Description</th>
<th>Institution</th>
<th>Data</th>
</tr>
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<tbody>
<tr>
<td>Cranium with partial cores, surface weathered</td>
<td>Now C.N.H.M. P-6832</td>
<td>Figured by Hay, 1913b, pl. 12, figs. 1, 2 (as B. occidentalis)</td>
</tr>
<tr>
<td></td>
<td>Formerly U.P. 13753</td>
<td>From tundra behind Point Barrow; collected by Stewart Culin (see Rhoads, 1897)</td>
</tr>
<tr>
<td></td>
<td>Now C.N.H.M. P-6833</td>
<td>Figured by Lucas, 1899a, pl. 75</td>
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<tr>
<td>Cranium with partial right core</td>
<td>A.M.N.H. 14303</td>
<td>Data lost, looks like Alaskan fossilization</td>
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<tr>
<td></td>
<td></td>
<td>Figured by Hay, 1913b, pl. 12, figs. 3, 4 (as B. occidentalis)</td>
</tr>
<tr>
<td>CANADA</td>
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<tr>
<td>Cranium with weathered partial horn-cores</td>
<td>Peter Redpath Mus. McGill Univ.</td>
<td>From near Dawson, Yukon Territory; collected by J. Dudley Bell, preceding 1927</td>
</tr>
<tr>
<td></td>
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<td>Figured by Clark, 1927, figs. 1, 2</td>
</tr>
<tr>
<td>Cranium with orbits</td>
<td>Geol. Mus. Brit. Columbia 2</td>
<td>From Bonanza Creek, Eldorado Claim, Yukon Territory; collected by W. J. Rendell</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Figured by Williams, 1937, pl. 2</td>
</tr>
<tr>
<td>Partial cranium and left horn-core</td>
<td>U.S.N.M.:V.P. 1584</td>
<td>From the Yukon or Kotlo River, Yukon Territory; collected by J. H. Turner</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Figured by Lucas, 1899a, pl. 73, 74</td>
</tr>
<tr>
<td>Partial cranium with sheaths</td>
<td>Memorial Mus. Golden Gate Park, San Francisco</td>
<td>From southeast of Dawson, Yukon Territory</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Figured by Hay, 1913b, pl. 14, fig. 5</td>
</tr>
<tr>
<td>Cranium with sheaths</td>
<td>Geol. Mus. Brit. Columbia 1</td>
<td>From Bonanza Creek, Examiner Pup Claim, Yukon Territory</td>
</tr>
<tr>
<td></td>
<td>A.M.N.H. 13721</td>
<td>Figured by Williams, 1937, pl. 1, figs. 1, 2</td>
</tr>
<tr>
<td>Complete skull, lacking part of right maxilla and premaxillae, no premolars, tooth wear (S-3)</td>
<td></td>
<td>From Fox Gulch Mine near Dawson, Yukon Territory; collected by George T. Coffee through L. S. Quackenbush</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Figured by Hay, 1913b, pl. 10, figs. 1, 2, 3a; 1914, pl. 40, figs. 1, 2 (as B. occidentalis); by Figgins, 1933, pl. 1, figs. 1, 2 (cited as standing for holotype of &quot;Stelabison occidentalis&quot;)</td>
</tr>
<tr>
<td>Partial skull with sheaths, lacking nasals, palate, and premaxillae</td>
<td>C.M. 3247</td>
<td>From near Dawson, Yukon Territory; collected by Frank Caldwell, 1907</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Figured by W. J. Holland, 1915, pl. 43</td>
</tr>
<tr>
<td>Cranium with partial orbits</td>
<td>Mus. Geol. and Surv. Canada 1</td>
<td>From Gold Run Creek, Claim 17, Klondike District, Canada, 15 feet below surface; collected by R. G. McConnell, 1900</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>From Dominion Creek, Claim 83, Klondike District, 30 feet below the surface; collected by W. G. Luker, 1902</td>
</tr>
<tr>
<td></td>
<td></td>
<td>From Bear Creek, Klondike District, 45 feet below surface; collected by W. G. Luker, 1902</td>
</tr>
<tr>
<td>Cranium with cores and nasals</td>
<td></td>
<td>From Bonanza Creek, Claim 39, Klondike District, 18 feet below the surface; collected by W. Ogilvie, 1898</td>
</tr>
<tr>
<td>Partial cranium with partial left core (young animal or small female)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Portion of horn-core and ?sheath</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Partial male skull, lacking horn-cores and nasals, P3-M3 alv., M4-M5, tooth wear (S-A)

D. BISON (PLATYKEROBISON),
NEW SUBGENUS
SUBGENOTYPE: Bison chaneyi Cook, 1928.
SUBGENERIC CHARACTERS (BASED ON MALE SKULLS)

Cores large to moderate, extending from skull in a slight posterior depressed, with the distal tips curve sharply upward with no posterior twist, unlike B. (Bison); proximally, the cores are prominently dorsoventrally flattened as opposed to all other subgenera of Bison; likewise, the horns of the known specimens of the subgenus display a tendency to be more posteriorly placed on the cranium; the superior longitudinal groove on the distal tips is prominent but tends to be proportionately smaller in later forms; cranium moderately broad. To date, no complete specimens are known exhibiting facial characters.

Earlier Pleistocene forms have larger horn-cores than later forms, suggesting regressive horn growth.

DISCUSSION

It is felt necessary to include certain species of Bison in this new subgenus, since four species are known which display prominently flattened horn-cores and other characters in common.

Individual specimens of this group are poorly represented in North America. However, members of the subgenus are also present in Europe; one cast of a skull from England is nearly a duplicate of the subgenotype. Figured specimens from other continental European localities also suggest relationship to this subgeneric group, but illustrations are often very deceiving, particularly in Bison, where standardized comparative positions have not been used. Platykerobison, new subgenus, is also represented in Siberia by the species B. (P.) pallasii (Baer, 1823).

1 From the Greek meaning "flat-horned bison."

From the Yukon Territory; collected by W. J. Rendell
Figured by Williams, 1937, pl. 3, figs. 1, 2 (figured as female skull, but here considered male because of basal horn-core diameter)

1. Bison (Platykerobison) chaneyi
(Cook, 1928)

From the early Pleistocene deposits, Wilbarger County, Texas
Plate 24, figures 1, 1A, 1B, of plastotype

TOTAL AVAILABLE SPECIMENS: 1

1. References for the holotype:

SPECIFIC CHARACTERS (BASED ON MALE SKULLS)

Cook's description of the holotype so adequately describes this species that the pertinent statements from his original description are quoted for comparison in this report.

"Horn-cores long, heavy, strongly curved; tips of horn-cores directed inward, suggesting strongly incurved horn-sheaths; horn-cores strongly flattened fore and aft at base, this flattening producing an upward arch near the base of the horn-sheaths, causing this portion of the horn-core to extend markedly behind the occipital crest; length of horn-core along upper curve exceeds the distance between the bases of the horns by 42 per cent, and the circumference at the base by 30 per cent; index of curvature 141 . . . .

"The shape of the horns is quite distinctive. The horn-cores are flattened to a notable degree at the base. . . . As viewed from the front, the horns have a peculiar arched effect, suggestive of a Cupid’s Bow, due to their flattening and widening. The shape of the horns and proportions are quite distinct from
## COMPARATIVE MEASUREMENTS OF HOLOTYPES OF B. (Platycerobison) chaneyi, B. (P.) geisti, B. (P.) pallasii (AFTER GROMOVA), AND A REFERRED CAST OF B. "priscus"

(Measurements in millimeters, figure 1C for key; indices in per cent, page 142.)

<table>
<thead>
<tr>
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<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Spread of horn-cores, tip to tip</td>
<td>1071</td>
<td>1020</td>
<td>810</td>
</tr>
<tr>
<td>2</td>
<td>Greatest spread of cores on out- side curve</td>
<td>1068</td>
<td>1125</td>
<td>851</td>
</tr>
<tr>
<td>3</td>
<td>Core length on upper curve, tip to burr</td>
<td>545</td>
<td>530</td>
<td>360</td>
</tr>
<tr>
<td>4</td>
<td>Length of core on lower curve, tip to burr</td>
<td>630</td>
<td>605</td>
<td>425</td>
</tr>
<tr>
<td>5</td>
<td>Length, tip of core to upper base at burr</td>
<td>440</td>
<td>400</td>
<td>280</td>
</tr>
<tr>
<td>12</td>
<td>Transverse diameter of core</td>
<td>147</td>
<td>142</td>
<td>121</td>
</tr>
<tr>
<td>6</td>
<td>Vertical diameter of core</td>
<td>114</td>
<td>111</td>
<td>88</td>
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<tr>
<td>7</td>
<td>Circumference of core at base</td>
<td>412</td>
<td>403</td>
<td>340</td>
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<tr>
<td>13</td>
<td>Width between bases of cores</td>
<td>355</td>
<td>300</td>
<td>—</td>
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<tr>
<td>14</td>
<td>Width of cranium between cores and orbits</td>
<td>325</td>
<td>339</td>
<td>294</td>
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<tr>
<td>15</td>
<td>Greatest postorbital width</td>
<td>305</td>
<td>332</td>
<td>272</td>
</tr>
<tr>
<td>8</td>
<td>Greatest width at auditory open- ings</td>
<td>—</td>
<td>420</td>
<td>356</td>
</tr>
<tr>
<td>9</td>
<td>Width of condyles O-N</td>
<td>149</td>
<td>152</td>
<td>136</td>
</tr>
<tr>
<td>10</td>
<td>Occipital crest to nasal-frontal suture</td>
<td>—</td>
<td>(302)</td>
<td>—</td>
</tr>
<tr>
<td>11</td>
<td>Occipital crest to upper border foramen magnum</td>
<td>140</td>
<td>135</td>
<td>120</td>
</tr>
<tr>
<td></td>
<td>Incidence of core curvature</td>
<td>185</td>
<td>185</td>
<td>158</td>
</tr>
<tr>
<td></td>
<td>Index of core compression</td>
<td>143</td>
<td>151</td>
<td>152</td>
</tr>
<tr>
<td></td>
<td>Index of core proportion</td>
<td>78</td>
<td>78</td>
<td>73</td>
</tr>
<tr>
<td></td>
<td>Index of core length</td>
<td>132</td>
<td>131</td>
<td>106</td>
</tr>
<tr>
<td></td>
<td></td>
<td>167</td>
<td>156</td>
<td>122</td>
</tr>
</tbody>
</table>

*Measurements in parentheses are approximate.

any described American species and suggest Asiatic relationships. . . .

The incurved tips of the horns furnish a character quite distinct from most American bisons, although it also occurs in B. alleni, and B. texanus . . .

"In size, the skull and horns of B. chaneyi compare best with those of the largest described species, notably B. alleni, B. regius and B. latifrons; but the proportions differ to a marked degree. . . . Were the whole skull preserved, it is probable that this list of divergencies would be further extended, and possibly further relationships disclosed.

"B. chaneyi is notably deep in the basi- cranial region, in relation to the width between the horns; and the horns are set relatively high on the head, nearer the occiput than in some types observed."

In the introduction to the description Cook
states "On the basis of the known evidence of all kinds at this time, it is the writer's belief that those deposits are of early Pleistocene age and probably Aftonian."

Other important details of minor horn direction are here included. Proximally, horn-cores are depressed one-third their dorsal length on the upper curve and directed in a moderate, posterior direction with relation to the median plane of the skull. The distal tips swing abruptly upward, are heavy and blunt, and have a strong superior longitudinal groove; the horn-cores lack the prominent posterior twist so evident in B. occidentalis; the cores are dorsoventrally compressed as in B. (Platycerobison) alaskensis and B. (Platycerobison) geisti, new species. Some variants of B. (Simobison) alleni tend to have compressed cores but not so prominently as in B. (Platycerobison).

DISCUSSION

It is to be noted that this species, although rare in North America, closely resembles a specimen referred by Lydekker (1898, p. 61, fig. 13) to Bison priscus from the Pleistocene brick-earth deposits near Ilford, Essex, England (B. M. No. 45392). A cast of this specimen is deposited in the United States National Museum (U.S.N.M.: V.P. No. 2077). As set forth in table 17, the measurements of the Old World cast and the holotype of B. (Platycerobison) chaneyi are specifically inseparable. Both have about the same proportion of skull and horn-cores preserved, making it possible to compare equivalent parts.

However, if B. (P.) chaneyi is represented in the Old World fauna by this referred specimen of the loosely defined Bison priscus, it is also necessary that B. priscus be more definitely defined before attempting to synonymize. This leaves open the possibility of referring the British Museum specimen to B. (P.) chaneyi or of synonymizing chaneyi with priscus, which does not appear logical. For the present, however, the species B. (P.) chaneyi is retained.

Since B. (P.) chaneyi has been found in the New World and a synonymous example exists in England, two possibilities for their relationship may be considered. The first and most probable is the migration of a circum-polar species to opposite regions; the second and less probable, an example of parallelism in which two like forms have developed from unlike parent stocks. In either case, the Pleistocene collections from the vicinity of Fairbanks do not contain a single example of this species, which undoubtedly passed through Alaska on its southward migration to the plains of North America.

A rare species, B. (Platycerobison) geisti, is represented in the Fairbanks fauna by individuals with much smaller and more retrogressed horn-cores but which retained the over-all attributes of the earlier Pleistocene species, chaneyi.

In size, B. (P.) chaneyi is smaller than B. (Gigantobison) latifrons, larger than most of the Alaska specimens of B. (Superbison) crassicornis, B. (Platycerobison) alaskensis, and B. (Bison) preoccidentalis, new species, and approximately equal to B. (Simobison) alleni.

As noted in the original description of this species, the dorsoventral compression of the basal portion of the horn-cores is pronounced. This core flatness is also present in about the same degree in geisti and alaskensis, the other North American species of Platycerobison.

2. Bison (Platycerobison) geisti,1 new species

From the late Pleistocene deposits near Fairbanks, Alaska, and northern Canada

Plate 25, figures 2, 2A, 2B

TOTAL AVAILABLE SPECIMENS: 4

1. References for here-referred specimens:

SPECIFIC CHARACTERS
(BASED ON MALE SKULLS)

Horn-cores among the smallest of Platycerobison proportionately approaching mem-

1 Named in honor of Otto William Geist, who has directed fossil collecting in the Fairbanks area for the University of Alaska and the Frick Laboratory since 1937.
bers of the subgenus *Bison*; core length on upper curve equal to or exceeding basal circumference or cranial width; cores strongly depressed about one-third their dorsal length below the plane of the frontals before swinging abruptly upward; proximally, cores are directed in a moderate, posterior direction, extending slightly posterior to the occipital plane, with no posterior twist to tips as opposed to similarly sized *B. (Bison) preocci-
dentalis* and *B. (Bison) occidentalis*, in which core tips have a posterior twist; distal tips of cores tend to be heavy and blunt with a moderate, superior longitudinal groove as in *B. (Platycerobison) chaneyi* and *B. (Simobison) allenii*. As in *chaneyi*, the cores appear to be set more posteriorly on the frontals, being nearer to the occiput; the result leaves less of the occipital region posterior to the horn-
cores than in *B. (Superbison) crassicornis* and *B. (B.) preocci-
dentalis*. As in the larger *B. (Platycerobison) alaskensis* and *B. (P.) chaneyi*, the cores are dorsoventrally compressed in cross section as opposed to the subcircular cross sections of *B. (S.) crassicornis*, *B. (B.) preocci-
dentalis*, *B. (B.) occidentalis*, *B. (B.) bison*, and *B. (Simobison) antiquus*.

As indicated in a paratype, the sheaths have sharply pointed tips, inwardly and posteriorly directed, although the cores are not.

Frontals vary from flat to slightly arched; orbits tubular and forwardly directed; nasals unknown; occipital region well developed with indications of squarish bump; facial proportions and length of skull as yet unknown; cranium moderate.

This species is also very closely related to *Bison (Platycerobison) pallasii* of Siberia which, no doubt, originated from the same parent stock. It is best to consider *pallasii* as specifically distinct for the present, since the cores of *geisti* are a little longer and are not so posteriorly directed; the occipital region is not so broad, and the cranium is not so highly arched or expanded as in *pallasii* (pl. 25, figs. 3, 3A, 3B).

**DISCUSSION**

The holotype of *B. (Platycerobison) geisti*, new species, and two referred crania represent less than 3 per cent of the male crania from the Fairbanks area. The core size, compression, and character of curvature distinguish *geisti* from the other species in the Alaskan assemblage. *B. (Platycerobison) alaskensis* is the only other species found in Alaska with strong horn-core compression. The available data are yet too incomplete to determine its affinities to *B. (P.) geisti*.

Examples of *geisti* are unknown from the southern portions of North America. A geo-
logically earlier but related form, *B. (P.) chaneyi*, is found in Texas, the holotype of which is much larger than known specimens of *geisti* but exhibits the general cranial char-
acters and core shape of the smaller species, *geisti*. This may be another example of retro-
gressive horn growth, in which the small species, *geisti*, represents a geologically later and retrogressed race of the same stock to which the larger *B. (P.) chaneyi* belonged.

A specimen from Old Crow River, Canada, has all the attributes of this species and is tentatively referred to it from figures, since the specimen was not available for examina-
tion.

Four male specimens are here recorded:

**ALASKA**

**HOLOTYPE**

Cranium with horn-cores and one partial orbit

U.A.-F.A.M. 46893

From near Fairbanks; collected by Otto

Wm. Geist, 1942

This paper, pl. 25, figs. 2, 2A, 2B

**REFERRED**

Cranium, lacking orbits, with partial sheaths

U.A.-F.A.M. 30552

From Cleary Creek, near Fairbanks; col-
lected by Peter Kaisen, 1929

This paper, pl. 25, figs. 1, 1A

Cranium with horn-cores and partial orbits

30581

From Cleary Creek; collected by A. S.

Wilkerson, 1931
SKINNER AND KAISEN: FOSSIL BISON

CANADA

REFERRED

Cranium with horn-cores

U.S.N.M.:V.P. 2643
From Old Crow River, Yukon Territory; collected by A. G. Maddren, 1904
Figured by Gilmore, 1908, pl. 12; by Hay, 1913b, pl. 11, figs. 3, 4; by Stehlin, 1931 (after Hay), figs. 1D, 3D

3. Bison (Platycerobison) alaskensis
(Rhoads, 1897)
From late Pleistocene deposits of central and northern Alaska
Plate 24, figures 3, 3A, 3B
TOTAL AVAILABLE SPECIMENS: 5

1. References for the holotype:


TABLE 18

MEASUREMENTS OF HOLOTYPE AND REFERRED MALE SPECIMENS OF B. (Platycerobison) alaskensis

(Measurements in millimeters, figure 1C for key; indices in per cent, page 142.)

