MIOCENE RHINOCEROSES FROM THE TEXAS GULF COASTAL PLAIN

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ABSTRACT—Four species of rhinoceros occur together in the Barstovian (middle Miocene) faunas of southeast Texas, a unique situation in the Miocene of North America. Two are assigned to normal contemporary High Plains species of *Aphelops* and *Teleoceras,* and two to dwarf species of *Peraceras* and *Teleoceras.* The dwarf *Peraceras* is a new species, *P. hessei.* The dwarf *Teleoceras* is assigned to Leidy's (1865) species "*Rhinoceros*" *meridianus,* previously referred to *Aphelops.* "*Aphelops*" *profectus* is here reassigned to *Peraceras.*

The late Arikareean (early Miocene) Derrick Farm rhino, erroneously referred to "*Caenopus premitis*" by Wood and Wood (1937), is here referred to *Menoceras arikarense. Menoceras barbouri* is reported from the early Hemingfordian (early Miocene) Garvin Gully local fauna of southeast Texas. The rhinos from the early Clarendonian Lapara Creek Fauna are tentatively referred to *Teleoceras* cf. *major.*

The three common genera of middle late Miocene rhinoceroses of North America (*Aphelops, Peraceras, Teleoceras*) are rediagnosed. *Aphelops* and *Peraceras* are more closely related to the Eurasian *Aceratherium* and *Chilotherium* (all four together forming the Aceratheriinae) than they are to the American *Teleoceras.* Contrary to Heissig (1973), *Teleoceras* is more closely related to the living rhinoceroses and their kin (together forming the Rhinocerotini) than it is to the Aceratheriinae.

INTRODUCTION

AMONG the first mammalian fossils described from Texas was a fragmentary upper molar of a rhinoceros from the Texas Gulf Coastal Plain. The specimen was given to J. Leidy by B. F. Shumard of St. Louis, Missouri. Leidy (1865) described this tooth, illustrated it (1869, Pl. 23, fig. 10; see Figure 10.1–10.3), and gave it the name *Rhinoceros meridianus.* The only locality information given by Leidy was that "it was derived from a tertiary [sic] deposit in Washington county [sic], Texas, and presents much the general aspect of the Mauvaises Terres fossils of the White River, Dakota, with which it is probably cotemporary [sic] in age" (1869, p. 229).

In 1875 and 1877, Cope referred some specimens from the Santa Fe Group of New Mexico to the species *meridianus,* but placed this species in his new genus *Aphelops.* Matthew (1932) pointed out that Cope's "*meridianus*" did not correspond well to Leidy's type specimen, and was not from Texas. Matthew considered the name *meridianus* indeterminate until adequate topotypes were known. Matthew (1932, fig. 2) also figured a specimen (UCMP 31043) from near the type locality that he believed to be representative of Leidy's species. Most authors since Matthew (e.g., Hesse, 1943; Quinn, 1955; Patton, 1969) have referred the larger rhinoceros material from the middle Miocene of Texas to "*Aphelops*" *meridianus,* if generic-level identification was attempted at all.

Hesse (1943) was the first author to recognize a smaller rhinoceros in the Texas Gulf Coast Barstovian faunas. He described and named a new species, *Aphelops rileyi,* in a manuscript that was incomplete at his death in 1944, and never published. This smaller rhinoceros material was referred to *Diceratherium* by Quinn (1955) and Patton (1969), apparently due to identifications made by H. E. Wood (J. A. Wilson, personal commun.). Quinn (1955, p. 75) mentioned a small rhinoceros "no larger than *Diceratherium,* but with characters of *Teleoceras* including the reduced number of cheek teeth," suggesting "a primitive but direct ancestor to the upper Miocene and Pliocene species." Quinn gave no catalogue number for this specimen. Based on this brief and nondiagnostic description, it is unlikely that he actually recognized the dwarf *Teleoceras,* since there is no complete skull of it in the Texas Memorial Museum collections. All of the "*Diceratherium*"-sized

skulls (probably in reference to *Menoceras arikarense,* the Agate Spring rhino) in the latter collection are of the dwarf *Peraceras.* Although many (but not all) advanced *Teleoceras* reduce the premolars and lose P2/2, this is not a diagnostic feature of the genus. Thus, "reduced number of cheek teeth" is not diagnostic of *Teleoceras.* In short, the published literature is in great confusion concerning Texas Gulf Coast Miocene rhinoceroses.

In 1936, the Frick Laboratory of the American Museum of Natural History began collecting in the Texas Gulf Coastal Plain. The excavations were supervised chiefly by N. Z. Ward, and continued until 1964. Most of the large collection from this area remains undescribed. Descriptions of some of the rodents (Wahlert, 1976), horses (MacFadden and Skinner, 1977, 1981; Skinner and MacFadden, 1977), protoceratid artiodactyls (Frick, 1937; Patton and Taylor, 1971, 1973), leptomerycids (Taylor and Webb, 1976), and oreodonts (Schultz and Falkenbach, 1941) have been published. While curating the rhinoceros material in the Frick Collection, the junior author found that the Barstovian Texas Gulf Coastal Plain faunas contained four sympatric species of rhinoceros. Two of these appeared to be similar to the High Plains *Aphelops megalodus* and *Teleoceras medicornutum,* but there was also a dwarf *Teleoceras* and a dwarf aceratherine rhinoceros present. The latter was first identified as a dwarf *Aphelops* (Prothero and Sereno, 1980), but comparison with more complete material in the Texas Memorial Museum collection has shown that the dwarf aceratherine is actually a dwarf *Peraceras.* The occurrence of four different rhinoceroses in the Texas Barstovian faunas probably caused some of the taxonomic confusion outlined above.

The interesting morphological and ecological implications of this occurrence are discussed elsewhere (Prothero and Sereno, 1982). In this paper, the systematics of the Miocene rhinoceroses of Texas are reviewed, and an attempt to clear up some of the confusion regarding the early, primitive members of the genera *Aphelops, Teleoceras,* and *Peraceras* is made.

Abbreviations. — AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York, N.Y.; F:AM, Frick Collection, American Museum of Natural History, New York, N.Y.; l.f., local fauna (sensu Tedford, 1970); MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; N, sample size; PU, Princeton University Museum, Princeton, N.J.; OR, observed range; s, standard deviation; TAM, Texas A&M University, College Station, Tex.; TMM, Texas Memorial Museum, University of Texas at Austin; UCMP, University of California Museum of Paleontology, Berkeley, Calif.; UNSM, University of Nebraska State Museum, Lincoln, Nebr.; USNM, United States National Museum, Washington, D.C.; $\bar{x}$, mean.

For ease of word processing, the system of dental abbreviations of Jepsen (1966) is adopted here. Thus, upper premolars and molars are indicated by upper case "P" or "M", lower premolars and molars by lower case "p" or "m".

A note on endings: the *-ceras* suffix in rhino genera (such as *Peraceras* or *Teleoceras*) is neuter in gender; the suffix *-ceros* (as in *Rhinoceros*) is masculine. Since adjectival species names must agree with the genus in gender (International Code of Zoological Nomenclature, Article 11, section g), a number of traditionally-accepted species names have been corrected. Thus, *Peraceras* has species *superciliosum* and *profectum*; *Teleoceras* has species *medicornutum, proterum,* and *meridianum.* Similarly, *Brachypotherium americanus* Yatkola and Tanner, 1979, is here amended to *B. americanum,* since the suffix *-therium* is also neuter.

LOCALITIES AND STRATIGRAPHY

The Miocene of the Texas Gulf Coastal Plain has been collected by a number of institutions over the years, but the major collections of fossil vertebrates are at the Texas Memorial Museum of the University of Texas at Austin, the Texas A&M University (presently on loan to the Texas Memorial Museum), and the Frick Collection of the American Museum of Natural History. Each institution has a distinct set of localities, listed in Table 1 and shown in Figure 1. The detailed locality information is given in Hesse (1943) and Patton and Taylor (1971, table 2).

TABLE 1—Areal distribution of fossil localities (see Figure 1).

Number	County	Fauna	Locality
1	Tyler	Burkeville	West of Doucette, near Woodville
1	Tyler	Cold Spring	TMM 40662, Belts Creek
2	Tyler	Cold Spring	TMM 30009, 31087, 8 mi southwest of Woodville
3	Polk	Burkeville	TMM 30157, Moscow l.f.
4	Polk	Cold Spring	Near Swartaut
5	Tyler	Cold Spring	TMM 40623, Push Creek
6	San Jacinto	Cold Spring	TMM 31219, Cold Spring l.f. (=F:AM Donohoe Farm)
6	San Jacinto	Cold Spring	McMurray Pits 1 and 2
6	San Jacinto	Burkeville	Trinity River Pit 1 (=TMM 40196)
6	San Jacinto	Burkeville	Stephen Creek
7	San Jacinto	Cold Spring	TMM 31191, San Houston l.f.
8	San Jacinto	Burkeville	TMM 31243, Point Blank l.f.
9	San Jacinto	Burkeville	TMM 31190, Point Blank l.f.
10	San Jacinto	Burkeville	TMM 31242, Point Blank l.f.
11	Walker	Garvin Gully	TMM 30873, Aiken Hill l.f.
12	Grimes	Burkeville	TMM 40290, near Navasota
13	Washington	?Burkeville	Leidy'd locality, fide Hesse, 1943
14	Washington	Cold Spring	TMM 31272, southeast of Chapell Hill
15	Washington	Garvin Gully	TMM 40106, Farm Road 244
15	Washington	Garvin Gully	TMM 31048, Garvin Gully l.f.
15	Washington	Garvin Gully	TMM 40067, Hidalgo Bluff
16	Washington	?Catahoula Fm.	Derrick Farm locality
17	Fayette	Burkeville	TMM 40127, north side of Cedar Creek, La Grange
18	Fayette	?Burkeville	TMM 31246, Swiss Alp
19	Lavaca	?Burkeville	Near Hallettsville (exact locality unknown)
20	Grimes	Cold Spring	TAM locality 19, Noble Farm l.f.
21	Bee	Lapara Creek	TMM 30896, Berclair l.f. (=Farish Ranch l.f.)
22	Bee	Lapara Creek	TMM 31132, Normanna l.f. (=Bridge Ranch l.f.)
23	Bee	Lapara Creek	TMM 31081, Berclair l.f.

Further details are available from the appropriate institution.

The mammalian stratigraphy of the Texas Gulf Coastal Plain has been extensively discussed (Hesse, 1943; Quinn, 1955; Wilson, 1956; Patton, 1969; Patton and Taylor, 1971, 1973), and will not be reviewed here. The correlations shown in Figure 2 are based on the latest studies of the faunas by a number of workers (Tedford et al., 1987), incorporating much unpublished information from the Frick Collection.

SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen, 1848
Suborder CERATOMORPHA Wood, 1937
Superfamily RHINOCEROTOIDEA Gill, 1872
Family RHINOCEROTIDAE Owen, 1845
Genus MENOCERAS Troxell, 1921
MENOCERAS ARIKARENSE (Barbour, 1906)
Figure 3.1–3.3, 3.6

Diceratherium arikarense BARBOUR, 1906, p. 316.
Diceratherium cooki PETERSON, 1906, p. 282.
Coenopus [sic] sp. GIDLEY, 1924 (in Deussen, 1924, p. 98, Pl. 28).
Caenopus cf. premitis Gregory and Cook. WOOD AND WOOD, 1937, p. 134.
Menoceras arikarense (Barbour). TANNER, 1969, p. 395.

Discussion.—The rhinoceros left maxilla with dP1,P2–4 from Derrick Farm, Washington County, Texas, had previously been assigned to the Oligocene genus Caenopus. This determination was based on its small size and supposed Oligocene provenance. Apparently the age determination prevented earlier authors from comparing the Derrick Farm rhino (USNM 6573) with another small rhinoceros, Menoceras arikarense, from the earliest Miocene of Agate Spring Quarry, Nebraska. USNM 6573 is virtually identical in size and morphology with the Agate Spring sample of M. arikarense (Figure 3.6, Table 2). Wood and Wood (1937) referred the Derrick Farm rhino to Caenopus cf. premitis, but this rhino is merely a variant of Trigonias osborni. The genus Caenopus is now considered to be a junior synonym of Subhyracodon, so the Derrick Farm rhino cannot be referred to this genus (Lucas et al., 1981). Morphologically, the Derrick Farm rhino is a poor match for "Caenopus." It has much weaker lingual cingula and a more fully bilophodont P4, with the metaloph directed posteriorly and unconnected to the protoloph.
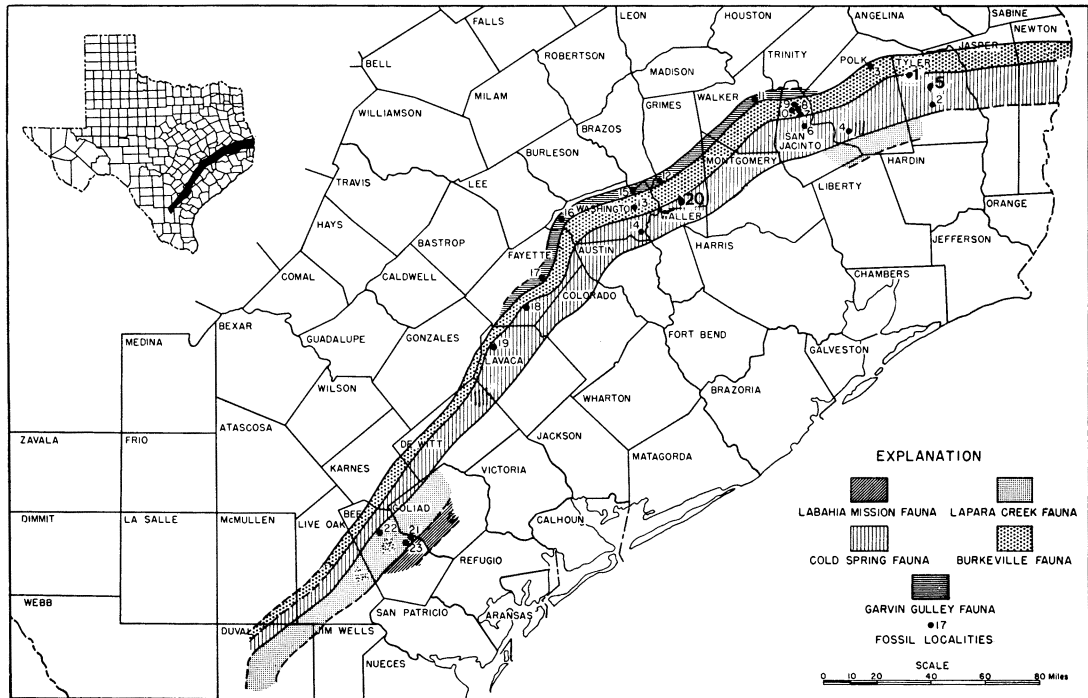
It is curious that this specimen was so badly

FIGURE *1*—Index map showing distribution of fossil localities described in Table 1. (After Quinn, 1955, fig. 5.)

misidentified, since both Wood and Gidley were certainly familiar with *Menoceras arikarense.* Specimens of *M. arikarense* are found in most of the major collections in the United States, and the rhino was first described in 1906 and thoroughly monographed by Peterson in 1920. Before 1969, *M. arikarense* was known as *Diceratherium cooki,* but Tanner (1969) showed that Troxell's (1921) distinction of the common Agate Springs Quarry rhinoceros, which he named *Menoceras,* from the John Day rhinoceros *Diceratherium* was correct. Tanner (1969) also pointed out that the species *arikarense* (Barbour, 15 June 1906) has two month's priority over Troxell's type species of *Menoceras, Diceratherium cooki* (Peterson, 31 August 1906). Perhaps the confusion of Wood and Gidley may be due to the supposed Oligocene age of USNM 6573. Recent workers have found that most of the Arikareean is also of Oligocene age (Tedford et al., 1987; Prothero and Rensberger, 1985). The age of the Agate Spring fauna is difficult to determine, but it is probably Aquitanian, or earliest Miocene (Hunt, 1972).

