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UNGULATES OF THE TOLEDO BEND LOCAL FAUNA (LATE ARIKAREEAN, EARLY MIOCENE), TEXAS COASTAL PLAIN

L. Barry Albright III[1]

ABSTRACT

The Toledo Bend Local Fauna includes the most diverse assemblage of mammals yet reported from the earliest Miocene Gulf Coastal Plain. Faunal affinities with the Buda Local Fauna of northern Florida, as well as with faunas of the northern Great Plains and Oregon, suggest a "medial" to late Arikareean age. Of 26 mammalian taxa represented, the 17 ungulates are discussed in this report; the carnivores, small mammals, and lower vertebrates are discussed elsewhere. All ungulate taxa are browsers rather than grazers, and many have not previously been recorded from the Gulf Coastal Plain. Riparian forms such as anthracotheres and tapirs account for a large percentage of mammalian remains recovered, although horses, rhinoceroses, and a small, new species of protoceratid, *Prosynthetoceras orthrionanus* sp. nov., are also common. Other ungulates include a small chalicothere, a new small rhinoceros, *Gulfoceras westfalli* gen. et sp. nov., and a giant entelodont. The abundance of protoceratids, tapirs, anthracotheres, and rhinoceroses, the absence of oreodonts, and the rarity of camelids at Toledo Bend contrasts with Arikareean faunas in Florida where protoceratids and anthracotheres are absent, tapirs and rhinos are extremely rare, oreodonts are present, and camelids are relatively common.

RESUMEN

La fauna local de Toledo Bend incluye el ensamble más diverso de mamíferos jamás reportado para el Mioceno más temprano de la Planicie Costera del Golfo, en Texas. Las afinidades faunísticas con la fauna local de Buda, del norte de la Florida y con la de las Grandes Planicies del Norte y de Oregon, sugieren una edad del Arikareano medio a tardío. De los 26 taxónes de mamíferos representados, los 17 ungulados se discuten en el presente reporte, en otros trabajos se discuten los carnívoros, pequeños mamíferos, y vertebrados primitivos. Todos los ungulados son ramoneadores más que pasteadores y muchos no han sido previamente descritos para la Planicie Costera del Golfo. Un gran porcentaje de los restos de mamíferos recuperados corresponde a formas ribereñas, tales como anthracotheros y tapires, aunque también son comunes los caballos, rinocerontes y una nueva especie de protocerátido pequeño, *Prosynthetoceras orthrionanus* sp. nov. Otros ungulados incluyen un pequeño chalicothero, un nuevo rinoceronte, *Gulfoceras westfalli* gen. et sp. nov., y un entelodonte gigante. La abundancia de protocerátidos, tapires, anthracotheros y rinocerontes; así como la ausencia de oreodontos y la rareza de camélidos en la curva de Toledo contrastan con las faunas Arikareanas en Florida donde los protocerátidos y anthracotheros están ausentes, los rinocerontes y tapires son extremadamente raros, los oreodontes están presentes y los camélidos son relativamente comunes.

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INTRODUCTION

The most diverse late Arikareean assemblage yet recorded from the Gulf Coastal Plain, the Toledo Bend Local Fauna, was recovered during summer months of 1989-90 from a submerged site in a canal that connects the Toledo Bend Reservoir with the Sabine River in Newton County, Texas. A detailed description of the site is provided in previous papers that focused on the lower vertebrate (Albright, 1994) and non-ungulate mammalian taxa (Albright, 1996), and on a comparison with other early Miocene faunas of the Gulf Coastal Plain and their relationship with faunas of the northern Great Plains as a function of dispersal and endemism (Albright, 1998a). This report, the last of a series on the Toledo Bend Local Fauna, provides the systematic account of all ungulates recovered with the exception of the tapir found there. The latter taxon, determined to represent a new genus, is described and discussed in Albright (1998b). Ungulates in addition to the tapir include two horses, three rhinoceroses, a chalicothere, an entelodont, three peccaries, an anthracothere, a camelid, two protoceratids, a hypertragulid, and an unidentified small artiodactyl. All are low-crowned browsing forms. Table 1 is an updated faunal list of all vertebrate taxa currently comprising the Toledo Bend Local Fauna.

Prior to study of the Toledo Bend Local Fauna, nearly all knowledge regarding the Arikareean Land Mammal "Age" for the Gulf Coastal Plain was based on a handful of assemblages in Florida such as the Buda, SB-1A, Franklin Phosphate Pit No. 2, Brookesville, White Springs, and Cow House Slough local faunas (see Albright, 1998a, and references within). Current study of the newly discovered Brookesville 2 Local Fauna by Florida Museum of Natural History personnel will add considerably to our understanding of this interval in this region (G. Hayes, pers. comm.). Localities in Texas, such as the Cedar Run Local Fauna, also have yielded mammals indicative of the Arikareean, yet the quality and

Table 1. Faunal list of all early Miocene vertebrates from the Toledo Bend Local Fauna. Compiled and updated from Albright (1991, 1994, 1996, and 1998) and Manning, (1990).

- Osteichthyes
  - *Lepisosteus* sp.
  - *Atractosteus spatula*
  - *Ictalurus punctatus*
  - *Micropterus* sp.
  - ?*Centropomus* sp.
- Amphibia
  - *Batrachosauroides* sp.
  - ?Sirenidae
- Reptilia
  - Trionychini
  - *Dermatemys* sp.
  - Emydid, small sp.
  - Emydid, large sp.
  - *Hesperotestudo* sp.
  - *Peltosaurus* sp.
  - *Anilioides nebraskensis*
  - Erycinaeid boid
  - *Alligator olseni*
  - *Gavialosuchus* sp.
- Mammalia
  - Insectivora sp. indet.
  - Rodentia
    - *Protospermophilus* sp.
    - *Neatocastor hesperus*
    - Eomyid or cricetid indet.
- Mammalia (cont.)
    - *Proheteromys toledoensis*
    - *Proheteromys sabinensis*
    - *Texomys* sp.
  - Carnivora
    - ?*Palaeogale* sp.
    - *Daphoenodon notionastes*
  - Perissodactyla
    - ?*Miohippus* sp.
    - *Anchippus texanus*
    - *Moropus* sp.
    - *Nexuotapirus marslandensis*
    - *Gulfoceras westfalli* n. gen. et sp.
    - *Diceratherium annectens*
    - *Diceratherium armatum*
  - Artiodactyla
    - ?*Dinohyus* sp.
    - "*Cynorca*" *sociale*
    - ?*Floridachoerus olseni*
    - ?*Hesperhys* sp.
    - *Arretotherium acridens*
    - *Nothokemas* sp.
    - *Prosynthetoceras orthrionanus* n. sp.
    - *Prosynthetoceras texanus*
    - *Nanotragulus* sp.
    - Small artiodactyl indet.

amount of material, as well as the diversity of taxa, is substantially less when compared with sites in Florida. The Toledo Bend Local Fauna is significant, therefore, because it finally provides a view into the Arikareean of the western region of the Gulf Coastal Plain that is based on an abundance of high quality fossils representing a wide diversity of species. As a consequence, new views regarding this distinct biogeographic province during the earliest Miocene, unrecognized when seen solely through the Florida "window," are now forthcoming.

Of additional importance is the interval of time represented by the Toledo Bend Local Fauna and by the correlative assemblages in Florida noted above. Recent magnetostratigraphic studies in northwestern Nebraska have determined that strata of the Arikaree Group (in which the defining faunas of the Arikareean Land Mammal "Age" originated) spanning the interval from about 27 to 22 Ma are apparently missing (MacFadden and Hunt, 1998). Importantly, it is the later part of this interval, the early part of the late Arikareean, thought to be sampled by these

Gulf Coastal Plain assemblages (Albright, 1998a). It may be, therefore, that the "endemic" early Miocene Gulf Coast fauna is, to some degree, an artifact of sampling a temporal interval not previously represented in the North American record.

The Toledo Bend Local Fauna differs from other early Miocene Coastal Plain faunas in a number of aspects. First is the unusual abundance of aquatic and riparian taxa such as fish, turtles, alligators, tapirs, anthracotheres, and protoceratids. Second, many of its members, such as the tapir and anthracothere, were previously known only from Arikareean faunas of the northern Great Plains. Third, many of its members are not shared with comparably aged faunas in Florida such as those noted above. Finally, grazing ungulates are absent.