<table>
<thead>
<tr>
<th>Key No.</th>
<th>Holotype</th>
<th>Referred</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P25226</td>
<td>46939</td>
</tr>
<tr>
<td>1</td>
<td>Spread of horn-cores, tip to tip</td>
<td>1115</td>
</tr>
<tr>
<td>2</td>
<td>Greatest spread of cores on outside curve</td>
<td>1130</td>
</tr>
<tr>
<td>3</td>
<td>Core length on upper curve, tip to burr</td>
<td>475</td>
</tr>
<tr>
<td>4</td>
<td>Length of core on lower curve, tip to burr</td>
<td>528</td>
</tr>
<tr>
<td>5</td>
<td>Length, tip of core to upper base at burr</td>
<td>400</td>
</tr>
<tr>
<td>12</td>
<td>Transverse diameter of core</td>
<td>129</td>
</tr>
<tr>
<td>6</td>
<td>Vertical diameter of core</td>
<td>95</td>
</tr>
<tr>
<td>7</td>
<td>Circumference of core at base</td>
<td>355</td>
</tr>
<tr>
<td>13</td>
<td>Width-between bases of cores</td>
<td>320</td>
</tr>
<tr>
<td>14</td>
<td>Width of cranium between cores and orbits</td>
<td>339</td>
</tr>
<tr>
<td>15</td>
<td>Greatest postorbital width</td>
<td>402</td>
</tr>
<tr>
<td>8</td>
<td>Greatest width at auditory openings</td>
<td>311</td>
</tr>
<tr>
<td>9</td>
<td>Width of condyles</td>
<td>160</td>
</tr>
<tr>
<td>O-N</td>
<td>Occipital crest to nasal-frontal suture</td>
<td>307</td>
</tr>
<tr>
<td>11</td>
<td>Depth, occipital crest to lower border foramen magnum</td>
<td>163</td>
</tr>
<tr>
<td></td>
<td>Index of core curvature</td>
<td>132</td>
</tr>
<tr>
<td></td>
<td>Index of core compression</td>
<td>74</td>
</tr>
<tr>
<td></td>
<td>Index of core proportion</td>
<td>134</td>
</tr>
<tr>
<td></td>
<td>Index of core length</td>
<td>140</td>
</tr>
</tbody>
</table>

*Bos priscus*, Lydekker, 1898, Wild oxen, sheep, and goats of all lands, p. 61.


2. References for here-referred specimens of *B. (P.) alaskensis*:


**Specific Characters**

(Based on Male Skulls)

Horn-cores tend to be moderately large, smaller than in *B. (Gigantobison) latifrons*, *B. (Simobison) alleni*, and *B. (Platycerobison) chaneyi*, equal in size to those of *B. (Superbison) crassicornis* variants but more dorso-ventrally compressed in cross section, larger than *B. (Platycerobison) geisti* and all *B. (Bison)* species; core curvature moderate to strong; core length on upper curve exceeding both basal circumference and cranial width; cores directed in moderate, posterior direction with respect to longitudinal axis of skull; distal tips not posteriorly twisted, being heavy and blunt with a moderate, superior, longitudinal groove, not to be confused with the basal longitudinal grooves resulting from age and growth; cores moderately depressed, rising well above the plane of the frontals, extending slightly posterior to occipital plane.

Frontals tend to be flat; cranial width moderately broad; sheaths, dentition, and anterior facial portions as yet unknown.

**Discussion**

The holotype of *B. (Platycerobison) alaskensis* was found on the tundra behind Point Barrow, one of the most northerly occurrences of *Bison*. Referred specimens of *B. (Superbison) crassicornis* were also found in the same locality.

Specimens referable to this species are still quite rare. The first specimen known (B.M. No. 91) was figured by Richardson (1852–1854, pl. 13, figs. 1, 2) and superficially resembles the holotype of *B. (Simobison) antiquus*. For this reason Allen (1876, p. 24) considered all Alaskan bison as *antiquus* and felt that *crassicornis* was a synonym of *antiquus*. When Rhoads named the species *B. alaskensis*, he accepted Allen's treatment for all the Alaskan specimens with the exception of the figured British Museum specimen (No. 91), which he considered the same as his new species, the holotype of which was a large, flat-horned specimen similar in size to most *crassicornis*, but differing in a marked degree because of horn-core compression. Lucas (1899a, p. 756) considered this species a synonym of *B. crassicornis* where it remained until Frick (1937, p. 592) again recognized it as representing another species in Alaska.

Although rare in occurrence and as yet imperfectly known, it has been considered expedient to continue the recognition of *B. (Platycerobison) alaskensis* until larger collections demonstrate that it is not a variation of horn-core flatness within the similarly sized *B. (S.) crassicornis* species. The much larger *B. (P.) chaneyi* from the southern regions of the United States represents a relative of this rare form, since its core flatness is also very pronounced. The new Alaskan species, *B. (P.) geisti*, is smaller than *B. (P.) alaskensis* and is considered different until more data are accumulated.

Five specimens are here recorded:
### E. Bison (Gigantobison),* New Subgenus

**Subgenotype:** *Bos latifrons* Harlan, 1825.

**Subgeneric Characters**
*(Based on Male Skulls)*

Cores extend from the skull in a moderate, posterior direction, not extending from the skull so straight as in *Simobison* or *Platycerobison*; varying in curvature from moderate to strongly curved, but never depressed as in *Simobison*, nor posteriorly twisted on the tips as in *Bison*, nor flattened as in *Platycerobison*; cores subcircular in cross section as in *B. (Bison), Superbison, and Simobison*; extremely large in size and proportion; smallest individuals larger than all other species of *Bison*; distal tips have a strong superior longitudinal groove, as in *Platycerobison* and *Simobison*; frontals vary from flat to slightly arched; cranium broad and modified to accommodate extremely large horn-cores.

Known specimens do not show so strong a tendency toward regressive horn growth as other subgenera. Largest of all *Bison*.

**Discussion**

It is felt that the recognition of a subgenus of *Bison* that will include the known giant forms will aid in understanding the *Bison*

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1. **Bison (Gigantobison) latifrons**

*(Harlan, 1825)*

From Middle Pleistocene deposits of Kentucky, Ohio, Florida, Oklahoma, Kansas, Nebraska, Texas, Arizona, California, and Mexico

Plate 26

**Total Available Specimens:** 20

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1. References for the holotype:
   - Great Indian Buffalo Peale, 1803, Phil. Mag., p. 325, fig. 6.
   - Aurochs Cuvier, 1808, Ann. Mus. d’Hist. Nat., Paris, vol. 12, p. 382, pl. 34, fig. 2; 1812, Ossements fossiles, vol. 4, p. 50, pl. 3, fig. 2; 1823, *op. cit.* [ed. 2], p. 143; 1825, *op. cit.*, ed. 3, p. 143, pl. 12, fig. 2; 1835, *op. cit.*, ed. 4, vol. 6, p. 287, pl. 22, fig. 2 (American specimen only).

*Bos latifrons* Harlan, 1825, Fauna Americana.

*Urus griseus* Bojanus, 1827, Nova Acta Acad. Caes. Leopoldino-Carolinae, vol. 13, p. 427. [Holotype mentioned in syntypic series as example No. 5, but not described or figured.]


2. References for the holotype of *Bison ferox* Marsh, 1877:


*Bison (Superbison) latifrons*, Schultze and Frankforter, 1946, Bull. Nebraska State Mus., vol. 3, no. 1, p. 4. ("Appears to be synonymous.")

3. References for the holotype of *Bos crampianus* Cope, 1894:

*Bison latifrons*, Hay, Robert, 1890, Bull. U. S. Geol. Surv., no. 57, p. 40. (Mentions a skull found in "earlier gravis" near Wellington. This may be the skull that Cope made the type of *Bos crampianus*.)


4. References for the holotype of *Bos arisonica* Blake, 1898:

*Bos arisonica* Blake, 1898, Amer. Geol., vol. 22, no. 2, p. 65.


5. References for the holotype of *Bison regius* Hay, 1913:


6. References for the holotype of *Bison angulauris* Figgins, 1933:


7. References for the holotype of *Bison rotundus* Figgins, 1933:


8. References for here-referred specimens of *B. (Gigantobison) latifrons*:

TABLE 19

SUMMARY OF MALE SKULL MEASUREMENTS AND INDICES OF B. (Gigantobison) latifrons AND MEASUREMENTS OF HOLOTYPE (A.N.S.P. No. 12993)

(Measurements in millimeters, figure 1C for key; indices in per cent, page 142.)

<table>
<thead>
<tr>
<th>Key No.</th>
<th>Holo-type</th>
<th>No. of Measurements</th>
<th>Summary</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Spread of horn-cores, tip to tip</td>
<td>— 10</td>
<td>1422 1758</td>
</tr>
<tr>
<td>2</td>
<td>Greatest spread of cores on outside curve</td>
<td>— 6</td>
<td>1560 1724</td>
</tr>
<tr>
<td>3</td>
<td>Core length on upper curve tip to burl</td>
<td>— 12</td>
<td>650 830</td>
</tr>
<tr>
<td>4</td>
<td>Length of core on lower curve, tip to burl</td>
<td>— 9</td>
<td>800 934</td>
</tr>
<tr>
<td>5</td>
<td>Length, tip of core to upper base at burl</td>
<td>— 8</td>
<td>680 810</td>
</tr>
<tr>
<td>12</td>
<td>Transverse diameter of core</td>
<td>179 15</td>
<td>140 162</td>
</tr>
<tr>
<td>6</td>
<td>Vertical diameter of core</td>
<td>155 15</td>
<td>123 144</td>
</tr>
<tr>
<td>7</td>
<td>Circumference of core at base</td>
<td>531 16</td>
<td>420 481</td>
</tr>
<tr>
<td>14</td>
<td>Width of cranium between cores and orbits</td>
<td>— 10</td>
<td>348 370</td>
</tr>
<tr>
<td>15</td>
<td>Greatest postorbital width</td>
<td>— 4</td>
<td>357 397</td>
</tr>
<tr>
<td>16</td>
<td>Width of skull at masseteric processes at M1</td>
<td>— 2</td>
<td>218 249</td>
</tr>
<tr>
<td>17</td>
<td>Greatest width at auditory openings</td>
<td>— 6</td>
<td>306 323</td>
</tr>
<tr>
<td>9</td>
<td>Width of condyles</td>
<td>165 8</td>
<td>140 157</td>
</tr>
<tr>
<td>O-N</td>
<td>Occipital crest to nasal-frontal suture</td>
<td>— 2</td>
<td>301 306</td>
</tr>
<tr>
<td>11</td>
<td>Occipital crest to lower border foramen magnum</td>
<td>186 7</td>
<td>151 176</td>
</tr>
<tr>
<td>F-P</td>
<td>Basilar length of skull</td>
<td>— 2</td>
<td>574 577</td>
</tr>
<tr>
<td>O-P</td>
<td>Over-all length of skull</td>
<td>— 1</td>
<td>— 640</td>
</tr>
<tr>
<td>19</td>
<td>P2-M3 alveolar length</td>
<td>— 1</td>
<td>— 162</td>
</tr>
<tr>
<td>20</td>
<td>M1-M3 alveolar length</td>
<td>— 2</td>
<td>97 104</td>
</tr>
<tr>
<td>M-P</td>
<td>Median length of premaxilla beyond P3</td>
<td>— 1</td>
<td>— 177</td>
</tr>
<tr>
<td>18</td>
<td>Rostral width at maxillary-premaxillary suture</td>
<td>— 1</td>
<td>— 126</td>
</tr>
</tbody>
</table>

Index of core curvature | — 8 | 110 118 | 131 |
Index of core compression | 87 15 | 80 89 | 93 |
Index of core proportion | — 10 | 147 176 | 210 |
Index of core length | — 6 | 209 245 | 300 |


**SPECIFIC CHARACTERS**

(Based on Male Skulls)

Horn-cores extremely large and long, length on upper curve greatly exceeding basal circumference or cranial width between horn-cores and orbits; cores subcircular in basal cross section; directed from a slight to moderate, posterior direction with respect to longitudinal axis of skull and extending posterior to the occipital plane; distal tips not posteriorly twisted, heavy and tapering with a moderately developed superior longitudinal groove; cores are not strongly depressed and vary from slight to strongly curved in a uniform manner, rising well above the frontals; fron-
t tendency to be flat to slightly arched and are posteriorly expanded to accommodate greatly enlarged horn-core bases; occipital region correspondingly specialized; proportionate cranial width broad; orbits tubular and anteriorly directed; anterior facial region tending to be slimmer with heavy nasal bones and well-developed masseteric processes.

Horn sheaths inwardly directed (as indicated by U.C.M.P. No. 4067).

Lower jaw as yet not definitely associated with a skull. Skelet al parts remain unknown but probably very large.

This species is the largest of the *Bison*. Female skulls are as yet unknown.

**DISCUSSION**

The largest of the bison species, *B. (Gigantobison) latifrons*, has not been observed in the Alaskan collection, although it appears to have been widespread in central North America and south into Mexico. The distribution map (p. 154) shows occurrences of identifiable horn-cores from California to Florida. Most of the literature giving geological data with finds of *latifrons* suggests an early to middle Pleistocene age. Apparently deposits containing fossils from this phase of the Pleistocene did not accumulate or are not yet discovered in Alaska. This may account for the unrecorded passage of *latifrons* from its presumably Old World sources of origin through the northern regions before it spread out over the southern part of North America, where it probably existed contemporaneously for a while with *B. (Simobison) alleni* and *B. (Platycerobison) chaneyi*. Much more extensive and accurate data are still to be desired on *latifrons* and its faunal associates. It appears that *latifrons* was not so strongly subjected to the processes of retrogressive horn growth as the other bison, for in the known material smaller-horned species in later Pleistocene deposits are not recognized.

Historic interest is centered on *latifrons* for it was the first species of fossil bison described from North America. Since Harlan's (1825, p. 273) first systematic naming, there has been a gradual accumulation of isolated specimens of this gigantic form. It is now possible to make some estimate of the range of specific variation. Many finds of this species have been described in the literature under various specific names with emphasis being placed on individual variations.

In view of the observed ranges of variation in both the living plains bison and the Pleistocene series of Alaskan *B. (Superbison) crassicornis*, it is well to reconsider all of the previously described *latifrons*-like species that are here considered synonyms. The holotype of each synonym is discussed in the chronological order in which it appeared. With the exception of *B. “arisonica,”* the holotype of each synonym has been measured and examined.

*Bison “ferox”* Marsh, 1877

The holotype is represented by the distal one-third to one-half of a very large horn-core which can now be recognized as belonging to *latifrons*. Marsh recognized it as different from known bison remains. Lucas (1899a, p. 767) continued to acknowledge Marsh's species but stated, “This species is based on an imperfect horn core, which indicates a species more nearly like *B. latifrons* in the shape of the horn cores than any other species.” Marsh’s original records show that the specimen was found along the Niobrara River in northern Nebraska where known Pleistocene deposits exist. Hay (1924, p. 199) indicated that he regarded *B. “ferox”* to be synonymous with *latifrons*. The fossilization of the specimen does not suggest a connection with the Hay Springs fauna.

*“Bos crampianus”* COPE, 1894

This specimen consists of the facial portion of a skull and two partial horn-cores. The size and curvature of the cores show them to be similar to “regius.” The basal portion of the cores are not preserved. The distal three-fifths of one and less than one-fifth of the other were found with the portion of the skull. Measurements obtained from the partial skull agree with a complete skull of *latifrons* from California figured by VanderHoof (1942, pls. 1, 2, figs. 2, 3, 4). The specimen also indicates an animal larger than any observed range of variation within the Alaskan *B. (Superbison) crassicornis* series. Lucas (1899a, p. 766) considered “*Bos crampianus*” as belonging to *Bison alleni* since he lacked the information now available on the size and
range of specimens referable to *latifrons*. A complete skull of *latifrons* is in the Wellington High School in Sumner County, Kansas (the type locality given by Cope for "*Bos crampsi- anus*"), and was identified from a photograph forwarded by Dr. Claude Hibbard, University of Kansas.

"*Bos arizonica*" Blake, 1898

The holotype of this species was described and never figured. Lucas (1899a, p. 768) considered the specimen to represent an individual of *B. latifrons*. The type specimen could not be located in the University of Arizona, its last recorded repository.

*Bison "regius"* Hay, 1913

Slight individual variations in horn-core and tooth pattern (p. 139) were considered important enough to warrant a specific name. The holotype is a young individual of an early S-2 tooth wear that accounts for the enamel foldings of the molars. Reentering folds may be observed as a rare variant in slightly worn teeth of other species of *Bison* and are a fixed character in *Bos taurus*. The age of the teeth indicates the possibility of continued growth and enlargement of the horn-cores if a comparison may be made with the stages of growth in the skulls of *B. (Bison) bison*. This specimen was originally considered as *B. latifrons* by Matthew (1909, p. 198). VanderHoof (1942, p. 5) considered *B. "regius"* different from the California skull of *latifrons* on the basis of tooth differences, apparently not considering that his specimen was an old individual of S-3 wear, in which age had simplified the enamel pattern of the fossettes, as compared to the relatively younger *B. "regius"* in which the unworn teeth show a more complex pattern.

*Bison "angularis" AND Bison "rotundus"* Figgins, 1933

The amount of difference exhibited by these specimens is well within the range of relative variation observed in the Alaskan series when compared with the illustrated horn-cores of *crassicornis*. These variants of *crassicornis* are completely intergrading and are considered one species. It seems that "*angularis*" and "*rotundus*" are individual variants of *latifrons*. These specimens were originally referred to *B. latifrons* by Cook (1931, pp. 273–280).

In the summarized table for this species, 12 original and one cast of 20 known specimens of this gigantic form have been measured. Measurements by other authors have been used for the remaining specimens where available. The accumulated data present an estimate of the range of variation to be expected when all the synonymous species are regarded as individuals of the *latifrons* population.

VanderHoof (1942, p. 10) suggested that the ratio of the length of the tooth row versus the length of the skull may have been one of the causes of the extinction of *latifrons* in competition with other smaller species of *Bison* which appeared to have larger teeth in proportion to the size of the skull. At present, recorded occurrences of the contemporaneous existence of *latifrons* and the smaller species of *Bison* are not demonstrated. The tooth proportion ratio is directly connected with age. For example, as the animal ages, the skull becomes longer and the tooth row shorter, the younger animal tending to have the higher ratio. The California specimen (U.C. M.P. No. 4067) is of an S-3 tooth wear and is, therefore, a mature individual.

