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NEW RECORDS OF LATE PLEISTOCENE UNGULATES (*BOOTHERIUM* AND *TAPIRUS*) FROM NORTH CENTRAL TEXAS

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ABSTRACT

Important specimens of the extinct muskox, *Bootherium bombifrons*, and tapir, *Tapirus veroensis*, representing new occurrences are reported from the late Pleistocene of broader north central Texas. Both taxa, the *Bootherium* in particular, are relatively poorly known from Texas. The muskox, a mature male, consists of a fairly complete cranium with a separate maxillary block. A detailed description of the cranium is provided, expanding our knowledge of *Bootherium* because most reports focus on their geographic and geologic context. The large size of the tapir suggests a re-examination of the species names applied to late Pleistocene (Rancholabrean) tapirs from Texas. Based upon its context near, but stratigraphically below, the Aubrey Clovis site, the tapir also implies a change in fauna and paleoenvironment before human occupation.

INTRODUCTION

Late Pleistocene mammalian faunas in northern and central Texas are typically dominated, in terms of number of specimens, by large ungulates and proboscideans, especially equids, *Bison*, mammoth and mastodon. We report the discovery of new and significant specimens of two of the less common ungulates in these faunas, a muskox (*Bootherium bombifrons*), represented by much of a skull, and a nearly complete tapir dentary (*Tapirus veroensis*).

Although the two specimens are from unrelated localities in broader north central Texas (Figure 1), their description and study are important contributions to our knowledge of late Pleistocene faunas of Texas and to the understanding of these species. The *B. bombifrons* specimen is a relatively complete skull of a large, older male. Although muskox remains are reported from other localities in Texas and elsewhere, those studies usually focused on geological context and provided only brief descriptions of the specimens. We provide a detailed description of the most complete muskox skull reported from Texas.

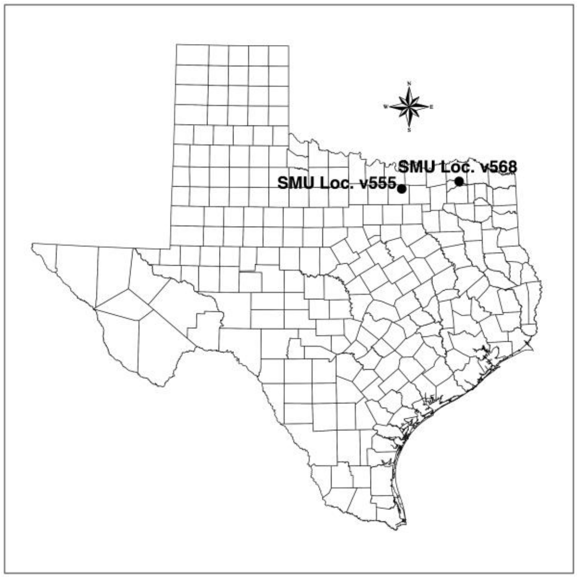

FIGURE 1. County outline map of Texas showing the localities for the *Bootherium bombifrons* (SMU 77689; SMU Loc. v568) and *Tapirus veroensis* (SMU 77673; SMU Loc. v555) specimens. Base map from Texas Parks and Wildlife, 2011, https://tpwd.texas.gov/gis/maps /images/texas-counties-black-text/view.

Despite its incompleteness, the *Tapirus* dentary represents one of the better specimens of tapir known from north central Texas. The size of the dentary and teeth calls into question the species allocation of large late Pleistocene (Rancholabrean) tapirs from this area (Slaughter, 1966; Lundelius and Slaughter, 1976). It is significant also in its occurrence just adjacent to the Aubrey Clovis archaeological site, Denton County, Texas (Ferring, 2001). The Aubrey site is noteworthy because the cultural occupation is bracketed by radiocarbon dates that are older than classically defined Clovis sites (Ferring, 2001; and see Haynes et al., 2007). It is sometimes considered a 'pre-Clovis' or 'proto-Clovis' complex (Morrow et al., 2012; Haynes, 2015). The tapir specimen was found at a level that is apparently lower in the local late Pleistocene terrace fill than the Aubrey human occupation, and it suggests a change in the fauna and paleoenvironment.

Institutional Abbreviations—HMS, Houston Museum of Natural Science, Houston, Texas; SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas; TMM, Texas Vertebrate Paleontology Collections, Jackson School Museum of Earth History, University of Texas at Austin, Austin, Texas; TMM-ETSU, see TMM above, formerly accessioned at East Texas State University, Commerce, Texas; TMM-TAMU, see TMM above, formerly accessioned at Texas A&M University, College Station, Texas.

SYSTEMATIC PALEONTOLOGY

Order Artiodactyla Owen, 1848
Family Bovidae Gray, 1821
Subfamily Caprinae Gray, 1821
Tribe Ovibovini (Gill, 1872) Simpson, 1945
Bootherium bombifrons (Harlan, 1825)
(Figures 2–6)

Referred Material—SMU 77689, an approximately 75% complete cranium with a separate block formed primarily by the maxillae and palatine bones including part of the left facial region, as well as the left M1–3 (alveoli for P2–P4) and right P4–M3 (alveoli for P2–P3).

Locality and Geologic Age—SMU Loc. v568, Lake Creek East, Sulphur River Formation, Lamar County, Texas. Latest Pleistocene based on known faunas from the Sulphur River Formation (e.g., Ben Franklin fauna; Slaughter and Hoover, 1963).