These factors can be attributed, in part, to the preservation of a paleoenvironment that apparently is rarely preserved in the early Miocene of North America—that of a subtropical to tropical coastal plain forest with a predominant fluvial component. In turn, the preservation of this environment was largely due to sedimentological influences imposed by a paleo-Mississippi River system that was migrating from east Texas to Louisiana during the late Oligocene-early Miocene (Galloway et al., 1986, 1991). Northern Florida, however, which undoubtedly shared similar climatic conditions during this interval, was not subjected to similar sedimentological influences, as is reflected in preservation there that is essentially limited to karst fissure infilling rather than strictly fluvial processes. In fact, the extent to which the Florida Platform was subaerially exposed during this interval is still poorly understood (see, e.g., Huddlestun, 1993, and Scott, 1997). This preservational bias may account for some of the faunal differences between the two areas, but ecological factors and distance from, or proximity to, the northern Great Plains may have contributed as well. Furthermore, vaguely defined temporal inequivalencies that may exist between the Toledo Bend site and those in Florida are difficult to resolve because of the lack of accurate geochronological control other than that provided by the mammals themselves. There are no radioisotopically dateable volcanic beds in appropriately aged strata of the Texas Coastal Plain or Florida, and magnetostratigraphy is also of limited use, as few, if any, of these sites occur in an amenable stratigraphic context; sites are either underwater or they exist as widely distributed isolated outcrops or karst fissure-fill deposits. Despite these limitations, the Toledo Bend assemblage still provides important new information toward an understanding of the vertebrate fauna that inhabited the Gulf Coastal Plain during the earliest Miocene, as well as toward the paleoecology and biogeography of the region. Further details of the paleoecology are provided in Albright (1991, 1994).

ABBREVIATIONS

Fossils from the Toledo Bend site are curated in the vertebrate paleontological collection of the Louisiana State University Museum of Geoscience, Baton Rouge, abbreviated throughout as LSUMG-V. Other abbreviations used are as follows: AC, Amherst College Museum, Amherst, Massachusetts; AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; CM, Carnegie Museum, Pittsburgh; F:AM, Frick:American Mammals collection at the AMNH; UF/FGS, Florida Geological Survey, now housed with the University of Florida (UF) collection at the Florida Museum of Natural History (FLMNH), Gainesville; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; SDSM, South Dakota School of Mines, Rapid City; TMM-TAMU, Texas Agricultural and Mechanical University collection at Texas Memorial Museum, Austin; UCMP, University of California Museum of Paleontology, Berkeley; UNSM, University of Nebraska State Museum, Lincoln; USNM, United States National Museum of Natural History, Smithsonian Institution; YPM, Yale Peabody Museum, New Haven. Capital letters "P" or "M" followed by a number refer to upper premolars and molars, respectively; lower case letters "p" or "m" followed by a number refer to lower premolars and molars, respectively. AP and TR refer to anteroposterior and transverse measurements, respectively. FAD denotes First Appearance Datum. All measurements are in millimeters. Subdivisions of North American Land Mammal Ages as used in this report (e. g., early late Arikareean) follow Tedford et al. (1987).

ACKNOWLEDGMENTS

This report is based on a detailed study of the Toledo Bend site completed as an M.S. thesis at Louisiana State University. J. Schiebout is thanked for her support as my major professor and for providing a Museum of Geoscience Research Grant that helped fund field work, travel, and other expenses. E. Manning first introduced me to the site, and to the amateurs who collected there previously, and made many of the initial identifications. L. Jacobs, R. Tedford, and M. Woodburne critically reviewed early manuscripts of the thesis and provided numerous helpful comments. Others who reviewed specific sections and provided helpful comments include M. Coombs, J. Hazel, R. Hunt, B. MacFadden, E. Manning, C. McCabe, J. Martin, and D. Prothero. R. Hunt and R. Tedford are additionally thanked for their careful review of the manuscript which resulted in this contribution, and for sharing with me over several years their vast knowledge of the Arikareean and Hemingfordian mammal ages. Similar discussions with D. Webb and G. Morgan were always enlightening, as well, and greatly appreciated.

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Gratitude is also extended to numerous avocational collectors. J. Hudson, of Baton Rouge, first brought the site to academic attention. K. Griffin from Lafayette, LA, and J. Stewart, from Leesville, LA, generously donated and made available many important specimens, including the tapir maxilla and the anthracothere ramus. R. Westfall, from Rosepine, LA, also donated and made available many interesting and important specimens, including the chalicothere teeth, some peccary teeth, and the well preserved dwarf rhino tooth. I additionally want to thank Mr. Westfall for help he provided during one field trip when we were plagued by truck problems. B. Fite is thanked for making available for study the only known virtually complete ramus of a small chalicothere. D. Cring, from the Department of Sociology and Anthropology, USL, Lafayette, also donated some specimens he had collected, and provided helpful discussions about the site early in my investigation. D. Lescinsky, L. Albright, S. McLaughlin, T. Delage, and E. Manning helped in the underwater exploration of the site and all found many important specimens.

Helpful discussions on the geology of the site were provided by J. Rogers, USGS retired, and P. Heinrich, then a Ph.D. candidate in the LSU Department of Geology. Mr. Rogers generously provided detailed, unpublished field and electric log data which accurately placed the site in stratigraphic context, as well as helpful discussions regarding the geology and stratigraphy of the western Louisiana-eastern Texas region. Mr. Rogers also found and donated a fragment of an entelodont tooth. Mr. Heinrich also visited the site and was helpful in interpreting its sedimentological aspects.

S. Murray and F. Demiers of the LSU Coastal Studies Institute provided much of the scuba equipment used in this investigation. Most photographs were taken and processed by LSU Coastal Studies Institute photographer K. Lyle. Others were taken by Erica Simons and Terry Lott of the Florida Museum of Natural History. Figure 1 was prepared by M. L. Eggert and C. Duplechin of the LSU Cartographic Services Division.

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GEOGRAPHIC AND GEOLOGICAL SETTING

Figure 1 shows the location of the Toledo Bend site in Newton County, Texas, approximately 27 km northeast of Burkeville in the "tailrace" canal that joins the Toledo Bend Reservoir to the Sabine River. The Sabine River marks the Texas/Louisiana state boundary and the site is about 400 m northwest of that boundary. As discussed at length in previous papers (Albright, 1991, 1994, 1996, 1998a, 1998b), the outcrop pattern of the Fleming and underlying Catahoula formations is mapped differently across the state line resulting in placement of the site in the upper part of the Catahoula Formation as mapped in Texas, but in the Carnahan Bayou Member of the Fleming Formation as mapped in Louisiana.

SEDIMENTOLOGICAL AND TAPHONOMIC CONTEXT

Most fossils from the Toledo Bend site were collected from a lag deposit that accumulated on the bottom of the canal since its excavation in 1969. The fossils originated and eroded from a paleochannel conglomerate that crops out immediately adjacent to the modern-day lag. Laminated floodplain siltstones lie stratigraphically above and below this outcrop. Because nearly all lower vertebrate

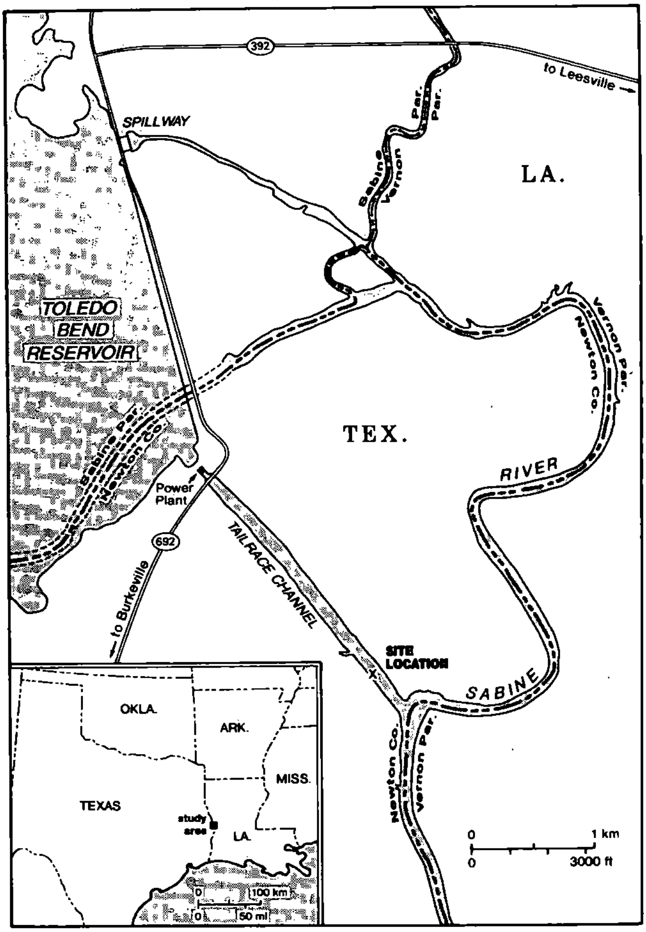

Figure 1. Location of Toledo Bend site in Newton County, Texas.

taxa in the fauna are indicative of quiet, slow-flowing bodies of water (Albright, 1994), and because Galloway et. al. (1986) considered the east Texas region as having very low relief during the early Miocene, the conglomeratic deposit was likely during an episode of violent flood mixing. There is no indication of sediment sorting throughout the deposit. Clay and siltstone rip-up clasts, quartz and chert pebbles, and bones and teeth of various sizes occur randomly distributed. No imbrication of pebbles is apparent, and there is no obvious indication of paleocurrent direction based on the few specimens collected *in situ*. The only graded bedding observed is at the top of the deposit where it abruptly grades into the overlying siltstone presumably after the high energy event subsided.