The summary of the ratio is given below:

<table>
<thead>
<tr>
<th></th>
<th>No. of Specimens</th>
<th>P4–M3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Range (in Per Cent)</td>
</tr>
<tr>
<td><em>B. (Bison) b. bison</em></td>
<td>29</td>
<td>24–32</td>
</tr>
<tr>
<td><em>B. (Bison) preocidentalis</em></td>
<td>7</td>
<td>24–27</td>
</tr>
<tr>
<td><em>B. (Superbison) crassicornis</em></td>
<td>8</td>
<td>23–26</td>
</tr>
<tr>
<td><em>B. (Gigantobison) latifrons</em> (after VanderHoof)</td>
<td>1</td>
<td>25</td>
</tr>
</tbody>
</table>
Twenty specimens are here recorded:

<table>
<thead>
<tr>
<th>Location</th>
<th>Specimen Description</th>
<th>Repository/Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>KENTUCKY</td>
<td>Partial cranium, left side, base of left horn-core</td>
<td>A.N.S.P. 12993</td>
</tr>
<tr>
<td></td>
<td>From 12 to 14 miles north of Big Bone Lick</td>
<td>Figured by Peale, 1803, fig. 6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>by Cuvier, 1808, pl. 34, fig. 2; 1812, ed. 1, pl. 3, fig. 2; 1823, [ed. 2], pl. 12, fig. 2; 1825, ed. 3, pl. 12, fig. 2; 1834, ed. 4 (atlas, 1836), pl. 173, fig. 2 (American specimen only); by Leidy, 1852c, pl. 1; by Rhoads, 1897, pl. 12, fig. 4</td>
</tr>
<tr>
<td></td>
<td>OHIO</td>
<td>A.M.N.H. 6840</td>
</tr>
<tr>
<td></td>
<td>Complete set of horn-cores with partial cranium</td>
<td>Figured by Allen, 1876, pl. 1; by Smith, 1886, pl. 1; by Lucas, 1899a, pl. 82; by Hay, 1913, vol. 46 (1914), pl. 19, fig. 1; 1914, pl. 42, fig. 1</td>
</tr>
<tr>
<td></td>
<td>Cranium with partial horn-cores, lacking orbits</td>
<td>U.S.N.M.:V.P. 1171</td>
</tr>
<tr>
<td></td>
<td>Part of cranium and right horn-core</td>
<td>From 2 miles south of Bradenton</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Figured by Simpson, 1930, p. 11, fig. 6</td>
</tr>
<tr>
<td></td>
<td>FLORIDA</td>
<td>A.M.N.H. 26828</td>
</tr>
<tr>
<td></td>
<td>Cranium with partial horn-cores, lacking orbits</td>
<td>From Withlacoochee River, Marion County; collected by D. Sheppard, 1891</td>
</tr>
<tr>
<td></td>
<td>Part of cranium and right horn-core</td>
<td>U.S.N.M.:V.P. 1171</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>OKLAHOMA</td>
<td>C.N.H.M. P-14636</td>
</tr>
</tbody>
</table>
|                  | Left horn-core with portion of center restored                                        | From Gage, Ellis County; collected by A.-
|                  | Basal portions of right and left horn-cores                                           | Schmalz, 1900                             |
|                  |                                                                                        | From Hardesty; collected by Mrs. Estelle McNew, 1940 |
|                  | NEBRASKA                                                                              | C.M.N.H. 1603                            |
|                  | Segment of large horn-core, lacking base and tip                                       | From northern Nebraska along the Niobrara River; collected by Eli Whitney, 1870 |
|                  |                                                                                        | Figured by Lucas, 1899a, pl. 81            |
|                  |                                                                                        | Holotype of B. “ferox” Marsh (see discussion, p. 206) |
|                  | Cranium with attached horn-cores and partial orbits                                   | Hastings Mus. No. 4710                    |
|                  |                                                                                        | From Sutton, Clay County; collected by A. M. Brookings, Director, Hastings Museum |

1 It is to be noted that the holotype is not from the fauna of Big Bone Lick, as indicated by several authors.
2 All references and figures cite the Cincinnati Society of Natural History as the repository for this specimen. In 1937, it was acquired through exchange by the American Museum of Natural History, where it is now A.M.N.H. No. 6840.
3 Smith, H. P., 1886, Jour. Cincinnati Soc. Nat. Hist., vol. 10, pl. 1. The above location for this specimen was taken from this publication. O. D. Norton, 1875, Amer. Jour. Sci., ser. 3, vol. 10, p. 386, gave Brush Creek, Adams County, as the location. This seems to be an extract from a newspaper account.
Cranium with horn-cores and partial orbits

C.M.N.H. 1187

Portion of skull anterior to orbits and parts of both horn-cores

A.N.S.P. 3

Skull with horn-cores, lacking premolars

A.M.N.H. 14346

Cranium with horn-cores attached, tips missing

K.U.M.V.P. 201

Partial right horn-core and cranium with condyles and partial orbit

U.N.S.M. 1-12-12-41

Partial cranium and horn-cores

Private Coll., Scott City, Kansas

(Now in Univ. of Nebraska)

Nearly complete skull, lacking teeth

Wellington High School, Sumner County, Kansas

Figured by Figgins (as specimen number C.M.N.H. No. 1164), 1931, pl. 1, fig. 2, no. 1, pl. 2, fig. 3, no. 1, and pl. 3, fig. 4, no. 1; 1933, pl. 4

Holotype of B. "angularis" Figgins (see discussion, p. 207)

From Dorchester, Saline County; collected by A. M. Brookings

Figured by Figgins, 1931, pl. 1, fig. 2, no. 2, pl. 2, fig. 3, no. 2, pl. 3, fig. 4, no. 2; 1933, pl. 5.

Holotype of B. "rotondus" Figgins (see discussion, p. 207)

From near Wellington, Sumner County

Figured by Cope, 1894, pl. 22, figs. 1-4; by Rhoads, 1897, pl. 22, fig. 5

Holotype of "Bos crampianus" Cope (see discussion, p. 206)

From Hoxie, Sheridan County; found by Frank Lee and Harley Henderson, 1902, and collected by Charles H. Sternberg

Figured by Sternberg, 1909, fig. 33; by Osborn, 1910, fig. 212 (a); by Hay, 1913, vol. 46 (1914), pl. 18, figs. 1, 2; 1914, vol. 23, pl. 42, figs. 2, 3

This paper, pl. 26, figs. 3, 3A, 3B

Holotype of B. "regius" Hay (see discussion, p. 207)

From 25 miles southeast of Coldwater, Comanche County; collected by James O'Connel, 1925

Figured by Martin, 1927, pl. 42, upper middle figures, pl. 43

From 15-16 miles west of Stockton, Rocks County; collected by George Sternberg, 1937. Later sent to the University of Nebraska State Museum

From Sand Pit near Scott City. Herbert Waite, U.S.G.S., measured and photographed the specimen

1 Martin, H. T., 1927, Kansas Univ. Sci. Bull. vol. 17, no. 7. These figures illustrate how changed a specimen may appear in respect to the horns when photographed from different angles.
ARIZONA

Partial horn-cores

Univ. Ariz.

Univ. Ariz. Last known

repository

From near Greaterville, Pima County
Never figured

Holotype of B. "arizonica" Blake (see
discussion, p. 207)

TEXAS

Craniun with partial horn-cores

B.M.1

20706

From near San Felipe, bank of Brazos
River, Austin County; collected by
William Huff, prior to 1846
Figured by Carpenter, 1846, fig. 1; by
Hay, 1913, vol. 46 (1914), pl. 19, fig. 3,
(after Carpenter)
Referred by Frick, 1937, to S. chaneyi

Craniun with horn-cores

Dr. Mark Francis

Collection

From near Beeville, Bee County; col-
lected by Ben Mattingly
Referred by Hay, 1927, p. 288, pl. 1,
fig. 2, to B. latifrons

CALIFORNIA

Complete skull with horn sheath molds

U.C.M.P.

4067

From MacArthur, Shasta County; found
in 1933 by Burnett Day and collected
by V. L. VanderHoof
Figured by VanderHoof, 1942, figs. 2, 3,
4, pl. 1, upper, middle figures

MEXICO

Craniun with attached horn-cores

Nat. Mus.

Mexico

From the Valley of Mexico
Figured by Villada, 1903, pl. 5

1 Hay, 1924, Carnegie Inst. Washington Publ., no. 322A, p. 189, cites references giving the present repository as
the British Museum, London, for the Carpenter specimen, which he referred to his species B. "regius".
REVISION, PART 2, BISON OF EURASIA

The literature on Eurasian bison is not easily reviewed for it must be translated from many languages. Excellent library facilities have made it possible to examine all of the earlier accounts which are interesting historically, and at the same time important, for among them are to be found the first valid scientific names applied to the living as well as the fossil bison. It has been necessary to follow the procedure of reestablishing very old names for a definite reason. The species *Bison priscus*, as currently used, is applied in an indeterminate manner and may apparently include any fossil bison regardless of size and other physical characters.

Bojanus originated the name *priscus* in 1827, when he listed five distinctly different bison skulls known to him at that time. His listing thus created a syntypic series of specimens that stood for *priscus*. Although he cited five specimens, only one may be used for the lectotype. The literary history of each specimen in the syntypic series was examined in order to verify the availability of one for consideration as a lectotype and to establish a set of physical characters that could be applied to the specific name of *priscus*. Examination disclosed that of the five specimens listed by Bojanus, three had been previously named by other authors, and one was of an indeterminate nature, never having been figured or described by Bojanus. It seems, however, that this specimen was later measured and discussed by von Meyer (1832 [1835], p. 133, no. 10), although he did not state that this was one of Bojanus’ examples. The location given in von Meyer’s description agrees with that of Bojanus.

Only one of Bojanus’ syntypic examples may unquestionably stand for the species *priscus*. Hilzheimer, as first reviser, selected this specimen in 1918 when he revised the species, and the present work has simply verified Hilzheimer’s selection. In this case it is possible to give only a few physical characters of the species, for, unfortunately, the lectotype is not completely figured and we cannot be sure that it is still in existence.

This portion of the report is confined entirely to findings in literature since it has been impossible to examine type specimens. The specific diagnoses of many of the older species have been redefined, but the conclusions have been drawn from the earlier descriptions, the type figures, and the measurements, when available. Since these works are not generally accessible, the liberty of copying and reproducing outline drawings of the figured types has been taken (after rescaling the figures to one-tenth), in order to facilitate comparison within this report.

The Eurasian listing presents *Bison* relationships as understood from the North American study. The taxonomic treatments consist of references concerning type descriptions or works pertaining to the status of each species. Several species have also been tentatively synonymized in order to clarify the Eurasian bison problem. The adopted practice has been that a species must stand on its own physical characters, and the first author definitely to apply a post-Linnaean name to a distinct *Bison* species has been credited with his observations.

LISTING OF EURASIAN BISON
BY SUBGENERA

The Eurasian *Bison* are here divided into one living and four extinct named subgenera and one unnamed subgenus. One other extinct subgenus, *Gigantobison*, which occurs in North America is not conclusively known. These subgenera embrace one living species and eight extinct species and five subspecies.

Family BOVIDAE Gray, 1821
Subfamily BOVINAE Gill, 1872
Genus BISON (Hamilton Smith, 1827)
A. Subgenus BISON

2 species and 6 synonyms

? Late Pleistocene and Recent.
Horn-cores moderate to small sized, subcircular in cross section and posteriorly twisted.

1. B. (Bison) bonasus (Linnaeus, 1758)
Recent European bison.
Former range in Lithuania and Caucasus.
Spread of horn-cores, 525–689 mm.
SYNONYMS

*Urus nostras* Bojanus, 1827
*Bison europaeus* von Meyer, 1832
*Bison bonasus caucasia* Grevé, 1906
*Bison caucasicus* Hilzheimer, 1909
*Bison kaukasikus* Hilzheimer, 1909

2. *B. (Bison) occidentalis primitivus* (Hilzheimer, 1909)

Late Pleistocene. Lena River of Siberia. Spread of horn-cores, 910 mm.

B. SUBGENUS SIMOBISON (Hay and Cook, 1930)

2 species

Early middle Pleistocene to sub-Recent. Horn-cores large to small sized extending from skull at approximately right angles.

1. *B. (Simobison) cesaris* (Schlotheim, 1820)

Geologic age unknown. Spread of horn-cores. Germany. Spread of horn-cores, (?1100 mm.).

2. *B. (Simobison) priscus* (Bojanus, 1827)

Geologic age unknown. Spread of horn-cores. Italy. Spread of horn-cores, (1126 mm.).

C. SUBGENUS SUPERBISON Frick, 1937

1 species and 6 synonyms

Late Pleistocene. Horn-cores large to moderate sized, proportionately long.

1. *B. (Superbison) crassicorns* (Richardson, 1854)

Late Pleistocene. Siberia, Russia, and Europe. Spread of horn-cores, 765–1360 mm.

SYNONYMS

*Bison europaeus lenensis* Hilzheimer, 1910
*Bison uniformis* Hilzheimer, 1910
*Bison priscus fraasi* Hilzheimer, 1918
*Bison priscus longicornis* Gromova, 1935
*Bison priscus ischerskii* Gromova, 1935
*Bison priscus deminutus* Gromova, 1935

D. PLATYCEROBISON, NEW SUBGENUS

1 species

Early to late Pleistocene. Horn-cores large to moderate sized, dorso-ventrally flattened.

1. *B. (Platycerobison) pallasii* (Baer, 1823)

Late Pleistocene. Siberia. Spread of horn-cores 842 mm.

E. GIGANTOBISON, NEW SUBGENUS

Not definitely known from Eurasia. Horn-cores extremely large and subcircular in cross section.

F. UNNAMED PRIMITIVE SUBGENUS

2 species

Late Pliocene and ? early Pleistocene. India and China.

1. *B. (Subgenus?) sivalensis* Lydekker, *ex* Falconer MS, 1878

? Pinjor stage of upper Siwaliks. Near Pinjor, India. Spread of horn-cores, (?less than 800 mm.)

2. *B. (Subgenus?) palaeosinensis* Chardin and Piveteau, 1930

Late Pliocene, Nihowan formation. Valley of Sangkan-ho River, China. Spread of horn-cores, 536 mm.

G. PARABISON, NEW SUBGENUS

2 species and 4 subspecies

Middle Pleistocene and sub-Recent. Horn-cores moderate to small sized, subcircular in cross section, posteriorly directed but not posteriorly twisted.

1. *B. (Parabison) exigus* (Matsumoto, 1915 [1927])

Subgenotypic species, post-Pleistocene. Northern China and eastern Mongolia. Spread of horn-cores, 700 mm.

1A. *B. (Parabison) exigus curvicornis* (Matsumoto, 1927)


1B. *B. (Parabison) exigus ?harbinensis*, new subspecies

Middle Pleistocene. Manchoukuo. Spread of horn-cores, 1008 mm.
2. B. (?Parabison) schoetensacki schoetensacki
(Freudenberg, 1910)

Late Pleistocene. Germany.
Spread of horn-cores, 870 mm.

2A. B. (?Parabison) schoetensacki mediator
(Hilzheimer, 1918)

Late Pleistocene. Germany.
Spread of horn-cores (700 mm.).

2B. B. (?Parabison) ?schoetensacki maior
(Hilzheimer, 1918)

Sub-Recent. Germany.
Spread of horn-cores, 650 mm.

A. BISON (BISON) (HAMILTON SMITH, 1827)

Two Eurasian species are recognized as belonging to the typical subgenus B. (Bison), the living species B. (Bison) bonasus and the fossil subspecies B. (Bison) occidentalis primitivus.

Apparently the specific members of B. (Bison) were more numerous in North America than in Europe and entirely lacking in Asia, for no examples of Bison appear in Asiatic literature that unquestionably could be assigned to the typical subgenus B. (Bison). The evidence suggests that the species of Bison in Asia proper are referable to B. (Parabison), new subgenus, or belong to a primitive, and as yet unnamed, subgenus of Bison. This may indicate that specific members of B. (Bison) developed in northern Siberia and Europe after their progenitors had migrated there from earlier sources of origin, presumably the Siwaliks and China, and that B. (Bison), as such, never returned to the region of their ancestral origin. Species closely paralleling B. (Bison) are found in their place which have been referred to the new subgenus B. (Parabison).

1. Bison (Bison) bonasus (Linnaeus, 1758)

LIVING BISON OF EUROPE

Plate 10, figures 4, 4A, 4B reverse

References for the species:
Lydekker, 1898, Wild oxen, sheep, and goats of all lands, p. 64.
Bos taurus bonasus, Kerr, 1792, The animal kingdom, or zoological system of the celebrated Sir Charles Linnaeus, p. 333.
Bos bison HAMILTON SMITH, 1827, in Cuvier, Georges, The animal kingdom, with additional descriptions of all the species hitherto named, and of many not before noticed, by Edward Griffith and others, vol. 4, p. 398.
Bos (Bison) bison HAMILTON SMITH, 1827, op. cit., vol. 5, p. 373.
Bison bonasus, Gray, 1850, Knowsley menagerie, p. 48.

SPECIFIC CHARACTERS
(BASED ON MALE SKULLS)

Horn-cores small in size, proportionately longer than in B. bison; core length on upper curve seldom exceeds the basal circumference or cranial width between the horn-cores and orbits; subcircular in basal cross section; posteriorly directed with respect to longitudinal axis of skull but not always extending posterior to the occipital plane; cores less posteriorly directed, more widespread, rising higher above the plane of the frontals, and distal tips less posteriorly twisted than in B. (B.) bison; superior longitudinal groove on tips weak or missing; cores vary in curvature from nearly straight to recurved.

Frontals tend to be flat, but arching is occasionally observed. The orbits are tubular and forwardly directed; in specimens observed, the supraorbital sulcus and foramina tend to remain open and unossified in old
TABLE 20
SUMMARY* OF MALE SKULL MEASUREMENTS AND INDICES OF B. (B.) bonasus COMPARED WITH AVERAGES OF B. (B.) b. bison AND B. (B.) b. athabascae
(Measurements in millimeters, figure 1C for key; indices in per cent, page 142.)

<table>
<thead>
<tr>
<th>Key No.</th>
<th>No. of Measurements</th>
<th>bonasus</th>
<th>bison</th>
<th>athabascae</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Spread of horn-cores, tip to tip</td>
<td>16</td>
<td>525</td>
<td>608</td>
</tr>
<tr>
<td>2</td>
<td>Greatest spread of cores on outside curve</td>
<td>7</td>
<td>540</td>
<td>649</td>
</tr>
<tr>
<td>3</td>
<td>Core length on upper curve, tip to burr</td>
<td>7</td>
<td>195</td>
<td>226</td>
</tr>
<tr>
<td>4</td>
<td>Length of core on lower curve, tip to burr</td>
<td>14</td>
<td>197</td>
<td>268</td>
</tr>
<tr>
<td>5</td>
<td>Length, tip of core to upper base at burr</td>
<td>16</td>
<td>147</td>
<td>187</td>
</tr>
<tr>
<td>12</td>
<td>Transverse diameter of core</td>
<td>13</td>
<td>67</td>
<td>79</td>
</tr>
<tr>
<td>6</td>
<td>Vertical diameter of core</td>
<td>13</td>
<td>57</td>
<td>71</td>
</tr>
<tr>
<td>7</td>
<td>Circumference of core at base</td>
<td>18</td>
<td>199</td>
<td>238</td>
</tr>
<tr>
<td>14</td>
<td>Width of cranium between cores and orbits</td>
<td>22</td>
<td>224</td>
<td>254</td>
</tr>
<tr>
<td>15</td>
<td>Greatest postorbital width</td>
<td>22</td>
<td>292</td>
<td>316</td>
</tr>
<tr>
<td>16</td>
<td>Anterior orbital width, at notch</td>
<td>11</td>
<td>226</td>
<td>246</td>
</tr>
<tr>
<td>17</td>
<td>Width of skull at masseter process at M$^1$</td>
<td>7</td>
<td>143</td>
<td>172</td>
</tr>
<tr>
<td>8</td>
<td>Greatest width at auditory openings</td>
<td>20</td>
<td>212</td>
<td>243</td>
</tr>
<tr>
<td>O-T</td>
<td>Length, occipital crest to tip of nasals</td>
<td>18</td>
<td>415</td>
<td>443</td>
</tr>
<tr>
<td>O-N</td>
<td>Length, occipital crest to nasal-frontal suture</td>
<td>18</td>
<td>210</td>
<td>257</td>
</tr>
<tr>
<td>10</td>
<td>Occipital crest to upper border of foramen magnum</td>
<td>19</td>
<td>75</td>
<td>95</td>
</tr>
<tr>
<td>11</td>
<td>Occipital crest to lower border of foramen magnum</td>
<td>17</td>
<td>124</td>
<td>142</td>
</tr>
<tr>
<td>F-P</td>
<td>Basilar length of skull</td>
<td>21</td>
<td>449</td>
<td>475</td>
</tr>
<tr>
<td>O-P</td>
<td>Over-all length of skull</td>
<td>19</td>
<td>490</td>
<td>526</td>
</tr>
</tbody>
</table>

* The measurements of bonasus are compiled from the literature cited in this paper, and the two skulls at our disposal. The averages of bison and athabascae are from tables 10, 11.

