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MORRIS F. SKINNER AND OVE C. KAISEN

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Volume 89, article 3, pages 123–256, text figures 1–5,
plates 8–26, tables 1–25, maps 1–3

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CONTENTS

TABLES

ILLUSTRATIONS

PLATES

(AT END)

TEXT FIGURES

MAPS

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 4838 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 reëxamination 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.* (*Simobison*) (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

Size Range in 10-mm. Groups	Male				Female			
	Right	Left	Total	Per cent of Total	Right	Left	Total	Per cent of Total
240–250	6	7	13	0.7	none	1	1	0.1
230–240	72	81	153	8.8	9	4	13	1.4
220–230	355	305	660	37.9	58	50	108	11.6
210–220	348	308	656	37.7	197	204	401	43.0
200–210	120	119	239	13.7	157	168	325	34.8
190–200	8	11	19	1.1	42	43	85	9.1
180–190	none	none			1	none	1	0.1
Totals	909	831	1740		464	470	934	

TABLE 2

SPECIMEN COUNT OF ALASKAN *Bison* METATARSI

Size Range in 10-mm. Groups	Male				Female			
	Right	Left	Total	Per cent of Total	Right	Left	Total	Per cent of Total
300–310	3	none	3	0.1	none	none	none	
290–300	12	8	20	1.5	none	none	none	
280–290	86	74	160	12.2	13	13	26	3.2
270–280	212	211	423	32.3	62	62	124	14.5
260–270	236	248	484	36.9	154	133	287	33.2
250–260	82	88	170	13.0	134	155	289	33.9
240–250	23	25	48	3.7	56	57	113	13.2
230–240	1	1	2	0.1	6	9	15	1.8
Totals	655	655	1310		425	429	854	

Total male metapodials, 3050 Total female metapodials, 1788

Grand total male and female metapodials, 4838

TABLE 3

MEASUREMENTS (IN MILLIMETERS) AND INDICES OF SELECTED SAMPLE OF MALE *Bison* METACARPI

U.A.-F: A.M. Number	Greatest Over-all Length	Transverse Diameters: Proximal End	Transverse Diameters: Center of Shaft	Transverse Diameters: Distal End	Anterior-Posterior Diameter at Center	Indices (%): Transverse Diameter at Center / Greatest Over-all Length
46816	248.5	90.0	54.2	95.2	37.2	21.8
46817	248.0	91.2	59.8	92.7	37.4	24.1
46818	243.3	97.5	59.8	98.2	40.8	24.6
46819	240.2	93.1	59.5	93.8	40.6	24.7
46820	238.0	96.2	61.2	97.6	37.5	25.7
46821	233.0	91.7	58.2	93.2	40.3	25.0
46822	232.0	93.3	57.3	91.2	38.1	24.7
46823	231.5	96.4	67.2	92.5	36.5	28.8
46824	226.2	95.3	60.2	97.2	39.3	26.6
46825	220.7	83.0	55.0	82.8	35.8	24.9
46826	220.0	92.5	62.5	95.7	37.8	28.4
46827	215.3	84.5	57.3	91.1	34.5	26.6
46828	213.1	81.5	53.3	82.2	34.2	25.0
46829	208.7	80.8	52.8	87.0	34.6	25.3
46830	203.0	78.1	52.3	81.0	33.5	25.7
46831	200.5	81.8	54.7	89.5	31.9	27.2
46832	199.8	82.2	58.7	85.7	34.4	29.4
46833	197.5	74.9	49.6	79.8	33.3	25.4
46834	192.8	74.2	48.2	80.0	31.8	25.1
46835	190.8	72.5	51.9	76.7	31.2	27.2
46836	190.5	73.5	50.8	76.2	30.4	26.2
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

U.A.-F: A.M. Number	Greatest Over-all Length	Transverse Diameters: Proximal End	Transverse Diameters: Center of Shaft	Transverse Diameters: Distal End	Anterior-Posterior Diameter at Center	Indices (%): Transverse Diameter at Center / Greatest Over-all Length
46837	304.2	70.2	50.0	85.2	43.9	16.4
46838	303.1	71.1	44.5	82.5	42.8	14.8
46839	296.7	71.2	44.6	79.2	44.2	15.0
46840	289.4	72.2	46.5	80.6	45.7	16.1
46841	282.6	73.2	49.1	83.6	46.5	17.4
46842	275.5	72.8	48.8	83.1	45.0	17.7
46843	270.0	66.0	39.8	77.7	43.9	14.7
46844	265.6	63.6	41.5	75.6	40.7	15.6
46845	257.0	64.8	43.1	73.6	42.2	16.8
46846	253.2	62.2	40.7	71.1	37.7	16.1
46847	250.3	61.0	38.0	72.2	38.2	15.2
46848	243.8	60.0	39.8	72.2	37.8	16.2
46849	236.0	60.0	40.9	70.5	35.5	17.3
Sample Average	271.3	66.8	43.6	77.4	41.4	16.1
Min./Max. (%)	77.7	81.9	76.0	82.7	76.5	85.6

TABLE 5

MEASUREMENTS (IN MILLIMETERS) AND INDICES OF SELECTED SAMPLE OF FEMALE *Bison* METACARPI

U.A.-F: A.M. Number	Greatest Over-all Length	Transverse Diameters: Proximal End	Transverse Diameters: Center of Shaft	Transverse Diameters: Distal End	Anterior-Posterior Diameter at Center	Indices (%): Transverse Diameter at Center / Greatest Over-all Length
46850	247.2	74.6	43.5	74.5	30.5	17.6
46851	235.5	76.0	45.7	79.6	33.2	19.4
46852	230.4	72.2	41.1	71.3	27.9	17.8
46853	225.7	76.0	41.4	76.0	28.0	18.4
46854	223.4	69.9	39.6	71.7	29.2	17.9
46855	223.0	78.3	45.1	84.0	34.0	20.2
46856	221.9	73.3	44.8	79.5	28.9	20.2
46857	220.0	72.0	41.1	75.5	29.0	18.7
46858	218.5	73.9	44.2	78.1	31.2	20.2
46859	215.4	69.6	37.7	70.3	29.1	17.5
46860	212.3	70.2	42.5	76.3	30.3	20.0
46861	211.2	72.0	43.6	78.0	31.4	20.6
46862	206.9	74.2	45.1	78.6	30.0	21.8
46863	203.7	66.8	40.0	67.9	27.7	19.6

TABLE 5 (*Continued*)

MEASUREMENTS (IN MILLIMETERS) AND INDICES OF SELECTED SAMPLE OF FEMALE *Bison* METACARPI

U.A.-F: A.M. Number	Greatest Over-all Length	Transverse Diameters			Anterior-Posterior Diameter at Center	Indices (%)
		Proximal End	Center of Shaft	Distal End		Transverse Diameter at Center / Greatest Over-all Length
46864	202.7	65.0	36.5	69.1	27.4	18.0
46865	200.6	65.1	40.0	70.4	27.5	20.0
46866	197.1	67.8	36.3	69.4	29.0	18.4
46867	195.5	63.4	36.9	71.1	28.6	18.9
46868	194.5	62.2	35.7	63.9	26.5	18.3
46869	185.5	64.1	37.6	70.9	27.1	20.2
Sample Average	213.5	69.3	41.3	72.9	28.9	19.2
Min./Max. (%)	75.0	79.5	78.2	76.1	75.2	80.4

TABLE 6

MEASUREMENTS (IN MILLIMETERS) AND INDICES OF SELECTED SAMPLE OF FEMALE *Bison* METATARSI

U.A.-F: A.M. Number	Greatest Over-all Length	Transverse Diameters			Anterior-Posterior Diameter at Center	Indices (%)
		Proximal End	Center of Shaft	Distal End		Transverse Diameter at Center / Greatest Over-all Length
46871	289.7	61.7	36.2	74.3	39.5	12.5
46872	283.8	58.0	35.5	67.7	37.4	12.5
46873	280.3	56.8	34.9	72.0	39.6	12.4
46874	271.0	60.6	36.5	71.7	40.4	13.5
46875	269.5	56.2	31.6	67.1	39.8	12.2
46876	262.4	62.0	33.8	69.4	40.0	12.9
46877	258.2	55.0	32.3	68.7	37.4	12.5
46878	253.7	54.2	31.3	65.7	35.5	12.3
46879	247.2	50.3	29.3	62.0	34.5	11.8
46880	240.0	52.5	28.8	64.9	36.4	12.0
46881	238.0	51.0	28.3	63.3	34.8	11.9
46882	237.3	46.0	28.0	57.5	29.5	11.8
46883	233.8	51.1	31.6	60.5	35.5	13.5
Sample Average	258.8	55.1	32.2	66.6	37.0	12.5
Min./Max. (%)	80.7	74.2	76.7	77.4	73.2	87.5

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 bovids. Young specimens are 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.)

TABLE 7

Mortality Rate as Shown by Alaskan *Bison* Rami

Stage of Wear	Right	Left	Totals	Per Cent of Totals
I-S	96	99	195	14.8
A-S	16	14	30	2.3
S-1[a]	33	19	52	3.9
S-2	50	43	93	7.0
S-3	229	193	422	32.0
S-4	273	257	530	40.0
Totals	697	625	1322	100.0

[a] 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 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 to allow for core growth. The young horn sheath is long, slender, and sharply tipped, with only a slight indication of the first seasonal rings at its base and these are widely spaced.

In fully mature and old individuals the later rings at the base of the sheath become pronounced and closely spaced, indicating that the sheath and cores are not elongating. This affords an estimate of individual age which is otherwise indicated by the wearing off and blunting of the sheath tips.

Allen (1876, pl. 8) has well illustrated a progressive growth series of living bison sheaths. Plate 17, this paper, shows the appearance of the fossil sheath of the mature Alaskan specimens of *B.* (*Superbison*) *crassicornis*.

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 P_4 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 M_3, and one other specimen had an extra style on both M_2 and M_3. 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.

Reëntering 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). Reëntering 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 reëntering fold on the posterior side of the posterior fossette, while that of *Bos* or domestic cattle has a prominent reëntering fold on the posterior side of the posterior fossette and, in addition, the anterior fossette has reëntering folds on both the anterior and posterior sides. The reëntering folds in the fossette 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 M_3 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 P_4 is the last tooth to form from the germ stage, and likewise to erupt in the dental series. The M_3 slightly precedes the P_4 (see pls. 12, 13).

In most cases, taken as a group the P_4 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* P_4's are tending to become more molariform. The rami of living *Bison* disclose a small, median, labial root on the P_4 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 dP_4 of both Pleistocene and living *Bison*.

In Recent *Bison* the crown of an unworn P_4 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 P_4, observed only in old age in the earlier *Bison*,

TABLE 8

DISTRIBUTION AND OCCURRENCE OF MALE *Bison* SKULLS AND HORN-CORES IN ALASKAN LOCALITIES

Collecting Localities	*Bison*				Totals	
	(*Superbison*) *crassicornis*	(*Bison*) *preoccidentalis*	(*Platycerobison*)		Number	Per Cent
			alaskensis	*geisti*		
Cleary Creek	53	8	—	2	63	34.2
Goldstream Creek	43	2	—	—	45	24.4
Fairbanks area	17	2	—	—	19	10.3
Fairbanks Creek	9	—	—	—	9	4.8
Engineer Creek	7	1	1	—	9	4.8
Cripple Creek	6	1	1	1	9	4.8
Ester Creek	8	—	—	—	8	4.3
Little Eldorado Creek	3	2	—	—	5	2.7
Livengood Creek	4	—	—	—	4	2.1
17 miles N. of Fairbanks	3	—	—	—	3	2.0
Chatham	2	1	—	—	3	2.0
Gilmore Creek	1	1	—	—	2	1.0
Ruth Creek	1	—	—	—	1	0.5
Pedro Creek	1	—	—	—	1	0.5
Moose Creek	1	—	—	—	1	0.5
Lillian Creek	1	—	—	—	1	0.5
Seward Peninsula at Candel (Eschscholtz Bay)	1	—	—	—	1	0.5

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:

Stage	No. of Specimens	Stage	No. of Specimens
A-S	3	S-3	11
S-1	2	S-4	24
S-2	1		

TABLE 9

Tabulation of Alaskan Male *Bison* Skulls, Crania, and Horn-cores Summarizing Condition of Preservation and Faunal Composition

Condition of Specimens	*Bison*				Totals	
	(*Superbison*) *crassicornis*	(*Bison*) *preoccidentalis*	(*Platycerobison*) *alaskensis*	(*Platycerobison*) *geisti*	Number	Per Cent
Complete skulls	4	3	—	—	7	4.0
Partial skulls	18	6	—	—	24	13.3
Crania, complete cores	47	6	—	1	54	29.4
Crania, one core complete	37	2	—	2	41	23.0
Crania, incomplete cores	51	1	—	—	52	29.0
Horn-cores only	—	—	2	—	2	0.1
Total specimen count	157	18	2	3	180	99.7
Per cent of specimens in U.A.-F:A.M. collection	87	10	1	2		
Skulls with basilar length	8	7	—	—	15	8.4
Skulls with dentitions	20	9	—	—	29	16.3
Skulls with mandibles	2	—	—	—	2	1.1
Complete and partial skulls with horn sheaths	9	7	—	—	16	9.0
Crania with one or both horn sheaths	34	1	—	1	36	20.0
Per cent of specimens with sheaths	27	45	—	33	—	av. *29*

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

SYNONYMY, 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.

$$\frac{\text{Horn-core length on lower curve (4)}^{1}}{\text{Distance, core tip to upper base at burr (5)}} \times 100$$
=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.

$$\frac{\text{Vertical diameter of core at base (6)}}{\text{Transverse diameter of core at base (12)}} \times 100$$
=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.

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

4. Horn-core length:

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

$$\frac{\text{Length of horn-core on upper curve, tip to burr (3)}}{\text{Width of cranium between horn-cores and orbits (14)}}$$
$\times 100$ =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 M^3 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.

$$\frac{\text{Alveolar length, } P^2-M^3 \text{ (19)}}{\text{Basilar length of skull (F–P)}} \times 100 = \text{index of}$$
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*

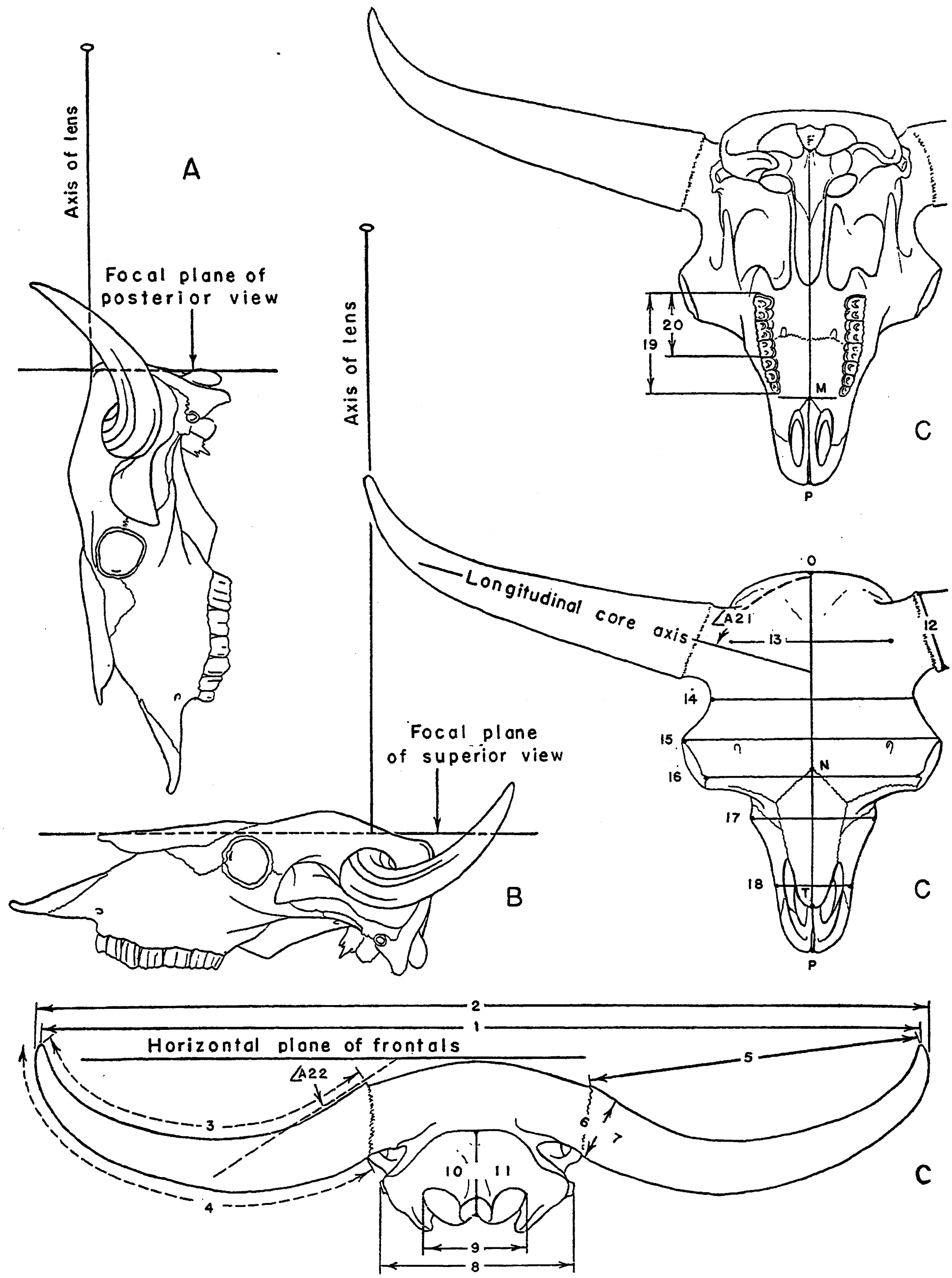
It was found necessary to develop a uniform system of individual age classification in *Bison* before attempting a segregation of cranial characters. The system, here illustrated in plates 8 to 13, is quite simple since *Bison* molars 1 to 3 erupt in a progressive order as the animal becomes mature. 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 P^2–P^4 in use; a small, prominent style present on dP^4; by the time this style


Axis of lens
A
Focal plane of posterior view
Axis of lens
20
19
M
P
C
O
Longitudinal core axis
A21
13
12
14
15
16
N
17
18
T
P
C
Focal plane of superior view
B
2
1
Horizontal plane of frontals
5
A22
3
6
7
4
10
11
9
8
C

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^1 starting to wear; M^2 worn on crown but style not worn; crown of M^1 worn off until style is well developed on pattern. At close of this stage M^2 style becomes worn; top of M^3 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^3 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^2 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^1 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^3 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*.

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.
9. Width of condyles.
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.
13. Width between bases of horn-cores.
14. Width of cranium between horn-cores and orbits.
15. Greatest postorbital width.
16. Angerior orbital width at notch.
17. Width of skull at masseteric processes above M^1.
18. Rostral width at maxillary-premaxillary suture.
19. P^2–M^3, alveolar length.
20. M^1–M^3, alveolar length.

- O–P. Length, over all, occipital crest to tip of premaxilla.
- F–P. Length, basilar, foramen magnum to tip of premaxilla.
- O–T. Length, occipital crest to tip of nasals.
- O–N. Length, occipital crest to nasal-frontal suture.
- M–P. Length, beyond P^2 to tip of premaxilla.
- N–T. Length of nasal bone.

21. Angle of posterior divergence of horn-core.
22. Angle of proximal horn-core depression.

INFERIOR DENTITION

Immaturity (I-S)

Plate 12, figures 1, 1A, 2, 2A, 3, 3A, 4, 4A

Milk premolars dP_2–dP_4 present. During this stage, the germs of the permanent molars M_1–M_3 are forming in a progressive order. At the close of this stage, germs of P_2–P_4 are forming. By the time dP_3 is shed, the germs of the molars are nearly formed, M_1 and M_2 are in use, and the germ of M_3 is erupting.

Early Adolescence (A-S)

Plate 12, figures 5, 5A

Deciduous P_4 is still retained, and permanent P_2 and P_3 are erupting. At the close of this stage, the style of M_1 is always worn, but never the style of M_2; M_3 has started to wear on the anterior lobe.

Late Adolescence (S-1)

Plate 13, figures 1, 1A

Most desirable for study; the style of M_1 worn, the style of M_2 unworn, the milk incisors and canines replaced by permanent incisors and canines, and the heel of M_3 starting to wear. This stage of wear continues until style of M_2 becomes worn.

Early Maturity (S-2)

Plate 13, figures 2, 2A

The style of M_2 becomes worn. By the close of this stage, P_2–P_4 are well worn and M_1 has been worn away from one-third to one-half its original length. The heel of M_3 is now in full wear.

Full Maturity (S-3)

Plate 13, figures 3, 3A

The style of M_3 becomes worn; the crowns of P_2–M_3 are now well worn. At the close of this stage, the anterior and posterior prongs of the roots of P_2–M_1 are exposed above the bone of the horizontal ramus. The style of M_1 has begun to disappear, and the styles of M_2 and M_3 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 M_1 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 M^3 is erupting. (For change in sheath appearance, see p. 138.)

IMMATURE SKULLS

Plate 8, figures 1–4

Tooth Wear (I-S) dP^2–dP^4 in wear M^1 unerupted	Skull small, one-half the length of adult; frontals and supraoccipital bones unfused; supraorbital foramen in open groove; orbits not prominently protruding; horn-cores have begun growth from frontals on a horizontal plane posterior to the orbits
dP^2–dP^4 in wear M^1 erupting	Skull enlarging to three-fifths the length of adult; frontals and supraoccipital bones unfused; supraorbital foramen in a deepening groove; orbits not prominently protruding; horn-cores have started to elongate but are not curved or large in circumference
dP^2–dP^4 in wear M^1 and M^2 erupted	Skull enlarging three-fourths to four-fifths the length of adult; frontals and supraoccipitals still unfused; 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*

an open porous texture of the bone not observed in maturity; the core surface is smooth and does not have longitudinal bony ridges extending from the burrs toward the tip as in old age

ADOLESCENT SKULLS

Plate 8, figure 5

Tooth Wear (A-S)
- dP^2 shed
- dP^3 and dP^4 retained
- P^2 and M^3 erupting

Skull four-fifths the length of adult; sutures of frontals and supraoccipitals still unfused; orbits more tubular but not prominently so; deep groove containing supraorbital foramen starting to enclose on posterior portion; horn-cores becoming larger in circumference and texture of bone finer and more compact; cores have almost reached mature length but are slender; sutures between frontals, lacrimals, and nasals unfused

Plate 9, figures 1, 2

Tooth Wear (S-1)
- dP^2–dP^4 shed
- P^2–P^4 slightly worn
- M^1 style beginning wear
- M^3 still unworn on posterior half

Skull approximating mature length; sutures of frontals and supraoccipitals still unfused; orbits tubular and slightly more prominent; cores enlarging in circumference, texture of bone becoming finer, and surface starting to develop longitudinal ridges of maturity; groove containing supraorbital foramen more enclosed; frontal, lacrimal, and nasal sutures unfused

SKULLS IN EARLY MATURITY

Plate 9, figure 3

Tooth Wear (S-2)
- M^1 style worn
- M^2 style worn to well worn
- M^3 style unworn

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 burr and longitudinal ridges becoming more prominent; groove containing supraorbital foramen still more enclosed; frontal, lacrimal, and nasal sutures unfused

FULLY MATURE SKULLS

Plate 9, figure 4, plate 10, figure 1

Tooth Wear (S-3)
- M^1 style $\frac{1}{2}$–$\frac{3}{4}$ worn
- M^2 style well worn
- M^3 style worn to well worn

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

Tooth Wear (S-4)
- M^1 style and fossettes gone
- M^2 fossettes and style well worn or missing
- M^3 style well worn

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 over all, 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.*) *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.

REVISION, 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, 485–662 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) alleni** (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 **SUPERBISON** FRICK, 1937
1 species

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

1. **B. (Superbison) 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, dorsoventrally 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. arizonica 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	*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*
1A. *Bison (Bison) bison athabascae* Rhoads, 1897 Mountain or woodland race	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 figginsi* (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*

D. BISON (PLATYCEROBISON), NEW SUBGENUS

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*) *geisti*, 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*) *alaskensis* (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*

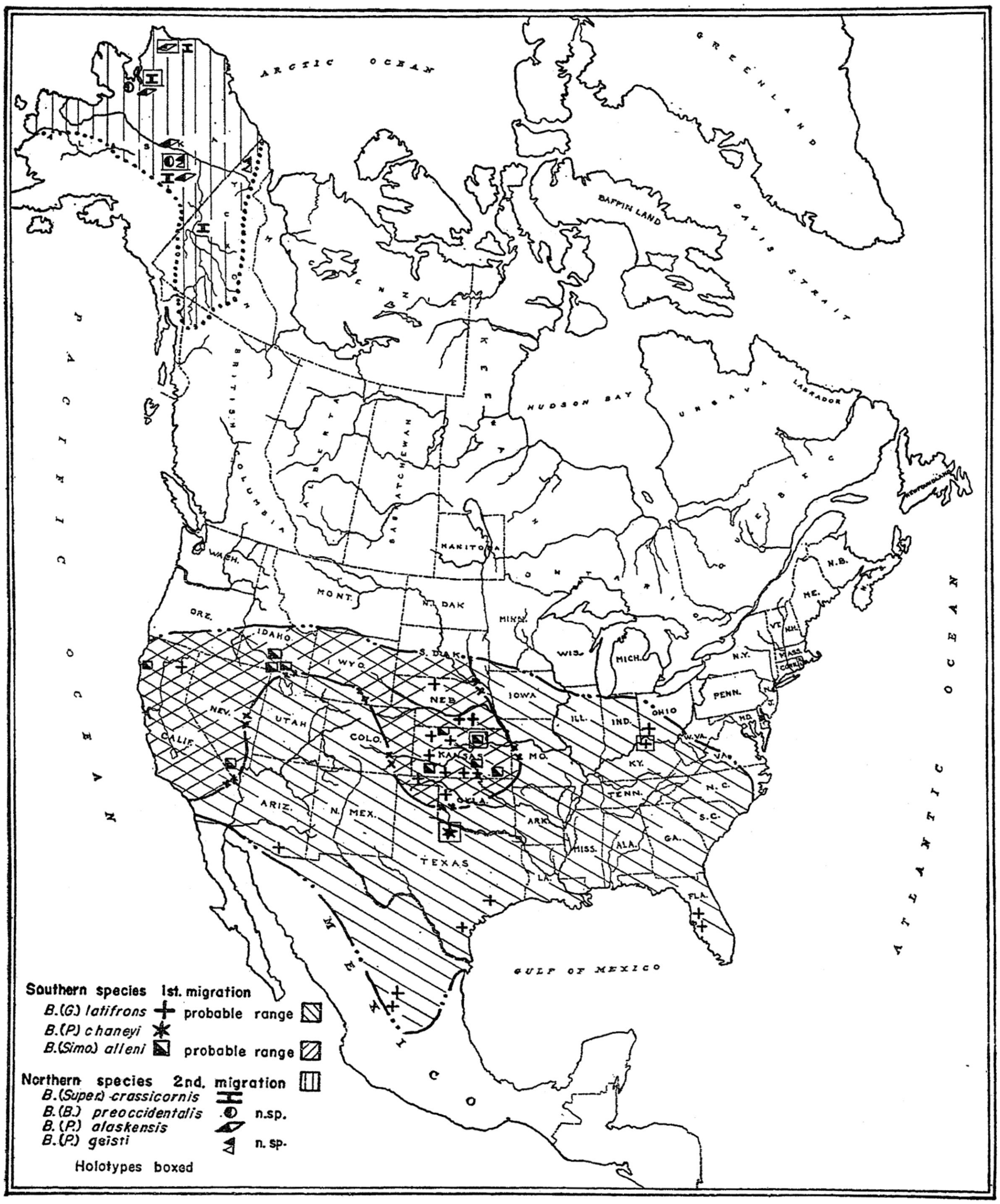
SUMMARY OF NORTH AMERICAN TYPES AND BEST FIGURED SPECIMENS

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	Figured Specimens Types or Referred
	A. BISON (BISON)
B. (*Bison*) *b. bison* Living	See Allen, 1876 This paper, pls. 8–11
B. (*Bison*) *occidentalis* Lucas, 1898 Cranium with 1 complete horn-core. U.S.N.M: V.P. No. 4157	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
B. (*Bison*) *preoccidentalis*, new species Complete skull with sheaths U.A.-F: A. M. No. 46885	Holotype: This paper, pl. 14, figs. 3, 3A, 3B, 3C
	B. BISON (SIMOBISON)
B. (*Simobison*) *antiquus antiquus* (Leidy, 1852) Partial horn-core A.N.S.P. No. 12990	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
B. (*Simobison*) *antiquus figginsi* (Hay and Cook, 1928) Crushed skull C.M.N.H. No. 574	Referred: Complete skull. See Hay and Cook, 1928, C.M.N.H. No. 1236. (Formerly holotype of *B.* "*taylori*" but provisionally referred to *figginsi*)
B. (*Simobison*) *alleni* (Marsh, 1877) Complete horn-core Y.P.M. No. 911	Referred: Complete skull. F.H.K.S.C. No. 40. This paper, pl. 16, figs. 2, 2A, plastotype, pl. 16, figs. 1, 1A
	C. BISON (SUPERBISON)
B. (*Superbison*) *crassicornis* (Richardson, 1854) Cranium, partial horn-cores B.M. 1-A, Beechey Collection	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
	D. BISON (PLATYCEROBISON)
B. (*Platycerobison*) *chaneyi* (Cook, 1928) Posterior cranium and horn-cores C.M.N.H. No. 1147	Holotype: No complete skull known. Plastotype: This paper, pl. 24, figs. 1, 1A, 1B
B. (*Platycerobison*) *geisti*, new species Posterior cranium U.A.-F: A.M. No. 46893	Holotype: No complete skull known. This paper, pl. 25, figs. 2, 2A, 2B
B. (*Platycerobison*) *alaskensis* (Rhoads, 1897) Cranium with horn-cores C.N.H.M. No. P25226	Holotype: No complete skull known. This paper, pl. 24, figs. 3, 3A, 3B
	E. BISON (GIGANTOBISON)
B. (*Gigantobison*) *latifrons* (Harlan, 1825) Partial cranium and left core A.N.S.P. No. 12993	Referred: Complete skull. See VanderHoof, 1942, U.C.M.P. No. 4067. This paper, holotype and referred specimens, pl. 26, holotype, figs. 1, 1A

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.

complished 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*) *alleni*, 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*) *alleni*, 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*) *alleni*, 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.