Yet, it is not even certain that the Derrick Farm specimen is Oligocene in age. Deussen (1924, p. 98) originally reported the specimen from the Oakville Formation and suggested that the rhino had affinities with middle or late Miocene forms. Weeks (1933, p. 456–457) and Wood and Wood (1937) were convinced that the specimen came from the Catahoula Formation, which was then considered Oligocene in age. J. A. Wilson (personal commun.) has examined the locality and suggests that the specimen could easily be derived from a channel from the overlying Oakville Formation (Figure 2). If it is truly from the Catahoula Formation, the Oligocene age of this unit is not well established, either. The Catahoula Formation is composed of subaerial braided stream deposits and contains no diagnostic marine fossils, only some plant fossils (Deussen, 1924, p. 95; McBride et al., 1968). The Oligocene age was suggested primarily by its position between the Miocene Oakville Formation and the Eocene Fayette Formation. McBride et al. (1968, p. 10) report a lead-alpha age on zircons from the lower part of the correlative Gueydan Formation in Live Oak County, Texas. This date of 24 ± 1 million years would place the Ca-
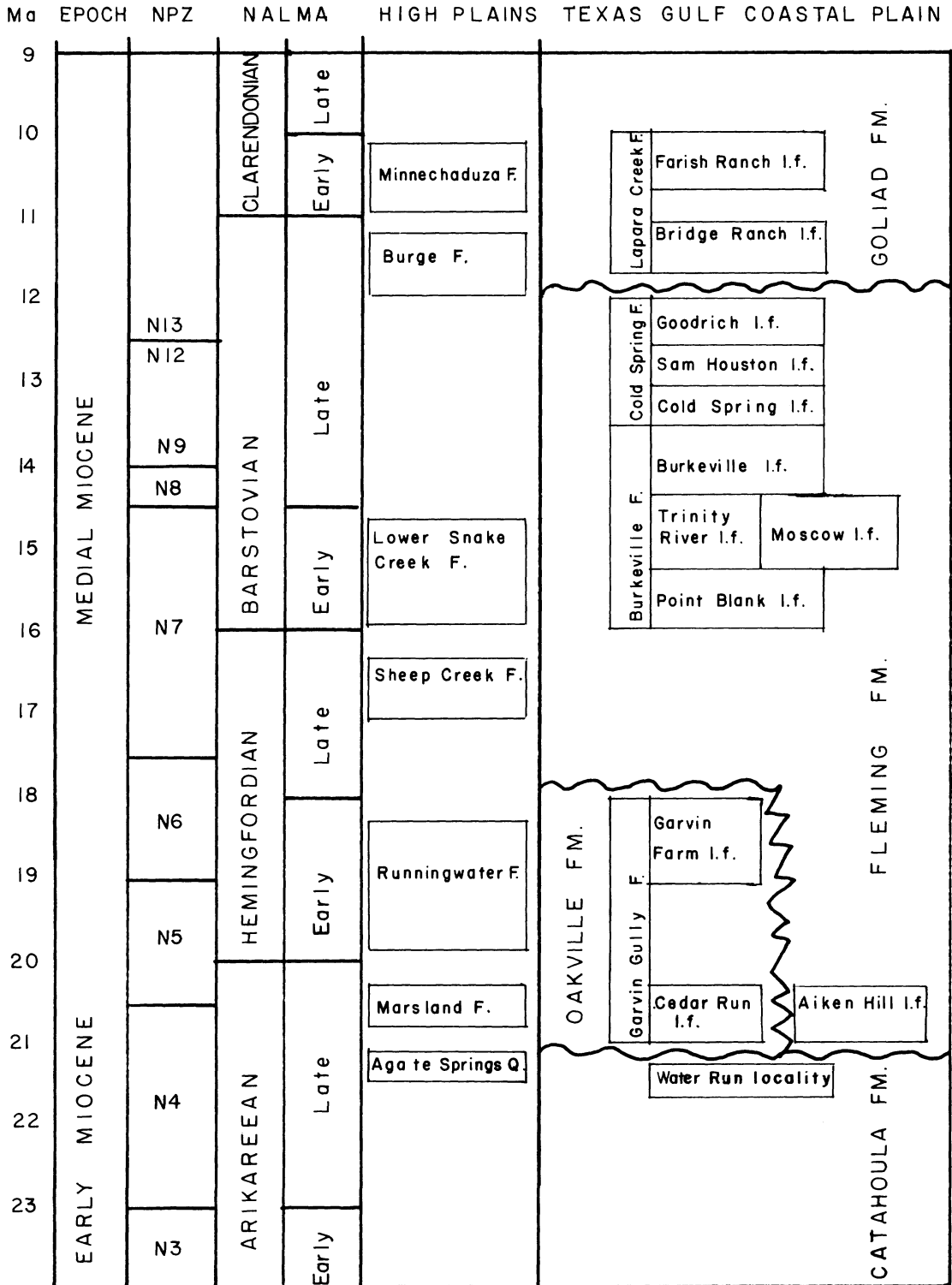
FIGURE 2—Stratigraphy of Miocene localities from the Texas Gulf Coastal Plain (after Tedford et al., 1987). Abbreviations: Ma, million years before present; NPZ, Neogene planktonic zones; NALMA, North American land mammal ages; F, Fauna; l.f., local fauna (sensu Tedford, 1970).
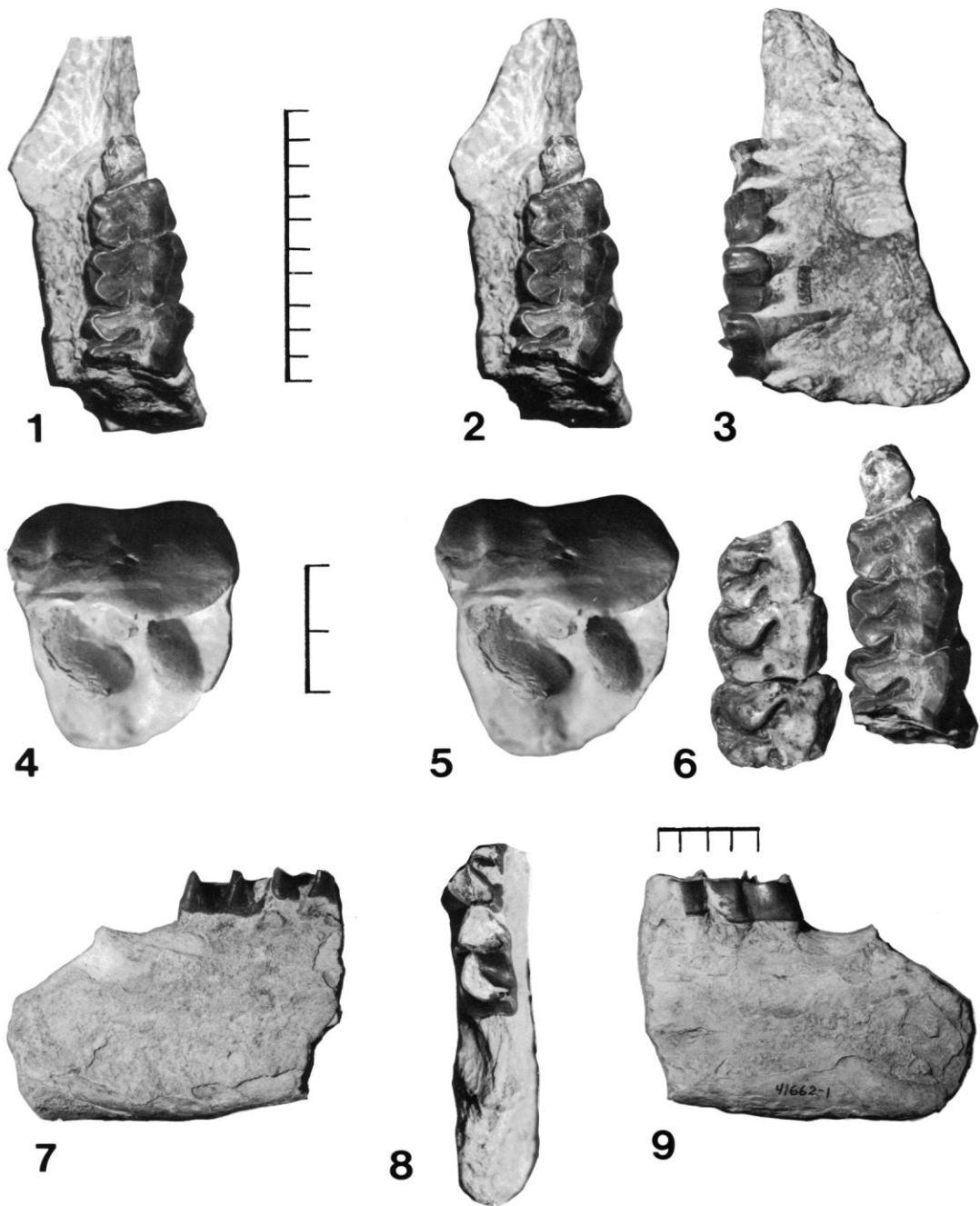
FIGURE *3—Menoceras* from the Texas Gulf Coastal Plain. *1, 2, Menoceras arikarense,* USNM 6573, stereopairs of crown view; *3,* same specimen, lateral view. *4, 5, Menoceras barbouri,* TMM 31048-48, stereopair of left dP4. *6,* Comparison of *M. arikarense*; left specimen is AMNH 86118 from Agate Spring Quarry; right specimen is USNM 6573 from Derrick Farm. *7–9, M. barbouri,* TMM 41662-1, left ramal fragment in medial, crown, and lateral views. Scales in cm.

TABLE 2—Measurements (in mm) of *Menoceras arikarense.*

	Derrick Farm rhino USNM 6573	Agate Spring *M. arikarense*[1]		
		N	x̄	s	OR
P2–4	63.0	7	64.7	3.0	59.6–68.5
P2 length	19.1	7	21.5	2.0	19.0–25.3
P2 width	27.5	7	26.8	1.0	25.3–28.6
P3 length	22.1	7	22.1	1.7	20.1–23.8
P3 width	33.0	7	33.6	2.7	31.1–37.4
P4 length	20.5	7	24.1	1.3	22.4–26.0
P4 width	35.0	7	36.4	2.3	33.3–39.2

[1] Agate Spring sample based on the following specimens: AMNH 86224, 86227, 86116, 86118, 86112, 14213, 26892.

tahoula Formation in the middle late Arikareean, very near the Oligocene–Miocene boundary. Thus, the upper part of the Catahoula Formation is probably late Arikareean (early Miocene), agreeing with the age suggested by the Derrick Farm rhino.

MENOCERAS BARBOURI
(Wood, 1964) n. comb.
Figure 3.4, 3.5, 3.7–3.9

Diceratherium (Menoceras) barbouri WOOD, 1964, p. 378.
Diceratherium sp. QUINN, 1955, p. 72.
Diceratherium sp. PATTON, 1969, p. 211.

Referred material.—TMM 41662-1, jaw fragment with m2-3, fragments of other teeth; TMM 31048-48, left dP4 (unworn); TMM 40067-124, immature right femur; TMM 40106-4, lumbar vertebra; TMM 40067-190, fragmentary skull with poor dentition; TMM 40067-71, tooth fragment; TMM 40067-178, broken metacarpals; TMM 40067-189, tooth fragments; TMM 31048-54, edentulous partial right lower jaw; TMM 31048-3, right lower molar (?m2); TMM 31048-39, tooth fragment.

Discussion.—Most of the Garvin Gully rhinoceros material is too poorly preserved to be identified. The most diagnostic specimen is TMM 41662-1, a partial left ramus with m3 and part of m2 (Figure 3.7–3.9). In size and morphology it most closely approaches specimens referred to "*Diceratherium*" *barbouri* (Table 3). It is clearly too large to be referred to *Menoceras arikarense*, and too small to be referred to *Menoceras marslandense.*

Wood (1964) placed *Diceratherium (Menoceras) barbouri* in the subgenus *Menoceras.* Tanner (1969) showed that *Menoceras* is a valid genus, although he did not mention *Menoceras barbouri. Diceratherium (Menoceras) barbouri* is here placed in the genus *Menoceras,* and removed from *Diceratherium.* Specimens from the Runningwater Formation ("B" Quarry, Bridgeport Quarries) were referred to *Menoceras falkenbachi* by Tanner (1972), who never mentioned *Menoceras barbouri* in his diagnosis of *M. falkenbachi,* and possibly they cannot be distinguished. They are nearly identical in size and morphology, so far as can be determined. *Menoceras falkenbachi* Tanner, 1972, is not synonymized with *M. barbouri* (Wood, 1964) here. Further comparisons, that are beyond the scope of the present paper, are necessary to establish this synonymy.

Whatever the status of *M. falkenbachi, M. barbouri* is certainly a valid taxon. It is restricted to the early Hemingfordian (Runningwater Formation in Nebraska, Thomas Farm fauna in Florida), and its occurrence in the Garvin Gully fauna is strong evidence for an early Hemingfordian age of TMM locality 41662.

The only other diagnostic rhino specimen from the Garvin Gully fauna is TMM 31048-

TABLE 3—Comparison of early Hemingfordian *Menoceras.*

Specimen	m3 length			m3 width		
	N	x̄	s	N	x̄	s
Garvin Gully rhino						
TMM 41662-1	1	37.2	—	1	21.5	—
M. barbouri						
MCZ 7445 (type)	1	38.6	—	1	23.0	—
M. falkenbachi						
UNSM 1241 (type)	1	39.9	—	1	22.5	—
M. marslandense						
Runningwater Fm.						
"B" Quarry	2	40.4	5.5	2	22.6	4.1
M. arikarense						
Agate Spring Quarry	14	34.2 (OR = 31.0–37.2)	1.7	14	19.5 (OR = 17.9–29.0)	4.0

48, an isolated right dP4 (Figure 3.4, 3.5). Its lophs are barely worn, which is unusual for a dP4, since it is one of the first deciduous teeth to erupt. The strong crochet and the size of the specimen are comparable to deciduous teeth of *M. "falkenbachi"* from Bridgeport Quarries found in the Harold Cook Collection now in the collections of the American Museum of Natural History. TMM 31048-48 seems to corroborate the Runningwater affinities of the Garvin Gully fauna.

Subfamily ACERATHERIINAE Dollo, 1885
Genus PERACERAS Cope, 1880

Type species.—*Peraceras superciliosum* Cope, 1880.

Revised diagnosis.—*Peraceras* is characterized by a number of derived features, including a brachycephalic skull with procumbent lambdoid crest and occiput, shortened nasals, flat dorsal skull profile, an upturned symphysis in females, a short diastema on the lower jaw, and lingual cingula on most of the lower teeth. It possesses the features that characterize the Aceratheriinae, including greatly reduced premaxilla and the loss of I1, nasal incision retracted to the level above anterior P4, brachydont teeth with weak antecrochets, and primitive rhinocerotid proportions. More derived species of *Peraceras* develop broad zygomatic arches, flaring lamboid crests which secondarily create a concave dorsal skull profile, massive broad postglenoid processes, and very large size.

PERACERAS HESSEI n. sp.
Figures 4–8

Aphelops n. sp. (small form) HESSE, 1943, p. 171.
Diceratherium sp. QUINN, 1955, p. 72–75.
Diceratherium sp. PATTON, 1969, p. 129.

Holotype.—TMM 31219-228, skull from Coldspring, Texas. Dentition worn almost to the alveoli (Figure 4.1–4.4).

Distribution.—Burkeville and Cold Spring faunas (early and late Barstovian, middle Miocene), Texas; late Barstovian of New Mexico.

Etymology.—In honor of Curtis J. Hesse, who first recognized and described the dwarf rhinoceroses.

Referred material.—Burkeville Fauna (early Barstovian): Swiss Alp locality (TMM 31246), Fayette Co., Texas: TMM 31246-1, badly damaged left maxilla with P3–M2. Woodville locality, Tyler Co., Texas: F:AM 108313,

left M3. Moscow l.f., Polk Co., Texas: TMM 31057-160, fragmentary left upper deciduous premolar; TMM 31057-43, fragmentary m2; TMM 31057-11, tusk fragments; TMM 31057-83, left m2; TMM 31057-35, carpals; TMM 31057-28, phalanx. Point Blank l.f., San Jacinto Co., Texas: TMM 31190-29, tibia; TMM 31190-30, femur. Locality 31242, San Jacinto Co., Texas: TMM 31242-30, femur. Trinity River Pit 1, San Jacinto Co., Texas: F:AM 108311, right M1–2; F:AM 108312, right P3; F:AM 108907, left m2; F:AM 108314, radius; F:AM 108315, radius; F:AM 108316, proximal ulna; F:AM 108318, metacarpal V; F:AM 108317, left navicular; F:AM 108298, proximal left metatarsal II; F:AM 108946, proximal left metacarpal II; F:AM 108945, proximal juvenile ulna.

Cold Spring Fauna (late Barstovian): Cold Spring l.f., San Jacinto Co., Texas: TMM 31219-228, skull (type); TMM 31219-227, skull; TMM 31219-229, skull; TMM 31219-225, jaw; TMM 31219-220, jaw; TMM 31219-231, left femur; TMM 31219-247, left femur; TMM 31219-244, left pelvis; TMM 31219-278, left ramus; TMM 31219-45, left ramus; TMM 31219-123, left i2; TMM 31219-226, right m3; TMM 31219-242, right p2; TMM 31219-1, magnum; TMM 31219-48, left femur; TMM 31219-46, radius; TMM 31219-238, right femur; TMM 31219-216, right i2; TMM 31219-193, isolated lower molars; TMM 31219-49, tibia; TMM 31219-209, atlas; TMM 31219-50, ulna. A. D. Donohoe Pit, San Jacinto Co., Texas: F:AM 108340, right and left rami. Four miles southeast of Chapell Hill, Washington Co., Texas: TMM 31272-24, calcaneum. Near Swartaut, Polk Co., Texas: F:AM 108264, right ramus with i2, p2–m3. Belts Creek, Tyler Co., Texas: TMM 40622-1, right maxilla with dP1–2. McMurray Pits 1 and 2, San Jacinto Co., Texas: F:AM 108268, left ramus with m1–3; F:AM 108267, right ramus with p2, m2–3; F:AM 108274, left tibia; F:AM 108307, skull with left and right P4–M3; F:AM 108337, 2 metatarsals III; F:AM 108336, 2 metatarsals II; F:AM 108335, 2 ectocuneiforms; F:AM 108334, left navicular; F:AM 108333, patella; F:AM 108332, astragalus; F:AM 108331, distal tibia; F:AM 108330, distal right femur; F:AM 108329, distal left femur; F:AM 108328, left tibia; F:AM 108327, right femur; F:AM 108326, 2 unciforms; F:AM 108322, proximal radius; F:AM 108319, right humerus; F:AM 108325, 2 magnums; F:AM 108324, 2 lunars; F:AM 108323, 5 scaphoids; F:AM 108321, radius; F:AM 108320, distal right humerus; F:AM 108310, damaged left M1–3; F:AM 108309, left M1; F:AM 108308, mandible; F:AM 108944, juvenile mandible with dp2–4, m1 erupting. Noble Farm, five miles east of Navasota, Grimes Co., Texas: TAM 2191, right M3, P2, m2; TAM 2674, symphysis with left i2; TAM 2591, palate with right P1–M2, left M2–3.