Age as opposed to B. (B.) bison (pl. 10). Overall and basilar length of skull slightly less than in B. (B.) bison. Cranial and facial proportions appear to be less but are proportionately about the same as in bison, and average proportionate differences seldom exceed 5 per cent, with the exception of the horn-cores.

Living external appearances noticeably different in two species; B. (B.) bison appears smaller, lighter, and with a deeper chest than B. (B.) bonasus, and has a heavier, shaggier hair growth on head and shoulders.

DISCUSSION

The Linnaean name bonasus for the wild bison of Europe has clear priority over all other names applied to this species. Although Linnaeus did not give extensive descriptions in his tenth edition, he cited two references which were well figured and indicated clearly that he had the European bison in mind.
when he classified them under the name *bonasus*. The specific name was not originated by Linnaeus, but since all zoologic nomenclature dates from his publication, he is to be credited with the usage.

Synonymies have been kept as brief as possible and only important changes in synonymous usages have been shown. Excellent information is to be found in some of the more recent publications concerning the preservation of this species, which now exists only on game preserves. It is not assumed that all published photographs are of full-blooded *bonasus* since they have been inbred with American bison. Concerning this, however, the records of the International Society for the Preservation of Wisents give much useful information on blood strains.

Two *bonasus* skulls have been located in North American collections, one in the American Museum of Natural History (pl. 10, figs. 4, 4A, 4B, rev.) and one in the United States National Museum. The measurements of these two skulls have been combined with measurements given by other authors, and a small population sample has been accumulated for comparison with the male skulls of the two North American subspecies of *Bison* (table 20). This table is not comparable to the summary tables of the North American subspecies, where we have personally measured all of the specimens and are assured of uniformity of method.

On examination of the table, it is to be noted that the subspecies *B. (B.) b. bison* and *B. (B.) b. athabascae* differ more from each other in some respects than do *B. (B.) b. bison* and *B. (B.) bonasus*. By this it is not implied that *bonasus* is subspecific to *bison*, although they interbreed freely and produce fertile offspring. It seems that here is a living example of geographic isolation in which both *bison* and *bonasus* originated from the same parent stock but have varied their modes of development to some slight extent aided by geographic isolation. From a liberal point of view, *bonasus*, *bison*, and *athabascae* could all bear subspecific relationship to each other.

The two fossil species *Bison* "*bonasus" mediator and *Bison* "*bonasus" maior* of Hilzheimer have been placed in closer relationship to *B. (?Parabison) schoetensacki* (Freudenberg, 1910), than to the living *bonasus*. Conclusions must be drawn from holotypes of these subspecies rather than from referred specimens. A parallel phylectic line of *Bison* seems to have existed in Eurasia until nearly recent times on a contemporaneous basis with the phylectic line which gave rise to *bonasus*. A similar condition also existed in North America in the relationship between *B. (Simobison) antiquus* and *B. (Bison) bison*. In North America and Europe, the specific members of the subgenus *Bison* are the last survivors.

There has been a tendency in the more recent papers to use the name "wisent" in an almost generic sense in an attempt to distinguish between North American and European bison.

The following names have been used so frequently in literature that they have been given special treatment.

*Bison "europaeus"* von Meyer, 1832


**DISCUSSION**

**TAXONOMIC CLASSIFICATION: Bison (Bison) bonasus** (Linnaeus, 1758).

The name "*europaeus*" is nearly as widely used for the living European bison as the name *bonasus* by which it should be known. Von Meyer was evidently the first writer to use the name, rather than Owen, who is generally credited with its origin. No attempt has been made to list all the synonymous usages of the name "*europaeus*" in literature. The adjectival usage of "European bison" has no doubt led to the development of the name "*europaeus*" as "American bison" led to the use of *B. "americanus."

*Bison bonasus* "caucasia" Grevé, 1906


*Bison causicasus* HILZHEIMER, 1909, Jahresh.


**Discussion**

**Taxonomic Classification:** *Bison (Bison) bonasus* (Linnaeus, 1758).

Translation of Grevé's paper indicates that he considered the Caucasian wisent, or *B. (Bison) bonasus*, a geographic race. The article gives useful historical data concerning the extermination and distribution of the race, but no physical characters. In 1909, Hilzheimer raised Grevé's unestablished geographic race to full specific rank, and figured a skull (No. 5737) from the Caucasus. He attributed differences of individual age and variability to specific distinctness. In November, 1935, Gromova pointed out that there apparently existed no basis in fact for the recognition of this form as a subspecies. From all figures and measurements observed, Gromova's opinion that the species or race "caucasicus" does not differ from the living European *Bison bonasus* seems correct.

2. *Bison (Bison) occidentalis primitivus* (Hilzheimer, 1909)

1. References for the holotype:


*Bison occidentalis*, HAY, 1913, Proc. U. S. Natl. Mus., vol. 46 (1914), p. 177. (Hay's statement "The curvature and direction of the horn-cores suggest strongly some specimens of *B. occidentalis*, and it seems possible that *B. primitivus* represents a specimen of the latter with unusually long horns.")

*Bison occidentalis primitivus* (Hilzheimer), Hilzheimer, 1918, Arch. Naturgesch., vol. 84, div. A, no. 6, p. 60.

Horizon and Locality: The lower Tunguska near Kisensk, on the Lena River, Siberia; collected in 1906 by Pfizenmayer. No geologic data given.

Holotype: Posterior portion of a cranium with complete horn-cores, in Stuttgart Natural History collections. No number given.

Illustrations: See Hilzheimer, 1909; also this paper, figure 5C, C'.

Measurements: Table 23, after Hilzheimer.

**Subspecific Characters**

*(Based on a Male Cranium)*

Horn-cores extend from the skull in a moderate posterior direction, are subcircular in basal cross section, not strongly depressed proximally before swinging upward on the distal half; distal tips are posteriorly twisted and moderately slender without a pronounced superior longitudinal groove. Cranium tends to be flat or slightly arched; orbits are tubular and forwardly directed.

Cores tend to be a little longer than in observed examples of North American *B. (Bison) occidentalis* and somewhat smaller, more curved and posteriorly twisted than in the Alaskan *B. (Bison) preeocidentalis*.

**Discussion**

**Tentative Taxonomic Classification:**

*Bison (Bison) occidentalis primitivus* (Hilzheimer, 1909).

Hilzheimer was probably correct in later recognizing his species as a race of *B. (Bison) occidentalis*. All the characters observed in the figured specimen are in agreement with the numerous examples observed in this study.

The specimen was found in Siberia and, since geologic data are lacking, may represent either a geographic or geologic race, but suggests the former. Continued recognition of *primitivus* as a race is advisable, since it is intermediate in size between *occidentalis* and *preeocidentalis*. For comparison within this report, a figure and measurements after Hilzheimer, 1909, have been included.

The name *B. "sibericus,"* as used by Hilzheimer, 1909, in his table of measurements, apparently indicated a valid species, although no mention of the name "sibericus" is to be found in the body of the text. Fortunately, Hilzheimer published a second work on bison in 1910, and in his footnote (loc. cit., p. 145), clarifies the status of *B. "sibericus"* by stating that he first intended to call the skull from Siberia that he figured and described in his text as *B. primitivus* by the specific name of "sibericus." This was inadvertently placed
in the measurement table. Therefore, the name "sibericus" is a synonym of *primitivus*.

**F. BISON (PRIMITIVE, UNNAMED SUBGENUS)**

**ASIATIC AND SIWALIK BISON**

The described *Bison* species from the general regions of China, Mongolia, and the Siwaliks, while distinctly *Bison*, are among the earliest forms and suggest a relationship to the genus *Leptobos*. Many of the intervening stages of *Bison* development are lacking in specimens from these regions for the geologically later species of *Bison* (?middle to late Pleistocene) are well advanced in horn-core and cranial enlargement.

The known material indicates the existence of not more than two subgenera from these regions. Expanded collections and research will no doubt bring to light additional species which may be allocated to the known subgenera. The earliest, and as yet unnamed, subgenus includes the primitive species *B. sivalensis* and *B. palaeosinensis*. The geologically later material is included in the new subgenus *Parabison*.

1. *Bison* (Subgenus?) *sivalensis* Lydekker, ex Falconer MS, 1878

References for the holotype:


### TABLE 21

**Measurements** of *Primitve Asiatic and Siwalik Bison*

(Measurements in millimeters, figure 1C for key; indices in per cent, page 142.)

<table>
<thead>
<tr>
<th>Key No.</th>
<th><em>Bison</em> (Subgenus?) <em>sivalensis</em></th>
<th><em>Bison</em> (Subgenus?) <em>palaeosinensis</em></th>
<th><em>Bison</em> (Subgenus?) <em>palaeosinensis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(Holotype) Female?</td>
<td>(Lectotype) Male</td>
<td>(Paratype) Female?</td>
</tr>
<tr>
<td>1</td>
<td>Spread of horn-cores, tip to tip</td>
<td>—</td>
<td>(536)</td>
</tr>
<tr>
<td>2</td>
<td>Greatest spread of horn-cores on outside curve</td>
<td>—</td>
<td>(693)</td>
</tr>
<tr>
<td>3</td>
<td>Horn-core length on upper curve, tip to burr</td>
<td>—</td>
<td>300</td>
</tr>
<tr>
<td>4</td>
<td>Length of horn-core on lower curve, tip to burr</td>
<td>—</td>
<td>(420)</td>
</tr>
<tr>
<td>5</td>
<td>Length, tip of horn-core to upper base at burr</td>
<td>—</td>
<td>200</td>
</tr>
<tr>
<td>12</td>
<td>Transverse diameter of horn-core</td>
<td>86</td>
<td>(80)</td>
</tr>
<tr>
<td>6</td>
<td>Vertical diameter of horn-core</td>
<td>66</td>
<td>(76)</td>
</tr>
<tr>
<td>7</td>
<td>Circumference of horn-core at base</td>
<td>254</td>
<td>(245)</td>
</tr>
<tr>
<td>14</td>
<td>Width of cranium between horn-cores and orbits</td>
<td>221</td>
<td>234</td>
</tr>
<tr>
<td>15</td>
<td>Greatest postorbital width</td>
<td>(242)</td>
<td>—</td>
</tr>
<tr>
<td>16</td>
<td>Anterior orbital width, at notch</td>
<td>(195)</td>
<td>—</td>
</tr>
<tr>
<td>17</td>
<td>Width of skull at masseteric processes at M¹</td>
<td>(141)</td>
<td>—</td>
</tr>
<tr>
<td>8</td>
<td>Greatest width at auditory openings</td>
<td>(194)</td>
<td>230</td>
</tr>
<tr>
<td>9</td>
<td>Width of condyles</td>
<td>99</td>
<td>102</td>
</tr>
<tr>
<td>O-N</td>
<td>Length, occipital crest to naso-frontal suture</td>
<td>(169)</td>
<td>(175)</td>
</tr>
<tr>
<td>10</td>
<td>Occipital crest to upper border of foramen magnum</td>
<td>(86)</td>
<td>91</td>
</tr>
<tr>
<td>11</td>
<td>Occipital crest to lower border of foramen magnum</td>
<td>122</td>
<td>131</td>
</tr>
</tbody>
</table>

* Index of horn-core curvature
* Index of horn-core compression
* Index of horn-core proportion
* Index of horn-core length

---

* Measurements in original description used where possible; our estimated measurements from type figures in parentheses.

Horizon and Locality: Near Pinjor, exact level unknown, probably belongs to the Pinjor stage of the Upper Siwaliks, data from Pilgrim, 1939.

Holotype: Of Lydekker, partial mature skull with orbits and occipital region; proximal one-half to one-third of right horn-core; lacking left horn-core, M1–M2 (worn). The holotype of Falconer, according to Pilgrim, 1939, “only known by a few indistinct sketches and some measurements. Its present whereabouts is unknown . . . in the collections of the Geological Survey of India in Calcutta (registered number B. 239).”

Illustrations: See Lydekker; also this paper, figure 2C, C'.

Measurements: Table 21, after Lydekker.

Specific Characters
(Based on ?Female Skull)

Small skull with horn-cores rising high on the frontals in a rather strong posterior direction and somewhat doroventrally flattened at the base; total length and curvature unknown; anterior facial region seems to be quite narrow in proportion to cranial width; occipital region tends to be narrow and high; orbits are forwardly directed and not strongly tubular.

Discussion

Tentative Taxonomic Classification: Bison (Subgenus?) sivalensis Lydekker ex Falconer MS, 1878.

This little-known form has many primitive characters, suggesting an ancestral Bison, and may prove to be of value in demonstrating the structural changes which took place in later Pleistocene Bison and in connecting the entire life history of Bison with some earlier bovid that cannot be called true Bison.

The Lydekker figure of the holotype of Bison sivalensis is lacking in many details, and only generalized characters can be determined. It appears that the holotype may be a female. If this is the case, more material belonging to this primitive race may be represented by Bison palaeosinensis Chardin and Piveteau, 1930 (this paper, fig. 2B, paratype). It does not seem advisable to synonymize palaeosinensis with sivalensis until there are more data. The figures given by Chardin and Piveteau indicate both male and female crania in their syntypic series. One of these specimens (?female) is similar to the holotype of sivalensis. If this later proves to be the case, it will be necessary to consider palaeosinensis a synonym of sivalensis (Article 27 c). Because of insufficient comparative data, a subgeneric classification for this primitive Bison is not suggested, but some such recognition may be necessary when more evidence accumulates.

2. Bison (Subgenus?) palaeosinensis
Chardin and Piveteau, 1930


Horizon and Locality: About 150 kilometers west of Peking, China, in the valley of the Sangkan-ho River. Late Pliocene, Nihowan formation.

Lectotype: Cranium with partial horns in the paleontological collections of the Muséum National d’Histoire Naturelle. Here selected from the syntypic series the male cranium and partial horn-cores, figured by Chardin and Piveteau, 1930, on plate 15, figures 1 and 1a, as typical of this species.

Illustrations: See Chardin and Piveteau, 1930; also this paper, figure 2A, A'.

Measurements: Table 21, after Chardin and Piveteau.

Specific Characters
(As Here Used, Based on Male Skull of Syntypic Series)

A small species of primitive bison with relatively large parietaIs and temporal fossae extending high up along the lateral sides of the cranium and separating the occiput more than in the later forms of bison; the occipital region is not so strongly developed and the core bases next to the skull are more strongly developed and relatively longer than in later bison; the horn-cores are posteriorly extended and moderately depressed on the proximal one-third of their length before curving
sharply upward with moderately recurved tips which appear to have a posterior twist; condition of orbits unknown, but frontals appear to be flat and not highly arched and expanded as in later bison.

Female characters (as observed in the figure of the paratype, Chardin and Piveteau, 1930, pl. 15, fig. 12, cranium B): cores directed in a strongly posterior direction, rising relatively high over frontals but untwisted; female strongly resembles holotype of B. sivalensis. (Compare outline sketches in this paper, fig. 2B and 2C'.)

Characters seen in the ramus of the syntypic series (Chardin and Piveteau, 1930, pl. 15, fig. 3) show that the angle between the horizontal and vertical portions of the ramus are more acute, the symphysis is shorter (indicating a shorter face), and the posterior angle of the horizontal ramus is larger and more posteriorly extended. The illustrations of referred dentitions (Chardin and Piveteau, 1930, pl. 16) indicate relatively small superior and simplified inferior premolars and an overall smallness of the teeth, as compared to the later bison forms. The molars still possess the internal enamel fold between the anterior and posterior lobes, a character used extensively in age classification.

**DISCUSSION**

**TENTATIVE TAXONOMIC CLASSIFICATION:**

*Bison* (Subgenus ?) palaeosinensis Chardin and Piveteau, 1930.

As suggested in the discussion of *B. sivalensis* (p. 218) it is entirely possible that *B. palaeosinensis* is a synonym, but it does not seem advisable definitely to synonymize this species until more evidence has accumulated. The syntypic series of Chardin and Piveteau contains both a male and female cranium, presumably of the same species. The female strongly resembles the holotype of *B. sivalensis*. In the outline sketches (fig. 2) the specimens are all in the same one-tenth scale, thus clearly demonstrating a great similarity of size which must eventually be taken into account.

Since Chardin and Piveteau studied a syntypic series of three skulls and designated no holotype it seems necessary to select one of these three specimens as a representative of *B. palaeosinensis*. The specimens were un-numbered in the original report, but the cranium considered to be that of a male (Chardin and Piveteau, 1930, pl. 15, figs. 1, 1a) in the collections of the Muséum National d'Histoire Naturelle is here called the lectotype. It is expedient to designate specimens with which each specific name can be associated in order to avoid confusion of usage as has been the case with *B. priscus*.

**G. BISON (PARABISON),**

**NEW SUBGENUS**

**SUBGENOTYPE:** Bison exiguus Matsumoto, 1915 (1927).

**SUBGENERIC CHARACTERS**

**(BASED ON MALE SKULLS)**

Cores moderately large to small in size, never so large as in Gigantobison; extend from the skull in a moderate to strongly posterior direction, never at right angles to the longitudinal axis of skull as in Simobison; cores may or may not be proximally depressed before swinging up on the tips with only a slight suggestion of, but as a rule with no, posterior twist, differing from the typical subgenus Bison in this respect; cores are heavy and robust with a tendency towards blunt tips that tend to be sharply curved upward although one subspecies has gently curved horns; cores tend to be round to semicircular in cross section and not dorsoventrally flattened as in Platycerobison; cranium moderately flat and varies from broad to rather narrow.

**DISCUSSION**

The members of this subgenus are confined to the Old World and so far have not been encountered in the North American bison fauna.

This group of bison species apparently has many close relationships to Superbison, Simobison, and the typical subgenus Bison, yet when any one of the species assigned to the new subgenus Parabison is examined closely some important physical character is found that will not permit placing that species in any of the related subgenera.

Specific members of this subgenus are widespread in Eurasia and may be easily confused with members of the subgenus Simo-

1 From the Greek meaning "near, relationship to."
### TABLE 22

Measurements* of Types of (Male) B. (Parabison) exiguis and B. ?(Parabison) schoetensacki

(Measurements in millimeters, figure 1C for key; indices in per cent, page 142.)

