

The Autochthonous
North American Musk Oxen
Bootherium, *Symbos*, and *Gidleya*
(Mammalia: Artiodactyla: Bovidae)

JERRY N. McDONALD
and
CLAYTON E. RAY

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ABSTRACT

McDonald, Jerry N., and Clayton E. Ray. The Autochthonous North American Musk Oxen *Bootherium*, *Symbos*, and *Gidleya* (Mammalia: Artiodactyla: Bovidae). *Smithsonian Contributions to Paleobiology*, number 66, 77 pages, 64 figures, 4 tables, 1989.—The history of taxonomy of the autochthonous genera of North American musk oxen—*Bootherium*, *Symbos*, and *Gidleya*—is reviewed. The bases upon which taxonomic judgments within the group have been made are identified. These bases are reevaluated in the light of current information on patterns of ontogenesis, sexual dimorphism, postmortem alteration of skeletal remains, and spatial and temporal distribution of musk ox records. The bases used by taxonomists in the past to justify separation of this musk ox group into multiple genera and species can be explained best as indices of sexual dimorphism or postmortem weathering and abrasion. All nominal species within *Bootherium*, *Symbos*, and *Gidleya* are, therefore, placed in synonymy with the senior name in the group, *Bootherium bombifrons* (Harlan, 1825). A revised diagnosis is provided for the monotypic species.

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The Autochthonous North American Musk Oxen *Bootherium*, *Symbos*, and *Gidleya* (Mammalia: Artiodactyla: Bovidae)

Jerry N. McDonald
and Clayton E. Ray

Introduction

Five genera of musk oxen (low-horned ovibovines) presently are recognized from the Quaternary of North America. Two of these genera (*Ovibos* and *Praeovibos*) were Holarctic in distribution, whereas the other three (*Bootherium*, *Symbos*, and *Gidleya*) are known only from the Nearctic.

Praeovibos Staudinger, 1908, at one time considered to be the earliest known representative of the musk ox group, is known from fossil skull material from at least 16 sites in Europe and Asia that date from the middle Pleistocene (i.e., the Günz, Mindel, and possibly Riss stages, and their equivalents) (Kahlke, 1964; Sher, 1974; Crégut-Bonnoure, 1984; Moigne, 1984). *Ovibos* Blainville, 1816, however, is also known from deposits possibly of Günz age at Süssenborn, East Germany (Kahlke, 1964; Kurtén, 1968; Crégut-Bonnoure, 1984), and was considered by Kahlke (1975) to be the oldest genus of musk ox. Recently, skeletal remains assigned to *Praeovibos* sp. have been reported from Venta Micena, Spain, and Casa Frata, Italy (Moyá-Solá, Augustí, Gibert, and Pons-Moyá, 1981; De Giuli and Masini, 1983), both of which, along with at least one of the Kolyma Basin sites in Siberia, are reported as predating those at Süssenborn.

The earliest records of *Ovibos* and *Praeovibos* from North America are from deposits presumed to be of Illinoian age near Nome and Fairbanks, Alaska, respectively (Péwé and Hopkins, 1967; Harington, 1970a). Nearctic records of *Praeovibos* are restricted to eastern Beringia (Fairbanks area, Alaska, Old Crow Basin, Yukon Territory, and Porcupine River, Yukon-Alaska), whereas cranial records of *Ovibos* extend from Alaska southward to Montana, Wyoming, Nebraska, Iowa, Illinois, Ohio, and the continental shelf of New Jersey

(Hay, 1923, 1924; Barbour, 1934; Harington, 1978; Walker, 1982; McDonald and Ray, unpubl. data).

The North American autochthons, *Bootherium* (Harlan, 1825), and *Symbos* (Leidy, 1852), appear simultaneously in deposits usually assigned to the Illinoian glaciation (= late Irvingtonian-early Rancholabrean land mammal ages). The earliest record of *Bootherium* is from Cripple Creek Sump (and possibly Gold Hill and Lower Cleary Creek) in the Fairbanks District, Alaska (Péwé and Hopkins, 1967; Péwé, 1975). Remains of *Symbos* of Illinoian age also have been recovered from Cripple Creek Sump, as well as from the North Prong Quarry (Mullen local faunas), Cherry County, Nebraska, and equivocally from the Conard Fissure, Newton County, Arkansas (Brown, 1908; Jakway, 1961a; Péwé and Hopkins, 1967; Martin, 1972). Both North Prong Quarry and Conard Fissure local faunas, however, present some problems of specimen identification or age assignment (see discussion, pp. 48-51). A *Symbos* specimen from sediments tentatively assigned to the late Illinoian (i.e., middle Rancholabrean) has been reported from Booth Canyon, Bonneville County, Idaho (White, 1985). The single specimen of *Gidleya* (Gidley, 1906), from Black Rocks, McKinley County, New Mexico, was considered at one time to date from the early Pleistocene because of its association "with camels and horses, animals of early Pleistocene age" (Hay, 1924:179). Now, however, the *Gidleya* record, and all *Bootherium* and *Symbos* records from localities other than those just mentioned, are considered to be either Sangamonian or Wisconsinan in age.

Praeovibos became extinct in Eurasia (Sher, 1974; Crégut-Bonnoure, 1984) near the end of the Middle Pleistocene (during the ?Riss glaciation). *Praeovibos* might have become extinct in North America before the Wisconsinan glaciation, but specimens assigned to this genus have been found at lower Cleary Creek, and have been identified tentatively from essentially late Wisconsinan faunules at Cripple Creek, Dome

Jerry N. McDonald, P.O. Box 10308, Blacksburg, Virginia 24062.
Clayton E. Ray, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Creek, Gold Hill, and lower Cleary Creek, Alaska. *Bootherium*, *Symbos*, and *Gidleya* appear to have become extinct by the end of the Wisconsinan glaciation. *Ovibos* became extinct in Eurasia around 3000 yr B.P., and survived into the historic period only in the higher latitudes of North America and Greenland (Allen, 1912, 1913; Harington, 1970a, 1970b; Crégut-Bonnoure, 1984).

The taxonomy of the autochthonous North American musk oxen has been unstable since the earliest recognized taxa were described in the second and third decades of the 19th century. Questions about the relationship between *Bootherium* and *Symbos* arose soon after the group was first revised by Leidy (1852a,b) and have continued, unresolved, to the present (e.g., Nelson and Neas, 1980; White, 1985; Nelson and Madsen, 1987). Another conspicuous taxonomic problem involving musk oxen concerns the status of *Gidleya*, a genus established originally as *Liops* on an extensively abraded partial cranium from New Mexico (Gidley, 1906). Although *Gidleya* has received attention from paleontologists throughout its eighty-year history (Cossmann, 1907; Allen, 1913; Troxell, 1915; Hay, 1922, 1924; Ryziewicz, 1933, 1955; Frick, 1937; Kretzoi, 1942; Harington, 1961; Romer, 1966), it has failed nonetheless to receive functional validation as a viable taxon. No less than 13 nominal species were erected within *Bootherium*, *Symbos*, and *Gidleya* between 1825 and 1942. Most of these species were established upon weak foundations—isolated teeth, isolated postcranial elements, or fragments of crania. Six of the 13 species already have been synonymized with more securely founded taxa, but the status of the remaining species also needs to be reevaluated.

Much of the reason for taxonomic instability at the generic level of the autochthonous North American musk oxen can be attributed to either failure to recognize sexual dimorphism and individual variation or assess differential postmortem alteration of various specimens. This circumstance is in part a result of very few specimens being available at the time for study and comparison. Furthermore, the questions being asked often were different from those being asked today. The arguments that have characterized this debate have endured long past their time in great part because a comprehensive review of the North American fossil musk ox group has not been undertaken since Allen did so in 1913. The taxonomy of the group has not benefited from the information and ideas acquired or developed during the last 75 years, and consequently the uncertainties related to the conceptualization and use of the three recognized genera are based to a surprising but real extent upon 19th century information and ideas.

Information acquired since 1913 relevant to the taxonomic status of *Bootherium*, *Symbos*, and *Gidleya* is herein updated and reevaluated. The 226 available specimens is much larger than the 16 or so known to Allen (who, apparently, personally examined only two of these). Consequently, patterns of morphological and geographical variation can be documented and analyzed with substantially greater resolution and confidence than was possible in 1913. More reliable dating methods

and inter-site correlations permit more confident assessments of chronology and contemporaneity of the three nominal genera. Data obtained from taxa closely related to musk oxen permit comparisons of patterns of individual morphological variation, sexual dimorphism, differential preservation and collection of male and female skeletal elements, and geographical distribution. Recent studies of taphonomy provide much useful information about the effects of weathering and abrasion processes on bones and teeth, and patterns of postmortem biological alteration of skeletal remains.

Our purpose is to reassess the relationships among the genera *Bootherium*, *Symbos*, and *Gidleya*. We first review the taxonomic history of the group, directing particular attention to the specific questions that have characterized the instability. In this same section we identify the morphological characters and other data that have been invoked to support the diverse perspectives that have characterized the debate. Next we present our views on the status of the nominal species within each of the three genera. In a third section we consider the relationship between *Gidleya* and *Symbos*. Lastly, we examine the validity of the various elements of the arguments over the relationship between *Bootherium* and *Symbos*, incorporating modern data and insights derived from studies of individual variation, sexual dimorphism, ontogenetic change, and temporal and spatial distribution patterns.

In this paper the names *Bootherium*, *Symbos*, and *Gidleya* are used as though they represented distinct taxa until we establish and summarize our case for their synonymy in the final section. We have omitted use of the diaeresis in *Bootherium* in accordance with Article 27 of the 3rd edition of the *International Code of Zoological Nomenclature*.

Abbreviations for institutional, departmental, and personal collections containing specimens used in this paper are identified in Appendix I.

ACKNOWLEDGMENTS.—The theme and scope of this paper was established in 1982 and 1983 during McDonald's tenure as a Smithsonian Postdoctoral Fellow, working with Ray, in the Department of Paleobiology, National Museum of Natural History. The paper was written in 1984 and 1985, since which time it has remained essentially unchanged save for adding new records and references to newly published factual information.

The ideas presented in this paper, however, have developed during our more than 30 years of combined research on musk and shrub oxen. During that period, we have benefited from the assistance and interest of many colleagues. For facilitating access to collections, for loaning specimens, for sharing unpublished information, and for conversation and debate, we thank the following people: William A. Akersten, Carol W. Allison, Donald Baird, Charles S. Bartlett, Jr., Stig M. Bergström, Robert C. Bright, Kenneth Caster, Charles S. Churcher, Vickie L. Clay, William A. Clemens, Jr., John Connaway, John P. Cook, Richard G. Corner, Richard A. Davis, A. Gordon Edmund, Ralph E. Eshelman, Anthony Fiorillo, Weldon D. Frankforter, Jr., Larry E. Freeman, Linda Gordon, Russell W. Graham, the late John E. Guilday, Carl E.

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History of Taxonomy of the Group

The first published record of a fossil musk ox from North America was Wistar's description and figures of a cranium with horn cores (ANSP 994; Figures 1–4) collected at Big Bone Lick, Kentucky, by William Clark in 1807 (Wistar, 1818; Rice, 1951). Wistar recognized the resemblance between some characters in his specimen and those of domestic cattle, sheep, and goats, and especially bison, but he gave no indication of having compared the specimen with the tundra musk ox, descriptions of which were available at that time (e.g., J  r  mie, 1720; Pennant, 1781, 1784; Blainville, 1816). Although Wistar realized that the cranium from Big Bone Lick was "very different from that of any animal now known here" (Wistar,

1818:379), he did not name this newly documented form of life (Wistar, 1818). Seven years later, Harlan (1825), in *Fauna Americana*, described *Bos bombifrons* on the basis of the Big Bone Lick cranium (ANSP 994; Figures 1–4). This species shared the genus *Bos* with *B. americanus* (now *Bison bison*) and the new species *B. latifrons* (now *Bison latifrons*); the tundra musk ox (*Ovibos moschatus*) was retained as a monotypic genus, following Blainville (1816). Both Wistar and Harlan placed the Big Bone Lick specimen near *Bison* because the skulls of both were similar in size, and the horn cores of each were rounded and projected laterally from the cranium distinctly anterior to the occipital crest. Harlan apparently overlooked the remnant lacrimal depression on the left side of the Big Bone Lick skull, for one diagnostic criterion of his genus *Bos* (and, erroneously, *Ovibos*) was the absence of a "lacrimal depression" (Harlan, 1825:264, 267).

In 1828, De Kay described and figured a second fossil musk ox specimen, a partial cranium with the bases of the horn cores, discovered at New Madrid, Missouri, following the famous earthquake of 1812. This specimen, too, was originally identified as "a petrified occiput, and the horn processes of the American Bison" but, in De Kay's opinion, "none of that genus are now to be found in our country, whose crania in the slightest degree resembles the one under consideration" (De Kay, 1828:285). Placing emphasis upon the flattened horn cores, De Kay correctly removed this specimen from the bison group and placed it with the musk oxen. Upon comparing the New Madrid specimen with Cuvier's description of *Ovibos moschatus*, however, De Kay recognized important differences in the character of the dorsal surface of the frontals (although De Kay allowed that his specimen, with its conspicuously roughened surface, could have been damaged or have lost the entire dorsal surface), the depth of the occipital surface (being greater in his specimen than in *Ovibos*), and "the most remarkable difference" (De Kay, 1828:287)—the position of the horns. The bases of the horn cores suggested to De Kay (1828:287, 289) that

the longest axis of the horns has been in the same direction with the bones of the face . . . or to speak more definitely, the axis of the longest diameter of the horns, is parallel with the bones of the palate.

These observed and inferred differences between the New Madrid specimen and existing descriptions of *Ovibos moschatus* led De Kay to consider affinities with fossil specimens from Siberia originally described by Pallas (1773) and Ozeretskovsky (1811), as reported by Cuvier in an unidentified edition of his *Recherches*. De Kay found sufficient support in Cuvier's comments about the Siberian specimens to erect a new species, *Bos pallasii*, to accommodate "the fossil crania of Pallas and Ozeretskovsky, and provisionally, the specimen from the banks of the Mississippi" (De Kay, 1828:291; our emphasis). The Siberian specimens of Pallas, however, earlier had been named *Ovibos pallantis* by Smith (1827), making *Bos pallasii* a junior synonym of the former. The New Madrid specimen was later referred to *Bootherium cavifrons* by Leidy



5 cm

FIGURE 1.—Holotype of *Bos bombifrons* Harlan, 1825 (ANSP 994), in dorsal view.



5 cm

FIGURE 2.—Holotype of *Bos bombifrons* Harlan, 1825 (ANSP 994), in right lateral view.



FIGURE 3.—Holotype of *Bos bombifrons* Harlan, 1825 (ANSP 994), in ventral view.



FIGURE 4.—Holotype of *Bos bombifrons* Harlan, 1825 (ANSP 994), in caudal view.

(1852b), and, although this specimen has been lost or destroyed, Leidy's decision seems to have been correct. De Kay's contribution to the nomenclatural history of the Pleistocene musk oxen of North America was that he was the first to recognize the occurrence of a fossil musk ox in North America, and he correctly identified the major morphological differences between *Ovibos* and what would become *Bootherium* (in part, then *Symbos*).

Leidy reviewed the extinct North American oxen in 1852. At that time, the only known specimen of *Bos bombifrons* was the holotype from Big Bone Lick, while at least 12 crania of the kind described by De Kay were known (Leidy, 1852b). In May 1852, Leidy (1852a:71) noted that both forms of musk oxen possessed

large larmiers or lachrymal depressions, as in the deer; and if these are possessed by the *Ovibos moschatus*, the two fossils would belong to the same genus as *Ovibos bombifrons* and *O. cavifrons*; but if they are not possessed by *Ovibos*, as is stated to be the case by Desmarest, the two latter species would form a new genus, for which the name *Bootherium* is proposed.

The genus *Bootherium*, containing two species (*B. bombifrons* and *B. cavifrons*), was erected in the formal review (Leidy, 1852b:12) on the basis of three diagnostic characteristics:

1. The os frontis rises into a hump, or forms a prominent process, from the sides of which arise the horn-cores.
2. The latter arise above and posterior to the orbits, but considerably in advance of the inion, and curve downwards in their course, but do not turn up at the tips, as in *Ovibos*.
3. The species possess lachrymal depressions, or larmiers, as well developed as in cervine animals.

The holotype for *B. cavifrons* (ANSP 12995; Figures 5–8) is a relatively well-preserved cranium lacking only the distal tip of the left horn core. This cranium was secured by Thomas Kite of Cincinnati, Ohio, “in the hut of an Indian, in which it was used as a seat and he was informed it was found in a neighboring gravelly bluff, near Fort Gibson, on the Arkansas River” (Leidy, 1852b:13) in what was then Indian Territory (now Oklahoma). Leidy's descriptions of this specimen and the *B. bombifrons* holotype are extensive and detailed, but he did not indicate explicitly those criteria considered to be specifically diagnostic. In the description of *B. bombifrons*, Leidy stated that the base of the cranium “is sufficiently well preserved to exhibit the peculiarities which associate it in the same genus with *Bootherium cavifrons*” (Leidy, 1852b:18), but he did not identify those unifying characteristics. Moreover, he did not mention one of the most conspicuous shared characters—the outward, downward, and forward curvature of the horn cores, clearly evident in both type specimens. (Leidy also did not comment on a small circular scar on the holotype of *B. cavifrons* located on the dorsal surface of the right frontal, above the orbit, resulting from a pathologic condition. This injury healed before the death of the individual, and resculpting restored the bone surface to near-normal configuration. This condition is apparent in fig. 1, pl. III of Leidy, 1852b, and in our Figure 5.)

Leidy's review was important in that it transferred Harlan's *Bos bombifrons* from the bison group to the musk ox group and placed both forms of fossil musk oxen in the same genus. However, Leidy did not establish the distinctiveness and integrity of *Bootherium* with the three diagnostic criteria he proposed. His first criterion actually consisted of two characters—either a hump or a prominent process of the frontal region—and he did not establish any reason why these two expressions should be shared within the same genus, or that each was species specific (although this is implied by his descriptions of the two specimens). The second and third criteria are characteristics of all low-horned musk oxen and, therefore, are not generically diagnostic. Certainly, the inadequacy of Leidy's generic diagnoses can be attributed to the fact that he had very little information about the structure of the skull of *Ovibos moschatus*, and that some of what had been published elsewhere was erroneous. Subsequent information about the morphology of *Ovibos* proved that the genus did have lacrimal depressions and its horn cores did not turn upward at the tips. In 1854, Leidy repeated his belief that the presence of lacrimal depressions in *Bootherium* separated that genus from *Ovibos*, and that *B. cavifrons* was further separated from *O. moschatus* by differing frontal characteristics—the presence of a deep fissure separating the bases of the horn cores in the latter whereas the horn core bases joined together and covered the entire length and breadth of the frontals in the former (Leidy, 1854).

A new species, *Ovibos maximus*, was named by Richardson in 1852 on a damaged fossil axis (HM 90/2; Figure 9) found at Eschscholtz Bay, Alaska. Richardson compared the fossilized axis with that of a young male *Ovibos moschatus* and concluded that the two bones, being of different sizes, represented different species. Without stating reasons, Richardson considered that the fossilized axis might belong to the same taxon that Leidy had called *Bootherium cavifrons* and thus proposed the synonymy of *O. maximus* and *B. cavifrons* (Richardson, 1852). Leidy quickly and effectively refuted Richardson's decision, and explicitly stated his opinion that there were no reasonable grounds for considering *Ovibos* and *Bootherium* to be synonymous (Leidy, 1854).

Rütimeyer (1865) and Dawkins (1867) referred Leidy's genus *Bootherium* to *Ovibos* on the grounds that *Ovibos*, like *Bootherium*, possessed lacrimal depressions. Rütimeyer (1865) further considered *B. cavifrons* and *B. bombifrons* to be actually male and female of the same taxon, and created a new species, *O. priscus*, to accommodate the pair. Leidy acknowledged that *Bootherium* might possibly belong within *Ovibos*, but he did not concur that the two forms were conspecific (Leidy, 1869). In 1872, Dawkins concluded that Leidy's *B. cavifrons* and *B. bombifrons* were conspecific and gave them the new combination *Ovibos cavifrons* (a name proposed earlier by Leidy), despite the fact that *bombifrons* was the senior specific epithet (Dawkins, 1872). The idea that the two forms were conspecific received mixed reception, some authors—including Lydekker (1885, 1898)—agreeing with

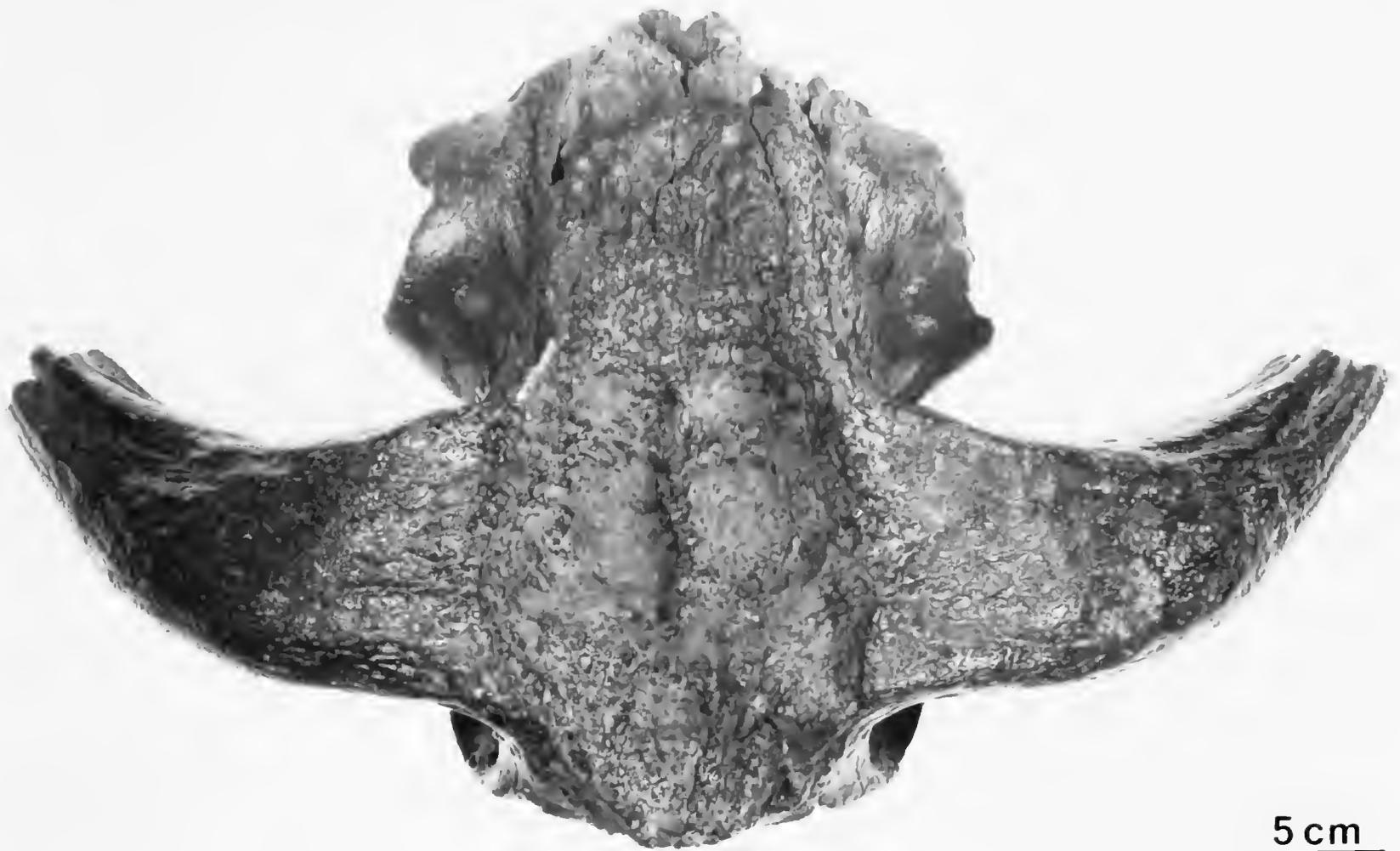


FIGURE 5.—Holotype of *Bootherium cavifrons* Leidy, 1852 (ANSP 12995), in dorsal view.



FIGURE 6.—Holotype of *Bootherium cavifrons* Leidy, 1852 (ANSP 12995), in left lateral view.

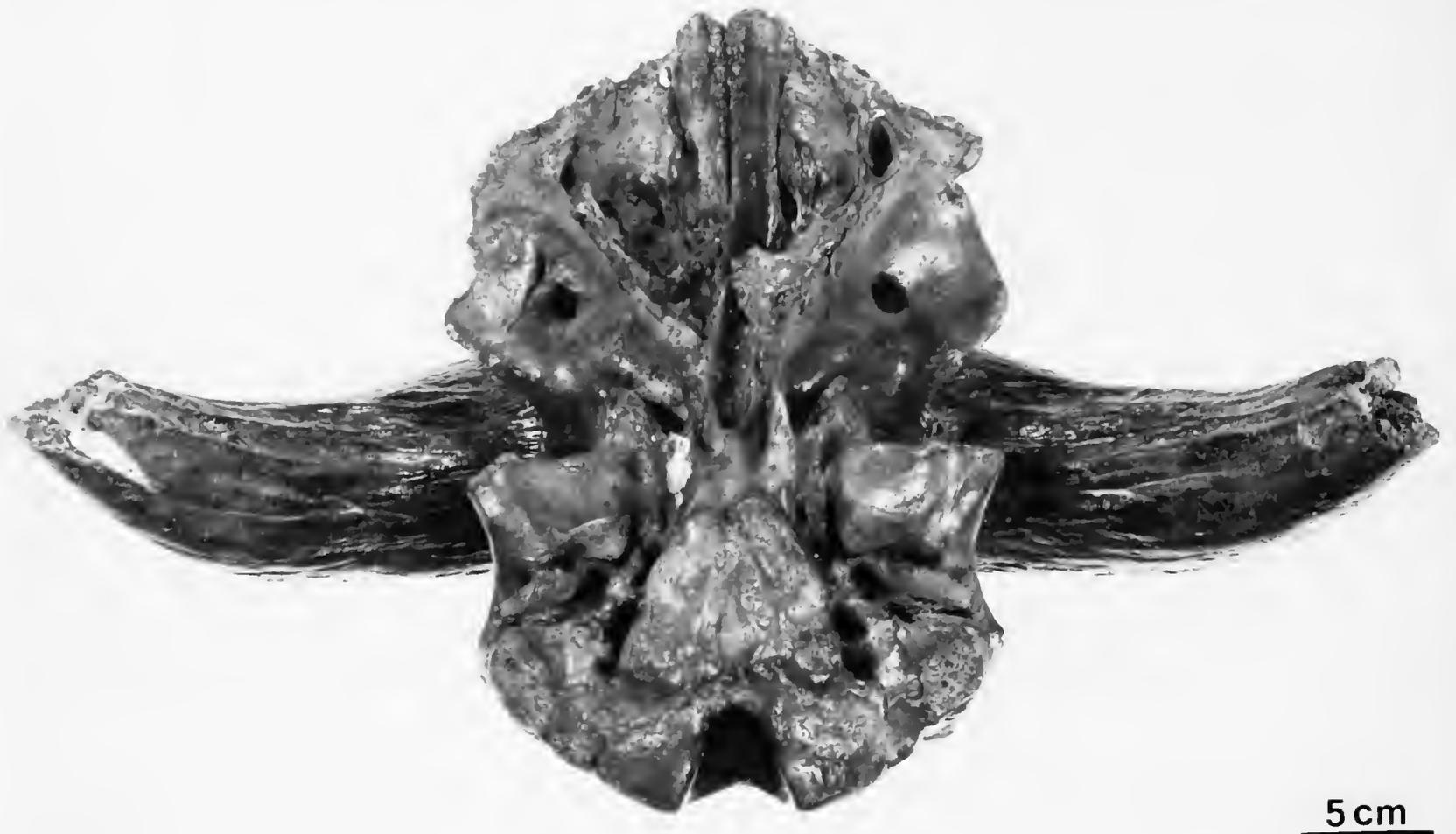


FIGURE 7.—Holotype of *Bootherium cavifrons* Leidy, 1852 (ANSP 12995), in ventral view.



FIGURE 8.—Holotype of *Bootherium cavifrons* Leidy, 1852 (ANSP 12995), in caudal view.

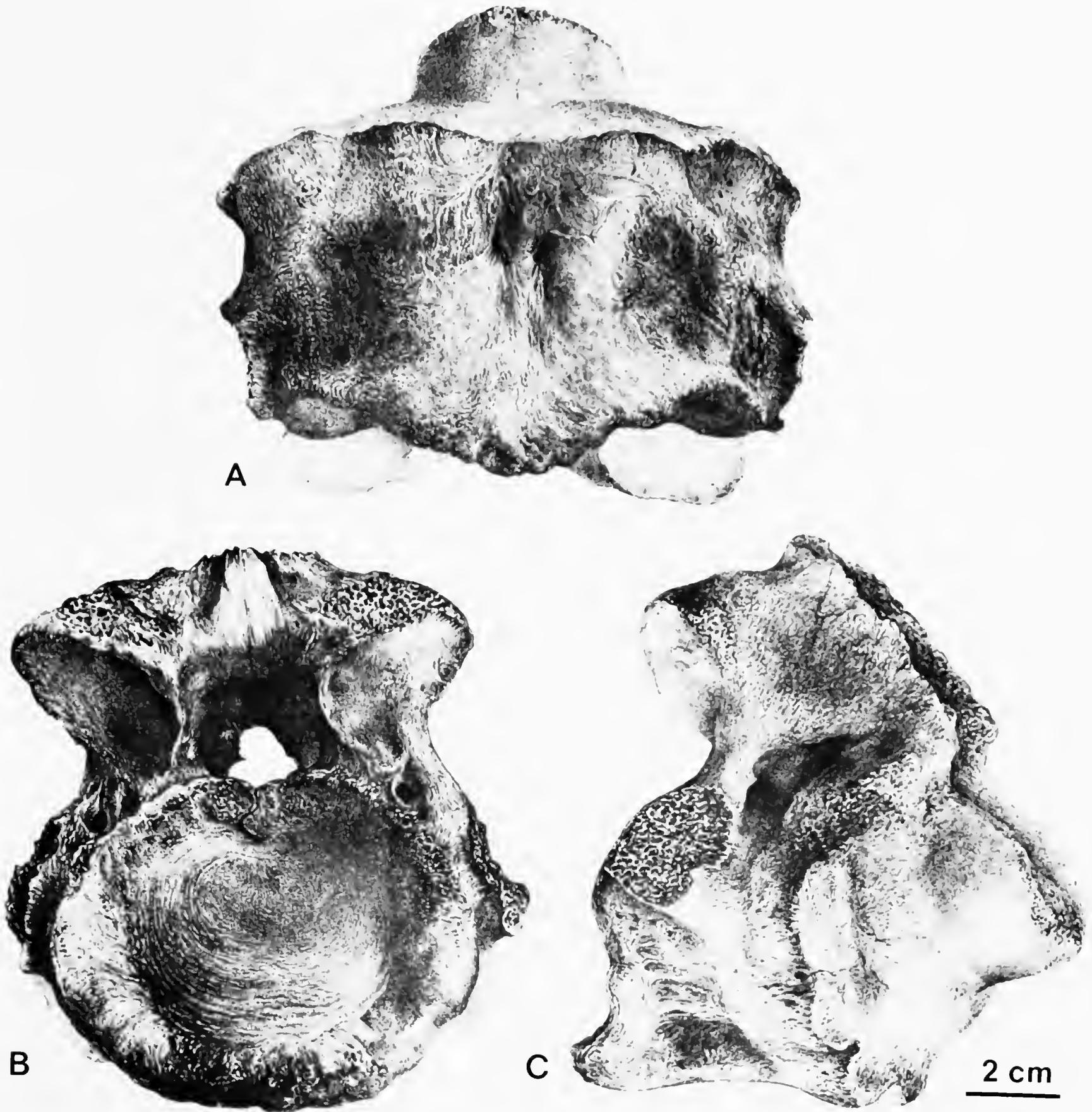


FIGURE 9.—Holotype of *Ovibos maximus* Richardson, 1852 (IHM 90/2), in A, ventral, B, caudal, and C, right lateral views.