Fleming Formation, level unknown: Hallettsville locality, Lavaca Co., Texas: TAM 2202, skull with left and right P4, M1–3.

Diagnosis.—Primitive, small-sized *Peraceras* with relatively robust limb elements, reduced occiput, and lambdoid crest with slight lateral flare.

Description.—The type specimen of *Peraceras hessei*, TMM 31219-228, is a skull that has been heavily restored with plaster
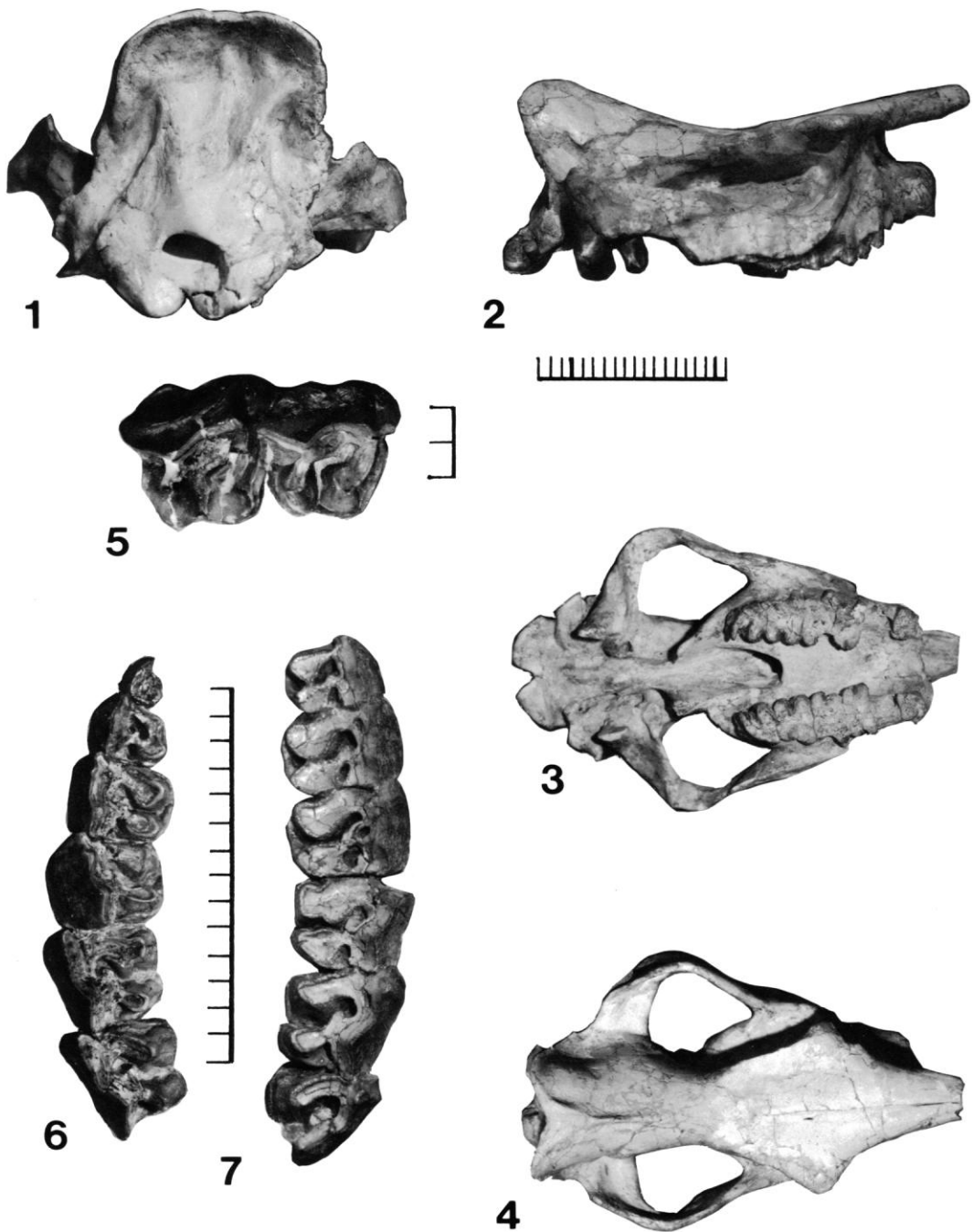
FIGURE *4—Peraceras hessei* n. sp. *1–4,* TMM 31219-228, holotype skull, in posterior, right lateral, palatal, and dorsal views; *5,* F:AM 108311, right dP3–4; *6,* TAM 2591, right dP1–M2; *7,* TMM 31219-227, left P2–M3. Scales in cm.
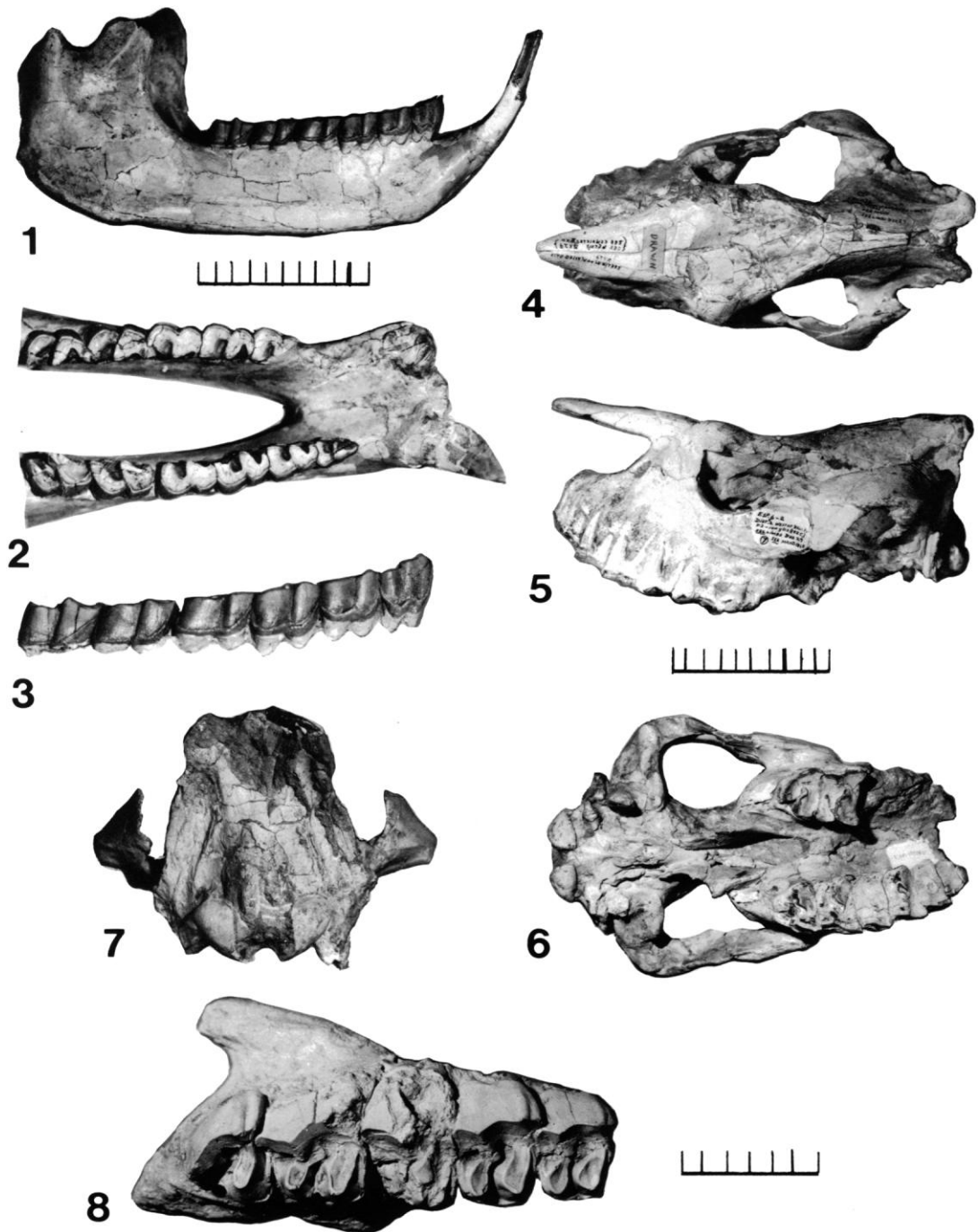
FIGURE 5—*Peraceras hessei* n. sp. *1–3,* TMM 31219-225, mandible, in right lateral view, crown view, and close-up of right lateral view of teeth; *4–7,* F:AM 109360, skull in dorsal, left lateral, palatal, and posterior views; *8,* UCMP 31043, right maxilla with P3–M3, crown view. Scales in cm.

TABLE 4—Skull and upper tooth measurements (in mm).

	Peraceras hessei TMM 31219-228 (type)	*P. hessei* (ref.) TMM 31219-227	*P. hessei* (ref.) TMM 31219-229	*P. hessei* (ref.) F:AM 108307	*P. hessei* (ref.) TAM 2591	*P. cf. hessei* F:AM 109360 (New Mexico)	*Peraceras profectum* (ref.) F:AM 108838	*Aphelops megalodus* AMNH 8292 (type)	*Teleoceras meridianum* (ref.) F:AM 108306	*Teleoceras medicornutum* AMNH 9832 (type)	*Teleoceras medicornutum* (ref.) F:AM 108838	*?Peraceras sp.* UCMP 31043
Foramen magnum to anterior P2	360.0	361.0	—	—	—	371.0	431.0	427.0	—	498.0	524.0	—
Occipital crest to tip of nasals	348.0	—	—	379.0	—	375.0	413.0	457.0	—	520.0	—	457.0
Zygomatic width	255.0	214.0	220.0	236.0	—	240.0	251.0	299.0	323.0	329.0	—	—
Palatal width	49.9	62.1	65.2	65.4	—	52.3	55.0	64.2	82.0	62.0	79.5	64.2
Lambdoid crest width between M3	133.0	107.0	150.0	150.0	—	142.0	163.0	186.0	179.0	252.0	214.0	—
P2–M3 length	166.0	168.0	—	—	—	196.0	227.0	225.0	—	253.0	273.0	—
M1–M3 length	92.0	90.0	96.0	98.0	—	104.0	126.0	129.0	138.0	153.0	162.0	116.0
P2 length	23.5	24.5	—	—	23.6	21.5	24.0	27.7	—	28.0	34.6	—
P2 width	28.2	32.0	26.5	—	27.4	32.2	43.1	36.7	—	35.5	39.0	—
P3 length	25.0	27.3	37.0	—	27.8	27.6	33.2	32.8	—	32.6	38.3	32.2
P3 width	31.0	37.8	29.6	—	36.4	44.6	56.9	46.1	—	49.5	53.5	43.6
P4 length	27.6	28.5	40.8	—	31.7	30.4	37.5	35.7	—	40.5	41.5	32.7
P4 width	41.5	37.8	31.5	—	39.5	49.0	60.4	49.4	—	60.0	62.7	50.3
M1 length	26.8	30.0	39.7	30.0	34.5	30.9	37.6	42.8	46.4	44.8	52.5	36.0
M1 width	40.4	35.6	33.7	43.8	37.5	49.6	58.0	57.8	61.2	67.5	73.8	58.7
M2 length	30.0	34.3	39.6	34.7	38.2	35.3	43.2	45.0	49.6	57.4	58.2	40.4
M2 width	41.0	37.6	32.0	41.5	37.5	51.0	61.0	59.0	68.3	68.5	73.1	52.0
M3 length	36.7	31.0	34.0	32.5	34.7	37.4	45.8	41.3	47.3	54.3	49.6	39.7
M3 width	37.0	35.4	—	37.4	35.8	46.4	59.0	51.0	51.0	66.8	59.5	47.4

(Figure 4.1–4.4). Enough bone is present, however, to ascertain that the original shape has been maintained. The skull of *P. hessei* has shortened, broad nasals characteristic of *Peraceras,* with a relatively flat dorsal profile. The lateral margins of the nasals curve under abruptly. The nasals are not fused. There is no sign of a nasal horn, although the anterior tip has been broken off. There are pronounced rugosities over the anterior part of the orbit. The flat dorsal surface of the frontals meets the parietal-occipital region with a sharp inflection. The lambdoid crests show little lateral flaring. There is a single narrow sagittal crest. The occiput is procumbent. The zygomatic arches are deep and widely flaring, but this may be an artifact of restoration. The premaxillae and the anterior part of the maxillae are missing from the type and other skull referred to *P. hessei.* The nasal incision is retracted to the level of anterior P4. There is a small infraorbital foramen anterior to the orbit at the posterior end of the nasal incision.

The basicranium of TMM 31219-228 is mostly plaster restoration. The confluent mastoid-paroccipital processes have been restored incorrectly. Comparison with less damaged skulls, such as TMM 31219-227, shows that the mastoid process is quite massive. A small but distinct parocciptal process is present (contrary to the restoration of the type). There is a shallow anteriorly-facing pocket between the mastoid and paroccipital processes. The postglenoid process is also massive, with a distinct ventral knob frequently found in *Peraceras.* The postglenoid process and the mastoid process are not confluent. The basicranial foramina and petrosal region are poorly preserved, although the hypoglossal foramen, posterior lacerate foramen, medial lacerate foramen, foramen ovale, and posterior opening of the alisphenoid canal can be distinguished on at least one skull. All of the skulls are too badly damaged to identify orbital foramina. The pterygoid flange shows a strong lateral flare in F:AM 108307. The palate is badly damaged in all specimens.

An additional skull referable to *P. hessei* (F:AM 109360, Figure 5.4–5.7) is the best preserved of any skull referable to this species. Although it is from the Barstovian of New Mexico, it is discussed in this paper because it shows the morphology of *P. hessei* prior to crushing and restoration. The basal tooth dimensions are larger than is typical for *P. hessei* (Table 4), but this is probably due to extreme wear. Lateral expansive deformation of the basal diameter of the teeth is common in very old individuals. Tooth row lengths, which are less susceptible to deformation with age, and all skull dimensions of F:AM 109360 are comparable to other specimens of *P. hessei.* The large collection of Frick New Mexico *Peraceras* was compared to the Texas material, but could not be included in this study.

The dentition of the type skull, TMM 31219-228, is worn almost to the alveoli and is missing P3 on both sides. The dentitions of TMM 31219-227 (Figure 4.7) and TAM 2591 (Figure 4.6) are much less worn and serve as the basis for this description. The upper teeth are brachydont, with unreduced premolars. A dP1 is present on TAM 2591. It has a very weak protoloph and a strong metaloph, with a closed medifossette. The upper premolars have strong continuous anterior, lingual, and posterior cingula; the molars have no cingula. P2 shows a strong protocone-hypocone connection, but all of the other premolars are molariform. The prefossette formed on P2 is elliptical in shape. On the relatively unworn P2 of TAM 2591, there is a small medifossette due to the contact of the crista and crochet. In the other premolars, however, the crochets are usually unconnected with the cristae. This feature is variable, however; in TMM 31219-227, the left P4 has a medifossette, but the right lacks it. The postfossettes in the premolars are generally circular or elliptical, with their long axes oriented parallel to the long axis of the skull. In P4 and the molars, the postfossettes become more triangular in shape, opening posteriorly.

The molars have strong parallel-sided lophs with weak antecrochets. Crochets are moderately well-developed on most molars, but cristae are usually absent. The molars have strong anterior cingula, but the lingual cingula are weak and do not connect the protoloph and metaloph. Posterior cingula are usually well-developed, passing labially to enclose triangular postfossettes. M3 is triangular, with a weak crochet and no antecrochet. The anterior cingulum on M3 is strong, but the posterior cingulum is absent except for a small spur (the remnant of the posterior metacone).

TABLE 5—Lower jaw and teeth measurements (in mm).

	P. hessei[1]			A. megalodus	T. meridianum[2]			T. medicornutum[3]		
	N	x̄	s	(type)	N	x̄	s	N	x̄	s
Mandible length	5	379.0	21	461.0	2	443.0	20	1	489.0	—
Top of condyle to angular process	6	159.0	20	208.0	2	200.0	20	1	247.0	—
Width symphysis at tusks	4	68.0	15	87.0	2	85.0	1	1	85.0	—
Length i3–p2 diastema	4	29.0	12	57.0	2	48.0	11	1	54.0	—
Depth of jaw below m1	7	69.0	5	74.0	2	69.0	17	2	90.0	4
p2–m3 length	5	183.0	13	217.0	0	—	—	0	—	—
i3 length	1	92.2	—	80.5	0	—	—	1	68.8	—
i3 basal diameter	2	26.9	2	32.5	0	—	—	1	22.5	—
p2 length	3	23.3	2	27.7	0	—	—	0	—	—
p2 width	3	16.8	0.4	36.7	0	—	—	0	—	—
p3 length	6	28.9	3	32.8	2	24.0	2	2	33.5	4
p3 width	6	22.1	2	46.1	2	21.6	4	2	26.5	1
p4 length	6	29.7	2	35.7	2	31.0	1	2	42.5	4
p4 width	6	24.1	6	49.4	2	28.0	6	2	31.1	1
m1 length	6	28.5	3	37.0	1	38.8	—	2	49.3	1
m1 width	6	25.6	7	29.0	2	31.3	2	2	35.8	1
m2 length	7	31.0	5	42.0	2	44.1	3	2	54.6	0.1
m2 width	7	25.8	7	27.7	2	29.4	3	2	36.6	0.6
m3 length	7	31.8	6	44.6	2	49.7	0.6	2	60.1	4
m3 width	7	26.0	8	27.2	2	29.8	3	2	35.6	4

[1] Sample of *Peraceras hessei* includes: TMM 31219-225, TMM 31219-220, TMM 31219-278, F:AM 108308, F: AM 108257, F:AM 108346, F:AM 108264.