<table>
<thead>
<tr>
<th>Key No.</th>
<th>Bison (Parabison) exiguis</th>
<th>Bison ?(Parabison) schoetensacki</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Exiguis Paratype</td>
<td>Curricornis Holotype</td>
</tr>
<tr>
<td>1</td>
<td>Spread of horn-cores, tip to tip</td>
<td>700</td>
</tr>
<tr>
<td>2</td>
<td>Greatest spread of cores on outside curve</td>
<td>—</td>
</tr>
<tr>
<td>3</td>
<td>Core length on upper curve, tip to buurr</td>
<td>320</td>
</tr>
<tr>
<td>4</td>
<td>Length of core on lower curve, tip to buurr</td>
<td>370</td>
</tr>
<tr>
<td>5</td>
<td>Length tip of core to upper base at buurr</td>
<td>275</td>
</tr>
<tr>
<td>12</td>
<td>Transverse diameter of horn-core</td>
<td>95</td>
</tr>
<tr>
<td>6</td>
<td>Vertical diameter of horn-core</td>
<td>95</td>
</tr>
<tr>
<td>7</td>
<td>Circumference of core at base</td>
<td>300</td>
</tr>
<tr>
<td>13</td>
<td>Width between bases of cores</td>
<td>—</td>
</tr>
<tr>
<td>14</td>
<td>Width of cranium between horn-cores and orbits</td>
<td>266</td>
</tr>
<tr>
<td>15</td>
<td>Greatest postorbital width</td>
<td>—</td>
</tr>
<tr>
<td>16</td>
<td>Anterior orbital width, at notch</td>
<td>—</td>
</tr>
<tr>
<td>8</td>
<td>Greatest width at auditory openings</td>
<td>—</td>
</tr>
<tr>
<td>9</td>
<td>Width of condyles</td>
<td>—</td>
</tr>
<tr>
<td>O-N</td>
<td>Length, occipital crest to nasal-frontal suture</td>
<td>—</td>
</tr>
<tr>
<td>10</td>
<td>Occipital crest to upper border of foramen magnum</td>
<td>—</td>
</tr>
<tr>
<td>11</td>
<td>Occipital crest to lower border of foramen magnum</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Index of horn-core curvature</td>
<td>135</td>
</tr>
<tr>
<td></td>
<td>Index of horn-core compression</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>Index of horn-core proportion</td>
<td>107</td>
</tr>
<tr>
<td></td>
<td>Index of horn-core length</td>
<td>120</td>
</tr>
</tbody>
</table>

* Measurements in original description used where possible; our estimated measurements from type figures in parentheses.

bison which also existed there. One Asiatic species and two subspecies are recognized in this subgenus that may well represent widely varying segments of one population, as in the case of Bison (Superbison) crassicornis from Alaska.

Matsumoto believed that species of the typical subgenus Bison (Bison) were present in China and Mongolia. The specimens so far figured are so distinctly different from those of North America that they have been included in the new subgenus B. (Parabison) rather than in B. (Bison). The present concept of the Bison distribution, on the basis of published figures, will not allow the placing of Matsumoto's subspecies B. "occidentalis" curvicornis in the same subgeneric group with the true occidentalis. The subspecies curvicornis has two characters in common with B. exiguis, also from Asia: the posteriorly directed and untwisted horn-cores. This group of Asiatic species may have been derived from the same parent stock as the North American species of B. (Bison), but it differed in some modes of development. It is possible to recognize and describe these differences which seem
applicable to several forms that may be considered specifically different. The recognition of Parabison, new subgenus, as here defined, will aid in understanding the ramifications of the worldwide relationships within the genus Bison and should be useful to the concept of distribution both geographically and in time.

The subgenotypic species is considered to be B. (Parabison) exiguus. It is not certain that the specimens on which this species was founded still exist, but excellent figures have been published. The concept and conclusions concerning Parabison were derived from these figures and from one example of this subgenus which is in the American Museum of Natural History collections, No. 17733. The specimen was obtained, according to Matthew (1921, p. 602), "from the older Pleistocene gravels of Great Barrington, near Cambridge [Eng] ..." In size, the specimen nearly duplicates the holotype of B. (Parabison) exiguus curvicornis from Mongolia, to which it is referred.

In the European area, Parabison has been tentatively considered to be represented by Bison ?(Parabison) schoetensacki.

1. Bison (Parabison) exiguus exiguus (Matsumoto, 1915)

1. References for the holotype:
   (The holotype is a right ramus; the first figured paratype is a partial cranium with a right horn-core.)

   Bison, n. sp., Koken, 1885, Palaeont. Abhandl., vol. 3, p. 65 (93), text fig. 2, pl. 2 (7), figs. 18, 19.
   Bison exiguus MATSUMOTO, 1915, Sci. Rept. Tohoku Imp. Univ., Sendai, ser. 2 (Geol.), vol. 3, no. 1, p. 32, pl. 12, fig. 10, pl. 13, figs. 7, 8 (non 4–6) [type ramus figured]; 1927, Sci. Rept. Tohoku Imp. Univ., Sendai, ser. 2 (Geol.), vol. 10, no. 3, pp. 51–52, pl. 25, figs. 1, 2 (this is the paratype, the first figured specimen from which the specific characters may be demonstrated).

   Horizon and Locality: (Holotype), Honan, northern China, post-Pleistocene; (paratype), border of eastern Mongolia, post-Pleistocene.


   Paratype: Partial cranium with left horn-core in Geological Institute, Tokyo. No number given, but on the illustration of the speci-

   men (Matsumoto, 1927, pl. 25, fig. 1) number 75 [or 3] 90 can be detected.

   Illustrations: Holotype, see Matsumoto, 1915; paratype, see Matsumoto, 1927, also this paper, figure 2D, D'.

   Measurements: For the paratype, table 22, after Matsumoto.

   Specific Characters
   (Based on a Specifically Indeterminate Ramus)

   Holotype: A small species of Bison. The tooth wear is S-1. P3–M2 equals 150 mm. Dental series of this size have been observed in the Alaskan collection, but only as rare examples.

   Specific Characters
   (Based on a Referred Male Cranium)

   Paratype: This specimen could be called a neotype, but since the holotype is not known to be lost, paratype seems the better usage. The referred cranium has the only characters that are specifically diagnostic.

   "Distinctly smaller than the former two [in this case referring to B. occidentalis and B. "occidentalis" curvicornis]. Horn-cores small in comparison to the size of the cranium; markedly flared backwards; not at all dipped downwards; strongly curved, so that their tips are directed upwards; circular in cross section, even the upper side being uniformly rounded; not at all flattened at the base" (after Matsumoto, 1927, loc. cit.). To these characters from the well-figured paratype may be added: the frontals appear to be rather flat and not highly arched; the cores have no posterior twist; the tips lack a pronounced superior longitudinal groove; the cores are heavily proportioned and robust. Contrary to Matsumoto, the cores seem slightly depressed on the proximal one-third of their length.

   Discussion

   The holotype of this species is a right ramus specifically beyond identification. A Bison ramus does not possess enough diagnostic characters to separate it from any of several other Bison species. Fortunately, Matsumoto later referred a partial skull to his species, thus giving it a set of usable charac-
ters. The referred cranium gives this species its diagnostic characters, although it can never be more than a referred specimen or, perhaps, a paratype.

The referred specimen indicates that *Bison (Parabison) exiguis exiguis* may be intermediate in size between the North American B. (Bison) *occidentalis* and B. (Bison) *bison athabascae*, differing subgenerically in that the horn-cores are not posteriorly twisted, though they are posteriorly directed. For the present, it seems best to place this species in the new subgenus *Parabison*.

1A. *Bison (Parabison) exiguis curvicornis*
(Matsumoto, 1927)

Reference for holotype:


**LOCALITY:** Eastern Mongolia and Siberia, Upper Pleistocene; collected by Saito Gratitude Foundation.

**HOLOTYPE:** Partial cranium with horn-cores, in the Institute of Geology and Paleontology, Tohoku Imperial University. No number given in description. We observed on plate 26, figure 1, the superior view of the holotype, the number 7589 (Matsumoto, 1927).

**ILLUSTRATIONS:** See Matsumoto, 1927; also this paper, figure 2E, E'.

**MEASUREMENTS:** Table 22, after Matsumoto.

**SPECIFIC CHARACTERS**
*(BASED ON A MALE CRANIUM)*

"... Horn-cores slightly flared backwards; markedly dipped downwards; strongly curved, so that their tips are directed upwards; roundedly triangular or oval in cross section; distinctly flattened at the base" (after Matsumoto, 1927, p. 55).

Observations of the type figure show that the cranium appears to be that of a male, and the tips of the cores are moderately blunt and robust with no indication of a posterior twist, also a pronounced superior longitudinal groove is lacking on the tips; occipital region is broad and well developed; frontals appear to be flat, and the cranium seems to be relatively narrow.

**DISCUSSION**

**TENTATIVE TAXONOMIC CLASSIFICATION:**
*Bison (Parabison) exiguis curvicornis* (Matsumoto, 1927)

On comparing the paratype of *Bison exiguis* and the holotype of *Bison "occidentalis" curvicornis* it appears that *curvicornis* is more closely related to *exiguis* than true *B. (Bison) occidentalis* of North America, for there is no indication of posterior twist in the horn-cores, so pronounced in *occidentalis*. This tendency for the cores to be posteriorly twisted is an important phyletic character in itself, one which is not strongly expressed in any subgeneric group of species except in the typical subgenus *B. (Bison)*. Strongly depressed horn-cores are not observed in true *occidentalis*, whereas *curvicornis* has strongly depressed horn-cores that curve sharply upward on the tips. Although *curvicornis* is larger in size than *exiguis*, it has more basic characters in common with it than with any North American *Bison* species.

Although the holotype of *curvicornis* comes from Mongolia, a referred specimen has been found in England and is in the collection of the American Museum of Natural History (see p. 223).

1B. *Bison (Parabison) exiguis ?harbinensis*,
new subspecies

1. References for the holotype:
*Bison species a*, Tokunaga and Naora, 1934, Report of the First Scientific Expedition to Manchoukuo, sect. 2, pt. 1, Waseda University, Tokyo, p. 83, pl. 25, fig. 1, 1a. (Also *Bison species b*, Tokunaga and Naora, 1934, *op. cit.*, pp. 85, 86, pl. 26, fig. 1, 1a, are referred to this new subspecies.)

**HORIZON AND LOCALITY:** Ho-chia-kou, 5 kilometers southwest of Harbin, Manchoukuo; reported as Middle Pleistocene. Collected by S. Tokunaga and party, 1934.

**HOLOTYPE:** Cranium with complete right and nearly complete left horn-cores, in collections of Waseda University, Tokyo. No number given (see Tokunaga and Naora); *Bison sp. a*, page 83, plate 25, figure 1, 1a.

**ILLUSTRATIONS:** See Tokunaga and Naora; also this paper, figure 2F, F'.
Measurements: This paper, table 22, after Tokunaga and Naora.

Specific Characters
(Based on a Male Cranium)

Horn-cores moderate in size and directed from the skull in a rather strongly posterior direction at an angle of approximately 64 degrees to the longitudinal axis of the skull; cores are proximally depressed 30 degrees below the plane of the frontals for about one-fourth their superior length before swinging gently upward, barely rising above the plane of the frontals; tips are heavy and robust and not posteriorly twisted; the cores are somewhat dorsoventrally flattened and more posteriorly directed and less curved than in either B. (Parabison) exigus exigus or B. (Parabison) exigus curvicornis; frontals tend to be flat and moderately broad; occipital region is well developed and broad.

Discussion

It seems best to consider this specimen provisionally as representative of a new sub-specific of Parabison.

This probable race is named after the geographic locality near which it was found, apparently in association with the works of ancient man. A set of outline figures (fig. 2F, F') of the holotype of B. (Parabison) exigus harbinensis are included for comparison with those of B. (P.) exigus exigus and B. (P.) exigus curvicornis which are likewise found in this general region. As more data accumulate these three races may prove to be distinct species or they may represent widely differing segments of one specific population.

2. Bison ?(Parabison) schoetensacki schoetensacki (Freudenberg, 1910)

References for the holotype:
Bison sp. nov. indt., SCHOTENSACK, 1908, Der Unterkiefer des Homo Heidelbergen, Leipzig, p. 14, table, p. 15.
Bison schoetensacki FREUDENBERG, 1910, Neues Jarhb. Min. Geol. Palaeont, vol. 2, p. 133 (specific name applied to Schoetensack material but no holotype designated); 1914, Geol. Palaeont. Abhandl., new ser., vol. 12, nos. 4/5, p. 82, pl. 4, fig. 6 (holotype designated on caption of pl. 4, fig. 6, as "Bison schoetensacki ... ". Typus der neuen Art, bzw. Unterart von Bison europaeus."

Note: Spelling of specific name changed in later work from schoetensacki to schoetensacki). SCHERTZ, 1936, Senckenbergiana, vol. 18, pp. 57-62.

Locality: The sands of Mauer, in the district of Heidelberg, Germany.

Holotype: Posterior cranial portion with both horn-cores, in Darmstadt Geologische Landesanstalt. No number given.

Illustrations: See Freudenberg, 1914; also this paper, figure 3C.

Measurements: Table 22, after Freudenberg.

Specific Characters
(Based on a Male Cranium)

Cores moderate to small, extending from the skull in a posterior direction with heavy, blunt tips that are curved sharply upward with little or no posterior twist. Cranium tends to be rather broad with forwardly directed orbits.

Discussion

Tentative Taxonomic Classification:
Bison ?(Parabison) schoetensacki schoetensacki (Freudenberg, 1910).

The subgeneric allocation of this species to Parabison is questionable because details of the physical characters in the holotype are shown only from a superior view. The details seem to be distinctive enough, however, to recognize schoetensacki as a full species. Some of the referred material may belong to other specific groups.

The species schoetensacki has previously been considered ancestral to the living B. (Bison) bonasus. This relationship is questionable, since all figured specimens of schoetensacki seem to lack the pronounced posterior twist of the horn-cores that is observed in figured skulls of bonasus. It seems that the progenitor of bonasus must also have a posterior twist to the cores. Such a specimen is known from Siberia, B. (Bison) occidentalis primitivus (Hilzheimer, 1909).

Table 22 and the holotypes shown in figure 3 demonstrate the pronounced similarity in horn-core size and shape between
schoetensacki, mediator, and maior. Considering the different angles from which these holotypic figures were originally photographed, the variations are hardly great enough to be of specific value, and since schoetensacki is apparently the first-named species of this particular horn-core type, mediator and maior have been tentatively associated with it.

2A. Bison ?(Parabison) schoetensacki mediator (Hilzheimer, 1918)

References for the holotype:

Horizon and Locality: Phoeben, Germany, 1874, in the clay pit of A. Schnetter, owner of a brick kiln; last interglacial period of Europe (Dietrich, 1932).

Holotype: Complete left horn-core and partial frontal bone to the median suture; catalogue 8, No. 235, in the Mark Museum Collection, Berlin.

Illustrations: See Hilzheimer, 1918; also this paper, figure 3D, D'.
Measurements: Table 22, after Hilzheimer.

Subspecific Characters
(Based on Male Horn-Core)

Cores extend from the skull in a moderate posterior direction, are subcircular in cross section and proximally depressed; core tips are heavy and blunt and curve sharply upward without a posterior twist as in B. (Parabison), but not in B. (Bison); frontals appear flat and moderately broad.

Discussion
Tentative Taxonomic Classification:
Bison ?(Parabison) schoetensacki mediator Hilzheimer, 1918).

Very little is known concerning this subspecies except the characters of the holotype. Although evidence suggests that this race lived until nearly Recent times, the horn-core characters indicate that it was not ancestral to the living bison of the Old World. Physical characters shown in the figured holotype of mediator differ from the figured remains of B. (Bison) bonasus in that the horn-cores lack the pronounced posterior twist present in the slightly smaller bonasus.

2B. Bison ?(Parabison) schoetensacki maior (Hilzheimer, 1918)

References for the holotype:
Bison bonasus maior HILZHEIMER, 1918, Arch. Naturgesch., vol. 84, div. A, no. 6, pp. 73–75, text figs. 22, 23.

Horizon and Locality: Hermsdorfer Fliess, Mark Brandenburg District, Germany. Alluvial or sub-Recent in age.


Illustrations: See Hilzheimer, 1918; also this paper, figure 3E, E'.
Measurements: Table 22, after Hilzheimer.

Subspecific Characters
(Based on a Male Cranium)

Horn-cores small but heavy and robust with blunt tips, extending from the skull in a moderate posterior direction, are proximally depressed and swing sharply up on the tips without a pronounced posterior twist to the cores; frontals broad and moderately arched with well-developed occipital region; orbits tubular and forwardly directed.

Discussion
Tentative Taxonomic Classification:
Bison? (Parabison)? schoetensacki maior (Hilzheimer, 1918).

There is some possibility (owing to the
angle from which the holotype was photographed) that this subspecies has more affinities to the living European bison, *bonasus*, than is apparent from the holotypic figure. A second specimen referred to this species by Hilzheimer in 1927 (loc. cit.) may be considered either a paratype or another subspecies as indicated in the taxonomy. It is well figured and indicates horn-core relationship to *B. (Parabison)* and not *B. (Bison)*.

From the information it seems that *maior* represents the small members of the specific population of *schoetensacki*. It may be more useful, however, to continue the recognition of *maior* as a subspecies until better population samples are known.

**B. Bison (Simobison) (Hay and Cook, 1930)**

The specific members of *B. (Simobison)* are well represented in both North America and Europe. Although no examples of this subgenus have been observed in Asiatic faunal literature, the possibility of *B. (Simobison)* existing in that region may not be precluded.

Two species of this subgenus are recognized in Europe, *B. (Simobison) cesaris* and *B. (Simobison) priscus*. Numerous figured examples of specimens referable to this subgenus are found in European literature. If they were segregated from specimens referable to *B. (Parabison)* and *B. (Platycerobison)*, it is possible that at least one or two other specific variations of *B. (Simobison)* might be recognized. As the subgeneric divisions of the genus *Bison* are now defined there is no reason to confuse *B. (Simobison)* with the other subgenera, i.e., *B. (Bison)*, *B. (Superbison)*, or *B. (Gigantobison)*.

1. *Bison* (Simobison) *cesaris* (Schlotheim, 1820)

1. References for the holotype:
1823, Ossements fossiles, ed. 2. vol. 4; 1825, op. cit., ed. 3, pp. 141, 142, pl. 12, figs. 1, 11.

*Bos cesaris* SCHLOTHEIM, 1820, Die Petrefacten-kunde, Gotha, p. 10 [cites Faujas, Essai de géologie, pl. 17, no. 1. This is seven years prior to Bojanus below]. HILZHEIMER, 1918, Arch. Naturgesch., vol. 84, div. A, no. 6, p. 60.


**LOCALITY:** The banks of the Rhine near Bonn in western Germany.

**HOLOTYPE:** Cranium with partial horn-cores, lacking the extreme tips, in the Paris Museum. No number given.

**ILLUSTRATIONS:** See Faujas and Cuvier; also this paper figure 3B, B'.

**MEASUREMENTS:** Table 23, after Faujas and Cuvier.

**SPECIFIC CHARACTERS**

**(BASED ON A MALE CRANIUM)**

Horn-cores of moderate size, extending at nearly right angles to the longitudinal axis of the skull; subcircular in cross section and proximally depressed before swinging slightly upward on the tips, which do not rise high above the frontals or have a posterior twist.

This species approximates the size of North American *B. (Simobison) antiquus* and would be separated from it with difficulty. The geographic separation seems to be the only basis for specific difference. (See table 23 for measurements.)

This specimen and the specific population which it represents may be easily assigned to the subspecies *Simobison*, for it has all of the subgeneric characters which are recognized in the North American members. Apparently the frontals of *Bison cesaris* are wider and much heavier than in the lectotype of *Bison priscus* Bojanus, as designated by Hilzheimer (1918, loc. cit.).