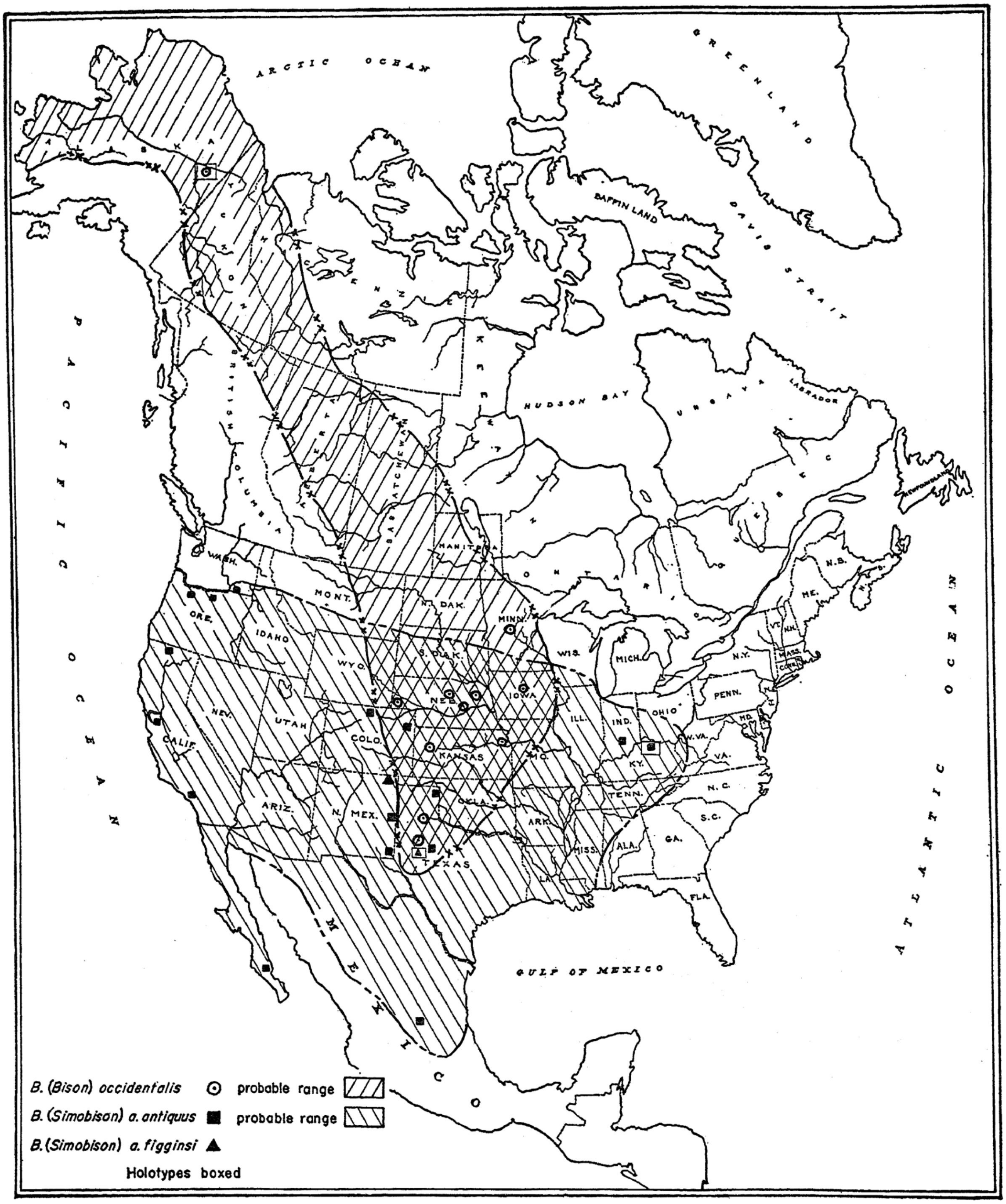
On the basis of occurrence, *crassicornis* was predominant and *preoccidentalis* was next, while *alaskensis* and *geisti* were extremely rare. They probably arrived from Eurasia during the start of the late Pleistocene, spreading over Alaska and most of the Yukon River drainage where their remains are 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*) *alleni* 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 Linnaeus, 1758 (in part), Systema naturae, ed. 10, vol. 1, p. 71. Gmelin, 1788, Systema naturae, vol. 1, p. 204.

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.

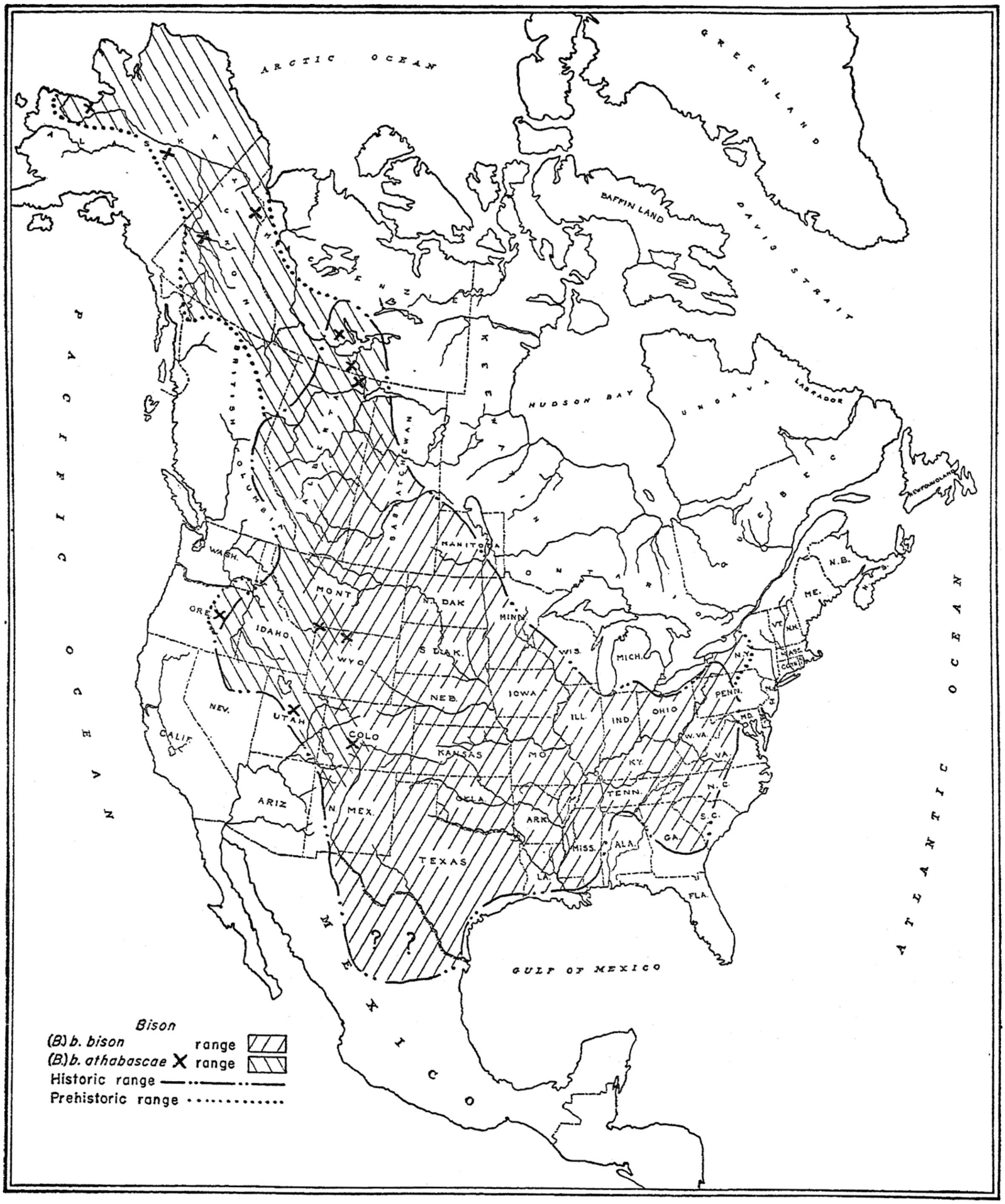
Bison, Knight, 1849, Sketches in natural history, vols. 5, 6, pp. 402, 408. Audubon and Bachman, 1851, The quadrupeds of North America, vol. 2, p. 32. Jordan, 1888, Manual of the vertebrate animals of northern United States, p. 337.

Stelabison Figgins, 1933, Proc. Colorado Mus. Nat. Hist., vol. 12, no. 4, pp. 17–19.

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.* (*Platycerobison*) *chaneyi*; *B.* (*Superbison*) *crassicornis*; *B.* (*Gigantobison*) *latifrons*; and the Eurasian *B.* (*Parabison*) *exiguus*.

[1] Circumstances make it necessary to cite *figginsi* as the type of the subgenus. See page 181.

Frick (1937, p. 567) erected the subgenus *Superbison* to include all the large horned forms. "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." This division was convenient. The present detailed studies have indicated the presence of several distinct horn-core forms within the large *Superbison*, and have suggested the possibility of a fourfold subdivision of the subgenus (i.e., *Bison*, *Simobison*, *Platycerobison*, and *Gigantobison*), each representing a distinct phyletic line and embracing forms (with the possible exception of *Gigantobison*) grading from larger-horned in the earlier Pleistocene to smaller-horned in the later Pleistocene and Recent.

This new subgeneric division of the members of the closely related genus *Bison* is proposed with the belief that the addition of new units will aid in the recognition of the phyletic lines. An understanding of all the species of the genus and their development is complex in many ways. Combined with the specific physical differences, the element of time, the isolating factors of nature, and distribution must be dealt with. All have played an important part in the production of the *Bison* species. On the other hand the recognition of the various *Bison* species has been based on populations, and a number of species have been synonymized, thus combining the population segments into complete blocks.

One genus, "*Stelabison*" Figgins, previously proposed, is here considered synonymous with *Bison*.

"*Stelabison*" Figgins, 1933

In 1933, Figgins (1933, pp. 17–21, pl. 1, figs. 1, 2) proposed a new bovid genus called "*Stelabison*," the generic distinction being founded on the presence of small external pillars on the M^2 and M^3. He stated: "A character so markedly at variance to its nearly total absence in other races of *Bison* makes advisable a new genus, in which to include all races having these pillars. It is therefore proposed that *Stelabison*, gen. nov., be recognized with *Bison occidentalis* as the type, the latter becoming *Stelabison occidentalis*." Figgins, however, figured in the same report the molars of his new subspecies, *Bison b. "hangtoni*," which also show external pillars. He explained their presence by calling them rudimentary, and he did not allocate his new subspecies to his new genus.

In the Alaskan collection of *B.* (*Superbison*) *crassicornis* and the new species *B.* (*Bison*) *preoccidentalis*, it is observed that of 31 skulls that have retained their dentition, seven, or 23 per cent, have external pillars. Except for the pillars, the skulls could in no way be separated from the others. Among seven palates and 90 maxillae, 17 examples, or 16 per cent, had external pillars, and, in addition, 43 out of several hundred isolated molars had pillars in all gradations of size.

It appears that the presence of external pillars is an erratic tendency toward a "mutation" and has so far been observed in *B.* (*Superbison*) *crassicornis*, *B.* (*B.*) *preoccidentalis*, *B.* (*Simobison*) *antiquus "taylori*," and *B.* (*Bison*) *bison*. Specimens having pillars are not otherwise separable from other referred specimens in the same species. For this reason, the genus "*Stelabison*" is here considered a synonym of *Bison*.

Although it was stated that *B. occidentalis* was the genotypic species, a referred specimen was used to represent the holotype. Figgins (1933, p. 18) stated: "As the type of *Bison occidentalis* consists of only the horn-cores, frontals and occipital, a question must attach to the characters of the dentition.The skull characters of No. 13721 [American Museum specimen] are quite similar to those of the type of *occidentalis* and until adequate studies of all of the northern bison prove otherwise, it seems best to follow Dr. Hay's course and recognize this skull as belonging to the last named race."

In this study of the Alaskan series, a direct comparison of A.M.N.H. No. 13721 with a cast of the holotype of *occidentalis* shows little agreement. The specimen is more readily placed with the larger *B.* (*Superbison*) *crassicornis*.

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 $\frac{4}{4}$ 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 primitivus* by Hilzheimer in 1909. If one can judge from the type figure and the size, this species is closely related to, if not synonymous 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 americanus, KNIGHT, 1849, Sketches in natural history, vols. 5, 6, p. 408. AUDUBON AND BACHMAN, 1851, The quadrupeds of North America, vol. 2, p. 32. ALLEN, 1876, Mem. Mus. Comp. Zool., vol. 4, p. 36. HORNADAY, 1889, Ann. Rept. Smithsonian Inst. for 1887, pt. 2 (1889), p. 367.

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 RHOADS (1897, p. 492) described *B. b. athabascae.*

Bison (*Bison*) *bison bison*, the typical subgenus automatically came into being when FRICK (1937, 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:

Bison sylvestris HAY, 1915, Proc. U. S. Natl. Mus., vol. 48, p. 515, pl. 30, figs. 1–4. FRICK, 1937 Bull. Amer. Mus. Nat. Hist., vol. 69, p. 581.

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

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

Bison bison pennsylvanicus Shoemaker, MILLER, 1923, Bull. U. S. Natl. Mus., no. 128, p. 494. FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 578, 593. KELLOGG, 1937, Proc. U. S. Natl. Mus., vol. 84, no. 3022, p. 475; 1939, Proc. U. S. Natl. Mus., vol. 86, no. 3051, p. 297. SCHORGER, 1944, Jour. Mammal., vol. 25, no. 5, pp. 313–315.

4. References for the holotype of *B. b. septemtrionalis* Figgins, 1933:

Bison bison septemtrionalis FIGGINS, 1933, Proc. Colorado Mus. Nat. Hist., vol. 12, no. 4, p. 28, pl. 7. FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, p. 592.

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 fontals 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-*

talis; masseteric processes seldom strongly developed; occipital region rounded and well developed; cranium tends to be moderate.

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 $\frac{4}{4}$ 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 Pliestocene 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, is so extensive that little can be added concerning this race that is not already known. Both Allen and Hornaday, in their time, have presented excellent historical accounts concerning *Bison* distribution and habits. As a result of Hornaday's efforts, there is preserved in the United States National Museum a splendid series of skulls, skeletons, and skins

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.)

Key No.		No. of Measurements	Summary		
			Min.	Av.	Max.
1	Spread of horn-cores, tip to tip	44	485	*581*	662
2	Greatest spread of cores on outside curve	30	534	*612*	687
3	Core length on upper curve, tip to burr	44	140	*186*	250
4	Length of core on lower curve, tip to burr	44	170	*233*	313
5	Length, tip of core to upper base at burr	44	135	*168*	210
12	Transverse diameter of core	44	68	*78*	95
6	Vertical diameter of core	44	64	*74*	91
7	Circumference of core at base	44	208	*235*	279
14	Width of cranium between cores and orbits	44	242	*264*	290
15	Greatest postorbital width	30	271	*317*	343
17	Width of skull at masseteric processes at M^1	30	171	*187*	210
8	Greatest width at auditory openings	30	222	*258*	275
9	Width of condyles	29	113	*125*	135
O-T	Occipital crest to tip of nasals	30	388	*437*	470
O-N	Occipital crest to tip of nasal-frontal suture	30	211	*241*	268
11	Depth, occipital crest to lower border foramen magnum	29	139	*150*	163
F-P	Basilar length of skull	43	454	*480*	503
O-P	Over-all length of skull	29	491	*541*	570
19	P^2–M^3 alveolar length	30	129	*147*	157
20	M^1–M^3 alveolar length	30	82	*91*	98
M-P	Median length of premaxilla beyond P^2	30	120	*138*	151
18	Rostral width at maxillary-premaxillary suture	30	92	*107*	119
	Index of horn-core curvature	44	120	*139*	182
	Index of horn-core compression	44	85	*95*	101
	Index of horn-core proportion	44	66	*79*	104
	Index of horn-core length	44	57	*71*	90

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^3 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"* Shoemaker, 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.

[1] Opinion No. 2, International Commission on Zoological Nomenclature.

1A. Bison (Bison) bison athabascae Rhoads, 1897

LIVING WOODLAND OR MOUNTAIN BISON

Present range restricted to type locality, Great Slave Lake, northern Canada; prehistoric range, Alaska, northern Canada, and Rocky Mountains southward as far as Colorado and Utah

Plate 10, figures 3, 3A, 3B, 3C

1. References for the holotype:

Bison bison athabascae RHOADS, 1897, Proc. Acad. Nat. Sci. Philadelphia, vol. 49, pp. 492–500.

2. References for the holotype of *B. b. oregonus* Bailey, 1932:

Bison bison oregonus BAILEY, 1932, Proc. Biol. Soc. Washington, vol. 45, p. 48. FIGGINS, 1933, Proc. Colorado Mus. Nat. Hist., vol. 12, no. 4, p. 32. STOCK, 1937, Westways, vol. 29, no. 2, p. 29. FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 578, 593.

3. References for the holotype of *B. b. haningtoni* Figgins, 1933:

Bison bison haningtoni FIGGINS, 1933, Proc. Colorado Mus. Nat. Hist., vol. 12, no. 4, pp. 30–32, pls. 8, 9. FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 578, 592.

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

Bison antiquus Leidy, ALLEN, 1876 (in part), Mem. Mus. Comp. Zool., vol. 4, no. 10, pp. 24–26, pl. 4, table 4 (see footnote p. 24, St. Michael specimen).

Bison occidentalis LUCAS, 1899, Proc. U. S. Natl. Mus., vol. 21, p. 758 (St. Michael specimen). OSGOOD, 1907, Proc. U. S. Biol. Soc. Washington,

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.)

Key No.		No. of Measurements	Summary Min.	Av.	Max.
1	Spread of horn-cores, tip to tip	9	585	*665*	736
2	Greatest spread of cores on outside curve	5	645	*683*	750
3	Core length on upper curve, tip to burr	9	155	*216*	260
4	Length of core on lower curve tip to burr	8	190	*255*	290
5	Length, tip of core to upper base at burr	7	150	*189*	200
12	Transverse diameter of core	8	81	*92*	108
6	Vertical diameter of core	8	72	*85*	97
7	Circumference of core at base	9	230	*271*	300
14	Width of cranium between cores and orbits	9	272	*288*	312
15	Greatest postorbital width	4	326	*355*	384
17	Width of skull at masseteric processes at M^1	3	179	*195*	204
8	Greatest width at auditory openings	7	185	*263*	296
9	Width of condyles	7	113	*130*	140
O-T	Occipital crest to tip of nasals	3	447	*477*	507
O-N	Occipital crest to tip of nasal-frontal suture	5	248	*286*	271
11	Depth, occipital crest to lower border foramen magnum	6	140	*149*	159
F-P	Basilar length of skull	3	525	*537*	555
O-P	Over-all length of skull	3	560	*573*	595
19	P^2–M^3 alveolar length	3	143	*148*	158
20	M^1–M^3 alveolar length	2	92	*92*	92
M-P	Median length of premaxilla beyond P^2	3	151	*160*	170
18	Rostral width at maxillary-premaxillary suture	3	108	*121*	130
	Index of horn-core curvature	7	126	*135*	149
	Index of horn-core compression	8	84	*92*	98
	Index of horn-core proportion	9	62	*80*	92
	Index of horn-core length	9	57	*75*	90

vol. 20, p. 265 (Pelly River specimen). HAY, 1913, Proc. U. S. Natl. Mus., vol. 46 (1914), pp. 175, 176 (U.S.N.M. No. 5513).

Superbison occidentalis (Lucas), FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, p. 591 (St. Michael specimen).

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

Bison americanus (Gmelin) Smith, ALLEN, 1876 (in part), Mem. Mus. Comp. Zool., vol. 4, no. 10, pp. 166–175 (a good summary of northern woodland bison).

Bison americanus, Var.?, SETON (THOMPSON), 1886, Proc. Canadian Inst., vol. 3, p. 114.

The "Wood" or "Mountain" Buffalo, HORNADAY, 1889, Ann. Rept. Smithsonian Inst., for 1887, pt. 2 (1889), pp. 407–412.

Bos [Bison] bison athabascae, LYDEKKER, 1898, Wild oxen, sheep, and goats of all lands, pp. 5, 50, 90, 91.

Bison, FRYXELL, 1926, Jour. Mammal., vol. 7, no. 2, pp. 102–109; 1928, *ibid.*, vol. 9, pp. 129–139.

Buffalo, MERRIAM, 1926, Jour. Mammal., vol. 7, pp. 211–214.

Northern Bison, SOPER, 1941, Ecol. Monogr., vol. 11, no. 4, pp. 349–412; 1942, Jour. Mammal., vol. 23, no. 2.

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
Mounted specimen	N.M.C. 299	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
		REFERRED
Skull	N.M.C. 625	From near Athabaska Lake, 1898
Skull	4538	From near Fort Smith, 1921
Skull, skin, and skeleton of old male	8755	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
Skull, skin, and skeleton of adult cow	10405	From Wood Buffalo Park, March, 1928
Skull, skin, and skeleton	Univ. Saskatchewan Coll.	From Wood Buffalo Park, Sept., 1927
Skull of young spike bull	A.M.N.H:M. 18163	From near Great Slave Lake, 1900; Bull. Amer. Mus. Nat. Hist., vol. 13, art. 6

Skull with skeleton; tooth wear (S-3)	A.M.N.H:M. 73615	From Alberta; collected by Rowen, 1926 This paper, pl. 10, figs. 3, 3A, 3B, 3C
Cranium with sheaths	123053	Collected by Canadian Park Services in 1930. Secured by G. G. Goodwin in 1937
Skull and skeleton	U.S.N.M:M. 172689	Collected by Harry V. Radford, 1910, northern Alberta
Cranium, partial and badly weathered	U.S.Bi.S. 177630	From near Fort Providence on north side of Great Slave Lake, Mackenzie; collected by H. V. Radford, 1910
Partial cranium with complete left core	177631	From west of Fort Smith, northern Alberta; collected by H. V. Radford, 1909
Cranium with horn-cores, unfossilized	U.S.N.M:V.P. 5513	From 12 miles above mouth of Pelly River, near Selkirk, Yukon Territory; collected by Charles Sheldon, 1905 Referred to *B. occidentalis* by Osgood, 1907; Hay, 1913b
Cranium with cores and orbits	16861	From Peel River, Yukon Territory; collected by E. A. Preble, 1904
		ALASKA
		REFERRED
Cranium with horn-cores, unfossilized	C.A.S. Coll.	From near St. Michael Figured by Allen, 1876, pl. 4, footnote, p. 24 Referred to *B. antiquus* by Allen; to *B. occidentalis* by Lucas, 1899a, and Hay, 1913b, and to *Superbison occidentalis* by Frick, 1937
Complete skull, tooth wear (S-3); completely unweathered	U.S.Bi.S. 223292	Found by an Indian in a cut bank of a creek near its mouth, and 30 miles above the mouth of the Tanana River. Obtained by Charles Sheldon, 1906
		WYOMING
		REFERRED
Complete skull, well-worn teeth (S-4)	U.S.Bi.S. 168816	From Big Horn Mountains on the west slope at 9000 feet
Seven crania, all of which have weathered surfaces	U.S.N.M:M. 120507 120508 120509 120510 120511 120512 221089	From Gardner River and Mammoth Hot Springs, Yellowstone Park; collected by E. A. Mearns, 1902
		COLORADO
		REFERRED
Adult male, mounted specimen	C.M.N.H. 2	From head of Rock Creek, northeast of South Park, South Park County; taken by Edwin Carter, 1872, at an altitude of 10,500 feet Figured by Figgins, 1933, pls. 8, 9 Holotype of *B. b. "haningtoni"*
Skull of adult male	1369	From Alma, Park County; altitude, 10,232 feet Figured by Figgins, 1933 Cotype of *B. b. "haningtoni"*
		UTAH
		REFERRED
Cranium	U.S.N.M:M. 14442	From Twelve Mile Creek Canyon near Gunnison; collected by J. W. Powell

OREGON

Referred

Male skull (S-4) and skeleton	U.S.Bi.S. 250145	From Malheur Lake; collected by George M. Benson, Nov., 1931 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, S-2	250094	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:

Referred

Skull	N.M.C. 11435	Collected by J. Dewey Soper, 1932, Blind Bull Lake
Skull	11436	Cabin 7, Murdock Creek
Skull, female	12091	Cabin 7, Murdock Creek
Skull with sheaths	A.M.N.H:M. 86950	From Alberta; collected by G. G. Goodwin, 1934
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. 263390	From near Government Hay Camp, 1936–1937
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:

Bison occidentalis LUCAS, 1898, Science, ser. 2, vol. 8, p. 678 (brief mention and description); 1899, Kansas, Univ. Quart., vol. 8, p. 17 (brief discussion on difference between *B. occidentalis* and *B. antiquus*); 1899, Proc. U. S. Natl. Mus., vol. 21, p. 758, pl. 65. GILMORE, 1908, Smithsonian Misc. Coll., vol. 51, p. 34. HAY, 1913, Proc. U. S. Natl. Mus., vol. 46 (1914), p. 167, pl. 9, figs. 3, 4; 1914, Ann. Rept. Iowa Geol. Surv. for 1912, vol. 23, p. 319, pl. 39, figs. 2, 3. BARBOUR AND SCHULTZ, 1936, Bull. Nebraska State Mus., vol. 1, no. 45, pp. 435, 436.

Superbison occidentalis (Lucas), FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, p. 591.

2. References for the holotype of *Bison kansensis* McClung, 1904:

Bison kansensis MCCLUNG, 1904, Trans. Kansas Acad. Sci., vol. 19, p. 157, fig. 10. HAY, 1913, Proc. U. S. Natl. Mus., vol. 44, pp. 584, 585. FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 575, 577, 583.

Bison occidentalis Lucas, HAY, 1924, Carnegie Inst. Washington Publ., no. 322A, p. 193.

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

Bison texanus HAY AND COOK, 1928, Proc. Colorado Mus. Nat. Hist., vol. 8, no. 2, pt. 1, p. 33; 1930, *ibid.*, vol. 9, no. 2, p. 25, pl. 8, figs. 3–5 (pls. 9 and 10 are reversed in this publication), pl. 10, figs. 1–3, pl. 11, fig. 1. FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 575, 577, 587.

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.)

Superbison occidentalis (Lucas, 1898), FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, p. 591.

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^3 of *Bison*.)

Bison (*Stelabison*) *francisi* (Figgins), FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, p. 586.

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

Bison antiquus Leidy, ALLEN, 1876 (in part), Mem. Mus. Comp. Zool., vol. 4, no. 10, pp. 24, 25, table 4 (U.S.N.M. No. 7529). STEWART, 1897, Kansas Univ. Quart., vol. 6, pp. 127, 130, text fig., pl. 17, fig. 2. SCHULTZ AND FRANKFORTER, 1946, Bull. Nebraska State Mus., vol. 3, no. 1, p. 7, chart 1, sp. no. 30323.

Bison occidentalis LUCAS, 1898, Proc. U. S. Natl. Mus., vol. 21, p. 758, pl. 66; 1899, Kansas Univ. Quart., vol. 8, p. 17, pl. 9, fig. 2. MCCLUNG, 1908, Kansas Univ. Sci. Bull., vol. 4, no. 10, pp. 249–252, pl. 14 (first figure of Kansas skeleton). HAY, 1914, Ann. Rept. Iowa Geol. Surv. for 1912, vol. 23, p. 319, text fig. 102, pl. 40, figs. 3, 4; 1913, Proc. U. S. Natl. Mus., vol. 46 (1914), p. 169, text figs. 4, 5, 6; 1924, Carnegie Inst. Washington Publ., no. 322A, pp. 193, 194; 1923, Proc. U. S. Natl. Mus., vol. 63 (1924), art. 5, pp. 1–8, pl. 1, figs. 1, 2, pl. 2, figs. 1, 2. BARBOUR AND SCHULTZ, 1932, Bull. Nebraska State Mus., vol. 1, no. 32, p. 263, text figs. 163, 164. SCHULTZ, 1934, Bull. Nebraska State Mus., vol. 1, no. 41, pt. 2, pp. 390, 391.

Bison oliverhayi FIGGINS, 1933, Proc. Colorado Mus. Nat. Hist., vol. 12, no. 4, p. 21 (a specimen from Scottsbluff Bison Quarry referred by Figgins to this species).

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).

Bison species, FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 577, 582, 583, 584.

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 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.)

Key No.		Holotype	No. of Measurements	Summary		
				Min.	Av.	Max.
1	Spread of horn-cores, tip to tip	706	13	670	*747*	875
2	Greatest spread of cores on outside curve	764	8	735	*782*	892
3	Core length on upper curve, tip to burr	295	12	222	*279*	330
4	Length of core on lower curve, tip to burr	365	12	275	*340*	405
5	Length, tip of core to upper base at burr	247	11	210	*243*	290
12	Transverse diameter of core	102	16	85	*98*	114
6	Vertical diameter of core	95	16	76	*91*	100
7	Circumference of core at base	300	16	253	*290*	336
14	Width of cranium between cores and orbits	297	12	277	*299*	340
15	Greatest postorbital width	360	8	328	*351*	400
17	Width of skull at masseteric processes at M^1	—	5	169	*187*	204
8	Greatest width at auditory openings	280	9	259	*275*	307
9	Width of condyles	129	8	124	*131*	147
O–T	Occipital crest to tip of nasals	—	5	471	*493*	543
O–N	Occipital crest to tip of nasal-frontal suture	267	8	229	*259*	273
11	Depth, occipital crest to lower border foramen magnum	177	6	136	*158*	177
F–P	Basilar length of skull	—	6	467	*516*	582
O–P	Over-all length of skull	—	6	505	*573*	630
19	P^2–M^3 alveolar length	—	6	137	*147*	160
20	M^1–M^3 alveolar length	—	5	84	*91*	102
M–P	Median length of premaxilla beyond P^2	—	5	143	*153*	168
18	Rostral width at maxillary-premaxillary suture	—	6	102	*115*	125
	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.*) *preoccidentalis*, 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.*) *b. athabascae*, is slightly larger but proportionately similar in all details, except 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 frontals 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)		Plastotype, this paper, pl. 14, figs. 2, 2A, 2B

REFERRED

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

MINNESOTA

REFERRED

Four skulls and other associated material:		From Sagamore Iron Mine, near Riverton; collected by F. W. Uhler on behalf of John A. Savage and Co.
Mature skull, lacking part of nasals and teeth	U.S.N.M:V.P. 10541	
Nearly complete skull; tooth wear (S-4)	10542	Figured by Hay, 1924, pls. 1, 2. Part of a composite mount
Cranium and horn-cores	10545	
Partial skull, top of cranium, and one horn-core, complete	10546	

IOWA

REFERRED

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

REFERRED

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

Complete skull and composite skeleton	U.N.S.M. 30323[1] (Formerly 2-10-6-32)	From Scottsbluff Bison Quarry, Scotts Bluff County; collected in 1932 Figured by Barbour and Schultz, 1936, Bull. Nebraska State Mus., vol. 1, p. 349, fig. 204
	Trailside Mus., Scottsbluff, Nebraska	
Male skull, lacking nasals Complete female skull	No. 1 (male) No. 2 (female)	From 7 miles south of McGrew, Banner County; collected by Joe and Lyle Horn, 1945. In private collection of H. C. Becker, Scottsbluff, Nebraska

KANSAS

Referred

Posterior portion of skull and partial right horn-core of young male	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*"
Complete skull lacking premolars; tooth wear (S-4)	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	3190	From Logan County; collected by H. T. Martin, 1895 Figured by Stuart, 1897, text fig. p. 130, pl. 17, fig. 2 (as *B. antiquus*, skull only); Lucas, 1899a, pl. 66 (skull only); McClung, 1908, pl. 14 (first figure of skull and skeleton); Hay, 1913, vol. 46 (1914), text figs. 4, 5, 6, 1914, vol. 23, text fig. 102; Barbour and Schultz, 1932, text fig. 164

TEXAS

Referred

Fragment of posterior cranium and portion of right horn-core	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*"
Complete skull and mandible; tooth wear (S-4)	C.M.N.H. 629	From near Michies, Dawson County Holotype of *B.* "*texanus*"
Partial skull	631	From same locality as above

CALIFORNIA

Tentatively Referred

Right horn-core and part of occiput	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

1. Reference for a here-referred specimen: *Superbison crassicornis* (Richardson), FRICK, 1937 (in part), Bull. Amer. Mus. Nat. Hist., vol. 69, p. 573, fig. 57, table, p. 575 (A.C.-F:A.M. No. 30595).

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

SUMMARY OF MALE SKULL MEASUREMENTS AND INDICES OF *B.* (*Bison*) *preoccidentalis* IN U.A.–F:A.M. COLLECTION AND MEASUREMENTS OF HOLOTYPE (U.A.–F:A.M. 46885)
(Measurements in millimeters, figure 1C for key; indices in per cent, page 142.)

Key No.		Summary				
		Holotype	No. of Measurements	Min.	Av.	Max.
1	Spread of horn-cores, tip to tip	875	18	740	*842*	925
	Spread of horns with sheaths, tip to tip	625	8	485	*632*	786
2	Greatest spread of cores on outside curve	898	17	792	*861*	958
	Greatest spread of horns with sheaths	964	8	829	*912*	1005
	Sheath length on upper curve	540	15	410	*478*	540
3	Core length on upper curve, tip to burr	395	32	315	*364*	415
	Difference between sheaths and core length	145	15	50	*100*	160
4	Core length on lower curve, tip to burr	435	32	370	*414*	464
5	Length, tip of core to upper base at burr	355	32	300	*332*	365
12	Transverse diameter of core	104	34	99	*108*	128
6	Vertical diameter of core	91	34	88	*97*	107
7	Circumference of core at base	302	34	295	*320*	361
14	Width of cranium between cores and orbits	269	18	250	*284*	305
15	Greatest postorbital width	325	16	321	*342*	368
17	Width of skull at masseteric processes	184	9	179	*184*	196
8	Greatest width at auditory openings	283	16	268	*284*	302
9	Width of condyles	138	18	130	*139*	148
O–T	Occipital crest to tip of nasals	502	4	480	*496*	514
O–N	Occipital crest to nasal-frontal suture	281	16	253	*274*	297
11	Occipital crest to lower border foramen magnum	161	18	153	*160*	175
F–P	Basilar length of skull	543	7	526	*539*	547
O–P	Over-all length of skull	604	7	577	*599*	629
19	P^2–M^3 alveolar length	148	15	147	*152*	158
20	M^1–M^3 alveolar length	93	15	91	*94*	97
M–P	Median length of premaxilla beyond P^2	160	7	147	*155*	165
18	Rostral width at maxillary-premaxillary suture	121	7	108	*117*	124
	Index of core curvature	123	32	112	*126*	134
	Index of core compression	87	18	83	*90*	94
	Index of core proportion	131	18	100	*113*	131
	Index of core length	147	18	110	*128*	152

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 P_4.