Rütimeyer and Dawkins, and others not (e.g., Rhoads, 1895; Osgood, 1905a; Allen, 1913). Rütimeyer (1865), however, had raised a major question about the relationship between *B. cavifrons* and *B. bombifrons* and, whether other authors agreed with him or not, none offered systematic arguments against either his or Dawkins' (1872) positions.

Rhoads identified another species of musk ox from a small cranial fragment found in a cave in Durham County, Pennsylvania (ANSP 29; Figures 10, 11). The specimen was considered initially to be part of the left horn core and adjacent frontal of a new species of bison to which Rhoads gave the name *Bison appalachicolus* (Rhoads, 1895). Reexamination of

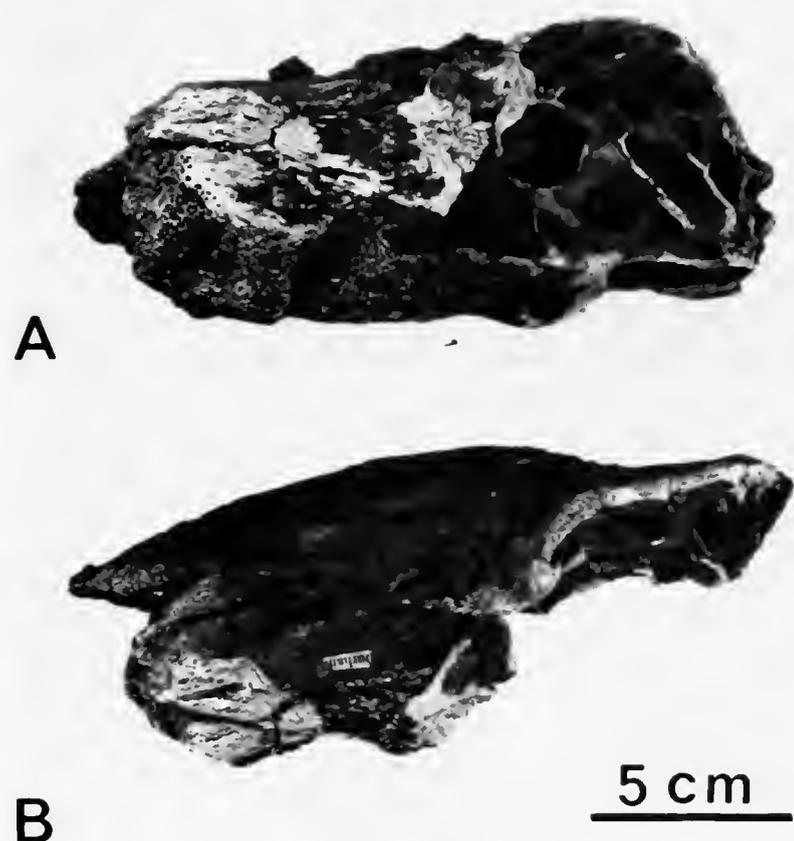


FIGURE 10.—Holotype of *Bison appalachicolus* Rhoads, 1895 (ANSP 29), in A, ventral, and B, rostral views.

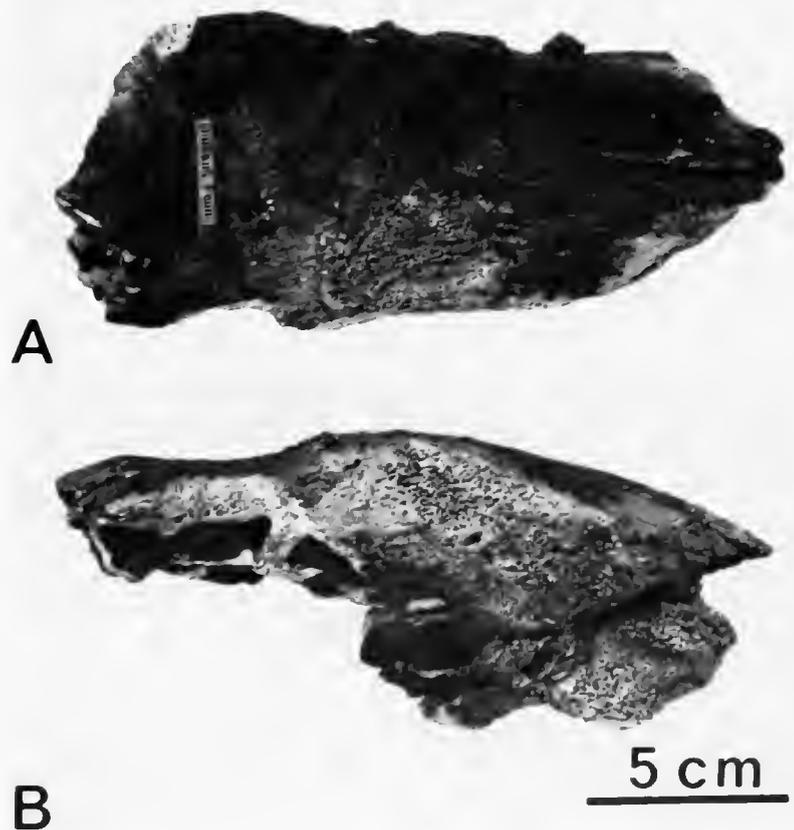


FIGURE 11.—Holotype of *Bison appalachicolus* Rhoads, 1895 (ANSP 29), in A, dorsal, and B, caudal views.

the specimen led Rhoads to conclude that it belonged to a musk ox, not bison, so he changed the name to *Ovibos (Bootherium?) appalachicolus* (Rhoads, 1897).

Osgood (1905a) reversed the trend toward synonymizing *Bootherium/Ovibos bombifrons* and *Bootherium/Ovibos cavifrons* when he created *Scaphoceros* to accommodate a nearly complete skull (USNM 2555; Figures 12–15) from the Yukon Territory that he described as *Scaphoceros tyrrelli*. Osgood transferred *Bootherium cavifrons* to *Scaphoceros* as *S. cavifrons*. Osgood rejected Rüttimeyer's *Ovibos priscus* as spurious and reinstated *B. bombifrons*, leaving it in a genus separate from *Scaphoceros*. (Following publication, *Scaphoceros* was found to be preoccupied and was replaced by *Symbos*; Osgood, 1905b). Osgood (1905a:181–183) justified and elaborated upon his decisions on the following grounds:

Since *bombifrons* and *cavifrons* have been considered by several authors as being not only congeneric but conspecific, the establishment of a separate genus for each may appear surprising. While it may be possible, from examination of figures only, to construct a hypothesis to the effect that *cavifrons* represents the male and *bombifrons* the female of one species, it is inconceivable that any modern taxonomist would reach such a conclusion after comparing the original types. These are now before me and with them are specimens of *S. tyrrelli* and of both sexes and young of *Ovibos moschatus*. From comparisons of these it is evident that, unless the disparity between the sexes in this case was vastly greater than in the recent genus *Ovibos*, *cavifrons* and *bombifrons* do not respectively represent the male and female of one species. Neither is *bombifrons* the young of any species, for the type gives every evidence of maturity.

The horn cores of the female *Ovibos* are essentially of the same character as those of the male. They are excessively flattened and directed downward close to the skull just as those of the male. Their bases approach each other over the top of the frontals increasing with age as in the male, the space between them being merely relatively greater than in the male. They are attached to the frontals only it is true, but this is the case with the immature male. Therefore the skull of the female has all the essential characters of the male but they are not as highly developed. The skull of *Bootherium bombifrons*, on the contrary, differs not in degree but in actuality from that of *Scaphoceros cavifrons* and *S. tyrrelli*. The horn cores are not flattened but are actually round or as nearly round as may be in a rough surfaced structure; they are directed away from the skull at a different angle; their attachment to the skull is entirely different; their bases do not approach each other in the least but on the contrary stand out from the skull on pedicels and have a distinct burr as in *Bison*. The frontal region between the horn pedicels is not flattened as in the female *Ovibos*, but is elevated and convex. The under side of the skull of the type of *bombifrons* is much injured but one conspicuous character is shown in which it differs from all the other species. This is found in the basisphenoid which is not deflected but has its lower surface in the same horizontal plane as that of the basioccipital and it has a sharp median ridge. The horn cores of *bombifrons* are essentially like those of *Bison* except that they turn downward instead of upward. However, other characters, notably the possession of deep lacrymal fossae, serve to distinguish it from *Bison*. In consideration of these various characters, the genus *Bootherium* with *Bos bombifrons* as the type seems to merit recognition. Thus far, only one specimen of this genus, the original type, has been found. Specimens of *S. cavifrons* and *S. tyrrelli*, however, have been secured at various localities among which are the following: Fort Gibson, Indian Territory; Council Bluffs, Iowa; New Madrid, Mo.; St Louis, Mo.; Benton Co., Mo.; Trumbull Co., Ohio; Brook Co., W. Va.; Pennsylvania; Anvik, Alaska, and Bonanza Creek, near Dawson, Yukon Territory. In this large number of specimens, if there were any females at all it is probable that there would be more than one. In order to give any semblance of certainty to the supposition that the differences between *bombifrons* and *cavifrons* are sexual, it is necessary to show that these differences are relatively the same that obtain

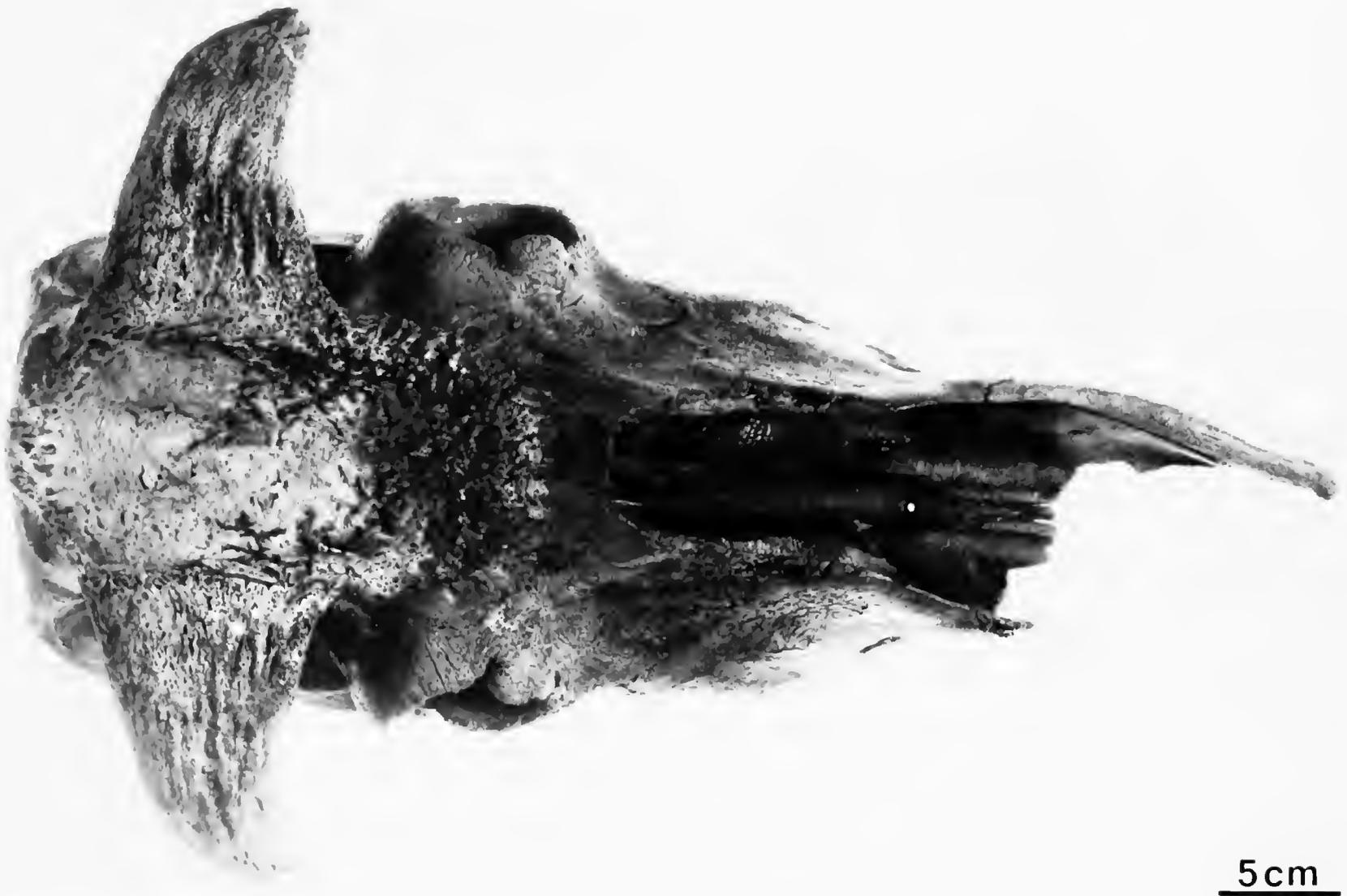


FIGURE 12.—Holotype of *Scaphoceros tyrrelli* Osgood, 1905 (USNM 2555), in dorsal view.



FIGURE 13.—Holotype of *Scaphoceros tyrrelli* Osgood, 1905 (USNM 2555), in right lateral view.

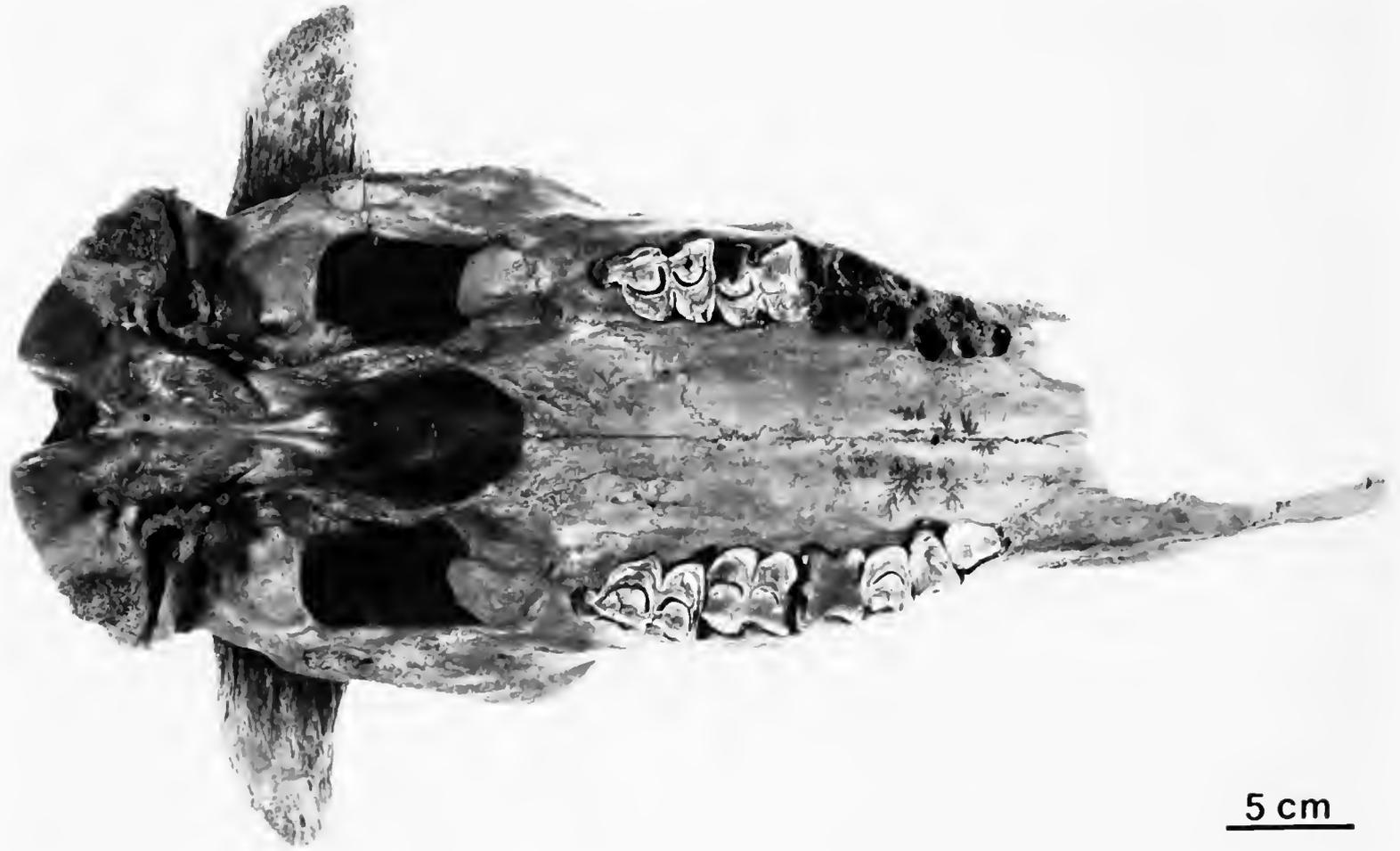


FIGURE 14.—Holotype of *Scaphoceros tyrrelli* Osgood, 1905 (USNM 2555), in ventral view.



FIGURE 15.—Holotype of *Scaphoceros tyrrelli* Osgood, 1905 (USNM 2555), in caudal view.

between the sexes in living species. This cannot be done, therefore it seems safer to treat the two animals as distinct. A much more reasonable assumption would be that *S. cavifrons* represents the male and *S. tyrrelli* the female of one species. The present objection to this is the fact that both have not been found in the same region.

From the foregoing excerpt, it can be seen that Osgood (1905a,b) considered the following facts important in separating *Symbos* and *Bootherium*:

1. The dimorphism between skulls of *Bootherium* and *Symbos* (Osgood's *Scaphoceros*) was greater than that between skulls of female and male *Ovibos moschatus*. (No number of specimens available was given, nor were quantitative comparisons of the dimorphism made.)

2. The shape of horn cores and the manner of their attachment to and development over the frontals differed qualitatively between *Bootherium* and *Symbos*.

3. The frontal region in *B. bombifrons* was elevated and convex, whereas that of *Symbos* "between bases of horn cores (was) surmounted by a prominent exostosis with an anterior bounding rim and a deep median excavation" (Osgood, 1905a:174).

4. The basisphenoid of *B. bombifrons* was not deflected from the basioccipital, and it contained a sharp median ridge on the ventral surface, whereas the basisphenoid in *Symbos* was deflected conspicuously and did not exhibit a sharp median ridge.

5. The sex ratio of skulls recovered (Osgood implied) should closely approximate the sex ratio of living wild populations. (No allowance was made for differential preservation or recovery of male and female skulls.)

Although Osgood had few specimens with which to work, including only a single specimen of the form he returned to *Bootherium bombifrons*, his ideas nonetheless have had great influence upon the study of Pleistocene musk oxen during the 20th century.

A new genus and species of musk ox was erected in 1906 by Gidley upon a partial cranium (USNM 5100; Figures 16–18) found during the construction of an irrigation dam near Black Rocks, McKinley County, New Mexico. Gidley (1906:165) acknowledged that "its incompleteness and poor condition make it a rather unsatisfactory type, yet there are sufficient distinctive characters preserved to warrant its description" which he gives as follows (Gidley, 1906:165–167):

LIOPS, new genus. [sic]

Generic characters.—Horn cores set wide apart and well back, as in *Ovibos*, but much less drooping; continuous with the frontals laterally, with no burrs or rugosities at base; smooth throughout. Parietals forming a large part of the occiput, which is high and narrow above. No true lambdoidal crest. Foramen magnum about one and one-half times greater in diameter than in *Ovibos*. Occipital condyles set widely apart, with their borders continuous with the surrounding bones. Tympanic bone roughly triangular in shape, very smooth and flat, with no bulla, and tightly inclosed by the surrounding elements. Post-glenoid process reduced to a low rounded knob.

LIOPS ZUNIENSIS, new species.

Type, top and back portion of skull, Cat. No. 5100, U.S.N.M. collection.

A striking feature of the portion of the skull preserved is its extreme

smoothness. Its angles are free from rugosities, and there are no sharp or roughened processes even in the tympanic and mastoid region. The horn cores are relatively longer, less robust, and less drooping than in *Ovibos* or *Simbas* [sic], the latter standing directly intermediate between *Liops* and *Ovibos* in this respect. Another striking feature is the position of the relatively large foramen magnum, which is confined entirely to the back or occipital face of the skull.

Gidley named the new genus *Liops*, with *Liops zuniensis* as the type species. *Liops* was twice preoccupied and, apparently, Gidley tried to change the generic name to *Lissops* in 1908. By that time, however, Cossmann had suggested replacing *Liops* with the valid name *Gidleya* which remains in current use (Cossmann, 1907; Gidley, 1908).

Gidley named two other extinct musk oxen in 1908 when he founded *Ovibos yukonensis* upon a partial skull (USNM 5728) from the Palisades along the Yukon River in Alaska and *Bootherium sargenti* upon a partial cranium (dorsal surface, part of left nasal, most of left horn core, and all of right horn core: GRPM 11-423-3101; Figures 19–21) from Moorland Swamp near Grand Rapids, Michigan. The Alaska specimen was correctly assigned to *Ovibos* and will not be considered further in this paper. Of *Bootherium sargenti*, Gidley (1908:683–684) said:

Species-characters.—Size about two-thirds that of *Ovibos moschatus*, somewhat larger than *B. bombifrons*; horn-cores comparatively large, well rounded, long and slender, horn-cores at base horizontally directed at right angles to the skull as in Plate LIX, fig. a, but curving downward and forward in graceful semi-spirals, ending in slender anteriorly directed tips (see Plate LIX, fig. b); orbits comparatively large, depressed below the arching frontals, with thin gently shelving borders, not tubular as in *Ovibos*. In the general form and contour of the skull and horn-cores this species, together with *B. bombifrons*, is strikingly different from other known species of the *Ovibovena*e [sic].

The type of *B. sargenti*, compared with that of *B. bombifrons*, shows the following resemblances: (1) The fragment preserved indicates a skull but little larger in size and of the same general proportions; (2) the position, form, and contour of the orbits as well as (3) the general appearance of the facial and posterior portions of the cranium (see Plate LIX, fig. c) are essentially alike. The horn-cores are also similarly placed, but the differences in their relative size, form and proportions are very marked. In *B. sargenti* the base of the horn-core is relatively heavier, is angular in front, and its superior border approaches much nearer the median frontal suture than in *B. bombifrons*. In addition, characteristic rugosities and markings on the frontals indicate that the horn-covering extended much beyond the horn-core base, nearly or quite meeting the one from the opposite side in the median line. In *B. bombifrons* the inter-horn space was apparently covered by a wide skin-band as in *Bos*. The horn characters seem sufficiently different to separate these species generically, but the other cranial characters denote generic relationship. Moreover it is possible that the extreme difference in type of horn-core may be due in part at least to difference in sex.

NOTES ON THE RELATIONSHIPS OF THE GENUS BOÖTHERIUM LEIDY.

The genus *Boötherium* has for some time been considered as closely allied to *Ovibos*, and by some authorities as synonymous with that genus. But in 1905 Mr. W. H. Osgood re-defined *Boötherium*, selecting *B. bombifrons* as the type, and transferred the remaining species, *B. cavifrons*, to a new genus, *Scaphoceros*, of which *S. tyrrelli* is the type. In the publication first cited Mr. Osgood has shown with good reason the untenability of the opinion held by Rüttimeyer and others regarding the types of *B. bombifrons* and *Ovibos* (*Symbos*) *cavifrons*, which they considered the female and male, respectively, of the same, or closely related, species. He has also pointed out that the type of *B. bombifrons* does not represent an immature male, but a fully adult



FIGURE 16.—Holotype of *Liops zuniensis* Gidley, 1906 (USNM 5100), in dorsal view.

individual. By an analogy similar to that employed by Osgood it is equally clear that the type of *B. sargenti* can not be referred on these grounds to any species of *Ovibos* or *Symbos*. The validity of the genus *Boötherium* therefore seems to be well established.

The separation of the two species originally referred to this genus permits the study of its relationships in a new light. As now known the genus presents quite as many bovine as ovibovine characters, and if referable to the Ovibovinae it is far removed from the other known genera of the group. From present evidence it seems probable that the finding of more complete material will show that, whether, generically distinct from each other or not, the species *B. bombifrons* and *B. sargenti* represent a distinct group, or subfamily, of the Bovidae. To this group may belong also the genus *Lissops* Gidley. Since, however, so little is known of the species of the group as a whole, owing to the lack of good material, it would be unwarrantable to separate them at present from the Ovibovinae.

A new species, *Symbos australis*, was erected upon three teeth (RM2, Lm2, Lm3: AMNH 11828; Figure 22) collected by Barnum Brown in 1904 at Conard Fissure, Newton County, Arkansas (Brown, 1908). Other ovibovine remains collected at the fissure and referred to *S. australis* included three premolars, an atlas, one or two proximal phalanges, and an ungual phalanx. (Brown reported one proximal phalanx on p. 203, but referred to two on p. 204. We are aware of only one such element among the ovibovine material from Conard Fissure

described by Brown.) Brown determined that the three molars were too large to belong to *Ovibos*, and sent the RM2 and the atlas to Osgood for comparison with the type specimens of *B. bombifrons*, *S. cavifrons*, and *S. tyrrelli*. Osgood concluded (Brown, 1908:203):

They evidently belong to a species different from the one on which I am working, *Symbos* (*Scaphoceros*) *tyrelli* [sic]. The tooth is somewhat smaller in my specimen, although the difference in condition makes it difficult to get an exact comparison. The atlas is much too small to fit on the condyle of my specimen or on that of the type of *Ovibos cavifrons* Leidy, with which I compared it in Philadelphia. The type of *O. bombifrons* is also in Philadelphia, but is very different from any of the other specimens and hardly needs to be considered.

Allen revised the North American musk oxen in 1913. Although his treatment of the fossil taxa was relatively superficial, he followed Osgood (1905a) in considering *Bootherium* and *Symbos* to be valid separate genera (Allen, 1913:209),

which, in the light of present knowledge, prove to be not only not congeneric, but not very closely allied. This interesting discovery is due to Osgood, whose paper on the status and relationships of *Bootherium* is entitled to high praise.

Allen (1913:210) considered that the following character



FIGURE 17.—Holotype of *Liops zuniensis* Gidley, 1906 (USNM 5100), in right lateral view.



FIGURE 18.—Holotype of *Liops zuniensis* Gidley, 1906 (USNM 5100), in caudal view.



FIGURE 19.—Holotype of *Bootherium sargenti* Gidley, 1908 (GRPM 11-423-3101), in dorsal view.



FIGURE 20.—Holotype of *Bootherium sargenti* Gidley, 1908 (GRPM 11-423-3101), in right lateral view.

differences satisfactorily separated *Bootherium* and *Symbos*:

1. *Bootherium* had *Bison*-like (round or sub-rounded) horns, whereas the horns of *Symbos*, unlike those of *Bison*, were flattened.

2. *Bootherium* had a smooth and sharply convex dorsal frontal surface, whereas the same surface in *Symbos* was an elongated trough covered with exostosis.

3. The ventral surface of the basisphenoid was continuous with that of the basioccipital in *Bootherium*, and it supported a

high ridge, whereas in *Symbos* the ventral surface of the basisphenoid was deflected from that of the basioccipital.

4. *Bootherium* had small but deep and sharply defined lacrimal fossae, whereas those of *Symbos* were shallow and less well defined.

5. *Bootherium* was much smaller than *Symbos*, based on the assumption that the holotype of *Bootherium bombifrons* was the skull "of a very old male, with all the sutures of the preserved part of the skull wholly obliterated by ankylosis."



FIGURE 21.—Holotype of *Bootherium sargenti* Gidley, 1908 (GRPM 11-423-3101), in caudal view.

Allen went on to say, however, that *Bootherium* did resemble *Symbos* in some characters, including those of the occipital condyles, the occipital plane, and the length and depth of the skull. Nonetheless, he concluded that *Bootherium* and the recently described shrub ox *Preptoceras* (Furlong, 1905) were “not closely related, but more nearly so than is either to any other known genus” (Allen, 1913:212), a decision that was based more upon the superficial impression of horn core similarity than a thorough systematic comparison of cranial structure in the two forms.

Bootherium sargenti, however, was transferred from *Bootherium* to *Symbos* by Allen (1913:215). The species

was founded on an imperfect skull . . . found in a swamp near Grand Rapids, Michigan. In the description comparison is strangely made with *Bootherium bombifrons*, with which it shares no essential feature. The horncores are attached to the skull as in the female of *Ovibos*, with about the same relative area of exostosis extending from the base over the lateral third or more of the frontals and not, as in *Bootherium*, supported on a pedicel and terminating in a burr as in *Bison*. The relationship of *Bootherium sargenti* is entirely with *Symbos*, and well fulfills the conditions that would be expected in the female of *S. cavifrons*.

Allen did not specify what conditions would be expected in the female of *Symbos*, nor did he consider the possibility, when discussing *S. tyrrelli*, that this form could be the female of *S. cavifrons*. Allen did, however, refer *S. australis* to *S. cavifrons* “as probably representing the female of that species” (Allen, 1913:215).

Allen upheld the distinctiveness of *Gidleya* (which he discussed under *Liops*). His description of the specimen (Allen, 1913:216) reads, in part, as follows:

The dense smooth natural surface of the bone is preserved over the greater part of the dorsal aspect of the skull, except laterally in the postorbital region; the surface elsewhere consists of the cancellous structure of abraded bone, the abrasions being in places quite superficial, as in the case of the horncores and upper surface of the skull, and elsewhere so deep as to greatly obscure or wholly obliterate important features, as the condyles, the characters of the mastoid and tympanic regions, and the occipital angles. The unabraded dorsal surface of the skull shows that it must have been that of an old animal, and probably that of a male, the sutures being entirely obliterated by ankylosis.

Continuing, Allen (1913:216) acknowledged that *Liops* was nearer *Symbos* than any other taxon, as Gidley (1906) had suggested.

A striking difference between *Liops* and both *Symbos* and *Ovibos* is the smoothness of the surface of the basal portion of the horncores and the entire absence of exostosis between the horn bases over the top of the skull, which is here smooth, with the same dense surface as that of the interorbital and preorbital portions.