**DISCUSSION**

Schlotheim's species *cesaris*, the first fossil *Bison* to receive a valid scientific name, remained in the obscurity of the loosely defined term and definition of Bojanus' specific name *priscus* for nearly 90 years, when Hay's work on *Bison* prompted Hilzheimer (1918, loc. cit.) to examine the literature, revise and select a lectotype for *Bison priscus* from the listed specimens of Bojanus, and bring out the fact that *Bison cesaris* was a valid species. The first figure and measurements of the holotype were given by Faujas-St.-Fond in his "Essai de géologie" (loc. cit.); later the place of origin for the holotype was given by him (1803, vol. 2, pp. 190, 191).

Faujas simply referred both his *Bison* and *Bos* material to the general term of fossil ox. It remained for Schlotheim, 1820, to be the first writer to give the Faujas figures valid scientific names. He called the *Bison, Bos cesaris* (Faujas, loc. cit., pl. 17, fig. 1), and the true *Bos or ox, Bos urus priscus* (Faujas, loc. cit., pl. 17, fig. 2).

Evidently Schlotheim chose his name *Bos cesaris* from the title of Faujas'* plate, for it read "Corones d'Aurochs Urus de Jules César." It is fitting but coincidental that the first specific name ever applied to fossil *Bison* was *cesaris*, since it was the leader of the named host of bison species to follow in the next 125 years. Schlotheim chose a natural subspecific name, *Bos urus priscus*, for the fossil ox, since *priscus* means "of or belonging to former times." This use of the name, in 1820, for a fossil ox in the genus *Bos* (International Rules of Zoological Nomenclature, Article 35), would clearly make a homonym of Bojanus' use of the name *priscus* (1827) when he applied it to fossil *Bison, also called *Bos* at that time. Fortunately, *Bison* has now been generically separated from *Bos* and Bojanus' name need not be rejected as a homonym (p. 232). The fact still remains that the Faujas specimen named by Schlotheim is still a holotype for a subspecies of *Bos* that must be reckoned with in any extensive revision of the fossil oxen of Europe.

The first fossil bison skull figured in literature, it seems, is referable to this species, but references to it under other names have appeared in the literature.

*Boves "uri fossil" BAER, 1823*


DISCUSSION

The figures and measurements suggest that this specimen is synonymous with *Bison* (*Simobison*) *cesaris* and not *priscus*. The specimen is of historical interest but has no outstanding differences from the holotype of *cesaris*.

2. *Bison* (*Simobison*) *priscus* (Bojanus, 1827)

**Selection of Lectotype by Elimination:** In order to clarify the taxonomic treatment of Bojanus' syntypic series of five specimens, they are listed in the same order used by Bojanus in 1827. For reasons indicated below, four of the five specimens are unavailable for consideration as lectotypes, leaving only one of the five examples available to represent Bojanus' species *Bison* *priscus*. Example No. 1: Previously named and therefore unavailable. See taxonomy of *B. (Platybo-*

**Lectotype:** Lombardy, Italy, valley of the Po River.

**Lectotype:** Nearly complete skull in the University of Pavia collection. (See Cuvier, 1825, Ossems fossils, ed. 3, vol. 4, p. 142.)

**Illustrations:** Cuvier, 1823 (Ossems fossils, ed. 2, pl. 11, fig. 5); also this paper, figure 3A.

**Measurements:** Table 23, after Cuvier, 1823.

**Specific Characters**

**(Based on a Male Skull)**

The horn-cores extend from skull at nearly right angles, are proximally depressed, and appear to be semicircular in cross section; tips curve upward with no posterior twist and may or may not rise high above the frontal plane, depending on the core length; frontals are moderately flat; orbits are tubular and forwardly directed; cranium appears somewhat narrower than in *B. (Simobison)* *cesaris*; anterior face relatively long and narrow; occipital region well developed.

The figures indicate a close relationship between *B. priscus* and *B. cesaris*. Apparently, *priscus* has longer-proportioned horns and narrower forehead than *cesaris*. This may not be of specific value. If this proves to be the case, *priscus* automatically becomes a synonym of *cesaris*, for no other examples of Bojanus' syntypic series can be used to establish the specific characters.

**Discussion**

**Taxonomic Classification:** *Bison* (*Simobison*) *priscus* (Bojanus, 1827).

As indicated above, the specific name of *priscus* was proposed by Bojanus in 1827 when he listed five fossil bison crania known to him and referred them to *Urus priscus*, using the name *priscus* to separate the fossil remains from those of living bison. Although Bojanus cited figures in other works, he gave...
Fig. 5. A, A'. Holotype of Bison "europaeus lenensis." B, B'. Holotype of B. "uriformis," synonyms of B. (Superbison) crassicornis. C, C'. Holotype of B. (Bison) occidentalis primitivus. See respective discussions for source of sketches. Approximately ×1/10.
neither figures nor descriptions for his specimens. A careful consideration of these specimens demonstrates that they belong to widely divergent forms of *Bison*. European and Asiatic writers use the name *B. priscus* almost universally for any fossilized bison skull, since the name implies “of or belonging to other times.”

We are not the first to be confronted with the problem of establishing a definite type or set of physical characters for this species. Hay, in 1913, pointed out the need for a re-vision of the fossil bison of Europe and indicated a laxity in the use of the name *priscus*. As a result, Hilzheimer (1918, *loc. cit.*) revised the syntopic series of Bojanus and selected Example No. 3 as standing for the type of *priscus*. As first reviser, this was Hilzheimer’s right and, according to the accepted practice, his selection became inviolable, and Bojanus’ Example No. 3, as of 1918, acquired the equivalent status of a holotype.

In 1932, Gromova (*loc. cit.*) in violation of this selection, set up as type of *priscus* Bojanus’ Example No. 1, which she excellently figured and extensively measured for the first time. Unfortunately, this specimen could never stand for the type of *priscus*, for it was clearly and definitely named *Boves pallasii* by Baer in 1823, and was not even available for Bojanus in his consideration of *priscus* (see this paper, p. 237).

We are in agreement with Hilzheimer’s selection of the lectotype, although our reasons for the recognition of Example No. 3 may differ from his. These reasons are based upon the fact that three of the five Bojanus examples were previously named and one was specifically indeterminate.

As Hilzheimer (1918, *ibid.*, vol. 84, p. 58) pointed out, Bojanus’ name *priscus* is in reality a homonym, for Schlotheim in 1820 applied the name *Bos urus priscus* to a subspecies of fossil oxen known throughout Europe as *Bos primigenius* Bojanus, 1827. Since this obvious error was not corrected for nearly a hundred years, Hilzheimer felt it best to retain the name *priscus* for the bison and *primigenius* for the oxen. This was a wise selection for no end of confusion would have resulted in discarding the Bojanus name and recognizing the Schlotheim name. It is no longer necessary to consider Bojanus’ *priscus* a homonym of Schlotheim’s *priscus*. Both were originally in the genus *Bos* but are now generically separated, Schlotheim’s name remaining in *Bos* and Bojanus’ name in *Bison*.

The specific distinctness of *priscus* still remains to be permanently established. It has been determined which specimen must be considered to demonstrate the physical characters of *priscus*. A complete set of measurements and figures is still lacking. It is not known to the present writers if this specimen still exists, but if it does, adequate descriptions for a universal understanding should be made available. Only by this means will the utter confusion in the usage of the name *priscus* be avoided.

The known and prominent features of both *B. priscus* and *B. cesaris* clearly demonstrate that a group of bison having physical characters we have attributed to the subgenus *Simobison* exists in both Europe and North America and possibly in Asia, although Asiatic occurrences are not well established.

C. BISON (SUPERBISON) FRICK, 1937

1. *Bison* (Superbison) *crassicornis* (Richardson, 1854)

In North America many examples of *B. (Superbison) crassicornis* were referred to other species, but no synonymous species have been described. In Eurasia this species has never been recognized, although nearly every size segment of the *crassicornis* population has been given specific identity. In consideration of the extensive Alaskan population sample, many of these Eurasian names appear to be based on synonymous examples of *crassicornis*.

The measurements of only the holotypes or lectotypes of the apparent synonyms are presented in table 24 for comparison with the range of size in the *crassicornis* specimens in table 16. Outline sketches (rescaled to the standardized one-tenth) have been reproduced from figures given by the original authors. These figures have been necessarily reproduced from their original viewpoints which do not always coincide with the standard viewpoints followed in this paper.

In Eurasia, *crassicornis* apparently ranged over most of northern Russia, Siberia, and down into Europe. In North America this
TABLE 24

Measurements* of "Holotypes" and "Lectotypes" of Eurasian Bison
Tentatively Referred to B. (Superbison) crassicornis
(Measurements in millimeters, figure 1C for key; indices in per cent, page 142.)

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Spread of horn-cores, tip to tip</td>
<td>1106</td>
<td>1165</td>
<td>1107 (1026)</td>
<td>--</td>
<td>710</td>
</tr>
<tr>
<td>2</td>
<td>Spread of horns with sheaths, tip to tip</td>
<td>1005</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>3</td>
<td>Greatest spread of cores on outside curve</td>
<td>(1164)</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>975</td>
</tr>
<tr>
<td>4</td>
<td>Greatest spread of cores with sheaths</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>975</td>
</tr>
<tr>
<td>5</td>
<td>Core length on upper curve, tip to burr</td>
<td>(500)</td>
<td>(476)</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>6</td>
<td>Length of core on lower curve, tip to burr</td>
<td>575</td>
<td>590</td>
<td>439</td>
<td>456</td>
<td>--</td>
</tr>
<tr>
<td>7</td>
<td>Length, tip of core to upper base at burr</td>
<td>414</td>
<td>440</td>
<td>387</td>
<td>347</td>
<td>--</td>
</tr>
<tr>
<td>12</td>
<td>Transverse diameter of core</td>
<td>121 (132)</td>
<td>106</td>
<td>120 (97)</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>13</td>
<td>Vertical diameter of core</td>
<td>108</td>
<td>--</td>
<td>97</td>
<td>110</td>
<td>--</td>
</tr>
<tr>
<td>14</td>
<td>Circumference of core at base</td>
<td>362</td>
<td>364</td>
<td>321</td>
<td>355</td>
<td>340</td>
</tr>
<tr>
<td>15</td>
<td>Width between bases of cores</td>
<td>388</td>
<td>--</td>
<td>340</td>
<td>365</td>
<td>--</td>
</tr>
<tr>
<td>16</td>
<td>Width of cranium between cores and orbits</td>
<td>313</td>
<td>305</td>
<td>292</td>
<td>313</td>
<td>317</td>
</tr>
<tr>
<td>17</td>
<td>Greatest postorbital width</td>
<td>(365)</td>
<td>340</td>
<td>--</td>
<td>384</td>
<td>360</td>
</tr>
<tr>
<td>18</td>
<td>Anterior orbital width, at notch</td>
<td>295</td>
<td>282</td>
<td>--</td>
<td>--</td>
<td>275</td>
</tr>
<tr>
<td>19</td>
<td>Width of skull at masseteric processes at M</td>
<td>(185)</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>(183)</td>
</tr>
<tr>
<td>20</td>
<td>Greatest width at auditory openings</td>
<td>297</td>
<td>290</td>
<td>284</td>
<td>--</td>
<td>294</td>
</tr>
<tr>
<td>21</td>
<td>Width of condyles</td>
<td>143</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>O-N</td>
<td>Length, occipital crest to nasal-frontal su-</td>
<td>289</td>
<td>--</td>
<td>--</td>
<td>(289)</td>
<td>(239)</td>
</tr>
<tr>
<td>22</td>
<td>Occipital crest to upper border of foramen magnum</td>
<td>(122)</td>
<td>99</td>
<td>107</td>
<td>--</td>
<td>97</td>
</tr>
<tr>
<td>23</td>
<td>Occipital crest to lower border of foramen magnum</td>
<td>(151)</td>
<td>--</td>
<td>147</td>
<td>--</td>
<td>141</td>
</tr>
<tr>
<td>F-P</td>
<td>Basilar length of skull</td>
<td>574</td>
<td>590</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>O-P</td>
<td>Over-all length of skull</td>
<td>648</td>
<td>655</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
</tbody>
</table>

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* Measurements in original description used where possible; our estimated measurements from type figures in parentheses.

species apparently did not move farther south than the headwaters of the Yukon before a climatic change or a return of adverse conditions halted its North American expansion. By the time favorable conditions again returned to the northern circumpolar region, *crassicornis* had evidently become extinct. No evidence is known which indicates that *cras-

HOLOTYPE: Partial skull with horn-sheaths lacking teeth, premaxillae, and nasals. No number given. In the Berlin palaeontological collections.

ILLUSTRATIONS: See Hilzheimer, 1910; also this paper, figure 5A, A'.

MEASUREMENTS: Table 24, after Hilzheimer.

SUBSPECIFIC CHARACTERS
(According to Hilzheimer, 1910)

A large subspecies of Bison europaeus. [B. "europaeus" is a synonym of Bison bonasus.] The horns are elevated above the frontal plane and posteriorly extended behind the occiput with the sheath tips curved inward. The sheath color is different from that of B. europaeus. [This would be the result of fossilization.] The occipital region is high as in B. europaeus forming a small saddle between the horns; frontals are slightly arched, more than in B. europaeus; the lacrimal bones are shaped as in B. europaeus and not as in B. priscus.

DISCUSSION

TENTATIVE TAXONOMIC CLASSIFICATION:
Bison (Superbison) crassicornis (Richardson, 1854) or possibly B. (Bison) occidentalis primitius (Hilzheimer, 1909).

This holotype is figured with horn-sheaths that disguise the diagnostic characters of the horn-cores. It is therefore inadvisable to place this specimen in exact synonymy with either crassicornis or primitius. It seems quite certain, however, that this specimen is not subspecific to the living B. (Bison) bonasus of Europe to which Hilzheimer assigned it by using the synonymous specific name of "europaeus."

The figures of the holotype show an apparent male skull. The horns extend from the skull in a moderate posterior direction, are proximally depressed, and appear to rise rather high above the frontals; the tips are posteriorly directed with a suggestion of a posterior twist. The cranial and facial characters are in no way diagnostic. The specimen could be related either to crassicornis or primitius, but since the cores are proximally depressed it appears that this tends to re-move the holotype from relationship with primitius and suggests crassicornis instead. A population sample centering around this holotype would certainly be conspecific with either crassicornis or occidentalis, depending on a more detailed examination.

If this specimen had not already been synonymous with one of the above species it would also have priority of name over like specimens which Gromova in 1935 classified under the name of B. "priscus deminutus."

Bison "uriformis" Hilzheimer, 1910

Reference for the holotype:
Bison uriformis HILZHEIMER, 1910, Sitzber. Gesellsch. Naturf. Fr., Berlin, no. 4, pp. 138, 139, text figs. 3, 4; 1918, Arch. Naturgesch., vol. 84, div. A, no. 6, pp. 84, 86, tables 1, 2.

HORIZON AND LOCALITY: Klinge near Kottbus in Brandenburg, a province of Prussia, on the Spree, about 70 miles southeast of Berlin. Found in an interglacial peat deposit.


ILLUSTRATIONS: See Hilzheimer, 1910; also this paper, figure 5B, B'.

MEASUREMENTS: Table 24, after Hilzheimer, 1910 and 1918.

SPECIFIC CHARACTERS
(According to Hilzheimer, 1910)

Frontals flat, almost slightly concave, the horn bases lying a bit higher than the central line. The horns point upwards right from the start with a slight twist around their own axis. Cores rise high over the frontal plane and are strongly curved with recurved tips. The strong curvature of the horns suggests the horn form of the aurochs, thus the specific name uriformis.

DISCUSSION

TENTATIVE TAXONOMIC CLASSIFICATION:
Bison (Superbison) crassicornis (Richardson, 1854).

Although the type figures of this species are not from a standard view, it seems that B. "uriformis" Hilzheimer could readily be placed in that segment of the Alaskan crassicornis population having strongly curved horn-cores which rise high above the frontals and are directed from the skull in a moderate,
posterior direction, but without a posterior twist to the core tips. The size of the horn-cores and the dimensions of the skull fit into the range of size in the Alaskan series.

The specimen cannot be referred to either Bison priscus Bojanus, fide Hilzheimer, 1918, or to Bison cesaris Schlotheim, 1820, for the cores of these two species are directed at right angles to the longitudinal axis of the skull without being strongly curved or highly elevated.

Bison “priscus fraasi” Hilzheimer, 1918

References for the holotype:


LOCALITY: The diluvial sands of Steinheim, on the Murr River, Württemberg, Germany; collected in 1908, no original geologic data given.

HOLOTYPE: Complete skull with horn-cores, P²–M¹ alv., M²–M³, No. 12043 in the Stuttgart Natural History collections.

ILLUSTRATIONS: See Hilzheimer, 1909; also this paper, figure 4A, A'.

MEASUREMENTS: Table 24, after Hilzheimer.

Subspecific Characters
(After Hilzheimer)

Frontals flat, not rising above the horn bases; horn curvature about like a half moon; horns extend proximally from the skull in a horizontal direction, then rise upward and are somewhat posteriorly twisted; tops of cores flattened; occipital region relatively broad; nasals narrow.

DISCUSSION

Tentative Taxonomic Classification:
Bison (Superbison) crassicornis (Richardson, 1854).

The type figure indicates another Eurasian example of the species crassicornis. There is no reason for considering it other than a synonym. The skull of the holotype is large and the horns extend in a moderate posterior direction with high-rising, posteriorly directed tips.

If the figures of a typical crassicornis specimen, U.A.—F.A.M. No. 46926 (which resembles the holotype of “fraasi”), are examined it is evident that “fraasi” is a member of the crassicornis population, bearing in mind, of course, that the above crassicornis specimen is only one of a race whose members vary in all degrees of shapes and sizes around it. The views of this Alaskan specimen are to be found on the following plates: lateral view, plate 22, figure 3; superior, plate 18, figure 7; and posterior, plate 19, figure 7.

Hilzheimer’s lateral and superior views of the holotype of “fraasi” were not taken from exactly the same angle as here used. For comparison, Hilzheimer’s figures have been reproduced in outline and rescaled to one-tenth (fig. 4A, A').

Bison “priscus longicornis” Gromova, 1935

References for syntypic series and lectotype:

LOCALITY: Siberia and Russia. Syntypic series from the lower Wolga near the village of Lutshka, not far from the city of Sarepta.

LECTOTYPE: Complete skull, at least one sheath, lacking nasals, P²–P³ alv., P⁴–M³. I.P.A.S. No. 2368.

ILLUSTRATIONS: See Gromova, 1935b, plate 7, figures 1, 2, 3; also this paper, figure 4B, B'.

MEASUREMENTS: Table 24, after Gromova.

Subspecific Characters
(After Gromova)

Large, long, and relatively slender horn-cores; skull large but relatively narrow.

DISCUSSION

Tentative Taxonomic Classification:
Bison (Superbison) crassicornis (Richardson, 1854).

The specimens Gromova assigned to the subspecies B. “priscus longicornis” appear
to represent a segment of the B. (Superbison) crassicornis population. In the Alaskan collection this segment has the long, posteriorly directed horn-cores that rise high above the frontal plane with a high index of horn-core curvature. As suggested on page 189, had these specimens been found separately, there would have been a tendency to recognize them as independent subspecies. Evidence does not permit this, for specimens having horn-core patterns that represent Gromova’s B. “priscus tscherskii” and B. “priscus diminutus” are also present in the crassicornis population sample and are completely intergrading in shape and size. It does not appear that B. “priscus longicornis” represents a distinct subspecies.