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*) *geisti*, 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*) *alleni*, 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, P^2–P^4 alv., M^1–M^3; 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

Male skulls and crania:		From near Fairbanks; collected by Peter C. Kaisen, 1929–1930; Albert S. Wilkerson, 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

Complete skull, P^2–M^2 alv., M^3; sheaths attached	U.A.-F:A.M. 46884	From lower Goldstream, 1939
Complete skull, P^2 alv., P^3–M^3	46886	From upper Cleary Creek, 1937
Skull lacking nasals, sheaths attached, P^2–M^3	46887	From Little Eldorado Creek, 1938
Skull lacking nasals, P^2, P^3 alv., P^4–M^3	46888	From lower Goldstream, 1939
Skull lacking nasals and right horn-core, left sheath attached, P^2–M^3	30530	From Cleary Creek, 1930
Skull lacking nasals, sheaths attached, P^2 alv., P^3–M^3	46889	From (?) upper Cleary Creek, 1937
Skull lacking nasals, premaxilla, sheaths attached, P^2–P^3 alv., P^4–M^3	46890	From Little Eldorado Creek, 1938
Skull lacking nasals, premaxilla, sheaths attached, P^2–M^1 alv., M^2–M^3	30567	From Cleary Creek, 1930
Cranium, partial orbit	30529	From Fairbanks area, 1929
Cranium, partial left core and partial orbits	30526	From Fairbanks area, 1929
Cranium, lacking orbits	30648	From upper Cleary Creek, 1934
Cranium, partial orbits	46891	From Cripple Creek, 1942
Cranium, partial right horn-core	30651	From upper Cleary Creek, 1934
Cranium, lacking left core and orbits	30541	From Cleary Creek, 1930
Cranium, partial orbits	30622	From Gilmore Creek, 1932
Cranium, partial orbits	46892	From Engineer Creek, 1942
Posterior cranium with horn-cores	U.S.N.M:V.P. 10891	From Kotzebue Sound, near Eschscholtz Bay, Seward Peninsula

B. BISON (SIMOBISON) (HAY AND COOK, 1930)

References for the subgenus:

Bison figginsi HAY AND COOK, 1928, Proc. Colorado Mus. Nat. Hist., vol. 8, no. 2, pt. 1, p. 33.

Simobison HAY AND COOK, 1930, Proc. Colorado Mus. Nat. Hist., vol. 9, no. 2, pp. 23–25, pl. 7, figs. 1, 2.

Bison (*Simobison*) (Hay and Cook), FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, p. 587.

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 dorsoventral 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 $\frac{4}{4}$ 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 mandible 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 premaxilla 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 premaxillae." 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 dP_4 has not been shed, and the heel of M_3 is not in wear, indicating a young animal. The skull has shed the dP^4, 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 dP_4 has been shed, and the ascending ramus and condyles are extended in a more posterior position with respect to the M_3.

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:

Bison antiquus LEIDY, 1852, Proc. Acad. Nat. Sci. Philadelphia, vol. 6, p. 117; 1852, Smithsonian Contrib. to Knowledge, vol. 5, art. 3, p. 11, pl. 2, fig. 1. ALLEN, 1876 (in part), Mem. Mus. Comp. Zool., vol. 4, no. 10. pl. 21. LUCAS, 1899, Kansas Univ. Quart., ser. A, vol. 8, pp. 17, 18, pl. 8; 1899, Proc. U. S. Natl. Mus., vol. 21, p. 759, pls. 67, 68. HAY, 1913, Proc. U. S. Natl. Mus., vol. 46 (1914), p. 164, fig. 1. FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 575, 576, 578. SCHULTZ AND FRANKFORTER, 1946, Bull. Nebraska State Mus., vol. 3, no. 1, p. 4, measurements, p. 7.

Bison crassicornis RICHARDSON, 1852–1854, The zoology of the voyage of H.M.S. "Herald," p. 139.

Bison antiquus? LEIDY, 1854, Proc. Acad. Nat. Sci. Philadelphia, vol. 7, p. 210 (Leidy stated "I think not the same as the *Bison crassicornis* Richardson, but probably it may be *Bison latifrons*").

Bison latifrons (Harlan), LEIDY, 1867, Proc. Acad. Nat. Sci. Philadelphia, p. 85; 1869, Jour. Acad. Nat. Sci. Philadelphia, p. 372; 1873, U. S. Geol. Surv. Terr., vol. 1, p. 253.

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

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

Bison latifrons (Harlan), LEIDY, 1867, Proc. Acad. Nat. Sci. Philadelphia, p. 85; 1869, Jour. Acad. Nat. Sci. Philadelphia, p. 373; 1873, U. S. Geol. Surv. Terr., vol. 1, p. 253, pl. 28, figs. 4, 5.

Bison antiquus Leidy, ALLEN, 1876, Mem. Mus. Comp. Zool., vol. 4, no. 10, p. 22. LUCAS, 1899, Proc. U. S. Natl. Mus., vol. 21, p. 759, pls. 69, 70 (*B. californicus* placed in synonymy with *B. antiquus*); 1899, Kansas Univ. Quart., vol. 8, p. 18. CHANDLER, 1916, Univ. California Publ., Bull. Dept. Geol., vol. 9, p. 124. HAY, 1927, Carnegie Inst. Washington Publ., no. 322B, pp. 121, 122.

Bison californicus RHOADS, 1897, Proc. Acad. Nat. Sci. Philadelphia, vol. 49, p. 501, pl. 12, fig. 2. FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 575, 577, 588.

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

Bison pacificus HAY, 1927, Carnegie Inst. Washington Publ., no. 322B, p. 118, fig. 1.

4. References for here-referred specimens:

Fossil Bison MIDDLETON AND MOORE, 1899, Proc. Indiana Acad. Sci., p. 178, fig., p. 179 (Earlham College *B. antiquus* specimen).

Bison antiquus, HAY, 1912, Geol. Surv. Indiana, 36th Ann. Rept., pp. 649–652, figs. 50, 51; 1914, Ann. Rept. Iowa Geol. Surv. for 1912, vol. 23, p. 317, figs. 100, 101; 1913, Proc. U. S. Natl. Mus., vol. 46 (1914), figs. 2, 3. CHANDLER, 1916, Univ. California Publ., Bull. Dept. Geol., vol. 9, pp. 124, 135, figs. 1a, 1b, 2a, 2b, 3a, 3b, 4a, 4b.

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.)

Key No.		Holo-type	No. of Measure-ments	Summary		
				Min.	Av.	Max.
1	Spread of horn-cores, tip to tip	—	10	816	*881*	975
3	Core length on upper curve, tip to burr	(283)	13	220	*281*	344
4	Length of core on lower curve, tip to burr	(360)	10	280	*336*	395
5	Length, tip of core to upper base at burr	(245)	8	197	*245*	280
12	Transverse diameter of core	122	13	92	*107*	122
6	Vertical diameter of core	102	14	90	*98*	108
7	Circumference of core at base	358	14	290	*320*	358
14	Width of cranium between cores and orbits	—	12	292	*319*	357
15	Greatest postorbital width	—	2	346	*353*	360
17	Width of skull at masseteric processes at M^1	—	4	188	*205*	218
O–T	Length, occipital crest to tip of nasals	—	4	482	*510*	527
O–N	Length, occipital crest to tip of nasal-frontal suture	—	11	240	*295*	350
F–P	Basilar length of skull	—	3	520	*545*	560
	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

Bison antiquus taylori (Hay and Cook, in part), BARBOUR AND SCHULTZ, 1941, Bull. Nebraska State Mus., vol. 2, no. 7, p. 68. U.N.S.M. No. 1-8-8-39. SCHULTZ, 1943, Amer. Antiquity, vol. 8, no. 3, p. 247.

Bison species, FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, p. 581.

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 Southwest 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 This paper, pl. 15, figs. 3, 3A

TEXAS

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 Figured by Leidy, 1873, pl. 28, figs. 4, 5; by Rhoads, 1897, pl. 12, fig. 2; by Lucas, 1899a, pls. 69, 70 This paper, pl. 15, figs. 4, 4A Holotype of *Bison "californicus"* Rhoads, 1897
Complete and partial skulls as listed by Chandler, 1916	U.C.M.P.	Four crania from Rancho La Brea Figured by Chandler, 1916
Partial horn-core	C.A.S. 7952	From near bed rock of Centennial Mine, Klamoth River, Siskiyou County, 1888 Figured by Hay, 1927, fig. 1 Holotype of *Bison "pacificus"* Hay, 1927 (This specimen, in the California Academy of Sciences, has had three other numbers, C.A.S. Nos. 10617, 15502, and 15355)

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 Figured by Hay, 1927, pl. 8, fig. 5, text fig. 3
Cranium with horn-cores	Univ. Oregon	From 5 or 6 miles east of The Dalles, Wasco County Figured by Condon, 1902, pl. 29

WASHINGTON

REFERRED

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

MEXICO

Referred

Partial skull, crushed, with P^2–P^4 alv., M^1–M^3	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 figginsi**[1] (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:

Bison figginsi Hay and Cook, 1928, Proc. Colorado Mus. Nat. Hist., vol. 8, no. 2, pt. 1, p. 33. Barbour and Schultz, 1932, Bull. Nebraska State Mus., vol. 1, no. 32, p. 268.

Simobison figginsi (Hay and Cook, 1928), Hay and Cook, 1930, Proc. Colorado Mus. Nat. Hist., vol. 9, no. 2, p. 23, pl. 7, figs. 1, 2. (Single specimen standing for type of genus *Simobison*.)

Bison (*Simobison*) *figginsi* (Hay and Cook), Frick, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, p. 587.

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 and Schultz, 1936, Bull. Nebraska State Mus., vol. 1, p. 436. Frick, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 575, 577, 585.

Stelabison occidentalis taylori, Figgins, 1933, Proc. Colorado Mus. Nat. Hist., vol. 12, no. 4, pp. 19, 20, 22, pl. 1, figs. 3, 4.

Bison antiquus taylori (Hay and Cook), Barbour and Schultz, 1936, Bull. Nebraska State Mus., vol. 1, pp. 434, 435.

3. References for holotype of *B. oliverhayi* Figgins, 1933:

Bison oliverhayi Figgins, 1933, Proc. Colorado Mus. Nat. Hist., vol. 12, no. 4, p. 21, pl. 2, figs. 5, 6, pl. 3. Barbour and Schultz, 1936, Bull. Nebraska State Mus., vol. 1, no. 45, p. 436. Frick, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 575, 577, 585.

4. References for holotype of *B. antiquus barbouri* Schultz and Frankforter, 1946:

Bison antiquus barbouri Schultz and Frankforter, 1946, Bull. Nebraska State Mus., vol. 3, no. 1, p. 7, fig. 1, chart 1 (sp. no. U.N.S.M. No. 30310).

5. References for here-referred specimens:

Bison sp. indet. Hay and Cook, 1930, Proc. Colorado Mus. Nat. Hist., vol. 9, no. 2, p. 30, pl. 9, fig. 1. (Note: Pls. 9 and 10 reversed in this report.)

(?) *Bison taylori* Hay and Cook, Frick, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, p. 585 (sp. no. 1237).

Bison occidentalis Lucas, Figgins, 1933, Proc. Colorado Mus. Nat. Hist., vol. 12, no. 4, pp. 20, 21 (sp. no. 1237).

Subspecific Characters (Based on Male Skulls)

The same general skull proportions and characters as in *B.* (*Simobison*) *a. antiquus*, except horn-cores tend to be longer and a little more posteriorly directed but not approaching *B.* (*Bison*); cores do not rise far above plane of frontals as in *antiquus* and therefore not as in *occidentalis;* frontals flat to slightly arched; orbits tubular and forwardly directed; anterior facial portions appear narrow; dental patterns, although similar to those of other bisons, tend to be slightly more complicated as in *B.* (*Simobison*) *antiquus antiquus.*

[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 subgenus. 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 antiquus* 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 M^3 (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

Skull, crushed, partial, lacking core tips, nasals, and premaxillae. Mounted on skeleton	C.M.N.H. 574	From Lone Wolf Creek, near town of Colorado, Mitchell County Figured by Hay and Cook, 1930

REFERRED

1945 bison find; parts of 50 or more individuals, some having complete skulls		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

Skull, slightly crushed, with horn-cores. Mounted on composite skeleton	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*"
Skull, crushed, lacking tip of right horn-core and most of left core	C.M.N.H. 1240	From Folsom Bison Quarry Figured by Figgins, 1933 Holotype of *B.* "*oliverhayi*"
Skull, young male or cow	1237	From Folsom Bison Quarry Figured by Hay and Cook, 1930
Male skull and composite skeleton, mounted	A.M.N.H. 33801	From Folsom Bison Quarry
Incomplete male skull with left core	33802	From Folsom Bison Quarry
Female skull	33803	From Folsom Bison Quarry
Female skull and composite skeleton	33804	From Folsom Bison Quarry

NEBRASKA

REFERRED

Cranium with complete horn-cores, lacking condyles	U.N.S.M. 30310	From west side of "Devils Gap" southwest of Gothenburg, Dawson County Holotype of *B. antiquus* "*barbouri*"

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

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

Plate 16, figures 2, 2A, referred skull from Kansas

TOTAL AVAILABLE SPECIMENS: 14 MALES

1. References for the holotype:

Bison alleni MARSH, 1877, Amer. Jour. Sci., ser. 3, vol. 14, p. 252. RHOADS, 1897, Proc. Acad. Nat. Sci. Philadelphia, vol. 49, p. 486, footnote 5, p. 488. LUCAS, 1899, Proc. U. S. Natl. Mus., vol. 21, p. 765, pls. 77, 78. GILMORE, 1908 (in part), Smithsonian Misc. Coll., vol. 51, p. 33, pl. 11 (a referred specimen of *B.* (*S.*) *crassicornis* is figured as *B. alleni*). HAY, 1913 (in part), Proc. U. S. Natl. Mus., vol. 46 (1914), p. 182, table, p. 183, text fig. 7, pl. 15, fig. 3, pl. 16, figs. 1, 2, pl. 17, figs. 1, 2 (referred specimens of *B.* (*S.*) *crassicornis* are described and figured as *B. alleni*); 1914 (in part), Iowa Geol. Surv. Ann. Rept. for 1912, vol. 23, p. 326, text fig. 103, pl. 41, figs. 1, 2 (referred specimens of *B.* (*S.*) *crassicornis* are figured as *B. alleni*). VANDERHOOF, 1942, Univ. California Publ., Bull. Dept. Geol., vol. 27, no. 1, p. 6.

Superbison alleni (Marsh), FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 575, 576, 582.

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

Bison willistoni MARTIN, 1924, Kansas Univ. Sci. Bull., vol. 15, no. 6, p. 273, pl. 26, fig. 1, pl. 27, figs. 3, 3a.

3. References for here-referred specimens:

Bison species, HIBBARD, 1939, Trans. Kansas Acad. Sci., vol. 42, p. 469, pl. 5, figs. 19, 20, 21, 22. (Two crania measured and figured.)

Bison aff. *occidentalis* Lucas, SIMPSON, 1933, Amer. Mus. Novitates, no. 667, p. 6, fig. 3.

TABLE 15

SUMMARY OF MALE SKULL MEASUREMENTS AND INDICES OF *B.* (*Simobison*) *alleni* AND MEASUREMENTS OF HOLOTYPE (Y.P.M. No. 911)

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

Key No.		Holo-type	No. of Measure-ments	Summary		
				Min.	Av.	Max.
1	Spread of horn-cores, tip to tip	—	5	1100	*1209*	1338
3	Core length on upper curve, tip to burr	640	10	400	*561*	720
4	Length of core on lower curve, tip to burr	740	10	480	*647*	890
5	Length, tip of core to upper base at burr	540	9	355	*471*	575
12	Transverse diameter of core	143	10	133	*151*	169
6	Vertical diameter of core	117	10	107	*124*	145
7	Circumference of core at base	417	11	378	*434*	495
14	Width of cranium between cores and orbits	—	5	334	*339*	350
15	Greatest postorbital width	—	4	330	*371*	428
17	Width of skull at masseteric processes at M^1	—	1	—	*230*	—
8	Greatest width at auditory openings	—	4	296	*309*	320
9	Width of condyles	—	4	139	*150*	160
O–T	Occipital crest to tip of nasals	—	1	—	*580*	—
O–N	Occipital crest to nasal-frontal suture	—	1	—	*345*	—
11	Occipital crest to lower border foramen magnum	—	2	155	*173*	190
F–P	Basilar length of skull	—	1	—	*620*	—
19	P^2–M^3 alveolar length	—	2	146	*152*	157
M–P	Median length of premaxilla beyond P^2	—	2	165	*167*	169
18	Rostral width at maxillary-premaxillary suture	—	2	134	*142*	149
	Index of core curvature	137	9	121	*135*	155
	Index of core compression	82	10	72	*82*	91
	Index of core proportion	153	10	100	*129*	164
	Index of core length	—	4	114	*142*	169

Bison alleni Marsh, LUCAS, 1899, Proc. U. S. Natl. Mus., vol. 21, pls. 79, 80. HAY, 1927, Carnegie Inst. Washington Publ., no. 322B, pp. 126, 127.

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.* (*Superbison*) *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 *alleni*, *chaneyi*, *latifrons*, and *B.* (*Platycerobison*) *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*) *preoccidentalis*, *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

REFERRED

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. Sternberg and Dale H. Hendrick, 1939 This paper, pl. 16, figs. 2, 2A
Cranium with complete left and partial right horn-core, associated ramus with M_1–M_3	K.U.M.V.P. 4634	From 7½ miles northeast of Newton, Harvey County; collected by Kenneth Scott, 1937 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

NEVADA

REFERRED

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

IDAHO

REFERRED

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

CALIFORNIA

REFERRED

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:

Super-bison FRICK, 1930, Nat. Hist., vol. 30, no. 1, pp. 71, 75, 78.

Superbison FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 567, 572.

Bison VANDERHOOF, 1942 (in part), Univ. California Publ., Bull. Dept. Geol. Sci., vol. 27, no. 1, p. 6.

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*[1] 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 urus, BUCKLAND, 1831, *in* Beechey, Narrative of a voyage to the Pacific, Appendix, vol. 2, pp. 334, 336, 339, pl. 3, fig. 1.

Bison crassicornis RICHARDSON, 1852–1854, Zoology of the voyage of H.M.S. "Herald," pp. 40–42, 139, pl. 9, figs. 1, 2, 3, 4. LEIDY, 1854, Proc. Acad. Nat. Sci. Philadelphia, vol. 7, p. 210. LUCAS, 1899, Proc. U. S. Natl. Mus., vol. 21, pp. 760, 761, 765. GILMORE, 1908, Smithsonian Misc. Coll., vol. 51, p. 31. HAY, 1913, Proc. U. S. Natl. Mus., vol. 46 (1914), pp. 179, 181. BARBOUR AND SCHULTZ, 1936, Bull. Nebraska State Mus., vol. 1, no. 45, p. 436. WILLIAMS, 1937, Trans. Roy. Soc. Canada, ser. 3, vol. 31, sect. 4, p. 108.

Bison latifrons (Harlan), LEIDY, 1869, Jour. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 7, p. 372.

Bison antiquus Leidy, ALLEN, 1876, Mem. Mus. Comp. Zool., vol. 4, no. 10, pp. 21, 24, 26, table 4. RHOADS, 1897, Proc. Acad. Nat. Sci. Philadelphia, vol. 49, pp. 489, 490, 491, 501.

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

Superbison crassicornis (Richardson), FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 573, 575, 577, 589. (An earlier adjectival use of super-bison by Frick, 1930, Nat. Hist., vol. 30, no. 1, pp. 71, 78, without direct mention of lectotype as such.)

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

Bison crassicornis Richardson, LUCAS, 1899, Proc. U. S. Natl. Mus., vol. 21, pp. 760, 761, pls. 73–76. WHITEAVES, 1903, Ottawa Nat., vol. 16, no. 12, pp. 240, 241. GILMORE, 1908, Smithsonian Misc. Coll., vol. 51, p. 31, pl. 4, fig. 2 (in part), pl. 10. HAY, 1913, Proc. U. S. Natl. Mus., vol. 46 (1914), pp. 179, 182, pl. 14, figs. 1, 2, 5. HOLLAND, 1915, Ann. Carnegie Mus., vol. 9, p. 225, pl. 43. CLARK, 1927, Canadian Field Nat., vol. 41, no. 3, pp. 45–47, figs. 1, 2. FRICK, 1930, Nat. Hist., vol. 30, no. 1, pp. 71, 78, figs. 71, 75. (First use of name now applied to subgenus *Superbison* describing *B. crassicornis* from Alaska, but here spelled "super-bison.") WILKERSON, 1932, Amer. Mus. Novitates, no. 525, p. 4, fig. 2. (Name used after Frick, but not taxonomically.) BARBOUR AND SCHULTZ, 1936, Bull. Nebraska State Mus., vol. 1, no. 45, p. 436. WILLIAMS, 1937, Trans. Roy. Soc. Canada, ser. 3, vol. 31, sect. 4, p. 105, pls. 1, 2, 3.

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.

Bison latifrons (Harlan), LEIDY, 1869, Jour. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 7, p. 372.

Bison antiquus Leidy, ALLEN, 1876, Mem. Mus. Comp. Zool., vol. 4, no. 10, p. 21 (see table, p. 26). RHOADS, 1897, Proc. Acad. Nat. Sci. Philadelphia, vol. 49, pp. 483, 484 (U. P. Nos. 13752, 13753; now C.N.H.M. Nos. P-6832, P-6833; see lists).

Bos priscus Bojanus, LYDEKKER, 1898, Wild

[1] VanderHoof (1942, p. 6) attempted to point out that he considered that *Superbison* should contain the small-horned individuals instead of the large-horned because of a plotted measurement factor which he did not clarify.

TABLE 16

SUMMARY OF MALE SKULL MEASUREMENTS AND INDICES OF *B.* (*Superbison*) *crassicornis* AND MEASUREMENTS OF LECTOTYPE (B.M. 1-A)[a]

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

Key No.		Lecto-type	No. of Measure-ments	Summary		
				Min.	Av.	Max.
1	Spread of horn-cores, tip to tip	—	118	765	*963*	1295
2	Greatest spread of cores on outside curve	—	108	790	*986*	1322
	Sheath length on upper curve	—	68	410	*584*	810
3	Core length on upper curve, tip to burr	—	208	295	*409*	610
	Difference between sheaths and core length	—	64	45	*148*	275
4	Length of core on lower curve, tip to burr	—	207	310	*458*	650
5	Length, tip of core to upper base at burr	—	207	280	*365*	530
12	Transverse diameter of core	109	291	90	*110*	137
6	Vertical diameter of core	95	291	82	*98*	118
7	Circumference of core at base	320	286	272	*324*	388
14	Width of cranium between cores and orbits	293	156	255	*288*	332
15	Greatest postorbital width	—	110	307	*349*	408
17	Width of skull at masseteric processes at M^1	—	21	177	*196*	213
8	Greatest width at auditory openings	275	131	250	*284*	314
9	Width of condyles	145	150	115	*136*	159
O–T	Occipital crest to tip of nasals	—	10	473	*491*	503
O–N	Occipital crest to nasal-frontal suture	246	107	235	*272*	315
11	Depth, occipital crest to lower border foramen magnum	158	153	141	*159*	185
F–P	Basilar length of skull	—	8	487	*523*	560
O–P	Over-all length of skull	—	8	558	*598*	642
19	P^2–M^3 alveolar length	—	37	131	*147*	166
20	M^1–M^3 alveolar length	—	30	72	*92*	115
M–P	Median length of premaxilla beyond P^2	—	8	137	*152*	161
18	Rostral width at maxillary-premaxillary suture	—	7	112	*120*	131
	Index of core curvature	—	207	107	*125*	153
	Index of core compression	—	157	81	*90*	103
	Index of core proportion	—	115	100	*126*	166
	Index of core length	—	113	110	*143*	189

[a] After Richardson or estimated from his figures.

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

Bison alleni Marsh, GILMORE, 1908, Smithsonian Misc. Coll., vol. 51, p. 33, pl. 11. HAY, 1913, Proc. U. S. Natl. Mus., vol. 46 (1914), pp. 182–192, text figs. 7, 8, 9, pl. 15, fig. 3, pl. 16, figs. 1, 2, pl. 17, figs. 1, 2 (Alaskan material); Ann. Rept. Iowa Geol. Surv. for 1912, vol. 23, p. 326, fig. 103, pl. 41, figs. 1, 2 (Alaskan material).

Bison occidentalis Lucas, HAY, 1913 (in part), Proc. U. S. Natl. Mus., vol. 46 (1914), pp. 167, 168, pl. 10, figs. 1, 2, 3a, pl. 11, figs. 1, 2, pl. 12, figs. 1, 2, 3, 4, pl. 13, figs. 1, 2, 3; 1914 (in part), Ann. Rept. Iowa Geol. Surv. for 1912, vol. 23, pl. 40, figs. 1, 2 (A.M.N.H. No. 13721 only).

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*).

Superbison occidentalis (Lucas), FRICK, 1937 (in part), Bull. Amer. Mus. Nat. Hist., vol. 69, p. 591 (A.M.N.H. No. 13721).

Superbison crassicornis (Richardson), FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 573, 575, 590, text fig. 57 (A.C.-F:A.M. Nos. 30600, 30568, 30523, 30601).

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 $\frac{4}{4}$ tend to be less molariform in *crassicornis* than in all the later species of *B.* (*Bison*) and *B.* (*Simobison*).

Discussion

Bison (*Superbison*) *crassicornis* was founded 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 segments of the *crassicornis*-like population have been described as distinct species or as subspecies of the loosely defined *Bison priscus*.

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

ALASKA

Lectotype

Cranium with partial horn-cores and orbits	B.M. 1-A	From Eschscholtz Bay; collected by Beechey on the voyage of H.M.S. "Blossom," 1825–1828 Figured by Buckland, 1831; by Richardson, 1852–1854 This paper, pl. 18, fig. 1, pl. 19, fig. 1

Referred

Male skulls and crania:		From near Fairbanks; collected by Peter C. Kaisen, 1929–1930; Albert S. Wilkerson, 1931; Ray Henricksen, 1932; John Dorsh, 1933–1936; Otto Wm. Geist, 1937–1942
Partial skull, lacking nasals and one-half premaxilla, P^2–M^3 alv.	U.A.-F:A.M. 30653	From Goldstream, 1933 This paper, pl. 20, fig. 1, pl. 21, fig. 2, pl. 22, fig. 1
Cranium with sheaths	30524	From Fairbanks area, 1929 Figured by Frick, 1930, vol. 30, no. 1, pp. 71, 75, lower right specimen
Cranium with sheaths, lacking one orbit	30619	From Cleary Creek, 1932 This paper, pl. 20, fig. 2, pl. 21, fig. 3
Cranium with partial orbits	46894	From Cripple Creek, 1941
Cranium with partial orbits and sheaths	30601	From Goldstream, 1931 Figured by Frick, 1937, fig. 57 This paper, pl. 17, fig. 7, pl. 20, fig. 4, pl. 21, fig. 5
Cranium with partial orbits	46895	From Ester Creek, 1942
Cranium with partial orbits	30623	From Cleary Creek, 1932
Cranium with partial orbits	30638	From Goldstream, 1933
Cranium, lacking orbits	30589	From Goldstream, 1931
Cranium with partial orbits	46896	From Fairbanks Creek, 1942
Cranium with partial cores and orbits	30593	From Cleary Creek, 1931
Cranium with one partial and one complete core, partial orbits	30645	From Cleary Creek, 1933
Partial cranium, lacking left core and orbits	30556	From Goldstream, 1930
Cranium with left partial core and orbit	30558	From 17 miles north of Fairbanks, 1930
Cranium with partial cores, lacking orbits	30628	From Fairbanks area, 1932
Cranium with one core, one partial core, no orbits	30615	From Cleary Creek, 1931
Cranium with partial cores, no orbits	30535	From Livengood Creek, 1930
Partial cranium with partial right core, lacks left side	30547	From Cleary Creek, 1930
Cranium with partial cores, lacking orbits	30588	From Goldstream, 1931
Cranium, lacking orbits	46897	From Ester Creek, 1942
Cranium with partial cores, lacks orbits	30602	From Cleary Creek, 1931

	U.A.-F:A.M.	
Cranium with partial cores, lacks orbits	30566	From Cleary Creek, 1930
Cranium with partial cores and orbits	30654	From Goldstream, 1929
Cranium with partial cores, lacks orbits	30515	From Goldstream, 1929
Cranium with partial cores and one partial orbit	30539	From Cleary Creek, 1930
Cranium with partial right core, lacking left core and orbit	30536	From Livengood Creek, 1930
Cranium with partial left core, lacking orbits	30534	From Livengood Creek, 1930
Complete skull, lacks right core tip, left core abnormally shaped and small, P^2–M^1 alv., M^2–M^3	46898	From Engineer Creek, 1941
Cranium with partial cores and orbits	30603	From Cleary Creek, 1931
Cranium with partial orbits	30594	From Chatham, 1931
Cranium with sheaths and partial orbits	30631	From Goldstream, 1933 This paper, pl. 17, fig. 1, pl. 18, fig. 3, pl. 19, fig. 3
Cranium	30649	From upper Cleary Creek, 1934
Cranium with partial orbits	30618	From Cleary Creek, 1932 This paper, pl. 18, fig. 2, pl. 19, fig. 2
Cranium, lacking orbits	30578	From Cleary Creek, 1931
Cranium with partial left core, lacking orbits	30607	From Cleary Creek, 1931
Cranium with partial orbits	46899	From Ester Creek, 1942
Cranium (immature) with partial orbits	46900	From Ester Creek, 1942
Cranium with partial orbits	30609	From Cleary Creek, 1931 This paper, pl. 21, fig. 1
Cranium with partial cores and orbits	30542	From Cleary Creek, 1930
Cranium with sheaths and partial orbits	C.M.N.H. 1368	From Fairbanks area, 1929
Skull with sheaths, lacking one-half premaxilla and nasals, P^2–P^3 alv., P^4, M^1 alv., M^2–M^3; also has mandible	U.A.-F:A.M. 46901	From Engineer Creek (Dawson cut), 1940 This paper, pl. 17, fig. 8, pl. 20, fig. 5, pl. 21, fig. 6, pl. 22, fig. 5
Skull lacking nasals and premaxilla, P^2–P^4 alv., M^1–M^2, M^3 alv.	46902	From Fairbanks Creek, 1940
Complete skull with sheaths, P^2–P^3 alv., P^4–M^3	46903	From Fairbanks Creek, 1940 This paper, pl. 17, fig. 3, pl. 20, fig. 3, pl. 21, fig. 4, pl. 22, fig. 4
Cranium with sheaths and partial orbits	46904	From Goldstream (banks near Fox), 1942
Cranium with left sheath and partial orbits	30512	From Cleary Creek, 1929
Partial cranium with one complete and one partial core, one partial orbit, lacks basicranium	30580	From Gilmore Creek, 1931
Cranium with partial orbits	46905	From Cripple Creek, 1942
Cranium, lacking orbits	30560	From Moose Creek, 1930
Partial cranium with one complete and one partial core, no orbits	30654A	From Fairbanks area
Cranium with partial orbits	30617	From Cleary Creek, 1932
Cranium, lacking left orbit	46906	From Engineer Creek, 1942
Cranium with one partial orbit	30582	From Cleary Creek, 1931
Cranium, lacking orbits	30635	From Goldstream, 1933
Cranium with partial orbits, lacking left core	30571	From Cleary Creek, 1931
Cranium with right orbit and partial left core	30613	From Cleary Creek, 1931