The ventral, caudal, and lateral surfaces of the skull, Allen stated, were greatly abraded.

Hay (1915) erected *Bootherium nivicolens* on the basis of a partial cranium (USNM 23241; Figure 23) from Eschscholtz Bay, Alaska, that possessed character states he considered different from or midway between *B. bombifrons* and *B. sargenti*. Most important among these were the outward orientation of the horn cores and the way in which they had burrs situated on distinct pedicels, as in *B. bombifrons*. The specimen also had exostosis extending over the dorsal surface of the pedicel onto the lateral edges of the dorsal surface of the frontals, as in *B. sargenti*. Hay also rejected Allen’s synonymizing of *B. sargenti* and *S. cavifrons*, arguing that it was unlikely that, among the 25 or so skulls known and assigned to *S. cavifrons*, only one would have belonged to a female. More likely, Hay maintained, the smaller specimens with exostosis-covered frontals and more feebly developed horn cores that were assigned to *Symbos* probably represented females. Hay (1915:527) also pointed out that one of the characteristic features of *Bootherium*, as identified by Allen, was

the abrupt downward slope of the dorsal outline of the skull posterior to the horn cores. The type skull of *B. sargenti* has a slope of the same region which lacks but a few degrees of being equal to that found in *Bootherium*

Elsewhere, Hay (1915:527) stated:

Notwithstanding the immense development of the horn-cores of the males of *Symbos cavifrons*, there is no such elevation of the region behind the orbits as we see in the case of *B. sargenti*

Four new species of Pleistocene musk oxen were named

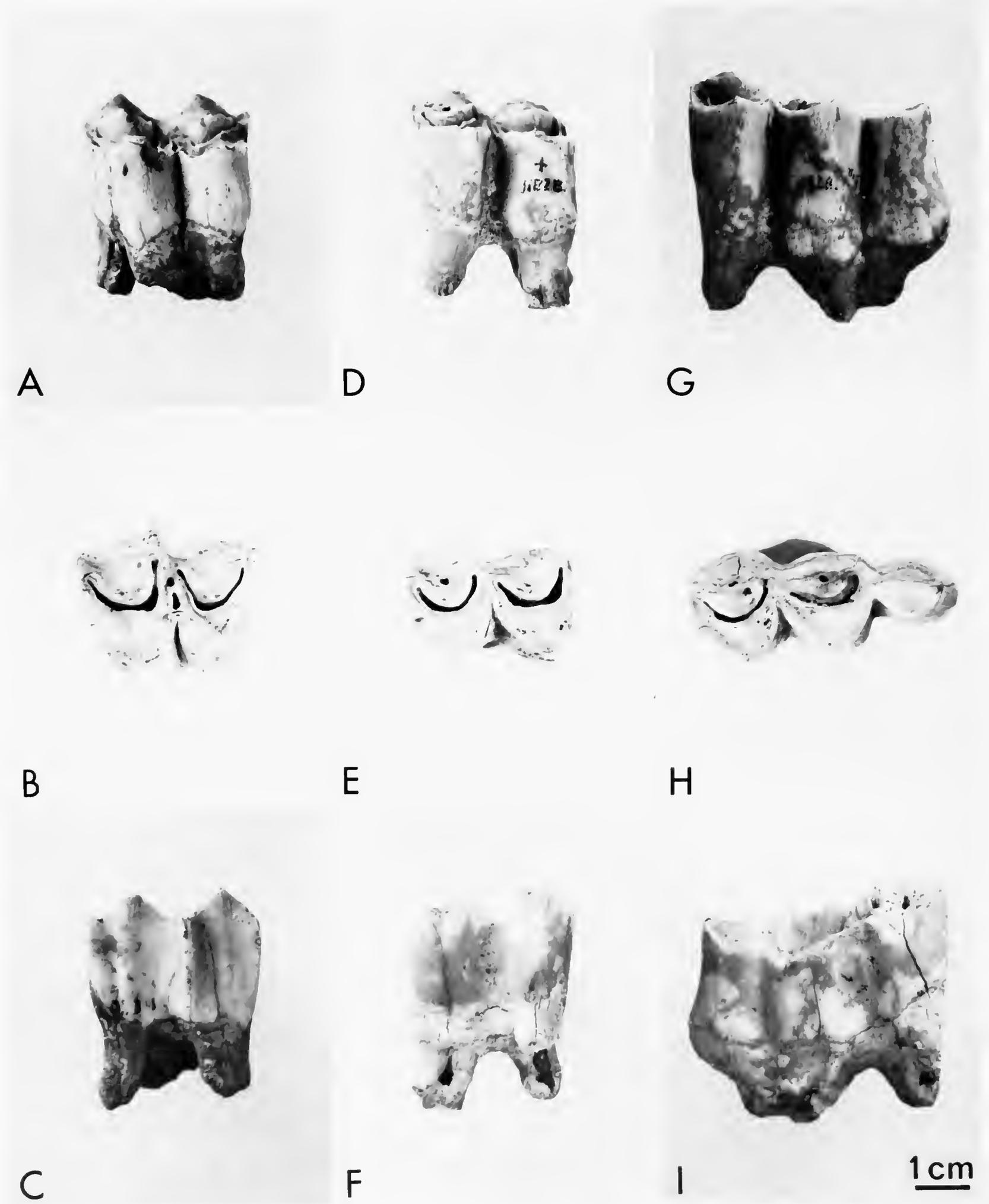


FIGURE 22.—Type of *Symbos australis* Brown, 1908 (AMNH 11828): RM2 in A, lingual, B, occlusal, and C, labial views; Lm2 in D, labial, E, occlusal, and F, lingual views; and Lm3 in G, labial, H, occlusal, and I, lingual views.



FIGURE 23.—Holotype of *Bootherium nivicolens* Hay, 1915 (USNM 2324), in dorsal view.

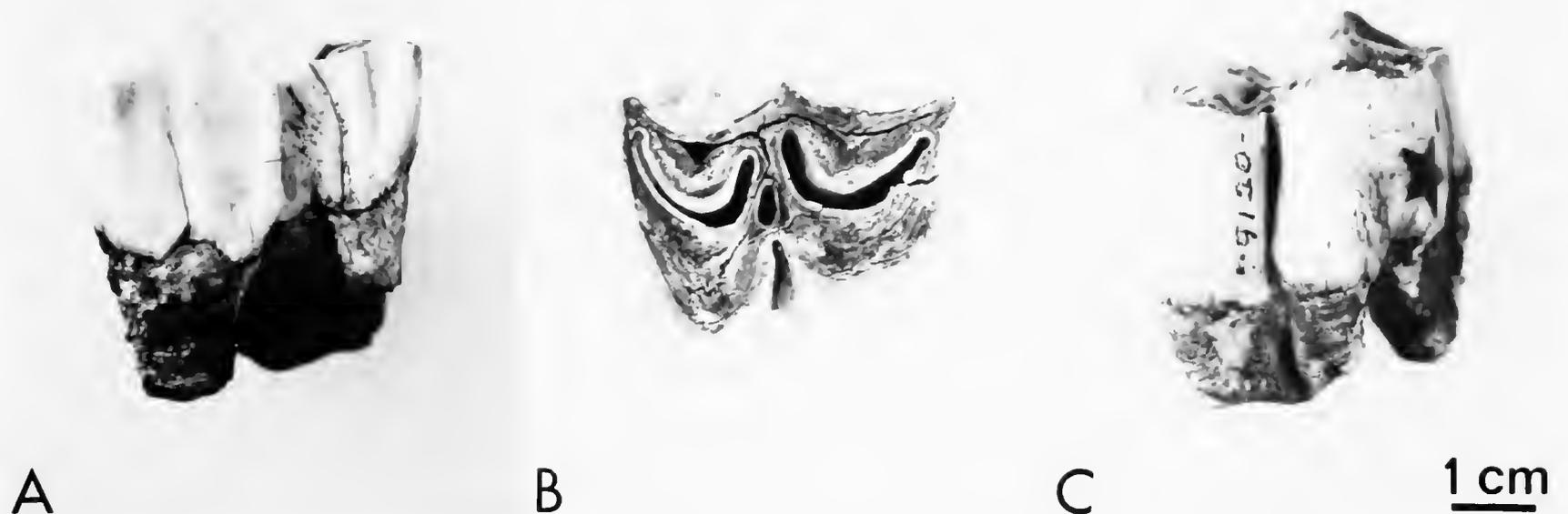


FIGURE 24.—Holotype of *Symbos promptus* Hay, 1920 (USNM 9120), in A, labial, B, occlusal, and C, lingual views.

from 1920 to 1942. *Symbos promptus* was founded upon an upper left third molar (USNM 9120; Figure 24) from near Afton, Oklahoma, the diagnosis given as simply “Upper molars with the external styles less strongly developed than in *S. cavifrons*; the fossetts less angular” (Hay, 1920:125). Barbour (1934) named *Symbos convexifrons* upon a nearly complete skullcap and right horn core (UNSM 39001; Figures 25–28) found in the North Prong Quarry in southern Cherry County,

Nebraska. “The brow of this specimen is notably convex, and this, coupled with the slope, length, and sweep of the horn cores, constitutes the main feature of this new species” (Barbour, 1934:295). *?Ovibos giganteus* was created by Frick (1937) with a large right humerus (F:AM 30498; Figure 29) from near Fairbanks, Alaska, as the holotype. Frick probably was stimulated to name this species after seeing what was (probably erroneously) then identified as the humerus of a



FIGURE 25.—Holotype of *Symbos convexifrons* Barbour, 1934 (UNSM 39001), in dorsal view.



FIGURE 26.—Holotype of *Symbos convexifrons* Barbour, 1934 (UNSM 39001), in right lateral view.



FIGURE 27.—Holotype of *Symbos convexifrons* Barbour, 1934 (UNSM 39001), in ventral view.



FIGURE 28.—Holotype of *Symbos convexifrons* Barbour, 1934 (UNSM 39001), in caudal view.

giant ovibovine from near the American Falls Reservoir, Idaho (Frick, 1937). The last North American musk ox to be named was *Bootherium brazosis*, erected upon a damaged partial cranium with partial horn cores (TAMC 2553; Figures 30–32) that was found in Brazos County, Texas (Hesse, 1942). Hesse considered his specimen to resemble *B. bombifrons* more than

any of the other nominal taxa, but it was differentiated from *B. bombifrons* by minor differences, some of which undoubtedly resulted from Hesse's having misoriented the specimen during study.

Hibbard and Hinds initiated a resurgence of attention to the relationship among *Bootherium* and *Symbos* species that has

A



B



5 cm

FIGURE 29.—Holotype of ?*Ovibos giganteus* Frick, 1937 (AMNH F:AM 30498), in A, cranial and B, caudal views.



FIGURE 30.—Holotype of *Bootherium brazosis* Hesse, 1942 (TAMC 2553), in dorsal view.



FIGURE 31.—Holotype of *Bootherium brazosis* Hesse, 1942 (TAMC 2553), in ventral view.



FIGURE 32.—Holotype of *Bootherium brazosis* Hesse, 1942 (TAMC 2553), in caudal view.

continued to the present. These authors stated "it is very likely that *Boötherium* is the female woodland musk ox since all specimens of *Symbos* based on skulls are considered as those of bulls" (Hibbard and Hinds, 1960:107). Harington (1961) disagreed, instead favoring Hay's (1915) separation of the two genera. Semken, Miller, and Stevens (1964) apparently adopted Allen's views, concluding that *Bootherium bombifrons* was not a female *Symbos* but that *B. sargenti*, which was erroneously placed within *Bootherium*, might be. Ray evaluated the status of *B. appalachicolus* and *B. brazosis* and concluded that both were better considered junior synonyms of *B. sargenti* than separate species. Ray also acknowledged the merit of the suggestions that *B. sargenti* could represent the female of *S. cavifrons*, and stated that failure to allow for weathering damage had vitiated much comparison and unwarranted differentiation in the past (Ray, 1966a,b). By 1977, Harington had come to accept the synonymy of *S. cavifrons* and *B. sargenti*, but "presuming the specimen of *Boötherium bombifrons* does not represent an abnormal individual, that species is probably not closely related to *Boötherium sargenti* or *Symbos cavifrons*" (Harington, 1977:880–881). Regarding the synonymy of *B. sargenti* and *S. cavifrons*, Harington (1977:882–883) wrote:

...the evidence supporting this view is very strong. The similar basic conformation of the horncores (as far as orientation and curvature are concerned); the smaller, thinner-roofed cranium; and the broad space between the horncore bases in the former species parallel the differences between male and female *Ovibos moschatus*: thus Sargent's muskox resembles what a female *Symbos cavifrons* would be expected to look like. In addition, *Boötherium sargenti* and *Symbos cavifrons* had similar geographic and habitat preferences (e.g. Alaska, Yukon Territory, Indiana, Michigan, Virginia (using *Boötherium* sp.), Utah, Missouri and Nebraska), and sometimes even from the same site and deposit (e.g. near Great Salt Lake, Utah, in the Bonneville sands and gravels (Stokes and Hansen 1937, p. 63), and evidently in the Goldstream Formation of Wisconsin age near Fairbanks, Alaska). In the conterminous United States, both species are concentrated within the same latitudinal range—usually south of the late Wisconsin fossil localities of the tundra muskox, *Ovibos moschatus*. Unlike *Soergelia*, *Praeovibos*, and *Ovibos*, which had Holarctic distributions during the Pleistocene, *Boötherium sargenti* and *Symbos cavifrons* are only known from North America. Geochronologically, both species appear during the Illinoian and become extinct near the close of the Wisconsin glaciation.

In the preceding excerpt, Harington advocated the comparison of patterns of both sexual dimorphism (without demanding exact duplication of character states between the sexes, as had earlier writers) and geographic and chronologic distribution in assessing the relationships between these two taxa.

Nelson and Madsen (1978) and Nelson and Neas (1980) recognized *Bootherium* and *Symbos* as distinct genera, but acknowledged that the status of most nominal species within *Bootherium* was still uncertain. Following Harington, Kurtén and Anderson (1980) placed *B. sargenti* in *S. cavifrons* while allowing *B. bombifrons* to stand, although with the admonition that "The status of the genus *Bootherium* is in doubt; it has often been considered to be congeneric with *Symbos*, but this is undemonstrated" (Kurtén and Anderson, 1980:334). Nelson and Madsen (1987) concurred with Harington (1977) and Kurtén and Anderson (1980) in synonymizing *S. cavifrons* and

B. sargenti (as *S. cavifrons*) while maintaining the validity of *B. bombifrons* as a distinct taxon. Neas has reversed his opinion held in 1980 that *Bootherium* and *Symbos* were distinct taxa and, with McDonald and Ray, views all nominal taxa within *Bootherium*, *Symbos*, and *Gidleya* as synonyms of *Bootherium bombifrons* (McDonald, 1986; Neas, 1986; McDonald and Ray, 1987, in press; Neas and Hoffmann, 1987; Neas and Parker, 1987).

The Content of *Bootherium*, *Symbos*, and *Gidleya*

Twelve nominal species of autochthonous North American musk oxen were erected between 1825 and 1942 within, or are referable to, the genera *Bootherium*, *Symbos*, and *Gidleya*. *Bootherium*, in the modern sense, at one time or another contained the five species *B.* (= *Bos*) *bombifrons* (1825), *B.* (= *Bison*) *appalachicolus* (1895), *B. sargenti* (1908), *B. nivicolens* (1915), and *B. brazosis* (1942). Ray placed *B. appalachicolus* and *B. brazosis* in synonymy with *B. sargenti*, and Harington did the same with *B. nivicolens* (Ray, 1966a,b; Harington, 1977). Allen (1913) attempted to place *B. sargenti* in synonymy with *Symbos cavifrons*, but this decision has met with mixed acceptance and the status of *B. sargenti* must, therefore, be reevaluated. *Bootherium bombifrons* was considered conspecific with *Symbos cavifrons* by Rüttimeyer (1865), Dawkins (1872), and their followers during the late part of the 19th century, but the two taxa have been considered generically distinct for most of their history. At present, most workers tend to recognize only a single species of *Bootherium*, *B. bombifrons*, while acknowledging that uncertainty in the taxonomic status of the group, and especially of *B. sargenti*, clearly exists.

Symbos has contained six species during its 135-year history, including *Symbos* (= *Bootherium*) *cavifrons* (1852), *S. tyrrelli* (1905), *S. australis* (1908), *S. promptus* (1921), *S. convexifrons* (1934), and *S.* (= ?*Ovibos*) *giganteus* (1937). Allen (1913) placed *S. australis* in synonymy with *S. cavifrons*, and Jakway (1961b) did the same for *S. convexifrons*. Among the remaining four species, only *S. cavifrons* is in use.

Gidleya has contained only a single species, *G.* (= *Liops*, *Lissops*) *zuniensis* (1906). Although this taxon has been recognized by several paleontologists since it was established, it has never received validation as a viable taxon.

The relationship of *Ovibos maximus* is uncertain; this taxon probably is properly placed within *Ovibos*, although conclusive determination of that fact must await further comparative study of the axes of the various ovibovine genera.

At present, then, there are seven nominal species standing within the three genera, five of the 12 named species having been placed previously, without subsequent rejection, in synonymy (Appendix II). The standing species are *B. bombifrons* (Harlan, 1825); *S. cavifrons* (Leidy, 1852); *S. tyrrelli* Osgood, 1905; *Gidleya zuniensis* (Gidley, 1906); *B. sargenti* Gidley, 1908; *S. promptus* Hay, 1920; and *S.* (= ?*Ovibos*) *giganteus* (Frick, 1937).

We are of the opinion that *B.* (= *Bos*) *bombifrons*, *B.*

(= *Bison*) *appalachicolus*, *B. sargenti*, *B. nivicolens*, and *B. brazosis* are conspecific. *Bootherium appalachicolus*, *B. brazosis*, and *B. nivicolens* have been synonymized with *B. sargenti* by Ray (1966a,b) or Harington (1977). *Bootherium bombifrons* and *B. sargenti* may be considered conspecific on the basis of morphological similarity of their cranial and horn core structure, especially (1) horn core size, shape, orientation, and cranial attachment, and (2) frontal configuration (Figures 1–3, 19–21). Aside from modest differences in the exact shape and size of character states—all of which can be attributed more satisfactorily to individual variation than to taxonomic distinctiveness—there are no significant morphological features present on the holotypes of these taxa sufficient to justify their taxonomic separation. Despite numerous statements and implications to the contrary, the differences in the size, shape, surface details, and orientation of character states between *B. sargenti* and *S. cavifrons* are much greater, qualitatively and quantitatively, than are those between *B. bombifrons* and *B. sargenti*. Detailed comparisons of character state differences, and discussions of the reasons for those differences among individuals and between sexes and taxa, are presented below (pp. 25–51).

We also are of the opinion that all nominal species within *Symbos* (including ?*Ovibos giganteus*) should be considered conspecific. *Symbos convexifrons* was established upon the dorsal half of a cranium and nearly complete right horn core (Figures 25–28). The dorsal surface of the right half of the braincase is preserved, whereas the frontoparietal sinuses are exposed on the left side (in ventral view). Several small fragments of bone have been reattached to the cranium with plaster. The diagnostic characters for *S. convexifrons* were the “notably convex” dorsal surface of the cranium, coupled with the slope, length, and sweep of the horn cores. Barbour (1934:295) also noted that “the horns rise from the side of the head.” Jakway (1961b), following Frick (1937:562), referred *S. convexifrons* to *S. cavifrons* on the grounds that (1) all other remains of *Symbos* from the North Prong Quarry and other sites in Nebraska were assignable to *S. cavifrons*, and (2) the “convexity between the horncores, the supranuchal, and the internal surface of the cranium” seemed to be pathological instead of taxonomically significant variations (Jakway, 1961b:115).

The holotype of *S. convexifrons* appears to represent a mature individual, based on the size of the specimen, the density of the horn core, and the absence of unfused sutures. This specimen is unusual, however, in several respects. (1) The horn core possesses a distinct burr line which delimits the horn core proper from the exostosis covering the intercornual surface of the cranium. (2) The base of the remaining horn core is situated abnormally low on the side of the cranium and the horn core emanates from the cranium at an unusually low angle but, based on differences in the planes of secondary bone medial to the bases of the horn cores, the left core was neither situated as low nor did it emanate at such an unusually low angle. (3) The longitudinal profile of the dorsal surface of the

cranium is flexed to an unusual degree. (4) The transverse profile of the dorsal surface of the cranium is asymmetrical. (5) The exostosis is distributed rather thinly and uniformly across the intercornual region. The exostosis extends rostrally only a short distance from the level of the horn cores and caudally only a short distance onto the parietal surface. No rim-like or shelf-like build-up of secondary bone is present at either the caudal or rostral edges, respectively, of the exostosis. (6) The horn core attaches only to the frontal bone.

We are of the opinion that the asymmetry of the transverse profile of the dorsal surface of the cranium in the holotype of *S. convexifrons* is probably attributable to a pathology of the right horn core. We were unable to locate any other natural asymmetries and consider the cranium—excluding the horn pathology and subsequent atypical development of the intercornual boss and associated exostosis—to be normally developed. Two fragments of the cranium—one including the insertion surface for the left *M. semispinalis capitis* and the other a portion of the left frontoparietal bones—were reattached at the wrong location during restoration. These artificial errors probably contributed to Jakway’s recognition of asymmetries in the supranuchal ridge and internal surface of the cranium. Aside from the asymmetry of the dorsal surface of the cranium in transverse profile and the low level of emanation of the right horn core, the holotype of *S. convexifrons* strongly resembles a cranium with horn cores (USNM 23548) found in the Ohio River below Augusta, Bracken County, Kentucky. The Kentucky specimen has a similarly flexed (longitudinally) dorsal surface of the cranium and—over the caudal part of the dorsal surface—a similar pattern of exostosis development. Other crania identified as *S. cavifrons* (e.g., AMNH F:AM 33129 from Lower Goldstream, Fairbanks District, Alaska) also exhibit marked flexion of the longitudinal profile of the dorsal surface, as do specimens identified as *Bootherium* (e.g., ANSP 994 from Big Bone Lick, Kentucky; USNM 23264 from Saltville, Virginia). We believe that the holotype of *S. convexifrons* represents a pathologic adult male with abnormal placement and orientation of the right horn core and the development of the keratinous boss over the dorsal surface of the cranium. When the evidence of this pathologic condition is put aside, we see nothing to justify recognition of *S. convexifrons* as a valid taxon distinct from *S. cavifrons*.

Allen’s (1913) referral of *S. australis* (founded upon three associated teeth, AMNH 11828; Figure 22) is reasonable, in part, but not conclusive. The RM2 and Lm2 are undifferentiable from the equivalent teeth in other specimens of *S. cavifrons*. The Lm3, however, differs somewhat from other m3s assigned to *S. cavifrons*. Specifically, the shape of the enamel border of the entoconulid-hypoconulid is conspicuously rounded (i.e., elliptical) in the holotype of *S. australis* (Figure 22). The same character in other m3s of *Symbos* is more complexly shaped, with an undulating lingual surface and a distinct terminal stylid at the caudal end. The unusual shape of the entoconulid-hypoconulid in the *S. australis* m3 could represent (1) an atypical tooth of *Symbos*, (2) a character state

typical of early *Symbos* that subsequently changed to the form found in late Wisconsinan *Symbos*, or (3) a tooth belonging to another large ovibovine, such as *Euceratherium*. (The teeth that constitute the type of *S. australis* are within the size range of the teeth of *Euceratherium*. The breadth of the occipital condyles in the holotype of *Euceratherium collinum* is 103 mm, and the breadth of the cranial articular cavities in the atlas from Conard Fissure is 107 mm.) Dental variation within the ovibovines, and especially shrub oxen, is not known sufficiently well to conclusively determine the identity of the teeth of the *S. australis* type specimen. The possibility exists that the three teeth forming the type of *S. australis* might represent more than one animal and, perhaps, more than one taxon. We feel that *S. australis* should be left in synonymy with *S. cavifrons* for now, but we also recognize that some or all of these teeth might, at some later date, be assignable to one or more other taxon/taxa.

Symbos tyrrelli was erected upon a nearly complete but unusually small skull (USNM 2555, the smallest skull for which quantitative information was available in 1905; Figures 12–15) from Bonanza Creek, Yukon Territory, at a time that few *Symbos* crania were known (Osgood, 1905a). Osgood used three character states to differentiate the Bonanza Creek specimen from *S. cavifrons*: the relatively small size, restricted development of exostosis, and shallow depth of the frontoparietal region. The holotype does not, however, possess any character of taxonomic significance that would set it apart, qualitatively or quantitatively, from *S. cavifrons* as that species is now conceived, based upon more than 150 known specimens. Specifically, the size of the skull and its various characters, the degree of exostosis development, and the depth of the frontoparietal sinus region of the Bonanza Creek specimen are all within the range of variation known for *S. cavifrons*. We feel that *S. tyrrelli* is conspecific with *S. cavifrons*.

Symbos promptus was founded upon an upper left third molar (USNM 9120; Figure 24) from near Afton, Oklahoma (Hay, 1920). This tooth is well worn; about one-third of the crown remains. The two criteria upon which the species was founded were the less extensive lateral development of the buccal styles and the more crescentic, less angular shape of the enamel border of the internal fossettes, relative to other known teeth of *Symbos*. Apparently, Hay compared the tooth from Afton only with two other specimens—the upper right second molar in the *S. australis* type tooth series and the superior molars in a *Symbos cavifrons* skull from near Manchester, Michigan (Hay, 1920). The tooth from Afton was worn more than either of the teeth with which it was compared. As wear progresses in the superior molars of *Symbos cavifrons*, the lateral extension of the buccal styles is reduced and the shape of the enamel border of the fossettes changes from a more angular or chevron shape to a more rounded or crescentic shape. The tooth from Afton is within the size range of the teeth of *Symbos cavifrons* (the size of the M3 of *Bootherium* is still unknown), and appears to be nothing more than a relatively well worn tooth assignable to that taxon. We feel that *S. promptus* is

properly a junior synonym of *S. cavifrons*.

Frick erected *Ovibos giganteus* upon a right humerus (AMNH F:AM 30498; Figure 29) from an unidentified site in the Fairbanks District, Alaska (Frick, 1937). Frick gave no reason for considering the holotype to be other than *Symbos* or *Bootherium*, nor were any diagnostic criteria given in the type description. Some of the incentive for establishing this species probably came from the discovery by J.W. Gidley, in 1929 and 1930, of what were considered to be remains of a giant ovibovine from southern Idaho. Two crania of *Symbos cavifrons* possessing unusually large horn cores were found in a gravel quarry near the American Falls Reservoir, and these might have inspired some notion of gigantic ovibovines from that area. In addition, a robust radioulna and an unusually long humerus from southern Idaho were also identified as ovibovines. The humerus was shown to Frick by Gidley, and might have been the specific stimulus that led Frick to recognize an extinct taxon of giant musk ox from Alaska. Actually, the radioulna (figure 26 in Gidley, 1930) was probably *Bison latifrons* and the humerus was probably *Camelops* sp. In the collection of fossils from southern Idaho in the National Museum of Natural History (USNM), there are no ovibovine limb bones, but there is a large *Bison* radioulna (USNM 13710) that can be identified as the one in Gidley's figure 26 and a *Camelops* humerus (USNM 392114) of similar size to that mentioned by Frick from Idaho (length estimated by Frick: 470 mm; length of USNM 392114, whose proximal end is abraded slightly: 458 mm). The humerus from near Fairbanks is ovibovine, it is similar in size and morphology to the humerus of an associated partial skeleton (F:AM A-204-4254) of *Symbos cavifrons* from Little Eldorado Creek, Alaska, and we refer it to that species.

Gidleya zuniensis was founded upon an extensively abraded cranium and carries only a single specimen, its holotype (USNM 5100; Figures 16–18).

The seven standing species of musk oxen within the genera *Bootherium*, *Symbos*, and *Gidleya* have been reduced to three species in three monotypic genera: *Bootherium bombifrons*, *Symbos cavifrons*, and *Gidleya zuniensis*. In the next two sections of this paper, we evaluate the relationships between the genera (1) *Gidleya* and *Symbos* and (2) *Bootherium* and *Symbos*, respectively.

The Relationship between *Gidleya* and *Symbos*

The genus *Gidleya* (= *Liops*, *Lissops*, sensu Gidley, 1906, 1908) was founded upon a partial skull (USNM 5100; Figures 16–18) found in 1905 during the construction of an irrigation dam on the Zuni Indian Reservation at Black Rocks, McKinley County, in western New Mexico. This specimen, along with a small collection of other vertebrate fossils (including *Mammothus columbi*, *Equus* sp. indet., and camel) was salvaged by the site engineer John B. Harper and transferred to the Smithsonian Institution through the efforts of F.E. Leupp, Commissioner of Indian Affairs.

The musk ox specimen from Black Rocks had been damaged extensively by abrasion. Most of the occipital surface is missing, both of the horn cores have been shortened and reduced in diameter by the loss of surface bone, the dorsal surface of the cranium has been abraded to the extent that several of the parietal and frontal sinus cells are exposed. The remainder of the specimen has had most surface detail completely removed or extensively rounded by abrasion. Most of the dense outer bone appears to have been removed prior to the time this specimen was unearthed, leaving cancellous bone exposed over much of the surface. The cells of the cancellous bone apparently filled with a fine grained chemical precipitate during or prior to the last phase of abrasion, giving the specimen an unnaturally smooth surface. Other parts of the remaining surface are not smooth, probably because of damage incurred during the excavation, drying, and handling of the specimen. (The smooth surface bone easily separates from the deeper bone at a nearly uniform depth.)

The poor condition of the specimen was acknowledged by Gidley in his type description of the genus (as *Liops*) and its sole species *G.* (= *Liops*) *zuniensis* (Gidley, 1906). The characters that Gidley considered to be taxonomically significant were all products of post-mortem alteration—the “extreme smoothness” of the skull, its angles “free from rugosities,” and absence of “sharp or roughened processes even in the tympanic and mastoid region,” horns “relatively longer, less robust and less drooping” than in *Ovibos* or *Symbos*, and “the relatively large foramen magnum, which is centered entirely to the back or occipital face of the skull” (Gidley, 1906:166–167).

With uncharacteristic oversight, Allen apparently regarded the abraded dorsal surface as being natural, writing “The dense smooth natural surface of the bones is preserved over the greater part of the dorsal aspect of the skull, except laterally in the postorbital region” (Allen, 1913:216). Allen correctly pointed out that Gidley had failed to recognize the extent to which the caudal, lateral, and ventral surfaces of the skull had been damaged, and that as a result Gidley had introduced errors into his generic diagnosis. Allen also noted that, while the Black Rocks specimen was about one-half the size of *Symbos* (Allen personally had examined only one *Symbos* specimen, AMNH 14365 from Hebron, Porter County, Indiana), its proportions were similar to those of *Symbos* (Allen, 1913).