Hilzheimer in 1918 selected the lectotype for B. priscus from the Bojanus syntypic series (this paper, p. 232). As first reviser, Hilzheimer selected a specimen that belongs in the subgenus Simobison, therefore removing for all time the possibility of assigning crassicornis-like specimens of the subgenus Superbison to the loosely defined priscus. Gromova evidently ignored Hilzheimer’s revision and did not recognize his lectotype.

It is to be noted that Gromova’s bibliography does not mention the works of Richardson, Lucas, Hay, or Gilmore, all of whom figured crassicornis examples. It must therefore be assumed that Gromova did not compare the Russian collections with previously named and figured examples of crassicornis with which they seem synonymous.

Bison “priscus tscherskii” Gromova, 1935


Locality: The lower course of the Jana River in northeastern Siberia. Geologic data unknown.

Lectotype: Complete cranium with horn-cores and partial orbits from Gromova’s syntypic series of eight partial skulls. See Gromova, 1935b, plate 8, figure 1; I.P.A.S. No. 4861.

Illustrations: See Gromova, 1935b, plate 8, figure 1; also this paper, figure 4C.

Measurements: Table 24, after Gromova.

Subspecific Characters
(After Gromova, in German Summary)

Skull small, horn-cores of medium size and slender, slightly curved upward; skull a little broader than the two last-named subspecies [subspecies refer to B. “priscus fraasi” and B. “priscus longicornis”]. The systematic independence of the subspecies is doubtful; in the future, it might be combined with other medium horned subspecies.

Discussion

Tentative Taxonomic Classification:
Bison (Superbison) crassicornis (Richardson, 1854).

The specimens Gromova assigned to the subspecies B. “priscus tscherskii,” appear to represent only a segment of the B. (Superbison) crassicornis population. In the Alaskan collection, this segment has the widespread depressed horn-cores that do not rise high above the frontals, and cores of this pattern range from small to large. When the “tscherskii” segment is separated from the rest of the series, a variety is suggested (p. 189), but with the evidence at hand of completely intergrading examples of horn-core patterns that make up the entire crassicornis population, the “tscherskii” pattern represents only one segment.

Gromova used a syntypic series of eight partial skulls to establish what was believed to represent a subspecies of Bison priscus. As indicated above, one of these skulls was selected as a lectotype. Its outline sketch is reproduced (fig. 4C) for comparison within this report.

For the same reason discussed in the close of the discussion of B. “priscus longicornis” (p. 236), it does not seem “tscherskii” can be considered a subspecies of priscus, but it is completely synonymous with the previously named crassicornis. The first spelling of the name “tscherskii” is used rather than “tscherskii” as later given by Gromova.
Bison "priscus deminutus" Gromova, 1935


Lectotype: Partial male cranium with horn-cores and orbits from Gromova's syntypic series. See Gromova, 1935b, plate 9, figure 1; I.P.A.S. No. 15020.

Illustrations: See Gromova, 1935b, plate 9, figure 1; also this paper, figure 4D.

Measurements: Table 24, after Gromova.

Subspecific Characters (After Gromova, in German Summary)

Medium-sized skull; horn-cores likewise medium sized but massive; cranial width similar to that in the variation tscherskii.

Discussion

Tentative Taxonomic Classification: Bison (Superbison) crassicornis (Richardson, 1854).

Gromova is not definite concerning the diagnostic characters of this subspecies of bison and its geographic occurrence. Therefore, the first figured specimen has been selected as the lectotype.

Presumably, Gromova intended this example to be representative of the subspecies "deminutus." It suggests, however, a segment of the Eurasian crassicornis population, the small-sized individuals which are completely intergrading with the larger members of the same population. An examination of the figure of the only specimen that is representative of the species priscus excludes the possibility of considering "deminutus" as subspecific to priscus since the lectotype of priscus belongs in the subspecies Simobison and not Superbison.

The first spelling of "deminutus" (Gromova, 1935a, p. 141) is used rather than "deminutulus," later used in the same work.

D. Bison (Platycerobison), New Subgenus

Examples of B. (Platycerobison) are the rarest of the later, more advanced Bison species. One species, B. (Platycerobison) pallasii, is known from Eurasia, the holotype of which was found in Siberia. It is possible that specimens referable to this subgenus may also be found in Asia. One example is also known from England but is referred to B. "priscus" at present. The measurements of a cast of this specimen are in table 17 and show that it nearly duplicates measurements of the holotype of B. (Platycerobison) chaneyi from Texas.

Other examples of this flat-horned subgenus are figured but unmeasured in European literature. It would be unwise, however, to enumerate them with only the figures as evidence. A careful reexamination of European specimens in the light of the present classifications will, no doubt, demonstrate the existence of other B. (Platycerobison) specimens which have been referred to the loosely defined B. "priscus."

Bison (Platycerobison) pallasii (Baer, 1823)

References for the holotype: "Gmelin, J., Reise Durch Siberian, Th. 3, 1752, 8" [after Gromova, 1935b].


Bones pallasii BAER, 1823, De fossilibus mammalium relickquis in Prussia, Regiomenti, Typis Hartungianis, pp. 27, 28. (First application of a scientific name to Bojanus' example No. 1 of his syntypic series standing for B. priscus.)


Bos (Bison) priscus VON MEYER, 1832, Palaeologica, p. 96.


Locality: The Ilga River, a tributary on the headwaters of the Lena River, near the city of Vercholsk in central Siberia; collected by J. Gmelin between 1730-1740. Geologic data unknown.

Holotype: Partial skull with horn-cores and sheaths, lacks palate and premaxillae; Pallas, 1768, figured the specimen with nasal bones, now missing. I.P.A.S. No. 11161.

Illustrations: See Gromova, V., 1932; also this paper, plate 25, figures 3, 3A, 3B.

Measurements: Table 17, after Gromova.

Subspecific Characters
(As Used by Gromova, in German Summary)

Skull medium sized, horn-cores small and massive, strongly compressed, receding far behind the frontal plane, strongly turned upwards.

Specific Characters
(Based on a Male Skull)

Gromova's excellent figures and extensive measurements of the holotype of this species aid greatly in its diagnosis and can be carried further.

Horn-cores among the smallest of known Platycerobison, proportionally approaching Bison, length on upper curve equal to or slightly exceeding basal circumference and cranial width, strongly depressed about one-third to one-half their dorsal length before swinging abruptly upward; directed in a rather strong posterior direction extending posterior to the occipital plane.

As compared to the closely related North American species B. (P.) geisti, the cores of B. (Platyobison) pallasii are more posteriorly directed, strongly depressed, and do not rise so high above the plane of the frontals (pl. 25). The cores are placed well back on the frontals which are broadly expanded and highly arched as opposed to the flat or moderately arched and expanded cranium of geisti. Occipital region is broad and flat as compared to the narrower, higher occipital region of geisti. The cores are strongly compressed dorsoventrally as in all Platycerobison and do not appear to be posteriorly twisted as in the subgenus Bison. The orbits are tubular and forwardly directed; the nasals (after Pallas, 1768) are moderately slender.

The size of the horn-cores removes this species from consideration within the subgenus Gigantobison; the core compression and, secondarily, core size distinguish it from the subgenera Bison, Superbison, Simobison, and Parabison which have subcircular horn-cores. The skull and horn-cores are smaller than in the North American Platycerobison species chaneyi and alaskensis.

Discussion

Taxonomic Classification: Bison (Platycerobison) pallasii (Baer, 1823).

The famous specimen that is considered the holotype of B. (Platycerobison) pallasii (Baer, 1823), was the second fossil bison skull to receive a properly applied scientific name. It was discovered in Siberia by Gmelin between 1730 and 1740, described and figured but not properly named by Pallas in 1768, and received its proper scientific name by Baer in 1823. This specimen has been figured after Pallas by numerous authors.

In 1932, Gromova presented the first set of photographic reproductions and an extensive series of measurements when the specimen was treated as the “type” of the sympatric series of B. priscus Bojanus, 1827. This specimen was Bojanus’ first listed example in the sympatric series that he considered Bos priscus. Bojanus did not recognize the priority of the name pallasii, which has remained in obscurity for 129 years.

Gromova (1935, loc. cit.) again used this specimen for the “type” of B. priscus. The priority of Baer’s name pallasii excluded the specimen from consideration by Gromova; moreover, Hilzheimer, 1918 (as first reviser of priscus, this paper, p. 229), had previously selected as lectotype the only available specimen of unnamed Bison in Bojanus’ list of the priscus examples. It is entirely possible that Baer’s paper was not available to Bojanus or Gromova.
Baer wrote as follows: "... Restat quartus Boum fossilium, quem Pallasium ad crania ex Sibiria translatam descripsit. Hujus speciei nostrum esse credimus, quia eundem animadvertimus. . . . .

"Caret haec species, e terrarum fundamento reviviscens, nomine proprio Divini Pallasii nominem immortale proponimus." We translate from the Latin as follows:
The fourth awaits [a name (Baer here is referring to the fourth specimen in his discussion)] fossil bovid, which description Pallas gave to the crania brought back from Siberia. [See footnote from Baer, below.] We believe ours to be of this species because we perceive on observation.... This species has been without a proper name ever since its restoration from the earth. We propose the immortal name of the admirable Pallas. (End of translation.)

From Baer only one intent can be interpreted. He clearly and definitely applied the name Boves pallasi to the specimen figured

"Novi comment. Acad. Petrop. T. XIII. p. 460. cum icono, quae denuo expressa exstat in Cuvieri opere de ossib. fossil."—with a figure which is again clearly shown in Cuvier's work on fossil bones. [Cuvier figures only one of the two specimens figured by Pallas and this is the holotype of pallasi.]

by Pallas and simply referred his own specimen (the fourth) to the species he was naming. It has later been proved that Baer's fourth specimen was a muskox-like horn, but since he only referred it to the Bison species he called pallasi, it has no bearing on the validity of the name when applied to Bison.

E. BISON (GIGANTOBISON), NEW SUBGENUS

No definite evidence of specimens belonging to the subgenus Gigantobison was found in the European literature. There is, however, a possibility that one or two specimens may be referred to Gigantobison, pending more information. Certain specimens (e.g., Hilsheimer, 1918, figs. 24, 25, and Owen, 1846, fig. 205) suggest that this subgenus existed in Europe during the Pleistocene. These specimens have been referred either to the genus Bison or classified in the loosely defined species priscus.

Geologic evidence in North America indicates that B. (G.) latifrons was one of the first arrivals from Asia during the latter part of the early or middle Pleistocene. Although no specimens are definitely known from Asia, future collections may produce remains referable to this subgenus.
INDETERMINATE AND INVALID BISON NAMES

SPECIFICALLY INDETERMINATE EUROPEAN SPECIES

Because of the physical nature of the types, three specific names of *Bos* or *Bison* in European literature may only be placed in an indeterminate category.

*Bos velanus* Robert, 1829


The name *Bos velanus* is based on a syntypic series of three specifically indeterminate specimens. Plate 4 in the 1829 report figures the distal end of a metapodial, a second phalanx, and an ungual phalanx. This species can only be considered indeterminate, for the specimens figured could belong to any of several fossil *Bison* or *Bos* species.

*Bos intermedius* de Serres, 1838


The name *Bos intermedius* when first used in 1838 was not associated with either a description or material. In 1839, however, definite examples and descriptions were designated. Unfortunately, the examples are so fragmentary that no specific allocation to the genera *Bos* or *Bison* is possible. For convenience the specimens cited in the rare 1839 publication are mentioned:

Plate 12, figure 8, a fragment of a bovid maxilla with P4–M2. Plate 13, figure 13, partial scapula; figure 14, humerus and radius; figure 15, metacarpal; figure 16, calcaneum and astragalus; figure 17, metatarsal. Plate 19, figure 12, second and third phalanges; figure 13, second and first phalanges.

*Bison minor* Owen, 1846


The specific name *minor* is based on a female ?*Bison* metacarpal which might be synonymous with any of several extinct *Bison* and should be considered specifically indeterminate, although the name must be retained (International Rules of Zoological Nomenclature, Article 27, part a).

ANIMAL REMAINS DESCRIBED AS BISON BELONGING TO OTHER FAMILIES OR GENERA

“*Bison* alticornis” Marsh, 1887


“*Bos* scaphoceras” Cope, 1894


Dr. F. A. Lucas (1899a, p. 756) discussed this type and concluded that it was more than likely the horn-core of a member of the genus *Ovis* rather than *Bison*.

“*Bison* appalachicorius” Rhoads, 1895


*Lepidosteus* bison, Leidy, 1860


Leidy was discussing a gar fish at this place and had no intention of originating a *Bison* name, as some literary references indicate.

**Nomina Nuda in North American Literature**

“*Bison laticornis*,” Leidy, McConnell, 1901, Summary Rept. Geol. Surv. Canada for 1900, p. 185 A.
McConnell’s use of the name “laticornis” is clearly a misstatement. He said, “Portion of a skull of extinct bison possibly B. laticornis, Leidy found in a layer of ‘muck.’” We are unable to locate such a name in Leidy’s works.


This is an obvious typographical error, in place of which Rhoads meant Bison latifrons.

? Nomina Nuda in Eurasian Literature


According to Göppert and von Meyer, these two species were described by Croizet and Jobert in their “Recherches sur les ossemens fossiles du department du Puy-de-Dôme, pet. in folio, tome I., avec 35 plll., Paris 1828.” Three copies of this book were examined and no references to, or descriptions of, elatus or giganteus were observed. Croizet and Jobert mentioned two “boeufs” in the faunal lists, but gave no name or description.

Nomina Nuda in Eurasian Literature


Both of these names are listed in the above “Nomenclator” without descriptions or author citations. No works antedating this citation could be located which used these names specifically.


It is evident that Hilzheimer confused his name B. “europaeus lenensis” and used B. “europaeus sibericus” since he gave no description of “sibericus.”


The name “Bison suessenbornensis” was mentioned by Freudenberg in discussing a bison collection that Wilhelm Staudinger studied in 1906 and was said to have called “Bison suessenbornensis” in an oral discussion. We were unable to find any written notice on the material by Staudinger who apparently did not formally name his bison material as Freudenberg suggests, for Freudenberg’s reference to the name is the only one we were able to find.


As the name is used here, it is either a misstatement or a synonym for the living European bison. Brentana (1929, pp. 91–117) supposedly used this name, but we were unable to locate a single reference to the nomen nudum “Bison primigenus” in Brentana’s work. No doubt this name has been confused with Bos primigenus, for no reference to a specimen belonging to the genus Bison and specifically described as primigenus was found.

European Homonym


This specific name must be considered a homonym for the specimen figured is not referable to B. (Gigantobison) latifrons (Harlan, 1825), and two Bison species cannot have the same specific name. Harlan used the name Bos latifrons in 1825 for the scientific name of the giant bison of North America. The actual types could in no way be considered synonyms.
The genus *Bison* constitutes a closely related group, the members of which differ principally in their horn-core growth. Differentiation based on dentition has proved to be unworkable; size and body proportions are not well enough known to be applied to overall specific diagnosis with any degree of assurance, since completely articulated skeletons are unknown for the majority of species.

The division of the genus *Bison* into six named subgenera and one primitive, tentatively unnamed subgenus, is based primarily on characters observed in skulls and identifiable patterns of horn-core growth. These subgenera should not be generically separated from *Bison*. The concept of each species has been founded, for the most part, on a population basis that may be continental in distribution but is still anchored to the "type" example.

The earliest geological examples of *Bison* appear in the late Pliocene of China. A bovid that may eventually prove to be the ancestor of this genus is yet to be demonstrated, but *Leptobos* appears to have some of the required characters. Too few characters are known concerning the primitive segment of the genus *Bison* to diagnose accurately subgeneric characters, and the early Pleistocene records are too inconclusive to bridge the gap between the primitive forms and the later Pleistocene ramifications of the genus.

By the close of early Pleistocene several species of *Bison* had reached the regions of Europe and Siberia, some of which crossed over into North America for the first time, under presumably favorable climatic conditions. Recurrent glaciation isolated and forced these first migrators southward to the plains of North America where they spread out and developed free of Eurasian influence. The descendants of this migration are now extinct. The living North American bison are the descendants of a later second migratory invasion from Siberia.

From Pliocene times up to and during the close of the early Pleistocene, *Bison* species appear to have been undergoing a process of progressive horn-core enlargement. It appears that with the possible exception of *B. (Giantobison) latifrons*, the geologically later *Bison* species began a process of retrogressive horn-core growth during middle Pleistocene times that apparently culminated in the extinction of the large-horned forms, and by Recent times, *B. (Bison) bonasus* was the sole survivor in Europe, and only the plains and woodland races of *B. (Bison) bison* remained in North America.

Before the subgeneric relationships of *Bison* may be clearly understood it is necessary to establish and evaluate the significance of patterns and modes of growth in skulls and more particularly the horn-cores. This has been one of the primary objects of the present work. Accurate geological evidence has been lacking in many cases but, where possible, the particular phase of the Pleistocene in which each species lived has been indicated.

When more extensive and concise geological information is available in conjunction with good population samples of the *B. (Bison)* species of North America, the demonstrated tendency for progressive average change in horn-core size will be most useful in estimating the time element. This will be particularly true in relationship to early man.

The conclusions concerning Eurasian bison are drawn from literature, but an attempt has been made to establish a type for each Eurasian name. Much remains to be done by students with access to actual Eurasian bison material.

Detailed conclusions concerning each recognized form may be found in the discussions or summaries of characters.

**SYNOPSIS**

Die Verfasser haben alle spezifischen Namen sowohl des nordamerikanischen als des eurasischen *Bison* in dieser Arbeit niedergelegt. Der erste nachlängliche Name jeder identifizierbaren spezifischen Form ist angekündigt. Es ist eine Standardmethode für die Behandlung des Themas versucht und illustriert worden. So sind zum Beispiel alle in den Tabellen benützten Schädelmasse in Abbildung 1C dargestellt, die somit als Schlüssel dient.

Obwohl die Gattung *Bison* auf Grund von
Schädelund Hornzapfenmerkmalen in sechs Untergattungen eingeteilt worden ist, bleiben diese nach wie nach wie vor Bison und sollten gattungsmässig nicht losgetrennt werden.

Vor allem muss eine genauere Anwendung des Namens Bison priscus geübt werden, damit ein Verständnis aller fossilen eurasischen Bison erzielt werden kann. Die syn-
typische Reihe von Bison priscus (Bojanus, 1827) wurde gründlich geprüft. Die Literatur über jedes Exemplar von Bojanus ist in dieser Schrift enthalten. Das Exemplar, welches für die Festlegung der spezifischen Merkmale benützt werden sollte, ist in Übereinstim-
mung mit der gebräuchlichen Auslegung der internationalen Regeln der zoologischen No-
menklatur identifiziert worden.

RÉSUMÉ

Les auteurs ont réuni en un seul rapport toutes les dénominations spécifiques du Bison
américain et eurasiatique. Le premier nom post-linnéen applicable à chaque forme
spécifique identifiable a été reconnu. Un essai d'établir une méthode de travail stand-
ardisée est présenté avec des explications. Ainsi, toutes les mensurations crâniennes
utilisées dans les tableaux sont expliquées sur la figure 1C, qui sert de clé.