Description—The cranium is well preserved, although the relatively more delicate structures and some processes, e.g., paraoccipital processes, are broken. There is no evidence of fluvial transport of the specimen. The anterior end of the snout is missing, but some of the roof of the nasal cavity is present a little anterior to the nasofrontal sutures. The dorsal and medial aspects of the orbits are preserved, as is the cranial base and occipital region. Horn cores are present on both sides: the left is essentially complete (except for its distal tip) and the right about 60% complete. There are no dentaries or postcrania associated with the cranium.

Anatomical terminology for *Bootherium* is from published records of Pleistocene muskoxen, and also is modified from that for bovines in Pasquini et al. (1995), Liebich and König (2007) and Habel and Budras (2011). Measurements of the dentition of SMU 77689 are in Table 1; those of the cranium of SMU 77689 and comparative specimens from Texas are in Table 2. Measurements used are adapted from Stefaniak et al. (2019:fig. 1), and also from McDonald (1985:table 1) and McDonald and Ray (1989:68).

Maxillary Block (Fig. 2)—The ventral surface of the maxillary block includes the entire length of the maxillae. The premaxillae are not preserved, and there is no evidence of the suture between them and the maxillae. Some of the posterolateral border of the palatine fissure is present on the left side. A distinctive gently curving crest (concave laterally) extends from the alveolus of P1 toward the premaxilla. The left and right maxillae and horizontal plates of the palatines form a gently concave surface with the suture between left and right sides slightly elevated. The palatomaxillary suture is at the anterior end of M3. Major palatine foramina are at the anterior end of the palatines. A distinctive minor palatine foramen is present posterior to the major on the left side. The bone forming the ventral border of the choanae is preserved, as is that forming the anterior border of the orbits. The maxillae posterolateral to M3 on both sides are broken. The most anteroventral aspect of the pterygopalatine fossae are present, and at their most ventral portion, the caudal palatine foramina.

On the left side, some of the lateral extent of the maxilla is preserved, including the infraorbital foramen (dorsal to P2), and the facial crest extending from the facial tubercle. Most of what remains of the lateral part of the maxilla on the right side is crushed. The dorsum of the block exposes the floor of the nasal cavity, formed by the maxillae and palatine bones. Palatine processes of the premaxillae and the vomer are not preserved.

Ventrolateral Views of the Skull (Figures 3, 4)—On the main (cranial) skull block, the lacrimal and frontal contributions to the orbits are preserved. The zygomatic components are lacking. The bases of the maxillae are anterior and the bases of the basisphenoids medial. Anteriorly, the roof of the nasal cavity is exposed. The openings of the nasolacrimal canals are preserved (Figure 4). The temporal fossa includes a deep slightly sinuous component between the suture between the temporal and parietal bones and the base of the horn core. This groove extends anteroposteriorly from the orbit to the dorsal edge of the mastoid process. An oval ethmoid foramen is present on the ventromedial wall of the orbit. Within the orbit, the supraorbital foramen is a large circular opening.

The bases of the pterygoid processes are preserved on either side of the basisphenoid. Damage to the body of the basisphenoid has resulted in a large cavitation within it. The basisphenoid is at an angle relative to the basioccipital: these two bones are not in the same horizontal plane. The morphology of the ventral surface of the basioccipital is as is typical for *B. bombifrons* (McDonald and Ray, 1989: 68): "…in

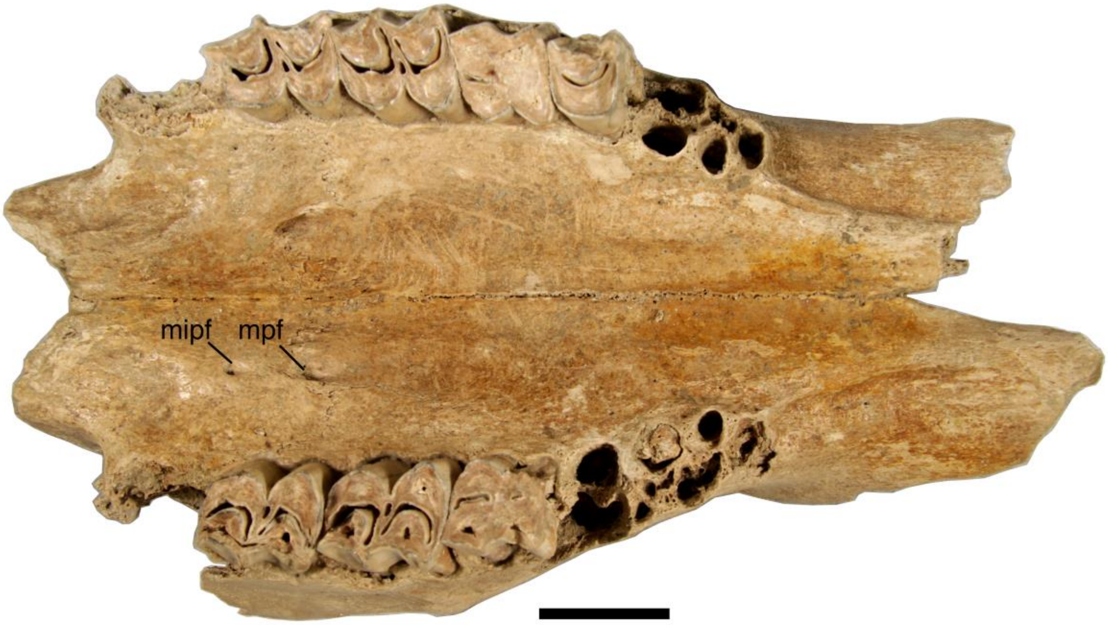

FIGURE 2. Ventral view of maxillary block of *Bootherium bombifrons*, SMU 77689, from Lamar County, Texas. Includes left M1–3 (alveoli for P2–P4) and right P4–M3 (alveoli for P2–P3). **Abbreviations**: **mipf**, minor palatine foramen; **mpf**, major palatine foramen. Scale equals 4 cm.