Patterson commented further upon the insecure foundation of *Gidleya* in some unpublished notes that he prepared after he received a cranium of *Symbos cavifrons* from near Grand Mesa, Delta County, Colorado (McDonald, 1985a), that was abraded somewhat like the type specimen of *Gidleya zuniensis*:

On comparing this (i.e., the Colorado) fragment with specimens of *Ovibos* and with published figures and descriptions of the various Pleistocene forms I was struck by its resemblance to Gidley's “*Liops*” *zuniensis* (*Gidleya zuniensis* Cossman [sic], 1907). The type of this species was found near Zuni, New Mexico and was also uncovered, curiously enough, during excavations for a dam. Dr. C. Lewis Gazin kindly arranged for a loan of the specimen, U. S. N. M. no. 5100.

Careful comparison of the two specimens permits no doubt that they are congeneric and little doubt, despite the somewhat larger size of the Colorado

specimen, that they are conspecific. The type is about as waterworn as is possible for a fossil to be and yet retain some character; so scoured is it that some portions could almost be described as polished. It is quite evident that Gidley completely underestimated the extent of the abrasion and was therefore badly led astray. I quote his diagnosis here, placing brackets around those “characters” that are certainly artificial.

Horn cores set wide apart and well back, as in *Ovibos*, but much less drooping, [continuous with the frontals laterally, with no burrs or rugosities at base; smooth throughout.] Parietals forming a large part of the occiput, which is high and narrow above. [No true lambdoidal crest.] Foramen magnum [about one and one half times] greater in diameter than in *Ovibos*. [Occipital condyles set widely apart, with their borders continuous with the surrounding bones.] Tympanic bone roughly triangular in shape [very smooth and flat with no bulla and tightly inclosed by the surrounding elements. Post-glenoid process reduced to a low rounded knob].

None of the characters that remains after this elimination distinguishes *Gidleya* from *Symbos* (Osgood 1905A and B) (Notes attached to letter: B. Patterson to C. E. Ray, 4 November 1968).

Gidley originally described this taxon under the name *Liops* (Gidley, 1906), but that name was preoccupied so Cossmann (1907) suggested replacing it with *Gidleya*. Gidley, perhaps realizing *Liops* was unavailable and not knowing of Cossmann's replacement, inserted—without explanation or reference to a specific specimen—the name *Lissops* in a subsequent manuscript when he alluded to the genus based on the Black Rocks specimen (Gidley, 1908). Allen (1913) and Troxell (1915) retained use of *Liops*, but most subsequent authors have referred to the genus as *Gidleya* (e.g., Hay, 1922, 1924; Ryziewicz, 1933, 1955; Kretzoi, 1942; Harington, 1961; Romer, 1966). Frick's placement of *Gidleya zuniensis* in *Ovibos*, as *O. zuniensis*, was done without explanation and has had no following (Frick, 1937). Although, based upon usage of the name, *Gidleya* has been considered a viable genus, the literature gives no indication that any specimen other than the holotype of *G. zuniensis* has ever been placed in the genus.

If allowance is made for the extensive loss of bone by battering and fine abrasion, the cranium upon which *Gidleya* was founded is undifferentiable from crania that would routinely be assigned to *S. cavifrons*. As Allen (1913) suggested and Patterson (n.d.) stated emphatically, the proportions and configuration of the vestigial characters are like those in *Symbos cavifrons*. The Black Rocks specimen is smaller than average (a condition exaggerated by its abraded condition), but it is still clearly within the range of variation for cranial characters of *S. cavifrons*. At least two other crania of *S. cavifrons* are now known from the Colorado Plateau (McDonald, 1985a; McDonald, Neusius, and Clay, 1987), so—although the Black Rocks specimen is a boundary record—it was found near the otherwise documented range of the species. We conclude that the Black Rocks specimen is simply an extensively abraded cranium representing *Symbos cavifrons*. *Gidleya zuniensis* should, therefore, be considered a junior synonym of *Symbos cavifrons*.

The Relationship between *Bootherium* and *Symbos*

The uncertainty about the biological relationship between *Bootherium* and *Symbos* is a direct result of different

interpretations of (1) morphological and preservational differences exhibited in the known skull characters and (2) sample sizes of representatives of the two groups. Most of the debate about the relationship of these two forms has involved a few specific morphological features of the cranium, the horn cores, and the lacrimal bones—all features that were known as early as Leidy's technical description of *Bootherium cavifrons* and *Bootherium bombifrons* (Leidy, 1852b). Specifically, the morphological characteristics that have been invoked to support opinions about the relationship between *Bootherium* and *Symbos* include (1) the general size of adult crania (Osgood, 1905a; Allen, 1913); (2) the size, shape, attachment, direction, and angle of emanation of the horn cores (Osgood, 1905a; Allen, 1913; Hay, 1914); (3) the configuration of the dorsal surface of the cranium (Leidy, 1852b; Osgood, 1905a; Allen, 1913; Hay, 1914, 1915); (4) the degree of flexion between the ventral surfaces of the basisphenoid and basioccipital bones at their junction, and the configuration of the ventral surface of the basisphenoid (Osgood, 1905a; Allen, 1913); and (5) the relative depth of the lacrimal fossae (Allen, 1913). In addition, the pronounced difference in the number of recovered *Bootherium* and *Symbos* skulls has been used as a basis for declaring the two forms taxonomically distinct (Osgood, 1905a; Hay, 1914). Presently, three arrangements of the relationship among nominal taxa within *Bootherium* and *Symbos* are advocated by different writers, including (1) *Bootherium* (including all nominal species) and *Symbos* (including all nominal species) are taxonomically distinct; (2) *Bootherium bombifrons* is taxonomically distinct from *Symbos* (including all nominal taxa in *Symbos*, as well as *B. sargentii* and its synonyms); and (3) *Bootherium* and *Symbos* are sexually dimorphic forms of the same taxon (at least genus, possibly species).

In essence, the morphological bases for the debate have not changed since Leidy's initial revision of the North American fossil oxen (Leidy, 1852b). Additional information on the cranial morphology of *Bootherium* and *Symbos* that has been produced since Leidy's time has served, instead, to document better the ranges of variation found within any given character rather than to identify new differences. Likewise, the larger number of specimens now known has allowed a better documentation of the distribution of the two forms without altering significantly the disproportionate numerical representation of the two forms. The position taken by specific authors who have been active in the debate has been reviewed in the second section of this paper. Here, we consider the various specific issues separately, first by reviewing the argument(s) as used by the principal advocate(s) and then discussing the validity of the argument in the light of currently available information.

DIFFERENCES IN THE SIZE OF *Bootherium* AND *Symbos* CRANIA

Difference in the size of crania of *Bootherium* and *Symbos* has been interpreted as representing both sexual dimorphism and a taxonomic characteristic. Although Leidy placed the two forms in different species, he did not mention that size

difference alone was a specific consideration in leading him to do so. Rüttimeyer (1865) and Dawkins (1872) attributed the size difference to sexual dimorphism. Dawkins (1872:29) stated that the skull of *B. bombifrons*

bears exactly the same relation to that of *B. cavifrons*, as the male to the female [sic; he has these reversed] Musk Sheep. It is therefore highly probable that *B. cavifrons* and *B. bombifrons* are the male and female of the same species.

Osgood, however, concluded that the disparity in size between the two forms "was vastly greater than in the recent genus *Ovibos*" (Osgood, 1905a:182) and proceeded to separate the two forms into *Bootherium* and *Symbos*. Allen (1913) accepted Osgood's conclusion about the taxonomic distinctiveness of *Bootherium* (as represented by *B. bombifrons*) and *Symbos*, but he moved the recently named *B. sargentii* (Gidley, 1908) to *Symbos*, stating "the relationship of *B. sargentii* is entirely with *Symbos*, and well fulfills the condition that would be expected in the female of *S. cavifrons*" (Allen, 1913:215). Allen did not enumerate the expected conditions, but he clearly was aware that the female skull should be smaller than that of the male. Hay (1914, 1915) felt that the range of sizes among specimens assigned to *Symbos* was adequate to accommodate both male and female individuals, and rejected Allen's placement of *B. sargentii* with *Symbos*. Hibbard and Hinds, however, returned to the position of Rüttimeyer (1865) and Dawkins (1872) when they wrote "it is very likely that *Bootherium* is the female woodland musk ox since all specimens of *Symbos* based on skulls are considered those of bulls" (Hibbard and Hinds, 1960:107).

All of the positions reviewed above were based upon the qualitative differences observed in available crania, which in most cases consisted of relatively few specimens or, in the cases of Rüttimeyer and Dawkins, illustrations only. Hay probably used the largest sample, which included some 25 specimens assigned to *Symbos* and four specimens assigned to *Bootherium*. None of these authors supported their position with focused discussions of patterns expected in sexually dimorphic forms of the same species. Neither did they quantify comparisons of *Bootherium* and *Symbos*, nor compare such patterns with those of dimorphism found in *Ovibos* or other closely related taxa.

Sexual dimorphism of the skeleton is an expected characteristic among species of Artiodactyla, with the skeleton of males typically being larger than that of females (Glucksmann, 1978; Nowak and Paradiso, 1983). Patterns of size distribution within known or inferred single-sex populations have been described for samples of crania representing species such as *Bison latifrons*, *Bison antiquus*, *Bison bison*, *Ovis catclawensis*, and *Rupicapra rupicapra caucasica* (Corner, 1977; McDonald, 1981; Koubek and Hrabě, 1983).

Patterns of size distribution recorded for historic and fossil populations of *Ovibos moschatus*, and *Bootherium* and *Symbos*, are presented in Figures 33 to 37. These histograms and scatterplots show that the *Bootherium* and *Symbos* samples possess about the same quantitative relationship to each other as do female and male *Ovibos moschatus*.

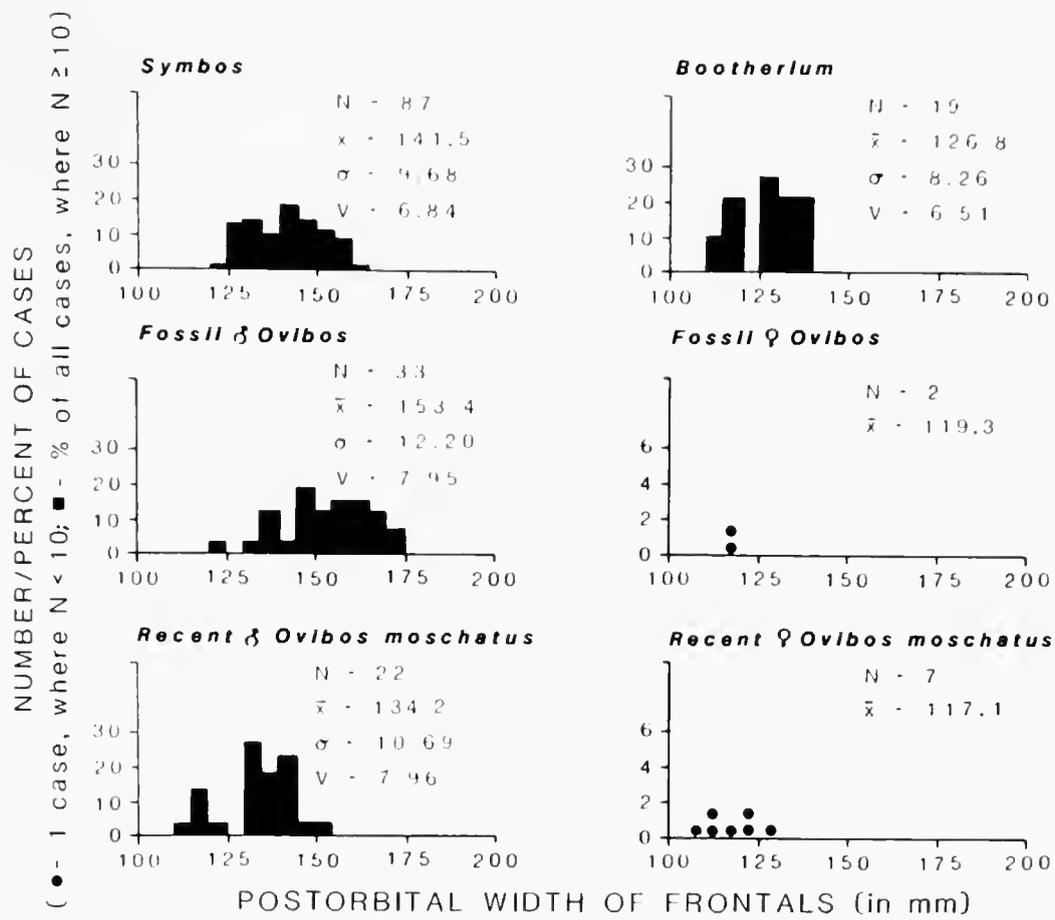


FIGURE 33.—Histogram showing distribution of measurements of postorbital width of frontals in *Bootherium*, *Symbolos*, and fossil and Recent samples of male and female *Ovibos moschatus*.

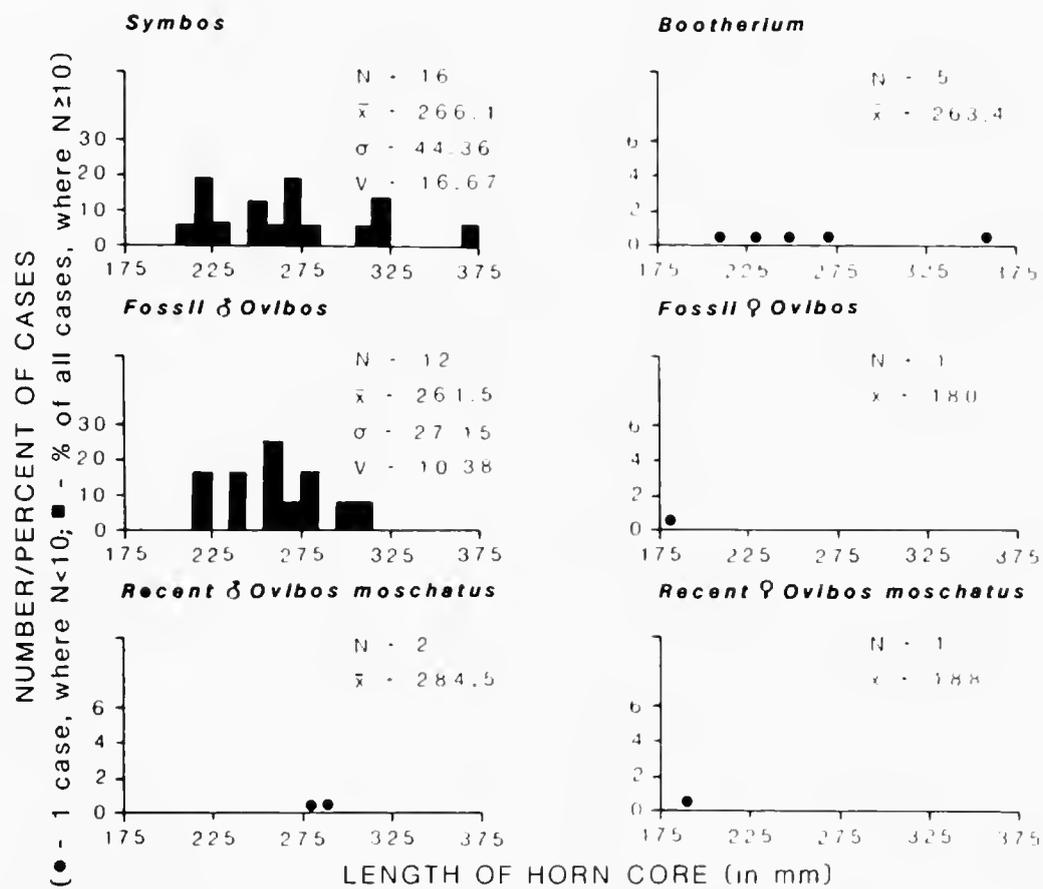


FIGURE 34.—Histogram showing distribution of measurements of length of horn core in *Bootherium*, *Symbolos*, and fossil and Recent samples of male and female *Ovibos moschatus*. (The small sample of *Ovibos moschatus* is due to the fact that most modern specimens still have the horn sheaths attached, making examination of the horn core impossible.)

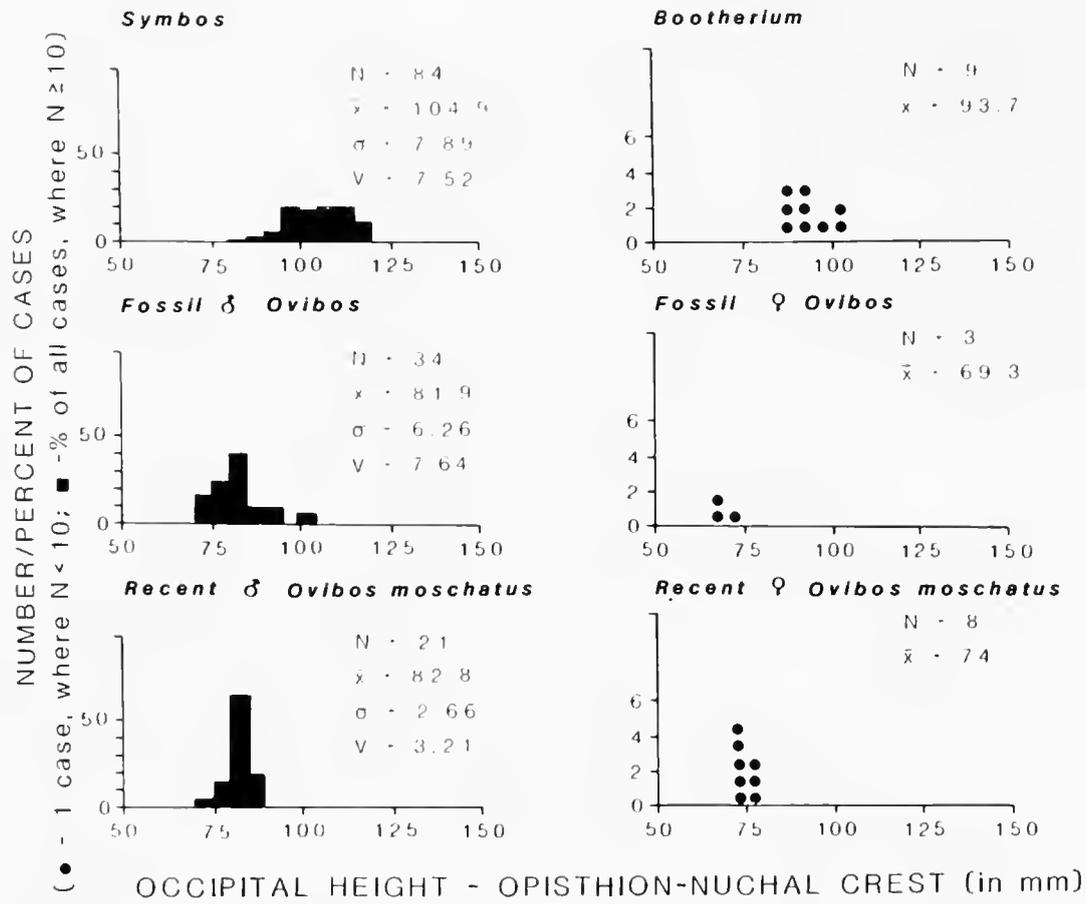


FIGURE 35.—Histogram showing distribution of measurements of occipital height in *Bootherium*, *Symbos*, and fossil and Recent samples of male and female *Ovibos moschatus*.

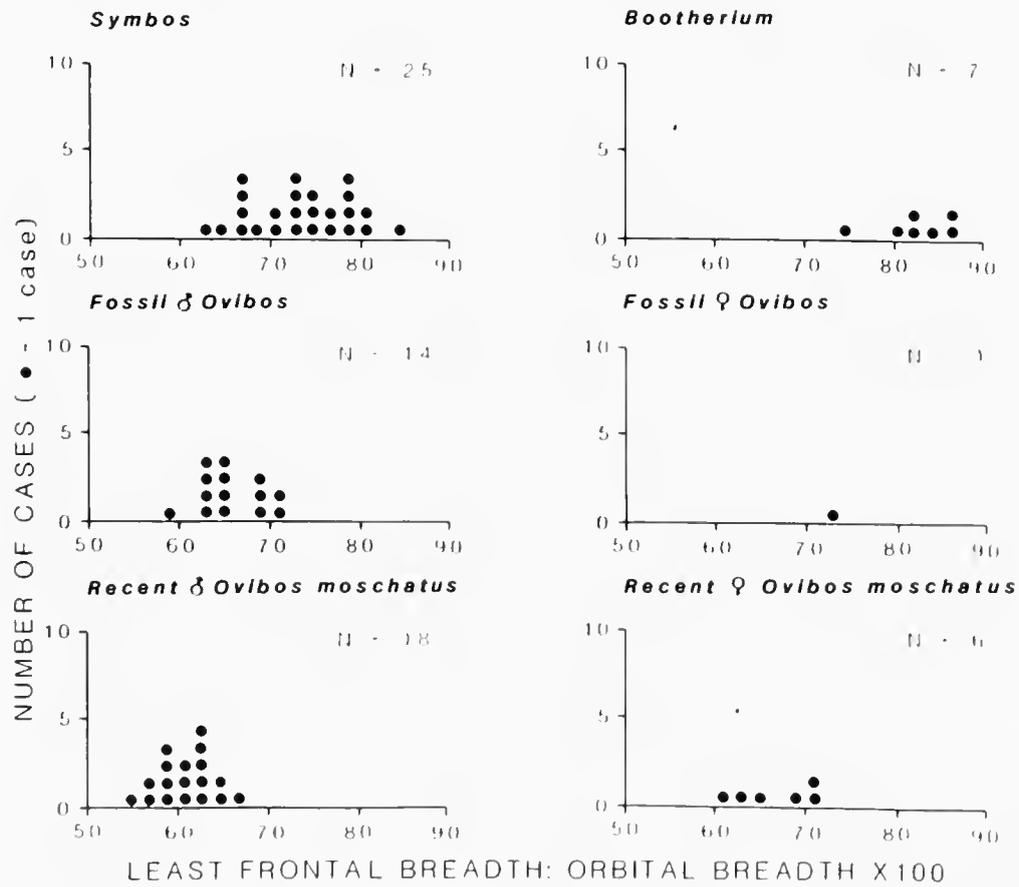


FIGURE 36.—Histogram showing distribution of ratio of least frontal breadth:orbital breadth $\times 100$ in *Bootherium*, *Symbos*, and fossil and Recent samples of male and female *Ovibos moschatus*. The greater the value, the less the orbits extend beyond the postorbital level of the frontals.

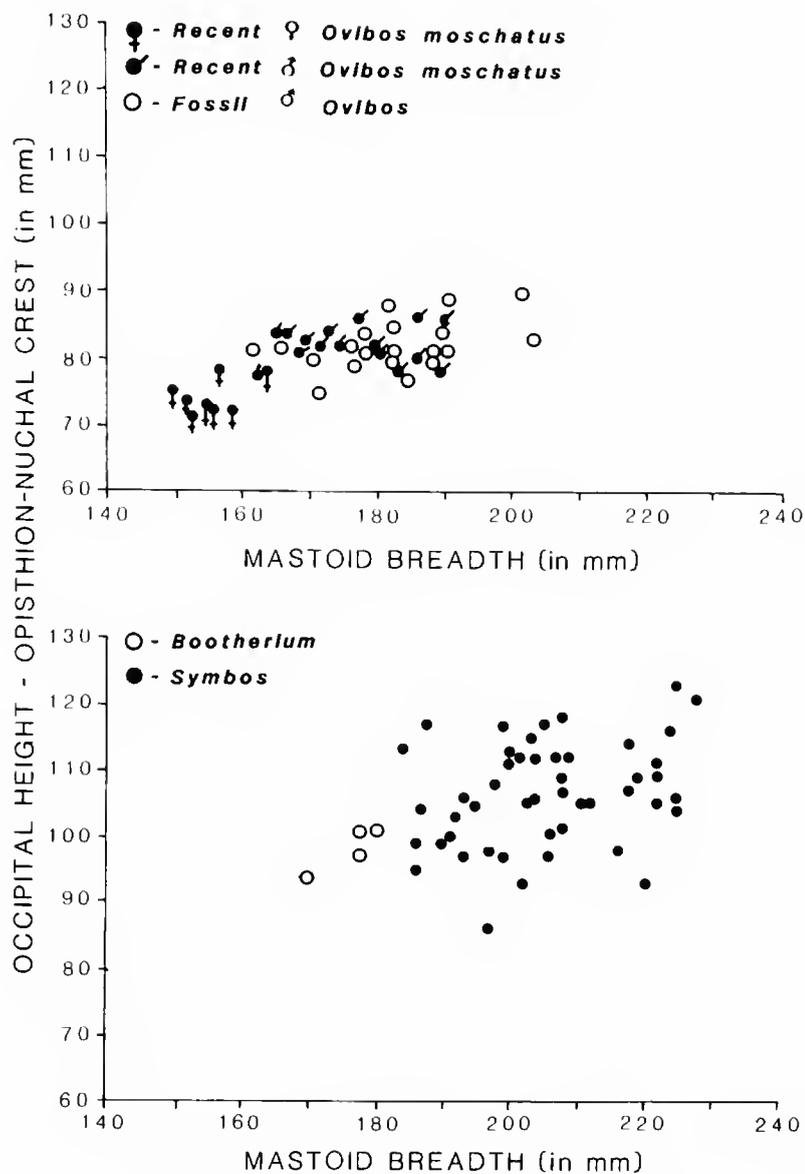


FIGURE 37.—Scatterplot showing sexual and taxonomic differences in the size and proportions of the occiput, as expressed by the height and breadth of the region: *Oribos moschatus* (top); *Bootherium* and *Symbolos* (bottom).

DIFFERENCES IN THE CHARACTERISTICS OF THE HORN CORES

Osgood (1905a) stressed differences in the horn cores of *Bootherium* and *Symbolos* as partial justification for placing the two forms in separate genera. Osgood noted the similarity between the horn cores of male and female *Oribos moschatus*, especially in their being “excessively flattened and directed downward close to the skull” with bases approaching “each other over the top of the frontals. . . . Therefore the skull of the female has all the essential characters of the male but they are not as highly developed” (Osgood, 1905a:182). Osgood used the male/female parallel in *Oribos moschatus* to compare and evaluate the horn cores of *Bootherium* and *Symbolos*. The horn cores of *Bootherium* were seen to differ from those of *Symbolos* in four respects: (1) they were rounded, not flattened, at the base; (2) they emanated from the cranium at a different angle; (3) their bases were ringed by a burr and not fused with exostosis; and (4) they were attached to the skull via pedicels attached to the frontals instead of merging indistinctly with the frontal and parietals. “A much more reasonable assumption

would be that *Symbolos cavifrons* represents the male and *Symbolos tyrrelli* the female of one species. The present objection to this is the fact that both have not been found in the same region” (Osgood, 1905a:183).

In describing the type specimen of *B. sargenti*, however, Gidley (1908) noted differences between the horn cores of that specimen and the *B. bombifrons* type, including the larger size, more angular base, and extension of the dorsal edge onto the frontals toward the median plane. The characteristics of the horn cores in the *Bootherium sargenti* holotype led Allen (1913) to consider it to be the female of *Symbolos cavifrons*. Hay considered the differences between *B. bombifrons* and *B. sargenti* to be taxonomically insignificant, and felt that the latter—along with his new species *Bootherium nivicolens* (possessing laterally directed horn cores and modest development of exostosis over the dorsal edge of the pedicel)—was properly placed in *Bootherium* (Hay, 1914, 1915).

Some facts are important in better understanding the role that horn core differences have had in the debate. The holotype of *Bootherium bombifrons* (Figures 1–4) represents an extreme among described specimens in the roundness of its horn cores at the base, the presence of a distinct burr at the base, and the placement of the horn core base upon a distinct, relatively elongated pedicel. The holotype of *Bootherium sargenti* (Figures 19–21) is extreme in the degree of development of exostosis over the dorsal surface of the frontals toward the median plane, in the rectangularity of the dorsal half of the base of the horn core, and the preservation of detailed features of the original bone surface. These two specimens, which still represent the extremes of many characters within the genus, were the first two crania of *Bootherium* to be reported and thus represent the foundation upon which conceptualization of the genus, and its first two nominal species, was based. (There has been no similar difficulty in evaluating the generic placement of nominal species within *Symbolos* that were based upon cranial material.) *Bootherium* specimens collected or recognized since 1915, when Hay described *Bootherium nivicolens*, have shown that the nature of horn core attachment to the frontals varies between the condition seen in the holotype of *Bootherium bombifrons* to that seen in *Bootherium sargenti* (Figures 1, 19, 38–42).

The development of horns and horn cores within *Oribos moschatus* has been described by Lönnberg (1900), Allen (1913), and Henrichsen and Grue (1980). The general pattern of horn core development is that the horn core appears upon the frontal bone by about 5–7 months of age and differentiates into a core and pedicel in both sexes by ~1.5 years. During the subsequent period of development, the direction at which the horn emanates from the frontals changes. The horn cores emanate initially in a lateral direction, but—after about 1.5 years of age—the cores shift to a more ventral orientation, reaching their maximum ventral deflection by about 4 years of age. The adult horn cores in both sexes have about the same orientation. Throughout the juvenile period (to ~3–4 years of age) the horn cores in both sexes remain attached to the frontals



FIGURE 38.—*Bootherium* sp. (F:AM 33195; Ester Creek, Alaska).

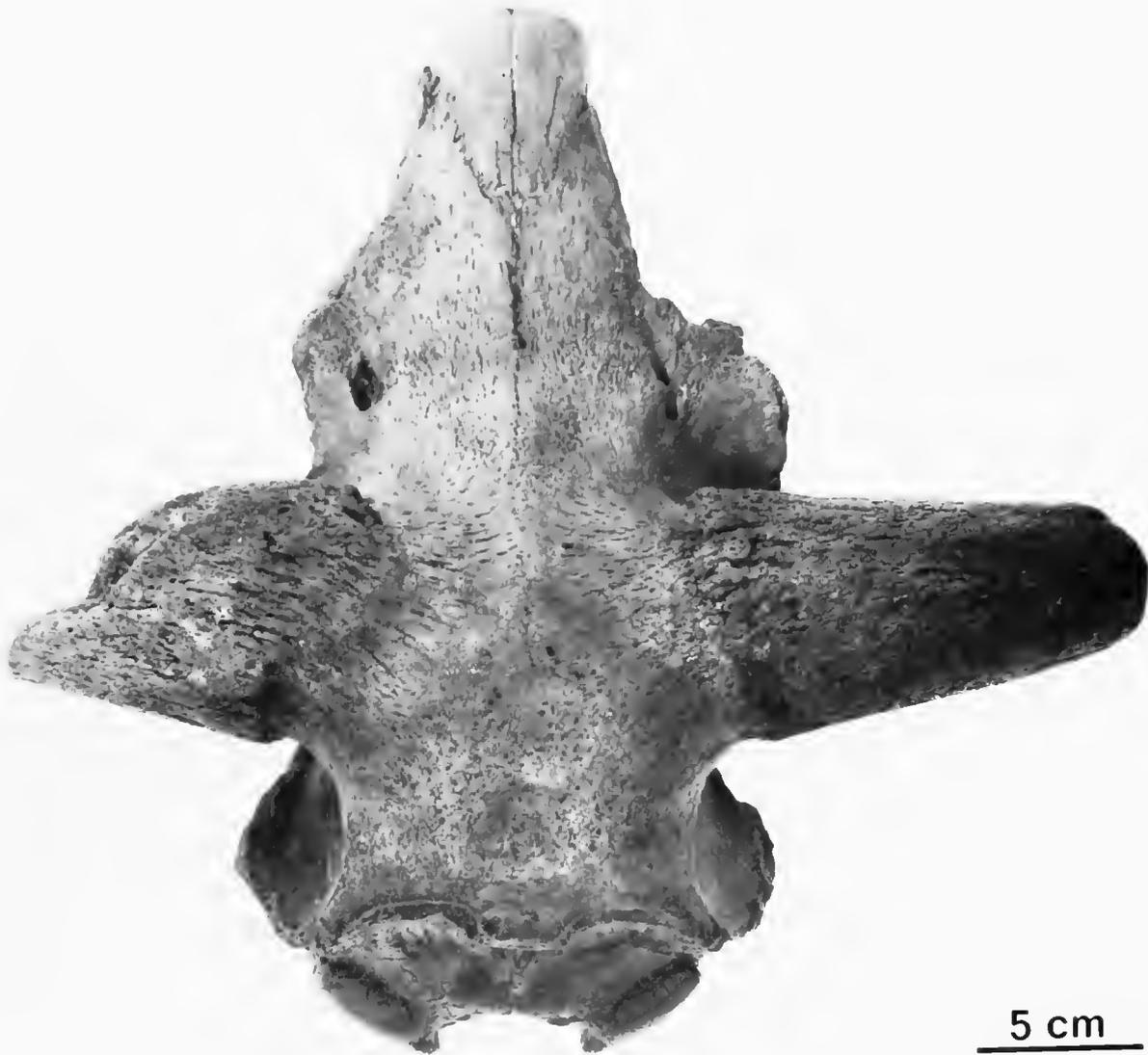


FIGURE 39.—*Bootherium* sp. (F:AM 33199; Fairbanks Creek, Alaska).