	U.A.-F:A.M.	
Cranium with partial cores, lacking orbits	30533	From Fairbanks area, 1929
Cranium with partial cores, lacking orbits	30528	From Cleary Creek, 1930
Cranium with partial cores, lacking orbits	30544	From Cleary Creek, 1930
Cranium with partial cores, lacking orbits	30550	From Cleary Creek, 1930
Cranium with partial orbits	46907	From Goldstream (banks near Fox), 1940
Cranium with partial left core and partial orbits	30596	From Cleary Creek, 1931
Cranium with partial cores and orbits	30612	From Cleary Creek, 1931
Cranium with partial cores and orbits	30583	From Cleary Creek, 1931
Cranium with partial left and fragment of right core, partial orbits	30587	From Goldstream, 1931
Cranium lacking right core and partial orbits	46908	From Ester Creek, 1942
Cranium with partial right core	46909	From Ester Creek, 1942
Cranium with partial cores and orbits	30513	From Cleary Creek, 1929
Cranium with partial orbits	46910	From Cripple Creek, 1942
Cranium with partial cores, lacking orbits	30517	From Goldstream, 1929
Cranium with partial right core and orbits	30600	From Goldstream, 1931 Figured by Frick, 1937, fig. 57
Skull, complete, with sheaths, P^2–P^4 alv., M^1–M^2, M^3 alv.	46911	From upper Cleary Creek (?), 1937 This paper, pl. 17, fig. 2, pl. 18, fig. 5, pl. 19, fig. 5, pl. 22, fig. 2
Skull, complete, P^2–P^3 alv., P^4–M^3	46912	From Cripple Creek, 1942
Partial skull with sheaths, lacking palate and premaxilla	46913	From Little Eldorado Creek, 1938
Cranium with sheaths, cores, and orbits	46914	From upper Cleary Creek, 1937 This paper, pl. 17, fig. 5, pl. 18, fig. 6, pl. 19, fig. 6
Cranium with sheaths, cores, and orbits	30592	From Cleary Creek, 1931
Cranium with sheaths and partial orbits	30555	From Ruth Creek, 1930
Cranium with left sheath and partial orbits	30632	From Goldstream at Fox, 1933
Skull with sheaths, lacking nasals and premaxilla, P^2 alv., P^3–M^3	46915	From Little Eldorado Creek, 1938
Skull with right sheath, lacking nasals and premaxilla, P^2–P^3 alv., P^4-M^3	46916	From upper Cleary Creek, 1937
Skull with partial left core, lacking nasals and premaxilla, P^2–P^4 alv., M^1–M^3	46917	From upper Cleary Creek, 1937
Skull, lacking right maxilla and premaxilla, P^2–P^4 alv., M^1–M^2	30647	From upper Cleary Creek, 1934
Skull, lacking nasals and premaxilla, P^2–M^3 alv.	46918	From second stripping area in Goldstream, 1937
Cranium with sheaths and partial orbits	30650	From Cleary Creek, 1934
Cranium with sheaths and partial orbits	30579	From Cleary Creek, 1931
Cranium with sheaths and partial orbits	30625	From Goldstream, 1933
Cranium with sheaths and partial orbits	46919	From Goldstream (banks near Fox), 1942

	U.A.-F:A.M.	
Cranium with left sheath and partial orbits	30634	From Goldstream, 1933
Cranium with partial orbits	30629	From Fairbanks area, 1932
Cranium with partial orbits	30621	From Cleary Creek, 1932
Cranium with partial orbits	46920	From Fairbanks Creek, 1942
Cranium with right sheath and partial orbits	46921	From Ester Creek, 1942
Cranium with partial orbits	46922	From Cripple Creek, 1942
Cranium lacking orbits	46923	From Ester Creek, 1942
Cranium with partial right core, lacking orbits	30511	From Cleary Creek, 1929
Cranium with partial orbits, lacking basicranium	30559	From 17 miles north of Fairbanks, 1930
Cranium lacking orbits	30637	From Goldstream, 1933
Cranium with partial left core and orbit, lacking right orbit	30605	From Cleary Creek, 1931
Cranium with partial cores and orbits	30627	From Cleary Creek, 1932
Cranium with right sheath and partial right orbit, lacking left side	30590 30599	From Goldstream, 1931
Cranium with right sheath and partial right orbit, lacking left side	30532	From Fairbanks area, 1929
Cranium with partial orbits and fragment of left core	30608	From Fairbanks area, 1931
Cranium with fragment of left core, lacking orbits	30614	From Goldstream, 1931
Cranium with partial left core, lacking orbits	30577	From Cleary Creek, 1931
Cranium, lacking left side and orbits	30537	From Goldstream, 1930
Cranium with fragment of left core and partial orbits	30562	From Fairbanks area, 1930
Cranium with fragment of cores and partial orbits	30620	From Cleary Creek, 1932
Cranium with sheaths and partial orbits	30527	From Cleary Creek, 1931
Cranium with partial orbits	30551	From Lillian Creek, 1930
Cranium with partial orbits	30569	From Goldstream Camp 21, 1930
Cranium with right sheath, partial left core and partial right orbit	30591	From Fairbanks Creek, 1931
Cranium with fragment of right core and partial orbits	30519	From Goldstream, 1930
Cranium with partial right core and partial orbits, lacking basicranium	30546	From Cleary Creek, 1930
Cranium with partial right core and partial orbits	46941	From Engineer Creek, 1942
Cranium with left sheath and partial left orbit, lacking right side	30540	From Cleary Creek, 1930
Cranium with fragment of cores and partial orbits	30549	From Cleary Creek, 1930
Partial cranium with left sheath, lacking right side	30563	From Fairbanks area, 1930
Skull with sheaths, lacking premaxilla and teeth	30510	From Fairbanks area, 1929 Figured by Frick, 1930, p. 75, bottom left
Skull, lacking premaxilla, P^2–P^4 alv., M^1–M^3	46924	From Engineer Creek, 1939
Skull, lacking left core, right nasal, and premaxilla, P^2–M^1 alv., M^2–M^3	46925	From Little Eldorado Creek, 1938

	U.A.-F:A.M.	
Complete skull with sheaths, P^2–P^4 alv., M^1–M^3	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
Cranium with right sheath and partial orbits	46927	From Seward Peninsula at Candle, 1941. [Candle is near Eschscholtz Bay, the type area for *B.* (*S.*) *crassicornis*]
Skull with left sheath, lacking nasals and premaxilla, P^2–M^1 alv., M^2–M^3	30633	From Goldstream, 1933
Cranium with sheaths	30520	From Goldstream, 1929
Partial skull with sheaths, partial premaxilla, P^2–M^3, left ramus	46928	From Cripple Creek, 1940
Skull, lacking nasals and premaxilla, P^2 alv., P^3–M^3	46929	From Fairbanks Creek, 1940
Skull, lacking nasals and premaxilla, P^2–M^1 alv., M^2, M^3 alv.	46930	From Engineer Creek, 1938
Skull, lacking nasals and premaxilla, P^2–P^4 alv., M^1–M^3	30640	From Goldstream at Fox, 1933
Skull, lacking nasals, premaxilla, and right horn-core, P^2–P^3 alv., P^4–M^3	46931	From upper Cleary Creek, 1937
Cranium with sheaths and partial orbits	30624	From Chatham, 1932
Cranium with left sheath	30521	From Pedro Creek, 1929
Cranium with right sheath and partial orbits	46932	From Livengood, 1941
Cranium with partial orbits	46933	From Fairbanks Creek, 1942
Cranium with one sheath and partial orbits	46934	From Goldstream (banks near Fox), 1942
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 with sheaths, lacking orbits	46936	From Fairbanks Creek, 1940
Cranium, lacking orbits	30545	From Cleary Creek, 1930
Cranium with partial left orbit, lacking right orbit	30654B	
Cranium with partial orbits	46937	From lower Goldstream, 1939
Cranium with partial orbits	30518	From Goldstream, 1929 Figured by Frick, 1930, p. 75, second from bottom right
Cranium, lacking orbits	30654C	
Cranium	30646	From upper Cleary Creek, 1934
Cranium with partial right core and partial orbits	30604	From Fairbanks area, 1931
Cranium, lacking left core and partial orbits	30598	From Fairbanks area, 1931
Cranium with partial cores and orbits	30610	From Cleary Creek, 1931
Cranium with partial right 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, lacking condyles and basicranium	30538	From Goldstream, 1930
Cranium with partial cores	30557	From 17 miles north of Fairbanks, 1930
Cranium with partial orbits	30514 30565	From Goldtsream, 1929, 1930

	U.A.-F:A.M.	
Cranium with right sheath and partial orbits	30561	From Cleary Creek, 1930
Cranium with partial orbits	30611	From Cleary Creek, 1931
Cranium with partial orbits	30586	From Goldstream, 1931
Cranium with weathered cores and partial orbits	30636	From Goldstream, 1933
Cranium with partial left core and partial orbits	30616	From Goldstream, 1931
Cranium with partial left core and partial orbits	30516	From Goldstream, 1929
Cranium with partial cores and orbits	30548	From Cleary Creek, 1930
Cranium with orbits and nasals	C.M.N.H. 1367	From Fairbanks area, 1929
Cranium with partial orbits, tips weathered	U.S.N.M:V.P. 5726	From Little Minook Creek near Rampart; collected by C. W. Gilmore, 1907 Figured by Gilmore, 1908, pl. 10; by Hay, 1913b, pl. 14, figs. 1, 2
Partial cranium, lacking tips	5727	From Little Minook Creek, 6 miles southeast of Rampart; collected by Bowen and Coole through C. W. Gilmore
Cranium of young animal	B.M. 24589	From Eschscholtz Bay: collected by Kellett, 1845–1851
A cast of this specimen is in the United States National Museum	U.S.N.M:V.P. 2078	Figured by Richardson, 1852–1854, as *Bison priscus?*, pl. 7, fig. 1, pl. 10, fig. 1; by Lucas, 1899a, pl. 76 (figure of cast, called *B. crassicornis*); by Hay, 1913b, pl. 13, figs. 2, 3 (figure of cast, as *B. occidentalis*), pp. 176, 177
Left horn-core with sheath of female	Richardson 105	From Eschscholtz Bay, Kellett's collection, 1845–1851 Figured by Richardson, 1852–1854, pl. 13, fig. 3 (as *B. priscus?*)
Cranium with weathered cores	U.S.N.M:V.P. 10607	From Tolovana River
Cranium with horn-cores	U.S.N.M:V.P. 5514	From Tanana River, 20 miles above mouth; collected by Charles Sheldon, 1906 Figured by Hay, 1913b, pl. 11, figs. 1, 2 (as *B. occidentalis*)
Cranium with sheaths, lacking orbits	2383	From Little Minook Creek, 8 miles southeast of Rampart; collected by McLain and Ballou Figured by Gilmore, 1908, pl. 11 (as *B. alleni*); by Hay, 1913b, pl. 15, fig. 3 (as *B. alleni*)
Complete skull with sheaths and mandible, also articulated cervicals, tooth wear (S-3)	7706	From Hunter Creek just below mouth of Dawson Creek about 6 miles southeast of Rampart; collected by James Nelson, 1912 Figured by Hay, 1913b, text figs. 7, 8, 9 (as *B. alleni*), pls. 16, 17; by Hay, 1914, text fig. 103, pl. 41, figs. 1, 2 (as *B. alleni*)
Cranium, lacking orbits	11980	From Kotzebue Sound; collected by H. B. Collins, 1929
Partial cranium, with core surfaces weathered	Formerly U.P. 13752	From tundra behind Point Barrow; collected by Stewart Gulin (see Rhoads, 1897)

	Now C.N.H.M. P-6832	Figured by Hay, 1913b, pl. 12, figs. 1, 2 (as *B. occidentalis*)
Cranium with partial cores, surface weathered	Formerly U.P. 13753	From tundra behind Point Barrow; collected by Stewart Culin (see Rhoads, 1897)
	Now C.N.H.M. P-6833	Figured by Lucas, 1899a, pl. 75
Cranium with partial right core	A.M.N.H. 14303	Data lost, looks like Alaskan fossilization Figured by Hay, 1913b, pl. 12, figs. 3, 4 (as *B. occidentalis*)

CANADA

Referred

Cranium with weathered partial horn-cores	Peter Redpath Mus. McGill Univ.	From near Dawson, Yukon Territory; collected by J. Dudley Bell, preceding 1927 Figured by Clark, 1927, figs. 1, 2
Cranium with orbits	Geol. Mus. Brit. Columbia 2	From Bonanza Creek, Eldorado Claim, Yukon Territory; collected by W. J. Rendell Figured by Williams, 1937, pl. 2
Partial cranium and left horn-core	U.S.N.M:V.P. 1584	From the Yukon or Kotlo River, Yukon Territory; collected by J. H. Turner Figured by Lucas, 1899a, pls. 73, 74
Partial cranium with sheaths	Memorial Mus. Golden Gate Park, San Francisco	From southeast of Dawson, Yukon Territory Figured by Hay, 1913b, pl. 14, fig. 5
Cranium with sheaths	Geol. Mus. Brit. Columbia 1	From Bonanza Creek, Examiner Pup Claim, Yukon Territory Figured by Williams, 1937, pl. 1, figs. 1, 2
Complete skull, lacking part of right maxilla and premaxillae, no premolars, tooth wear (S-3)	A.M.N.H. 13721	From Fox Gulch Mine near Dawson, Yukon Territory; collected by George T. Coffee through L. S. Quackenbush 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 "*Stelabison occidentalis*")
Partial skull with sheaths, lacking nasals, palate, and premaxillae	C.M. 3247	From near Dawson, Yukon Territory; collected by Frank Caldwell, 1907 Figured by W. J. Holland, 1915, pl. 43
Cranium with partial orbits	Mus. Geol. and Surv. Canada 1	From Gold Run Creek, Claim 17, Klondike District, Canada, 15 feet below surface; collected by R. G. McConnell, 1900
Cranium with cores and nasals	2	From Dominion Creek, Claim 83, Klondike District, 30 feet below the surface; collected by W. G. Luker, 1902
Partial cranium with partial left core (young animal or small female)	3	From Bear Creek, Klondike District, 45 feet below surface; collected by W. G. Luker, 1902
Portion of horn-core and ?sheath	4	From Bonanza Creek, Claim 39, Klondike District, 18 feet below the surface; collected by W. Ogilvie, 1898

	C.M.	
Partial male skull, lacking horn-cores and nasals, P^2–M^1 alv., M^2–M^3, tooth wear (S-4)	Geol. Mus. Brit. Columbia 3	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)

D. BISON (PLATYCEROBISON),[1]
NEW SUBGENUS

SUBGENOTYPE: *Bison chaneyi* Cook, 1928.

SUBGENERIC CHARACTERS
(BASED ON MALE SKULLS)

Cores large to moderate, extending from skull in a slight posterior direction with a tendency to be proximally depressed, while 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 retrogressive 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 preent 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. *Platycerobison*, new subgenus, is also represented in Siberia by the species *B.* (*P.*) *pallasii* (Baer, 1823).

[1] From the Greek meaning "flat-horned bisons."

1. Bison (Platycerobison) 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:

Bison chaneyi COOK, 1928, Proc. Colorado Mus. Nat. Hist., vol. 8, no. 3, pp. 34–36, figs. 1, 2. VANDERHOOF, 1942, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 27, no. 1, p. 6, par. 4.

Bison species, FIGGINS, 1931, Proc. Colorado Mus. Nat. Hist., vol. 10, no. 3, p. 22, pl. 1, fig. 2, no. 3, pl. 2, fig. 3, no. 3, pl. 3, fig. 4, no. 3.

Superbison chaneyi (Cook), FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 573–575, 577, 586.

Bison (*Superbison*) *alleni*, SCHULTZ AND FRANKFORTER, 1946, Bull. Nebraska State Mus., vol. 3, no. 1, p. 6.

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

TABLE 17

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.)

Key No.		Holotype of *chaneyi* C.M.N.H. 1147	Cast of Referred *B.* "*priscus*" U.S.N.M:V.P. 2077	Holotype of *geisti* U.A.-F:A.M. 46893	Holotype of *pallasii* I.P.A.S. 11161
1	Spread of horn-cores, tip to tip	1071	1020	810	(842)[a]
2	Greatest spread of cores on outside curve	1068	1125	851	(860)
3	Core length on upper curve, tip to burr	545	530	360	(332)
4	Length of core on lower curve, tip to burr	630	605	425	384
5	Length, tip of core to upper base at burr	440	400	280	287
12	Transverse diameter of core	147	142	121	116
6	Vertical diameter of core	114	111	88	82
7	Circumference of core at base	412	403	340	312
13	Width between bases of cores	355	300	—	308
14	Width of cranium between cores and orbits	325	339	294	306
15	Greatest postorbital width	—	420	356	368
8	Greatest width at auditory openings	305	332	272	294
9	Width of condyles	149	152	136	(137)
O-N	Occipital crest to nasal-frontal suture	—	(302)	—	308
10	Occipital crest to upper border foramen magnum	140	135	120	108
11	Occipital crest to lower border foramen magnum	185	185	158	158
	Index of core curvature	143	151	152	134
	Index of core compression	78	78	73	70
	Index of core proportion	132	131	106	(107)
	Index of core length	167	156	122	(109)

[a] 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 basicranial 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 circumpolar 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 protion 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:

Bison occidentalis, Gilmore, 1908, Smithsonian Misc. Coll., vol. 51, p. 34, pl. 12. Hay, 1913, Proc. U. S. Natl. Mus., vol. 46 (1914), table, p. 168 (U.S.N.M:V.P. No. 2643), pl. 11, figs. 3, 4. Stehlin, 1931, Eclogae Geol. Helvetiae, vol. 24, p. 279, figs. 1D, 3D.

Superbison occidentalis (Lucas), Frick, 1937 (in part), Bull. Amer. Mus. Nat. Hist., vol. 69, p. 591 (U.S.N.M:V.P. No. 2643).

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*) *preoccidentalis* 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*) *alleni*. 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.*) *preoccidentalis*. 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.*) *preoccidentalis*, *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 geologically 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 characters and core shape of the smaller species, *geisti*. This may be another example of retrogressive 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 examination.

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; collected 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

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 deposts of central and northern Alaska

Plate 24, figures 3, 3A, 3B

TOTAL AVAILABLE SPECIMENS: 5

1. References for the holotype:

Bison alaskensis RHOADS, 1897, Proc. Acad. Nat. Sci. Philadelphia, vol. 49, pp. 490, 491, pl. 12 figs. 3, 6.

Bison crassicornis Richardson, LUCAS, 1899, Proc. U. S. Natl. Mus., vol. 21, p. 761. HAY, 1913 (in part), Proc. U. S. Natl. Mus., vol. 46 (1914), table, p. 179 (sp. no. 6834), p. 180, par. 3, pl. 14, figs. 3, 4. WILLIAMS, 1937 (in part), Trans. Roy.

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.)

Key No.		Holotype C.N.H.M. P25226	Referred U.A.-F:A.M. 46939	U.A.-F:A.M. 46940	U.S.N.M:V.P. 11964
1	Spread of horn-cores, tip to tip	1115	—	—	—
2	Greatest spread of cores on outside curve	1130	—	—	—
3	Core length on upper curve, tip to burr	475	520	—	—
4	Length of core on lower curve, tip to burr	528	580	—	—
5	Length, tip of core to upper base at burr	400	465	—	—
12	Transverse diameter of core	129	150	145	120
6	Vertical diameter of core	95	105	113	91
7	Circumference of core at base	355	425	402	330
13	Width between bases of cores	320	—	—	—
14	Width of cranium between cores and orbits	339	—	—	—
15	Greatest postorbital width	402	—	—	—
8	Greatest width at auditory openings	311	—	—	—
9	Width of condyles	160	—	—	—
O-N	Occipital crest to nasal-frontal suture	307	—	—	—
11	Depth, occipital crest to lower border foramen magnum	163	—	—	—
	Index of core curvature	132	126	—	—
	Index of core compression	74	70	78	76
	Index of core proportion	134	122	—	—
	Index of core length	140	—	—	—

Soc. Canada, sect. 4, vol. 31, pp. 108, 109 (holotype listed).

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

Superbison alaskensis (Rhoads), FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 573–575, 578, 592.

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

Bison crassicornis RICHARDSON, 1852–1854 (in part), Zoology of the voyage of H.M.S. "Herald," pp. 42, 43, pl. 13, figs. 1, 2 (sp. no. 91). LEIDY, 1854, Proc. Acad. Nat. Sci. Philadelphia, vol. 7, p. 210. LUCAS, 1899 (in part), Proc. U. S. Natl. Mus., vol. 21, pp. 760, 761 (sp. no. 91), table, p. 765.

Bison latifrons (Harlan), LEIDY, 1869, Jour. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 7, p. 373.

Bison antiquus Leidy, ALLEN, 1876 (in part), Mem. Mus. Comp. Zool., vol. 4, no. 10, p. 24, table, p. 26 (sp. no. 91).

Bison alaskensis RHOADS, 1897, Proc. Acad. Nat. Sci. Philadelphia, vol. 49, pp. 490, 491 (sp. no. 91).

Superbison crassicornis (Richardson), FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, p. 589 (sp. no. 91).

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 dorsoventrally 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:

ALASKA

	Holotype	
Posterior cranium and horn-cores	C.N.H.M.[1] P25226	From tundra behind Point Barrow Figured by Rhoads, 1897, pl. 12, figs. 3, 6; by Hay, 1913b, pl. 14, figs. 3, 4 This paper, pl. 24, figs. 3, 3A, 3B
	Referred	
Complete right horn-core	U.A.-F:A.M. 46939	From Cripple Creek near Fairbanks; collected by Otto Wm. Geist, 1942 This paper, pl. 24, figs. 2, 2A
Basal fragment of left horn-core	46940	From Engineer Creek near Fairbanks; collected by Otto Wm. Geist, 1940
Partial left horn-core	U.S.N.M:V.P. 11964	From Walson Creek, Rampart; collected by Frank Reinosky, 1929
Partial (?) left horn-core	B.M. 91	From Eschscholtz Bay; collected by Kellett, 1845–1851 Figured by Richardson, 1852–1854, pl. 13, figs. 1, 2

E. BISON (GIGANTOBISON),[2] 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 retrogressive 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* problems of both the Old and New Worlds. A liberal view of specific distinction in this subgenus would include six previously described species. As it is, all six species are considered synonyms of *B.* (*Gigantobison*) *latifrons* (Harlan, 1825). The degree of proportionate size and shape differences is no greater than that observed in living plains bison or the Alaskan *B.* (*Superbison*) *crassicornis*, although it is more spectacular. The known specimens are extremely rare, but they present a clearly definable specific population. The physical characters of these giants do, however, suggest a closer relationship to *Superbison*, as here used, than any of the other subgenera.

[1] The holotype was described by Rhoads as being No. 13754 in the collection of the Museum of Science and Arts in the University of Pennsylvania. In December, 1901, this specimen was sent to the Chicago Natural History Museum where it is now C.N.H.M. No. P25226.

[2] From the Greek meaning "giant or mighty bison."

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

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, Ossemens 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,

p. 273. LYDEKKER, 1898, Wild oxen, sheep, and goats of all lands, p. 92.

Urus priscus 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.]

Bos priscus, VON MEYER, 1832, Nova Acta Acad. Caes. Leopoldino-Carolinae, vol. 17 (1835), pp. 140, 141, table p. 168.

Bison latifrons (Harlan), LEIDY, 1852, Proc. Acad. Nat. Sci. Philadelphia, vol. 6, p. 117; 1852, Smithsonian Contrib. Knowl., vol. 5, art, 3, p. 8, pl. 1. ALLEN, 1876, Mem. Mus. Comp. Zool., vol. 4, no. 10, p. 7 (see Allen for complete synonymy of *latifrons* from 1803 to 1876). RHOADS, 1897, Proc. Acad. Nat. Sci. Philadelphia, vol. 49, pl. 12, fig. 4. LUCAS, 1899, Proc. U. S. Natl. Mus., vol. 21, p. 767. HAY, 1913, Proc. U. S. Natl. Mus., vol. 46 (1914), p. 192; 1923, Carnegie Inst. Washington Publ., no. 322, p. 265. VANDERHOOF, 1942, Univ. California Publ., Bull. Dept. Geol., vol. 27, no. 1, p. 3 (best illustration of species).

Superbison latifrons (Harlan), FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 575, 576, 578.

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

Bison ferox MARSH, 1877, Amer. Jour. Sci., ser. 3, vol. 14, p. 252. LUCAS, 1899, Proc. U. S. Natl. Mus., vol. 21, p. 767, pl. 81. SCHULTZ, 1934, Bull. Nebraska State Mus., vol. 1, no. 41, pp. 359 (table "A"), 391.

Bison latifrons (Harlan), HAY, 1924, Carnegie Inst. Washington Publ., no. 322A, p. 199.

Superbison ferox (Marsh), FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 575, 583.

Bison (*Superbison*) *latifrons*, SCHULTZ 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 gravels" near Wellington. This may be the skull that Cope made the type of *Bos crampianus*.)

Bos crampianus COPE, 1894, Proc. Acad. Nat. Sci., Philadelphia, vol. 9, p. 456, pl. 22, figs. 1–4.

Bison alleni Marsh, RHOADS, 1897, Proc. Acad. Nat. Sci. Philadelphia, vol. 49, footnote, p. 486, p. 488, pl. 12, fig. 5. LUCAS, 1899, Proc. U. S. Natl. Mus., vol. 21, pp. 756, 765, 766.

Superbison crampianus (Cope), FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 575, 582.

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

Bos arizonica BLAKE, 1898, Amer. Geol., vol. 22, no. 2, p. 65.

Bison latifrons (Harlan), LUCAS, 1899, Proc. U. S. Natl. Mus., vol. 21, pp. 756, 768.

Superbison arizonica (Blake), FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 575, 587.

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

Bison latifrons (Harlan), MATTHEW, 1909, Science, new ser., vol. 29, p. 198. STERNBERG, 1909, The life of a fossil hunter, fig. 43. OSBORN, 1910, The age of mammals in Europe, Asia and North America, fig. 212 (a).

Bison regius HAY, 1913, Proc. U. S. Natl. Mus., vol. 46 (1914), pp. 192–197, text fig. 10, pl. 18; 1914, Ann. Rept. Iowa Geol. Surv. for 1912, vol. 23, p. 327, pl. 42, figs. 2, 3. COOK, 1928, Proc. Colorado Mus. Nat. Hist., vol. 8, no. 3, pp. 35, 36. VANDERHOOF, 1942, Univ. California Publ., Bull. Dept. Geol., vol. 27, no. 1, pp. 5, 8.

Superbison regius (Hay), FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 575, 582.

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

Bison latifrons (Harlan), COOK, 1931 (Aug.), Jour. Mammal., vol. 12, pp. 275–277.

Bison species, FIGGINS, 1931 (Sept.), Proc. Colorado Mus. Nat. Hist., vol. 10, no. 3, p. 22, pl. 1, fig. 2, no. 1, pl. 2, fig. 3, no. 1, pl. 3, fig. 4, no. 1.

Bison angularis FIGGINS, 1933, Proc. Colorado Mus. Nat. Hist., vol. 12, no. 4, p. 23, pl. 4. SCHULTZ, 1934, Bull. Nebraska State Mus., vol. 1, no. 41, pp. 359 (table "A"), 390.

Superbison angularis (Figgins), FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 575, 584.

Bison (*Superbison*) *latifrons*, SCHULTZ AND FRANKFORTER, 1946, Bull. Nebraska State Mus., vol. 3, no. 1, p. 4.

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

Bison latifrons (Harlan), COOK, 1931 (Aug.), Jour. Mammal., vol. 12, pp. 275, 277.

Bison species, FIGGINS, 1931 (Sept.), Proc. Colorado Mus. Nat. Hist., vol. 10, no. 3, p. 22, pl. 1, fig. 2, no. 2, pl. 2, fig. 3, no. 2, pl. 3, fig. 4, no. 2.

Bison rotundus FIGGINS, 1933, Proc. Colorado Mus. Nat. Hist., vol. 12, no. 4, p. 24, pl. 5. SCHULTZ, 1934, Bull. Nebraska State Mus., vol. 1, p. 359 (table "A"), p. 391. VANDERHOOF, 1942, Univ. California Publ., Bull. Dept. Geol., vol. 27, no. 1, pp. 6, 7.

Superbison rotundus (Figgins), FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, pp. 575, 584.

Bison (*Superbison*) *latifrons*, SCHULTZ AND FRANKFORTER, 1946, Bull. Nebraska State Mus., vol. 3, no. 1, p. 4.

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

Great Fossil Ox CARPENTER, 1846, Amer. Jour. Sci., ser. 2, vol. 1, p. 245, figs. 1, 2.

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.)

Key No.		Holotype	No. of Measurements	Summary		
				Min.	Av.	Max.
1	Spread of horn-cores, tip to tip	—	10	1422	*1758*	2129
2	Greatest spread of cores on outside curve	—	6	1560	*1724*	1945
3	Core length on upper curve tip to burr	—	12	650	*830*	1115
4	Length of core on lower curve, tip to burr	—	9	800	*934*	1156
5	Length, tip of core to upper base at burr	—	8	680	*810*	1020
12	Transverse diameter of core	179	15	140	*162*	184
6	Vertical diameter of core	155	15	123	*144*	164
7	Circumference of core at base	531	16	420	*481*	546
14	Width of cranium between cores and orbits	388	10	348	*370*	402
15	Greatest postorbital width	—	4	357	*397*	434
17	Width of skull at masseteric processes at M^1	—	2	218	*219*	220
8	Greatest width at auditory openings	—	6	306	*323*	340
9	Width of condyles	165	8	140	*157*	175
O–N	Occipital crest to nasal-frontal suture	—	2	301	*306*	310
11	Occipital crest to lower border foramen magnum	186	7	151	*176*	188
F–P	Basilar length of skull	—	2	574	*577*	580
O–P	Over-all length of skull	—	1	—	*640*	—
19	P^2–M^3 alveolar length	—	1	—	*162*	—
20	M^1–M^3 alveolar length	—	2	97	*104*	110
M–P	Median length of premaxilla beyond P^2	—	1	—	*177*	—
18	Rostral width at maxillary-premaxillary suture	—	1	—	*126*	—
	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

Bison latifrons (Harlan), ALLEN, 1876, Mem. Mus. Comp. Zool., vol. 4, no. 10, p. 11, pl. 1 (first figure of Ohio specimen). LUCAS, 1899, Proc. U. S. Natl. Mus., vol. 21, p. 769, pl. 82. HAY, 1913, Proc. U. S. Natl. Mus., vol. 46 (1914), pl. 19, fig. 1. MARTIN, 1927, Kansas Univ. Sci. Bull., vol. 17, no. 7, pls. 42, 43. SIMPSON, 1930, Amer. Mus. Novitates, no. 406, p. 11, fig. 6. VANDERHOOF, 1942, Univ. California Publ., Bull. Dept. Geol., vol. 27, no. 1, pp. 3–8, text figs. 2, 3, 4, pls. 1, 2.

Bos latifrons Harlan, VILLADA, 1903, An. del Mus. Nac. Mexico, vol. 7, pp. 448, 449, pl. 5.

Superbison species FRICK, 1937, Bull. Amer. Mus. Nat. Hist., vol. 69, p. 580.

Superbison chaneyi, FRICK, 1937 (in part), Bull. Amer. Mus. Nat. Hist., vol. 69, p. 586 (Carpenter specimen only).