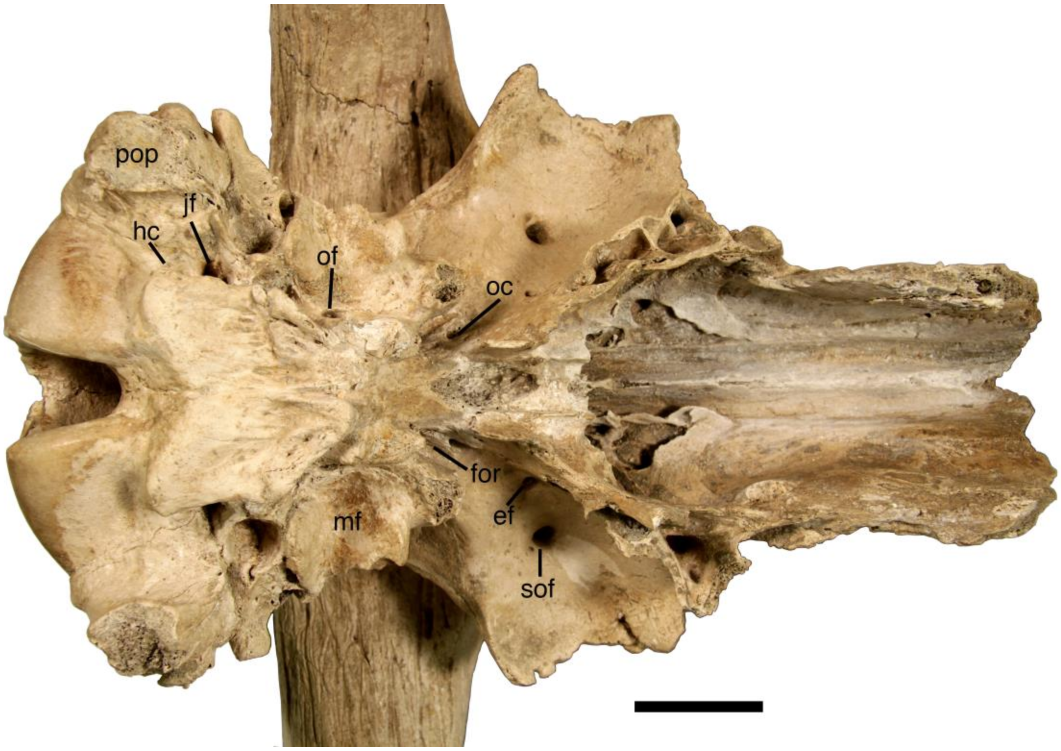

FIGURE 3. Ventral view of the cranium of *Bootherium bombifrons*, SMU 77689, from Lamar County, Texas. **Abbreviations**: **ef**, ethmoid foramen; **for**, foramen orbitorotundum; **hc**, hypoglossal canal; **jf**, jugular foramen; **mf**, mandibular fossa; **oc**, optic canal; **of**, oval foramen; **pop**, paraoccipital process; **sof**, supraorbital foramen. Scale equals 5 cm.