Almost all bones show at least some degree of abrasion, although very few are worn beyond recognition and most, although fragmented, show only light to moderate wear and/or polishing. Exceptions include bone recently eroded from the paleochannel deposit that fractured during the process. Well rounded bone cobbles illustrate the most extreme cases of wear. Many specimens were likely exposed to streamflow abrasion or subjected to numerous episodes of transport and reworking prior to entrapment in the Toledo Bend deposit (see Behrensmeyer, 1982). Supporting this, a highly worn entelodont astragalus was found *in situ*, whereas another, virtually unworn specimen was found free in the modern lag deposit. Fossils in the lag deposit are additionally subjected to abrasion caused by strong currents produced during electricity generation (there is a hydroelectric plant at the head of the canal). These currents not only facilitate erosion of fossils from their matrix, but also churn the bottom sediments, thus exposing fossils previously eroded and deposited into the lag.

No remains were found in an articulated or partially articulated state, nor were any complete, unbroken bones found except isolated elements of the manus and pes (rare vertebrae were recovered in worn, but relatively complete condition). The frequency of occurrence of various elements recovered is largely a function of the mechanical stability of those elements. Teeth, teeth fragments, and manus and pes elements make up the greatest percentage of remains recovered. Of the isolated teeth collected, none retain their complete root system and most consist of only the crown. Mandibular fragments are uncommon. Skull material is limited to those parts of relatively greatest mechanical strength including rare maxillary fragments, isolated petrosals, and other bones of the ear region. Similarly, limb bone material is limited primarily to fragments of the proximal and distal ends. Because the scapula and pelvis are readily transported and abraded (Voorhies, 1969), recovered fragments of these elements also include only their strongest parts, the glenoid region of the former and the acetabular part of the latter.

Presently the Toledo Bend Local Fauna does not include a large enough series of any one taxon to perform population studies. Stage of tooth wear indicates a mixture of all age groups. From the diversity of the fauna and the condition of the remains recovered, the fossils from Toledo Bend, although concentrated in the deposit by a flood event, appear to represent an attritional mode of mortality. The accumulation of remains in a channel deposit, combined with (1) many abraded elements, (2) the absence of certain elements and concentration of others, and (3) the lack of articulated skeletons and/or complete skulls, limb bones, etc., provides evidence indicating that most, if not all, of the fossils were variably subjected to episodes of reworking prior to their final emplacement in the Toledo Bend deposit (see Behrensmeyer, 1982). Further details on the taphonomy of the Toledo Bend site can be found in Albright (1991).

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order PERISSODACTYLA Owen, 1848
Family EQUIDAE Gray, 1821
?*Miohippus* sp.

Figure 2

Type Species.—*Miohippus annectens* Marsh, 1874

Referred Specimens.—LSUMG V-2509, incisor; V-2510, left M3; V-2251, right upper cheek tooth; V-2252, partial left lower m3; V-2511, left astragalus; V-2512, partial right cuboid; V-2513, distal metapodial III; V-2514, proximal phalanx of medial digit; V-2515, two proximal phalanges of lateral digits; V-2768, proximal phalanx of lateral digit.

Description.—V-2510 is thought to be an M3 based on the lack of interstitial wear on the posterior surface (Fig. 2A). The labial surface of the paracone and metacone is broad anteroposteriorly and ribbed. The parastyle and mesostyle, but not the metastyle, are prominent. An anterior cingulum is continuous with the parastyle. There is no lingual cingulum. The metaconule is submerged within the metaloph. The metaloph has no crochet or plications, and it meets a lingually directed spur originating from the ectoloph (the medicrista). The hypostyle shows the "type 3" morphology of Prothero and Shubin (1989:144, fig. 10.1). Cement is entirely absent. The tooth measures 13.7 mm AP by 15.5 mm TR. Another upper cheek tooth, V-2251, differs from V-2510 in having a non-connected metaloph. Although the partial m3 (V-2252) shows no trace of a cingulum, it may have been worn away, as the tooth is highly water-worn. The astragalus measures 22.3 mm proximo-distally by 17.5 mm transversely.

Discussion.—Tentative referral to *Miohippus* is based on dental similarity to a small horse in the collections of the FLMNH referred to cf. *Miohippus* from the late early Arikareean Cow House Slough Local Fauna, Hillsborough County, Florida (Morgan, 1994). It is important to note, however, that the distinction between later members of *Miohippus* and early members of *Archaeohippus* (extinction of

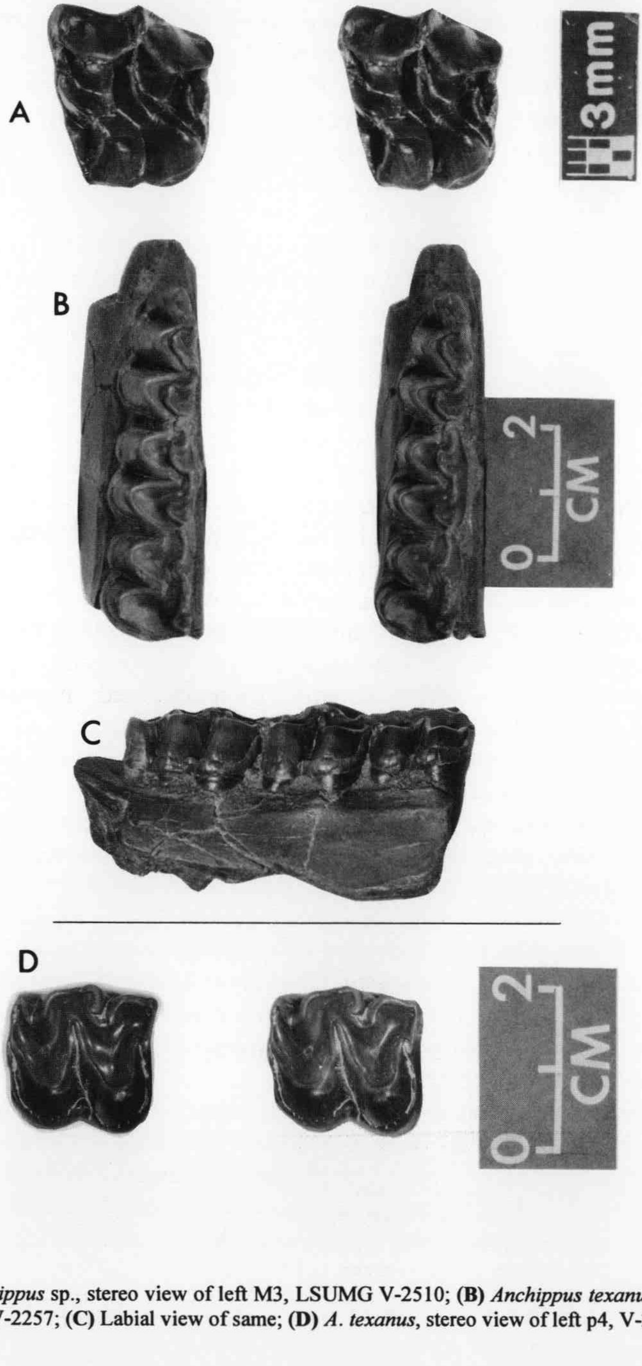

Figure 2. **(A)** ?*Miohippus* sp., stereo view of left M3, LSUMG V-2510; **(B)** *Anchippus texanus*, stereo view of right m1-3, V-2257; **(C)** Labial view of same; **(D)** *A. texanus*, stereo view of left p4, V-2526.

Miohippus and first appearance of *Archaeohippus* overlaps in the Arikareean) based solely on dentition remains tenuous, at best, and both groups are long overdue for a major revision. Typically, distinction centers around the connection of the metaloph to the ectoloph, i. e., not connected in *Miohippus*, connected in *Archaeohippus* (Stirton, 1940; Prothero and Shubin, 1989:169). However, many specimens referred to *Miohippus* show the connected condition, including F:AM specimens 116414, 116415, and 116416 from the "lower *Protoceras* channels" of Washington County, South Dakota (labeled *M. gidleyi*), and AMNH specimens 12917d and 19914 from the "lower Rosebud" near Porcupine Creek, South Dakota, whereas specimens of *A. blackbergi* in the large sample from the early Hemingfordian Thomas Farm Local Fauna, Florida, rarely show an unconnected metaloph. Additionally problematic are several specimens from other Arikareean localities in Florida, other than Cow House Slough, that show an intermediate, very weakly connected condition such as that seen in LSUMG V-2510. On the other hand, V-2251, as noted above, retains the disconnected condition more typical of *Miohippus*.