[2] Sample of *Teleoceras meridianum* includes: F:AM 108839, F:AM 108338.

[3] Sample of *Teleoceras medicornutum* includes: AMNH 9832 (holotype), F:AM 108349.

The best preserved mandible is TMM 31219-225 (Figure 5.1), which is complete except for a broken left i2 and p2. The symphysis has a strong upward inflection and short diastema that is characteristic of *Peraceras*. Although the type specimen of the genus, *P. superciliosum,* lacks a mandible, several workers (Stock and Furlong, 1926; Dalquest and Hughes, 1966) have correctly surmised that jaws in their collections (Clarendonian forms, probably females, referable to *P. superciliosum*) with upturned symphyses and short diastemata might belong to *Peraceras.* Associated skull and mandibles of *P. profectum* in the Frick Collection have shown this to be true. The right tusk in TMM 31219-225 is large and pointed with a strong medial ridge. It flares only slightly away from the midline. Its elongate shape is characteristic of a male tusk. F:AM 108267 has an i2 alveolus of the appropriate small size and stout shape for a female. The posterior part of the jaw shows the normal aceratherine angle, condyle, and coronoid process.

The lower teeth are brachydont with the stereotyped rhinocerotid pattern. There is no dp1, and p2 overhangs the diastema. The lower premolars and molars all have strong labial cingula. Each cingulum extends anterodorsally to the surface of the preceding tooth. Small cingula are present also on the lingual side of the tooth, but are usually distinct only along the base of the protolophid.

Postcranial skeleton.—Most of the postcranial material of *P. hessei* comes from McMurray Pit Number 2 and has undergone much crushing and plastic deformation. Thus, the comparisons given below must be interpreted with caution, since it is likely that many of the differences observed may be due to postmortem effects. The postcranial elements described here are shown in Figures 6–8 and Table 5. No vertebrae, scapulae, or ribs are yet known for *P. hessei.*

The humerus (Figure 6.1, 6.2) shows relatively little rugosity on the lateral epicondyle and medial border of the olecranon fossa. The radius (Figure 6.5) is quite small; on the proximal end the bicipital rugosity and the ulnar facets are very weak. The distal lateral facets for the ulna (Figure 6.3, 6.4) are also weakly developed. The facets for the carpals
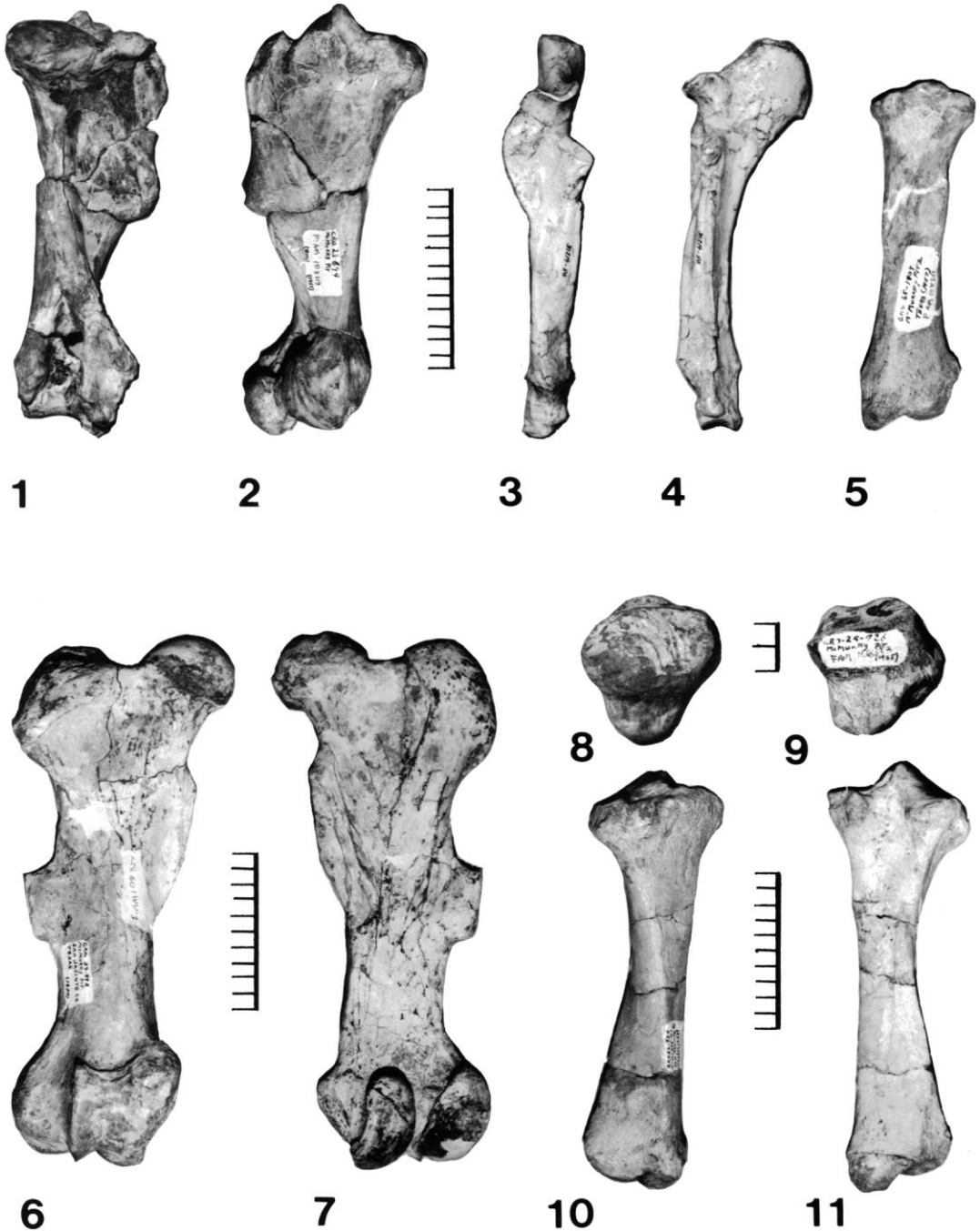
FIGURE 6—*Peraceras hessei* n. sp. *1*, *2*, F:AM 108319, humerus; *3*, *4*, TMM 31219-50, ulna; *5*, F:AM 108321, radius; *6*, *7*, F:AM 108327, femur; *8*, *9*, F:AM 108333, patella; *10*, *11*, F:AM 108274, tibia. Scales in cm.
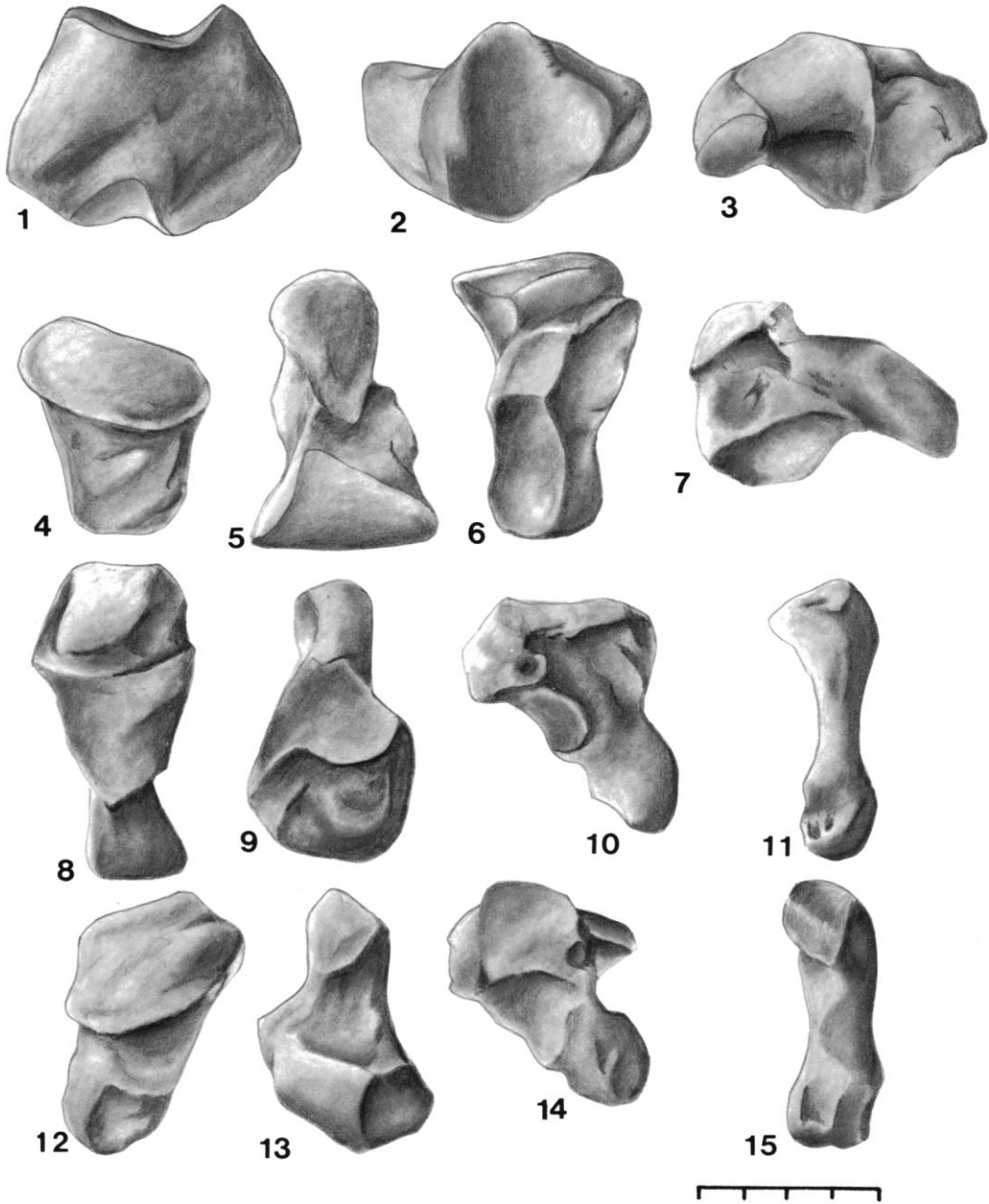
FIGURE 7—*Peraceras hessei* n. sp. Manus elements. *1–3*, F:AM 108323a, right scaphoid, in lateral, proximal, and distal views; *4–7*, F:AM 108324a, left lunar, in dorsal, proximal, distal, and left lateral views; *8–10*, F:AM 108325a, right magnum, in distal, dorsal, and left lateral views; *12–14*, F:AM 108326b, right unciform, in dorsal, proximal, and left lateral views; *11, 15*, F:AM 108318, right metacarpal V in lateral and posterior views. Scale in cm.

are very deep. The ulna has a short but slender shaft that is reduced relative to the size of the proximal end. The lateral articulation for the humerus and radius bears only a faint ridge separating the two bones. The greater

sigmoid cavity is broadly arched, with a distinct facet for the medial condyle of the humerus.

The manus (Figure 7) of *P. hessei* is known only from the scaphoid, lunar, magnum, un-

ciform, and metacarpals III and V. The scaphoid (Figure 7.1–7.3) has the basic primitive aceratherine shape, except that the radial facet is smaller and less convex. The anterior dorsal lunar facet is small and poorly developed. There is no posterior lunar facet. The lunar (Figure 7.4–7.7) is gracile, and the ulnar facet is separated from the body of the lunar by a constriction. The lunar bears a sulcus separating the ulnar facet from the unciform facet. The magnum (Figure 7.8–7.10) is gracile, with a large unciform facet and a sulcus between the facets for metacarpal II and the scaphoid. The metacarpal III facet of the magnum is also reduced. The unciform (Figure 7.12–7.14) is gracile, with a less robust posterior process. Metacarpal II is quite small, and the facet for metacarpal III and the posterior rugosity are less well developed. A tiny, reduced metacarpal V (Figure 7.11, 7.15) that could only belong to *P. hessei* is also present in the collection. Contrary to Wood (1964), both *Peraceras* and *Aphelops* had phalanx-bearing fifth metacarpals, now known from large quarry samples of both rhinos.

Besides the flattening due to postmortem crushing, the femur (Figure 6.6, 6.7) has a broadly flared greater trochanter with a triangular proximal surface. The anterior face of the greater trochanter bears a strong crest. The third trochanter is rectangular in shape, with sharp proximal and distal borders. The tibia (Figure 6.10, 6.11) has a slender shaft and a narrow, laterally-truncated fibular facet. No fibula is known for *P. hessei.* The patella (Figure 6.8, 6.9) is relatively thin and gracile and lacks a ridge on the distal tuberosity.

The pes of *P. hessei* (Figure 8) is known from the astragalus, navicular, ectocuneiform, and metatarsals II and III. The astragalus (Figure 8.1–8.3) has a lateral calcaneal facet which is broader and less concave. There is a distinct fossa lateral to the sustentacular facet. The navicular (Figure 8.4–8.6) has distinct distal facets. The ectocuneiform (Figure 8.7–8.9) is quite small and has suffered the effects of proximodistal crushing. Metatarsal III (Figure 8.10–8.12) is gracile, and the phalangeal articulation extends further anteroproximally. Metatarsal II is also very gracile and bears a reduced facet for metatarsal III.

Discussion. —Hesse (1943) first recognized a small aceratherine rhinoceros in the collections from the Texas Gulf Coastal Plain. In his unpublished manuscript (kindly furnished by J. A. Wilson), he wrestled with the problem of the similarity of primitive Barstovian rhinoceroses. The confusion among *Aphelops, Teleoceras,* and *Peraceras* in the literature was compounded by taxonomic concepts that were based on more derived forms. The Frick Collection has greatly improved the sample of late Hemingfordian and Barstovian rhinoceroses and will make it possible to clear up some of taxonomic confusion that presently exists.

Primitively, *Aphelops* and *Peraceras* are so similar in all but certain skull features that we were also confused about the affinities of the dwarf aceratherine (Prothero and Sereno, 1980). Uncrushed skulls with complete dentitions from the Texas Memorial Museum collections clearly show that this dwarf is a primitive *Peraceras.* The reasons for this confusion are discussed above. Many of the characters that presently define *Peraceras* are true only of the later, more derived species such as *P. superciliosum.* The present comparisons are made chiefly with undescribed *Peraceras* material from the Barstovian of New Mexico, Colorado, and Nebraska, which is assigned to *P. profectum.* The diagnosis of the genus *Peraceras* has been revised to reflect this. Comparisons of *Aphelops, Peraceras,* and *Teleoceras* based on Frick Collection specimens are given in Tables 4–6.

Peraceras hessei is clearly a dwarf species, rather than a primitively small, earlier member of the genus, because it is the smallest aceratherine rhinoceros in North America. Its contemporary sister-species, *P. profectum,* is 20 percent larger. Most other aceratherines, including *Aphelops, Aceratherium* s.s., and *Chilotherium,* are even larger than *P. profectum.* Indeed, *P. hessei* is the smallest post-Hemingfordian rhinoceros of any kind that is known. The small size is not due to sexual dimorphism for several reasons: 1) extreme sexual dimorphism in size is almost unknown among rhinocerotids (Laurie, 1982); 2) both male- and female-shaped lower incisors are present in the collection; 3) there are no *P. profectum* in the Texas faunas.