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; frontals tending 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 slender 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. Skeletal 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.* "*arizonica*," 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 crampianus*"), 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. Reëntering 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-core variations 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:

	No. of Specimens	$\frac{P^2\text{–}M^3}{\text{Over-all Skull Length}}$	
		Range (in Per Cent)	Average (in Per Cent)
B. (*Bison*) *b. bison*	29	24–32	*26*
B. (*Bison*) *preoccidentalis*	7	24–27	*26*
B. (*Superbison*) *crassicornis*	8	23–26	*25*
B. (*Gigantobison*) *latifrons* (after VanderHoof)	1	25	

Twenty specimens are here recorded:

	KENTUCKY	
	HOLOTYPE	
Partial cranium, left side, base of left horn-core	A.N.S.P. 12993	From 12 to 14 miles north of Big Bone Lick[1] Figured by Peale, 1803, fig. 6; 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 This paper, pl. 26, figs. 1, 1A
	OHIO	
	REFERRED	
Complete set of horn-cores with partial cranium	A.M.N.H.[2] 6840	From Brush Creek, Brown County, 1869 Figured by Allen, 1876, pl. 1; by Smith,[3] 1886, pl. 1; by Lucas, 1899a, pl. 82; by Hay, 1913, vol. 46 (1914), pl. 19, fig. 1; 1914, pl. 42, fig. 1 This paper, pl. 26, figs. 2, 2A
	FLORIDA	
	REFERRED	
Cranium with partial horn-cores, lacking orbits	A.M.N.H. 26828	From 2 miles south of Bradenton Figured by Simpson, 1930, p. 11, fig. 6
Part of cranium and right horn-core	U.S.N.M:V.P. 1171	From Withlacoochee River, Marion County; collected by D. Sheppard, 1891
	OKLAHOMA	
	REFERRED	
Left horn-core with portion of center restored	C.N.H.M. P-14636	From Gage, Ellis County; collected by A. Schmalz, 1900
Basal portions of right and left horn-cores	C.M.N.H. 1603	From Hardesty; collected by Mrs. Estelle McNew, 1940
	NEBRASKA	
	REFERRED	
Segment of large horn-core, lacking base and tip	Y.P.M. 910	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.

		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)
Cranium with horn-cores and partial orbits	C.M.N.H. 1187	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. "rotundus"* Figgins (see discussion, p. 207)

KANSAS

REFERRED

Portion of skull anterior to orbits and parts of both horn-cores	A.N.S.P. 3	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)
Skull with horn-cores, lacking premolars	A.M.N.H. 14346	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)
Cranium with horn-cores attached, tips missing	K.U.M.V.P. 201	From 25 miles southeast of Coldwater, Comanche County; collected by James O'Connel, 1925 Figured by Martin,[1] 1927, pl. 42, upper middle figures, pl. 43
Partial right horn-core and cranium with condyles and partial orbit	U.N.S.M. 1-12-12-41	From 15–16 miles west of Stockton, Rooks County; collected by George Sternberg, 1937. Later sent to the University of Nebraska State Museum
Partial cranium and horn-cores	Private Coll., Scott City, Kansas (Now in Univ. of Nebraska)	From Sand Pit near Scott City. Herbert Waite, U.S.G.S., measured and photographed the specimen
Nearly complete skull, lacking teeth	Wellington High School, Sumner County, Kansas	From 1½ miles southeast of Wellington, Sumner County, in the Turner pit, 1940. Data taken from photograph of specimen. This is from the same area as Cope's *"Bos crampianus"*

[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	
	REFERRED	
Partial horn-cores	Univ. Ariz. Last known repository	From near Greaterville, Pima County Never figured Holotype of *B.* "*arizonica*" Blake (see discussion, p. 207)
	TEXAS	
	REFERRED	
Cranium 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*
Cranium with horn-cores	Dr. Mark Francis Collection	From near Beeville, Bee County; collected by Ben Mattingly Referred by Hay, 1927, p. 288, pl. 1, fig. 2, to *B. latifrons*
	CALIFORNIA	
	REFERRED	
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	
	REFERRED	
Cranium 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 reëstablishing 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, ? late Pleistocene. Germany.
Spread of horn-cores, (?1100 mm.).

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

Geologic age unknown, ? late Pleistocene. 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) crassicornis** (Richardson, 1854)

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

SYNONYMS

Bison europaeus lenensis Hilzheimer, 1910
Bison uriformis Hilzheimer, 1910
Bison priscus fraasi Hilzheimer, 1918
Bison priscus longicornis Gromova, 1935
Bison priscus tscherskii Gromova, 1935
Bison priscus deminutus Gromova, 1935

D. **PLATYCEROBISON,** NEW SUBGENUS
1 species

Early to late Pleistocene.
Horn-cores large to moderate sized, dorsoventrally 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) exiguus** (Matsumoto, 1915 [1927])

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

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

Upper Pleistocene. Eastern Mongolia and Siberia.
Spread of horn-cores, 960 mm.

1B. **B. (Parabison) exiguus ?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:

Bos bonasus LINNAEUS, 1758, Systema naturae, ed. 10, vol. 1, p. 71; 1766, *op. cit.*, ed. 12, p. 99. LYDEKKER, 1898, Wild oxen, sheep, and goats of all lands, p. 64.

Bos taurus ferus, GMELIN, 1788, Systema naturae, ed. 13, vol. 1, p. 202.

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.

Urus nostras BOJANUS, 1827, Nova Acta Acad. Caes. Leopoldino-Carolinae, vol. 13, p. 413.

Bison europaeus VON MEYER, 1832, Nova Acta Acad. Caes. Leopoldino-Carolinae, vol. 17 (1835), p. 131, table, p. 168. OWEN, 1848, Proc. Zool. Soc. London, p. 126. LA BAUME, 1908, Schr. Naturf. Gesellsch. Danzig, new ser., vol. 12, no. 3, p. 56.

Bos (*Bison*) *bonasus*, WAGNER, 1838, *in* Schreber, Die Säugethiere in Abbildungen nach der Natur, mit Beschreibungen, pt. 5, vol. 2, p. 1481.

Bison bonassus, GRAY, 1850, Knowsley menagerie, p. 48.

Bison bonasus, FLOWER AND GARSON, 1884, Catalogue Osteological Museum College of Surgeons, pt. 2, p. 232. HILZHEIMER, 1918, Arch. Naturgesch., vol. 84, div. A, no. 6, p. 41. MELNYK, 1932, Ber. der Internatl. Gesellsch. zur Erhaltung des Wisents, vol. 3, no. 3, p. 169 ff.

Wisent, VON LEITHNER, 1927, Ber. der Internatl. Gesellsch. zur Erhaltung des Wisents, vol. 2, no. 1, p. 19, pp. 29–31, pl. 2, figs. 25, 26. MOHR, 1939, Bijd. tot de Dierk., vol. 27, p. 441, figs. 1–15.

Bison bonasus bonasus, GROMOVA, 1935 (November), Trav. Inst. Zool. Acad. Sci. URSS, vol. 2, p. 198, table 8.

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 widespreading, 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[a] 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.)

Key No.		No. of Measurements	*Bison* (*Bison*) *bonasus* Min.	*bonasus* Av.	*bonasus* Max.	*bison bison* Av.	*bison athabascae* Av.
1	Spread of horn-cores, tip to tip	16	525	*608*	689	*581*	*665*
2	Greatest spread of cores on outside curve	7	540	*649*	744	*612*	*683*
3	Core length on upper curve, tip to burr	7	195	*226*	262	*186*	*216*
4	Length of core on lower curve, tip to burr	14	197	*268*	310	*233*	*255*
5	Length, tip of core to upper base at burr	16	147	*187*	223	*168*	*189*
12	Transverse diameter of core	13	67	*79*	86	*78*	*92*
6	Vertical diameter of core	13	57	*71*	85	*74*	*85*
7	Circumference of core at base	18	199	*238*	268	*235*	*271*
14	Width of cranium between cores and orbits	22	224	*254*	284	*264*	*288*
15	Greatest postorbital width	22	292	*316*	242	*317*	*355*
16	Anterior orbital width, at notch	11	226	*246*	281	—	—
17	Width of skull at masseteric process at M^1	7	143	*172*	191	*187*	*195*
8	Greatest width at auditory openings	20	212	*243*	273	*258*	*263*
O-T	Length, occipital crest to tip of nasals	18	415	*443*	478	*437*	*477*
O-N	Length, occipital crest to nasal-frontal suture	18	210	*257*	273	*241*	*286*
10	Occipital crest to upper border of foramen magnum	19	75	*95*	118	—	—
11	Occipital crest to lower border of foramen magnum	17	124	*142*	160	150	149
F-P	Basilar length of skull	21	449	*475*	516	*480*	*537*
O-P	Over-all length of skull	19	490	*526*	580	*541*	*573*
	Index of horn-core curvature	14	123	*143*	180	*139*	*135*
	Index of horn-core compression	13	79	*90*	100	*95*	*92*
	Index of horn-core proportion	7	74	*90*	100	*79*	*80*
	Index of horn-core length	7	74	*86*	96	*71*	*75*

[a] 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). Over-all 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 phyletic line of *Bison* seems to have existed in Eurasia until nearly recent times on a contemporaneous basis with the phyletic 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

Bison europaeus VON MEYER, 1832, Nova Acta Acad. Caes. Leopoldino-Carolinae, vol. 17 (1835), p. 131, table, p. 168. OWEN, 1848, Proc. Zool. Soc. London, p. 126. HILZHEIMER, 1910, Sitzber. Gesellsch. Naturf. Fr., Berlin, no. 4, p. 145. LA BAUME, 1908, Schr. Naturf. Gesellsch., Danzig, new ser., vol. 12, p. 56, table 4.

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 bonasus caucasia GREVÉ, 1906, Zool. Beob., vol. 47, no. 9, pp. 269–272.

Bison kaukasikus HILZHEIMER, 1909, Jahresh. Ver. Vater. Naturk., Württemberg, vol. 65, pl. 7.

Bison caucasicus HILZHEIMER, 1909, Jahresh.

Ver. Vater. Naturk., Württemberg, vol. 65, pp. 250–252, 257, table 1.

Bison bonasus ?caucasicus GROMOVA, 1935 (November), Trav. Inst. Zool. Acad. Sci. URSS, vol. 2, p. 198, table 5 (questions distinctness of this subspecies).

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 primitivus HILZHEIMER, 1909, Jahresh. Ver. Vater. Naturk., Württemberg, vol. 65, pp. 254–256, pl. 7, figs. 6, 6a, table, p. 266 [measurements given under synonymus name, "*sibericus*" Hilzheimer, 1909]; 1910, Sitzber. Gesellsch. Naturf. Fr. Berlin, no. 4, p. 145 [see footnote 1, *B.* "*sibericus*" synonymized with *B. primitivus*].

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.* (*B.*) *occidentalis* and somewhat smaller, more curved and posteriorly twisted than in the Alaskan *B.* (*B.*) *preoccidentalis*.

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 *preoccidentalis*. 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

TABLE 21

MEASUREMENTS[a] OF PRIMITIVE ASIATIC AND SIWALIK *Bison*

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

Key No.		*Bison* (Subgenus?) *silvalensis* (Holotype) Female?	*Bison* (Subgenus?) *palaeo-sinensis* (Lectotype) Male	*Bison* (Subgenus?) *palaeo-sinensis* (Paratype) Female?
1	Spread of horn-cores, tip to tip	—	(536)	(545)
2	Greatest spread of horn-cores on outside curve	—	(693)	(572)
3	Horn-core length on upper curve, tip to burr	—	300	235
4	Length of horn-core on lower curve, tip to burr	—	(420)	—
5	Length, tip of horn-core to upper base at burr	—	200	220
12	Transverse diameter of horn-core	86	(80)	(70)
6	Vertical diameter of horn-core	66	(76)	—
7	Circumference of horn-core at base	254	(245)	—
14	Width of cranium between horn-cores and orbits	221	234	220
15	Greatest postorbital width	(242)	—	—
16	Anterior orbital width, at notch	(195)	—	—
17	Width of skull at masseteric processes at M^1	(141)	—	—
8	Greatest width at auditory openings	(194)	230	210
9	Width of condyles	99	102	100
O-N	Length, occipital crest to nasal-frontal suture	(169)	(175)	(165)
10	Occipital crest to upper border of foramen magnum	(86)	91	—
11	Occipital crest to lower border of foramen magnum	122	131	129
	Index of horn-core curvature	—	(210)	—
	Index of horn-core compression	77	(95)	—
	Index of horn-core proportion	—	(120)	—
	Index of horn-core length	—	127	—

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

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:

Bos sivalensis FALCONER, 1868, Palaeont. Mem., vol. 1, pp. 280, 555 (not figured but measurements given).

Bison sivalensis (Falconer), LYDEKKER, 1878, Palaeont. Indica, ser. 10, vol. 1, p. 122, pls. 15, 17, fig. 1 (Mem. Geol. Surv. India). Type designated and figured by Lydekker from Falconer's MS.

Bison sivalensis Lydekker *ex* Falconer MS, PILGRIM, 1939, Mem. Geol. Surv. India, new ser., vol. 26, mem. no. 1, pp. 325–327.

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, M^1–M^3 (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 dorsoventrally 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

References for the syntypic series and lectotype: *Bison palaeosinensis* CHARDIN AND PIVETEAU, 1930, Ann. Paléont., Paris, vol. 19, pp. 84–86, pl. 15, figs. 1 and 1a (lectotype, male cranium), fig. 2 (paratype, ?female), pl. 16, figs. 1 (partial skull), 2 (superior dentition), 3, 3a (inferior dentition).

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 horn-cores 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 parietals 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 unnumbered 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),[1] 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."

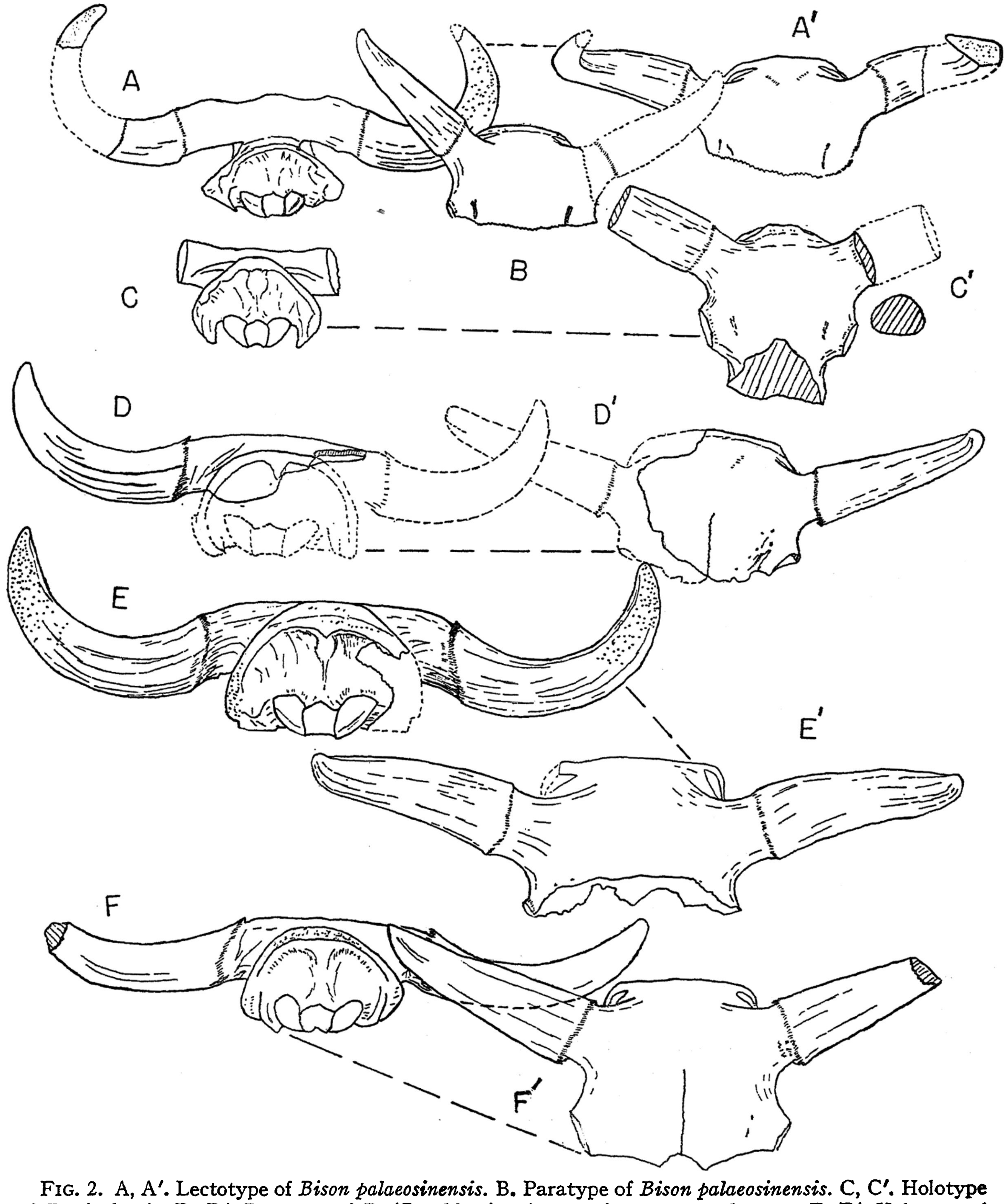


FIG. 2. A, A'. Lectotype of *Bison palaeosinensis*. B. Paratype of *Bison palaeosinensis*. C, C'. Holotype of *B. sivalensis*. D, D'. Paratype of *B. (Parabison) exiguus exiguus*, new subgenus. E, E'. Holotype of *B. (Parabison) exiguus curvicornis*. F, F'. Holotype of *B. (Parabison) exiguus ?harbinensis*, new subspecies. See respective discussions for source of sketches. Approximately $\times 1/10$.

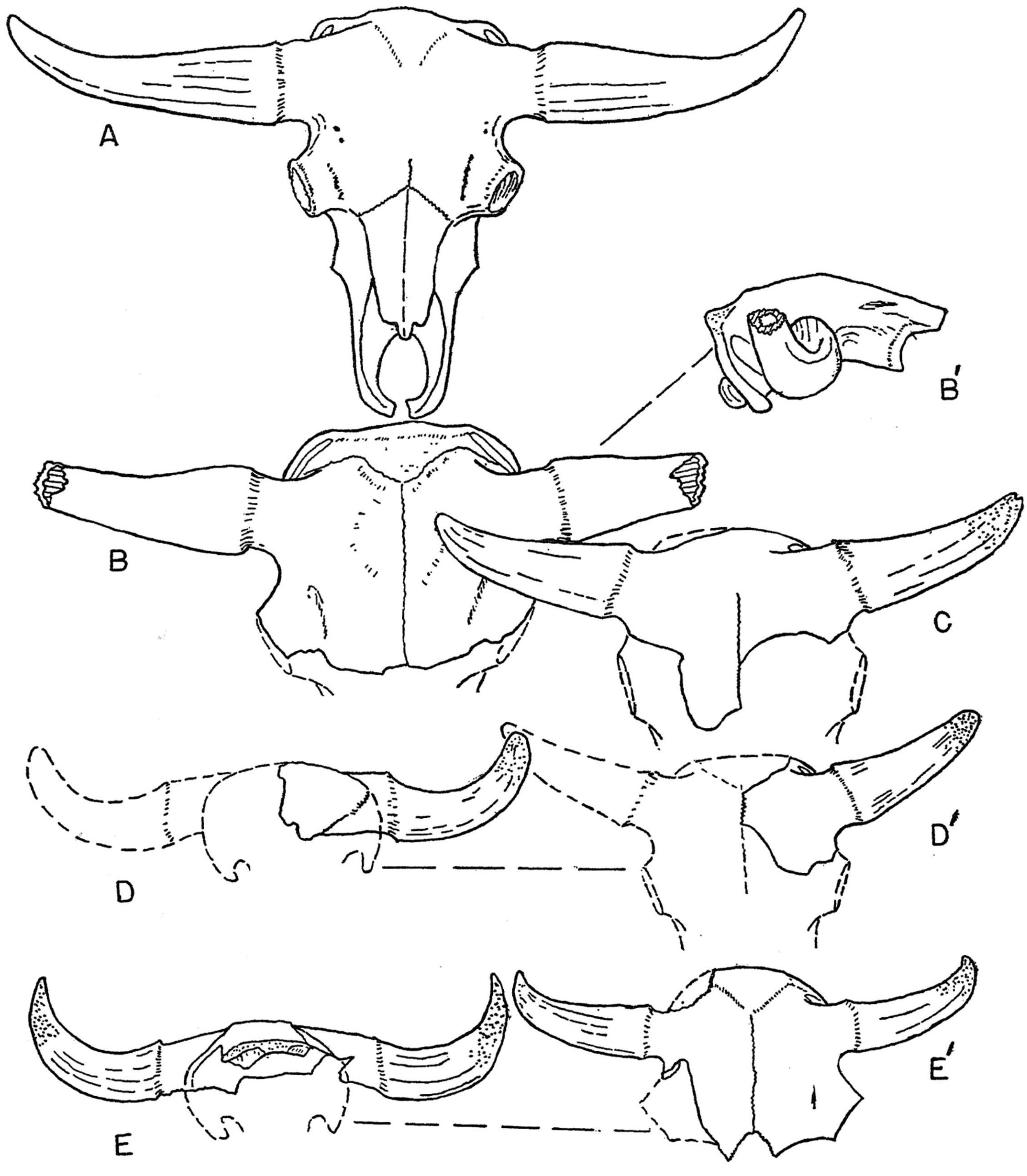


FIG. 3. A. Lectotype of *Bison* (*Simobison*) *priscus*. B, B'. Holotype of *B.* (*Simobison*) *cesaris*. C. Holotype of *B. ?*(*Parabison*) *schoetensacki schoetensacki*, new subgenus. D, D'. Holotype of *B. ?*(*Parabison*) *schoetensacki mediator*. E, E'. Holotype of *B. ?*(*Parabison*) *?schoetensacki maior*. See respective discussions for source of sketches. Approximately ×1/10.

TABLE 22

MEASUREMENTS[a] OF TYPES OF (MALE) *B.* (*Parabison*) *exiguus* and *B.* ?(*Parabison*) *schoetensacki*

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

Key No.		*Bison* (*Parabison*) *exiguus*			*Bison* ?(*Parabison*) *schoetensacki*		
		exiguus Paratype	*curvicornis* Holotype	?*harbinensis* Holotype	*schoetensacki* Holotype	*mediator* Holotype	*maior* Holotype
1	Spread of horn-cores, tip to tip	700	960	(1008)	870	(700)	650
2	Greatest spread of cores on outside curve	—	—	—	—	—	695
3	Core length on upper curve, tip to burr	320	385	(352)	255	(248)	(241)
4	Length of core on lower curve, tip to burr	370	475	(440)	—	329	333
5	Length tip of core to upper base at burr	275	315	(332)	—	230	188
12	Transverse diameter of horn-core	95	123	113	118	105	89
6	Vertical diameter of horn-core	95	105	104	98	96	81
7	Circumference of core at base	300	360	(339)	(339)	348	288
13	Width between bases of cores	—	—	256	300	—	—
14	Width of cranium between horn-cores and orbits	266	335	296	333	(270)	(255)
15	Greatest postorbital width	—	358	320	—	—	338
16	Anterior orbital width, at notch	—	—	270	—	—	—
8	Greatest width at auditory openings	—	336	246	—	—	—
9	Width of condyles	—	155	—	—	—	—
O-N	Length, occipital crest to nasal-frontal suture	—	—	274	(269)	—	(251)
10	Occipital crest to upper border of foramen magnum	—	123	—	—	—	—
11	Occipital crest to lower border of foramen magnum	—	175	156	—	—	—
	Index of horn-core curvature	135	151	(132)	—	143	177
	Index of horn-core compression	100	85	92	83	91	91
	Index of horn-core porportion	107	107	(104)	(75)	(71)	(84)
	Index of horn-core length	120	115	(119)	(77)	(92)	(95)

[a] 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. exiguus*, 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 [England] . . . " 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) ex[i]guus 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 ex[i]guus MATSUMOTO, 1915, Sci. Rept. Tohôku 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. Tohôku 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.

HOLOTYPE: Right ramus with P_2, alv. P_3–P_4, M_1–M_3, in the Geological Institute, Tokyo. No number given.

PARATYPE: Partial cranium with left horn-core in Geological Institute, Tokyo. No number given, but on the illustration of the specimen (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. P_2–M_3 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 characters. 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*) *exiguus exiguus* 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) exiguus curvicornis (Matsumoto, 1927)

Reference for holotype:

Bison occidentalis, MATSUMOTO, 1918, Sci. Rept. Tohôku Imp. Univ., Sendai, Japan, ser. 2 (Geol)., vol. 3, no. 2, p. 85 (in part), pl. 27, figs. 1, 2.

Bison occidentalis curvicornis MATSUMOTO, 1927, Sci. Rept. Tohôku Imp. Univ., Sendai, Japan, ser. 2 (Geol.), vol. 10, no. 3, pp. 52–55, pl. 26, figs. 1, 2, 3.

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, Tohôku 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*) *exiguus curvicornis* (Matsumoto, 1927).

On comparing the paratype of *Bison exiguus* and the holotype of *Bison "occidentalis" curvicornis* it appears that *curvicornis* is more closely related to *exiguus* 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 *exiguus*, 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) exiguus ?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*) *exiguus exiguus* or *B.* (*Parabison*) *exiguus 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 subspecies 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*) *exiguus ?harbinensis* are included for comparison with those of *B.* (*P.*) *exiguus exiguus* and *B.* (*P.*) *exiguus 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 schoentensacki** (Freudenberg, 1910)

References for the holotype:

Bison sp. nov. indt., SCHOETENSACK, 1908, Der Unterkiefer des Homo Heidelbergensis, Leipzig, p. 14, table, p. 15.

Bison schötensacki 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 *schötensacki* to *schoetensacki*). SCHERTZ, 1936, Senckenbergiana, vol. 18, pp. 57–62.

Bison europaeus schoetensacki Freudenberg, HILZHEIMER, 1918, Arch. Naturgesch., vol. 84, div. A, no. 6, p. 71.

Bison priscus schoetensacki Freudenberg, GROMOVA, V., 1935, Trav. Inst. Zool. Acad. Sci. URSS, vol. 2, p. 196.

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:

Bison bonasus mediator HILZHEIMER, 1918, Arch. Naturgesch., vol. 84, div. A, no. 6, pp. 67–73, text figs. 18, 19. DIETRICH, 1932, Zeitschr. Deutschen Geol. Gesellsch., vol. 84, pp. 198, 209, 210. GROMOVA, V., 1935 (November), Trav. Inst. Zool. Acad. Sci., URSS, vol. 2, pp. 188, 198. SCHERTZ, 1936, Senckenbergiana, vol. 18, pp. 65, 67.

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 *mediator* is recognized as a subspecies of *schoetensacki*, additional evidence may show that the difference is only a variation within a population.

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.

Bison bonasus major HILZHEIMER, 1927, Ber. Internatl. Gesellsch. zur Erhaltung des Wisents, vol. 2, no. 2, pp. 159–162, text figs. 1, 2. (Hilzheimer changed the spelling of his specific name *maior* to "*major*" and figured another skull. The discussion indicates that "*major*" is the same subspecies as *maior*.) GROMOVA, V., 1935 (November), Trav. Inst. Zool. Acad. Sci., URSS, vol. 2, p. 183 (Russian), p. 198 (German summary).

HORIZON AND LOCALITY: Hermsdorfer Fliess, Mark Brandenburg District, Germany. Alluvial or sub-Recent in age.

HOLOTYPE: Partial cranium with horn-cores, partial orbits, lacking basal occipital region. In the collections of the Geological-Palaeontological Museum, Berlin. Inventory Number 1909, No. 17.

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

TABLE 23

MEASUREMENTS[a] OF TYPES OF MALE SKULLS AND CRANIA OF *B.* (*Bison*) *occidentalis primitivus*, *B.* (*Simobison*) *cesaris*, AND *B.* (*Simobison*) *priscus*
(Measurements in millimeters, figure 1C for key.)

Key No.		*Bison* (*Bison*) *occidentalis primitivus* Holotype	*Bison* (*Simobison*) *cesaris* Holotype	*Bison* (*Simobison*) *priscus* Lectotype
1	Spread of horn-cores, tip to tip	910	927+	1126
3	Core length on upper curve, tip to burr	—	380+	(380)
4	Length of core on lower curve, tip to burr	465	—	—
5	Length, tip of core to upper base at burr	340	—	—
12	Transverse diameter of core	—	—	(112)
7	Circumference of core at base	370	—	(350)
14	Width of cranium between cores and orbits	310	(325)	(261)
15	Greatest postorbital width	370	(390)	(329)
16	Anterior orbital width, at notch	—	—	(260)
17	Width of skull at masseteric processes at M^1	—	—	(200)
8	Greatest width at auditory openings	290	350	—
O-T	Length, occipital crest to tip of nasals	—	—	(481)
O-N	Length, occipital crest to nasal-frontal suture	—	300	(257)
10	Occipital crest to upper border of foramen magnum	—	130	—
11	Occipital crest to lower border of foramen magnum	110	170	—
O-P	Over-all length of skull	—	—	610

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

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:

Boeuf fossile (fossil ox), FAUJAS-ST.-FOND, 1803, Ann. Mus. d'Hist. Nat., Paris, vol. 2, pp. 190, 191, pl. 43, figs. 1, 2; 1803, ed. [*non viso*], 1805, ed. [*viso*], 1809, ed. [*viso*] Essai de géologie, vol. 1, p. 354, pl. 17, fig. 1.

Aurochs, CUVIER, G., 1808, Ann. Mus. d'Hist. Nat., Paris, vol. 12, p. 381, pl. 34, figs., 1, 11;

1823, Ossemens fossiles, ed. 2. vol. 4; 1825, *op. cit.*, ed. 3, pp. 141, 142, pl. 12, figs. 1, 11.

Bos cesaris SCHLOTHEIM, 1820, Die Petrefactenkunde, 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.

Urus priscus BOJANUS, 1827, Nova Acta Acad. Caes. Leopoldino-Carolinae, vol. 13, div. 2, p. 427. [No figures or descriptions. List of known specimens with figure references, example No. 2 of syntypic series.]

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 subgenus *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 "Cornes d'Aurochs Urua 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

Skull of an ox, KLEIN, 1732, Phil. Trans., London, vol. 37, no. 426, p. 427, figs. 1–3.

Buffalorum PALLAS, 1768, Novi Comment. Acad. Sci. Imp. Petropol., vol. 13 (1769), p. 462.

Aurochs, Cuvier, 1808, Ann. Mus. d'Hist. Nat., Paris, vol. 12, p. 381; 1825, Ossemens fossiles, ed. 3, vol. 4, p. 140.

Boves uri fossil Baer, 1823, De fossilibus mammalium reliquiis in Prussia, p. 25.

Bos priscus, Göppert and von Meyer, 1848, *in* Bronn, Handbuch einer Geschichte der Natur, vol. 3, p. 172.

Bos (Bison) priscus Bojanus, von meyer, 1832, Palaeologica, Frankfurt am Main, p. 97.

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. (Platycerobison) pallasii* (Baer, 1823), this paper, page 237

Example No. 2: Previously named and therefore unavailable. See taxonomy of *B. (Simobison) cesaris* (Schlotheim, 1820), this paper, page 227

Example No. 3: This is the lectotype. See references following this list

Example No. 4: Specifically indeterminate. Bojanus did not give the specific description or figures for his own species. Therefore this specimen was never figured, but according to him this example was found in the province of Erfelden near the Rhine and was placed in the Darmstadt Museum. The identity of this specimen must be considered doubtful (see von Meyer, 1832 [1835], p. 133, No. 10)

Example No. 5: Previously named and therefore unavailable. See taxonomic treatment for *B. (Gigantobison) latifrons* (Harlan, 1825), this paper, page 203

References for lectotype (Bojanus' Example No. 3):

Aurochs, Cuvier, 1823, Ossemens fossiles, ed. 2, vol. 4, pl. 11, fig. 5; 1825, *op. cit.*, ed. 3, vol. 4, p. 142; 1835, *op. cit.*, ed. 4, vol. 6, p. 285; 1836, *op. cit.*, atlas, vol. 2, pl. 172, fig. 5.

Urus priscus Bojanus, 1827, Nova Acta Acad. Caes. Leopoldino-Carolinae, vol. 13, p. 427.

Bos priscus, von Meyer, 1832, Nova Acta Acad. Caes. Leopoldino-Carolinae, vol. 17 (1835), p. 139, table p. 168.

Bison priscus, Hilzheimer, 1918, Arch. Naturgesch., vol. 84, div. A, no. 6, p. 60. Gromova, V., 1932, Zool. Anz., vol. 99, pp. 207, ff.

Locality: Lombardy, Italy, valley of the Po River.