Upper cheek teeth of ?*Miohippus* sp. from Toledo Bend and Florida differ from those of *Archaeohippus blackbergi* (also known from the early Hemingfordian Garvin Gully Fauna, Texas) in larger size and absence of a crochet or plications on the metaloph. ?*Miohippus* sp. also has an anteroposteriorly broader ectoloph than does *A. blackbergi* and the cingulum labial to the metacone does not continue posteriorly into as prominent a metastyle. *Archaeohippus minimus* (Douglass, 1899), *A. ultimus* (Cope, 1886), and *A. mourningi* (Merriam, 1913) are larger than *A. blackbergi* and they have additional plications on the metaloph. The lower cheek tooth of ?*Miohippus* sp. is slightly lower crowned than in *Archaeohippus blackbergi*, and the "V" shaped trigonid and talonid in the latter appear anteroposteriorly broader and rounder in the former. Although not comparable due to lack of material in the Toledo Bend hypodigm, R. Hunt (pers. comm., 1998) also noted that lower premolars are conspicuously broader transversely than the molars in *Miohippus*, whereas in *Archaeohippus* there is less of a size difference between p4 and m1.

Subfamily EQUINAE Gray, 1821
Genus *Anchippus* Leidy, 1868
Anchippus texanus Leidy, 1868
Figures 2, 3

Anchippus texanus Leidy, 1868
Anchippus texanus Leidy, 1869
Parahippus texanus (Leidy). Gidley, 1907
Parahippus texanus (Leidy). Osborn (1918)
Parahippus texanus (Leidy). Stirton, 1940
Parahippus cf. *P. texanus* (Leidy). Forsten, 1975, in part

Table 2. Measurements of dentition of *Anchippus texanus*. [a] LSUMG V-2620, right maxillary fragment with P3-M1; [b] LSUMG V-2257, right ramal fragment with m1-3; [c] LSUMG V-2259, right ramal fragment with dp4-m1; [d] LSUMG V-2530, right ramal fragment with m1-2; [e] LSUMG V-2531.

	ECTL	AP	TR		AP	TR
P2		17.5	17.7	p3	16.9	14.4
		19.8	19.5	p4	17.9	17.0
P3	19.0[a]	17.3	21.2	m1	15.0[b]	12.3
P4	18.6[a]	17.8	22.0		14.1[d]	12.4
	18.0	17.0	22.6		14.7[c]	10.0
M1	18.5[a]	17.2	21.5	m2	15.2[b]	12.0
	–	16.3	21.6		14.3[d]	12.7
	17.8	17.0	22.0		15.7	12.2
	17.4	16.6	22.4		14.1[e]	13.0
M2	18.1	17.6	23.4	m3	19.1[b]	11.1
M3	17.5	15.5	21.5		20.4	10.0
	17.7	16.3	21.0			

Holotype.—ANSP 11275, left M1 or M2 from "Hutchen's well," Washington County, Texas.

Referred Specimens.—**Toledo Bend**: LSUMG-V-2516, three incisors; V-2517, two right P2s; V-2518, right P2; V-2519, right P4; V-2520, worn right upper cheek tooth; V-2248, right M1; V-2521, right M1?; V-2522, left M2; V-2523, right M3; V-2524, left M3; V-2620, right maxillary fragment with P3-M1; V-2525, left p3; V-2526, left p4; V-2531, right m2; V-2527, left m2; V-2528, left m3; V-2529, partial right lower cheek tooth; V-2259, right ramal fragment with dp4-m1; V-2530, right ramal fragment with m1-2; V-2257, right ramal fragment with m1-3; V-2532, scapula fragments; V-2533, proximal left radius; V-2534, two distal radius fragments; V-2535, two proximal ulna fragments; V-2536, right magnum; V-2537, two distal tibia fragments; V-2538, seven astragali; V-2767, two astragali (juvenile); V-2539, calcanea fragments; V-2540, left and right cuboid; V-2541, left and partial right navicular; V-2542, partial ectocuneiform; V-2543, sesamoid fragment; V-2769, two proximal lateral metapodials; V-2544, distal lateral metapodial; V-2545, three proximal metatarsal III fragments; V-2546, two distal metapodial III fragments; V-2547, distal metatarsal III; V-2548, three proximal phalanges; V-2258, proximal phalanx; V-2549, four medial phalanges; V-2550, proximal lateral phalanx. **Cedar Run Local Fauna**: TMM 40068-7, left M3.

Description.—Measurements of upper and lower cheek teeth are provided in Table 2. The incisors from Toledo Bend have cupped crowns and the cheek teeth show a primitive "parahippine" morphology. Upper cheek teeth (Fig. 3A-F) lack cement and a lingual cingulum. The metaloph is non-plicated and its connection to the ectoloph is at a primitive stage in that a lingually directed blade derived from the ectoloph connects with a labially directed extension of the metaconule. The

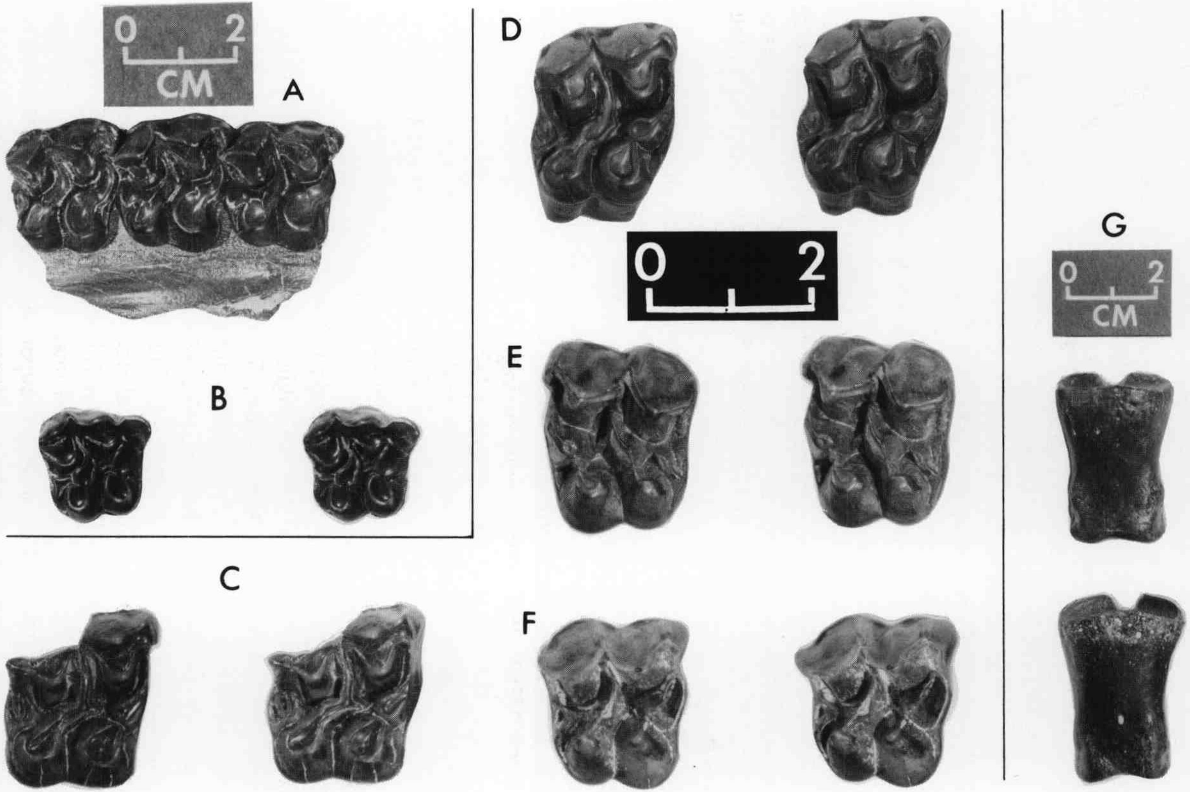

Figure 3. *Anchippus texanus*. **(A)** Right P3-M1, LSUMG V-2620; **(B)** Stereo view of right P2, V-2518; **(C)** Stereo view of right M1?, V-2521; **(D)** Stereo view of right M1?, V-2248; **(E)** Stereo view of left M2?, V-2522; **(F)** Stereo view of right M3, V-2523; **(G)** Proximal phalanges, V-2258 (top), V-2549 (bottom).

ectoloph is ribbed with the rib on the paracone being generally more prominent than that on the metacone. The parastyle and mesostyle are prominent. As seen in unworn specimens, the anterior cingulum is shelf-like between the protocone and protoconule, and continuous with the parastyle. The protocone and protoconule are entirely separated to the extent that even in medium wear stage their dentine does not merge. Dentine of the two cusps does not unite until the grinding surface of the tooth is highly worn as in V-2519, 2520, and 2620. Prominence of the metaconule varies, but it can always be distinguished from the hypocone by an anterior and posterior constriction on the metaloph.

The crochet varies from non-existent (V-2523 and V-2620), to a slight trace (V-2519 and V-2248), to relatively prominent (V-2520 and V-2524). In no case does the crochet connect to the protoconule except in P2 (V-2518). The hypostyle in V-2521, 2522, and 2620 resembles the "Type 3" hypostyle of Prothero and Shubin (1989:144, fig. 10.1). In other cheek teeth, the hypostyle is triangular and encloses a hypostylar fossette. The dentine of the hypostyle is not continuous with that of the metaloph, each being bound by its own enamel until extreme stages of wear. P4 and M1 are nearly the same size, and M2-3 are progressively smaller, but not to the point where M3 would be considered reduced.