There is, however, an intermediate-sized aceratherine, UCMP 31043 (Figure 5.8), from J. Fietsam's Farm, east of Ammansville, Fay-
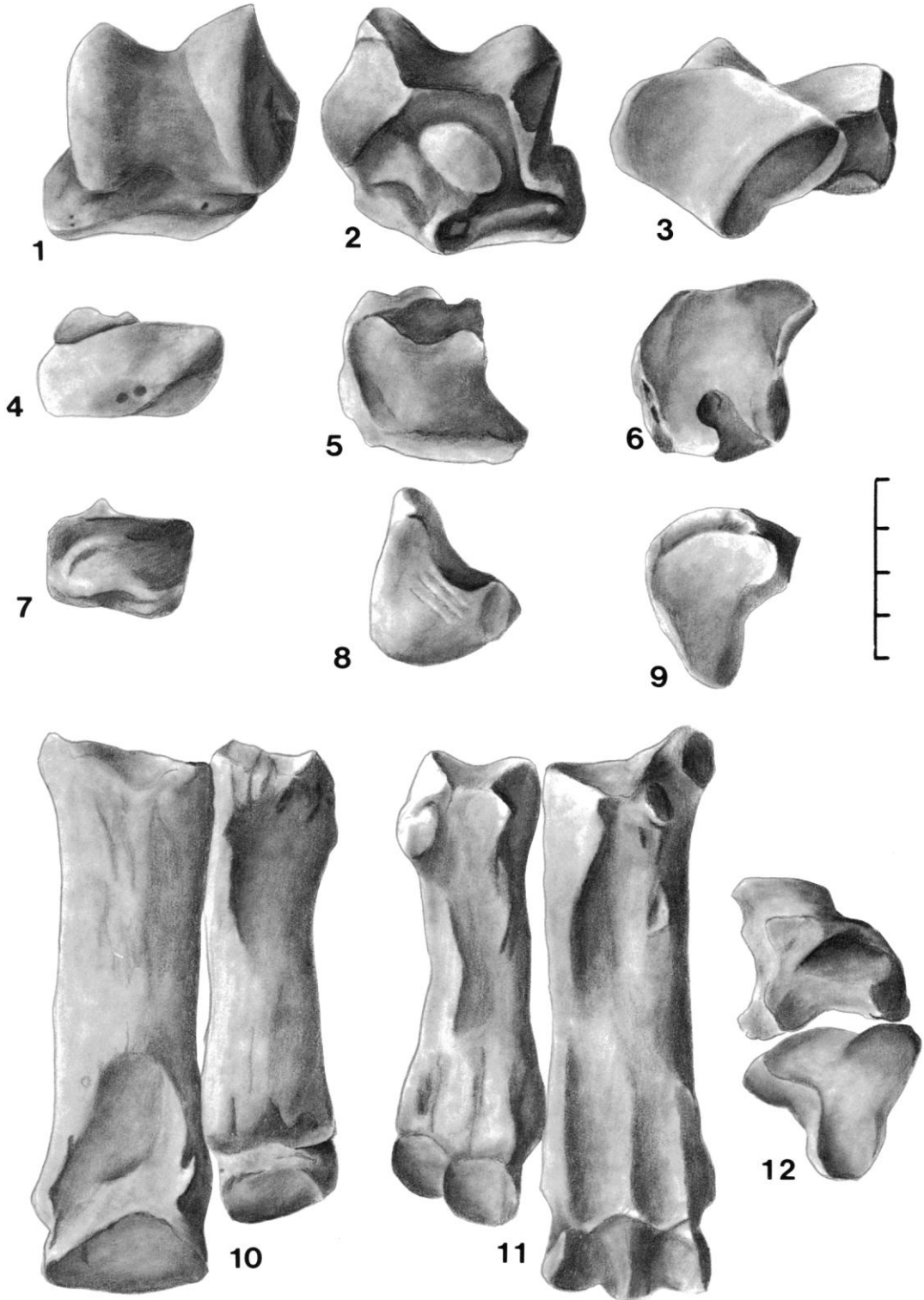
FIGURE 8—*Peraceras hessei* n. sp. Pes elements. *1–3,* F:AM 108332, left astragalus, in dorsal, plantar, and distal views; *4–6,* F:AM 108334, left navicular, in dorsal, proximal, and distal views; *7–9,* F:

ette County, Texas. This locality (Figure 1) would appear to be part of the Cold Spring Fauna, based on its stratigraphic position. Matthew (1932, p. 420) referred this specimen (possibly on the basis of location alone) to *Aphelops meridianus,* but, as discussed below, Leidy's type of *meridianus* is not an *Aphelops* at all, but a *Teleoceras.* UCMP 31043 consists of a right maxilla with P3–M3. It is brachydont with weak antecrochets. Both features suggest a primitive aceratherine. Since primitive *Aphelops* and *Peraceras* cannot be distinguished on upper dentitions alone, the specimen could be referred to either genus. In size (Figure 5.8, Table 4) it is much smaller than *A. megalodus* or *P. profectum,* and larger than *P. hessei.* In tooth area it matches the New Mexico specimen of *P. hessei* (F:AM 109360). But, as pointed out above, this individual has unusually large tooth area for *P. hessei* because of its extreme tooth wear. A species assignment for UCMP 31043 is not made until a thorough review of the New Mexico material is done.

PERACERAS PROFECTUM
(Matthew, 1899) n. comb.
Figure 9

Aceratherium profectum MATTHEW, 1899, p. 71.
Aphelops profectus (Matthew). MATTHEW, 1901, p. 358.
Aphelops profectus (Matthew). OSBORN, 1904, p. 317.
Peraceras n. sp. TANNER, 1976, p. 50.
Diceratherium jamberi TANNER, 1977, p. 121.

Holotype.—AMNH 9082, a lower jaw with m3, fragments of upper teeth, right squamosal region of the skull, and atlas.

Discussion.—The type of "*Aceratherium*" *profectum,* AMNH 9082, consists of fragmentary right and left rami, with both left and right m3. Other fragments include a skull fragment consisting of the right postglenoid process, posterior portion of the right zygomatic arch, and associated occipital and paroccipital bones, and additional skull and tooth fragments. All are from the Barstovian Pawnee Creek Formation, Logan County, Colorado. The type rami compare extremely well
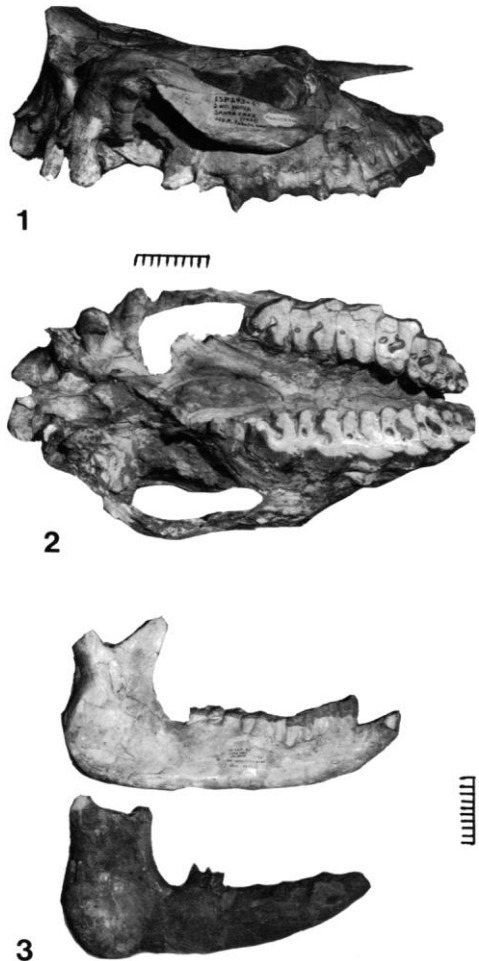

FIGURE 9—*Peraceras profectum.* *1, 2,* F:AM 108338, referred skull, right lateral and palatal views; *3,* F:AM 108338, right ramus, and AMNH 9082, holotype ramus. Scale in cm.

(Figure 9.3) with a skull and mandible (F:AM 108338, Figure 9.1, 9.2) from the Barstovian of New Mexico (specifically, from the Pojoaque Member of the Tesuque Formation). Both F:AM 108338 and AMNH 9082 show the characteristic features of *Peraceras*: short, upward-inflected symphysis and short diastema, and lingual cingula on the lower molars. The skull shows additional *Peraceras* features, such as the procumbent and laterally

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AM 108335a, right ectocuneiform, in dorsal, proximal, and distal views; *10–12,* F:AM 108337a, right metatarsal III, and F:AM 108336b, right metatarsal II, in dorsal, plantar, and proximal views. Scale in cm.

TABLE 6—Measurements of postcranial skeleton (in mm).

	Peraceras hessei			Aphelops megalodus			Teleoceras meridianum			Teleoceras medicornutum		
	N	x̄	s	N	x̄	s	N	x̄	s	N	x̄	s
Scapula length	0	—	—	0	—	—	1	239.6	—	0	—	—
Scapula width	0	—	—	0	—	—	1	173.0	—	0	—	—
Humerus length	1	262.0	—	4	307.3	17	3	264.0	10	2	365.5	2
Humerus, proximal width	1	113.6	—	4	119.1	6	2	86.4	0.1	3	131.6	10
Humerus, midshaft width	1	45.1	—	5	47.0	6	6	47.8	3	3	55.1	2
Humerus, distal width	1	66.5	—	5	94.7	7	6	87.7	3	3	114.2	17
Radius length	1	217.0	—	5	264.2	18	2	215.3	14	2	299.5	8
Radius, midshaft width	3	40.0	8	5	41.3	2	2	41.9	2	3	47.8	1
Radius, distal width	3	61.7	2	5	74.9	10	3	77.0	6	2	89.4	2
Ulna length	1	263.0	—	1	348.0	—	0	—	—	0	—	—
Ulna, olecranon to sigmoid notch	1	79.8	—	4	96.6	15	0	—	—	2	94.0	7
Ulna, midshaft width	2	30.0	0.2	4	36.5	4	0	—	—	2	47.6	5
Scaphoid, lateral width	5	42.9	4	5	51.4	2	2	54.1	0.1	1	64.6	—
Scaphoid, proximodistal length	5	26.7	2	5	34.8	1	2	27.1	0.5	1	35.3	—
Metacarpal II length	1	80.2	—	4	109.6	9	2	92.7	2	5	113.9	2
Metacarpal II width	1	21.1	—	6	29.8	6	2	31.2	4	5	43.4	2
Metacarpal III length	0	—	—	4	120.5	4	2	103.7	1	4	125.2	9
Metacarpal III width	0	—	—	4	36.5	3	2	43.8	2	4	50.9	2
Femur length	6	345.7	10	5	387.8	13	1	398.0	—	2	415.0	7
Femur, proximal width	4	130.7	8	3	150.4	9	1	144.8	—	2	149.8	3
Femur, midshaft width	4	38.8	7	4	57.4	10	1	64.3	—	4	66.5	5
Femur, distal width	6	90.8	9	5	108.8	2	2	110.2	1	2	115.1	7
Tibia length	3	263.7	8	3	290.3	20	4	218.0	7	6	271.4	13
Tibia, proximal width	1	84.5	—	3	93.3	6	4	98.6	7	7	110.3	9
Tibia, midshaft width	3	36.2	7	5	40.4	5	4	40.4	6	8	48.5	3
Tibia, distal width	2	66.0	2	6	72.1	7	4	70.2	5	8	85.3	3
Astragalus, lateral width	1	49.6	—	7	61.4	4	0	—	—	2	71.6	2
Astragalus, proximodistal length	1	49.2	—	7	58.8	2	0	—	—	2	68.4	5
Navicular width	2	35.3	3	2	41.2	0.5	2	39.3	2	1	55.0	—
Navicular, proximodistal length	2	14.6	1	2	17.0	2	2	15.4	1	1	20.4	—
Metatarsal III length	2	101.4	5	3	99.1	3	1	87.1	—	4	113.7	5
Metatarsal III width	2	26.8	1	3	26.3	3	1	31.5	—	4	45.9	3

flaring occiput, short pointed nasals, flat dorsal skull profile, and laterally-broadened postglenoid process. The rami of F:AM 108338 are very similar in size to the holotype, AMNH 9082 (Table 7). It seems clear that "*Aceratherium*" *profectum* should be referred to *Peraceras*.

Tanner (1977) described a skull from the late Barstovian Jamber l.f., lower Valentine Formation, Boyd County, Nebraska. Tanner considered this fauna to be lower Pliocene in age, but the late Barstovian is now considered to be middle Miocene (Tedford et al., 1987). Tanner (1976, 1977) wrestled with assigning this skull (UNSM 62048) to *Peraceras* or to *Diceratherium,* but eventually named it a new species, *Diceratherium jamberi.* The only feature of the specimen that suggests diceratherine affinities is very slight rugosities on the nasals, which Tanner considered to be evidence for paired nasal ridges. However, upon examination of this specimen, the insignificant roughening on the nasals does not bear any close resemblance to the true ridges of *Diceratherium.*

In every other feature, including size, "*Diceratherium jamberi*" is almost a perfect match for *Peraceras profectum* (Table 7). Tanner (1977) may not have realized what primitive *Peraceras* looked like, since most published descriptions of the genus are based on very derived, late forms such as *P. superciliosum.* All of the features cited by Tanner as evidence for diceratherine affinities are features that are also found in primitive aceratherines. Thus, *Diceratherium jamberi* is considered a junior synonym of *Peraceras profectum.* This synonymy eliminates the anomalously late occurrence of *Diceratherium* suggested by Tanner.

Genus APHELOPS Cope, 1874

Revised diagnosis.—*Aphelops* shows the derived features of a dorsally-arched nasofrontal profile (primitively flat) and an unusually long diastema between the i2 (lower tusk) and the first premolar. In most other features, *Aphelops* retains the primitive aceratherine condition, including: greatly reduced premaxilla and loss of I1; broad, unfused, hornless nasals with only slightly downturned lateral edges; nasal incision retracted to the level above anterior P4; brachydont teeth without cement; upper molars with

Table 7—Measurements (in mm) of *Peraceras profectum.*

Character	Holotype AMNH 9082	F:AM 108338	"D. jamberi" UNSM 62048
Length, angle to symphysis	400	422	—
Length, angle to condyle	215	195	—
Length, diastema	34	31	—
Depth below p3	70	77	—
Depth below m2	82	84	—
m3 length	43.5	45.5	—
m3 width	26.0	28.1	—
Occipital condyle to nasals	—	450	470
Occipital crest to nasals	—	415	453
Occipital condyle to dP1	—	440	440
Occipital crest to narial notch	—	348	354
Foramen magnum to palatal notch	—	250	237
Narial notch to tip of nasals	—	107	107
Zygomatic breadth	—	258	277
Width between M2	—	168	170
Occipital height	—	177	162
Occipital width	—	159	165
Width of occipital condyle	—	92	104
dP1–M3 length	—	238	236
M1–3 length	—	126	123
dP1–P4 length	—	120	115
dP1 length	—	19	23
dP1 width	—	18	20
P2 length	—	24	29
P2 width	—	43	39
P3 length	—	33	32
P3 width	—	56	48
P4 length	—	38	33
P4 width	—	60	57
M1 length	—	38	40
M1 width	—	58	55
M2 length	—	43	43
M2 width	—	61	60
M3 length	—	46	47
M3 width	—	59	58

weak antecrochets; primitive lambdoid crests (skull triangular in posterior view); narrow zygomatic arches; lower tusk (i2) sub-circular in cross section; and primitive rhinocerotid skeletal proportions. Contrary to Quinn (1955) and Patton (1969, p. 119), *Aphelops* is not particularly "long-legged," relative to more primitive (or the living) rhinos. It only seems so in contrast to the unusually short-legged *Teleoceras,* with which it is frequently found. Later, more derived species of *Aphelops* develop mesodont teeth, further nasal incision retraction, and long slender nasals.
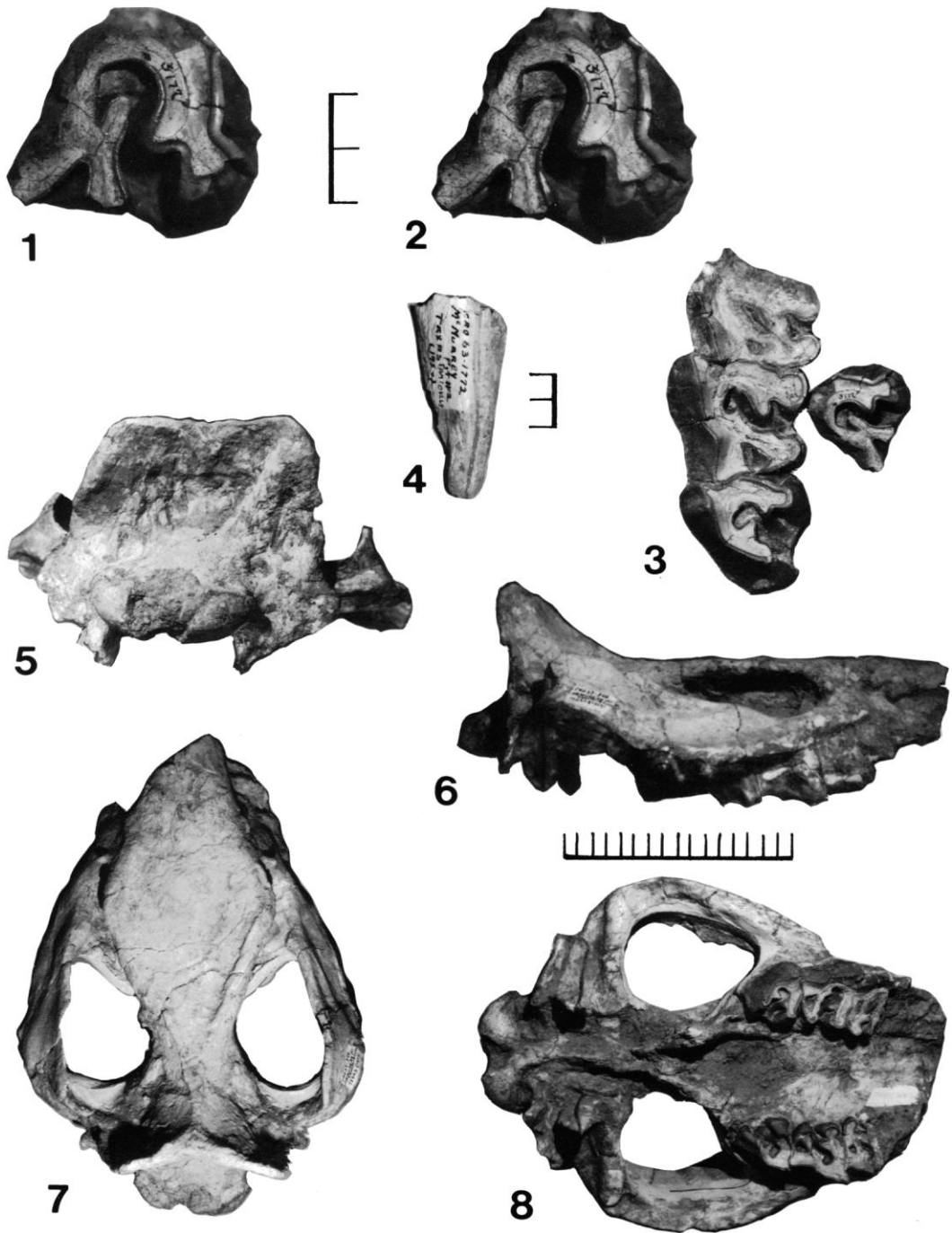
FIGURE *10—Teleoceras meridianum* n. comb. *1, 2,* USNM 3177, stereopair of holotype right ?M2; *3,* comparison of USNM 3177 (right) with right M1–3 of F:AM 108306 (left); *4,* F:AM 108269, isolated nasals, dorsal view; *5–8,* F:AM 108306, referred skull, posterior, right lateral, dorsal, and palatal views. Scales in cm.