5 cm

FIGURE 40.—*Bootherium* sp. (BYUG 834; Utah County, Utah).



5 cm

FIGURE 41.—*Bootherium* sp. (USNM 347315; Dare County, North Carolina).



FIGURE 42.—*Bootherium* sp. (USNM 23264; Saltville, Virginia).

by a distinct pedicel while enlarging in length and diameter (especially in antero-posterior diameter). The horn cores of males enlarge more than do those of females. The adult horn core is slightly more rounded in females than in males.

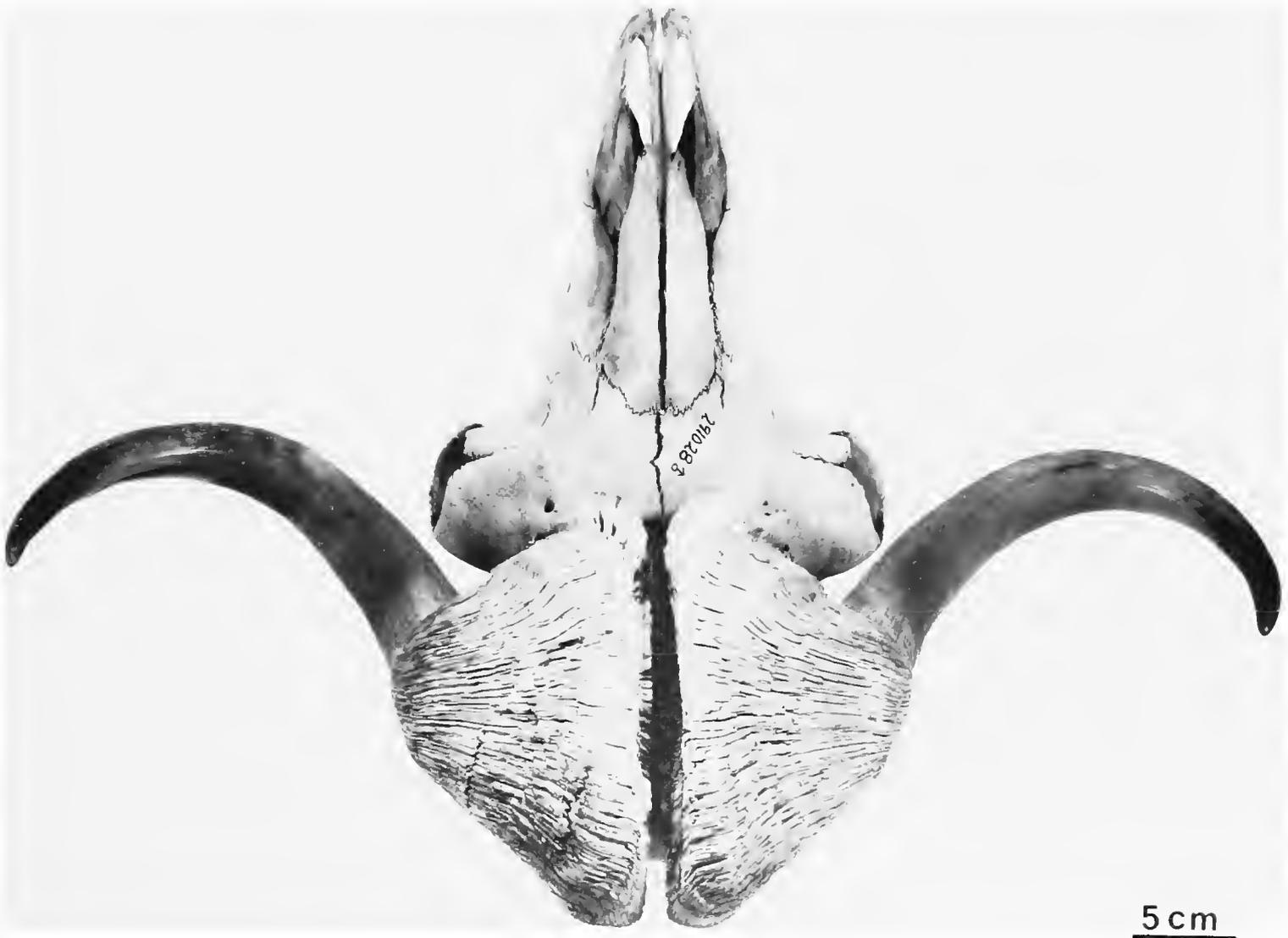
When the horn cores have reached their maximum ventrad extent (reached at ~3 years in females; 4 years in males), continued enlargement of the horn sheath at the base is accompanied by the deposition of secondary bone over all or part of the pedicel and onto part of the dorsal surface of the cranium (Figures 43–51). The deposition of most of the secondary bone appears to take place over a relatively brief period (1–2 years) and is much more pronounced and extensive in males than in females. The deposition of secondary bone at the base of the horn core in females appears to be limited primarily to rough pitted-and-ridged bone that Leidy (1852b) called “exostosis.” This exostosis develops first over the dorsal edge of the pedicel, extending mediad, rostrad, and ventrad beyond the edge of the pedicel. Later, the exostosis spreads caudad onto the frontal bone. The base of the horn core, and the associated exostosis, is confined to the frontal bone in adult females. Thin laminae of bone that probably developed between the integument and the base of the keratinous horn sheath have been observed in well-prepared and cautiously handled specimens (e.g., USNM 283599; USNM 291025) (Figure 52). In males, the secondary bone consists of both rough pitted-and-ridged exostosis where the horn sheath lies near or in contact with the bones of the cranial surface, and dense bone, especially beneath the rostrad and

laterad edges of the exostosis. Secondary bone in males occurs over much of the dorsal surface of the cranium, from the base of the horn core to within a few millimeters of the median plane, and from about or near the caudal edge of the parietals rostrad over the frontals to about the level of the caudal edge of the orbits. Typically, a smooth-surfaced longitudinal groove located over the median separates the secondary bone surfaces (Figures 45, 51), but occasionally these secondary surfaces coalesce over part of the length of the median groove. A small shallow depression often occurs in the median groove just rostrad of the frontoparietal suture (in female skulls, a somewhat larger shallow depression often occurs centered on the median of the parietal surface). The development of secondary bone at the base of the horn core in males enlarges the base to the extent that it spreads onto the lateral edge of the parietal bones and thus, in the adult, the base of the horn core attaches to both the frontal and parietal bones.

The horn cores of *Bootherium* exhibit some characteristics that parallel the patterns seen in female *Ovibos moschatus*, but differ in others. The range of differing shapes of the base of the horn cores in all known specimens of *Bootherium*, correlated with the extent of secondary bone deposition, is similar to the ontogenetic pattern seen in *Ovibos moschatus*. *Bootherium*

FIGURE 43 (top).—*Ovibos moschatus* (USNM 291025; Prince Patrick Island, N.W.T., Canada), female, in dorsal view.

FIGURE 44 (bottom).—*Ovibos moschatus* (USNM 291028; Prince Patrick Island, N.W.T., Canada), male, in dorsal view.



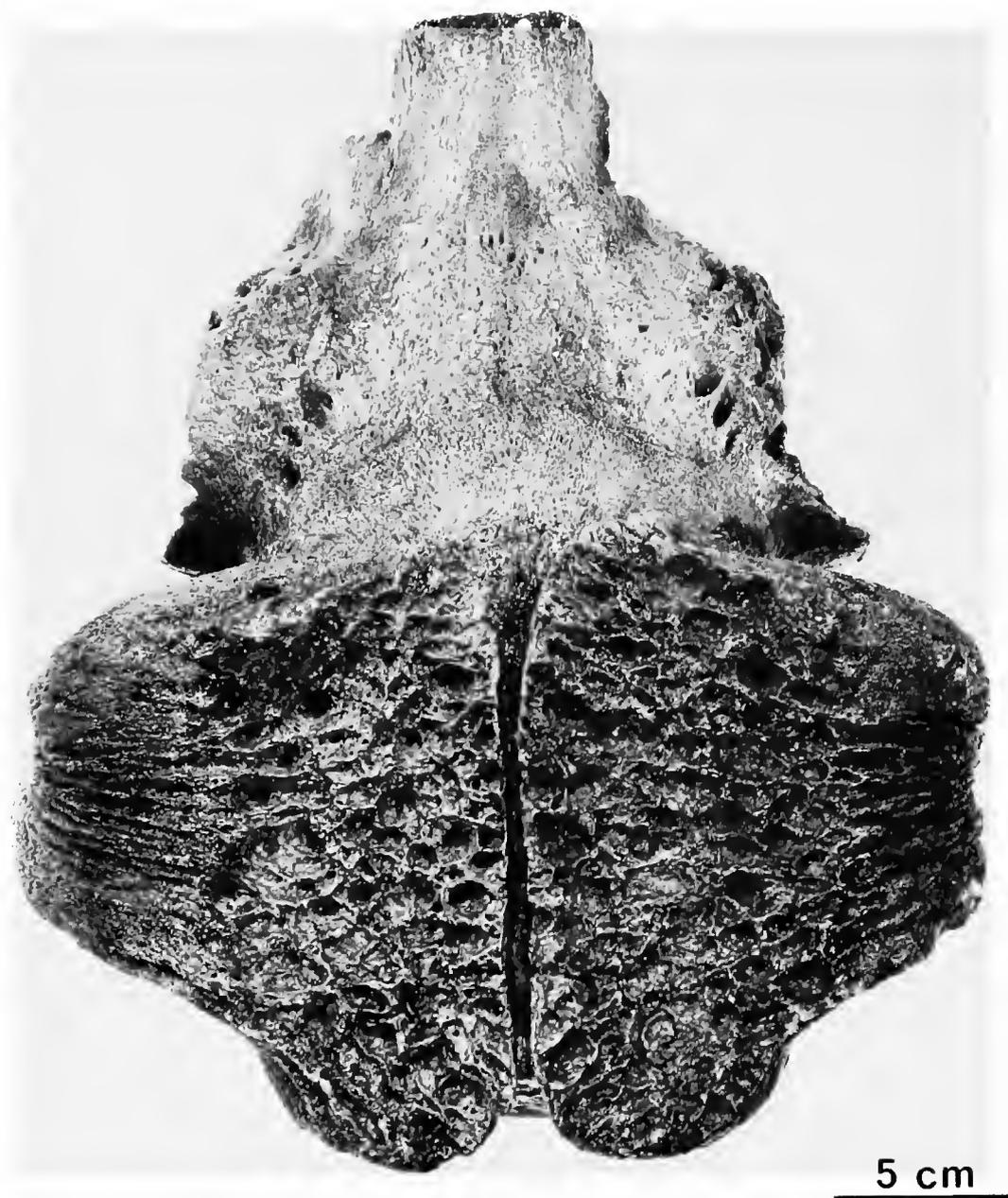


FIGURE 45.—*Ovibos proximus* (= *Ovibos moschatus*) Bensley, 1923 (ROM Mam 31E.6.4; East Toronto, Ontario), male, in dorsal view.

specimens with exostosis developed have more rostrocaudally elongated (angular or rectangular) shapes of the bases of the horn cores than do specimens without exostosis. The horn cores become increasingly rounded distally in all specimens. The pattern of development of exostosis is also similar in *Bootherium* and female *Ovibos moschatus*. Secondary bone appears first over the dorsal surface of the pedicel, then spreads mediad, rostrad, and ventrad until it finally obscures the pedicel and forms directly on the frontal surface. Exostosis in *Bootherium* does not extend onto the parietal surface, even in the holotype of *Bootherium sargenti* (GRPM 11-423-3101; Figure 19). The horn cores of adult *Bootherium*, unlike those of *Ovibos moschatus* females, emanate in a lateral direction, then trend downward, forward, and—distally—sometimes slightly outward and away from the face (Figures 1, 19, 23, 30, 38–42). The horn sheath extended even farther downward and forward,

and—in the only specimen which we have seen in which the sheath is preserved—the tip appears to have curved slightly inward toward the face (Figures 53–55). As all known *Bootherium* specimens are adults, the range of development of exostosis in *Bootherium* is probably indicative of the degree of variation in the development of the adult horn sheath rather than of any age variation in the individuals constituting the *Bootherium* sample.

No juvenile specimens representing *Symbos* are known for certain (although the juvenile musk ox remains from Frankstown Cave, Blair County, Pennsylvania, might represent *Symbos*; Peterson, 1926). The horn cores of *Symbos* are markedly elongate in a rostrocaudal direction at the base (e.g., Figures 5, 6, 12, 13), being flat to concave in this direction on the dorsal surface and convex on the ventral surface. Distally, the horn cores become subrounded, then rounded. The horn



FIGURE 46.—*Ovibos moschatus* (USNM 291025; Prince Patrick Island, N.W.T., Canada), female, in left lateral view. (Scale bar = 5 cm.)



FIGURE 47.—*Ovibos moschatus* (USNM 291028; Prince Patrick Island, N.W.T., Canada), male, in left lateral view. (Scale bar = 5 cm.)



FIGURE 48.—*Ovibos proximus* (= *Ovibos moschatus*) Bensley, 1923 (ROM Mam 31E.6.4; East Toronto, Ontario), male, in left lateral view.

cores in adult specimens attach to both the frontal and parietal bones, and blend imperceptibly with what appears to be secondary bone that covers most or all of the dorsal surfaces of the cranium between the bases of the horn cores, and from near the caudal edge of the parietals rostrad across the frontals to near the level of the rostral edges of the orbits. Most of the secondary bone is rough pitted-and-ridged or honeycombed exostosis that probably developed under the keratinous horn sheath (Figures 5, 12, 56, 57, 59), but what appears to be dense bone underlies or borders the rostral extension of the exostosis. A shallow depression is obvious over the median, just rostrad of the parietofrontal suture, in specimens with weakly developed or no exostosis in that region (Figure 51). The horn cores of *Symbos* emanate in a lateral direction, then trend downward, forward and—near the tip—somewhat outward away from the face, as in *Bootherium*.

The horn cores of *Bootherium* and *Symbos* share some common characteristics, including the angle of emanation from the cranium, their longitudinal shape, and their cross-sectional shape. The horn core characteristics of *Bootherium* and *Symbos* also parallel those of female and male *Ovibos moschatus* in many respects. The female *Ovibos moschatus* and *Bootherium* horn cores attach to the frontals only, whereas those of male *Ovibos moschatus* and *Symbos* attach to both the frontal and parietal bones. Male and female *Ovibos moschatus* horn cores have similar orientations and longitudinal and cross-sectional shapes, while differing mainly in absolute size. The horn cores of *Bootherium* and *Symbos* also have similar orientations and

longitudinal and cross-sectional shapes, while differing mainly in absolute size. Secondary bone deposits are extensive over the dorsal surface of the frontals and parietals in male *Ovibos moschatus* and *Symbos*, but are much less extensive and are restricted to the frontals in female *Ovibos moschatus* and *Bootherium*. The principal character considered here in which no direct parallel is seen between female *Ovibos moschatus* and *Bootherium* is the total absence of a visible pedicel to support the horn core in female *Ovibos moschatus*, and the corresponding weaker development of basal exostosis in *Bootherium* compared to female *Ovibos moschatus*. We interpret this difference as evidence that the development of the base of the horn sheath in *Bootherium*, relative to that of *Symbos*, was less extensive than that of female *Ovibos moschatus* relative to male *Ovibos moschatus*. This conforms to a pattern of greater sexual dimorphism in horns seen in other Rancholabrean ungulates, such as *Bison latifrons* and *Bison antiquus*, compared to related Holocene forms, such as *Bison bison* (McDonald, 1981).

FIGURE 49 (top).—*Ovibos moschatus* (USNM 291025; Prince Patrick Island, N.W.T., Canada), female, in caudal view. (Scale bar = 5 cm.)

FIGURE 50 (center).—*Ovibos moschatus* (USNM 291028; Prince Patrick Island, N.W.T., Canada), male, in caudal view.

FIGURE 51 (bottom).—*Ovibos proximus* (= *Ovibos moschatus*) Bensley, 1923 (ROM Mam 31E.6.4; East Toronto, Ontario), male, in caudal view.





FIGURE 52.—*Ovibos moschatus* (USNM 291025; Prince Patrick Island, N.W.T., Canada), female, in caudal view. Dense secondary bone has built up medial to the bases of both horn cores and more porous shelf-like accumulations of exostosis project medially from the bases of both horn cores. These exostotic laminae are easily broken off.

DIFFERENCES IN THE DORSAL SURFACE OF THE CRANIUM

Leidy (1852b) identified two expressions of the dorsal surface of the cranium as representative of his genus *Bootherium*. This surface in *Bootherium cavifrons* was described as being formed of “a very remarkable process, covering the os frontis like a huge exostosis,” which united the bases of the horn cores.

The whole process is remarkably rough and tuberculated, and presents, in some degree, the appearance of an exostosis, the result of disease. Its upper surface is depressed into a concavity, deepest between the horn-cores and divided at bottom by a prominent median ridge (Leidy, 1852b:13).

Of the cranium of *Bootherium bombifrons*, Leidy (1852b: 17–18) wrote:

The os frontis, instead of forming an exostosis-like process, as in *Bootherium cavifrons*, rises gradually from its commencement anteriorly, and forms a sort of hump The highest portion of the os frontis is between the posterior part of the bases of the horn-cores Anteriorly to this most elevated part, the os frontis inclines at an angle of about 45°, but posteriorly has a less degree of inclination The (parietal) surface . . . is moderately convex, and presents a broad shallow impression at its central part.

Clearly, the character of this surface differs between the two forms to a great degree. Some authors subsequent to Leidy have invoked these differences to separate the two forms taxonomically. Osgood wrote that the bases of horn cores of *Bootherium bombifrons* “do not approach each other in the least” and “The frontal region between the horn pedicels is not flattened as in the female *Ovibos*, but is elevated and convex” (Osgood, 1905a:182). Allen (1913) and Hay (1914, 1915) also considered the differences in the configuration of the dorsal surface of the cranium to be taxonomically significant (yet, inexplicably, Allen still referred *B. sargenti* to *Symbos* even though the dorsal surface of the cranium in the only known specimen was distinctly flexed in typical *Bootherium* fashion).

De Kay (1828) and Leidy (1852b) both recognized that the dorsal surface of the *Symbos* cranium they described probably had been altered by some physical or biological agency. De Kay considered that the New Madrid specimen could have developed the dorsal surface conditions by either disease or breakage—he even went so far as to suggest that the entire natural dorsal surface might be missing from his specimen.



FIGURE 53 (top).—*Bootherium bombifrons* (AMNH F:AM 30508; Fairbanks District, Alaska), female, in dorsal view.

FIGURE 54 (left).—*Bootherium bombifrons* (AMNH F:AM 30508; Fairbanks District, Alaska), female, in left lateral view.

FIGURE 55 (bottom).—*Bootherium bombifrons*(AMNH F:AM 30508; Fairbanks District, Alaska), female, in caudal view.





FIGURE 56.—*Symbos cavifrons* (AMNH F:AM 33124; upper Cleary Creek, Alaska), male, in dorsal view.



FIGURE 57.—*Symbos cavifrons* (AMNH F:AM 33124; upper Cleary Creek, Alaska), male, in right lateral view.



FIGURE 58.—*Symbolos cavifrons* (AMNH F:AM 33124; upper Cleary Creek, Alaska), male, in ventral view.



FIGURE 59.—*Symbolos cavifrons* (AMNH F:AM 33124; upper Cleary Creek, Alaska), male, in caudal view.

Leidy mentions only disease as a possible cause for the exostosis. We do not know of subsequent attempts to explain this condition in *Symbos*, but it is our opinion—as stated above—that the exostosis consists of secondary bone deposited in association with the development of the bases of the horn sheath in the adult animal, as in *Ovibos moschatus*. (Lönnerberg (1900) and especially Allen (1913) have discussed the formation of exostosis in *Ovibos moschatus*.) As the keratinous sheath enlarges, dense and porous secondary bone forms over the frontals and parietals where the sheath and bone surface come into contact. As noted above, most dense bone occurs beneath and along the edges of the rostrad zone of exostosis. This builds up on the dorsal surface and changes its morphology accordingly. Exostosis normally covers most of the dorsal surface of the cranium, producing an elliptical rim that more or less identifies the outline of the fused bases of the horn sheaths and contains a trough within (Figures 5, 12, 56). Normally, a conspicuous build-up of exostosis occurs transversely across the parietals forming the caudal end of the intercornual trough. The floor of the trough is normally covered by exostosis. A median ridge of exostosis, apparently formed where the bases of the horn sheath grew together, occurs in some specimens (such as the holotype of *Symbos cavifrons*) but not all. On the floor of the trough in some specimens is what appears to be unaltered primary bone; in such cases, the frontal suture line and the shallow depression rostrad of the frontoparietal suture are visible (Figure 60). In some specimens (e.g., USNM 2556, USNM 23548) much of the natural primary bone of the dorsal surface appears to have been resorbed (Figure 61), exposing the sinuses of the frontoparietal region. Regardless of the degree of modification of the dorsal surface, the addition of dense and porous secondary bone to the dorsal surface of the cranium of *Symbos* specimens, or the resorption of primary bone, changes the topography of this surface. Two specimens (F:AM A-204-4254; USNM 23548) in which the dorsal surface of the cranium is not completely covered by exostosis indicate that *the primary natural parietofrontal surface is flexed longitudinally*, with the peak of flexion occurring toward the rostrad edge of the parietal bones. In both specimens the parietal surface trends rostradorsad from the nuchal crest until reaching its apex, then it trends rostroventrad until fusing with the frontals. A shallow depression occurs over the median just rostrad of the frontoparietal suture in F:AM A-204-4254 (Figure 60). The dorsal surface of the frontal bones is generally parallel to a plane passing through the nuchal crest and the dorsal edge of the orbits. This might represent the orientation of the primary surface. Alternatively, secondary dense bone might have been deposited over the rostrad part of the surface which resulted in its rostrad end being built up. Based on information from these specimens, it is our opinion that the dorsal surface of the typical cranium of *Symbos* is naturally flexed, with the apex being in the parietal region, and that this characteristic would be visible were it not obscured by the resculpturing effect of secondary bone deposition associated with the spread of the horn sheaths across the frontoparietal surface. If our

reasoning is correct, then the structure of the dorsal surface of the crania of *Bootherium* and *Symbos* is much more nearly alike than has been thought previously. The superficial differences of the cranial surface between *Bootherium* and *Symbos* are attributable more to anatomical conditions and physiological processes associated with the exaggerated dimorphism of the horns in these two forms than to any inherent differences in the primary morphology of the cranium proper.

DIFFERENCES IN THE BASIOCCIPITAL-BASISPHENOID FLEXION

Osgood (1905a:182) introduced the opinion that two characters of the basisphenoid were of taxonomic significance.

The under side of the skull of the type of *bombifrons* is much injured but one conspicuous character is shown in which it differs from all the other species. This is found in the basisphenoid which is not deflected but has its lower surface in the same horizontal plane as that of the basioccipital and it has a sharp median ridge.

Allen (1913:212) accepted Osgood's conclusions, stating (when comparing the *B. bombifrons* holotype with *Bison*, *Ovibos*, *Symbos*, and *Liops*):

Another feature that sharply differentiates this skull from the above-named genera is that the ventral surface of the basisphenoid, as noted by Osgood, is in the same plane as that of the basioccipital, not sharply depressed (in ventral view) as in all of the others. Besides this, the ventral surface of the basisphenoid rises into a sharp ridge along the median line to a height of from 2 mm. to about 6 mm.

Most specimens assigned to *Bootherium* that have been described in the literature consist of isolated horn cores or the dorsal part of the cranium. Consequently, this character has been used to differentiate between *Bootherium* and *Symbos* less often than have the more conspicuous or frequently represented characters described above.

The degree of flexion between the basioccipital and basisphenoid bones appears to be related to both age and sex. Based upon a sample of 44 crania of *Ovibos moschatus* collected during the 19th and 20th centuries, the ventral surface of the basioccipital-basisphenoid bones lies nearly on the same plane in both sexes at birth. The degree of flexion of both surfaces increases with age to maturity, and it increases to a greater extent in males than in females (Table 1). The angle of flexion of these two bones in 11 *Bootherium* and 74 *Symbos* crania presents almost exactly the same pattern and relationship as was found in a sample of 58 adult crania of Recent and fossil *Ovibos moschatus* (Figure 62).

The ridge on the ventral surface of the basisphenoid that

FIGURE 60 (top).—*Symbos cavifrons*(AMNH F:AM A-204-4254; Little Eldorado Creek, Alaska), male, in dorsal view showing partly unfused frontal sutures along midline and adjacent areas of unaltered primary surface bone.

FIGURE 61 (bottom).—*Symbos cavifrons* (USNM 23548; Ohio River, Bracken County, Kentucky), male, in dorsal view. The frontal sinuses were probably exposed as a result of resorption of the primary roof of the frontal bone during the development and/or maintenance of the keratinous boss over the dorsal surface of the cranium.



TABLE 1.—Basioccipital-basisphenoid flexion in sub-adult *Ovibos moschatus*; except for the fetus, age estimates are based primarily upon tooth eruption and wear patterns, and follow Allen (1913), Tener (1965), and Henrichsen and Grue (1980). The age of some specimens is known.

Specimen number	Age	Sex	Angle of flexion
USNM 134406	fetus	?	180°
USNM 261770	6 mos.	F	171°
USNM 261769	4–6 mos.	M	174°
USNM 261771	1 yr	F	170°
USNM 291026	1 yr	F	164°
USNM 261772	1 yr	F	170°
USNM 14444	1 yr	F?	163°
USNM 255549	1 yr	M	158°
USNM 5094	1 yr	M	156°
USNM 288026	2.5 yrs	M	157°
UAF 7544	2.5 yrs	M	161°
USNM 251409	3 yrs	F	161°
USNM 256709	3 yrs	M	159°
USNM 291027	3 yrs	M	160°
USNM 257912	4 yrs	F	164°
USNM 251408	4 yrs	M	152°
UAF 15855	5 yrs	M	151°
Mean of adults >5 yrs:		F (N=5) M (N=22)	160.2° 150.2°

Osgood and Allen mentioned is a variable character that appears on all of the *Bootherium* crania for which the character can be assessed. A trace of a ridge occurs on the ventral surface of the basisphenoid of some female *Ovibos moschatus*. This character appears to be typical of specimens assigned to *Bootherium*, but we consider it of no taxonomic value.

DIFFERENCES IN DEPTH OF THE LACRIMAL FOSSAE

Leidy observed the presence of lacrimal fossae in both *Bootherium cavifrons* and *Bootherium bombifrons*, describing that of the former as “a deep lenticular depression, or larmier, such as exists in the Deer and Sheep” and that of the latter as “a remarkably deep fossa, or larmier, which appears to have been hemispherical, but, in the specimen, the lower portion is broken away” (Leidy, 1852b:13, 18). One characteristic of *Bootherium* given by Allen (1913:210) was “the presence of small but deep and sharply defined lacrymal fossae.” These are the only allusions to this character in a taxonomic context of which we are aware.

The specific shape and size of the lacrimal fossae are variable among individuals, but generally they are larger and better defined in specimens assigned to *Symbos* than those assigned to *Bootherium*. We consider differences in the size of the lacrimal fossae to be of no taxonomic value.

DIFFERENCES IN THE NUMBER OF *Bootherium* AND *Symbos* SPECIMENS

The number of known specimens referred to *Symbos* increased slowly but continuously during the 19th century and the early part of the 20th Century. Although De Kay (1828) had

but a single cranial specimen, Leidy (1852b) had access to eight such specimens, Allen (1913:214) acknowledged knowing of “at least 11” localities from which *Symbos* specimens had been reported (actually only eight of these localities had produced *Symbos* remains, and they a total of 12 whole or partial crania), and Hay claimed to have examined 25 specimens by 1915 (Hay, 1914, 1915). The only *Bootherium* cranium known to exist with certainty for some 90 years was the holotype for *Bootherium bombifrons* (Wistar, 1818; Harlan, 1825; Leidy, 1852b). A second specimen was described by Rhoads in the 1890s, originally as *Bison appalachicolus*, then *Ovibos (Bootherium?) appalachicolus* (Rhoads, 1895, 1897). Gidley described a third specimen as *Bootherium sargenti* in 1908. Other records followed, but always fewer than *Symbos*.

Both Osgood (1905a) and Hay (1914, 1915) invoked the difference in the number of specimens of *Bootherium* and *Symbos* as probable evidence that the two forms represented different taxa. Osgood, noting that *Symbos* specimens had been reported from 10 localities by the time of his writing, stated as one reason that *Bootherium* should be separated from *Symbos*: “In the large number of specimens, if there were any females at all it is probable that there would be more than one” (Osgood, 1905a:183). Hay objected to Allen’s (1913) putting *Bootherium sargenti* in *Symbos* and defended this position by writing “If the Grand Rapids skull is the female of *Symbos cavifrons*, it is very remarkable that only one female should be discovered among 25 specimens” (Hay, 1914, 1915:527).

Many additional crania referred to either *Bootherium* or *Symbos* have been found since 1915. The most productive locality has been the Fairbanks, Alaska, mining district where, from 1937 to 1960, Otto Geist collected literally thousands of vertebrate fossils for Childs Frick and, to a lesser extent, the University of Alaska (Keim, 1969). Isolated specimens or small numbers of specimens have, however, been collected at numerous other localities throughout much of the United States and western Canada. The proportion of *Symbos* to *Bootherium* records, however, has not changed substantially. We have examined 175 *Symbos* and 51 *Bootherium* crania for use in this paper. Our *Bootherium*:*Symbos* ratio of .29 is not greatly different from Allen’s (3:12; .25) ratio.