Lower cheek teeth (Fig. 2B, C, D) show a prominent anterior, posterior, and labial cingulum and lack cement. The p3-4 are wider transversely than m1-3 with p4 being the widest. V-2531, an m2, shows a separated metaconid and metastylid, but not as separated as in lower molars of *Parahippus leonensis*. Crown height is lower than in *P. leonensis*, resembling more closely that found in the type specimen of *P. pawniensis* (AMNH 9085).

Appendicular skeleton (Fig. 3G): Proximal phalanges of digit III are distinctly broader for their length than those of *P. leonensis*, but not as broad for their length as in *Anchitherium clarencei* from Thomas Farm. The distal tibia fagments have highly oblique astragalar facets, the medial of which is narrower and deeper than the lateral. The nine astragali show a wide range of size variation.

Discussion.—Referral to *Anchippus texanus* is based on the similarity of the teeth in size and morphology to the (admittedly poor) type specimen from "Hutchen's Well" in Washington County, Texas (Leidy, 1868), and because of the uncertain status of the genus *Parahippus* (see discussion in Voorhies, 1990:A170-A171). Recovery of the type from a well precludes accurate stratigraphic placement, although Forsten (1975) referred a tooth from another site in Washington County, the Cedar Creek fossil locality, to this species. Wood and Wood (1937) correlated the Cedar Creek assemblage (Cedar Run Local Fauna of Tedford et al., 1987) to faunas from the Harrison Formation in the northern Great Plains. Although illustrations of the type specimen (Leidy, 1869; Osborn, 1918) show an anterior cingulum that continues lingually around the protocone, personal observation of a cast of the specimen shows that this lingual continuation is exaggerated in the illustrations and that the cingulum actually ends before rounding the lingual surface of the protocone.

Similarity of tooth morphology suggests that *Anchippus texanus*, *Parahippus nebrascensis*, and *Parahippus wyomingensis* may be closely related. The resemblance between *A. texanus* and *P. nebrascensis* was noted by Peterson (1907), Osborn (1918), Matthew (1913; see Osborn 1918:79, 84), and Schlaikjer (1937). The type of *P. nebrascensis* from the "upper Harrison beds" of Sioux County, Nebraska (Peterson, 1907), and AMNH 12924, a specimen from the "Upper Rosebud" referred to *P. texanus* by Osborn (1918), differ from Toledo Bend specimens in larger size, stronger crochets, less conical hypocones, and less constricted separation between the protocone and protoconule. The relative degree of hypsodonty is similar. *Parahippus wyomingensis*, from the "lower part of the upper Harrison formation in the Goshen Hole Area, Wyoming" (Schlaikjer, 1937:255), is also larger, although one anomalously large lower premolar from Toledo Bend (V-2519) closely resembles the p4 of the type specimen (MCZ 6390).

Teeth of the type specimen of *P. tyleri* Loomis (1908) differ from *A. texanus* in being larger, more hypsodont, in having a less conical and more anteroposteriorly crescentic hypocone and protocone, and a more crescentic metaloph resulting in the hypocone being positioned posterior to the metacone rather than directly lingual to it. Also, the paracone rib is reduced in *P. tyleri*. Although Loomis (1908:164) listed the type (AC 1079) from "the upper part of the Lower Harrison beds, 8 miles northeast of Agate, Sioux County, Nebraska," Cook and Cook (1933) listed it from the Upper Harrison beds of Nebraska, and R. Tedford (written comm., 1990) also suggested that the type locality was more likely in the Upper Harrison or Runningwater formations. *Parahippus tyleri* is probably a latest Arikareean to early Hemingfordian form and therefore not likely ancestral to *P. nebrascensis* as Loomis suggested.

The type specimen of *P. pawniensis* (AMNH 9085) differs from Toledo Bend specimens in having a weakly plicated metaloph, a reduced M3, and a less distinct posterior constriction between the protocone and protoconule. The prominent labial cingulum on the lower cheek teeth from Toledo Bend is absent on the m3 of the *P. pawniensis* type specimen. Gidley (1907) described the type from the Pawnee Creek beds, Colorado, which were not clearly differentiated from the Martin Canyon Formation of early Hemingfordian age (Tedford et al., 1987). The dental morphology of AMNH 9085 suggests an older age, and specimens from the early Hemingfordian Flint Hill Local Fauna, South Dakota, (e.g., UCMP 32360, 32622, and 37285) and from late Arikareean deposits near the Lusk area, Wyoming (e.g., F:AM 109859), have also been referred to this species.

North American species of *Anchitherium* differ from *Anchippus texanus* in larger size, lack of a ribbed paracone and metacone resulting in a strongly W-shaped ectoloph, absence of a crochet, and a reduced M3. Also, in *Anchitherium*, the metaloph is not always connected to the ectoloph (e.g., early Arikareean F:AM specimens from "Harris Ranch just north of the Pine Ridge Reservation" and AMNH 105167 from the John Day Formation, as well as UF 22137 [a cast of a specimen] from the late Arikareean "Harrison beds near Van Tassell, Wyoming").

The M3 of the type specimen of *Anchitherium navasotae* Hay (1924) from the Garvin Gully Fauna (TMM-TAMU 2385) is generally similar to some of the Toledo Bend cheek teeth (e. g., V-2522), but differs in having a paracone that is higher than the metacone (in the Toledo Bend teeth they are of equal height), in having a relatively low metaloph and protoloph resulting in shallow pre- and post-fossettes in contrast to deep ones in the Toledo Bend teeth, and in having a more oblique ectoloph. *Kalobatippus agatense* is similar in size to *Anchippus texanus*, but differs from the latter in the same manner as does *Anchitherium*. A review of *Kalobatippus* and *Anchitherium* is currently underway by B. MacFadden (pers. comm., 1998).

Lower premolars referred to *Anchitherium navasotae*, also cataloged under TMM-TAMU 2385, are indistinguishable from those of the Toledo Bend species, sharing the slightly separated metaconid and metastylid and a continuous anterior, labial, and posterior cingulum with no lingual cingulum. However, in *Anchitherium clarencei* from Thomas Farm, both upper and lower cheek teeth, as well as post-cranial elements such as astragali, are much larger than similar elements from Toledo Bend.

Forsten (1975:20) referred two upper cheek teeth, one from Cedar Creek (i.e., Cedar Run Local Fauna) and one from Hidalgo Bluff, Washington County, Texas, to *Parahippus* cf. *P. texanus* and additionally noted the absence of this species at Thomas Farm. In her descriptions she noted that the protocone and protoconule were of nearly equal size and that the teeth had a subtriangular outline caused by a protocone "centrally situated and larger than the reduced hypocone." Personal observation found this statement true only for the Hidalgo Bluff specimen, TMM 40067-63, but not for the Cedar Run tooth, TMM 40068-7. The Cedar Run tooth referred to *P.* cf. *P. texanus*, a left M3, closely resembles LSUMG-V 2523, a right M3 in the following features: size, lack of cement, relatively tall protoloph and metaloph resulting in deep anterior and posterior fossettes, distinct ribbing on the ectoloph with the paracone rib the more prominent, a simple crochet not connected to the protoloph, a larger protocone than hypocone, a simple, connected metaloph with no plications other than the crochet, and a protoloph with a distinct anterior and posterior groove constricting the protocone from the protoconule. Differences are minor including, in TMM 40068-7, a slightly more prominent crochet, the lack of an anterior cingulum, a less bulbous parastyle, and a posteriorly notched hypostyle. The type specimen of *Anchippus texanus* also has a posteriorly notched hypostyle.

In contrast to Forsten's (1975) findings, the Hidalgo Bluff tooth, TMM 40067-63, appears to belong to a separate species, as it differs considerably from the Cedar Run and Toledo Bend teeth. The Hidalgo Bluff tooth must certainly be the one to which Forsten referred when she noted the subtriangular outline resulting from a centrally located protocone. TMM 40067-63 additionally differs in smaller size, presence of cement in the fossettes, a weak protocone-protoconule separation, a crescentically-shaped rather than conical protocone, a strongly posteriorly-directed metaloph, and greater hypsodonty. Overall, TMM 40067-63 appears most similar to teeth of *Parahippus leonensis*, with the exception of a non-plicated metaloph, and it is to this species that this tooth is here referred. Compared with *P. leonensis*, the most common horse at Garvin Gully and Thomas Farm, the Toledo Bend teeth (and TMM 40068-7) are slightly larger, relatively less hypsodont, lack cement, have a less crescentic, less posteriorly directed protoloph and metaloph, a more conical protocone, protoconule, and hypocone, and a simple metaloph.

Another specimen in Forsten's (1975) hypodigm of *P.* cf. *P. texanus*, TMM 40623-9 from Push Creek, Tyler County, Texas, shares few similarities with TMM 40068-7, TMM 40067-63, the Toledo Bend teeth, or the type of *Anchippus texanus*. TMM 40623-9 resembles most closely *Anchitherium* in having an almost W-shaped ectoloph with no ribs and a plicated metaloph that does not connect to the ectoloph. There is abundant cement and there is no posterior constriction between the protocone and protoconule. Based on the above comparisons, it is here concluded, in contrast to Forsten's findings, that TMM 40068-7, TMM 40067-63, and TMM 40623-9 each belong to separate species and that only TMM 40068-7 should be referred to *A. texanus*.