Quoique le genre Bison ait été divisé en six sous-genres, déterminés par des caractères
particuliers du crâne et des cornillons, ces sous-genres continuent néanmoins d'être
dans les limites du genre Bison et ne doivent pas en être séparé génériquement.

Il est nécessaire tout d'abord de réduire l'usage du nom Bison priscus, pour éclaircir
la question du Bison en Eurasie. La série
syntypique du Bison priscus (Bojanus, 1827) a cet effet, a été revisée minutieusement.
L'histoire littéraire de chacun des spécimens de Bojanus est inclue dans ce mémoire. Le
spécimen qui doit être employé pour établir les caractéristiques du Bison priscus a été
identifié selon les conventions établis par les Règles Internationales de Nomenclature
Zoologique.
**TABLE 25**

**Résumé of Horn-Core Indices**
(Data taken from tables 10–22; indices in per cent, page 142.)

<table>
<thead>
<tr>
<th>Name</th>
<th>Horn-core Index of</th>
<th>Curvature</th>
<th>Compression</th>
<th>Proportion</th>
<th>Length</th>
</tr>
</thead>
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<tr>
<td>A. Bison (Bison)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>a B. (B.) bison bison</td>
<td></td>
<td>120</td>
<td>139</td>
<td>182</td>
<td>85</td>
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<tr>
<td>a B. (B.) bison athabascae</td>
<td></td>
<td>126</td>
<td>135</td>
<td>149</td>
<td>84</td>
</tr>
<tr>
<td>e B. (B.) bonasus</td>
<td></td>
<td>123</td>
<td>143</td>
<td>180</td>
<td>79</td>
</tr>
<tr>
<td>a B. (B.) occidentalis</td>
<td></td>
<td>121</td>
<td>140</td>
<td>169</td>
<td>86</td>
</tr>
<tr>
<td>a B. (B.) prooccidentalis</td>
<td></td>
<td>112</td>
<td>126</td>
<td>134</td>
<td>83</td>
</tr>
<tr>
<td>B. Bison (Simobison)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<td>a B. (S.) antiquus antiquus</td>
<td></td>
<td>128</td>
<td>138</td>
<td>147</td>
<td>83</td>
</tr>
<tr>
<td>a B. (S.) alleni</td>
<td></td>
<td>121</td>
<td>135</td>
<td>155</td>
<td>72</td>
</tr>
<tr>
<td>C. Bison (Superbison)</td>
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<td></td>
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<td>a B. (S.) crassicornis</td>
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<td>107</td>
<td>125</td>
<td>153</td>
<td>81</td>
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<td>D. Bison (Platycerobison)</td>
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<td>a B. (P.) chaneyi</td>
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<td></td>
<td>78</td>
<td></td>
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<td>a B. (P.) alaskensis</td>
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<td>132</td>
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<td>74</td>
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<td>a B. (P.) geistii</td>
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<td>152</td>
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<tr>
<td>e B. (P.) pallasi</td>
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<td>134</td>
<td></td>
<td>70</td>
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<td>E. Bison (Gigantobison)</td>
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<td></td>
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<td></td>
</tr>
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<td>B. (G.) latifrons</td>
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<td>110</td>
<td>118</td>
<td>131</td>
<td>80</td>
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<td>F. Bison (subgenus?)</td>
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<td></td>
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<tr>
<td>e B. (?) palaeosinensis</td>
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<td>(210)</td>
<td></td>
<td>(95)</td>
<td></td>
</tr>
<tr>
<td>G. Bison (Parabison)</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>e B. (P.) exiguus exiguus</td>
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<td></td>
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<td>e B. (P.) exiguus curvicornis</td>
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<td></td>
<td>85</td>
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<td>e B. (P.) exiguus hortinensis</td>
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<td>(132)</td>
<td></td>
<td>92</td>
<td></td>
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<td>B. (P.) (Parabison)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>e B. (P.) schoetensacki schoetensacki</td>
<td></td>
<td>—</td>
<td></td>
<td>83</td>
<td></td>
</tr>
<tr>
<td>e B. (P.) schoetensacki medior</td>
<td></td>
<td>143</td>
<td></td>
<td>91</td>
<td></td>
</tr>
<tr>
<td>e B. (P.) schoetensacki maior</td>
<td></td>
<td>177</td>
<td></td>
<td>91</td>
<td></td>
</tr>
</tbody>
</table>

1. a, North American occurrence.
2. e, Eurasian occurrence.
3. *, extinct.
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**TSCHERSKI, J. D.**
SKINNER AND KAISEN: FOSSIL BISON


VAN DER VLERK, I. M.

WAGNER, JOHANN ANDREAS

YOUNG, CHUNG-CHIEN
EXPLANATION OF PLATES

All views of skulls and horn-cores are at an approximate scale of one-tenth, lateral views of rami at one-fourth, and occlusal views of denticitions at one-half.

PLATE 8
Superior, posterior, lateral, and dental views of immature male B. (B.) bison bison (Linnaeus, 1758), showing age development of skulls and examples of tooth wear in youth.
1, 1A, 1B, 1C. A.M.N.H.: M. No. 19393. Tooth wear, I-S.
4, 4A, 4B, 4C. A.M.N.H.: M. No. 130212. Tooth wear, I-S.

PLATE 9
Superior, posterior, lateral, and dental views of mature male B. (B.) b. bison, showing changes of skull during early maturity, and examples of tooth wear.
1, 1A, 1B, 1C. A.M.N.H.: M. No. 3757. Tooth wear, S-1.

PLATE 10
Superior, posterior, lateral, and dental views, showing comparison of living races of B. (Bison) in North America and Europe, mature (old age) male skulls.
1, 1A, 1B, 1C. B. (B.) b. bison; A.M.N.H.: M. No. 5477. Tooth wear, S-3.

PLATE 11
Superior, posterior, lateral, and dental views, showing development of female B. (B.) bison bison skulls from youth to old age.
1, 1A, 1B, 1C. A.M.N.H.: M. No. 130213. Tooth wear, I-S.

PLATE 12
Lateral and dental views showing tooth development in Bison rami, immature to adolescent. Sample selected from Alaskan collection.
1, 1A. U.A.-F: A.M. No. 46501. Tooth wear, I-S.
2, 2A. U.A.-F: A.M. No. 46502. Tooth wear, I-S.
4, 4A. U.A.-F: A.M. No. 46504. Tooth wear, I-S.

PLATE 13
Lateral and dental views of tooth development in Bison rami, early maturity to old age.

PLATE 14
Superior, posterior, and lateral views giving a comparison of males of B. (Bison) species with male and female B. (Simobison) antiquus on plate 15.
1, 1A. B. (Bison) bison bison ref. from Montana; A.M.N.H.: M. No. 16318.
2, 2A. B. (Bison) occidentalis Lucas, from Alaska; U.S.N.M.: V.P. No. 4157.
3, 3A, 3B, 3C. Holotype of B. (Bison) preocci-
dentalis, new species, from Alaska; U.A.-F: A.M. No. 46885.

PLATE 15
Superior, posterior, and lateral views of examples of male and female B. (Simobison) an-
tiquus compared with males of B. (Bison) species on plate 14.
1, 1A. Holotype of B. (Simobison) antiquus an-
tiquus (Leidy, 1852), from Big Bone Lick, Ken-
tucky; A.N.S.P. No. 12990.
2, 2A, 2B. Female B. (Simobison) antiquus an-
tiquus ref., from Rancho La Brea, California-
C.M. No. 10195, courtesy of Mr. J. Le Roy Kay;
3. 3A. B. (Simobison) a. antiquus, ref., male from near Clovis, New Mexico; A.N.S.P. No. 10226.
4. 4A. B. (Simobison) a. antiquus, ref., male from Philaritos Valley, California; A.N.S.P. No. 297.
5. 5A, SB (rev.). B. (Simobison) a. antiquus, ref., male from Baja, Lower California, Mexico; F: A.M. No. 42885.

PLATE 16
Superior and posterior views showing B. (Simobison) and B. (Bison).
1. 1A. Plastotype of B. (Simobison) alleni (Marsh, 1897), from Blue River, Kansas; Y.P.M. No. 911.
2. 2A. (Simobison) alleni, ref., male from near Lenora, Kansas; F.H.K.S.C. No. 40, courtesy of Mr. George F. Sternberg.
4. 4A. B. (Bison) occidentalis, ref., male from near Lawrence, Kansas; K.U.M.V.P. No. 2827, photographs by J. C. Fishel, courtesy of Dr. Claude Hibbard.

PLATE 17
Posterior views of a male population sample with horn sheaths attached, showing examples of Bison (Superbison) crassicornis, ref., from near Fairbanks, Alaska.
1. U.A.-F:A.M. No. 30631 (see pl. 18, fig. 3; pl. 19, fig. 3).
2. U.A.-F:A.M. No. 46911 (see pl. 18, fig. 5; pl. 19, fig. 5; pl. 22, fig. 2).
3. U.A.-F:A.M. No. 46903 (see pl. 20, fig. 3; pl. 21, fig. 4; pl. 22, fig. 4).
4. U.A.-F:A.M. No. 30523 (see pl. 18, fig. 4; pl. 19, fig. 4).
5. U.A.-F:A.M. No. 46914 (see pl. 18, fig. 6; pl. 19, fig. 6).
6. U.A.-F:A.M. No. 46926 (see pl. 18, fig. 7; pl. 19, fig. 7; pl. 22, fig. 3).
7. U.A.-F:A.M. No. 30601 (see pl. 20, fig. 4; pl. 21, fig. 5).
8. U.A.-F:A.M. No. 46901 (see pl. 20, fig. 5; pl. 21, fig. 6; pl. 22, fig. 5).

PLATE 18
Superior views of male examples of Bison (Superbison) crassicornis (Richardson, 1854) from Alaska. Also subgenotypic species.
1. Lectotype. B.M. No. 1A, from Eschscholtz Bay (see pl. 19, fig. 1), rescaled from Richardson's original figures.
2-7. B. (S.) crassicornis ref., from near Fairbanks, Alaska.
2. U.A.-F:A.M. No. 30618 (see pl. 19, fig. 2).
3. U.A.-F:A.M. No. 30631 (see pl. 17, fig. 1; pl. 19, fig. 3).
4. U.A.-F:A.M. No. 30523 (see pl. 17, fig. 4; pl. 19, fig. 4).
5. U.A.-F:A.M. No. 46911 (see pl. 17, fig. 2; pl. 19, fig. 5; pl. 22, fig. 2).
6. U.A.-F:A.M. No. 46914 (see pl. 17, fig. 5; pl. 19, fig. 6).
7. U.A.-F:A.M. No. 46926 (see pl. 17, fig. 6; pl. 19, fig. 7; pl. 22, fig. 3).

PLATE 19
Posterior views of male examples of Bison (Superbison) crassicornis (Richardson, 1854) from Alaska.
1. Lectotype. B.M. No. 1A, from Eschscholtz Bay (see pl. 18, fig. 1), rescaled from Richardson's original figures.
2-7. B. (S.) crassicornis ref., from near Fairbanks, Alaska.
2. U.A.-F:A.M. No. 30618 (see pl. 18, fig. 2).
3. U.A.-F:A.M. No. 30631 (see pl. 17, fig. 1; pl. 18, fig. 3).
4. U.A.-F:A.M. No. 30523 (see pl. 17, fig. 4; pl. 18, fig. 4).
5. U.A.-F:A.M. No. 46911 (see pl. 17, fig. 2; pl. 18, fig. 5; pl. 22, fig. 2).
6. U.A.-F:A.M. No. 46914 (see pl. 17, fig. 5; pl. 18, fig. 6).
7. U.A.-F:A.M. No. 46926 (see pl. 17, fig. 6; pl. 18, fig. 7; pl. 22, fig. 3).

PLATE 20
Superior views of referred male B. (Superbison) crassicornis examples from near Fairbanks, Alaska.
1. U.A.-F:A.M. No. 30653 (see pl. 21, fig. 2; pl. 22, fig. 1).
2. U.A.-F:A.M. No. 30619 (see pl. 21, fig. 3).
3. U.A.-F:A.M. No. 46903 (see pl. 17, fig. 3; pl. 21, fig. 4; pl. 22, fig. 4).
4. U.A.-F:A.M. No. 30601 (see pl. 17, fig. 7; pl. 21, fig. 5).
5. U.A.-F:A.M. No. 46901 (see pl. 17, fig. 8; pl. 21, fig. 6; pl. 22, fig. 5).

PLATE 21
Posterior views of referred male B. (Superbison) crassicornis examples from near Fairbanks, Alaska.
2. U.A.-F:A.M. No. 30653 (see pl. 20, fig. 1; pl. 22, fig. 1).
3. U.A.-F:A.M. No. 30619 (see pl. 20, fig. 2).
4. U.A.-F:A.M. No. 46903 (see pl. 17, fig. 3; pl. 20, fig. 3; pl. 22, fig. 4).
5. U.A.-F:A.M. No. 30601 (see pl. 17, fig. 7; pl. 20, fig. 4).
6. U.A.-F:A.M. No. 46901 (see pl. 17, fig. 8; pl. 20, fig. 5; pl. 22, fig. 5).
PLATE 22

Lateral views of B. (Superbison) crassicornis, referred male (1–5) and female (6–11) examples from near Fairbanks, Alaska.

1. U.A.-F:A.M. No. 30653 (see pl. 20, fig. 1; pl. 21, fig. 2).
2. U.A.-F:A.M. No. 46911 (see pl. 17, fig. 2; pl. 18, fig. 5; pl. 19, fig. 5).
3. U.A.-F:A.M. No. 46926 (see pl. 17, fig. 6; pl. 18, fig. 7; pl. 19, fig. 7).
4. U.A.-F:A.M. No. 46903 (see pl. 17, fig. 3; pl. 20, fig. 3; pl. 21, fig. 4).
5. U.A.-F:A.M. No. 46901 (see pl. 17, fig. 8; pl. 20, fig. 5; pl. 21, fig. 6).
6. U.A.-F:A.M. No. 30614 (see pl. 23, figs. 1, 1A).
7. U.A.-F:A.M. No. 30575 (see pl. 23, figs. 2, 2A).
8. U.A.-F:A.M. No. 46870 (see pl. 23, figs. 3, 3A).
9. U.A.-F:A.M. No. 30658 (see pl. 23, figs. 6, 6A).
10. U.A.-F:A.M. No. 30642 (see pl. 23, figs. 7, 7A).
11. U.A.-F:A.M. No. 46942 (see pl. 23, figs. 8, 8A).

PLATE 23

Superior and posterior views of female B. (Superbison) crassicornis, referred, from near Fairbanks, Alaska.

1. 1A. U.A.-F:A.M. No. 30614 (see pl. 22, fig. 6).
2. 2A. U.A.-F:A.M. No. 30575 (see pl. 22, fig. 7).
3. 3A. U.A.-F:A.M. No. 46870 (see pl. 22, fig. 8).
5. 5A. U.A.-F:A.M. No. 30658 (see pl. 22, fig. 9).
6. 6A. U.A.-F:A.M. No. 30642 (see pl. 22, fig. 10).
8. 8A. U.A.-F:A.M. No. 46942 (see pl. 22, fig. 11).

PLATE 24

Superior, posterior, and lateral views of large specific examples of Bison (Platycerobison), new subgenus. (See pl. 25.)
1, 1A, 1B. Plasotype of B. (Platycerobison) chaneyi (Cook, 1928), subgenotype, from near Vernon, Texas; C.M.N.H. No. 1147.
3, 3A, 3B. Holotype of B. (Platycerobison) alaskensis (Rhoads, 1897), from near Point Barrow, Alaska; C.N.H.M. No. P25226.

PLATE 25

Superior, posterior, and lateral views of small specific examples of Bison (Platycerobison) new subgenus. (See pl. 24.)
1, 1A. Paratype of B. (Platycerobison) geisti, new species, from near Fairbanks, Alaska; U.A.-F:A.M. No. 30552.
3, 3A, 3B. Holotype of B. (Platycerobison) palasi (Baer, 1823), from the Ilga River, west of Lake Baikal, Siberia. Reproductions rescaled after Gromova, 1932; I.P.A.S. No. 11161.

PLATE 26

Superior, posterior, and lateral views of examples of B. (Gigantobison), new subgenus, in comparison with an example of the typical subgenus, B. (Bison).
1, 1A. Holotype of B. (Gigantobison) latifrons (Harlan, 1825), from 12 to 14 miles north of Big Bone Lick, Kentucky; A.N.S.P. No. 12993. Also subgenotypic species.
2, 2A. B. (Gigantobison) latifrons, ref., from Brown County, Ohio. A.M.N.H. No. 6840.
3, 3A, 3B. B. (Gigantobison) latifrons, ref., from near Hoxie, Kansas. This specimen is not to 1/10 scale; 3 and 3B are larger; 3A is smaller. A.M.N.H. No. 14346.
4, 4A, 4B. B. (Bison) b. bison, ref., or typical plains bison from Montana; A.M.N.H. No. 16295. Compare with 2, 2A, which are the same 1/10 scale.
PLATES 8–26
Development of male skulls and dentition of B. (B.) b. bison (youth). Skulls × 1/10, teeth × 3/4
Development of male skulls and dentition of *B. (B.) b. bison* (maturity). Skulls × 1/10, teeth × ½
Mature males. 1, 2. B. (B.) b. bison. 3. B. (B.) h. athabascae. 4. B. (B.) bonasus. Skulls $\times 1/10$, teeth $\times \frac{3}{4}$.
Development of female *B. (B.) bison* (youth to old age). Skulls × 1/10, teeth × 1/2.
Tooth wear and development in *Bison* rami (immature and adolescent). Lateral × ¾, occlusal × ¾
Tooth wear and development in *Bison* rami (early maturity to old age). Lateral × 3/4, occlusal × 3/4
1. B. (B.) bison, referred. 2. B. (B.) occidentalis, platsyte. 3. B. (B.) proceridentalis, new species, holotype. X 1/10
1. B. (Sinochoerus) antiquus, holotype. 2. Female, referred. 3, 4, 5. Males, referred. × 1/10
B. (Superbison) crassicornis, referred, male population sample of Alaska. $\times 1/10$. (See pls. 18–22)
Male B. (Superbison) crassicornis. 1. Lectotype, after Richardson. 2-7. Referred. X 1/10. (See pls. 17, 19, 22)
Male *B. (Superbison) crassicornis*. 1. Lectotype, after Richardson. 2-7. Referred. × 1/10. (See pls. 17, 18, 22)
Male B. (Superbison) crassicornis, referred. × 1/10. (See pls. 17, 21, 22)
Male B. (Superbison) crassicornis, referred. × 1/10. (See pls. 17, 20, 22)
B. (Superbison) crassicornis, referred. 1–5. Male (see pls. 17–21). 6–11. Female (see pl. 23). × 1/10
B. (Superbison) crassicornis, referred, female population sample from Alaska (see pl. 22). × 1/10
B. (Pleurotectum), new subgenus. 1. B. (P.) shawei, holotype. 2. B. (P.) dekerensis, referred. 3. B. (P.) dekerensis, holotype. \( \times 1/10 \)
B. (Polyceros), new subgenus. 1, 2. Paratype and holotype, respectively, of B. (P.) goliath, new species. 3. B. (P.) pellesii, after Gromova, 1932. X 1/10