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

Illustrations: Cuvier, 1823 (Ossemens fossiles, 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

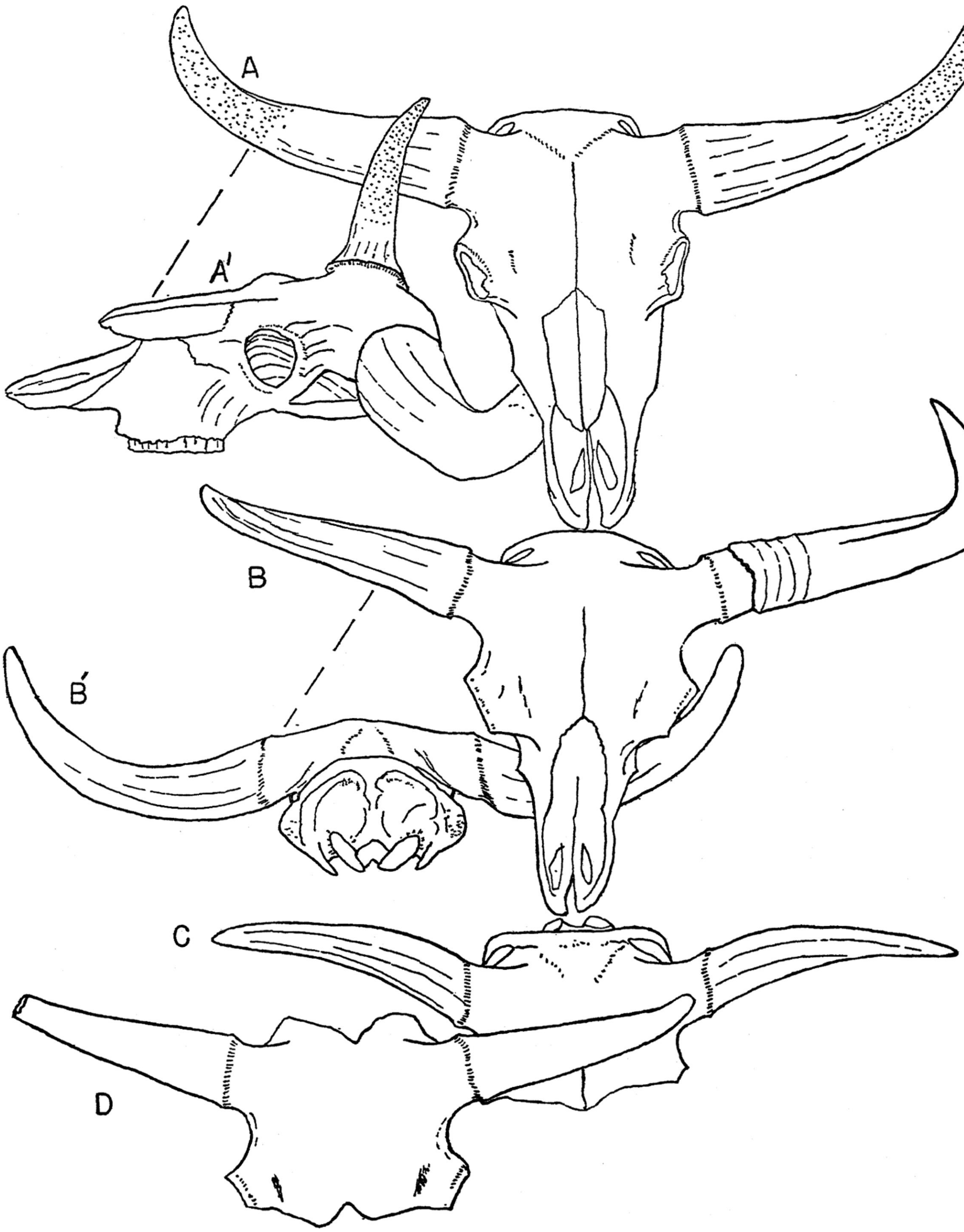


FIG. 4. Synonyms of *Bison* (*Superbison*) *crassicornis*. A, A'. Holotype of *B.* "*priscus fraasi.*" B, B'. Lectotype of *B.* "*priscus longicornis.*" C. Lectotype of *B.* "*priscus tcherskii.*" D. Lectotype of *B.* "*priscus deminutus.*" See respective discussions for source of sketches. Approximately ×1/10.

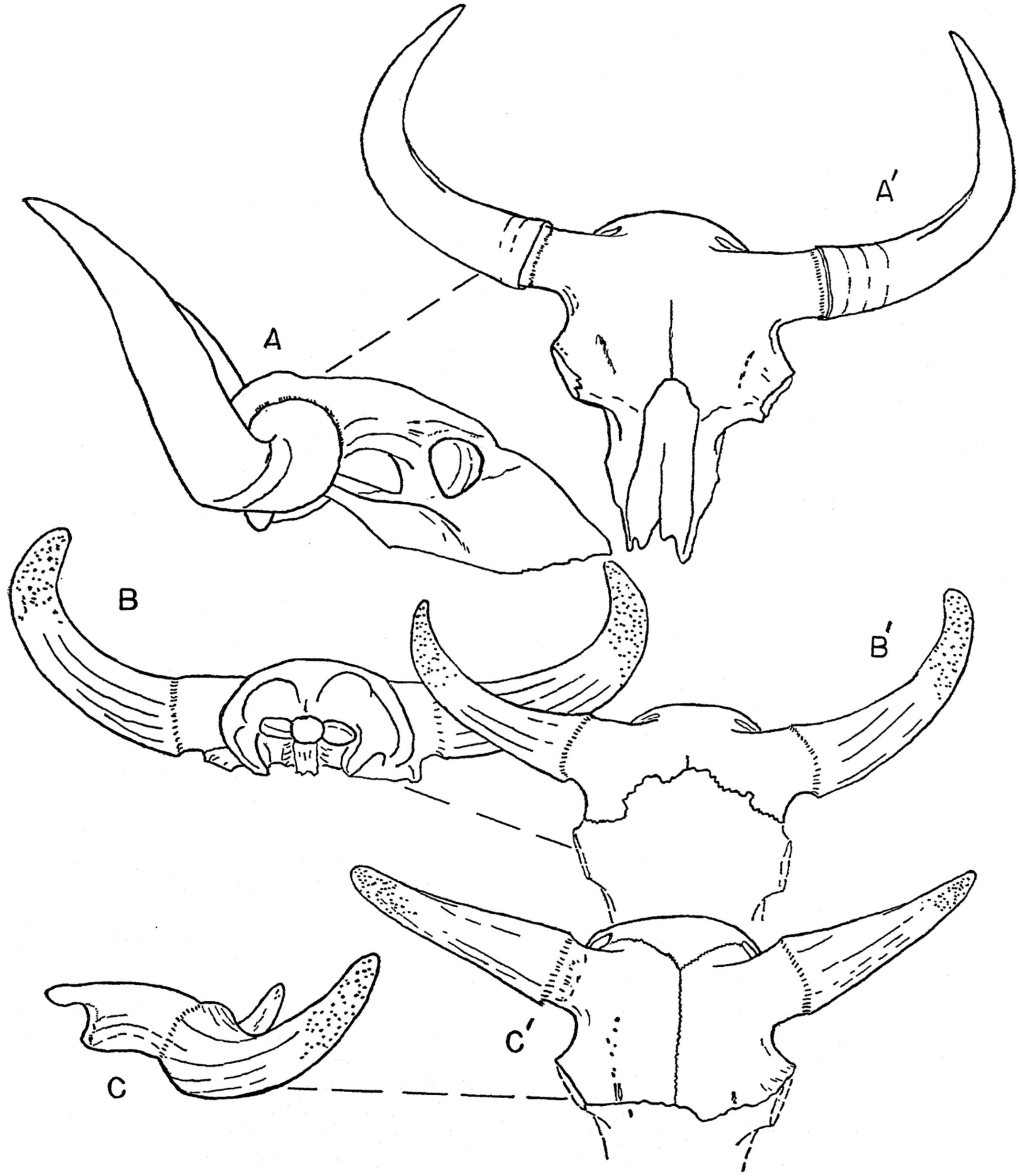


FIG. 5. A, A'. Holotype of *Bison "europaeus lenensis."* B. B'. Holotype of *B. "uriformis,"* synonyms of *B.* (*Superbison*) *crassicornis*. C, C'. Holotype of *B.* (*Bison*) *occidentalis primitivus*. See respective discussions for source of sketches. Approximately ×1/10.

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 revision of the fossil bisons of Europe and indicated a laxity in the use of the name *priscus*. As a result, Hilzheimer (1918, *loc. cit.*) revised the syntypic 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 bisons 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[a] 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.)

Key No.		*Bison "priscus longicornis"* Lectotype I.P.A.S. 2368	*Bison "priscus fraasi"* Holotype S.N.H. 12043	*Bison "priscus tscherskii"* Lectotype I.P.A.S. 4861	*Bison "priscus deminutus"* Lectotype I.P.A.S. 15020	*Bison "europeaus lenensis"* Holotype	*Bison "uriformis"* Holotype M.P.M. 7856
1	Spread of horn-cores, tip to tip	1106	1165	1107	(1026)	—	780
	Spread of horns with sheaths, tip to tip	1005	—	—	—	710	—
2	Greatest spread of cores on outside curve	(1164)	—	—	—	—	895
	Greatest spread of cores with sheaths	—	—	—	—	975	—
3	Core length on upper curve, tip to burr	(500)	(476)	—	—	—	—
4	Length of core on lower curve, tip to burr	575	590	439	456	—	571
5	Length, tip of core to upper base at burr	414	440	387	347	—	324
12	Transverse diameter of core	121	(132)	106	120	(97)	—
6	Vertical diameter of core	108	—	97	110	—	—
7	Circumference of core at base	362	364	321	355	340	383
13	Width between bases of cores	388	—	340	365	—	—
14	Width of cranium between cores and orbits	313	305	292	313	317	302
15	Greatest postorbital width	(365)	340	—	384	360	—
16	Anterior orbital width, at notch	295	282	—	—	275	—
17	Width of skull at masseteric processes at M¹	(185)	—	—	—	(183)	—
8	Greatest width at auditory openings	297	290	284	—	294	292
9	Width of condyles	143	—	—	—	—	—
O-N	Length, occipital crest to nasal-frontal suture	289	—	—	(289)	(239)	—
10	Occipital crest to upper border of foramen magnum	(122)	99	107	—	97	126
11	Occipital crest to lower border of foramen magnum	(151)	—	147	—	141	167
F-P	Basilar length of skull	574	590	—	—	—	—
O-P	Over-all length of skull	648	655	—	—	—	—
	Index of horn-core curvature	139	134	113	131	—	—
	Index of horn-core compression	89	—	92	92	—	—
	Index of horn-core proportion	(138)	(130)	—	—	—	—
	Index of horn-core length	(160)	(156)	—	—	—	—

[a] 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 *crassicornis* ever reached the more southern portions of North America.

Bison "europaeus lenensis" Hilzheimer, 1910

1. Reference for the holotype:
Bison europaeus lenensis HILZHEIMER, 1910, Sitzber. Gesellsch. Naturf. Fr., Berlin, no. 4, pp. 143–145, text figs. 8, 9.

HORIZON AND LOCALITY: Wilui River, left tributary of the Lena River in Siberia. No geologic data given.

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 primitivus* (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 *primitivus.* 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 *primitivus,* but since the cores are proximally depressed it appears that this tends to remove the holotype from relationship with *primitivus* 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.

HOLOTYPE: Posterior cranium with complete horn-cores. In Mark Provincial Museum collections, No. 7856.

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:

Bison priscus Bojanus, Hilzheimer, 1909, Jahresh. Ver. Vater. Naturk., Württemberg, vol. 65, pp. 252–254, pl. 7, figs. 2, 29, table 266 (No. 12034).

Bison priscus fraasi Hilzheimer, 1918, Arch. Naturgesch., vol. 84, div. A, no. 6, p. 66. Gromova, V., 1935 (November), Trav. Inst. Zool. Acad. Sci. URSS, vol. 2, p. 197.

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, P^2–M^1 alv., M^2–M^3, No. 12043 in the Stuttgart Natural History collections.

Illustrations: See Hilzheimer, 1909; also this paper, figure 4A, A′.

Measurements: Table 24, after Hilheimer.

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:

Bison priscus longicornis Gromova, V., 1935 (August), Trav. Inst. Paleozool. Acad. Sci. URSS, vol. 4, pp. 137–147, text fig. 1a [lectotype, No. 2368], table 1 [type description in Russian with German summary]; 1935 (November), Trav. Inst. Zool. Acad. Sci., URSS, vol. 2, pp. 105–124 [Russian], p. 196 [German summary], pl. 7, figs. 1, 2, 3 [No. 2368]. Entire syntypic series shown in pls. 3–7, inclusive.

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, P^2–P^3 alv., P^4–M^3. 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 deminutus"* 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

References for the syntypic series and lectotype:
Bison priscus tscherskii GROMOVA, V., 1935 (August), Trav. Inst. Paleozool. Acad. Sci. URSS, vol. 4, p. 139 [not figured but name mentioned]; 1935 (November), Trav. Inst. Zool. Acad. Sci. URSS, vol. 2, pp. 133–137 [type description in Russian], p. 197 [summary in German], pl. 8, figs. 1–4 [syntypic crania, lectotype here designated as fig. 1, I.P.A.S. No. 4861].

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 widespreading 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 *"tsherskii"* as later given by Gromova.

Bison "priscus deminutus" Gromova, 1935

References for the syntypic series and lectotype: *Bison priscus deminutus* GROMOVA, V., 1935 (August), Trav. Inst. Paleozool. Acad. Sci. URSS, vol. 4, p. 141 [not figured but name mentioned]; 1935 (November), Trav. Inst. Zool. Acad. Sci. URSS, vol. 2, pp. 124–133 [type description in Russian], pp. 197–198 [summary in German], pl. 9, fig. 1, 2 [syntypic crania, lectotype here designated as fig. 1, I.P.A.S. No. 15020].

LOCALITY: Indefinite localities in Europe and northern Asia. Presumably of late Pleistocene age.

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 subgenus *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].

crania Buffalorum gigantea, PALLAS, 1768, Novi Comment. Acad. Sci. Imp. Petropol., vol. 13 (1769), pp. 460–468, pl. 11, figs. 1, 2. Note: Pallas did not apply a specific name.

Aurochs, CUVIER, G., 1808, Ann. Mus. d'Hist. Nat., Paris, vol. 12, p. 386, pl. 34, figs. 4, 5; 1812, Ossemens fossiles, vol. 4, pp. 54–59, pl. 3, figs. 4, 5; 1823, *op. cit.,* [ed. 2]; 1825, *op. cit.,* ed. 3, vol. 6, p. 144, pl. 12, figs. 4, 5; 1835, *op. cit.,* ed. 4, vol. 6, p. 289 [vol. 2 of atlas, 1936], pl. 173, figs. 4, 5 [Cuvier's figures after Pallas, 1768].

Boves pallasii BAER, 1823, De fossilibus mammalium reliquiis in Prussia, Regiomonti, Typis Hartungianis, pp. 27, 28. (First application of a scientific name to Bojanus' example No. 1 of his syntypic series standing for *B. priscus.*)

Urus priscus BOJANUS, 1827, Nova Acta Acad. Caes. Leopoldino-Carolinae, vol. 13, pt. 2, p. 427 [holotype mentioned in syntypic series as example No. 1, but not described or figured].

Bos (*Bison*) *priscus* VON MEYER, 1832, Palaeologica, p. 96.

Bison priscus, TSCHERSKI, 1892, Mém. Acad. Imp. Sci., St. Pétersbourg, ser. 7, vol. 40, no. 1 (1893), pp. 76–85. HAY, 1913, Proc. U. S. Natl. Mus., vol. 46 (1914), p. 161, pl. 8, fig. 3 (after

Pallas). HILZHEIMER, 1918, Arch. Naturgesch., vol. 84, div. A, no. 6, p. 59. GROMOVA, V., 1932, Zool. Anz., vol. 99, pp. 207–221, text figs. 1–5 [holotype of *pallasii* well figured and measured].

Bison priscus priscus GROMOVA, V., 1935 (August), Trav. Inst. Paleozool. Acad. Sci. URSS, vol. 4, pp. 141, 146; 1935 (November), Trav. Inst. Zool. Acad. Sci. URSS, vol. 2, pp. 93–95 [Russian], p. 196 [German], pl. 1, figs. 1, 2, pl. 2, figs. 1, 2, tables 1, 4, 5, 7, and map.

LOCALITY: The Ilga River, a tributary on the headwaters of the Lena River, near the city of Vercholensk 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.* (*Platycerobison*) *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* (*Platybison*) *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. The 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 syntypic series of *B. priscus* Bojanus, 1827. This specimen was Bojanus' first listed example in the syntypic 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 translata descripsit.* Hujus speciei nostrum esse credimus, quia eundem animadevertimus. . . . .

"Caret haec species, e terrarum fundo reviviscens, nomine proprio Divini Pallasii nomen 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 pallasii* to the specimen figured 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 *pallasii*, it has no bearing on the validity of the name when applied to *Bison*.

" *Novi comment. Acad. Petrop. T. XIII. p. 460. cum icone, quae denuo expressa exstat in Cuvieri opere de ossib. fossil."—with a figure which is again clearly shown in Curvier's work on fossil bones. [Cuvier figures only one of the two specimens figured by Pallas and this is the holotype of *pallasii*.]

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., Hilzheimer, 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

Bos velanus Robert, 1829, Ann. Soc. Agr. Sci., Arts, and Comm. du Puy, vol. 4, p. 84, pl. 4, figs. 1, 2, 3; 1830, Ann. Sci. Lettres, Ind. l'Auvergne, Acad. Sci. Belles-Lettres et Arts, Clermont-Ferrand, vol. 3, p. 403 [an extract of the 1829 paper].

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

Bos intermedius de Serres, 1838, Essai sur les cavernes a ossements et sur les causes qui les y ont accumulés, ed. 3, Montpellier, pp. 159, 205 [name mentioned but no description given]. De Serres, Dubrueil, and Jeanjean, 1839, Recherches sur les ossemens humatiles des cavernes de Lunel-Viel, Montpellier, pp. 205–209, pl. 12, fig. 8, pl. 13, figs. 13, 14, 15, 16, 17, pl. 19, figs. 12, 13. Göppert and von Meyer, 1848, *in* Bronn, Heinrich, Handbuch einer Geschichte der Natur, vol. 3, p. 172.

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 P^4–M^2. 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

Bison minor Owen, 1846, A history of British fossil mammals and birds, p. 497, text fig. 206. Freudenberg, 1914, Geol. Palaeont. Abhandl., new ser., vol. 12, table 93, pp. 95, 96.

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

Bison alticornis Marsh, 1887, Amer. Jour. Sci., vol. 34, p. 323, figs. 1, 2.
Ceratops alticornis (Marsh), Marsh, 1889, *ibid.*, vol. 38, pp. 174, 175.

"Bos" scaphoceras Cope, 1894

Bos scaphoceras Cope, 1894, Jour. Acad. Nat. Sci. Philadelphia, vol. 9, p. 457, pl. 22, figs. 5–9.

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" appalachicolus Rhoads, 1895

Bison appalachicolus Rhoads, 1895, Proc. Acad. Nat. Sci. Philadelphia, vol. 47, p. 248.
Ovibos (*Boötherium?*) *appalachicolus* (Rhoads), Rhoads, 1897, *ibid.*, vol. 49, p. 492.

Lepidosteus bison, Leidy, 1860

Lepidosteus bison, Leidy, 1860, *in* Holmes, Francis S., Post-pliocene Fossils of South Carolina, p. 118.

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.

"*Bison patifrons*," RHOADS, 1895, Proc. Acad. Nat. Sci. Philadelphia, vol. 47, p. 248.

This is an obvious typographical error, in place of which Rhoads meant *Bison latifrons*.

? Nomina Nuda IN EURASIAN LITERATURE

Bos elatus and *Bos giganteus* Croizet and Jobert, GÖPPERT AND VON MEYER, 1848, *in* Bronn, Heinrich, Handbuch einer Geschichte der Natur, vol. 3, pp. liii, lxxi, 172.

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-Dome, pet. in folio, tome I., avec 35 pll., 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

Bison fossilis and *Bos colossus*, GÖPPERT AND VON MEYER, 1848, *in* Bronn, Heinrich, Handbuch einer Geschichte der Natur, vol. 3, p. 169 (*B. fossilis*) and p. 172 (*Bos colossus*).

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.

"*Bison europaeus sibericus*" HILZHEIMER, 1910, Sitzber. Gesellsch. Naturf. Fr., Berlin, no. 4, p. 145.

It is evident that Hilzheimer confused his name *B. "europaeus lenensis"* and used *B. "europaeus sibericus"* since he gave no description of "*sibericus*."

"*Bison suessenbornensis*," FREUDENBERG, 1914, Geol. Paleont. Abhandl., Jena, new ser., vol. 12, nos. 4/5, p. 86.

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.

"*Bison primigenus*," AHERNS, 1933, Jour. Mammal., vol. 14, p. 80.

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

Bos latifrons FISCHER DE WALDHEIM, 1830, Bull. Soc. Imp. Nat. Moscou, 2d année, pp. 81–84, pl. 2.

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.

CONCLUSIONS

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.* (*Gigantobison*) *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 nachlinnéische Name jeder identifizierbaren spezifischen Form ist anerkannt worden. 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 *Bisons* und sollten gattungsmässig nicht losgetrennt werden.

Vor allem muss eine genauere Anwendung des Namens *Bison priscus* geübt werden, damit ein Verständnis aller fossilen eurasischen *Bisons* erzielt werden kann. Die syntypische 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 Uebereinstimmung mit der gebräuchlichen Auslegung der internationalen Regeln der zoologischen Nomenklatur identifiziert worden.

RÉSUMÉ

Les auteurs ont réuni en un seul rapport toutes les dénominations spécifiques du *Bison* americain et eurasiatique. Le premier nom post-linnéen applicable a chaque forme spécifique identifiable a été reconnu. Un essai d'établir une méthode de travail standardisée est presenté avec des explications. Ainsi, toutes les mensurations crâniennes utilisées dans les tableaux sont expliquées sur la figure 1C, qui sert de clef.

Quoique le genre *Bison* ait été divisé en six sous-genres, determinés 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 réstreindre 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 caractèristiques du *Bison priscus* a été indentifié 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.)

Name	Horn-core Index of											
	Curvature			Compression			Proportion			Length		
	Min.	Av.	Max.	Min.	Av.	Max.	Min.	Av.	Max.	Min.	Av.	Max.
A. *Bison* (*Bison*)												
a[1] *B.* (*B.*) *bison bison*	120	*139*	182	85	*95*	101	66	*79*	104	57	*71*	90
a *B.* (*B.*) *bison athabascae*	126	*135*	149	84	*92*	98	62	*80*	92	57	*75*	90
e[2] *B.* (*B.*) *bonasus*	123	*143*	180	79	*90*	100	74	*90*	100	74	*86*	96
a*[3] *B.* (*B.*) *occidentalis*	121	*140*	169	86	*93*	104	85	*97*	110	88	*95*	112
a* *B.* (*B.*) *preoccidentalis*	112	*126*	134	83	*90*	94	100	*113*	131	110	*128*	152
B. *Bison* (*Simobison*)												
a* *B.* (*S.*) *antiquus antiquus*	128	*138*	147	83	*93*	108	68	*88*	100	66	*89*	114
a* *B.* (*S.*) *alleni*	121	*135*	155	72	*82*	91	100	*129*	164	114	*142*	169
C. *Bison* (*Superbison*)												
a* *B.* (*S.*) *crassicornis*	107	*125*	153	81	*90*	103	100	*126*	166	110	*143*	189
D. *Bison* (*Platycerobison*)												
a* *B.* (*P.*) *chaneyi*		*143*			*78*			*132*			*167*	
a* *B.* (*P.*) *alaskensis*		*132*			*74*			*134*			*140*	
a* *B.* (*P.*) *geisti*		*152*			*73*			*106*			*122*	
e* *B.* (*P.*) *pallasii*		*134*			*70*			(*107*)			*109*	
E. *Bison* (*Gigantobison*)												
B. (*G.*) *latifrons*	110	*118*	131	80	*89*	93	147	*176*	210	209	*245*	300
F. *Bison* (subgenus?)												
e* *B.* (?) *palaeosinensis*		(*210*)			(*95*)			(*120*)			*127*	
G. *Bison* (*Parabison*)												
e* *B.* (*P.*) *exiguus exiguus*		*135*			*100*			*107*			*120*	
e* *B.* (*P.*) *exiguus curvicornis*		*151*			*85*			*107*			*115*	
e* *B.* (*P.*) *exiguus ?harbinensis*		(*132*)			*92*			(*104*)			(*119*)	
Bison ?(*Parabison*)												
e* *B. ?*(*P.*) *schoetensacki schoetensacki*		—			*83*			(*75*)			(*77*)	
e* *B. ?*(*P.*) *schoetensacki mediator*		*143*			*91*			(*71*)			(*92*)	
e* *B. ?*(*P.*) *?schoetensacki maior*		*177*			*91*			(*84*)			(*95*)	

[1] a, North American occurrence.
[2] e, Eurasian occurrence.
[3] *, extinct.

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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 dentitions 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.

2, 2A, —, 2C. A.M.N.H.:M. No. 77897. Tooth wear, I-S.

3, 3A, 3B, 3C. A.M.N.H:M. No. 100027. Tooth wear, I-S.

4, 4A, 4B, 4C. A.M.N.H:M. No. 130212. Tooth wear, I-S.

5, 5A, 5B, 5C. A.M.N.H:M. No. 98958. Tooth wear, A-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.

2, 2A, 2B, 2C. A.M.N.H:M. No. 16326. Tooth wear, S-1.

3, 3A, 3B, 3C. A.M.N.H:M. No. 130209. Tooth wear, S-2.

4, 4A, 4B, 4C. A.M.N.H:M. No. 16299. Tooth wear, S-3.

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.

2, 2A, 2B, 2C. *B.* (*B.*) *b. bison;* A.M.N.H:M. No. 5475. Tooth wear, S-4.

3, 3A, 3B, 3C. *B.* (*B.*) *b. athabascae;* A.M.N.H:M. No. 73615. Tooth wear, S-3.

4, 4A, 4B (rev.). *B.* (*B.*) *bonasus;* A.M.N.H:M. No. 35490. 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.

2, 2A, 2B, 2C. A.M.N.H:M. No. 70376. Tooth wear, S-1.

3, 3A, 3B, 3C. A.M.N.H:M. No. 332. Tooth wear, S-2.

4, 4A, 4B, 4C. A.M.N.H:M. No. 10729. Tooth wear, S-3.

5, 5A, 5B, 5C. A.M.N.H:M. No. 19380. Tooth wear, S-4.

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.

3, 3A. U.A.-F:A.M. No. 46503. Tooth wear, I-S.

4, 4A. U.A.-F:A.M. No. 46504. Tooth wear, I-S.

5, 5A. U.A.-F:A.M. No. 46505. Tooth wear, A-S.

PLATE 13

Lateral and dental views of tooth development in *Bison* rami, early maturity to old age.

1, 1A. U.A.-F:A.M. No. 46506. Tooth wear, A-S, just at start of S-1 wear stage.

2, 2A. U.A.-F:A.M. No. 46511. Tooth wear, S-2.

3, 3A. U.A.-F:A.M. No. 46514. Tooth wear, S-3.

4, 4A. U.A.-F:A.M. No. 46516. Tooth wear, S-4.

5, 5A. U.A.-F:A.M. No. 46518. Tooth wear, S-4.

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, 1B. *B.* (*Bison*) *bison bison* ref. from Montana; A.M.N.H:M. No. 16318.

2, 2A, 2B. Plastotype of *B.* (*Bison*) *occidentalis* Lucas, from Alaska; U.S.N.M:V.P. No. 4157.

3, 3A, 3B, 3C. Holotype of *B.* (*Bison*) *preoccidentalis*, 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*) *antiquus* compared with males of *B.* (*Bison*) species on plate 14.

1, 1A. Holotype of *B.* (*Simobison*) *antiquus antiquus* (Leidy, 1852), from Big Bone Lick, Kentucky; A.N.S.P. No. 12990.

2, 2A, 2B. Female *B.* (*Simobison*) *antiquus antiquus* 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, 5B (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. *B.* (*Simobison*) *alleni*, ref., male from near Lenora, Kansas; F.H.K.S.C. No. 40, courtesy of Mr. George F. Sternberg.

3, 3A. *B.* (*Simobison*) *?alleni*, ref., ?female from Great Falls, Montana; A.M.N.H. No. 14479.

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.

1. U.A.-F:A.M. No. 30609.
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).

4, 4A. U.A.-F:A.M. No. 30643.

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).

7, 7A. U.A.-F:A.M. No. 46943.

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.

2, 2A, *B.* (*Platycerobison*) *alaskensis*, ref., from near Fairbanks, Alaska; U.A.-F:A.M. No. 46939.

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.

2, 2A, 2B. Holotype of *B.* (*Platycerobison*) *geisti*, new species, from near Fairbanks, Alaska; U.A.-F:A.M. No. 46893.

3, 3A, 3B. Holotype of *B.* (*Platycerobison*) *pallasii* (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*).

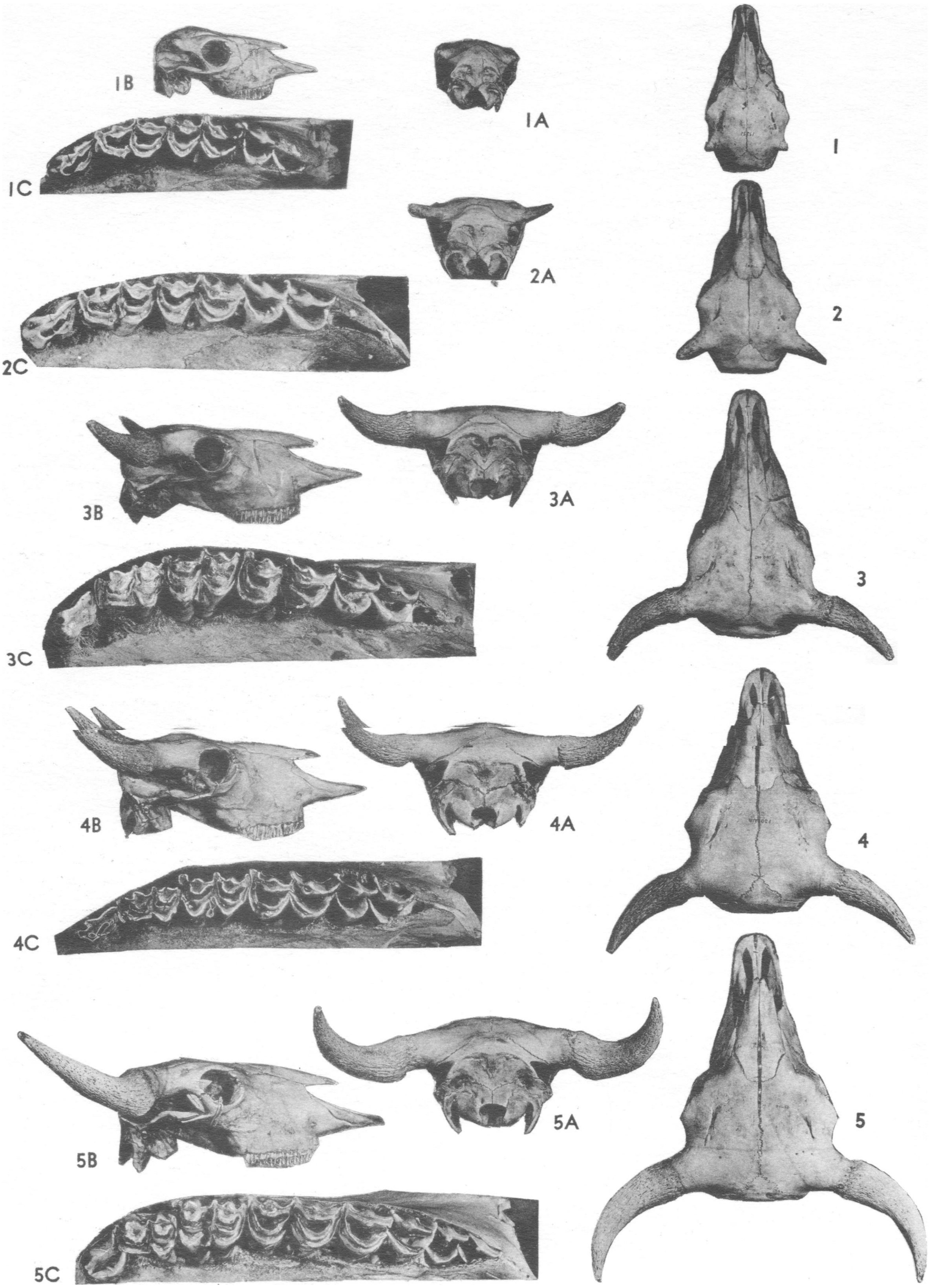
1, 1A. Holotype of *B.* (*Gigantobison*) *latifrons* (Harlan, 1825), from 12 to 14 miles north of Big Bone Lick, Kentucky; A.N.S.P. No. 12993. Also subgenotypic species.