Although lower cheek teeth from Toledo Bend vary in size (Table 2), this is likely due to sexual dimorphism rather than multiple species. In contrast to earlier studies by Simpson (1932), Quinn (1955), and particularly White (1942), who suggested the presence of as many as seven different species of horses at Thomas Farm, Hulbert (1984), in a detailed population dynamics study of *P. leonensis* from Thomas Farm, documented sexual dimorphism and concluded that it was "a good indication that [the] social structure [of *P. leonensis*] still resembled that of earlier, browsing equids."

Family CHALICOTHERIIDAE Gill, 1872
Subfamily SCHIZOTHERIINAE Holland and Peterson, 1914
Genus *Moropus* Marsh, 1877
Moropus sp.
Figure 4

Type Species.—*Moropus distans* Marsh, 1877

Referred Specimens.—LSUMG V-2703, partial right P2; V-2490, right m1 or m2; V-2489, right ramal fragment with m3; V-2408, distal left tibia; V-2409, distal left tibia; V-2410, right astragalus; V-2260, right metatarsal IV; LSUMG V-2411, proximal phalanx of digit IV; V-2261, proximal phalanx of digit III; V-2412, proximal phalanx; V-2413, proximal phalanx; V-2414, medial phalanx.

Description.—In its broken state the partial P2 measures about 15.3 mm AP by about 14 mm TR. There is a prominent, shelf-like anterior cingulum and a strong posterior cingulum continuous with a lingual cingulum (Fig. 4B). The anterior and lingual cingula only just meet at the anterolingual corner of the tooth. A conical, unworn protocone is the only lingual cusp. Extending labially from the protocone is

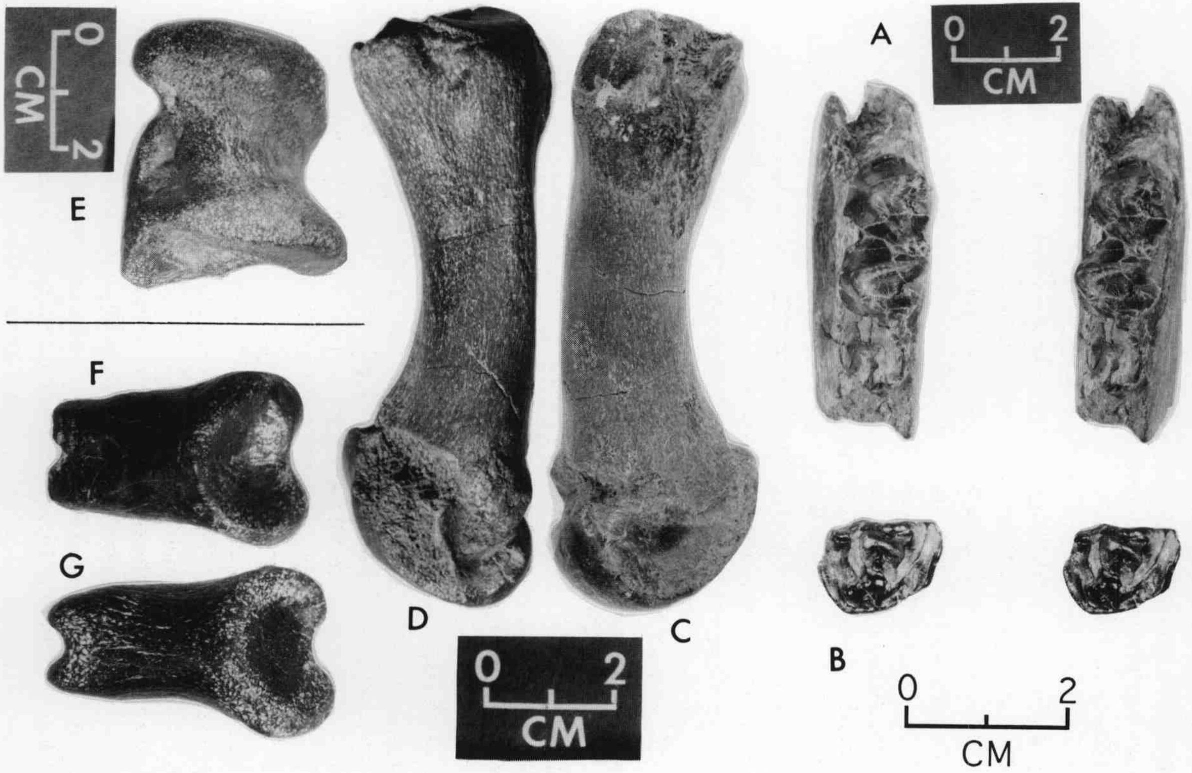

Figure 4. *Moropus* sp. **(A)** Stereo view of right m2, LSUMG V-2489; **(B)** Stereo view of right P2, V-2703; **(C)** Medial view of right Mt IV, V-2260; **(D)** Lateral view of same; **(E)** Right astragalus, V-2410; **(F)** Proximal phalanx, V-2261; **(G)** Proximal phalanx, V-2411.

a prominent protoloph and metaloph, the former more worn than the latter. Although damaged labially, the paracone was at least as prominent as the protocone. This tooth shows the wear pattern noted by Coombs (1978, 1979) of both *Moropus oregonensis* and *Tylocephalonyx skinneri* where the protoloph and the metaloph become worn before the protocone.

The m1 measures 25.0 mm AP by 14.0 mm TR. It has a prominent anterior and posterior cingulum and a small cingular segment at the labial entrance of the valley between the trigonid and talonid. The talonid is larger than the trigonid. Measuring about 11.0 mm AP by 12.5 mm TR, the trigonid resembles that of a right lower molar from the Buda Local Fauna (Frailey, 1979) that measures 10.3 mm AP by 13.0 mm TR. That from Buda, however, is relatively less hypsodont than the Toledo Bend specimen and it has no cingula.

The relatively unworn state of the m2 (Fig. 4A) shows a separated metaconid and metastylid. The trigonid and talonid are nearly the same size. Although partially broken, the labial cingular segment is more prominent in m2 than in m1. The tooth measures 29.2 mm AP and 15.4 mm TR.

The medial malleolus of the two distal tibia fragments is not nearly so prominent as in *Moropus elatus*. Resembling *M. elatus*, however, is the broad and shallow lateral astragalar facet (see Coombs, 1978:34-45). The medial facet is narrower and deeper than the lateral, but not nearly to the extent seen in horses, rhinos, and tapirs. V-2409 measures 44.4 mm TR and 33.2 mm AP; V-2408 measures 36.2 TR by 29.4 mm AP.

The astragalus measures 40.5 mm transversely by 36.4 mm dorsoventrally. It resembles that of *M. elatus*, and differs from that of horses and rhinos in having a broad sulcus between the medial and lateral trochleae, a highly reduced neck, and a navicular facet that does not extend laterally to the distal termination of the lateral trochlea (Fig. 4E).

The metatarsal (Mt) IV has separate dorsal and volar facets on the medial surface for articulation with the Mt III (Fig. 4C). The volar facet, though somewhat abraded, is smaller than the dorsal facet. The area just distal to the dorsal and volar Mt III facets is rugosely textured for muscle attachment. The cuboid facet has a roughly rectangular outline with its transverse diameter the greatest. There is no distinct ectocuneiform facet. The cross-sectional outline of the shaft is roughly quadrate. Immediately proximal to the dorsal surface of the distal articular surface is a chevron-shaped sulcus. Proximal and medial phalanges do not unite to form a duplex digit, apparently common in other species (Fig. 4F, G). Proximal phalanx measurements are provided in Table 3. The medial phalanx from Toledo Bend measures 24.5 mm in length, 16.5 mm in distal width, and 19.0 mm in proximal width.

Discussion.—Chalicothere remains from the Coastal Plain were previously known only from the Buda Local Fauna (Patton, 1967c; Skinner, 1968; Patton and Webb, 1970; Coombs, 1978; Frailey, 1979; and Coombs, 1989). Several additional

Table 3. Measurements of proximal phalanx for specimens of Moropus sp. from Toledo Bend and Buda local faunas. * Frailey (1979).