APHELOPS MEGALODUS (Cope, 1873)

Aceratherium megalodum COPE, 1873, p. 1.
Aphelops megalodus (Cope). COPE, 1874, p. 520.
Aphelops sp. (large) HESSE, 1943, p. 171.

Holotype. — AMNH 8292, a complete male skull and jaws from the late Barstovian of the Pawnee Creek area, northeast Colorado.

Distribution. — Burkeville and Cold Spring faunas (early and late Barstovian, middle Miocene), Texas Gulf Coastal Plain, and in many other Barstovian localities outside of Texas.

Referred material. — Burkeville Fauna (early Barstovian): Trinity River Pit 1, San Jacinto Co., Texas: F:AM 108892, 2 metacarpals V; F:AM 108906, 4 fibulae; F:AM 108905, 3 tibiae; F:AM 108904, 3 patellae; F:AM 108903, 4 patellae; F:AM 108902, 3 partial femora; F:AM 108901, 2 femora; F:AM 108900, partial ulna; F:AM 108899, 2 radii; F:AM 108898, 4 humeri; F:AM 108927, 3 metacarpals IV; F:AM 108926, 3 metacarpals III; F: AM 108925, 4 metacarpals II; F:AM 108924, entocuneiform; F:AM 108923, 2 ectocuneiforms; F:AM 108922, 2 naviculars; F:AM 108921, pisiform; F:AM 108920, trapezoid; F:AM 108919, 3 unciforms; F:AM 108918, 3 unciforms; F:AM 108917, cuneiform; F:AM 108916, 2 lunars; F:AM 108915, 4 scaphoids; F:AM 108914, 3 calcanea; F:AM 108913, 3 calcanea; F:AM 108912, 3 calcanea; F:AM 108911, 3 astragali; F:AM 108910, 4 astragali; F:AM 108909, 2 M1's; F:AM 108908, left M3; F:AM 108931, 2 metatarsals IV; F:AM 108930, 3 metatarsals III; F:AM 108929, 2 metatarsals II. Woodville localities, Tyler Co., Texas: F:AM 108932, proximal right scapula; F:AM 108943, left metacarpal II; F:AM 108942, right metacarpal III; F:AM 108941, right metatarsal III; F:AM 108940, left metatarsal IV; F:AM 108938, 3 isolated worn upper molars; F:AM 108936, left calcaneum; F:AM 108935, right scaphoid; F:AM 108934, right calcaneum; F:AM 108933, proximal ulna.

Cold Spring Fauna (late Barstovian): Two miles northeast of Cold Spring, San Jacinto Co., Texas: F:AM 108956, juvenile mandible with dp2-4 and m1 erupting. Three miles north of Cold Spring, San Jacinto Co., Texas: F:AM 108955, right femur. Near Swartaut, Polk Co., Texas: F:AM 108939, right M1; F:AM 108937, right i2. McMurray Pits, San Jacinto Co., Texas: F:AM 108959, patella; F:AM 108958, 3 tibiae; F:AM 108957, 3 femora; F:AM 108954, right metatarsal II; F:AM 108953, left metacarpal II; F:AM 108952, right metatarsal III; F: AM 108950, 3 calcanea; F:AM 108951, astragalus; F: AM 108949, cuboid; F:AM 108948, 3 fibulae; F:AM 108947, 2 proximal ulnae.

Diagnosis. — Smaller than all other species of *Aphelops*. Nasal incision not retracted further than above anterior P4 (to posterior P4 in *A. malacorhinus*, to M1 in *A. mutilus*).

Discussion. — Although there is a large amount of *Aphelops* material from Texas, no complete skulls are yet known to show conclusively that it is *Aphelops* and not *Peracer-*

as. The lower jaw material, however, has the procumbent symphysis, long diastema, and lack of cingula characteristic of *Aphelops* and not of *Peraceras.* The postcranial material is all too large to belong to *P. profectum* and is comparable in size to *A. megalodus* material from the early Barstovian of Colorado and Nebraska, particularly the sample from the Olcott Formation (lower Snake Creek Fauna in Figure 2) of Sioux County, Nebraska. A full description of the Texas material is beyond the scope of the present paper, since it would necessitate a full revision and redescription of the genus *Aphelops.*

Subfamily RHINOCEROTINAE
Gray, 1821 (expanded)
Tribe TELEOCERATINI Hay, 1902
Genus TELEOCERAS Hatcher, 1894

Revised diagnosis. — *Teleoceras* is derived in many features, including hypsodont teeth, strong antecrochets, greatly reduced premolars with loss of dP1/1 and occasional loss of P2/2, thick cement on teeth, narrow nasals with strong downturned lateral edges, enlarged premaxilla and I1, broad zygomatic arches, flaring lambdoid crests (skull semicircular in posterior view), a small terminal nasal horn and fused nasals, lower tusk (i2) teardrop-shaped in cross section, and characteristic body proportions of a barrel-shaped trunk and short, robust limbs.

TELEOCERAS MEDICORNUTUM Osborn, 1904
Figure 11.4

Teleoceras medicornutus OSBORN, 1904, p. 319.

Holotype. — AMNH 9832, a complete skull and jaws from the late Barstovian of the Pawnee Creek area, northeast Colorado (Galbreath, 1953).

Distribution. — Burkeville Fauna (early Barstovian, middle Miocene), Texas Gulf Coastal Plain, and in many other early and late Barstovian localities outside Texas.

Referred material. — Burkeville Fauna (early Barstovian): Localities near Doucette and Woodville, Tyler Co., Texas: F:AM 108893, left metacarpal II; F:AM 108892, left lunar; F:AM 108891, right and left distal humeri; F:AM 108890, right astragalus; F:AM 108889, broken left m2; F:AM 108888, broken right m1; F:AM 108887, right i2; F:AM 108886, left ramus with m2-3; F:AM 108897, right metacarpal IV; F:AM 108896, left metacarpal II; F:AM 108895, right metatarsal IV; F:AM 108894, left metatarsal III. Trinity River Pit 1, San Ja-

TABLE 8—M1–3 lengths (in mm) of selected samples of *Teleoceras*.

Sample	N	x̄	s	OR
T. medicornutum, late Barstovian, Burge Mbr., Valentine Fm., Nebr.	5	156.8	4.1	154–163
T. medicornutum, holotype, late Barstovian, Pawnee Creek Fm., Colo.	1	154.3	—	—
T. major, holotype, early Clarendonian, Cap Rock Mbr., Ash Hollow Fm., Nebr.	1	157.0	—	—
T. major, early Clarendonian, Cap Rock Mbr., Ash Hollow Fm., Nebr.	6	158.2	7.8	148–170
T. cf. *major,* early Clarendonian, Lapara Creek Fm., Tex.	3	161.0	5.5	157–167
T. major, late Clarendonian, Merritt Reservoir Member, Ash Hollow Fm., Nebr.	13	154.2	7.8	142–164
T. fossiger, early Hemphillian, Ogallala Fm., Kans.	13	172.4	6.1	161–183
T. fossiger, holotype, early Hemphillian, Ogallala Fm., Kans.	1	187.5	—	—
T. proterum, early Hemphillian, Mixson's Bone Bed, Fla.	2	148.0	2.8	146–150

cinto Co., Texas: F:AM 108837, left p2; F:AM 108836, m3; F:AM 108835, right p2–3; F:AM 108350, right ramus with m2–3; F:AM 108349, left ramus with symphysis and p3–m3; F:AM 108838, partial skull; F:AM 108840, right m2; F:AM 108841, right p2; F:AM 108844, left I2; F:AM 108845, atlas; F:AM 108846, 3 vertebrae; F:AM 108847, caudal vertebrae; F:AM 108848, back of skull; F:AM 108849, right humerus; F:AM 108850, left humerus; F:AM 108851, proximal right humerus; F:AM 108852, juvenile right humerus; F:AM 108853, proximal right humerus; F:AM 108854, 3 radii; F:AM 108855, 2 ulnae; F:AM 108856, 3 broken femora; F:AM 108857, 2 partial fibulae; F:AM 108858, distal tibia; F:AM 108881, 4 metacarpals IV; F:AM 108880, 3 metacarpals III; F:AM 108879, 5 metacarpals II; F:AM 108878, 2 ectocuneiforms; F:AM 108877, left navicular; F:AM 108876, 4 cuboids; F:AM 108875, 3 magnums; F:AM 108874, 3 trapezoids; F:AM 108873, 4 pisiforms; F:AM 108872, 3 cuneiforms; F:AM 108871, 4 lunars; F:AM 108870, right unciform; F:AM 108869, right scaphoid; F:AM 108868, 3 patellae; F:AM 108867, 4 patellae: F:AM 108866, 3 left calcanea; F:AM 108865, 3 right calcanea; F:AM 108864 4 astragali; F:AM 108863, 4 astragali; F:AM 108862, 2 partial tibiae; F:AM 108861, 2 tibiae; F:AM 108860, 3 tibiae; F:AM 108859, 2 tibial fragments; F:AM 108885, 3 metatarsals IV; F:AM 108884, 4 metatarsals III; F:AM 108883, 2 metatarsals II.

Diagnosis. —P3/3 less reduced than all other species of *Teleoceras* except *T. meridianum.* Teeth less hypsodont. Nasal incision not retracted further than above anterior P3. Larger than *T. meridianum.*

Discussion. —The most remarkable Texas specimen referred to *T. medicornutum* is F:AM 108838, a complete skull. The dentition shows the normal *Teleoceras* condition with strong antecrochets and hypsodonty, and the teeth are relatively unworn. The striking feature of this specimen is that both M3's have a distinct, isolated cusp (Figure 11.4) at the posteromedial end of the metaloph. No other rhinoceros that we have seen shows this. Such a feature might be considered the basis for a new species under a typological species concept. However, comparison of other isolated

M3's from the same quarry, Trinity River Pit 1, shows none with this condition. F:AM 108838 shows so little wear that the isolation of the anomalous cusp would disappear in older wear stages. The split between the cusp and the metaloph is very shallow and would disappear with wear. Thus, it is felt that this feature is a dental anomaly, possibly caused by an epigenetic disturbance in the development of the teeth. Similar dental anomalies are discussed by Archer (1975), Taylor (1982), and Rose and Smith (1979). Such a disturbance would have to have occurred very early in development, since it occurs on both sides. Butler (1967) suggested that bilaterally symmetrical dental anomalies result from disturbances in the migration of mesenchyme from the neural crest cells.

The remaining material of *T. medicornutum* compares favorably with the type and with referred material from the Barstovian of New Mexico, Colorado, and particularly the large samples from the Olcott Formation (Lower Snake Creek Fauna) of Nebraska. A full description of this material is beyond the scope of the present paper, since it would necessitate a full revision and redescription of the Teleoceratini.

TELEOCERAS cf. MAJOR Hatcher, 1894

Teleoceras major HATCHER, 1894, p. 149.
Teleoceras proterus (Leidy). QUINN, 1955, p. 72.
Teleoceras proterus (Leidy). PATTON, 1969, p. 214.

Discussion. —A large sample of Lapara Creek *Teleoceras,* including many good skulls and postcranial bones, is stored at the Texas Memorial Museum. A full description of this material is postponed until a complete revision of *Teleoceras* can be undertaken. These Lapara Creek rhinos were referred to *Teleoceras proterus* by Quinn (1955), and his iden-

tification was followed by Patton (1969). But a preliminary comparison of this material (Table 8) indicates that it is within the range of size variation of *T. medicornutum* or *T. major,* rather than the smaller Hemphillian rhino, *T. proterum,* or the large Hemphillian form, *T. fossiger.* The Lapara Creek rhinos are also less hypsodont than *T. proterum* and lack the medifossettes seen on the molars of this species. Temporarily the Lapara Creek rhinos are referred to *T.* cf. *major* (the typical early Clarendonian form, which it most closely matches) until a full revision of *Teleoceras* can be attempted.

The occurrence of *T.* cf. *major* (known from the early Clarendonian) in the Lapara Creek Fauna agrees with the late Barstovian–early Clarendonian age of this fauna (Patton, 1969; Tedford et al., 1987). *Teleoceras proterum,* on the other hand, is known only from the Hemphillian of Florida.

TELEOCERAS MERIDIANUM
(Leidy, 1865) n. comb.
Figures 10–14

Rhinoceros meridianus LEIDY, 1865, p. 176; 1869, p. 229, Pl. 23.
Aphelops meridianus (Leidy). COPE, 1875, p. 495 (type specimen only).

Holotype. — USNM 3177, broken ?M2.

Distribution. — Burkeville and Cold Spring faunas, early and late Barstovian (middle Miocene), Texas Gulf Coastal Plain.

Referred material. — Burkeville Fauna (early Barstovian): West of Doucette, northwest of Woodville, Tyler Co., Texas: F:AM 108261, right mandible with p2–4. Trinity River Pit 1, San Jacinto Co., Texas: F:AM 108263, left and right juvenile edentulous rami; F:AM 108260, right I1; F:AM 108259, right metatarsal III; F:AM 108258, left metatarsal IV: F:AM 108257, left metatarsal IV: F:AM 108256, scaphoid; F:AM 108255, unciform; F:AM 108254, magnum; F:AM 108253, humerus; F: AM 108842, right M3; F:AM 108843, left M3.

Cold Spring Fauna (late Barstovian): Two miles below Swartaut, Polk Co., Texas: F:AM 108272, left juvenile ramus with dp1–2; left ramal fragment with m2. A. D. Donohoe Pit, San Jacinto Co., Texas: F:AM 108265, left and right rami with p3–m3. Cold Spring l.f., San Jacinto Co., Texas: TMM 31219-223, scapula. McMurray Pits, San Jacinto Co., Texas: F:AM 108262, proximal tibia; F:AM 108266, skull and mandible; F:AM 108273, right M2; F:AM 108270, right i2; F:AM 108306, skull; F:AM 108269, proximal nasal bones; F:AM 108305, 2 I1; F: AM 108304, 2 scaphoids; F:AM 108303, cuneiform; F: AM 108302, pisiform; F:AM 108301, magnum; F:AM 108300, unciform; F:AM 108299, 3 ectocuneiforms; F: AM 108298, cuboid; F:AM 108297, 2 naviculars; F:AM 108296, 3 metatarsals IV; F:AM 108295, patella; F:AM

108294, 5 metacarpals II; F:AM 108292, distal femur; F:AM 108293, 2 metacarpals III; F:AM 108291, proximal femur; F:AM 108290, juvenile femur; F:AM 108289, tibia; F:AM 108288, tibia; F:AM 108287, tibia; F:AM 108286, 2 i2; F:M 108285, femur; F:AM 108284, humerus; F:AM 108283, distal radius; F:AM 108282, radius; F:AM 108281, humerus; F:AM 108280, humerus; F:AM 108279, humerus; F:AM 108278, humerus; F:AM 108277, humerus; F:AM 108276, radius; F:AM 108275, radius; F:AM 108339, mandible with left p2–m3, right p3–m3; F:AM 108348, cuneiform; F:AM 108347, right i2; F:AM 108346, cervical vertebra; F:AM 108345, thoracic vertebrae; F:AM 108342, juvenile skull; F:AM 108341, juvenile skull with left and right dP1–4, M1; F:AM 108839, mandible with left p3–m3, right p2–m3.

Barstovian localities (horizon unknown): McKenney Place, near Stephen Creek, San Jacinto Co., Texas: F: AM 108344, magnum. One-half mile south of Williamson's Farm, near Stephen Creek, San Jacinto Co., Texas: F:AM 108343, distal right humerus.

Diagnosis. — *Teleoceras meridianum* is by far the smallest of known species of *Teleoceras.* It also has relatively robust limbs.