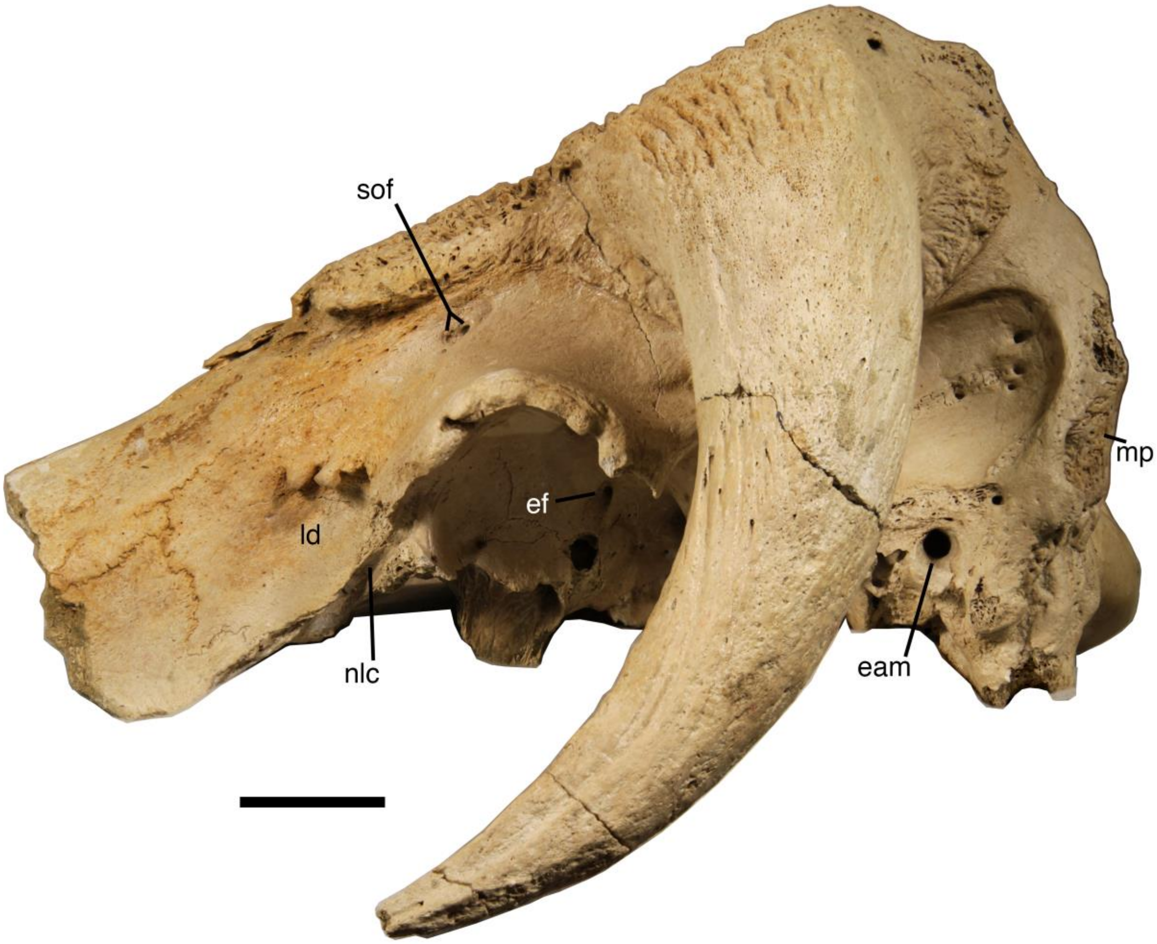

FIGURE 4. Left lateral view of the cranium of *Bootherium bombifrons*, SMU 77689, from Lamar County, Texas. **Abbreviations**: **eam**, external auditory meatus**;** **ef**, ethmoid foramen; **ld**, lacrimal depression; **mp**, mastoid process; **nlc**, nasolacrimal canal; **sof**, supraorbital foramen**.** Scale equals 5 cm.

the shape of pentagonal shield with caudal half of lateral edges lying nearly parallel to each other and the midline, and rostral half of lateral edges converging rostrally toward the midline. A ridge of bone oriented rostrocaudally typically occurs over part of the midline." Dorsolateral to the basisphenoid is the optic canal, and posterior to it the foramen orbitorotundum. Within the most posterior aspect of the basisphenoid, near its contact with the oblique edge of the basioccipital, is the large oval foramen. Just posterolateral to the oval foramen is a smaller foramen. Lateral to the oval foramen, the medial aspect of the mandibular fossa is preserved on both sides. The mandibular fossa is at an angle of 90° to the retroarticular process. The concavities housing the styloid processes are present bilaterally, but in both, the actual processes are not preserved. The tympanic bullae are indistinct, with the middle ear components encased in heavy bone. The external auditory meatus is distinctive on both sides (seen best on Figure 4). Posteromedial to the concavity for the styloid process is the large jugular foramen. The stylomastoid foramen (obscured on the left side; not observable in the Figures) is just anterior to the base of the paraoccipital process. The smaller hypoglossal canals (both obscured by matrix) are posterior to the jugular foramina.

Dorsolateral Views of the Skull (Figures 4, 5)—In lateral view, the dorsal surface of the cranium is flexed at about the expected location of the frontoparietal suture. The posterior approximately 110 mm of the nasal bones are preserved to the indistinct nasofrontal sutures. The lateral sides of the skull preserve some of the maxillae and lacrimal bones. On the left side, there are a couple strong spurs of bone protruding into the distinct lacrimal depression

TABLE 1. Measurements (in mm) of the upper dentition of SMU 77689, a mature male *Bootherium bombifrons* from Lamar County, Texas.

Tooth position	Side	Measurement
P4L	Right	19.4
P4W	Right	27.8
M1L	Right	28.5
M1W	Right	27.5
M1L	Left	26.8
M1W	Left	27.4
M2L	Right	34.1
M2W	Right	30.4
M2L	Left	33.5
M2W	Left	29.6
M3L	Right	36.6
M3W	Right	27.8
M3L	Left	34.3*
M3W	Left	28.3

*Low estimate because is missing the distal spur.

(larmier), which housed the preorbital gland. The lateral walls of the nasolacrimal canals are not preserved. Two supraorbital foramina are present on each side, about 65 mm medial to the orbital rim, and just lateral to the edge of the dorsal exostosis. The orbital rim protrudes significantly laterally. The area between the horn cores is deeply excavated (at its maximum about 44 mm deep) and covered with heavily developed exostosis that obscures the frontoparietal suture. The exostosis extends from about the level of the nasofrontal suture to about 31 mm anterior to the external occipital protuberance. The bases of the horn cores originate from the frontal and parietal bones, extend laterally, and then curve downward, forward and outward.

Occipital View of the Skull (Figure 6)—The occipital region is essentially complete. Most dorsal is a continuation of the parietal bones with heavy exostosis. There are no observable sutures demarcating the interparietal bone. The occipital bone is heavy and rugose, suggesting extensive muscle attachment. A prominent nuchal line forms the dorsal border of the supraoccipital component of the occipital bone. There is some loss of bone from the distinct external occipital protuberance. Deep roughly almond-shaped indentations extend laterally from the external occipital protuberance. The occipital condyles are roughly triangular in outline and form much of the border of the oval foramen magnum. Openings for the hypoglossal canals are observable within the foramen magnum. Only the bases of the massive paraoccipital processes are preserved. The mastoid processes are highly rugose elongate masses along the lateral borders of the occiput.