	Toledo Bend			Buda*
	V-2262	V-2412	V-2411	UF 24130
Length	32.3	34.6+	41.8	45.7
Proximal width	25.4	25.8	24.6	26.5
Distal width	16.2	17.2	16.4	18.5
Depth at dorsal margin of metapodial facet	22.0	20.3	20.2	21.3
Depth at volar termination of distal articulating surface	16.9	18.8	16.5	16.8

specimens closely resembling those from Buda were recently recovered from a undisclosed locality in Pasco County, Florida, but are retained in a private collection unavailable for study. Additional taxa from this locality indicate age equivalence with the Buda Local Fauna (pers. observ., 1998). Another specimen recently recovered from the panhandle region of Florida, and also retained in a private collection, consists of a nearly complete right ramus with p3-m3, missing p2. This specimen, a cast of which is housed at the FLMNH (UF 180233), represents a smaller individual than those represented by material from Toledo Bend, which, in turn are slightly smaller than the specimens from Buda. Sexual dimorphism, well documented in the Chalicotheriidae (Coombs, 1975), may account for these variations in size. Late Arikareean and Hemingfordian species from the High Plains (e.g., *Moropus elatus* and *M. hollandi*; see Coombs, 1978, 1989) are considerably larger.

Other small North American chalicotheres are known from the John Day Formation, Oregon, and include the genoholotype *Moropus distans* Marsh (1877) and *M. oregonensis* (Leidy, 1873). Coombs (1978, 1989) suggested that these two species may be conspecific. Although Frailey (1979) concluded that the Buda species was not *M. oregonensis* based on the quadrangular shape of M1 (UF 24131), Coombs (pers. comm., 1996) found that UF 24131 is more likely a dP4 (and the "M2" an M1) noting that dP4 is typically more quadrate and less elongate than M1. Lack of matching elements precludes direct comparisons between the Oregon and Toledo Bend specimens, but the P2 from Toledo Bend is the size expected for *M. oregonensis* based on the P3-4 of the latter (see Coombs, 1978:46). All specimens from the John Day Formation for which there is reliable stratigraphic data originate from strata overlying a tuff dated by C. Swisher at 22.6 Ma (R. Hunt and E.

Table 4. Measurements and proportions of Mt IV for various specimens of *Moropus*. MXL = maximum length; MXDW = maximum distal width; MNSW = minimum shaft width; L/DW = length/distal width; L/MNSW = length/minimum shaft width. * Frailey (1979:147); ** Coombs (1978:39).

	Toledo Bend V-2260	Buda* UF 24129	St. Gérand**	*M. hollandi* F:AM 54903**	*M. elatus*** (apx rng)
MXL	86.6	93.7	88.9	129.8	124-165
MXDW	25.0	26.2	28.0	38.5	35-51
MNSW	17.4	18.0	19.8	27.5	23-36
L/DW	3.46	3.57	3.20	3.4	3.2-3.8
L/MNSW	4.97	5.2	4.5	4.7	4.8-5.5

Stepleton to T. Fremd, pers. comm., 1996). Small chalicotheres also occur in the Aquitanian St. Gérand-le-Puy fauna of France, the upper boundary of which is placed at about 20.52 Ma by Berggren et al. (1995).

The Mt IV from Toledo Bend differs from the Buda specimen in smaller size and in having a triangular, rather than rounded, volar facet. The smaller size, less robust build, and less rugosely textured area of muscle attachment of the Toledo Bend specimen relative to the Buda specimen may be due to sexual dimorphism. Proximal and medial phalanges from Toledo Bend are also smaller and less robust than those from Buda (Table 3).

Neither the Toledo Bend nor the Buda Mt IV show a distinct facet for the ectocuneiform. Coombs (1978) listed an ectocuneiform facet on the Mt IV as diagnostic of the genus *Moropus*. The absence of this feature resembles the condition in the large, dome-skulled chalicothere, *Tylocephalonyx* (Coombs, 1979). However, Coombs (1978) also noted that in *M. elatus* only the proximal one-fourth of the dorsal Mt III facet articulates with the Mt IV facet of the ectocuneiform. Thus, the articulation may have been minimal in the Toledo Bend and Buda species, and not obvious without the associated Mt III and ectocuneiform.

Although the Mt IV from Toledo Bend is substantially smaller than that of *M. elatus* and *M. hollandi*, the length to distal width ratios and the length to minimum shaft width ratios are similar (Table 4). A Mt IV from St. Gérand shares similar ratios, but differs from the Toledo Bend specimen in having a distinctly divided dorsal facet on the medial side for articulation with both the ectocuneiform and the Mt III. Also, the volar facet in the St. Gérand specimen is relatively larger than in the Toledo Bend or Buda specimens.

Family TAPIRIDAE Burnett, 1830

Genus *Nexuotapirus* Albright, 1998b

Nexuotapirus marslandensis (Albright, 1998b)

Nexuotapirus marslandensis (Schoch and Prins, in Schoch, 1984). Albright, 1998b

See Albright (1998b) for a description and discussion of the tapir from Toledo Bend.

Family RHINOCEROTIDAE Owen, 1845

Gulfoceras, gen. nov.

Type Species.—*Gulfoceras westfalli.*
Etymology.—See below.
Diagnosis.—As for species.

Gulfoceras westfalli gen. et sp. nov.

Figure 5

Holotype.—LSUMG V-2622, right M3.

Referred Specimens.—LSUMG V-2249, left M3; V-2621, right M3; V-2574, left astragalus.

Etymology.—*Gulfoceras*, rhinoceros from the Gulf Coastal Plain; *westfalli*, for Mr. Robert Westfall, an enthusiastic avocational collector who made available to the LSU Museum of Geoscience the holotype, as well as many other important specimens.

Diagnosis.—Much smaller than *Menoceras* and *Diceratherium*. Smaller but similar relative hypsodonty to *Subhyracodon*. Less prominent crochet than *Menoceras*. M3 lacks continuous lingual cingulum and groove on protoloph to mark protocone.

Description.—In contrast to the highly worn condition of V-2249 and V-2621, the type specimen, V-2622, is a lightly worn specimen in excellent condition (Fig. 5A, B). The later measures 26.8 mm AP by 30.5 mm TR. The maximum, slightly worn crown height is 27.6 mm. There is an anterior cingulum and a weak posterior cingulum. The lingual cingulum is not continuous. There is no cristid but there is a sharp ridge that begins at the apex of the hypocone and descends the anterior surface. Once worn, this ridge becomes a simple crochet as seen in V-2249. V-2249 measures 23.0 mm AP and, in its broken state, about 27.5 mm TR. The transverse width would have been only slightly greater were it not broken. There is a simple crochet and a simple cristid. Most enamel is worn off the tooth. V-2621 is slightly larger than V-2249 and is also highly worn. It measures 25.3 mm AP, but its broken state prevents a transverse measurement.

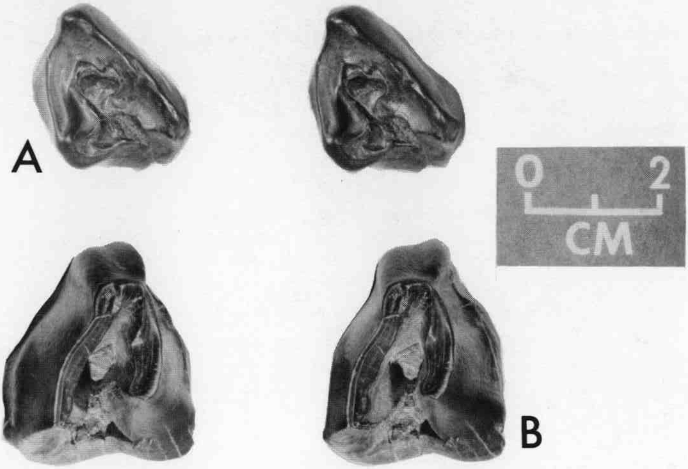

Figure 5. *Gulfceras westfalli* gen. et sp. nov., **(A)** Worn left M3, LSUMG V-2249; **(B)** Right M3, V-2622.

The astragalus is similar in size to those of *Anchippus texanus* and *Nexuotapirus marslandensis*. It resembles the tapir more closely than the horse in the broader angle between the two trochleae and in a relatively shallow, rather than deep, sustentacular facet. It further resembles the tapir in that the medial surface of the medial trochlea is relatively flat, whereas in the horse the medial surface of the medial trochlea has a distinct flange that follows the curvature of the trochlea. In the rhino and horse, but not the tapir, the medial trochlea contacts or merges with the navicular facet. The astragalus of the Toledo Bend chalicothere differs substantially in having a shallower angle between trochleae, a transversely reduced navicular facet, and a transversely expanded sustentacular facet.

Discussion.—Although material representing this tiny rhino is limited, comparisons have found no currently described species to which these specimens can be referred. Thus it seems reasonable to conclude that yet another Gulf Coastal Plain endemic species has been discovered (see below). The diminutive *Hyracodon* may have lasted into the early Arikareean (Prothero et al., 1989), but M3 of *Hyracodon* differs from the Toledo Bend teeth in having an ectoloph that extends posteriorly beyond the metaloph resulting in a vaguely "π" shaped occlusal outline.

The taxon with an M3 most closely resembling the Toledo Bend tooth is the common Orellan rhino, *Subhyracodon*. General shape and hypsodonty are essentially the same, although the M3 of *Subhyracodon* is larger in size, it lacks the ridge that ascends the anterior surface of the hypocone, and it has a prominent lingual cingulum that is continuous with the anterior cingulum.