Description. — The type specimen, USNM 3177, has a strong crochet and antecrochet, and is very hypsodont, with a narrow, slit-shaped medifossette. All of these features are well matched by the right M2 of F:AM 108306 (Figure 10.3), a skull from the McMurray Pit locality. USNM 3177 and the M2 of F:AM 108306 are also closely comparable in size, although this is difficult to measure precisely, since the ectoloph of the type is so badly broken and F:AM 108306 is more worn than the type. The only morphological differences between the two are due to differences in wear. The crochet of F:AM 108306 is worn down to the base, and the postfossette is more triangular and open. Since USNM 3177 is clearly a teleoceratine and there are no other *Teleoceras* from Texas that match it in size; F: AM 108306 is referred to *Teleoceras meridianum.*

F:AM 108306 (Figure 10.5–10.8) has been badly crushed dorsoventrally, so it is difficult to interpret the shape of the skull. The nasals, premaxillae, and part of the maxilla have been badly broken. An isolated anterior portion of the nasal bones from the same pit (F:AM 108269) shows the characteristic fusion, strongly downturned lateral edges, and terminal horn rugosity of *Teleoceras* despite its unusually small size (Figure 10.4). The frontals and parietals have been broadened and flattened by postmortem crushing. The occiput, however, is relatively undeformed and
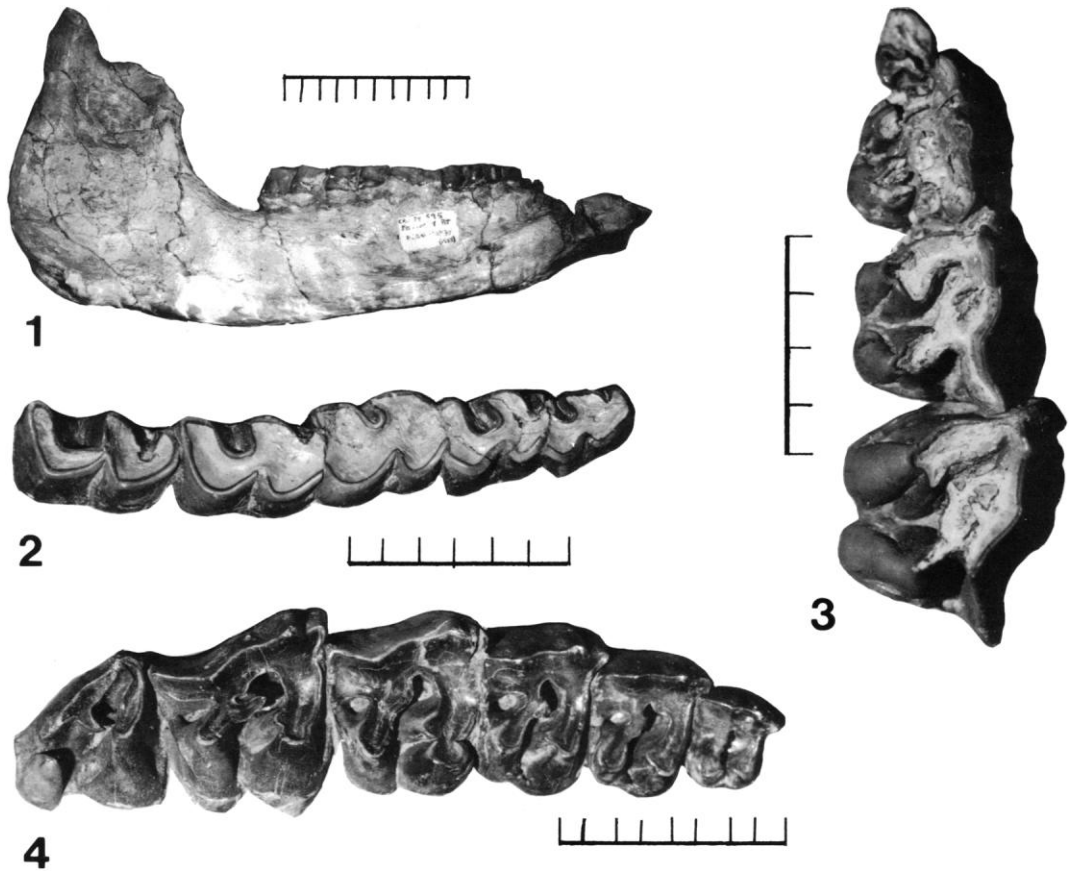
FIGURE *11–Teleoceras. 1, 2, Teleoceras meridianum,* F:AM 108839, right lateral view of mandible and crown view of teeth; *3,* F:AM 108341, left dP1–4, crown view. *4, Teleoceras medicornutum,* F:AM 108838, right P2–M3, showing peculiar isolated metaloph cusp on M3. Scales in cm.

has a broad, flaring lambdoid crest. The zygomatic arches are also broad and flaring. The nasal incision is retracted to the level above anterior P3.

The basicranium is poorly preserved. The postglenoid processes are relatively narrow and slender. The mastoid process is a flaring, slender wing fused to the postglenoid process. Both paroccipital processes are broken off, but they were apparently narrow and slender. The rest of the basicranium is too poorly preserved to distinguish foramina or other detailed structures. The pterygoid flanges are short and stubby. The sulcus anterolateral to the pterygoid flange is distinct. The secondary palate terminates at the level medial to anterior M3.

No incisors or premolars are preserved on F:AM 108306. However, there are a number of isolated I1's in the sample from the McMurray Pit that show the characteristic bladelike shape of *Teleoceras.* There are no upper premolars known for *T. meridianum.* M1–3 are present on both sides of F:AM 108306. Although very worn, they are clearly very hypsodont. All three molars have strong antecrochets. M1 is so worn that the antecrochet has enclosed a prefossette; the postfossette is nearly circular. M2 (as in the type specimen) has a distinct protocone, a strong antecrochet, and the base of what was once a prominent crochet. M3 has a strong crochet and antecrochet. There are no cingula on the upper molars.

The mandible (Figure 11.1, 11.2) has a procumbent symphysis and long diastema. Isolated lower tusks of both male (F:AM 108270) and female (F:AM 108286A–B) morphology are known. The coronoid, condyles, and angle of the jaw are robust. The lower premolars

FIGURE *12—Teleoceras meridianum* limb elements. *1, 2,* F:AM 108279, humerus; *3,* F:AM 108276, radius; *4,* TMM 31219-223, scapula; *5,* F:AM 108285, femur; *6, 7,* F:AM 108288, tibia-fibula; *8, 9,* F:AM 108295, patella. Scales in cm.
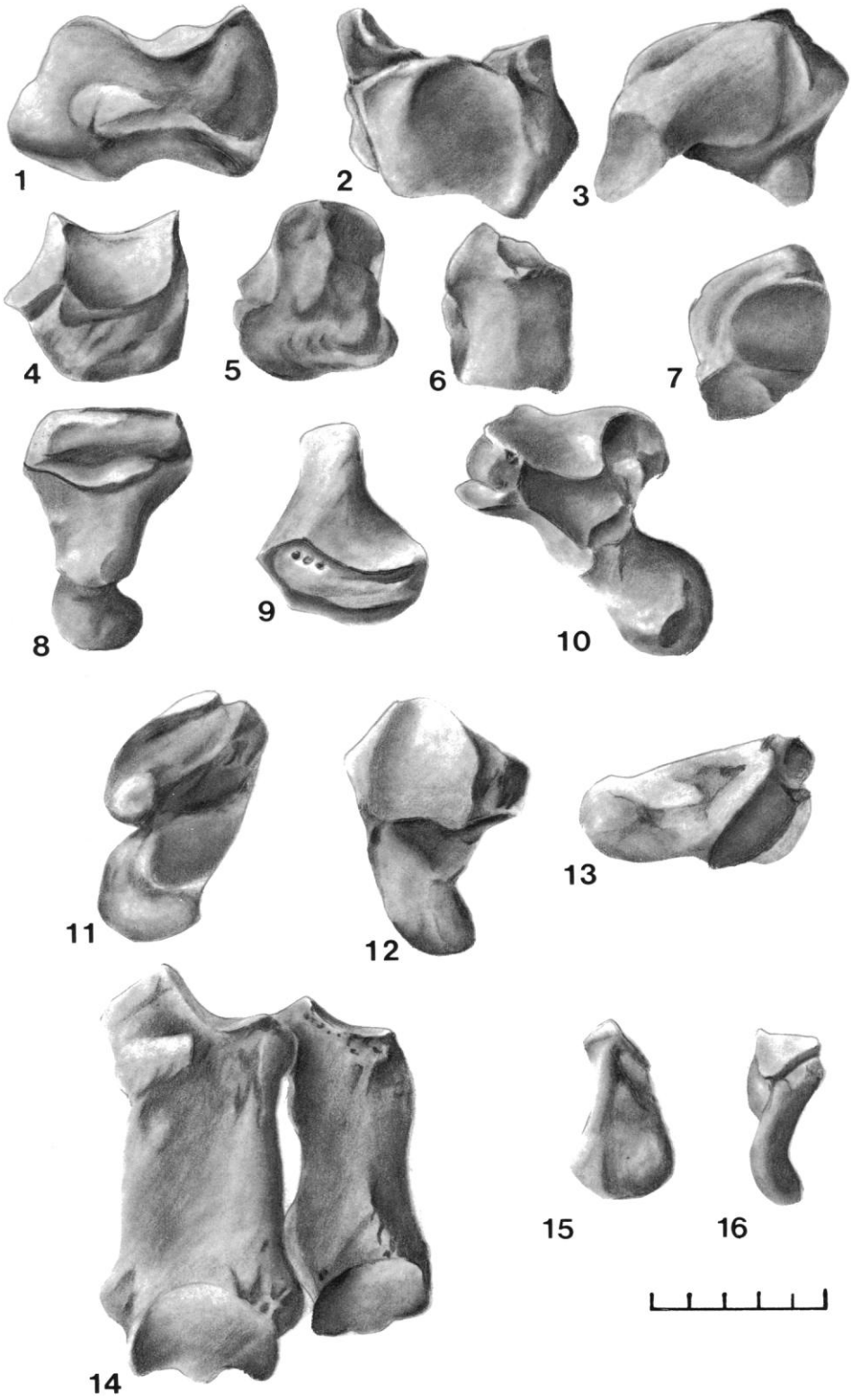
are highly reduced. Lower p2 is missing in all specimens, although there is a small alveolus for it in some. The lower molars are very hypsodont and lack cingula. The lower cheek tooth pattern is typically rhinocerotid.

Two nearly complete juvenile skulls also occur in the McMurray Pit. The larger one, F:AM 108341, has dP1–4 and the M1 still deep in the alveolus. The smaller, F:AM 108342, has dP2–4 and the tip of M1 just above the gumline. DP1 (Fig. 11.3) consists of a simple ectoloph with a metaloph at right angles to it. DP2–4 all have high-crowned ectolophs, strong anterior cingula, strong antecrochets, and lobate crochets that meet the crista to form a medifossette. The crochet is longest and most intricately lobate on dP4. The sutures of these skulls are unfused, the zygoma are narrow, the supraorbital rugosities are undeveloped, and the occiput is unflared; all of these features might be expected in a juvenile skull.

Postcranial skeleton. — A few badly broken vertebrae and some rib fragments are all that are known of the axial skeleton of *T. meridianum.* The scapula (Figure 12.4) is known from TMM 31219-223. It was badly broken and has been incorrectly restored in plaster. It appears to lack a posterior flexure of the scapular spine and the triangular proximal end. The parts that are original bone, however, show that the scapula was broad and robust, but relatively small.

Most of the limb elements of *T. meridianum* are from the McMurray Pit and have undergone crushing and plastic deformation. The humerus (Figure 12.1, 12.2) is known from a number of good specimens. It has a weakly developed deltopectoral crest and lateral epicondyle. The deltopectoral crest lacks a prominent anterolateral process. The radius (Figure 12.3) is drastically shortened relative to its diameter. The facets and rugosities on the proximal and distal ends are relatively indistinct. No ulna is known for *T. meridianum.*

The manus (Figure 13) of *T. meridianum* is known from the scaphoid, cuneiform, magnum, unciform, pisiform, and metacarpals II and III. They all show a marked dorsoventral compression. The scaphoid (Figure 13.1–13.3) is very flattened proximodistally. It has a distinct posterior lunar facet. The magnum (Figure 13.8–13.10) has a relatively large posterior (plantar) process, with no indication of modification for a magnum-unciform articulation (Harrison and Manning, 1983). The cuneiform (Figure 13.4–13.7) is very dorsoventrally flattened, with an indistinct posterior process. The unciform (Figure 13.11–13.13) is transversely flattened, with an indistinct cuneiform facet. The pisiform (Figure 13.15, 13.16) has a reduced distal swelling relative to the size of the articular facets. Metacarpal II (Figure 13.14) is stubby and anteroposteriorly flattened. Metacarpal III is also stubby and flattened, with a distinct proximal facet for metacarpal IV.

The femur (Figure 12.5) is robust and has been subjected to anteroposterior crushing. The greater trochanter is relatively less robust, without an anteroproximal ridge. The patellar trochlea of the femur is narrow, and the tibial trochlea is relatively reduced. The tibia (Figure 12.6, 12.7) has a less distinct proximal tuberosity. The fibula is a robust splint that apparently was fused to the tibia at its proximal end. The pes (Figure 14) of *T. meridianum* is known from the cuboid, navicular, ectocuneiform, and metatarsal IV. The cuboid (Figure 14.1–14.3) is dorsoventrally crushed, with a large facet for metatarsal IV. The navicular (Figure 14.4–14.6) has distinct facets for the ectocuneiform and mesocuneiform. The ectocuneiform (Figure 14.7–14.9) is dorsoventrally flattened. Metatarsal IV (Figure 14.10–14.11) is short, robust, and shows little lateral curvature.

In summary, the postcranial skeleton of *T. meridianum* shows many of the same trends seen in *Peraceras hessei*: smaller size, fewer rugosities, weakly developed articular sur-

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FIGURE *13—Teleoceras meridianum,* manus elements. *1–3,* F:AM 108304a, right scaphoid, in left lateral, proximal, and distal views; *4–7,* F:AM 108303, right cuneiform, in right lateral, dorsal, proximal, and distal views; *8–10,* F:AM 108301, right magnum, in proximal, dorsal, and left lateral views; *11–13,* F:AM 108300, right unciform, in right lateral, proximal, and left lateral views; *14,* F:AM 108293b, right metacarpal III, and F:AM 108294b, right metacarpal II, in dorsal view; *15, 16,* F:AM 108302, right pisiform, in plantar and left lateral views. Scale in cm.
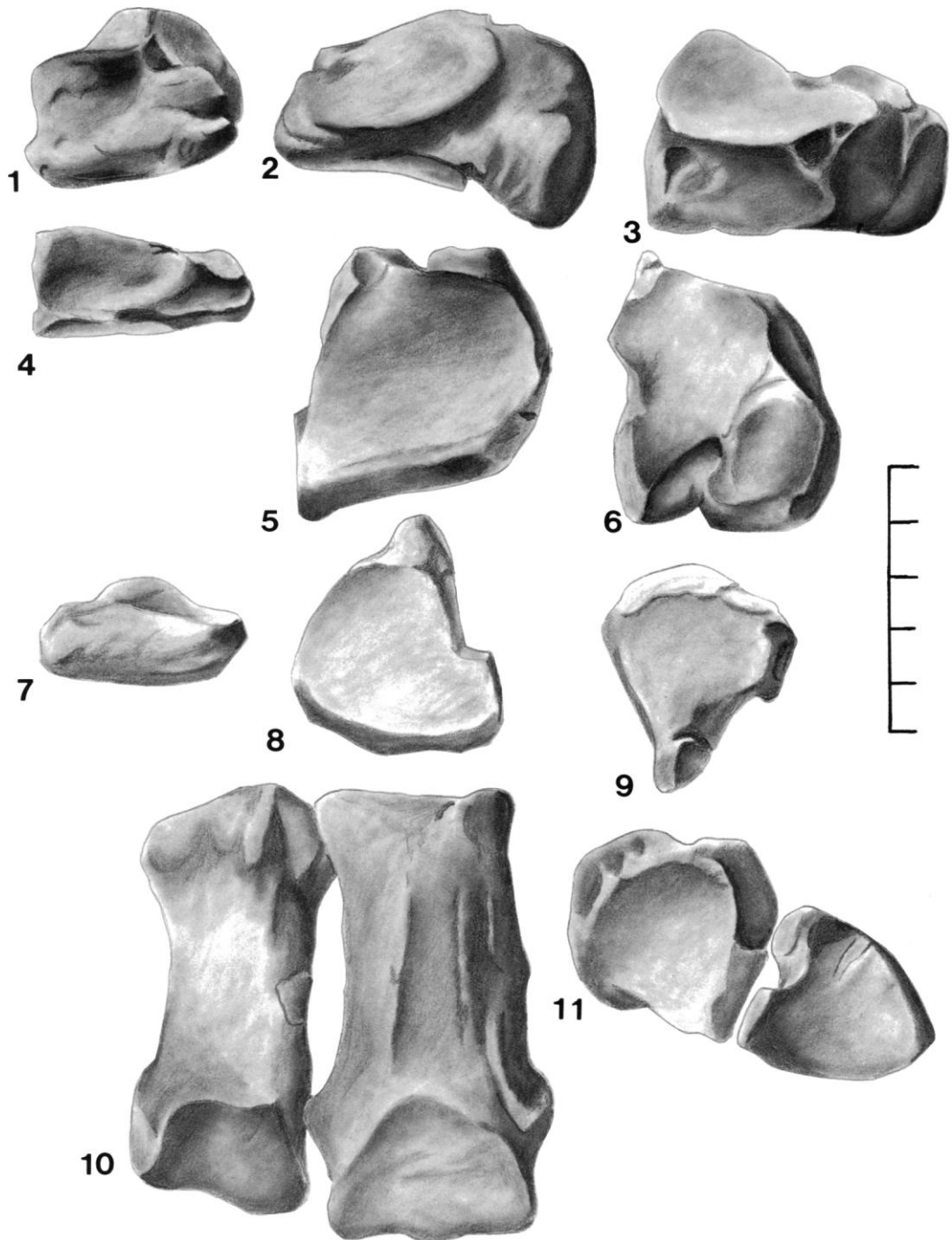
FIGURE *14—Teleoceras meridianum,* pes elements. *1–3,* F:AM 108298, left cuboid, in dorsal, left lateral, and proximal views; *4–6,* F:AM 108297b, right navicular, in dorsal, proximal, and distal views; *7–9,* F:AM 108229b, right ectocuneiform, in dorsal, proximal, and distal views; *10, 11,* F: AM 108296a, right metatarsal IV, and F:AM 108259, right metatarsal III, dorsal and proximal views. Scale in cm.
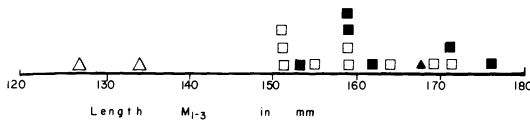
FIGURE *15*—Comparison of m1–3 lengths of late Barstovian *Teleoceras*. Solid squares = male *T. medicornutum,* Frick Horse and Mastodon Quarry, Pawnee Creek Fm., Colorado. Open squares = female *T. medicornutum,* Horse and Mastodon Quarry. Solid triangle = type specimen of *T. medicornutum,* Pawnee Creek Fm., Colorado. Open triangles = *T. meridianum,* Texas Gulf Coastal Plain.

faces, and increased robustness relative to size. Many of these features must be interpreted with caution. Most of the elements of both *T. meridianum* and *P. hessei* come from the McMurray Pit, where they have undergone considerable crushing and plastic deformation. Some of the flattening described above is certainly due to these postmortem effects.