Discussion—SMU 77689 is assigned to *B. bombifrons* based on the possession of several diagnostic characters from McDonald and Ray's (1989) extensive study of indigenous North American muskoxen. These include the morphology of the horn cores: 1) semi-elliptical at the base with the ventral surface semicircular in cross section and the dorsal surface flat (and then distally more concave in cross section); 2) horn cores originating from the lateral edge of the dorsum of the cranium about midway between the orbits and occipital region; 3) horn cores extending laterally, then downward, forward and outward, with their tips rounded distally; and 4) tips terminating anterior to the level of the bases of the horn cores (SMU 77689 terminating just anterior to the anterior end of the orbit). Other diagnostic characters that can be observed on SMU 77689 include: 1) flexed dorsal surface of the cranium; 2) orbits below dorsal surface of the frontals; 3) occipital surface bell-shaped and about as deep as wide; 4) upper molars lacking cementum; and 5) upper molars lacking accessory styles or ribs external to the enamel wall between the protocone-hypocone. The morphology of the basioccipital of SMU 77689 is as is typical (although not exclusively diagnostic) for *B. bombifrons* (see above; McDonald and Ray, 1989). On the upper molars, an accessory internal fossette is found within the dentine at the junction of the protocone and hypocone. McDonald and Ray (1989) noted that presence of this fossette is uncommon in *B. bombifrons*. McDonald and Ray (1989) provided a range of measurements for some parts of the cranium that they considered to be diagnostic for *B. bombifrons*. These measurements include: 1) diameter of base of horn core along the rostrocaudal axis (male $\bar{x}$ = 109 mm, OR = 86 – 146 mm, N = 94 and female $\bar{x}$ = 74 mm, OR = 61 – 96 mm, N = 74); 2) length of horn core from base (burr line) to tip along the dorsal surface (male $\bar{x}$ = 266 mm, OR = 206 – >400 mm, N = 16 and female $\bar{x}$ = 263 mm, OR = 210 – 356 mm, N = 5); and 3) mean postorbital width:orbital width ratio. Measurements of SMU 77689 for 1) (115 mm) fall within the range given above for male *B. bombifrons*, and for 2) (432 mm), at the uppermost end of the range for males. The incompleteness of the orbits of SMU 77689 may explain why the postorbital width:orbital width ratio for SMU 77689 (1.9) is 3x the mean given for *B. bombifrons* (0.64, N = 33).

In addition to the two measurements above, McDonald and Ray (1989) suggested other characters useful for distinguishing male versus female *B. bombifrons*. For example, the bases of the horn cores fused to both the frontal and parietal bones, as is seen in SMU 77689. Compared to females, males generally have extensive development of secondary bone (exostosis) on the dorsum of the skull. On SMU 77689, exostosis covers the dorsum from the anterior aspect of the orbits to the occiput. McDonald and Ray (1989) noted that the burr lines in males are typically

FIGURE 5. Dorsal view of the cranium of *Bootherium bombifrons*, SMU 77689, from Lamar County, Texas. Scale equals 10 cm.

TABLE 2. Measurements of SMU 77689, a mature male *Bootherium bombifrons* from Lamar County, Texas, and comparative measurements of other Texas *B. bombifrons* (TMM-ETSU 5301 from McDonald and Echols, 1990; SMU 69127 from McDonald, 1985). Measurements made are adapted from Stefaniak et al. (2019:fig. 1; their measurement number indicated as #). All measurements in mm.

	Specimen number		
Measurement	SMU 77689	TMM-ETSU 5301	SMU 69127
Greatest breadth basioccipital	86	77	90
Greatest breadth across nasals (#13)	87	—	—
Minimum frontal breadth (#27)[a]	154	—	137
Greatest frontal breadth (#28)	254	—	—
Minimum orbital breadth (across frontals; #29)	230	—	—
Orbital width (#23)	80*	—	—
Greatest breadth at bases paraoccipital processes (#18)	213	—	—
Greatest mastoid breadth (#19)	215	—	—
Greatest height occiput (akrocranium[b] to basion, #24)	132	—	136[c]
Minimum height occiput (nuchal line to opisthion)	109	113	111
Greatest breadth occipital condyles (#17, primary)	135	137	136
Greatest breadth foramen magnum (#32)	35	42	29
Minimum breadth between bases horn cores (#14)	82	—	148
Minimum occipital breadth below horn cores (#30)	148	—	—
Greatest (oro-aboro) diameter of the horn core base (#11)[d]	115*	120	115R-123L
Length horn core from base (burr line) to tip along dorsal surface	432*	—	—

*Approximate

[a] Equivalent to postorbital width of McDonald and Ray (1989)

[b] Akrocranium = external occipital protuberance

[c] Greatest height occipital region, nuchal line to basion (McDonald, 1985)

[d] Equivalent to McDonald and Ray (1989) diameter of base of horn core along rostrocaudal axis

obscured by secondary bone. On SMU 77689 this is true for the dorsal surface of the skull, but the burr lines are distinctive elsewhere.

Heavy occlusal wear on the M1s of SMU 77689 suggest an older individual. Allen (1913:fig. 18) figured an extant *Ovibos moschatus* adult female with dental wear similar to the fossil, and labeled it “about 12 years old”, suggesting an approximate ontogenetic age for SMU 77689.