Among bovids the skull of females typically is smaller, lighter, and less strongly fused by suturing than is the skull of males. These differences in size and structure render the female skull more susceptible than that of the male to destruction by weathering, abrasion, decomposition, carnivory, gnawing, or trampling. Three female and 38 male records of fossilized crania of *Ovibos moschatus* are known from North America, giving a female:male sex ratio of .08 for a group whose sexual dimorphism is well documented and widely accepted (McDonald, unpubl. data). Howard Hutchison (pers. comm.) observed in the Canadian arctic that the skulls of female *Ovibos moschatus* were more easily and readily destroyed by wolves than were the skulls of males. If female skulls are the more easily destroyed, then it is reasonable to expect them to be recovered less often than male skulls. There also appears to be a general collecting bias against salvaging the smaller, possibly

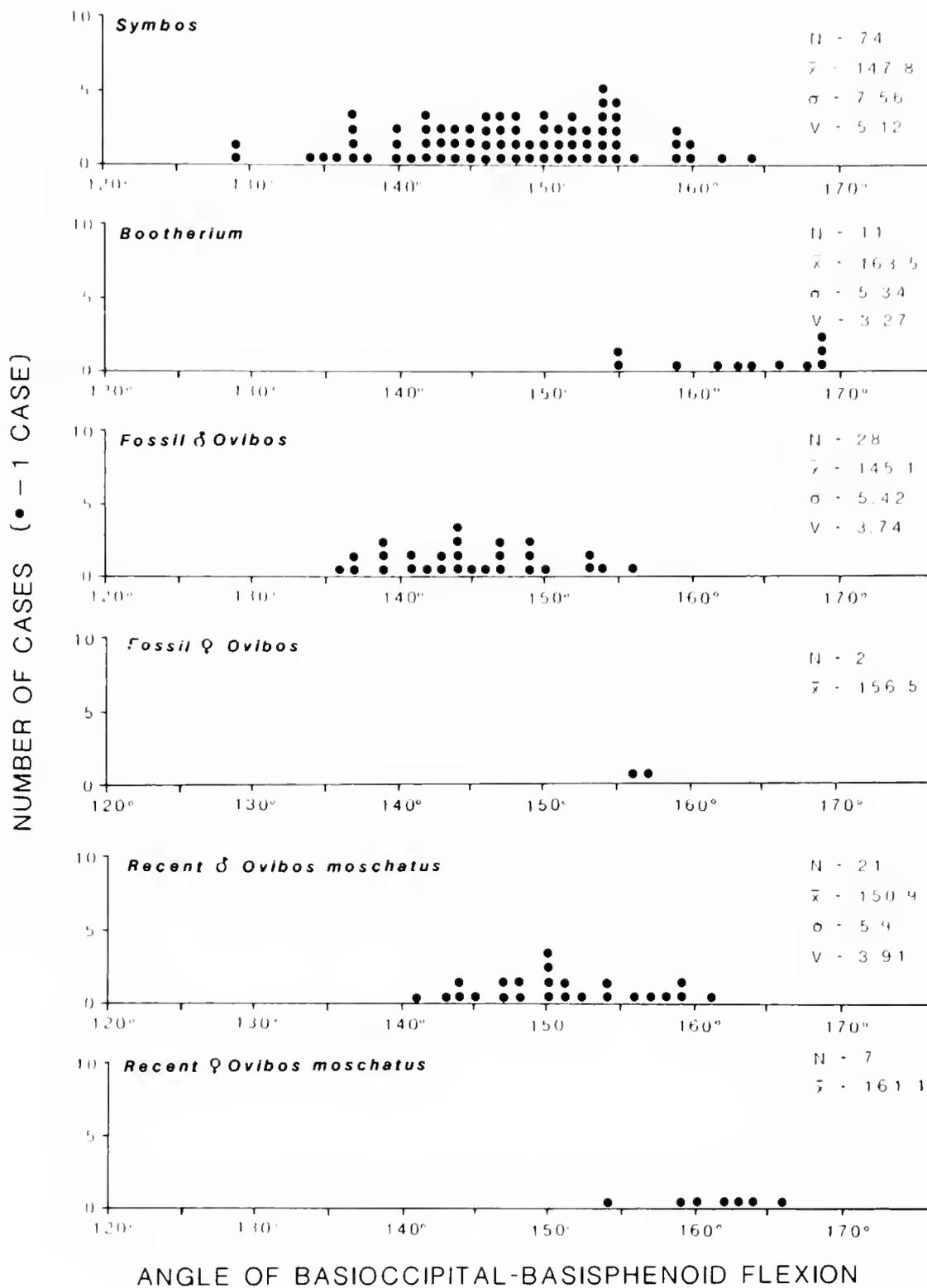


FIGURE 62.—Histograms showing the distribution of measurements of the angle of divergence between the basioccipital and basisphenoid bones in *Bootherium*, *Symbos*, and male and female samples of fossil and Recent *Ovibos moschatus*.

more fragmented female skull. This has been observed among some collectors of *Bison bison* crania in Texas, and museum collections of some modern taxa often are biased against females. The National Museum of Natural History collections of *Bison bison*, *Budorcas taxicolor*, and *Ovibos moschatus*, for example, are biased in favor of males (11♀ : 27♂ males, adult sample only; 5♀ : 11♂; 11♀ : 23♂, respectively) (McDonald, 1981, unpubl. data). Sex ratios for other samples of Recent and fossil bovids are given in Table 2. Based upon the sex ratio of samples in published reports and museum collections known to us, there are typically fewer females than male specimens in collections of bovid crania. It is our opinion that the ratio of

Bootherium:*Symbos* crania is within the limits of what could be expected as a sex ratio for a randomly collected sample of fossil crania in a single taxon. Certainly, the *Bootherium*:*Symbos* ratio presents no valid, persuasive basis for claiming that the two forms are taxonomically distinct.

SIMILARITIES IN THE MORPHOLOGY AND DISTRIBUTION OF *Bootherium* AND *Symbos* SPECIMENS

Even though the debate over the relationship between *Bootherium* and *Symbos* focused upon characters that differed between *Bootherium* and *Symbos*, several characters have been

TABLE 2.—Sex ratios for selected samples of bovid crania.

Sample	No. of females	No. of males	F:M ratio	Source
<i>Bison bison bison</i>	39	153	.254	McDonald, 1981
<i>Bison antiquus occidentalis</i>	30	115	.260	McDonald, 1981
<i>Bison antiquus antiquus</i>	31	107	.288	McDonald, 1981
<i>Bison latifrons</i>	10	80	.125	McDonald, 1981
<i>Ovibos moschatus</i> (Recent)	15	36	.417	McDonald, unpubl.
<i>Ovibos moschatus</i> (Recent)	26	31	.839	Allen, 1913
<i>Ovibos moschatus</i> (Fossil)	3	38	.079	McDonald, unpubl.
<i>Rupicapra rupicapra caucasica</i>	13	30	.433	Koubek and Hrabě, 1983
<i>Ovis catclawensis</i>	2	4	.500	Corner, 1977

identified in the literature that are similar in the two forms. Comparison of the technical descriptions of *Bootherium cavifrons* and *Bootherium bombifrons* provided by Leidy (1852b) indicates many similarities between the types of his two species, including the longitudinal growth form of the horn cores, the lateral emanation of the horn cores and their placement about midway between the levels of the orbits and the occipital plane, the shape and surface detail of the occiput, the presence of lacrimal fossae and grooves, the shape of the temporal fossae, the foramen magnum and processes of the ventral surface of the cranium, and the configuration and relative size of the occipital condyles. Allen (1913) conceded that several important characters were similar in *Bootherium* and *Symbos*, including the occipital condyles, the surface of the occiput, and the general proportions (great depth and length relative to breadth) of the skull.

Additional characters can be added to the list of similarities shared by *Bootherium* and *Symbos*. The frontoparietotemporal suture in both *Symbos* and *Bootherium* typically exhibits the same rostrocaudal orientation (i.e., roughly horizontal). The crania of male and female *Ovibos moschatus* share a common orientation of this suture line, but the orientation differs between *Ovibos moschatus* and *Bootherium/Symbos*. The mandibular dentition of *Bootherium* is now known from a mummified carcass collected by Otto Geist in 1940 at Fairbanks Creek, Alaska (McDonald, 1984b). Although this individual was a subadult (~2.3 years of age) at death and all permanent teeth had not developed, those that are present are indistinguishable from the teeth of *Symbos*.

In addition to morphological similarities between the crania of *Bootherium* and *Symbos*, the two forms share a similar pattern of spatial and temporal distribution. The spatial distribution of *Bootherium* and *Symbos* crania, based almost entirely upon specimens we have examined personally or from photographs, are shown in Figures 63 and 64. (Provenience data are presented in Tables 3 and 4.) These illustrations include all boundary records of which we are aware. Records without figures are not included in our data set; their inclusion would change only the density, not the spatial extent, of records. The major features of similarity between the distribution of records of *Bootherium* and *Symbos* include (1) their

concentration in Alaska and the mid-latitude belt of ~35°–45° N; (2) their southernmost extent on the coastal plain of Texas and Louisiana; (3) their absence in the extreme southeastern and southwestern corners of the continental United States; and (4) their absence over most of the glaciated northeastern one-third of the continent. *Bootherium* and *Symbos* are known only from the United States and Canada. Although Harington has noted that the holotype of *Ovibos recticornis*, from Radotin, Czechoslovakia, closely resembles *Symbos* (Ryziewicz, 1933; Harington, 1977), we suspect that this poorly known species is referable to *Praeovibos*.

The temporal distribution of *Bootherium* and *Symbos* is also broadly similar, but reliable stratigraphic and chronologic information exists for relatively few specimens. Available information indicates that *Bootherium* and *Symbos* were essentially Rancholabrean in age. Both *Bootherium* and *Symbos* have been found in the Cripple Creek Sump loess in central Alaska,

a mass of loess (possibly rebedded) of Illinoian age that was deposited on a down-warped or down-faulted surface of auriferous gravel beneath the present valley of Cripple Creek in the Fairbanks district.... (Péwé and Hopkins, 1967:269).

Symbos remains also have been reported from deposits of Illinoian age (and assigned to the late Irvingtonian) in Nebraska and Arkansas, but both of these records are weak. Jakway (1961a,b) reported *Symbos* in the Mullen local fauna, which he assigned to the early Illinoian. Jakway regarded this fauna as mixed, including some elements that predated the Illinoian and, possibly, some that post-dated the early Illinoian. Martin subsequently reported that, based upon restudy of the Mullen fauna and additional excavations at the locality (UNSM Cr-10), "the reworking was more extensive than Jakway had supposed" (Martin, 1972:174). Martin recognized at least two separate faunas within the Mullen assemblage, based upon the microtine rodent component: Mullen I, which he assigned tentatively to the early Kansan, and Mullen II, which was assigned to the early Illinoian. Martin did not discuss the status of *Symbos* within his revision of the fauna, but Kurtén and Anderson (1980) report that *Symbos*, along with *Bison* and *Alces*, were probably intrusives that post-dated Mullen II. The Conard

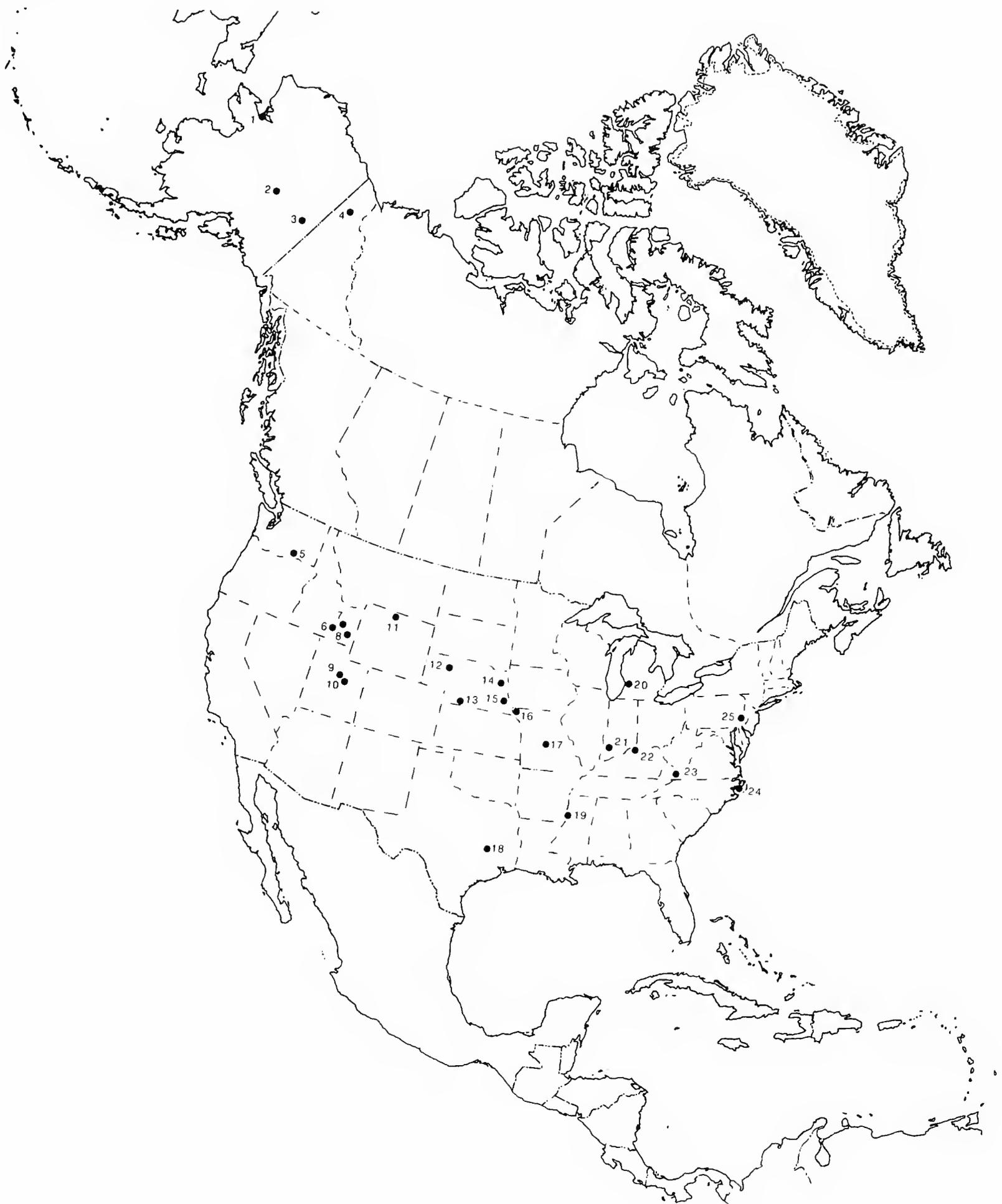


FIGURE 63.—The spatial distribution of cranial records of *Bootherium* used in this study (cf. Table 3).

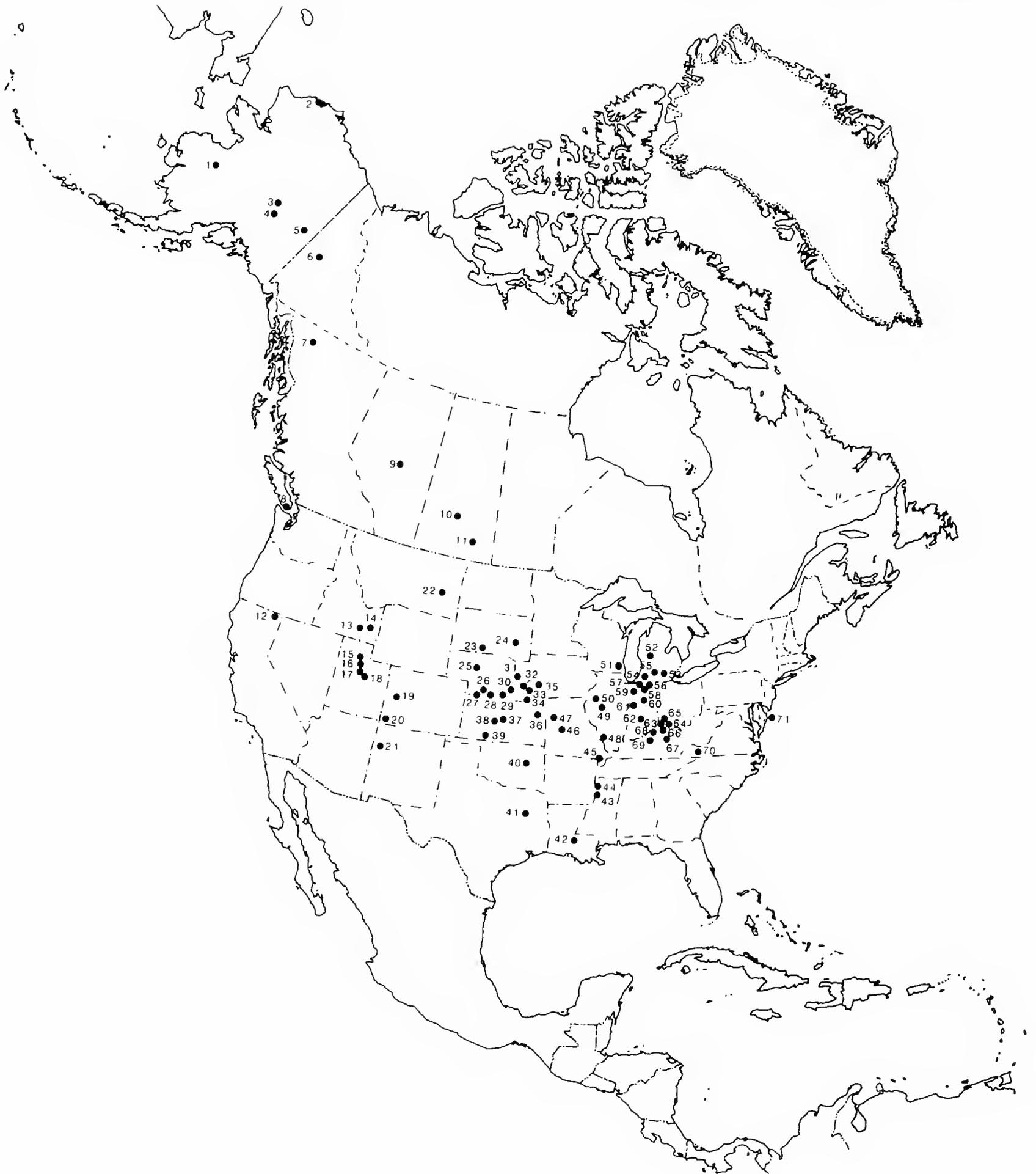


FIGURE 64.—The spatial distribution of cranial records of *Symbos* used in this study (cf. Table 4).

Fissure local fauna is considered to represent a single biostratigraphic unit assigned tentatively to the Irvingtonian, but—according to Kurtén and Anderson (1980:26), who did not enumerate the reasons for their position—this age assessment is “in dispute.” This local fauna was originally described by Brown (1908). Graham later collected and studied new material—primarily *Blarina*, with other small mammals—from this site, and considers its assignment to the late Irvingtonian to be correct (Graham, 1972, and pers. comm.). The ovibovine remains from Conard Fissure include three molars which were made the type of a new species, *S. australis*, along with some premolars and postcranial elements that were referred to *S. australis* by Brown (1908). Most of the teeth reported by Brown are of the size and configuration of those of *Symbos*, and their assignment to that genus was reasonable, but one (the Lm3) differs in detail from the corresponding tooth in other specimens assigned to *Symbos* and all are within the size range of corresponding teeth of *Euceratherium*. In addition, a tooth row collected at Conard Fissure by James H. Quinn is more similar to what are presumed to be the teeth of *Soergelia* than to those of any other known ovibovine taxon. The unequivocal presence of *Symbos* remains in both the pre-Rancholabrean fraction of the Mullen, and the Conard Fissure, local faunas is, therefore, not established.

Most specimens of *Symbos* and *Bootherium* are known or considered to date from the late Wisconsinan (Tables 3 and 4, Appendix III). The geologically youngest record of *Symbos*, based upon a radiocarbon-dated fourth lumbar vertebra from the associated skeleton (including skull) found near Scotts, Kalamazoo County, Michigan, is $11,100 \pm 400$ yr B.P. (M-1402)(Semken, Miller, and Stevens, 1964). A date of $10,370 \pm 160$ yr B.P. (I-8582) on *Bison* bone has been obtained on the Lost Chicken Creek fauna, which includes *Symbos*. *Equus* bone from the same fauna, however, yielded a date of $26,760 \pm 300$ yr B.P. (SI-355), and no dates have been obtained directly on remains of *Symbos* from the site (Harrington, 1978). The only radiocarbon dates obtained directly from *Bootherium* specimens were determined from hair (SI-454: $17,210 \pm 500$ yr B.P.) and scalp tissue (SI-455: $24,140 \pm 2200$ yr B.P.) from the frozen carcass of a subadult (F:AM A-293-5268) found at Fairbanks Creek, Alaska, in 1940 (Péwé, 1975; McDonald, 1984b) and from a horn sheath (SI-292: $22,540 \pm 900$ yr B.P.) on a cranium from the same locality (Péwé, 1975). Although not derived from the tissue of the animal itself, a radiocarbon date of $17,200 \pm 600$ yr B.P. (W-1617) was obtained on matrix from the cranial cavity of the holotype of *Bootherium bombifrons* (from Big Bone Lick, Kentucky). The geologically youngest radiocarbon date associated with *Bootherium* remains is $13,130 \pm 330$ yr B.P. (A-2985) obtained on spruce wood from the base of a lacustrine mud at Saltville, Virginia, in which the remains of both *Bootherium* and *Symbos* have been found (McDonald, 1984a).

Specimens of *Symbos* and *Bootherium* have been found together at several sites (Tables 3 and 4), including at least eight of the Fairbanks district sites (Cripple Creek and Cripple Creek

Sump, Dome Creek, Engineer Creek, Ester Creek, Fairbanks Creek, Gold Hill, lower Goldstream, and upper Cleary Creek); Lost Chicken Creek, Alaska; the Provo Formation near Slate Canyon, Utah County, Utah (Stokes and Hansen, 1937), Natural Trap Cave, Wyoming (Gilbert and Martin, 1984), Big Bone Lick, Kentucky, and Saltville Valley, Virginia (Ray, Cooper and Benninghoff, 1967; McDonald and Bartlett, 1983; McDonald, 1984a). These localities are widely distributed throughout the *Bootherium/Symbos* range, and both forms have been recovered from other deposits that are known or considered to be contemporaneous. *Bootherium* and *Symbos* were, therefore, contemporaneous as well as sympatric.

Conclusions

In the preceding sections we have reviewed the history of taxonomy of the autochthonous genera of musk oxen in North America, and the arguments that have been invoked during the past 135 years to justify decisions about the relationships between the nominal genera *Bootherium* and *Symbos* (including *Gidleya*). We have also discussed each issue individually in the light of current information and modern concepts, and presented evidence that allows the interpretation of all issues as characteristics or functions of sexual dimorphism. Specifically, we re-evaluated differences in the absolute size of crania; the size, shape, attachment, direction, and angle of emanation of the horn cores; the configuration of the dorsal surface of the cranium; the degree of flexion between the ventral surfaces of the basisphenoid and basioccipital bones at their junction; the relative depth of the lacrimal fossae; and the absolute number of recovered skulls of *Bootherium* and *Symbos*. In addition, we have introduced new perspectives on the relationship between these two forms—including similarities in the primary morphology of the cranium and horn cores in *Bootherium* and *Symbos*, and morphological parallels between *Bootherium/Symbos* and *Ovibos*—and attempted to show that these perspectives, too, allow recognition of the two nominal genera as sexually dimorphic forms of a single genus. *Symbos*, therefore, must be suppressed as a junior synonym of *Bootherium*, leaving *Bootherium* as the sole genus of musk oxen autochthonous to North America.

There is presently no strong evidence that more than one species exists within *Bootherium*. The range of quantitative variation within the male and female samples is continuous, as is most qualitative variation, presenting patterns of variation harmonious with that expected in a representative sample population of a large mammal taxon that ranged over half of North America for some 500,000 years. The caution that the collective sample of *Symbos* (now male *Bootherium*) crania might represent more than one species (McDonald, 1985b) is still applicable, since some qualitative differences (e.g., shape of the frontoparietotemporal suture; depth of the frontoparietal sinus region; configuration of the basioccipital bone) do occur among crania of both male and female *Bootherium*. Instances of atypical characters are rare, and appear to be randomly

TABLE 3.—Records of *Bootherium* mapped in Figure 63.

Locality		Specimen		
No.	Name	No.	Description	Provenience
1	Eschscholtz Bay, Alaska	USNM 2324	skullcap with both horn cores	on the shores of Eschscholtz Bay, probably at Elephant Point
2	Fairbanks area, Alaska	A-284-2044	left horn core with adjacent frontal	Cripple Creek
2	Fairbanks area, Alaska	A-284-8280	partial cranium with partial horn cores	Engineer Creek
2	Fairbanks area, Alaska	A-284-8281	skullcap with horn cores	Engineer Creek
2	Fairbanks area, Alaska	A-293-5268	mummified carcass	Fairbanks Creek; 64°58'N, 147°10'W
2	Fairbanks area, Alaska	A-325-8392	partial left horn core	Engineer Creek
2	Fairbanks area, Alaska	A-459-2014	partial left horn core with adjacent frontal	Cripple Creek
2	Fairbanks area, Alaska	A-521-4247	right horn core with adjacent frontal	Cripple Creek
2	Fairbanks area, Alaska	F:AM 30499	partial cranium with base of right horn core	Upper Cleary Creek
2	Fairbanks area, Alaska	F:AM 30500	skullcap with horn cores and supra-orbital region	?
2	Fairbanks area, Alaska	F:AM 30508	cranium with horn cores with both sheaths largely intact	creek near Fairbanks (Péwé, 1975)
2	Fairbanks area, Alaska	F:AM 33101	skullcap with partial horn cores	Cripple Creek
2	Fairbanks area, Alaska	F:AM 33102	right horn core	Cripple Creek Sump
2	Fairbanks area, Alaska	F:AM 33103	partial skullcap with partial right horn core	Cripple Creek Sump
2	Fairbanks area, Alaska	F:AM 33194	skullcap with partial horn cores	Dome Creek
2	Fairbanks area, Alaska	F:AM 33195	cranium with horn cores	Ester Creek
2	Fairbanks area, Alaska	F:AM 33196	partial skullcap and left horn core	Fairbanks Creek
2	Fairbanks area, Alaska	F:AM 33197	skullcap with partial horn cores	Fairbanks Creek
2	Fairbanks area, Alaska	F:AM 33198	skullcap with partial horn cores	Fairbanks Creek
2	Fairbanks area, Alaska	F:AM 33199	cranium with horn cores	Fairbanks Creek
2	Fairbanks area, Alaska	F:AM 33207	cranium with partial horn cores; part of face	Fairbanks Creek
2	Fairbanks area, Alaska	F:AM 33208	skullcap with base of left horn core	Gold Hill
2	Fairbanks area, Alaska	F:AM 33220	skullcap with partial horn cores	bank opposite Fox—Goldstream
3	Lost Chicken Creek, Alaska	UAF V-54-158	cranium with horn cores	near head of Lost Chicken Creek; 64°03'N, 141°53'W
4	Old Crow River, Yukon Territory	NMC 10536	partial right horn core and adjacent frontal	bank of Old Crow River; 67°47'N, 139°57'W
5	Benton County, Washington	WSU uncataloged	cranium with partial horn cores	Umatilla Mammoth Site, near Wal-lula Gap, on Columbia R. ~1 mi upstream from Umatilla, Oregon
6	Minidoka County, Idaho	LACM 16888	cranium with partial horn cores	from 12' depth, gravel pit 1 mi W of Minidoka Dam, N side of Snake R. (LACM loc. 6671); NE 1/4, Sec. 1, T9S, R25E, Lake Walcott Quad, USGS 7.5' series
7	Power County, Idaho	UVP 083	skullcap with horn cores	intersection of Oregon Trail and Elevator Streets, American Falls; NE 1/4, Sec. 29, T7S, R31E, American Falls Quad, USGS 7.5' series
8	Bannock County, Idaho	IMNH 17124	skullcap and horn cores	from 12' depth, Arimo Gravel Pit; SE 1/4, SW 1/4, Sec. 19, T10S, R37E, Arimo Quad, USGS 7.5' series
9	Utah County, Utah	lost; no number	partial skullcap and partial left horn core	near Pleasant Grove
10	Utah County, Utah	BYUG 834	cranium with partial horn cores	about 50' below surface, Provo City Upper Gravel Pits, near Slate Canyon; SW 1/4, Sec. 8, T7S, R3E, Provo Quad, USGS 7.5' series
11	Big Horn County, Wyoming	KUMNH 6135	skullcap and horn cores	Natural Trap Cave

TABLE 3.—Continued.
(Locality/Specimen No. repeated from left half of table for ease of reference.)

Locality No.	Specimen No.	Stratigraphic unit	Geologic age	Principal published description(s)
1	USNM 2324			Hay, 1915 (pl. 31: fig. 1)
2	A-284-2044			unpublished
2	A-284-8280			unpublished
2	A-284-8281			unpublished
2	A-293-5268		radiocarbon age: 17,210 ± 500 yr (SI-454; on hair) and 24,140 ± 2,200 yr (SI-455; on muscle) B.P.	Guthrie, 1972:300 (photograph); McDonald, 1984b
2	A-325-8392			unpublished
2	A-459-2014			unpublished
2	A-521-4247			unpublished
2	F:AM 30499			unpublished
2	F:AM 30500			unpublished
2	F:AM 30508		radiocarbon age: 22,540 ± 900 yr B.P. (SI-292 on horn sheath)	unpublished
2	F:AM 33101			unpublished
2	F:AM 33102			unpublished
2	F:AM 33103			unpublished
2	F:AM 33194			unpublished
2	F:AM 33195			unpublished
2	F:AM 33196			unpublished
2	F:AM 33197			unpublished
2	F:AM 33198			unpublished
2	F:AM 33199			unpublished
2	F:AM 33207			unpublished
2	F:AM 33208			unpublished
2	F:AM 33220			unpublished
3	UAF V-54-158			unpublished
4	NMC 10536			Harington, 1977 (fig. 83)
5	WSU uncataloged		(?)Late Wisconsinan (probably dates "shortly after 13,000 yr B.P.," Lyman and Livingston, 1983)	unpublished
6	LACM 16888		Late Pleistocene	White, 1985
7	UVP 083	?Equivalent to B layer (= Rainbow Beach Section), American Falls Formation	?~26,500 ± 500 yr B.P.	Nelson and Madsen, 1987 (fig. 1)
8	IMNH 17124	Lake Bonneville gravels		White, 1985 (figs. 2A, 3A)
9	lost; no number			unpublished
10	BYUG 834	(?)Provo Formation	(?)Lake Bonneville age	Stokes and Hansen, 1937 (fig. 1, bottom)
11	KUMNH 6135		Late Wisconsinan	Nelson and Madsen, 1987 (fig. 7)

TABLE 3.—Records of *Bootherium* mapped in Figure 63 (continued).