2, 2A. *B.* (*Gigantobison*) *latifrons*, ref., from Brown County, Ohio. A.M.N.H. No. 6840.

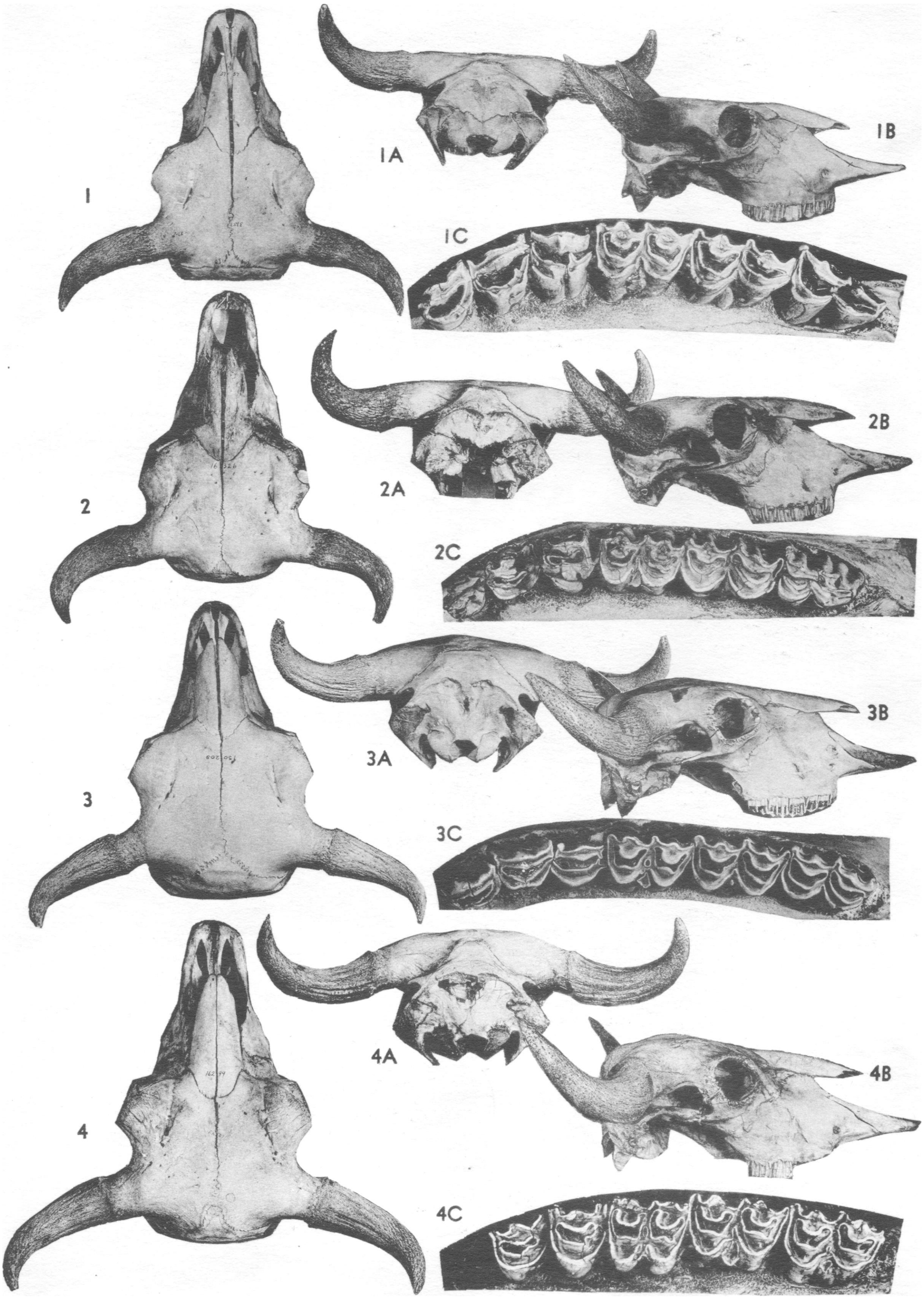
3, 3A, 3B. *B.* (*Gigantobison*) *latifrons*, ref., from near Hoxie, Kansas. This specimen is not to 1/10 scale: 3 and 3B are larger; 3A is smaller. A.M.N.H. No. 14346.

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.

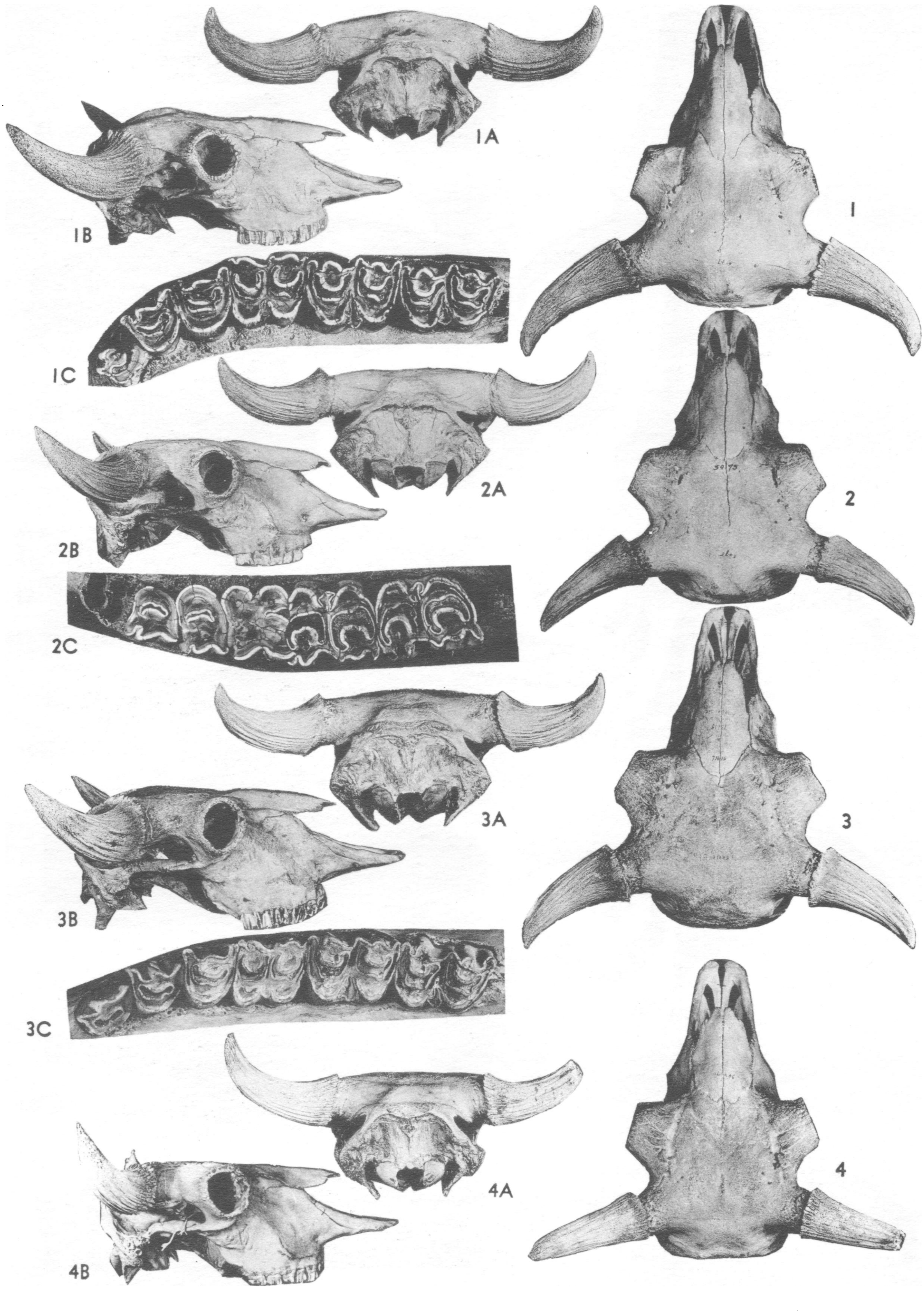
PLATES 8–26



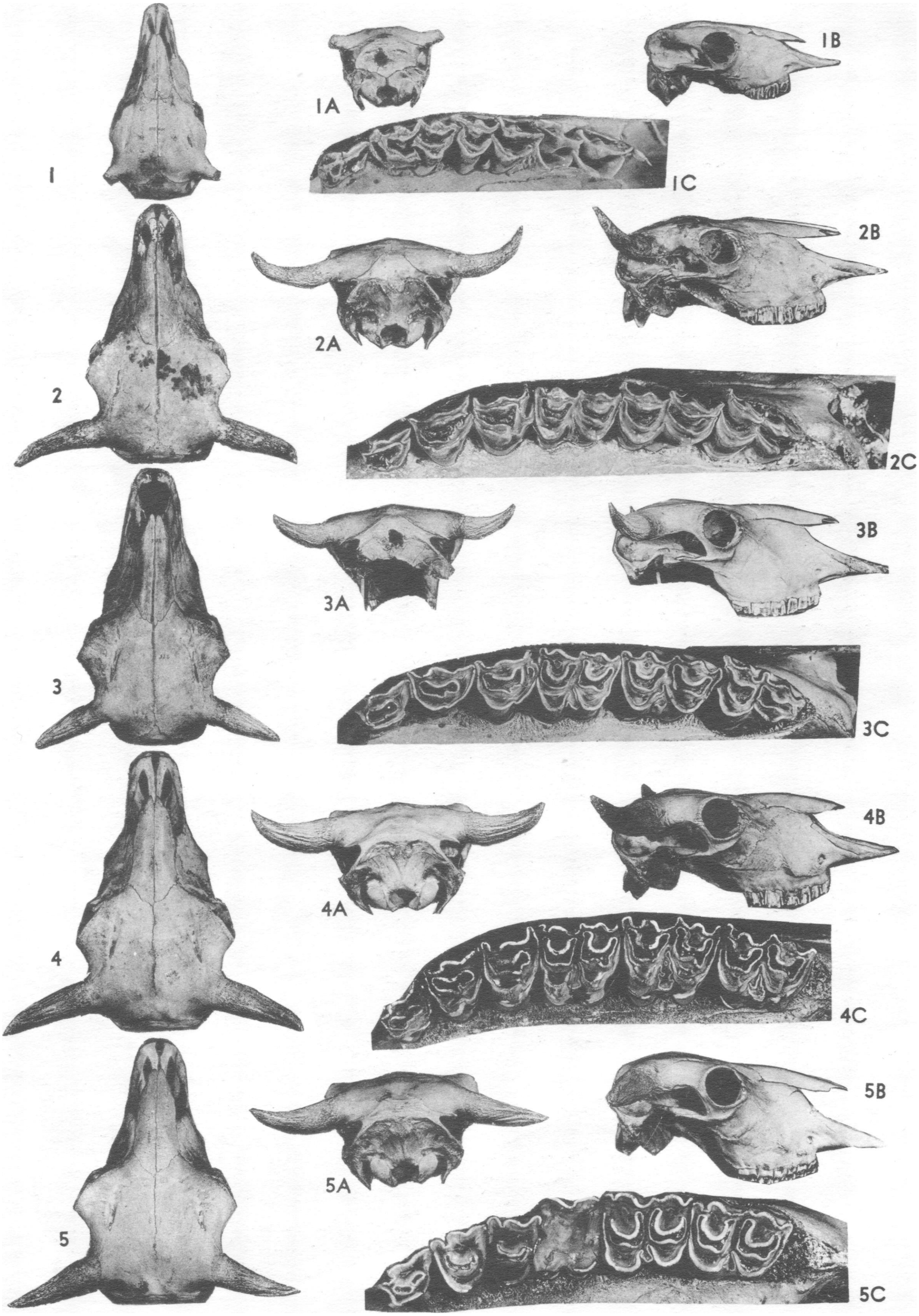
Development of male skulls and dentition of *B.* (*B.*) *b. bison* (youth). Skulls × 1/10, teeth × ½



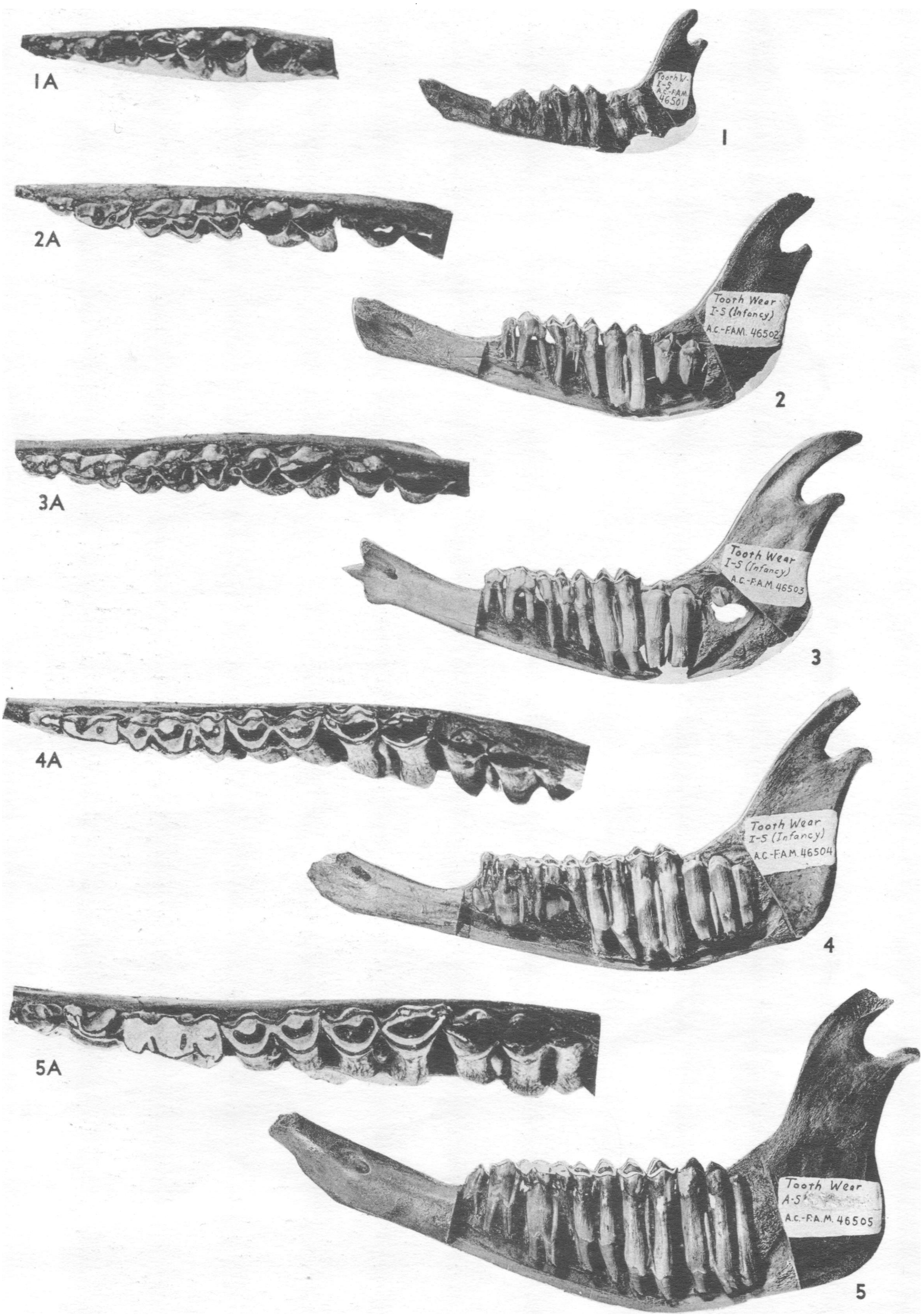
Development of male skulls and dentition of *B.* (*B.*) *b. bison* (maturity). Skulls × 1/10, teeth × ½



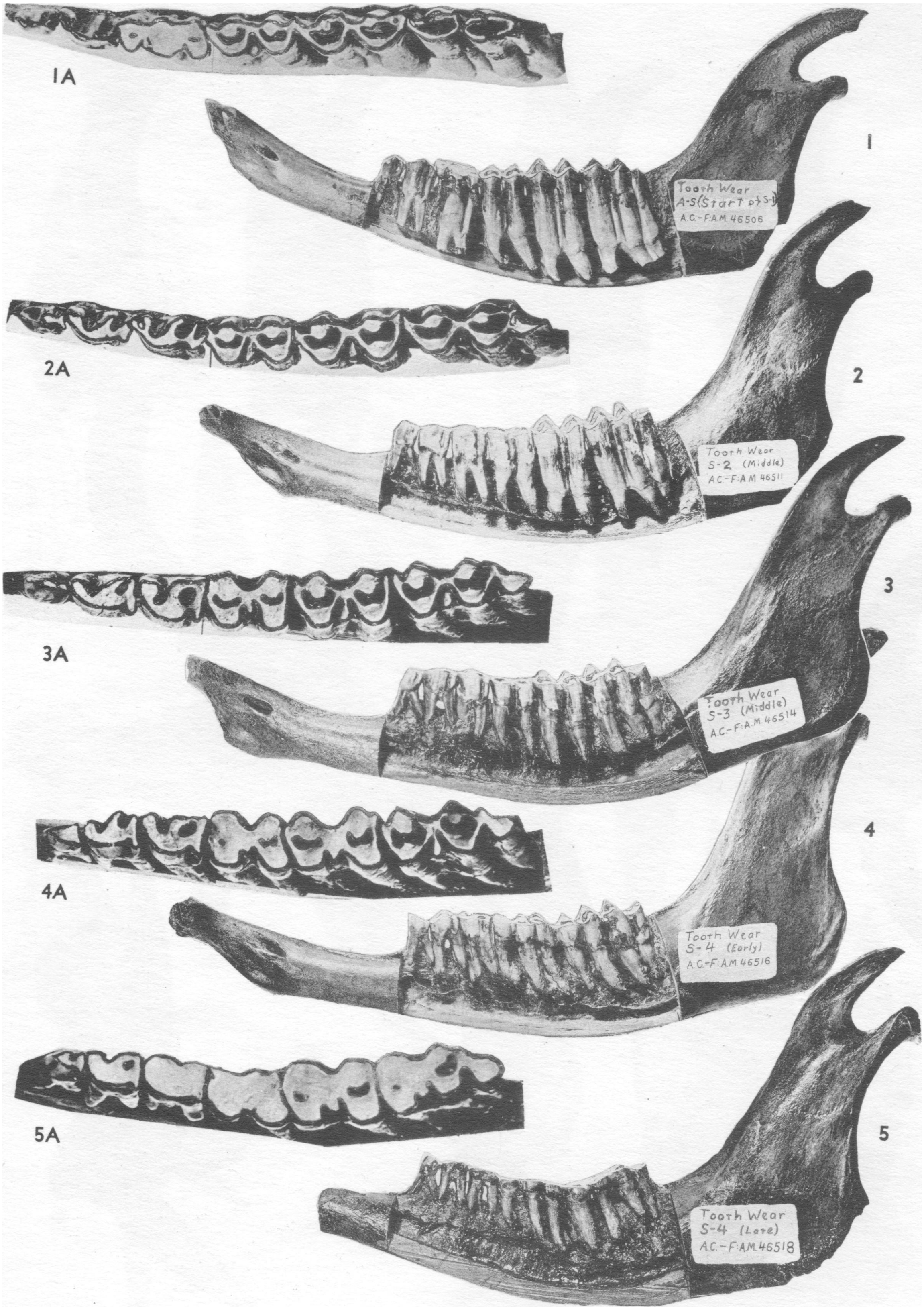
Mature males. 1, 2. *B.* (*B.*) *b. bison.* 3. *B.* (*B.*) *b. athabascae.* 4. *B.* (*B.*) *bonasus.* Skulls × 1/10, teeth × ½



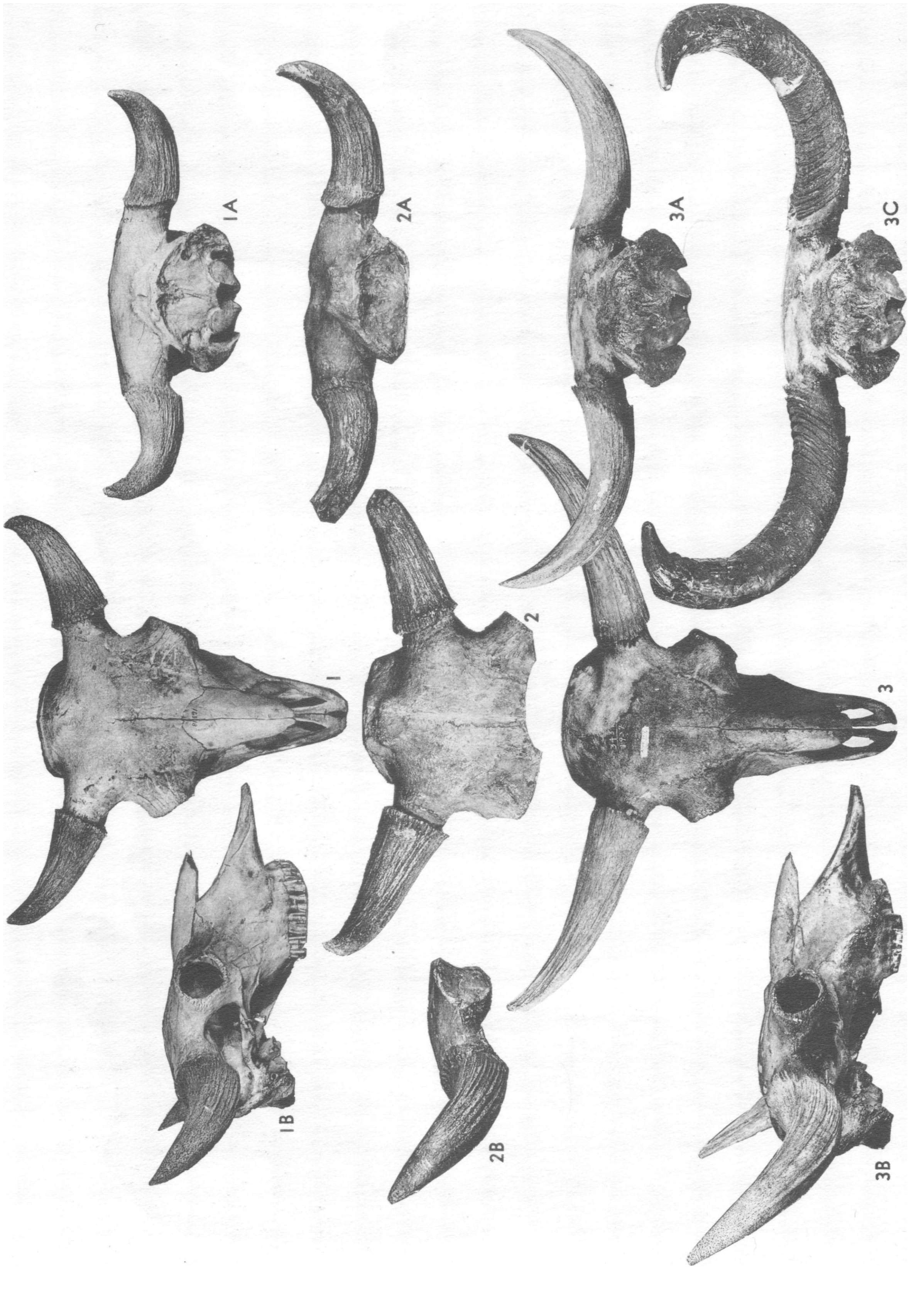
Development of female *B.* (*B.*) *bison* (youth to old age). Skulls × 1/10, teeth × ½



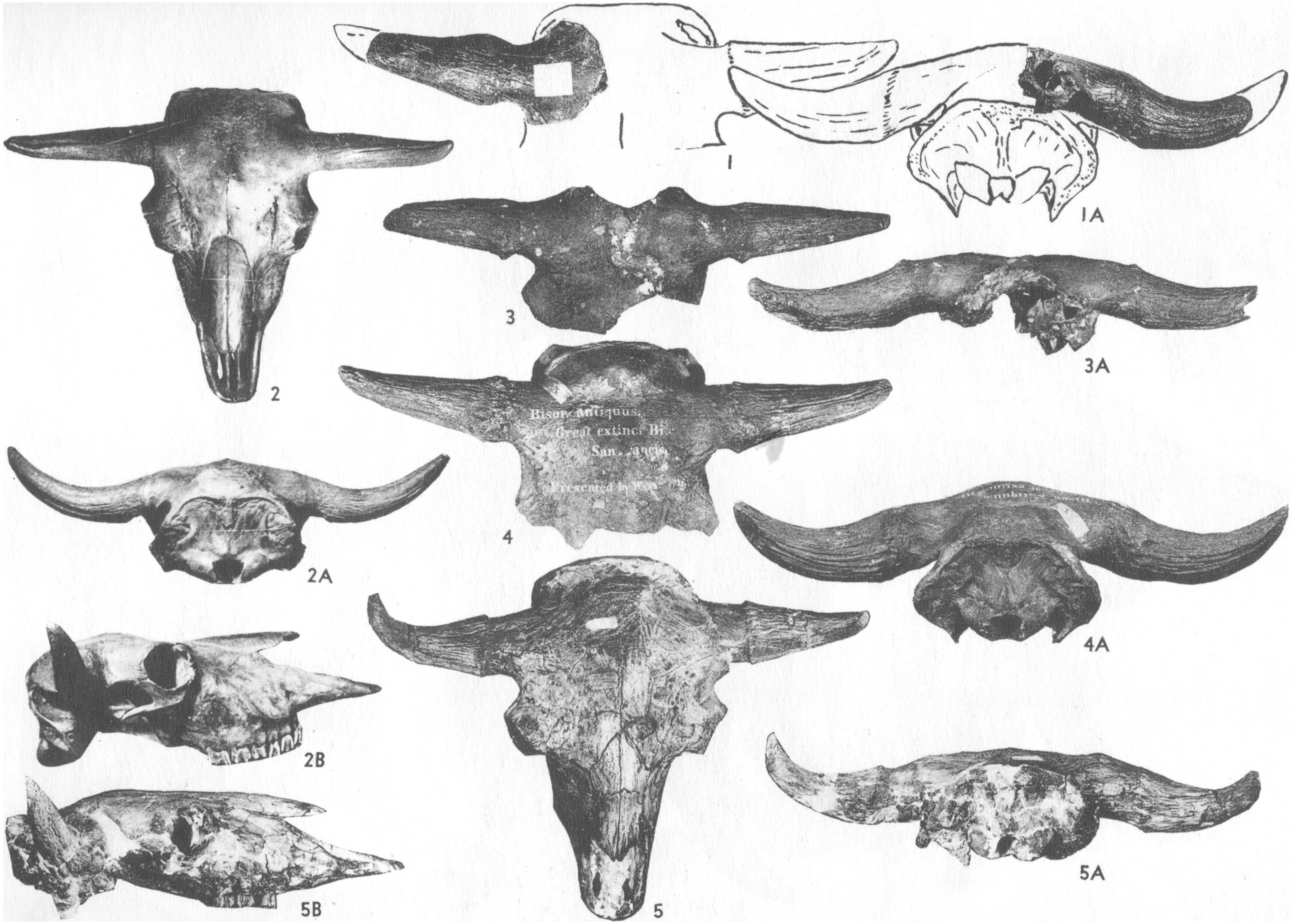
Tooth wear and development in *Bison* rami (immature and adolescent). Lateral × ¼, occlusal × ½



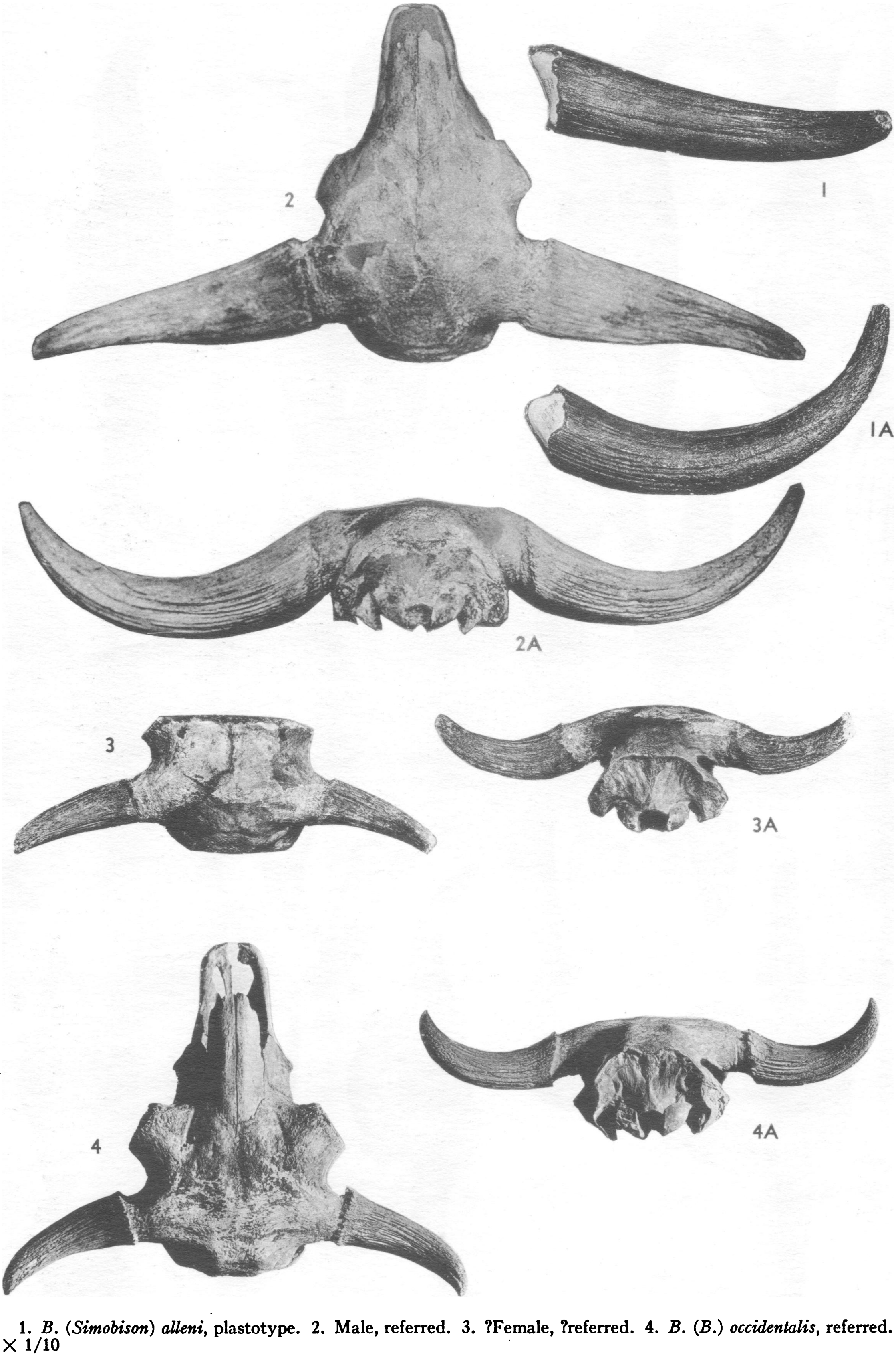
Tooth wear and development in *Bison* rami (early maturity to old age). Lateral × ¼, occlusal × ½