Multiple genera and species of fossil muskoxen in North America were synonymized by McDonald and Ray (1989) under *Bootherium bombifrons*. This species can be distinguished from modern *Ovibos moschatus* on both morphological and phylogenomic grounds (McDonald and Ray, 1989; Campos et al., 2010). Specimens that were previously referred to *Symbos cavifrons* are now considered to be males of *Bootherium* (McDonald and Ray, 1989; Bover et al., 2018). *Bootherium bombifrons* is autochthonous to and was the most widely distributed Quaternary muskox (McDonald and Ray, 1989). It has been recovered from sediments dating near the Irvingtonian-Rancholabrean boundary to about 11,000 ^{14}C years BP (McDonald and Ray, 1989; Campos et al., 2010). Although the remains of *Bootherium* are not uncommon from some parts of North America, for example the midwestern United States, specimens from the south, including Texas, are rare (McDonald and Ray, 1989; Campos et al., 2010). There are currently three other published records of muskox crania from Texas. Hesse (1942) described an incomplete cranial roof and horn cores of *Bootherium brazosis* (later assigned to *B. sargenti* by Ray, 1966) from Pleistocene deposits in Brazos County, Texas (TMM-TAMU 2553, adult female). This species was synonymized with *Bootherium bombifrons* by McDonald and Ray (1989). McDonald (1985) described a partial cranium of a muskox from Kaufman County, Texas, which he originally referred to *Symbos* sp. (SMU 69127). The geologic age of the specimen was estimated to be 21,000 – 24,000 years BP or possibly as much as 75,000 years BP (pers. comm. B. Slaughter, October 27, 1983 in McDonald, 1985:312). This specimen (an adult male) was later also referred by McDonald and Ray (1989) to *Bootherium bombifrons*. McDonald and Echols (1990) described the third cranium (a male) from Texas, which was found along the South Sulphur River in Hunt County, Texas (TMM-ETSU 5301; considered to be latest Wisconsin [late Rancholabrean] in geologic age). They referred the Hunt County specimen to *Bootherium bombifrons*. Comparative measurements of the other Texas *B. bombifrons* from the published literature are in Table 1. For all of these (except minimum breadth between bases of the horn cores), the measurements are comparable to those of SMU 77689 (i.e., within the range of expected individual variation or measurement error).

TABLE 3. Measurements (in mm) of SMU 77673, *Tapirus veroensis*, left dentary, from Denton County, Texas.

Tooth position	Measurement	Comments
p3L	22.7	—
p3W	>19.0	Buccal side damaged
p4L	24.8	—
p4W	25.3	—
m1L	24.8*	Buccal side damaged
m1W	22.6	Damaged, W at anterior base
m2L	27.7	—
m2W	23.1	—
m3L	30.4	—
m3W	23.2	—
m1–m3L	83.7	—
p3–m3L	129.8	—
p2–m3L (estimate)	153	From anterior p2 crown base
Dentary L (as preserved)	357	Posterior coronoid process missing

*Approximate

The only other fossil muskox from Texas is a third phalanx. Lundelius (1967:table 1) listed an Ovibovine (extinct genus) from Cave Without a Name, Kendall County, Texas. He listed the site as dating to 10,900 ± 190 years BP. McDonald and Echols (1990) examined a cast of this specimen (‘UT 40450-1625’; now TMM 40450-1625), and they considered it to conform most closely to that from the pes of *Bootherium* (=*Symbos*) *bombifrons*. It is interesting to note that no specimens of muskoxen occur in the Hill-Shuler faunas near Dallas (Slaughter et al., 1962; Slaughter and Hoover, 1963; Slaughter, 1966), despite extensive collections, nor in the Ben Franklin fauna (Slaughter and Hoover, 1963), which is in the vicinity of where SMU 77689 was collected. This absence may be a result of general rarity, plus a preference for more northern habitats.

Order Perissodactyla Owen, 1848
Family Tapiridae Gray, 1821
Tapirus veroensis Sellards, 1918
(Figure 7)

Referred Material—SMU 77673, left dentary and symphysis, including partial right i1–3, crown

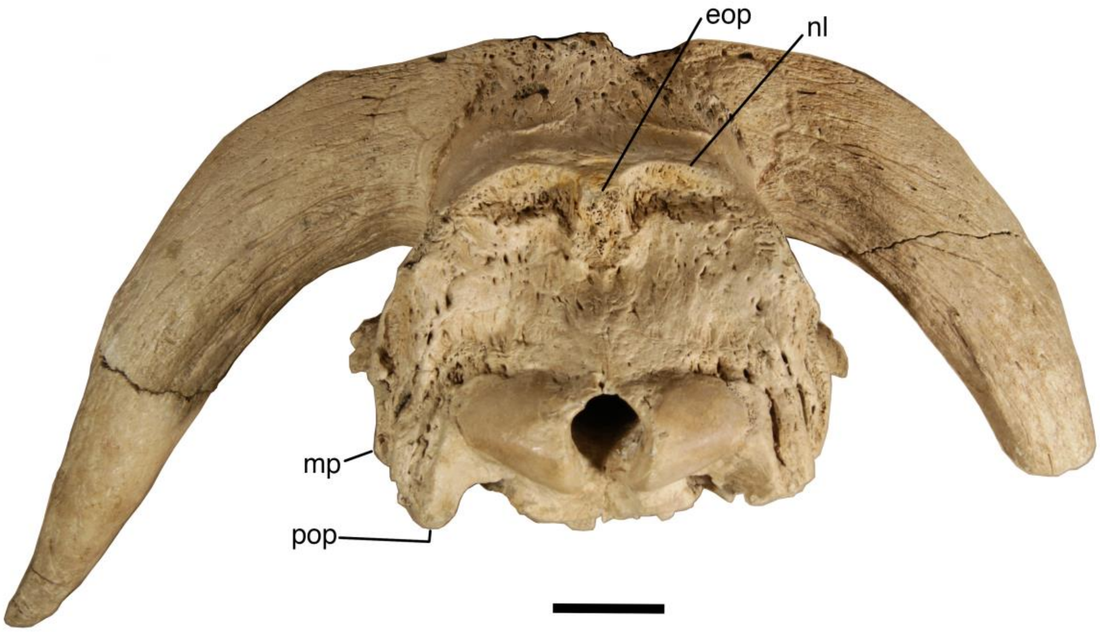

FIGURE 6. Occipital view of the cranium of *Bootherium bombifrons*, SMU 77689, from Lamar County, Texas. **Abbreviations**: **eop**, external occipital protuberance; **mp**, mastoid process; **nl**, nuchal line; **pop**, paraoccipital process. Scale equals 5 cm.

bases of both canines, the anterior crown base of p2, and p3–m3.