Locality		Specimen		
No.	Name	No.	Description	Provenience
12	Sheridan County, Nebraska	UNSM 9-418-39	left horn core	Pit 4, Johndreau Quarry 1. E 1/2, Sec. 25, T31N, R41W
12	Sheridan County, Nebraska	UNSM 10-419-39	partial cranium with base of left horn core	Pit 4, Johndreau Quarry 1. E 1/2, Sec. 25, T31N, R41W
13	Hitchcock County, Nebraska	UNSM 18-11-36	cranium with partial horn cores	Trenton Gravel Pit
14	Cuming County, Nebraska	UNSM 603-46	cranium with horn cores	gravel pit at W edge West Point (UNSM loc. Cm-3); SW 1/4, NW 1/4, Sec. 34, T22N, R6E
15	(?)Douglas County, Nebraska	UNSM 193-25-5-27	cranium with partial horn cores	(?)near Omaha
16	Atchinson County, Missouri	KUMNH Cast 345	left horn core	from gravel bar ~4 mi SW of Fairfax; SE 1/4, SE 1/4, Sec. 36, T64N, R41W
17	Cooper County, Missouri	Widel collection	skullcap with partial horn cores	dredged from Lamine R. (?)14 mi S of Blackwater; Sec. 22, T46N, R19W
18	Brazos County, Texas	TAMC 2553 ¹	partial cranium with partial horn cores	from sandbar in or along Brazos R. at Pitts Bridge
19	Bolivar County, Mississippi	McKay collection	partial cranium with partial horn cores	from sand bar in Mississippi R. near Rosedale
20	Muskegon County, Michigan	GRPM 11-423-3101	dorsal cranium and horn cores	about 2'-3' deep, Moorland Swamp, Charles McKay Farm, 3 mi NE of Moorland. NE 1/4, Sec. 16, T10N, R14W
21	Gibson County, Indiana	USNM 24885	skullcap with partial horn cores; associated occiput and basicranium probably of same individual	at 5'-20' depth in gravel pit "somewhere" east of East Mt. Carmel
22	Boone County, Kentucky	ANSP 994	cranium with horn cores and orbital region	Big Bone Lick (Clark-Jefferson Collection)
22	Boone County, Kentucky	UNSM 1111	fragmentary skullcap and horn cores	Big Bone Lick (University of Nebraska collection)
23	Smyth County, Virginia	USNM 23264	cranium with partial horn cores	Saltville Valley
23	Smyth County, Virginia	USNM 392115	fragment of proximal right horn core	Saltville Valley
23	Smyth County, Virginia	Space collection	fragment of frontal bone with base of left horn core ²	Saltville Valley
23	Smyth County, Virginia	Stephens collection	fragment of frontal with base of left horn core	Saltville Valley
24	Dare County, North Carolina	USNM 347315	cranium with partial horn cores and parts of face	in surf, Oregon Inlet
25	Bucks County, Pennsylvania	ANSP 29	small part of right horn core and adjacent cranium	from a closed limestone crevice in Durham Cave, along bank of Delaware R. near Riegelsville

¹This specimen is now a part of the collections of the Texas Memorial Museum, University of Texas, Austin, Texas.

²This specimen was in the Rufus Pickle collection when it was examined by Ray in 1965. The Pickle collection was subsequently sold to Ralph Space of Sussex, New Jersey. This specimen could not be located when the Space collection was examined by McDonald in December 1984.

TABLE 3.—Continued.
(Locality/Specimen No. repeated from left half of table for ease of reference.)

Locality No.	Specimen No.	Stratigraphic unit	Geologic age	Principal published description(s)
12	USNM 9-418-39			unpublished
12	USNM 10-419-39		Middle Pleistocene (Yarmouthian)	unpublished
13	USNM 18-11-36			unpublished
14	USNM 603-46		Middle to Late Wisconsinan (Frankforter, 1950:45)	unpublished
15	USNM 193-25-5-27			Barbour, 1931 (fig. 146)
16	KUMNH Cast 345			Neas and Parker, 1987 (fig. 1)
17	Widel collection			Holmes, 1960 (fig. 225)
18	TAMC 2553			Hesse, 1942 (pl. 18); Ray, 1966b (figs. 1, 2)
19	McKay collection			unpublished
20	GRPM 11-423-3101			Gidley, 1908 (pl. 59)
21	USNM 24885			unpublished
22	ANSP 994		matrix from cranium radiocarbon dated at 17,200 ± 600 yrs B.P. (W- 1617)	Wistar, 1818 (pl. 9: figs. 10, 11)
22	USNM 1111		(?)Late Wisconsinan	unpublished
23	USNM 23264	(?)Unit W4 (Late Wisconsinan fluvial gravels) (McDonald, 1984a) ³	radiocarbon age of Unit W4: between 27,000 ± 900 (A-2986) and 14,480 ± 300 (Beta-5701) yrs B.P.	Ray, Cooper, and Benninghoff, 1967 (pl. 65: figs. 2, 3; pl. 66: figs. 1-3)
23	USNM 392115		(?)Late Wisconsinan	unpublished
23	Space collection		(?)Late Wisconsinan	unpublished
23	Stephens collection		(?)Late Wisconsinan	unpublished
24	USNM 347315			Ray, 1983:3 (photographs)
25	ANSP 29			Rhoads, 1895, 1897; Ray, 1966a

³Based on information obtained from excavations at Saltville since October 1980, all known vertebrate fossils from this locality are presumed to date from the late Wisconsinan or Holocene. No remains of extinct vertebrate taxa have been found in deposits of Holocene age, and no vertebrate fossil bearing deposits have been found that date >27,000 yr B.P. (McDonald, 1984a).

TABLE 4.—Records of *Symbos* mapped in Figure 64.

Locality		Specimen		
No.	Name	No.	Description	Provenience
1	Anvik, Alaska	USNM 2378	partial right horn core	Anvik
2	Point Barrow, Alaska	BM(NH) 10462	cranium with partial horn cores	Port (= Point) Barrow
3	Lillian Creek District, Alaska	BLM uncataloged	cranium with horn cores	Tucker Mine, Lillian Creek
4	Fairbanks area, Alaska	A-204-4254	cranium with horn cores and left maxillary, left mandible, and several postcranial elements	Little Eldorado Creek
4	Fairbanks area, Alaska	F:AM 30501	cranium with left horn core; part of face	lower Cleary Creek; found in place 90' below surface
4	Fairbanks area, Alaska	F:AM 30505	cranium with horn cores	?
4	Fairbanks area, Alaska	F:AM 30506	cranium with partial horn cores	?
4	Fairbanks area, Alaska	F:AM 33124	skull lacking nasals, part of premaxillaries; still has horn sheaths	upper Cleary Creek
4	Fairbanks area, Alaska	F:AM 33125	cranium with partial horn cores	Lower Goldstream Creek
4	Fairbanks area, Alaska	F:AM 33126	skullcap with partial horn cores	lower Goldstream Creek
4	Fairbanks area, Alaska	F:AM 33127	cranium with partial horn cores	lower Goldstream Creek
4	Fairbanks area, Alaska	F:AM 33128	cranium with bases of horn cores	lower Goldstream Creek
4	Fairbanks area, Alaska	F:AM 33129	cranium and base of right horn core	lower Goldstream Creek
4	Fairbanks area, Alaska	F:AM 33130	cranium with partial horn cores	lower Goldstream Creek
4	Fairbanks area, Alaska	F:AM 33131	cranium with partial horn cores	Fairbanks Creek
4	Fairbanks area, Alaska	F:AM 33132	partial cranium with partial horn cores	Fairbanks Creek
4	Fairbanks area, Alaska	F:AM 33133	cranium with bases of horn cores	Fairbanks Creek
4	Fairbanks area, Alaska	F:AM 33134	cranium with partial horn cores	Fairbanks Creek
4	Fairbanks area, Alaska	F:AM 33135	cranium with partial right horn core	Fairbanks Creek
4	Fairbanks area, Alaska	F:AM 33136	cranium with partial horn cores	Fairbanks Creek
4	Fairbanks area, Alaska	F:AM 33137	cranium with partial horn cores	Fairbanks Creek
4	Fairbanks area, Alaska	F:AM 33138	cranium with bases of horn cores	Fairbanks Creek
4	Fairbanks area, Alaska	F:AM 33139	left horn core and part of cranium	Fairbanks Creek
4	Fairbanks area, Alaska	F:AM 33140	cranium with partial horn cores	Fairbanks Creek
4	Fairbanks area, Alaska	F:AM 33141	cranium with partial horn cores	Fairbanks Creek
4	Fairbanks area, Alaska	F:AM 33142	cranium with horn cores	Fairbanks Creek
4	Fairbanks area, Alaska	F:AM 33143	cranium with partial horn cores	Engineer Creek
4	Fairbanks area, Alaska	F:AM 33144	cranium with bases of horn cores	Engineer Creek
4	Fairbanks area, Alaska	F:AM 33145	cranium	Engineer Creek
4	Fairbanks area, Alaska	F:AM 33146	cranium with partial left horn core	Engineer Creek
4	Fairbanks area, Alaska	F:AM 33147	partial cranium	Engineer Creek
4	Fairbanks area, Alaska	F:AM 33148	cranium with horn cores	Engineer Creek
4	Fairbanks area, Alaska	F:AM 33149	skullcap with bases of horn cores	Engineer Creek
4	Fairbanks area, Alaska	F:AM 33150	cranium with bases of horn cores	Cripple Creek
4	Fairbanks area, Alaska	F:AM 33153	cranium with partial horn cores	Engineer Creek
4	Fairbanks area, Alaska	F:AM 33154	cranium with partial horn cores	Engineer Creek
4	Fairbanks area, Alaska	F:AM 33155	cranium with partial horn cores	Cripple Creek
4	Fairbanks area, Alaska	F:AM 33156	skullcap with partial horn cores	Cripple Creek
4	Fairbanks area, Alaska	F:AM 33157	cranium with left horn core	Cripple Creek
4	Fairbanks area, Alaska	F:AM 33158	skullcap with horn cores	Cripple Creek
4	Fairbanks area, Alaska	F:AM 33159	cranium with horn cores; partial face	Cripple Creek
4	Fairbanks area, Alaska	F:AM 33160	cranium with partial horn cores	Cripple Creek
4	Fairbanks area, Alaska	F:AM 33161	cranium	Cripple Creek
4	Fairbanks area, Alaska	F:AM 33162	cranium with partial horn cores	Cripple Creek
4	Fairbanks area, Alaska	F:AM 33164	cranium with right horn core	Cripple Creek
4	Fairbanks area, Alaska	F:AM 33167	skullcap	Cripple Creek
4	Fairbanks area, Alaska	F:AM 33168	cranium with partial horn cores	Cripple Creek Sump
4	Fairbanks area, Alaska	F:AM 33169	cranium with bases of horn cores	Cripple Creek Sump

TABLE 4.—Continued.
(Locality/Specimen No. repeated from left half of table for ease of reference.)

Locality No.	Specimen No.	Stratigraphic unit	Geologic age	Principal published description(s)
1	USNM 2378			unpublished
2	BM(NH) 104			unpublished
3	BLM uncataloged			unpublished
4	A-204-4254		radiocarbon age: >40,000 yr B.P. (SI-291: on fecal pellets) ¹	unpublished
4	F:AM 30501			unpublished
4	F:AM 30505			unpublished
4	F:AM 30506			unpublished
4	F:AM 33124		radiocarbon age: 25,090 ± 1070 yr B.P. (SI-850: on horn sheath)	unpublished
4	F:AM 33125			unpublished
4	F:AM 33126			unpublished
4	F:AM 33127			unpublished
4	F:AM 33128			unpublished
4	F:AM 33129			unpublished
4	F:AM 33130			unpublished
4	F:AM 33131			unpublished
4	F:AM 33132			unpublished
4	F:AM 33133			unpublished
4	F:AM 33134			unpublished
4	F:AM 33135			unpublished
4	F:AM 33136			unpublished
4	F:AM 33137			unpublished
4	F:AM 33138			unpublished
4	F:AM 33139			unpublished
4	F:AM 33140			unpublished
4	F:AM 33141			unpublished
4	F:AM 33142			unpublished
4	F:AM 33143			unpublished
4	F:AM 33144			unpublished
4	F:AM 33145			unpublished
4	F:AM 33146			unpublished
4	F:AM 33147			unpublished
4	F:AM 33148			unpublished
4	F:AM 33149			unpublished
4	F:AM 33150			unpublished
4	F:AM 33153			unpublished
4	F:AM 33154			unpublished
4	F:AM 33155			unpublished
4	F:AM 33156			unpublished
4	F:AM 33157			unpublished
4	F:AM 33158			unpublished
4	F:AM 33159			unpublished
4	F:AM 33160			unpublished
4	F:AM 33161			unpublished
4	F:AM 33162			unpublished
4	F:AM 33164			unpublished
4	F:AM 33167			unpublished
4	F:AM 33168			unpublished
4	F:AM 33169			unpublished

¹Several fecal pellets resembling those of *Ovibos moschatus* were found associated with this skeleton, parts of which were articulated by mummified connective tissue. The skeleton, however, does contain three *Bison* bones and one *?Ovibos moschatus* rib, so the association between the *Symbos* skeleton and the fecal matter, although probable, is not established with certainty.

TABLE 4.—Records of *Symbos* mapped in Figure 64 (continued).

Locality		Specimen		
No.	Name	No.	Description	Provenience
4	Fairbanks area, Alaska	F:AM 33170	cranium with partial horn cores	Cripple Creek Sump
4	Fairbanks area, Alaska	F:AM 33171	partial cranium with bases of horn cores	Cripple Creek Sump
4	Fairbanks area, Alaska	F:AM 33172	skullcap and partial left horn core	Ester Creek
4	Fairbanks area, Alaska	F:AM 33173	partial cranium with partial horn cores	Ester Creek
4	Fairbanks area, Alaska	F:AM 33174	skullcap with partial horn cores	Ester Creek
4	Fairbanks area, Alaska	F:AM 33175	cranium with partial horn cores	Ester Creek
4	Fairbanks area, Alaska	F:AM 33176	cranium with base of right horn core	Little Eldorado Creek
4	Fairbanks area, Alaska	F:AM 33177	cranium with partial horn cores	Little Eldorado Creek
4	Fairbanks area, Alaska	F:AM 33178	cranium with partial right horn core	Little Eldorado Creek
4	Fairbanks area, Alaska	F:AM 33179	cranium with partial horn cores	Livengood Creek
4	Fairbanks area, Alaska	F:AM 33180	cranium with partial horn cores	Livengood Creek
4	Fairbanks area, Alaska	F:AM 33181	skullcap with partial horn cores	Bear Creek
4	Fairbanks area, Alaska	F:AM 33182	cranium with horn cores; part of face	Dawson Cut, Engineer Creek
4	Fairbanks area, Alaska	F:AM 33183	cranium with partial horn cores	Dawson Cut
4	Fairbanks area, Alaska	F:AM 33184	cranium with bases of horn cores	Dawson Cut
4	Fairbanks area, Alaska	F:AM 33185	cranium with horn cores	Dome Creek
4	Fairbanks area, Alaska	F:AM 33186	cranium with partial horn cores	Dome Creek
4	Fairbanks area, Alaska	F:AM 33188	cranium with horn cores	(?)Flatt Creek
4	Fairbanks area, Alaska	F:AM 33189	cranium with right horn core	Gold Hill
4	Fairbanks area, Alaska	F:AM 33190	cranium with partial left horn cores	Gold Hill
4	Fairbanks area, Alaska	F:AM 33191	skullcap	Gold Hill
4	Fairbanks area, Alaska	F:AM 33192	cranium with partial horn cores	Tofty
4	Fairbanks area, Alaska	F:AM 33193	skull	?
4	Fairbanks area, Alaska	F:AM 34610	cranium with partial horn cores	(?)Chat. (= Chatam?)
4	Fairbanks area, Alaska	F:AM 34611	cranium with partial horn cores	Ester Creek
4	Fairbanks area, Alaska	F:AM 34612	cranium with partial horn cores	?
4	Fairbanks area, Alaska	F:AM 34613	cranium with right horn core	?
4	Fairbanks area, Alaska	F:AM 34614	cranium with partial horn cores	?
4	Fairbanks area, Alaska	F:AM 34615	cranium with partial horn cores	Ester Creek
4	Fairbanks area, Alaska	F:AM 34616	cranium with bases of horn cores; part of face	Goldstream Creek
4	Fairbanks area, Alaska	F:AM 34617-A	cranium with bases of horn cores	?
4	Fairbanks area, Alaska	F:AM 34617-B	cranium with partial left horn core	? ²
4	Fairbanks area, Alaska	F:AM 34617-C	partial cranium with bases of horn cores	?
4	Fairbanks area, Alaska	F:AM 34617-D	cranium and partial right horn core	?
4	Fairbanks area, Alaska	F:AM 34617-F	skullcap and left horn core	?
4	Fairbanks area, Alaska	F:AM 34617-G	partial cranium	?
4	Fairbanks area, Alaska	F:AM 34617-I	skullcap with bases of horn cores	upper Cleary Creek
4	Fairbanks area, Alaska	F:AM 34617-?	cranium with partial right horn core	(?)upper Cleary Creek ³
5	Lost Chicken Creek, Alaska	NMC 25892	cranium with partial horn cores	near head of Lost Chicken Creek; 64°03'N, 141°53'W
5	Lost Chicken Creek, Alaska	UAF V-54-197	cranium with horn cores	near head of Lost Chicken Creek
5	Lost Chicken Creek, Alaska	USNM 372807	dorsal cranium with partial horn cores; caudal part of face	Lost Chicken Creek
6	Dawson area, Yukon Territory	NMC 8837	cranium with horn cores	Dawson area, exact locality unknown
6	Dawson area, Yukon Territory	NMC 29229	cranium with partial horn cores	Dawson area
6	Dawson area, Yukon Territory	USNM 2555	70' below surface in gravcls, Lovett Gulch, Bonanza Creek	
6	Dawson area, Yukon Territory	USNM 2556	partial cranium with partial horn cores	Bonanza Creek
6	Dawson area, Yukon Territory	USNM 12135	partial skullcap with base of right horn core	note with specimen: "From Dan Coate, Dawson. Y.T."

²The abbreviation "Cl." is written on this specimen, but it is faint and additional information about provenience could be missing.

³What appears to be the abbreviation "U. Cl." is written on the specimen, but it is faint and additional information about provenience could be missing.

TABLE 4.—Continued.
 (Locality/Specimen No. repeated from left half of table for ease of reference.)

Locality No.	Specimen No.	Stratigraphic unit	Geologic age	Principal published description(s)
4	F:AM 33170			unpublished
4	F:AM 33171			unpublished
4	F:AM 33172			unpublished
4	F:AM 33173			unpublished
4	F:AM 33174			unpublished
4	F:AM 33175			unpublished
4	F:AM 33176			unpublished
4	F:AM 33177			unpublished
4	F:AM 33178			unpublished
4	F:AM 33179			unpublished
4	F:AM 33180			unpublished
4	F:AM 33181			unpublished
4	F:AM 33182			unpublished
4	F:AM 33183			unpublished
4	F:AM 33184			unpublished
4	F:AM 33185			unpublished
4	F:AM 33186			unpublished
4	F:AM 33188			unpublished
4	F:AM 33189			unpublished
4	F:AM 33190			unpublished
4	F:AM 33191			unpublished
4	F:AM 33192			unpublished
4	F:AM 33193			unpublished
4	F:AM 34610			unpublished
4	F:AM 34611			unpublished
4	F:AM 34612			unpublished
4	F:AM 34613			unpublished
4	F:AM 34614			unpublished
4	F:AM 34615			unpublished
4	F:AM 34616			unpublished
4	F:AM 34617-A			unpublished
4	F:AM 34617-B			unpublished
4	F:AM 34617-C			unpublished
4	F:AM 34617-D			unpublished
4	F:AM 34617-F			unpublished
4	F:AM 34617-G			unpublished
4	F:AM 34617-I			unpublished
4	F:AM 34617-?			unpublished
5	NMC 25892		radiocarbon age: 20,500 ± 390 yr B.P. (I-10649: on bone)	Harington, 1980 (figs. 13–15)
5	UAF V-54-197			unpublished
5	USNM 372807			unpublished
6	NMC 8837			Harington, 1977 (fig. 84)
6	NMC 29229			Harington, 1977 (fig. 85)
6	USNM 2555			Osgood, 1905a (pl. 37: fig. 2; pl. 38: fig. 2; pl. 39: fig. 1; pl. 40: fig. 2)
6	USNM 2556			unpublished
6	USNM 12135			unpublished

TABLE 4.—Records of *Symbos* mapped in Figure 64 (continued).

Locality		Specimen		
No.	Name	No.	Description	Provenience
7	Dease Lake, British Columbia	BCPM 680	cranium	from alluvium in the vicinity of Dease Lake
8	Saanich Peninsula, British Columbia	BCPM 69:014	partial cranium with partial horn cores	from Butler Brothers gravel pit at Keatings Cross Road, N of Victoria, on Saanich Peninsula, Vancouver Island, 48°33'54"N, 123°25'05"W
9	Ft. Saskatchewan, Alberta	UAI uncataloged	cranium with partial horn cores	at Steele Brothers of Canada gravel pit, ~3 mi SW of Ft. Saskatchewan. SE 1/4, Sec. 14, T54, R33, W4; 53°39'40"N, 113°17'W
10	Saskatoon, Saskatchewan	GMUS VM462	cranium with partial horn cores	
11	Fort Qu'Appelle, Saskatchewan	NMC 11859	skull	Bliss Gravel Pit, Fort Qu'Appelle
11	Fort Qu'Appelle, Saskatchewan	SMNH P100.63	partial cranium with partial horn cores	Bliss Gravel Pit, Fort Qu'Appelle; SW 1/4, SW S, 7T, 21R, 13W, 2
11	Fort Qu'Appelle, Saskatchewan	SMNH P100.84	partial cranium with partial horn cores	(?)Bliss Gravel Pit, Fort Qu'Appelle
11	Fort Qu'Appelle, Saskatchewan	SMNH P1675.1	cranium with partial horn cores	Sangsten Gravel Pit, Fort Qu'Appelle. 14T, 21R, 14W, 2
12	Modoc County, California	UCMP 58219	cranium with horn cores; part of left maxillary	John St. Gravel Pit, ~5--6 mi N of Cedarville; SW 1/4, NW 1/4, Sec. 17, T43N, R16E
13	Minidoka County, Idaho	IMNH 2598	cranium with horn cores	Acequia Gravel Pit, 2.5 mi E of Acequia; NE 1/4, Sec. 8, T9S, R25E, Acequia Quad, USGS 7.5' series
14	Power County, Idaho	USNM 13694	partial skull with partial horn cores	gravel quarry near east end of American Falls Dam
14	Power County, Idaho	USNM 13695	cranium with partial horn cores	gravel quarry near east end of American Falls Dam
15	Salt Lake County, Utah	UUVP 8540	skull with horn cores	Hardman Gravel Pits, N edge of Salt Lake City. NE 1/4, Sec. 32, T1N, R1E, Fort Douglas Quad, USGS 7.5' series
15	Salt Lake County, Utah	UUVP 8536	cranium with horn cores	from ~6' beneath surface in sands and gravels, (?)91 East South Temple, Salt Lake City; SW 1/4, T1N, R1E, Salt Lake City North Quad, USGS 7.5' series ⁴
16	Salt Lake County, Utah	YPM uncataloged	partial cranium with horn cores	Salt Lake City
17	Utah County, Utah	BYUG 102	cranium with horn cores	from ~15' beneath terrace surface in gravels and sands, Provo City Upper Gravel Pits, near Slate Canyon. SW 1/4, Sec. 8, T7S, R3E, Provo Quad, USGS 7.5' series
18	Utah County, Utah	BYUG 103	partial cranium with horn cores	from ~120' below terrace level, in built deposits of upper Lake Bonneville shoreline, Grant Lloyd Gravel Pit at Utah Bay, ~2 mi E of Santaquin
18	Utah County, Utah	USNM 17914	partial cranium and horn cores	from sand lens within gravel deposit, southern Utah Valley, 1 mi NE of Santaquin

⁴The provenience data refer to a specimen reported by Chadbourne (1871). Nelson and Madsen (1978) presumed UUVP 8536 to be that specimen, but definitive identification of the specimen as that described by Chadbourne is lacking.

TABLE 4.—Continued.
(Locality/Specimen No. repeated from left half of table for ease of reference.)

Locality No.	Specimen No.	Stratigraphic unit	Geologic age	Principal published description(s)
7	BCPM 680			Harington, 1968 (figs. 1-3)
8	BCPM 69:014	from lower half of Saanichton gravels	~19,000 yr B.P. (Harington, 1975; after Halstead, 1968:1411)	Harington, 1975 (figs. 7-10)
9	UAI uncataloged		probably of late Pleistocene age (Harington, 1977:901)	Harington, 1975 (figs. 3, 4)
10	GMUS VM462	Riddell Member, Floral Formation	probably Sangamonian	Skwara and Walker, in press
11	NMC 11859	4th gravel bed, Echo Lake Gravels	probably Sangamonian, possibly Wisconsinan interstadial, in age. Molluscs from sand overlying 4th gravel bed radiocarbon dated >30,000 yr B.P. (GSC-987)	Khan, 1970 (pls. 23-25)
11	SMNH P100.63		probably Sangamonian	Khan, 1970 (pls. 28, 29)
11	SMNH P100.84			unpublished
11	SMNH P1675.1			Khan, 1970 (pls. 26, 27)
12	UCMP 58219			unpublished
13	IMNH 2598			White, 1985 (figs. 2C, 3C)
14	USNM 13694			White, 1985
14	USNM 13695			White, 1985
15	UVP 8540	Alpine Formation	Early Lake Bonneville age	Nelson and Madsen, 1978 (figs. 2-5)
15	UVP 8536	(?)Provo Formation	(?)Late Lake Bonneville age	Hay, 1927 (pl. 1: fig. 3)
16	YPM uncataloged			unpublished
17	BYUG 102	(?)Provo Formation or (?)post-Provo sediments	(?)Late Lake Bonneville age (Bissell, 1963) ⁵	Stokes and Hansen, 1937 (fig. 1, top specimen)
18	BYUG 103	(?)Bonneville Formation	(?)Medial Lake Bonneville age (Bissell, 1963)	unpublished
18	USNM 17914	Alpine Formation	Early Lake Bonneville age (Bissell, 1963)	unpublished

⁵Stokes and Hansen (1937) reported this specimen to be from gravels and sands of late Bonneville age (= Provo Formation), but Nelson and Madsen (1978), following Bissell (1963), consider the specimen to have come from fan sediments of post-Bonneville age.

TABLE 4.—Records of *Symbos* mapped in Figure 64 (continued).

Locality		Specimen		
No.	Name	No.	Description	Provenience
19	Delta County, Colorado	PM 526	cranium with bases of horn cores	along or near Oak Creek. Sec. 14 or 15, T13S, R96W Hells Kitchen Quad, USGS 7.5' series
20	Montezuma County, Colorado	DAP 23	partial cranium with partial horn cores, complete cervical vertebral series and most of thoracic vertebral series	from loess on Grass Mesa. NE 1/4, Sec. 7, T38N, R15W, Trimble Point Quad, USGS 7.5' series
21	McKinley County, New Mexico	UNSM 5100	cranium with partial horn cores	Black Rocks irrigation dam site, 4.5 mi E of Zuni. Zuni Quad, USGS 7.5' series
22	Custer County, Montana	Payes collection	partial cranium with partial left horn core	from gravel pit ~12 mi E of Miles City
23	Bennett County, South Dakota	Rice collection	cranium with partial horn cores and caudal part of face	from fine gravel lens in loess on Don Rice farm, Tuthill; NE 1/4, Sec. 8, T37N, R35W
24	Aurora/Douglas County, South Dakota	WHOM 18661	cranium with horn cores	from gravel pit ~4 mi N of Corsica
25	Cherry County, Nebraska	UNSM 39000	skull	from North Prong Quarry (UNSM loc. Cr-102), N side of North Branch of Middle Loup River, ~12 mi NW of Mullen; NW 1/4, Sec. 18, T25N, R34W
25	Cherry County, Nebraska	UNSM 39001	skullcap with right horn core	from North Prong Quarry (UNSM loc. Cr-102), N side of North Branch of Middle Loup River, ~12 mi NW of Mullen; NW 1/4, Sec. 18, T25N, R34W
26	Frontier County, Nebraska	UNSM 1108-48	cranium with partial horn cores	Medicine Creek Dam
27	Red Willow County, Nebraska	UNSM 1112	cranium with horn cores	from gravel pit near McCook
28	Furnas County, Nebraska	UNSM 4-10-95	cranium with partial horn cores	found during construction of Chicago, Burlington and Quincy Railroad, 2 mi E of Cambridge
29	Franklin County, Nebraska	UNSM uncataloged	right horn core	?
30	Clay County, Nebraska	UNSM 4-10-30 ⁶	cranium with partial horn cores	from sand pit on Spring Ranch
31	Cuming County, Nebraska	UNSM uncataloged	cranium with partial horn cores	East Pit, West Point
32	Otoe County, Nebraska	UNSM 20-10-04	cranium with horn cores	from gravel bed ~1' thick, 32' beneath surface, Eugene Munn farm 5 mi S of Nehawka and 15 mi NW of Nebraska City. NW 1/4, Sec. 1, T9N, R13E
33	Gage County, Nebraska	UNSM 22-11-30	cranium with partial horn cores	from coarse gravel, 12' beneath surface, G.O. McClung farm, 4 mi E and 2 mi S of Beatrice
34	Jefferson County, Nebraska	UNSM 15-11-00	partial cranium with partial horn cores	near Endicott
35	Pottawattamie County, Iowa	SUI 107	cranium with horn cores	from loess 12' beneath surface, 130' above Missouri R. at Council Bluffs
36	Wyandotte County, Kansas	KUVP 54004	cranium with partial horn cores	from N bank of Kansas R. NW 1/4, SE 1/4, Sec. 29 T11S, R24E
36	Wyandotte County, Kansas	KUVP 58013	cranium with partial horn cores	from channel of Kansas R. NW 1/4, Sec. 5, T12S, R23E
37	Ellsworth County, Kansas	AMNH 12699	cranium with bases of horn cores	(?)near Wilson ⁷
38	Russell County, Kansas	FHSM 11545	skullcap and partial horn cores	from a sand and gravel quarry along a tributary of Big Creek, 3 mi S and 3 mi E of Gorham, SW 1/4, T14S, R15W

⁶This specimen is a cast of the original in the Hastings Museum, Hastings, Nebraska.⁷This specimen was purchased from Jacob Fowler at Wilson, Kansas, by Charles Sternberg for E.D. Cope. There is no indication that the specimen was found at or near Wilson.

TABLE 4.—Continued.
(Locality/Specimen No. repeated from left half of table for ease of reference.)