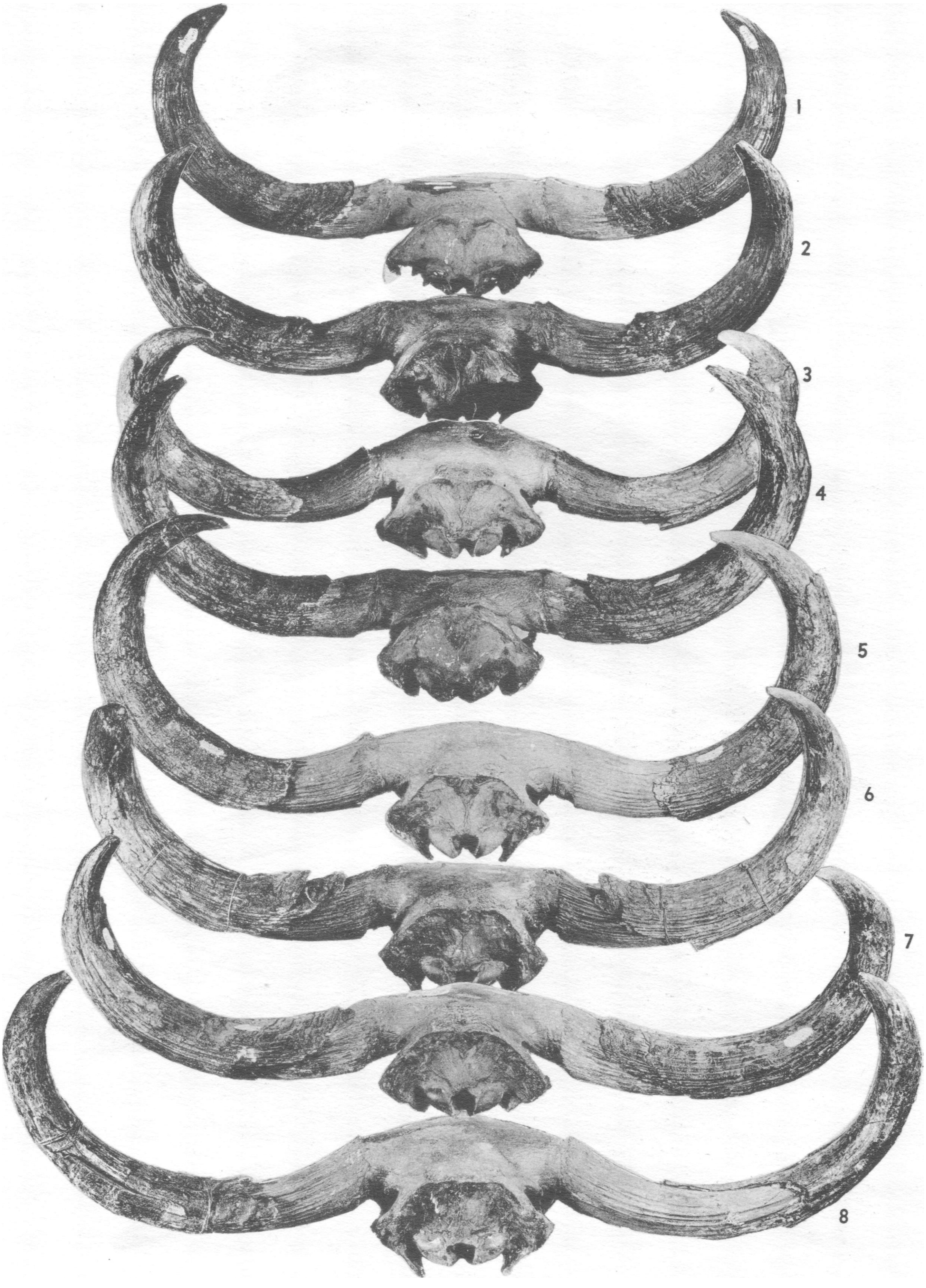
1. *B.* (*B.*) *b. bison*, referred. 2. *B.* (*B.*) *occidentalis*, plastotype. 3. *B.* (*B.*) *preoccidentalis*, new species, holotype. × 1/10



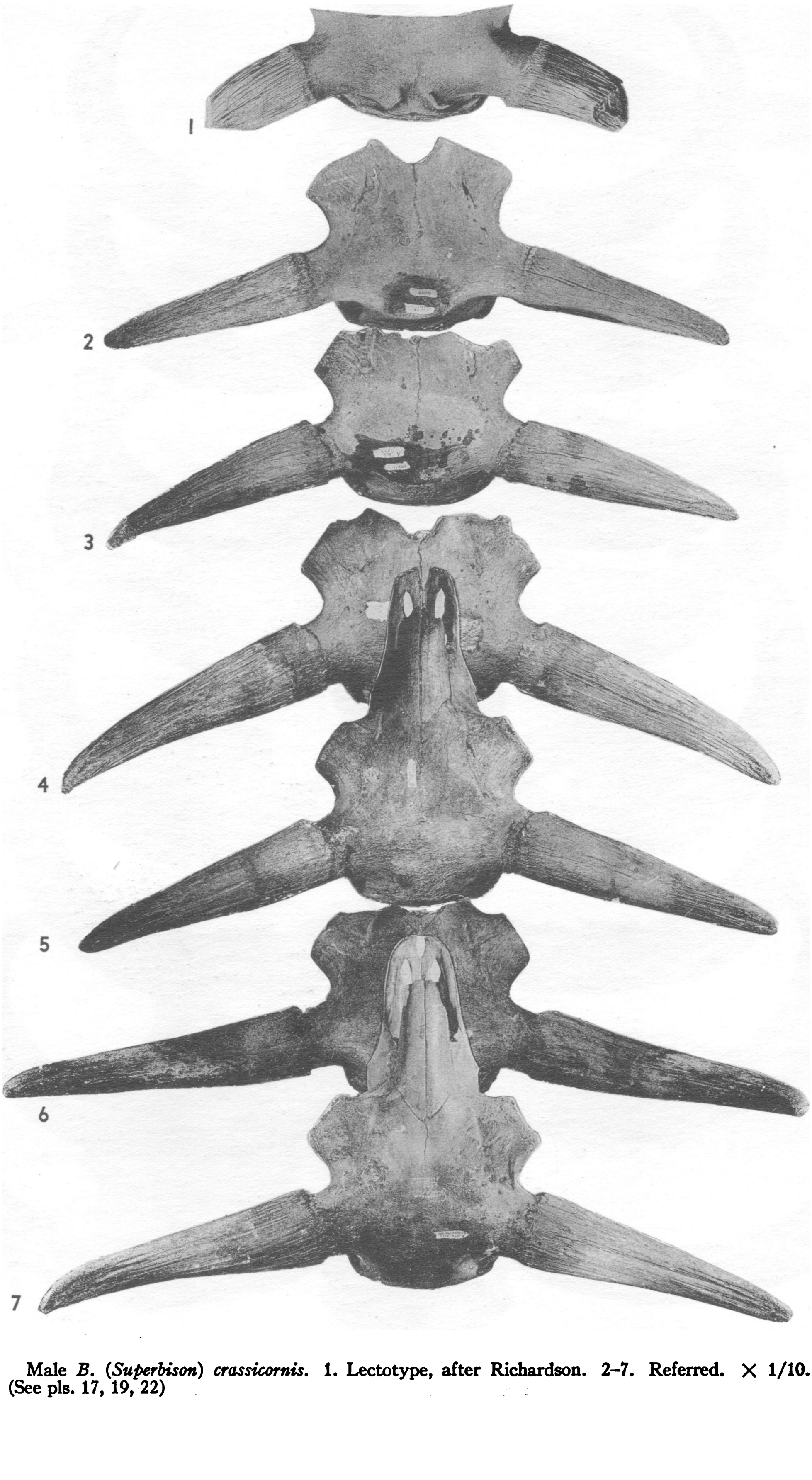
1. *B. (Simobison) antiquus antiquus*, holotype. 2. Female, referred. 3, 4, 5. Males, referred. × 1/10



1. *B.* (*Simobison*) *alleni*, plastotype. 2. Male, referred. 3. ?Female, ?referred. 4. *B.* (*B.*) *occidentalis*, referred. × 1/10

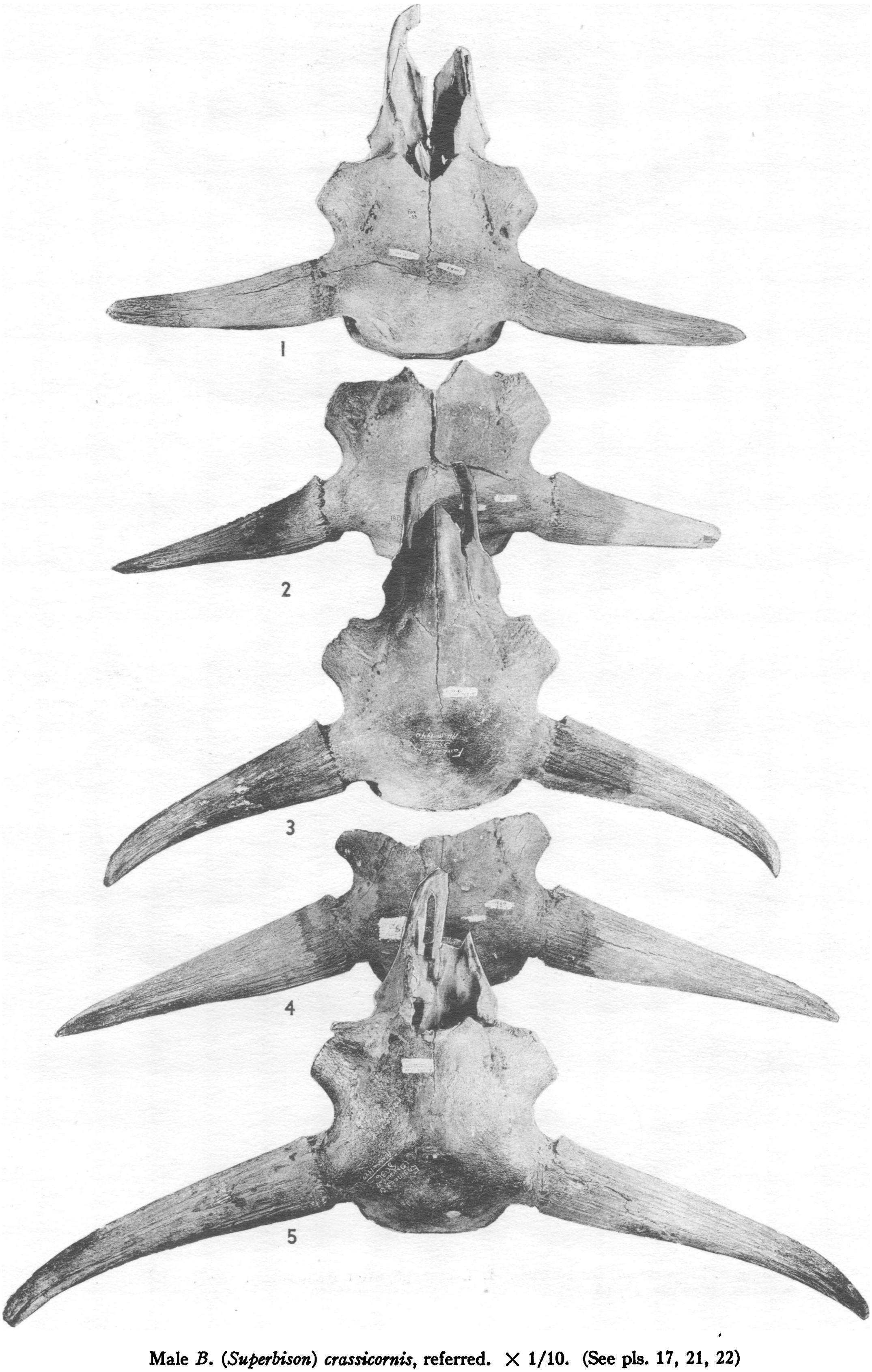


B. (*Superbison*) *crassicornis*, referred, male population sample of Alaska. × 1/10. (See pls. 18–22)



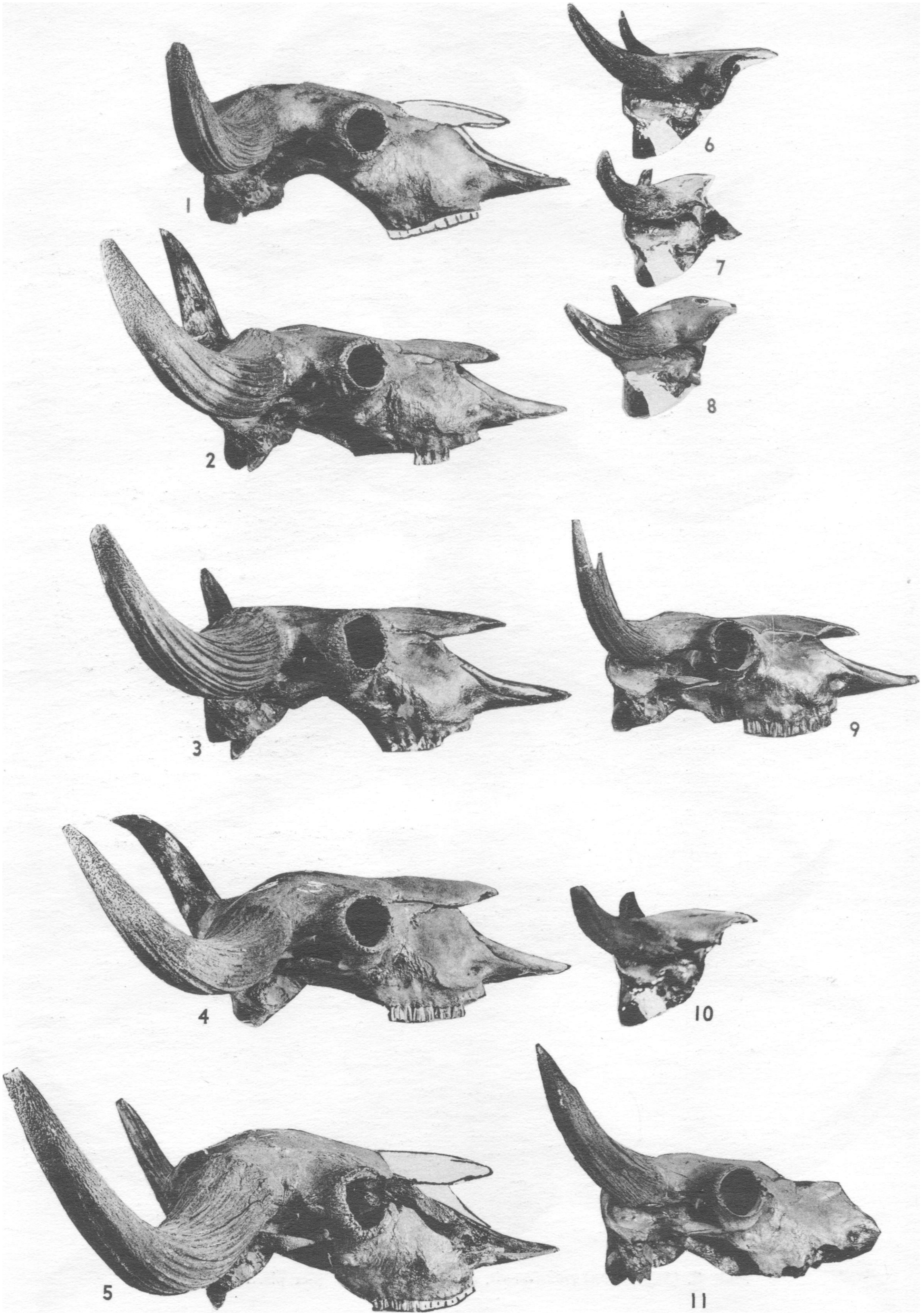
Male *B.* (*Superbison*) *crassicornis*. 1. Lectotype, after Richardson. 2–7. Referred. × 1/10. (See pls. 17, 19, 22)

Male *B.* (*Superbison*) *crassicornis*. 1. Lectotype, after Richardson. 2–7. Referred. × 1/10. (See pls. 17, 18, 22)

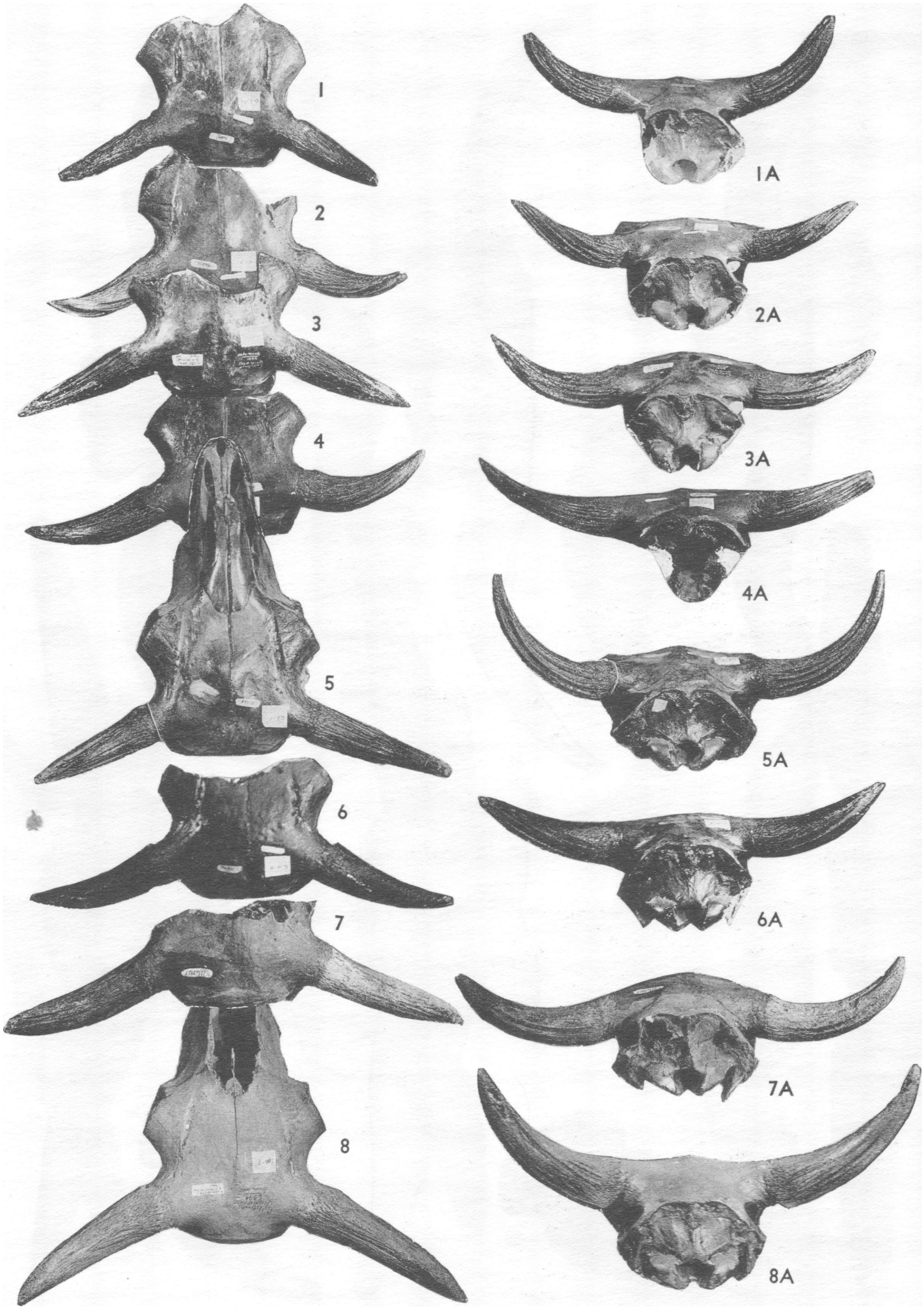


Male *B.* (*Superbison*) *crassicornis*, referred. × 1/10. (See pls. 17, 21, 22)

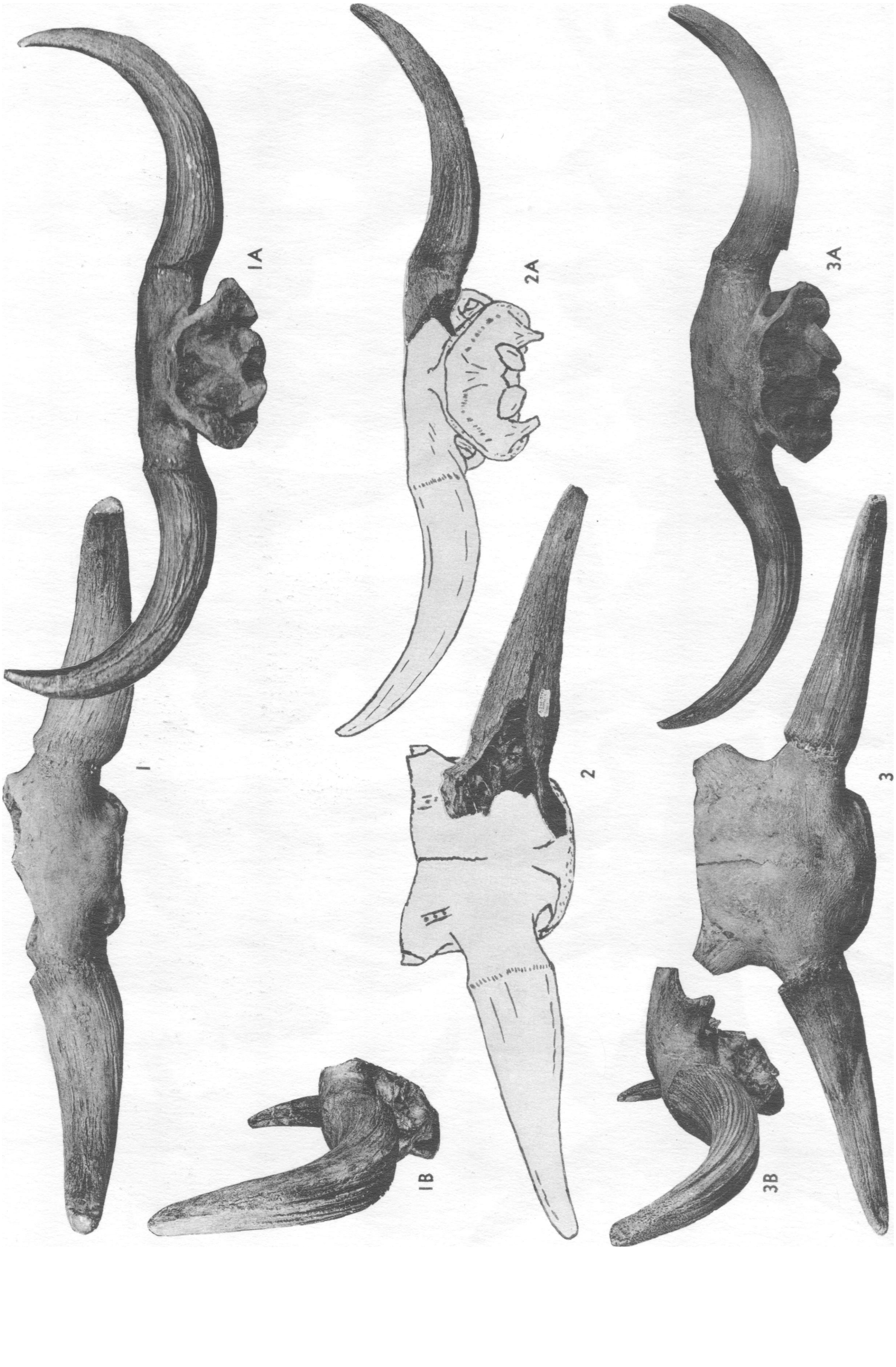
Male *B.* (*Superbison*) *crassicornis*, referred. × 1/10. (See pls. 17, 20, 22)



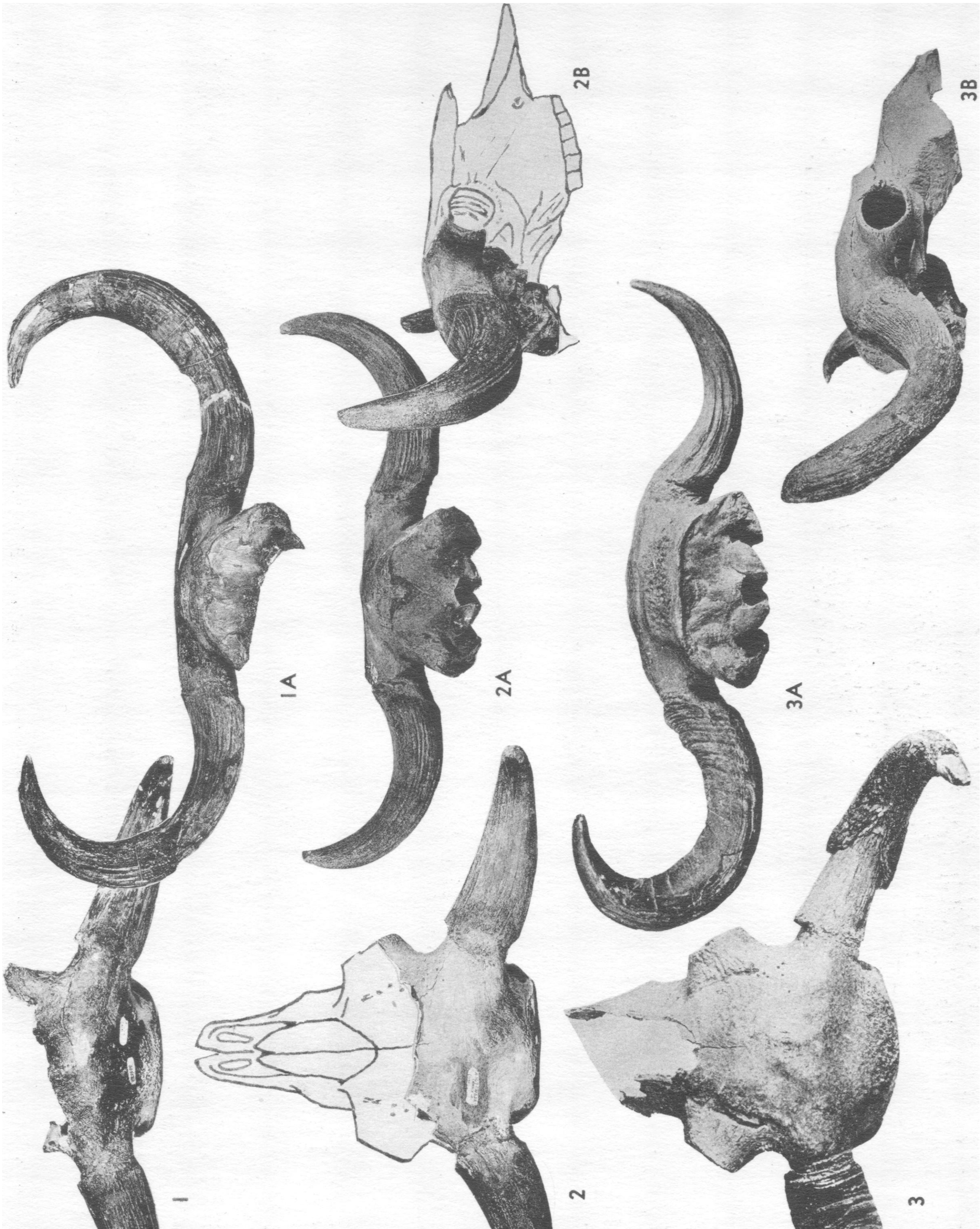
B. (*Superbison*) *crassicornis*, referred. 1–5. Male (see pls. 17–21). 6–11. Female (see pl. 23). × 1/10



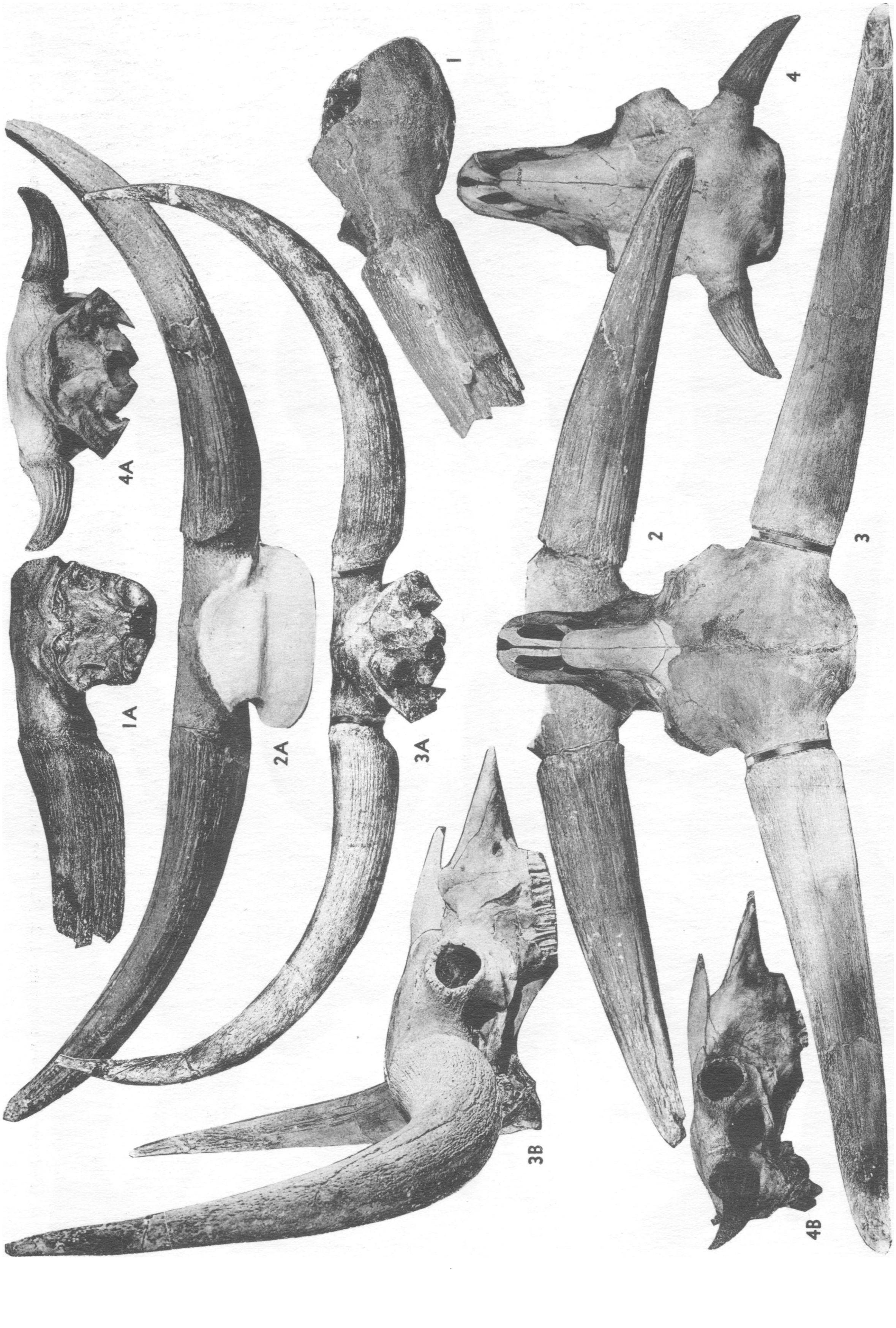
B. (Superbison) crassicornis, referred, female population sample from Alaska (see pl. 22). × 1/10



B. (*Platycerobison*), new subgenus. 1. *B.* (*P.*) *chaneyi*, plastotype. 2. *B.* (*P.*) *alaskensis*, referred. 3. *B.* (*P.*) *alaskensis*, holotype. × 1/10



B. (*Platycerobison*), new subgenus. 1, 2. Paratype and holotype, respectively, of *B.* (*P.*) *geisti*, new species. 3. *B.* (*P.*) *pallasii*, after Gromova, 1932. × 1/10



B. (*Gigantobison*), new subgenus, compared to *B.* (*Bison*). 1. *B.* (*G.*) *latifrons*, holotype. 2, 3. *B.* (*G.*) *latifrons*, referred. 4. *B.* (*B.*) *b. bison*, referred. × 1/10