Locality and Geologic Age—SMU Loc. v555, Ray Roberts Lake Spillway, Elm Fork of the Trinity River, Denton County, Texas. SMU 77673 was found approximately 700–800 m east of the Aubrey Clovis site excavations, in the Elm Fork valley, at the base of the exposed terrace fill section. The Clovis occupation at the Aubrey site has radiocarbon dates that average 11,565 ^{14}C years BP (Ferring, 2001). Below this level, Ferring (2001) reported radiocarbon dates as old as circa 14,200 ^{14}C years BP within the local terrace fill sequence. This provides a minimum date for the underlying, and lowest unit in the sequence (undated Unit A). Ferring (2001) suggested that Unit A deposition began approximately 18,000–19,000 years BP. The tapir specimen is tentatively correlated with Unit A because of its occurrence in the lowest exposed outcrop level locally.

Description—The cheek toothrow is almost complete, but missing most of p2, and with some damage to p3 and m1 (Figure 7). Both of the latter teeth have their buccal surfaces spalled-off, therefore width measurements for these teeth are too low (Table 3). All the teeth from p3 through m2 show significant crown wear, with m1 being the most heavily worn. The specimen is a full adult because m3 is fully erupted (Figure 7B), and has some wear on the posterior loph, but no dentine is exposed (Ray and Sanders, 1984; Hulbert et al., 2009).

Dental measurements for SMU 77673 (Table 3) fall toward the upper end of the range of variation of *Tapirus veroensis* specimens as regarded by Lundelius and Slaughter (1976: table 3). The attribution of some large fossil tapir specimens to *T. veroensis* by Lundelius and Slaughter (1976) was questioned by Ray and Sanders (1984), who advocated for recognition of *Tapirus haysii* as the valid name for large tapirs from the early and middle Pleistocene of the central and eastern United States. Based solely on size, SMU 77673 might be regarded as *T. haysii*. However, pending discovery of definitive specimens of that taxon from latest Pleistocene (late Rancholabrean) faunas, the SMU specimen is conservatively regarded as a large individual of *T. veroensis*. More complete skull material is needed to corroborate this allocation (see below).

Discussion—There has been debate about the species of *Tapirus* that are present in the middle and late Pleistocene of eastern and central North America (Lundelius and Slaughter, 1976; Ray and Sanders, 1984; Hulbert, 1995, 2010; Hulbert et al., 2009). The species *T. veroensis* is based upon excellent skull material from the late Pleistocene (Rancholabrean) of Florida (Sellards, 1918; Lundelius and Slaughter, 1976; Ray and Sanders, 1984). Smaller late Pleistocene tapirs from many localities in central and

FIGURE 7. *Tapirus veroensis*, SMU 77673, from Denton County, Texas. Includes left dentary and symphysis, partial right i1–3, crown bases of both canines, and left anterior crown base of p2, plus p3–m3. **A**, lateral view; **B**, occlusal view. Scales equal 4 cm.

eastern North America have been referred to this species. Several larger Pleistocene species have been named from earlier (Irvingtonian) deposits in the same region, but those species were based mostly on incomplete type specimens (Ray and Sanders, 1984). Subsequent discoveries of more complete material from both Irvingtonian and Blancan deposits have facilitated better descriptions of one large tapir, now synonymized under *Tapirus haysii* (Ray and Sanders, 1984; Hulbert, 1995). Additional new species of early Pleistocene tapirs have also been named (Hulbert, 2010). In western North America, similar large, middle Pleistocene and small, late Pleistocene tapirs have been named as other species (Jefferson, 1989). Skull measurements for eastern and central North American Pleistocene tapirs are clearly separated (using mean size) into distinct large (early) and small (late) Pleistocene tapir species populations. However, the size ranges of some dental measurements for *T. veroensis* overlap with those of *T. haysii* (Lundelius and Slaughter, 1976; Hulbert, 1995, 2010). The controversy is, therefore, what to call some larger specimens of latest Pleistocene (Rancholabrean) tapirs that are known from both the East and the West (Ray and Sanders, 1989; Jefferson, 1989; Graham, 2003; Graham et al., 2019). This is especially problematic for specimens from Texas, many of which are intermediate in size (Lundelius and Slaughter, 1976).

Extensive collections from the late Pleistocene (Rancholabrean) terrace deposits of the Trinity River in north central Texas were summarized by Slaughter et al. (1962). Tapirs are rare in those collections (isolated postcrania, teeth and dentaries; Table 4), and they were noted to be rather small in size (similar to *T. veroensis*), but referred only to '*Tapirus* sp.,' by Slaughter et al. (1962). Slaughter (1966) later described a new specimen (SMU 60600) from one of these localities (Moore Pit), a tapir partial left dentary (Table 4). Based upon its size, he referred the dentary to *T. copei* (=*T. haysii*). That allocation was not mentioned in Lundelius and Slaughter (1976), but it was followed by Graham (2003) and Graham et al. (2019). No tapir specimens were found in the Clear Creek fauna, which is quite near the Ray Roberts Lake spillway locality (Slaughter and Ritchie, 1963).