Locality No.	Specimen No.	Stratigraphic unit	Geologic age	Principal published description(s)
19	PM 526		found (probably redeposited) in sediments that were probably of Holocene age	McDonald, 1985a (figs. 2-6)
20	DAP 23	Mesa Verde (= Sage Plain) Loess	radiocarbon age: 15,970 ± 155 yr B.P. (SI-6137: on bone)	McDonald, Neusius, and Clay, 1987 (fig. 5)
21	UNSM 5100			Gidley, 1906 (figs. 1-3)
22	Payes collection			unpublished
23	Rice collection			unpublished
24	WHOM 18661		Pleistocene	Pinsof, 1986 (fig. 15)
25	UNSM 39000	(?)Crete Sand and Silt from Terrace 4 fill	Illinoian (Jakway, 1961a,b); (?) post-Illinoian (Kurtén and Anderson, 1980:32)	unpublished
25	UNSM 39001	(?)Crete Sand and Silt from Terrace 4 fill	Illinoian (Jakway, 1961a,b); (?)post-Illinoian (Kurtén and Anderson, 1980:32)	Barbour, 1934 (figs. 173, 174)
26	UNSM 1108-48			unpublished
27	UNSM 1112			Corner, 1977 (fig. 3B)
28	UNSM 4-10-95			Barbour, 1931 (fig. 140)
29	UNSM uncataloged			unpublished
30	UNSM 4-10-30 ⁸	Grand Island Formation	Kansan (Schultz, 1934)	Barbour, 1931 (fig. 144)
31	UNSM uncataloged			unpublished
32	UNSM 20-10-04			Barbour, 1931 (fig. 142)
33	UNSM 22-11-30			Barbour, 1931 (fig. 143)
34	UNSM 15-11-00			Barbour, 1931 (fig. 141)
35	SUI 107			unpublished
36	KUVP 54004			Nelson and Neas, 1980 (fig. 3A)
36	KUVP 58013			Nelson and Neas, 1980 (fig. 4A)
37	AMNH 12699			unpublished
38	FHSM 11545		Late Pleistocene	Nelson and Neas, 1980 (fig. 5B)

⁸This specimen is a cast of the original in the Hastings Museum, Hastings, Nebraska.

TABLE 4.—Records of *Symbos* mapped in Figure 64 (continued).

Locality		Specimen		
No.	Name	No.	Description	Provenience
39	Comanche County, Kansas	FHSM 8138	cranium with partial horn cores	along Salt Fork of Arkansas R., 12 mi S of Coldwater. Either NW 1/4, NW 1/4, T34S, R18W or NE 1/4, NE 1/4, T34S, R19W
40	(?)Muskogee County, Oklahoma	ANSP 12995	cranium with horn cores	reportedly collected by an Indian from a gravelly bluff on the Arkansas R., near Fort Gibson
41	Kaufman County, Texas	SMU-SMP 69127	cranium with bases of horn cores	from shallow fluvial deposit along E side of Little Brushy Creek, ~2.24 km WSW of City Hall, Kaufman
42	West Feliciana Parish, Louisiana	LSUMZ 17814	partial cranium and base of left horn core	from stream sediments along E side of Bayou Sara, near mouth of Gales Creek
43	Bolivar County, Mississippi	WMHS 85.14	cranium with partial horn cores	from gravel bar in Mississippi R. W of Scott
44	Coahoma County, Mississippi	Connaway collection (#284)	partial cranium with bases of horn cores	from gravel bar in Mississippi R. at Friars Point
45	New Madrid County, Missouri	uncataloged (lost)	cranium with partial horn cores	New Madrid, probably from alluvium on floodplain of Mississippi R.; specimen was "ejected by the shock of an earth quake in 1812"
46	Benton County, Missouri	ANSP 12996	partial cranium	(?)along Osage R., near (?)Tackner
46	Benton County, Missouri	ANSP 12997	partial cranium	(?)along Osage R., near (?)Tackner
46	Benton County, Missouri	ANSP 12998	partial cranium	(?)along Osage R., near (?)Tackner
46	Benton County, Missouri	ANSP 12999	partial cranium	(?)along Osage R., near (?)Tackner
46	Benton County, Missouri	ANSP 13000	partial horn core	(?)along Osage R., near (?)Tackner
47	Lafayette County, Missouri	USNM 8361	cranium	from bed of recently abandoned channel of Missouri R., Wellington
48	Mississippi River, Missouri or Illinois	unknown	cranium with bases of horn cores	dredged from Mississippi R. a few mi S of Grand Tower, Illinois
49	Sangamon County, Illinois	Broughton collection	partial cranium with partial right horn core	from gravel pool surrounded by clay ~65' beneath surface, Sangamon Valley Sand and Gravel Company gravel pit 8.5 mi E of Springfield. SW 1/4, Sec. 36, T16N, R4W, Springfield East Quad, USGS 7.5' series
50	Mason County, Illinois	USNM 7800	cranium with horn cores	Manito. Sec. 22, T23N, R6W, Manito Quad, USGS 15' series
51	Kenosha County, Wisconsin	PM 14679	skullcap with partial left horn core	near Wilmot
52	Newaygo County, Michigan	GRPM 12539	cranium with left horn core and dorsal parts of face	from marl pit between Croton Dam and Newaygo
53	Washtenaw County, Michigan	UMMP 3450	skull	from bog, 4' beneath surface of deposit, William J. Schlicht farm, about 0.5 mi NW of Manchester. Near center of NW 1/4, NW 1/4, Sec. 1, T4S, R3E
54	St. Joseph County, Michigan	Yoder collection	skull	recovered by dragline from beneath Marl Lake, on Ray Yoder property, 3 mi SE of White Pigeon. Sec. 17, T8S, R11W
55	Kalamazoo County, Michigan	KPM A2146-61:379	skull, part of right mandible, and all or part of 10 postcranial elements	from marl deposit 0.5 mi S of Scotts. Sec. 25, T3S, R9W
56	La Grange County, Indiana	uncataloged	cranium with horn cores and parts of face	from peat bog on Lester Egli farm, 2.5 mi N of Wolcottville. NE 1/4, NE 1/4, SE 1/4, Sec. 21, T36N, R10E, Wolcottville Quad, USGS 7.5' series
57	St. Joseph County, Indiana	?	?	from 0.6 mi W of North Liberty

TABLE 4.—Continued.
(Locality/Specimen No. repeated from left half of table for ease of reference.)

Locality No.	Specimen No.	Stratigraphic unit	Geologic age	Principal published description(s)
39	FHSM 8138		Late Pleistocene	Nelson and Neas, 1980 (fig. 5A)
40	ANSP 12995			Leidy, 1852b (pl. 3, pl. 4: fig. 1)
41	SMU-SMP 69127		Wisconsinan, probably dating to between 24,000 and 21,000 yrs B.P., perhaps to as much as 75,000 yr B.P.	McDonald, 1985b (figs. 2-5)
42	LSUMZ 17814		probably redeposited from sediments of medial to late Wisconsinan age (-38,000-10,000 yrs B.P.)	McDonald and Corkum, 1987 (fig. 2)
43	WMHS 85.14			unpublished
44	Connaway Collection (#284)			unpublished
45	uncataloged (lost)			De Kay, 1828 (pl. 6: figs. 1-3)
46	ANSP 12996			unpublished
46	ANSP 12997			unpublished
46	ANSP 12998			unpublished
46	ANSP 12999			unpublished
46	ANSP 13000			unpublished
47	USNM 8361			unpublished
48	unknown			Galbreath, 1974 (fig. 1)
49	Broughton collection			Ray, Wills, and Palmquist, 1968
50	USNM 7800			Ray, Wills, and Palmquist, 1968
51	PM 14679			unpublished
52	GRPM 12539			Frankforter, 1966 (pl. 2)
53	UMMP 3450			Case, 1915 (pls. 1, 2)
54	Yoder collection			Semken, Miller, and Stevens, 1964 (pl. 129: fig. 2)
55	KPM A2146-61:379		radiocarbon age: 11,100 ± 400 yr B.P. (M-1402: on bone)	Semken, Miller, and Stevens, 1964 (pl. 129: fig. 3: pl. 130)
56	uncataloged			Rarick and Wayne, 1969 (photographs, pp. 10, 11)
57	?			Lyon, 1926 (fig. 1)

TABLE 4.—Records of *Symbos* mapped in Figure 64 (continued).

Locality		Specimen		
No.	Name	No.	Description	Provenience
58	Kosciusko County, Indiana	CMNH 11744	partial skullcap with partial horn cores	found in ditch being dug in swamp near North Webster
59	Porter County, Indiana	AMNH 14365	skull	from ~7' beneath surface in mixture of sand and clay, ~6 mi E of Hebron
60	Miami County, Indiana	MCHS 170.56	skull	from muck on Homer Fenters farm, S of Macy, Allen Township. S 1/2, Sec. 24 or NE 1/4, Sec. 25, T29N, R3E, Macy Quad, USGS 7.5' series
60	Miami County, Indiana	USNM 8574	skull	Union Township
61	Montgomery County, Indiana	USNM 14428	skull	from fluvial sediments along Mill Creek, on Ingersol farm, Ripley Township
62	Bartholomew County, Indiana	AMNH 13830	cranium	washed from alluvium overlying 10'-20' of glacial gravel along East Fork of White River, near Walesboro
63	(?)Hamilton County, Ohio	UCM 37882	cranium with left horn core	from "local gravels" in or near Cincinnati
64	Hamilton County, Ohio	CM P55	cranium with partial horn cores	from ~10' beneath surface in outwash gravels, SE 1/4, NE 1/4, SE 1/4, Sec. 10, T1N, R1E, Hooven Quad, USGS 7.5' series
65	Warren County, Ohio	CM P54	cranium with partial horn cores	from ~14' beneath surface in gravels, near Little Miami River, S of Foster
66	Bracken County, Kentucky	USNM 23548	cranium with horn cores	from Ohio R. below Augusta
67	Nicholas County, Kentucky	YPM 13133	cranium with bases of horn cores	Blue Licks region
68	Boone County, Kentucky	Be-Cr uncataloged	cranium with right horn core	Big Bone Lick
68	Boone County, Kentucky	MCZ 9117	cranium with partial horn cores	Big Bone Lick (Shaler collection)
69	Spencer County, Kentucky	USNM 1988	partial cranium with partial horn cores	along Salt River
70	Smyth County, Virginia	Space collection (#3144)	cranium with partial horn cores	Saltville Valley
70	Smyth County, Virginia	Space collection (#3145)	cranium with partial horn cores	Saltville Valley
70	Smyth County, Virginia	USNM 23577	cranium with partial horn cores	Saltville Valley
71	Continental Shelf off New Jersey	PU 16340	partial left horn core and frontal	Continental Shelf, 40 mi SE of Atlantic City

distributed in time and space; they do not cluster in a biologically or taxonomically meaningful way. At present, then, we consider the autochthonous North American musk oxen to be monotypic, consisting only of *Bootherium bombifrons*.

Bootherium bombifrons is the largest known Pleistocene musk ox of North America—heavier, longer limbed, and proportionately shorter (craniocaudally) than *Ovibos moschatus* and, probably, *Praeovibos* spp. The degree of sexual dimorphism appears to have been relatively great within this species, but a more nearly definitive assessment of this condition must await the comparative study of postcranial specimens representing both sexes. The skull of *B. bombifrons* is relatively longer and deeper than that of *Ovibos*; the dorsal half of the cranium is narrow relative to the ventral half; and the

orbits protrude little relative to those of *Ovibos* and *Praeovibos*. The horn cores of males are longer and deflected downward more than are those of females. The bases of the horn sheaths extended over the dorsal surface of the cranium and fused at the midline in males, but probably extended only slightly over the dorsal surface of the cranium, if at all, in females. Technical descriptions of the cranium of males (given as *Bootherium cavifrons* or *Symbos cavifrons*) have been presented by Leidy (1852b) and Semken, Miller, and Stevens (1964); the female skull (as *Bootherium bombifrons*) has been most thoroughly described by Leidy (1852b). Technical descriptions of parts of the adult male postcranial skeleton have been provided by Semken, Miller and Stevens (1964), McDonald and Bartlett (1983), and McDonald, Neusius, and Clay (1987).

TABLE 4.—Records of *Symbos* mapped in Figure 64 (continued).
(Locality/Specimen No. repeated from left half of table for ease of reference.)

Locality No.	Specimen No.	Stratigraphic unit	Geologic age	Principal published description(s)
58	CMNH 11744			unpublished
59	AMNH 14365			Hay, 1912 (figs. 49, 50)
60	MCHS 170.56			Richards and Wepler, 1985 (fig. 1)
60	USNM 8574			unpublished
61	USNM 14428			Lyon and Hall, 1937 (pls. 1, 2)
62	AMNH 13830			unpublished
63	UCM 37882			McDonald and Davis, in press (fig. 2)
64	CM P55		Wisconsinan	McDonald and Davis, in press (fig. 3)
65	CM P54		Wisconsinan	Anonymous, 1965:31 (photo); McDonald and Davis, in press (fig. 4)
66	USNM 23548			unpublished
67	YPM 13133			unpublished
68	Be-Cr uncataloged		(?)Late Wisconsinan	unpublished
68	MCZ 9117		(?)Late Wisconsinan	unpublished
69	USNM 1988			unpublished
70	Space collection (#3144)			unpublished
70	Space collection (#3145)			unpublished
70	USNM 23577			unpublished
71	PU 16340			Parris, 1983 (fig. 4)

Systematic Hierarchy

Class MAMMALIA Linnaeus, 1758

Order ARTIODACTYLA Owen, 1848

Family BOVIDAE Gray, 1821

Genus *Bootherium* (Harlan, 1825)

Bootherium bombifrons (Harlan, 1825)

"A head very different from any now known here. . . . An animal nearly allied to the bison," Wistar, 1818:379-380.

Bos bombifrons Harlan, 1825:271.

Ovibos bombifrons.—Leidy, 1852a:71.

Ovibos cavifrons Leidy, 1852a:71. [New synonymy.]

Bootherium cavifrons (Leidy).—Leidy, 1852b:12. [New synonymy.]

Bootherium bombifrons.—Leidy, 1852b:17.

Ovibos priscus Rüttimeyer, 1865:328.

Bison appalachicolus Rhoads, 1895:248.

Ovibos (Bootherium?) appalachicolus Rhoads, 1897:492.

Scaphoceros tyrrelli Osgood, 1905a:173. [New synonymy.]

Scaphoceros cavifrons.—Osgood, 1905a:182. [New synonymy.]

Symbos tyrrelli.—Osgood, 1905b:224 [misspelling]. [New synonymy.]

Symbos cavifrons.—Osgood, 1905b:224. [New synonymy.]

Symbos tyrrelli.—Gidley, 1906:682. [New synonymy.]

Liops zuniensis Gidley, 1906:166.

Gidleya zuniensis.—Cossmann, 1907:64. [New synonymy.]

Bootherium sargenti Gidley, 1908:683.

Lissops zuniensis (Gidley, 1908:684). [New synonymy.]

Symbos australis Brown, 1908:203.

Bootherium nivicolens Hay, 1915:523.

Symbols promptus? Hay, 1920:109 [misspelling]. [New synonymy.]

Symbos promptus Hay, 1920:115. [New synonymy.]

Symbos convexifrons Barbour, 1934:295.

?*Ovibos giganteus* Frick, 1937:556. [New synonymy.]

?*Ovibos zuniensis*.—Frick, 1937:557. [New synonymy.]

Bootherium brazosis Hesse, 1942:78.

Bootherium appalachicolus.—Ray, 1966:4.

Symbos giganteus.—McDonald and Bartlett, 1983:454. [New synonymy.]

?*Ovibos australis*.—McDonald and Bartlett, 1983:458.

ORIGINAL DESCRIPTION.—C. Wistar provided an informal description of what later became the holotype for *Bootherium bombifrons* in 1818 in the paper "An Account of Two Heads Found in the Morass, Called the Big Bone Lick, and Presented to the Society, by Mr. Jefferson" (Wistar, 1818). The scientific name *Bos* (= *Bootherium*) *bombifrons* was created by Richard Harlan in 1825 in *Fauna Americana* (Harlan, 1825:271).

TYPE SPECIMEN AND REPOSITORY.—*Bootherium bombifrons* is monotypic. The holotype is ANSP 994, a cranium with the greater parts of both horn cores. This specimen is located in the Department of Geology, Academy of Natural Sciences, Philadelphia, Pennsylvania.

TYPE LOCALITY.—Big Bone Lick, Boone County, Kentucky.

DISTRIBUTION.—*Bootherium bombifrons* was the most widespread of the musk oxen to inhabit North America during the Quaternary; the other taxa were *Praeovibos* spp. and *Ovibos moschatus*. Of these taxa, only *Bootherium bombifrons* was autochthonous to North America.

Bootherium bombifrons is known from about the Irvingtonian–Rancholabrean boundary (or, from ~500,000 yr B.P.) to about 10,000 yr B.P. Remains of this species have been recovered from throughout Anglo-America except the north-eastern quarter, and the extreme southwestern and southeastern corners, of the region.

DIAGNOSIS.—Horn cores subcircular to semielliptical in cross section at the base—ventral surface semicircular in rostrocaudal cross section, dorsal surface semicircular through flat to concave in rostrocaudal cross section. Horn cores emanate from lateral edge of dorsal surface of cranium, approximately midway between occipital and orbits. Horn cores emanate in lateral direction, then trend downward, forward, and outward becoming more nearly round distally. Tips terminate rostral to level of bases of horn cores, near or at level of orbits. Diameter of base of horn core along rostrocaudal axis ranges from 61 mm to 146 mm (N = 121). Length of horn core, base (burr line) to tip along dorsal surface, ranges from 210 mm to >400 mm (N = 16).

Dorsal surface of cranium flexed; point of flexion near parietofrontal juncture. Orbits situated below level of dorsal surface of frontals, and extend but little beyond postorbital margin of frontals. Mean postorbital width:orbital width ratio is .64 (N = 33). Line of frontoparietotemporal sutures is typically relatively straight and oriented horizontally. Nasofrontal suture line shaped like flat-bottomed V. Occipital surface about as deep as wide; silhouette of occipital surface is bell-shaped.

(In ventral view, basioccipital typically is in shape of pentagonal shield with caudal half of lateral edges lying nearly parallel to each other and the midline, and the rostral half of lateral edges converging rostrally toward the midline. A ridge

of bone oriented rostrocaudally typically occurs over part of the midline. The shape and surface configuration of the basioccipital bone is often considered to be diagnostic, but specimens of *Bootherium bombifrons* are known in which the basioccipital is indistinguishable from the same element in typical specimens of *Ovibos moschatus*. Conversely, specimens of *Ovibos moschatus* are known that possess basioccipital bones indistinguishable from the same element in specimens of *Bootherium bombifrons*.)

Superior molars typically are without (1) cementum, (2) accessory style or rib external to enamel wall between protocone-hypocone, and (3) accessory internal fossette within dentine field at juncture of protocone-hypocone. (Exceptions to 1 and 2 are rare, and to 3 are uncommon.)

DIFFERENTIAL DIAGNOSIS OF MALES.—Horn cores semielliptical in cross section at base—dorsal surface flat to concave in rostrocaudal cross section. Bases of horn cores fused to both frontal and parietal bones, and burr line typically blurred by deposits of secondary bone. Diameter of base of horn core along rostrocaudal axis ranges from 86 mm to 146 mm (N = 94; \bar{x} = 109 mm). Length of horn core, base (burr line) to tip along dorsal surface, ranges from 206 mm to >400 mm (N = 16; \bar{x} = 266 mm—this mean is based on a range of 206–369 mm; the longest horn cores known are incomplete, with remaining sections being about 400 mm in length). Dorsal surface of cranium typically covered with deposits of secondary bone (both dense and exostotic bone) from about level of orbits to about level of occiput.

DIFFERENTIAL DIAGNOSIS OF FEMALES.—Horn cores subrounded to semielliptical in cross section at base—dorsal surface semicircular to flat in rostrocaudal cross section at base. Bases of horn cores fused with frontals only, and preserve distinct burr line. Diameter of horn core at base along rostrocaudal axis ranges from 61 mm to 96 mm (N = 27; \bar{x} = 74 mm). Length of horn core, base (burr line) to tip along dorsal surface, ranges from 210 mm to 356 mm (N = 5; \bar{x} = 263 mm). Dorsal surface of cranium with little or no deposits of secondary bone. If present, secondary bone is more extensive at level of rostral edge than at medial or caudal edge of base of horn cores.

DIFFERENTIAL DIAGNOSIS OF OTHER NORTH AMERICAN MUSK OXEN.—Horn cores of *Ovibos moschatus* compressed dorsoventrally; elliptical to semielliptical in cross section at base along rostrocaudal axis; emanate in ventro-lateral direction; and are straight. Tip of horn core terminates below, or just rostral to, level of base of horn core. Diameter of base of horn core along rostrocaudal axis ranges from 62 mm to 204 mm (N = 41). Length of horn core, base (burr line) to tip along dorsal surface, ranges from 180 mm to 311 mm (N = 16). Dorsal surface of cranium not markedly flexed between occiput and level of orbits; secondary bone typically does not coalesce over midline. Tubular orbits extend relatively far lateral to postorbital edges of frontal bones. Mean postorbital width:orbital width ratio is .54 (N = 34). Nasofrontal suture line shaped like the letter W. Silhouette of occipital surface is semielliptical;

transverse width typically is greater than dorsoventral depth. Superior molars typically (1) lack cementum, (2) contain accessory rib between protocone-hypocone, and (3) contain circular accessory enamel eyelet within dentine field near juncture of protocone-hypocone.

Horn cores of *Praeovibos* spp. are triangular to subelliptical (with long axis oriented dorsocaudally-ventrorostrally) in cross section at the base. Base of horn core is fused with dorsolateral angle of cranium, and rises above dorsal surface of cranium. Horn cores emanate in a ventrolateral and rostral direction;

straight or curved slightly rostral; tips are below, or rostral to, level of base of horn core. Little or no secondary bone is deposited on dorsal surface of cranium medial to base of horn core. Frontoparietal sinuses are shallow. Dorsal surface of cranium is not markedly flexed between occiput and level of orbits. Orbits are markedly tubular and extend far lateral to postorbital edges of frontals. The postorbital width:orbital width ratio in the only specimen for which measurements are available is .45.

Appendix I

Abbreviations for Institutional, Departmental, and Private Collections Used in This Study

<i>Institutional Collections</i>			
A	Frick Collection (field numbers), Department of Vertebrate Paleontology, American Museum of Natural History, New York, New York	MCHS	Miami County (Indiana) Historical Society Museum, Courthouse, Peru, Indiana
AMNH	American Museum of Natural History, New York, New York	MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
ANSP	Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania	NMC	National Museum of Natural Sciences, Ottawa, Ontario
BC	Behringer-Crawford Memorial Museum, Covington, Kentucky	PM	Field Museum of Natural History, Chicago, Illinois
BCPM	British Columbia Provincial Museum, Victoria, British Columbia	PU	Princeton University Museum of Natural History, Princeton University, Princeton, New Jersey (vertebrate paleontology collections now at Peabody Museum of Natural History, Yale University, New Haven, Connecticut)
BLM	Fairbanks District, Bureau of Land Management, Fairbanks, Alaska	ROM	Royal Ontario Museum, Toronto, Ontario
BM(NH)	British Museum (Natural History), London, England	SMNH	Museum of Natural History, Regina, Saskatchewan
BYUG	Department of Geology Museum, Brigham Young University, Provo, Utah	SMU-SMP	Shuler Museum of Paleontology, Department of Geology, Southern Methodist University, Dallas, Texas
CM	Cincinnati Museum of Natural History, Cincinnati, Ohio	SUI	Museum of Natural History, University of Iowa, Iowa City, Iowa
CMNH	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania	TAMC	Texas A&M College (now University) collections (vertebrate paleontology collections now at Texas Memorial Museum, University of Texas, Austin, Texas)
DAP	Anasazi Heritage Museum, Cortez, Colorado	UAI	University of Alberta, Edmonton, Alberta
F:AM	Frick Collection (cataloged specimens), Department of Vertebrate Paleontology, American Museum of Natural History, New York, New York	UAF	Otto Geist Museum, University of Alaska, Fairbanks, Alaska
FHSM	Sternberg Memorial Museum, Fort Hays State University, Hays, Kansas	UCM	Department of Geology Museum, University of Cincinnati, Cincinnati, Ohio
GMUS	Geology Museum, University of Saskatchewan, Saskatoon, Saskatchewan	UCMP	Museum of Paleontology, University of California, Berkeley, California
GRPM	Grand Rapids Public Museum, Grand Rapids, Michigan	UMMP	Museum of Paleontology, University of Michigan, Ann Arbor, Michigan
HM	Haslar Museum, England	UNSM	University of Nebraska State Museum, University of Nebraska, Lincoln, Nebraska
IMNH	Idaho Museum of Natural History, Idaho State University, Pocatello, Idaho	USNM	former United States National Museum, collections deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.
KPM	Kalamazoo Public Museum, Kalamazoo, Michigan	UUVP	Utah Museum of Natural History, University of Utah, Salt Lake City, Utah
KUMNH	Museum of Natural History, University of Kansas, Lawrence, Kansas	UVP	Antiquities Section, Division of State History, Salt Lake City, Utah
LACM	Natural History Museum of Los Angeles County, Los Angeles, California		
LSUMZ	Museum of Zoology, Louisiana State University, Baton Rouge, Louisiana		

WHOM	W.H. Over State Museum, Vermillion, South Dakota	Connaway	John Connaway, Archaeological Survey, Mississippi Department of Archives and History, Clarksdale, Mississippi (1988)
WMHS	Winterville Mounds Historic Site, Greenville, Mississippi	McKay	McKay Collection, Archaeological Survey, Mississippi Department of Archives and History, Clarksdale, Mississippi (1988)
WSU	Laboratory of Anthropology, Washington State University, Pullman, Washington	Payes	Mitchell L. Payes, Tucson, Arizona (1974)
YPM	Peabody Museum of Natural History, Yale University, New Haven, Connecticut	Rice	Don Rice, Tuthill, South Dakota (1985)
	<i>Private Collections</i>	Space	Ralph Space, Sussex, New Jersey (1984)
	(Most recent date of record in parentheses)	Stephens	Garland S. Stephens, Wytheville, Virginia (1965)
Broughton	Robert D. Broughton, Springfield, Illinois (1967)	Widel	Phillip Widel, Blackwater, Missouri (1967)
		Yoder	Ray Yoder, White Pigeon, Michigan (1964)

Appendix II

Chronology of Nominal Species Referable to Musk Oxen in the Genera *Bootherium*, *Symbos*, and *Gidleya*

1. *Bos* (= *Bootherium*, *Ovibos*) *bombifrons*
Big Bone Lick, Kentucky
ANSP 994; cranium with partial horn cores
Harlan, 1825
Stands as senior name in the group.
2. *Bootherium* (= *Ovibos*, *Scaphoceros*, *Symbos*) *cavifrons*
Near Fort Gibson, Oklahoma
ANSP 12995; cranium with partial horn cores
Leidy, 1852b
Referred, this paper, to *B. bombifrons*.
3. *Ovibos maximus*
Eschscholtz Bay, Alaska
HM 90/2; abraded axis
Richardson, 1852
Stands; generic identity uncertain, but probably *Ovibos*.
4. *Bison* (= *Bootherium*, *Ovibos*) *appalachicolus*
Durham Cave, Bucks County, Pennsylvania
ANSP 29; cranial and right horn core fragment
Rhoads, 1895
Referred to *B. sargenti* by Ray, 1966a.
5. *Scaphoceros* (= *Symbos*) *tyrrelli*
Bonanza Creek, Yukon Territory
USNM 2555; nearly complete skull
Osgood, 1905a
Referred, this paper, to *B. bombifrons*.
6. *Liops* (= *Gidleya*, *Lissops*, *Ovibos*) *zuniensis*
Black Rocks, New Mexico
USNM 5100; extensively abraded cranium with partial
horn cores
Gidley, 1906
Referred, this paper, to *B. bombifrons*.
7. *Bootherium sargenti*
Moorland Swamp, Michigan
GRPM 11-423-3101; skull cap with horn cores
Gidley, 1908
Referred to *S. cavifrons* by Allen, 1913; returned to
Bootherium by Hay, 1914; referred, this paper, to *B.*
bombifrons.
8. *Symbos* (= ?*Ovibos*) *australis*
Conard Fissure, Arkansas
AMNH 11828; 3 molar teeth
Brown, 1908
Referred to *S. cavifrons* by Allen, 1913.
9. *Bootherium nivicolens*
Eschscholtz Bay, Alaska
USNM 2324; skullcap with horn cores
Hay, 1915
Referred to *B. sargenti* by Harington, 1977.
10. *Symbos promptus*
Afton, Oklahoma
USNM 9120; upper left third molar
Hay, 1920
Referred, this paper, to *B. bombifrons*.
11. *Symbos convexifrons*
Cherry County, Nebraska
UNSM 39001; skullcap with right horn core
Barbour, 1934
Referred to *S. cavifrons* by Jakway, 1961b.
12. *Ovibos* (= *Symbos*) *giganteus*
Near Fairbanks, Alaska
AMNH F:AM 30498; right humerus
Frick, 1937
Referred, this paper, to *B. bombifrons*.
13. *Bootherium brazosis*
Brazos River, border of Brazos County, Texas
TAMC 2553; partial cranium with partial horn cores
Hesse, 1942
Referred to *B. sargenti* by Ray, 1966b.

Appendix III

Radiocarbon Dates on *Bootherium* and *Symbos* Specimens

Bootherium

1. a. A-293-5268
Fairbanks Creek, Alaska
Hair
SI-454
17,210 ± 500 yr B.P.
Péwé, 1975; McDonald, 1984b
- b. A-293-5268
Fairbanks Creek, Alaska
Tissue from beneath scalp
SI-455
24,140 ± 2,200 yr B.P.
Péwé, 1975; McDonald, 1984b
2. F:AM 30508
Creek near Fairbanks
Horn sheath
SI-292
22,540 ± 900 yr B.P.
Péwé, 1975

Symbos

1. A-204-4254
Little Eldorado Creek, Alaska
Fecal material
SI-291
>40,000 yr B.P.
Péwé, 1975
2. F:AM 33124
Upper Cleary Creek, Alaska
Horn sheath
SI-850
25,090 ± 1070 yr B.P.
Péwé, 1975
3. F:AM A-651-3006
Dome Creek, Alaska
Horn sheath

- SI-851
17,695 ± 445 yr B.P.
Péwé, 1975
4. NMC 25892
Lost Chicken Creek, Alaska
Bone
I-10649
20,500 ± 390 yr B.P.
Harrington, 1980
5. DAP 23
Grass Mesa, Colorado
Bone
SI-6137
15,970 ± 155 yr B.P.
McDonald, Neusius, and Clay, 1987
6. KPM A2146-61:379
Scotts, Michigan
Bone
M-1402
11,100 ± 400 yr B.P.
Semken, Miller, and Stevens, 1964
7. UMMP 34124
Climax, Michigan
Bone
M-639
13,200 ± 600 yr B.P.
Hibbard and Hinds, 1960
Notes: This number was given to three vertebrae (atlas, axis, and 3rd cervical) of a large musk ox that was determined to be *Symbos cavifrons* on the basis of the large atlas fitting the *Symbos cavifrons* skull (UMMP-3450) from the Schlecht farm in Washtenaw County, Michigan. The atlas was considered to be too large for *Ovibos* and *Bootherium* (Hibbard and Hinds, 1960).

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