Discussion. —The history of Leidy's type specimen of *"Rhinoceros" meridianus* is discussed in the introduction. Most authors have referred it to *Aphelops meridianus* or considered it indeterminate. However, it appears that none of these authors actually examined the type specimen in making these state-

TABLE *9*—Summary of occurrences.

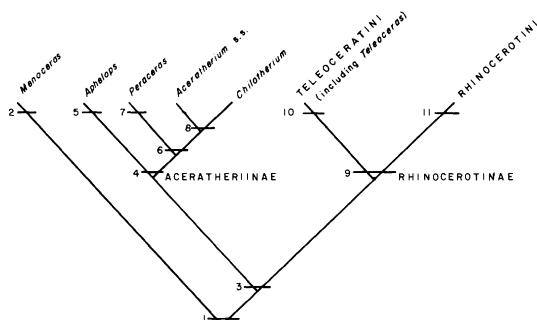| Locality	Menoceras arikarense	Menoceras barbouri	Peraceras hessei	Aphelops megalodus	Teleoceras meridianum	Teleoceras medicornutum	Teleoceras cf. major
DERRICK FARM (USNM)							
(?Late Arikareean) ?Catahoula Formation	X						
GARVIN GULLY FAUNA (Early Hemingfordian) Oakville Formation							
TMM 41662		X					
TMM 40106		X					
TMM 40667		X					
TMM 31048		X					
BURKEVILLE FAUNA (Early Barstovian) Fleming Formation							
TMM 31190 Point Blank l.f.			X	X	X		
TMM 31242			X	X	X		
TMM 31243			X				
TMM 31246 Swiss Alp			X	X	X		
TMM 40127					X		
TMM 31057 Moscow l.f.			X	X	X	X	
TMM 40290				X			
Trinity River Pit 1 (F:AM)			X	X	X	X	
TMM 40196 (Trinity River Pit 1)					X		
Doucette-Woodville area (F:AM)			X	X	X	X	
COLD SPRING FAUNA (Late Barstovian) Fleming Formation							
McMurray Pits 1 and 2 (F:AM)			X	X	X		
Near Swartaut (F:AM)			X	X	X		
Noble Farm (TAM)			X		X	X	
Halletsville (TAM)			X				
TMM 31191 San Houston l.f.					X		
TMM 31219 Cold Spring l.f.			X	X	X		
TMM 30009 Woodville southwest					X		
TMM 31272 Chapell Hill			X				
TMM 40623 Push Creek							
TMM 40622 Belts Creek			X				
LAPARA CREEK FAUNA (Early Clarendonian) Goliad Formation							X

FIGURE *16* —Hypothesis of relationships of North American Miocene rhinos. Derived character states at numbered nodes explained in text.

ments. The specimen (USNM 3177) is a badly broken left upper ?M2 (Figure 10.1, 10.2). It is very hypsodont and has a strong antecrochet. Both of these features characterize *Teleoceras* and not *Aphelops* or *Peraceras*. "*Rhinoceros*" *meridianus* is clearly a species of *Teleoceras*.

This conclusion is strengthened by comparison with the material described above, particularly the skull F:AM 108306, shown in Figure 10.3–10.8. Matthew (1932, p. 420) considered *meridianus* indeterminate until an adequate topotype is found. Unfortunately, Leidy's locality data are so vague that it cannot be determined with certainty whether the specimens came from the Burkeville or Cold Spring level in Washington County. Hesse (1943) was of the opinion that Leidy's localities were from the Burkeville level, but this is not certain. Almost no other Barstovian rhinoceros material is known from Washington County. If the concept of type area can be extended 75 miles to the east, then the material from the Cold Spring level in San Jacinto County described above serves admirably as a topotype. Even if the type area is considered restricted to Washington County, the type of *meridianus* is still not indeterminate, since it matches the San Jacinto County specimens described above so closely. Thus, *Teleoceras meridianum* is a valid species, presently the oldest (1865) described species that can be referred to the genus. The genus *Teleoceras* was established by Hatcher in 1894, based on the species *T. major* from the early Clarendonian of Nebraska. *Aphelops fossiger* Cope, 1878, from the early Hemphillian of Kansas, was assigned to *Teleoceras* at a later date.

Teleoceras meridianum is as striking an example of dwarfing as *Peraceras hessei,* since it undergoes a 20 percent size reduction. It is clearly a dwarf species, since it is smaller than any known teleoceratine, Eurasian or North American, including its primitive sister-taxon *Brachypotherium americanum. Teleoceras meridianum* is also slightly smaller than undescribed teleoceratines from the late Hemingfordian Sheep Creek Formation of Nebraska in the Frick Collection. These are the oldest and most primitive *Teleoceras* known, but description of this material is beyond the scope of the present paper.

Sexual dimorphism as a cause for the small size of *T. meridianum* can be ruled out, since: 1) there is no large *Teleoceras* in the large samples of late Barstovian Texas faunas; 2) extreme size dimorphism is unknown in the rhinocerotids (Laurie, 1982); and 3) both male- and female-shaped lower tusks are present in the sample of *T. meridianum.* In Figure 15, *T. meridianum* is compared with the large samples of *T. medicornutum* from the Frick Mastodon and Horse Quarry of the Barstovian Pawnee Creek Formation of Colorado. *Teleoceras meridianum* is clearly much smaller than any individual of *T. medicornutum.* Although late Barstovian Texas Gulf Coast faunas contain only *T. meridianum,* the early Barstovian faunas contain both *T. meridianum* and *T. medicornutum* (Table 9). These two rhinos were clearly sympatric and very distinct in size from one another, as can be seen by comparison of the material of both rhinos from Trinity River Pit 1. It is unclear why *T. medicornutum* was absent from Texas in the late Barstovian, when it was very common in High Plains faunas from the late Barstovian of Colorado, Nebraska, and New Mexico. Further study of teleoceratine systematics and biogeography promises some interesting results.

RELATIONSHIPS OF THE NORTH AMERICAN MIOCENE RHINOCEROSES

The systematic significance of the distinguishing characters of the various Gulf Coast rhino genera can only be understood from a broader perspective of North American Miocene rhinoceroses. A broader review of the systematic relationships of the higher groups of rhinos has been provided elsewhere (Prothero et al., 1986). The relevant parts of that study are summarized here.

Menoceras is more closely related to higher rhinos than to primitive ones such as *Diceratherium*. This is suggested by the following characters: strong upper molar crochets; I2 lost; reduced sagittal crest; reduced premaxillary; nasal incision over posterior P2; basicranium shortened relative to palate; upper molar lingual cingula weak or absent; and shallow anteroventral notch on atlas (node 1 in Figure 16). The taxon "Diceratheriinae" as used to unite these two genera (e.g., Heissig, 1973) is a rare example of a strictly polyphyletic (rather than paraphyletic) mammalian taxon, since the paired nasal horns are convergently obtained in *Menoceras* and *Diceratherium*. The genus *Menoceras* is further characterized by the presence of twinned bulbous terminal nasal horns in the males and a vestigial metacarpal and posterodorsal zygomatic tuberosities (node 2). *Menoceras* is a very short-lived genus, ranging only from the latest Arikareean (the Agate fauna and its equivalents) to the early Hemingfordian (the fauna of the Runningwater Formation and its equivalents).

Aceratherines, teleoceratines, and rhinocerotinines (see characterizations following) can be united on the basis of fully bilophodont upper premolars and an overall increased size (reversed in the dwarf forms discussed earlier) (node 3). These Eurasian groups underwent an Aquitanian (early Miocene) diversification which apparently led to the formation of the three major groups of Miocene rhinos.

The first of these major groups, Aceratheriinae, was first used by Matthew (1931) in the sense intended here. They are characterized by a nasal incision retracted to a position over anterior P4 (and, presumably, by an expanded upper lip), premaxillae greatly reduced (with I1 greatly reduced or lost), and reduction of the medial flange of the lower tusk (i2) (node 4). Postcranially, the American aceratheres remain almost entirely primitive in contrast to *Teleoceras*. The group appeared in North America in the middle Hemingfordian (fauna of the Box Butte Formation), probably as an immigrant from Eurasia. The aceratherines may have supplied the competition that caused the extinction of the long-lived American *Diceratherium* lineage.

The genus *Aphelops* has been more or less clearly understood since 1873. The type

species was placed in the genus *Aceratherium* originally by Cope. The only major confusion in the history of the genus was the placement of the species *fossiger* in *Aphelops* by Cope in 1877. It was not until much later that *fossiger* was properly placed in Hatcher's 1894 genus *Teleoceras*. *Aphelops* starts as a relatively primitive aceratherine, with the following derived characters: nasofrontal profile dorsally arched and the i2/dp1 diastema slightly lengthened (node 5). The genus ranges from late Hemingfordian to late Hemphillian in America and may be represented in the Vindobonian of Asia. It is a very useful genus biostratigraphically, as it appears to steadily increase in size from the middle Clarendonian until the late Hemphillian. It is one of the few lines which does not get smaller in the late Hemphillian.

A few characters suggest that the other aceratherines are more closely related to each other than they are to *Aphelops*—a flattened dorsal skull profile and shortened nasals (node 6). This suggests that the one American acerathere (*Peraceras*) is closer to the Eurasian aceratheres than to the other American one (*Aphelops*).

The genus *Peraceras* is the least well understood of the American Miocene rhinos. This is true for many reasons: primitively it resembles *Aphelops*; the derived forms mimic *Teleoceras* in several ways; it has a very short range in time; and, most importantly, it is common only in a few faunas. It is distinguished by the following characters: occiput procumbent; mandibular symphysis upturned in females (with i2/dp1 diastema shortened); a lingual cingulum usually present on the lower cheek teeth; i2 (the lower tusk) very reduced in females; the lambdoid crest slightly broadened (more so in derived forms); and the post-glenoid process slightly broadened laterally (node 7). The primitive species of the genus have not been discussed until the present paper. *Peraceras* ranges at least from the early Barstovian (and probably earlier) until the middle Clarendonian (the Ricardo fauna). The type specimen of *Peraceras superciliosum* from the Republican River Valley of south-central Nebraska, sometimes thought to be Hemphillian (Osborn, 1904), is probably of late Barstovian or early Clarendonian age (R. H. Tedford, personal commun.). The smaller (*P. profectum*) and larger (*P. superciliosum*) species are

apparently common in a few late Barstovian sites such as the Pojoaque fauna from New Mexico (F:AM) for the former and the Hotell Ranch fauna from Nebraska (UNSM) for the latter. *Peraceras* apparently became less common by the Clarendonian and was gone before the late Clarendonian. This may have been due to competition with *Teleoceras*. The history of *Peraceras* appears to be that of an unsuccessful bid by an aceratherine to compete with *Teleoceras*. Many of the features of the large *Peraceras* appear to be poor imitations of *Teleoceras* features—large proportioned, high crowned molars; small proportioned premolars; broad zygomatic arch; flaring lambdoid crest; downturning of the lateral edges of the nasals; and a brachycephalic skull.

One might conclude from *Peraceras* that it was futile for an aceratherine to try to compete with the grazing teleoceratines. But the success of the sister lineage of *Peraceras* in Eurasia (*Aceratherium* s.s. and *Chilotherium*) contradicts this. *Chilotherium,* in particular, achieved tremendous success in terms of numbers and distribution as a grazer in the late Miocene (Turolian). The success of *Chilotherium* probably had much to do with the competitive defeat of the teleoceratine *Brachypotherium* in Eurasia. The Eurasian higher aceratherines are characterized by their slightly parasaggital temporal crests and slightly laterally flared lower tusks (i2) (node 8).

Heissig (1973) suggested that teleoceratines were closely related to aceratherines (he placed them as tribes of his Aceratheriinae). All characters he cited were either primitive for both groups (larger lower tusk, absence of nasal horn, short mandibular symphysis, articulation of the radius with the cuneiform, unequally curved dorsal surfaces of the carpals and tarsals, and presence of manus digit V) or derived for only the Teleoceratini (presence of a small nasal horn, upper molars with a strong antecrochet, and articulation of the ulna with the lunar). Heissig cited both presence and absence of the last character in his diagnosis of Aceratheriinae.

In contrast to Heissig's view, several characters suggest that teleoceratines are more closely related to rhinocerotinines than they are to aceratherines. These features include: small terminal nasal horn present (expanded in rhinocerotinines) on fused terminal nasals;

lambdoid crest expanded laterally; a posterior articulation between the scaphoid and the lunar; and reduced bony bar between the foramen ovale and the foramen lacerum medium (node 9). Because of these characters, it is recommended that Rhinocerotinae be expanded to include the tribe Teleoceratini as well as the tribe Rhinocerotini, and that Aceratheriinae be confined to Heissig's Aceratherini.

The teleoceratines are distinguished by hypsodont teeth, strong upper molar antecrochets, reduced premolars (P2/2 lost in derived forms), premaxilla and upper tusk (I1) enlarged, lateral edges of the nasals strongly downturned, torso lengthened and barrel-like, limbs shortened (carpals and tarsals "compressed" dorsoventrally), zygomatic arch broadened, calcaneal tuber elongate, skull brachycephalic, and nasal incision retracted to over the anterior part of P3 (node 10). They are one of the most distinctive of all higher rhinocerotid taxa.

The relationship of the American *Teleoceras* to the Afro-Eurasian *Brachypotherium* was recognized early (Pavlow, 1892) and was given formal taxonomic recognition by Osborn in 1900. Teleoceratines appear to have migrated to North America from Eurasia in the Hemingfordian and persisted in North America until extinction in the latest Hemphillian. During almost its entire range, *Teleoceras* is by far the most common American Miocene rhino. It has been suggested (e.g., by Matthew, 1932) that *Teleoceras* does not survive as long as *Aphelops* in America, but this is refuted by its presence in several very late Hemphillian faunas (faunas of the upper Bone Valley Formation, Florida; upper Bidahochi Formation, Arizona; Eden l.f., California; Sawrock l.f., Kansas). The confusion was due to the peculiar rarity of *Teleoceras* in several late Hemphillian faunas (Coffee Ranch, Texas, and Edson, Kansas) when compared to *Aphelops*. These are some of the few instances when *Teleoceras* is not the dominant rhino in the fauna.

It is curious that *Teleoceras* material was described repeatedly long before Hatcher recognized it as a distinct genus in 1894—"*Rhinoceros*" *meridianus* Leidy, 1865; "*Aphelops*" *fossiger* Cope, 1878; "*Rhinoceros*" *proterus* Leidy, 1885; and "*Eusyodon maximus*" Leidy, 1886 ("*Eusyodon*" was originally described as a pig tusk, but is an i2 of

Teleoceras proterum). Why the founders of American vertebrate paleontology never recognized the distinct nature of *Teleoceras* is a mystery, since it is distinctive even with the most fragmentary material.

Misunderstanding of *Teleoceras* evolution could also be a hindrance to American biostratigraphy. Unlike *Aphelops, Teleoceras* does not gradually increase its size through time. The largest *Teleoceras* are not the youngest ones. Like many early Hemphillian taxa (*Aepycamelus, Yumaceras, Tapirus, Calippus, Nimravides, Pliohippus, Neohipparion, Epicyon, Leptarctus, Macrogenis, Illingoceras, Barbourofelis, Indarctos, Prosthennops*), *Teleoceras fossiger* is unusually large. This fact could be incorrectly interpreted to make it appear that early Hemphillian ("Kimballian") *Teleoceras* is more advanced than the smaller late Hemphillian one.

Rhinocerotinines are, by far, the most diversified and widespread of all higher rhinos. This group includes all five of the living species of rhinoceroses (Javan, Indian, Sumatran, black, and white) as well as the long lineages of woolly rhinoceroses and elasmotheres. The entire group is characterized by an anteroventrally extended nasal tip (allowing space for the expanded nasal horn boss) and by slightly parasaggital temporal crests (node 11).

SUMMARY

The oldest rhinoceros presently known from the Texas Gulf Coastal Plain is *Menoceras arikarense* from the Derrick Farm locality (?Catahoula Formation). It is comparable to late Arikareean rhinos from Agate Spring Quarry, Nebraska. The rhinos from the Garvin Gully Fauna (early Hemingfordian) are referred to *Menoceras barbouri* (n. comb.), also known from the Runningwater Formation of Nebraska and the Thomas Farm local fauna of Florida. Barstovian faunas from the Texas Gulf Coastal Plain contain four species of rhinoceros: the common High Plains forms *Teleoceras medicornutum* and *Aphelops megalodus,* and the dwarf species *Teleoceras meridianum* n. comb. and *Peraceras hessei* n. sp. As far as known, this represents the only instance of a North American Miocene fauna with four sympatric species of rhinoceros. The early Clarendonian Lapara Creek Fauna contains *Teleoceras* cf. *major.*

An hypothesis of relationships is proposed for the common North American Miocene rhinoceros genera, *Aphelops, Peraceras,* and *Teleoceras. Aphelops* and *Peraceras* are included in the subfamily Aceratheriinae, along with the European genera *Chilotherium* and *Aceratherium* s.s. *Teleoceras* (a member of the tribe Teleoceratini) is more closely related to the Rhinocerotini (which includes all living species) than it is to the Aceratheriinae. To reflect this, the usage of the subfamily Rhinocerotinae is expanded to include the tribes Teleoceratini and Rhinocerotini.

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