TABLE 4. *Tapirus* specimens from the late Pleistocene (Rancholabrean) Trinity River terraces, north central Texas.

Specimen number	Locality	Element
SMU 60093	Moore Pit (SMU Loc v148)	Metacarpal III, Lt.
SMU 60110	Moore Pit (SMU Loc v148)	Dentary, Lt., edentulous, fragmentary
SMU 60600	Moore Pit (SMU Loc v148)	Dentary, Lt., m2–m3
SMU 62743	Moore Pit (SMU Loc v148)	MX, Lt., anterior fragment
SMU 60301	Hickory Creek (SMU Loc v153)	mX, Lt.
SMU 60360	Wood Pit (SMU Loc v145)	Dentary, Lt., fragment
SMU 60621	Opitz Pit (SMU Loc v189)	Metapodial, distal
SMU 75361	Forney Dam (SMU Loc v337)	Dentary, Rt.; Maxillae, Rt., Lt., fragmentary
SMU 61858	Liberty Grove (SMU Loc v466)	M2?, Lt., anterior; p3, Rt.
SMU 76403	Liberty Grove (SMU Loc v466)	Metatarsal III, Lt.

Perhaps the best Pleistocene specimen of tapir from Texas is a partial skull from the area around the dam of what is now Livingston Lake (San Jacinto/Polk counties, southeast Texas; HMS 160; SMU Loc. v220) (Slaughter, 1965; Lundelius and Slaughter, 1976). Recognizing that many late Pleistocene tapirs from Texas are large (see Lundelius, 1972), an expanded concept of the species *Tapirus veroensis* was proposed by Lundelius and Slaughter (1976), and the Livingston Lake specimen was referred to that species. However, they also suggested that Rancholabrean tapirs from Texas may represent a new subspecies (also see Ray and Sanders, 1984). In the broader north central Texas area, the previously most complete tapir specimen is from the Lake Ray Hubbard area (SMU Loc. v337; "Forney Reservoir Basin", in Slaughter and Thurmond, 1965:1) in Kaufman County, Texas. It consists of fragmentary maxillae and a partial dentary (Lundelius and Slaughter, 1976; Table 4). The Forney Reservoir specimen comes from terrace deposits of an eastern branch of the Trinity River, and it was referred to *Tapirus haysii* by Graham (2003) based upon its size.

The specimen described here (SMU 77673) is large, and the length of the cheek tooth series and molar series is well within the range for *T. haysii* (Table 3), as tabulated by Hulbert et al. (2009) and Hulbert (2010). Until definitive specimens of the latter species are described from the late Rancholabrean of North America, it seems prudent not to extend its temporal range, and therefore, the Ray Roberts specimen is retained within an expanded concept of *T. veroensis*.

The new specimen also has paleoenvironmental implications. Late Pleistocene records of *Tapirus* are widespread in eastern North America, especially in forested settings, along the coast, and along major rivers. Tapirs are much less common at this time on the Great Plains and on the Colorado Plateau (Agenbroad and Downs, 1984; Graham et al., 2019). At the coastal late Pleistocene site of Ingleside, Texas, *Tapirus* specimens are relatively common (Lundelius, 1972). In contrast (as noted above), their abundance in late Pleistocene localities in north central Texas is quite low. The presence of tapirs in these faunas indicates forested, or woodland/shrubland environments, and fossil and modern tapirs have been shown to have had or have a diet of C^3 plants (DeSantis and MacFadden, 2007; DeSantis, 2011). As in other western and Great Plains sites, tapirs may have been restricted to riparian forests or woodlands (Agenbroad and Downs, 1984). Modern tapirs are largely restricted to warm tropical and sub-tropical environments, and to wet forested areas (DeSantis, 2011; Graham et al., 2019). The modern mountain tapir is an exception, living in colder high altitude and mostly forested environments (Downer, 2001). This led Graham et al. (2019) to argue that late Pleistocene North American tapirs became adapted to cold environments independently from the extant mountain tapir.

No tapir specimens are associated with the Aubrey (proto-) Clovis occupation level (Ferring, 2001). Fauna from the site includes specimens of many small vertebrates, but only bison, horse and ground sloth among large mammals (Yates and Lundelius in Ferring, 2001). Large mammals are represented by very few individuals (Ferring, 2001). A good pollen record from that site indicates a mostly open flora overall, with the upland covered in a treeless aster prairie, which has no modern analog (Hall, 2019). Woodlands were restricted to a riparian habitat of small trees (Hall, 2019). Other pollen records from this time in central and north central Texas also indicate vegetation that included extensive grassland savannas and open woodlands on the uplands (Bryant and Holloway, 1985; Cordova and Johnson, 2019). The presence of a tapir in deposits below the level of occupation suggests that a more forested or woodland habitat may have existed there prior to the time of the human occupation, at least in the riparian settings.

SUMMARY AND CONCLUSIONS

This paper describes two large Pleistocene ungulates, *Bootherium bombifrons* and *Tapirus* *veroensis*, both of which are relatively poorly known from Texas. The *Bootherium* cranium, SMU 77689, is a large male. It is the most complete skull of this taxon from Texas and provides for a detailed description. Measurements of the skull are comparable to those of other *B. bombifrons* from Texas.

The large tapir specimen, SMU 77673, is retained within *T. veroensis*, until more definitive material of *T. haysii* is described from the latest Pleistocene (late Rancholabrean). The occurrence of such a large forest or woodland inhabitant just below the level of the Aubrey archaeological site indicates a change in the fauna in the area and suggests a shift in the paleoenvironment at the end of the Pleistocene.

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