Table 5. Upper cheek teeth measurements for various specimens of *Diceratherium*. a= approximate; * = average of Peterson's (1920) and Troxell's (1921) measurements. The first column includes Toledo Bend specimens referred to *D. annectens*. The last column is the specimen referred to *D. armatum*.

		Toledo Bend	*D. annectens* YPM 10001	*D. annectens* AMNH 7324	*D. "nanum"* AMNH 7325	*D. "nanum"* AMNH 7343	*D. "armatum"* ACM 1828
P1:	L	18.9	20.4	19.0	20.0		
	W	18.3	17.2	17.0	16.0		
P2:	L	21.8	23.2	24.0			24.3
	W	24.4	27.8	a28.0			30.5
P3:	L	25.7	27.5	28.0		23.9	28.9
	W	30.0	34.3	35.0		26.7	37.2
P4:	L	27.7, 27.5	28.8	30.0			31.0
	W	33.7, 33.8	37.1	39.0			40.4
M1:	L			35.0			
	W			41.0			
M2:	L	41.7		40.0			40.8
	W	45.0		41.0			41.8
M3:	L	39.5		33.0			34.4
	W	41.8		38.0			42.2

Prothero and Manning (1987) described dwarf rhinoceroses from the Barstovian of the Texas Coastal Plain and Prothero and Sereno (1982:24-26), in discussing these dwarf forms, noted that the Miocene faunas of the Gulf Coast were characterized by a "high degree of endemism" and an "unusually high diversity of forms" apparently due to the mixing of endemic coastal forms with High Plains immigrants. The Toledo Bend Local Fauna clearly indicates at least limited mixing with faunas from the High Plains by the mutual occurrence of *Arretotherium*, *Nexuotapirus*, *Nanotragulus*, *"Cynorca,"* and *Diceratherium* in both regions (see Albright, 1998a, and below).

The occurrence of "dwarf" rhinoceroses, chalicotheres, and amphicyonids in the Gulf Coastal Plain, to their exclusion in the paleontologically well sampled northern Great Plains, would seem to confirm the unique paleoenvironmental

Table 5. Extended

		D. sp. AMNH 7342	*D.* sp. AMNH 7346	*D. armatum** YPM 10003	*D. gregorii* AM 12933	Toledo Bend V-2560
P1:	L		19.7	29.0	21.0	
	W		17.0	25.5	20.0	
P2:	L			32.0	26.0	
	W			39.5	32.0	
P3:	L			37.0	31.0	
	W			46.0	44.0	
P4:	L	28.5		39.0	34.0	35.4
	W	32.7		50.0	48.0	44.5
M1:	L			48.0	38.0	
	W			53.0	45.0	
M2:	L			54.0	45.0	
	W			55.0	47.0	
M3:	L			46.0	38.0	
	W			50.0	44.0	

setting of this region and its amenability to endemic evolution. However, as noted earlier, the Toledo Bend Local Fauna may sample a temporal interval missing in strata of the northern Great Plains thus biasing the apparent endemic nature of the Gulf region during the Arikareean. In other words, are these small forms the primitive members of lineages that would attain greater size upon dispersal elsewhere? This is supported by the fact that the small Gulf Coast chalicothere and amphicyonid probably predate the much larger and morphologically more derived *Moropus elatus* and *Daphoenodon superbus* from late Arikareean faunas of the Great Plains. Hence, "dwarf" as used above is not meant to imply a size decrease from a larger ancestral member of the lineage.

Subfamily DICERATHERIINAE Dollo, 1885
Genus *Diceratherium* Marsh, 1875

In addition to *Gulfoceras westfalli,* discussed above, two larger rhinoceroses also occur at Toledo Bend based primarily on the presence of two larger, yet significantly different sized P4s and magna. The larger of the two is referred to *Diceratherium armatum*; the smaller to *D. annectens.* It should be noted, however, that comparison with specimens at the ACM, AMNH, MCZ, and YPM resulted in the conclusion that there exists considerable confusion regarding the distinction between *Diceratherium armatum* Marsh (1875), *D. annectens* (Marsh, 1873), and *D. gregorii* Peterson (1920).

The type specimens of *D. armatum* (the genoholotype) and *D. annectens* were originally described from the middle John Day Formation, Oregon. Peterson (1920) noted that both were from the same horizon, and Tanner (1969) determined from YPM records that they were collected at "Turtle Cove." Although Macdonald (1963) reported that *D. annectens* had not been recovered in the Wounded Knee faunas, South Dakota, Prothero et al. (1989) reported both males and females of *D. armatum* and *D. annectens* from the early late Arikareean 77 Hill Quarry near Lusk, Wyoming. The type specimen of *D. gregorii* is from the "Lower Rosebud beds, near Rosebud Indian Agency, South Dakota" (Peterson, 1920:421).

Peterson (1920) considered only two of six John Day species of *Diceratherium* to be valid (*D. armatum* and *D. annectens*), placing the others *incertae sedis.* He synonymized *D. nanum* Marsh (1875) with *D. annectens,* and erected a new species, *D. gregorii,* for material from the High Plains. Agreeing with Peterson's conclusions, Troxell (1921) nonetheless erected two more species from the John Day, *D. lobatum* and *D. cuspidatum.* Green (1958:588) considered *D. gregorii* a valid taxon and reported additional specimens from "a nodular zone above the basal ash" in South Dakota. The "basal ash" is the Rockyford Ash at the base of the early Arikareean Sharps Formation (see Tedford et al., 1987, 1996, for further discussion). Later, Macdonald (1963, 1970) reported *D. gregorii* from the Wounded Knee Sharps Fauna. Green (1958) also concluded that *D. armatum,* with which he synonymized *D. lobatum,* occurred in South Dakota. For reasons discussed below, it is suggested here that *D. cuspidatum* be synonymized with *D. annectens.* The validity of *D. gregorii,* in my opinion, remains questionable pending a thorough review of the genus.

The largest Toledo Bend rhino material, including a large P4 and fragments of the zygoma, post-glenoid process, and distal femur, are virtually identical to material referred to *D. armatum* from the 77 Hill Quarry and to some specimens from the John Day Formation (e. g., AMNH 7321). With the exception of the large P4, the remainder of the upper cheek teeth are substantially smaller than those of the type specimen of *D. armatum* (YPM 10003). These teeth compare well with those of the type specimen of *D. annectens* and the type specimen of *D. nanum* (= *D. annectens*), YPM 10001 and AMNH 7324, respectively, and with other specimens referred to *D. annectens* including YPM 11184 and YPM 12493. They also compare well with AC 1828 and AC 4509 labeled *D. armatum*, although more likely representing *D. annectens* based on size (see Table 5).

The late Arikareean-early Hemingfordian immigrant *Menoceras* Troxell (1921), from early Miocene faunas of the Great Plains and Coastal Plain (Prothero and Manning, 1987), has a number of derived characters absent in the Toledo Bend rhinos. These include the prominent, highly plicated crochet and the weak to absent lingual cingula in the upper molars and increased hypsodonty of the lower molars (Prothero et al., 1986; Prothero et al., 1987; Prothero et al., 1989). Whether the weak to absent upper molar cingulum is truly a derived feature is debatable. Cingulum prominence is often variable and Wood (1964), in describing the type specimen of *Menoceras barbouri*, noted complete lingual cingula on P4-M3. Most post-cranial elements from the Toledo Bend species are larger than those of both *Menoceras arikarense* (Barbour, 1906) and the larger *M. barbouri* (Wood, 1964) (including the still larger *M. marslandensis* Tanner, 1969, which was synonymized with *M. barbouri* by Prothero et al., 1989:328).

Note: In his discussion of the Rhinocerotidae, Prothero (1998:600) listed *Menoceras barbouri* and *Floridaceras whitei* as occurring in the Toledo Bend Local Fauna, evidently following the preliminary faunal list of Manning (1990). More detailed study revealed that this material represents *Diceratherium annectens* and *D. armatum*. Thus, the record of *Menoceras* and *Floridaceras* at Toledo Bend is in error.

Diceratherium annectens (Marsh, 1873)
Figures 6-9

Rhinoceros annectens Marsh, 1873
Diceratherium nanum Marsh, 1875
Diceratherium annectens (Marsh). Loomis, 1908
Diceratherium annectens (Marsh). Peterson, 1920
Diceratherium cuspidatum Troxell, 1921

Holotype.—YPM 10001, upper left premolars with associated upper incisor. "lower to middle John Day Formation" (Peterson, 1920:417).

Referred Specimens.—LSUMG V-2250, left I1; V-2526, left I1; V-2527, left P1; V-2528, left P2; V-2529, right P2; V-2530, right P3; V-2531, left P3 fragment; V-2532, left P3 fragment; V-2533, left P4; V-2534, right P4; V-2535, right P4 fragment; V-2572, upper cheek tooth (dP4?) fragment; V-2536, right M1 or M2 (worn); V-2265, right M2; V-2266, left M3; V-2537, upper tooth fragments; V-2538, right p2; V-2539, right p3; V-2763, right p3, figured; V-2540, right m1? in jaw fragment; V-2541, talonid of right m2; V-2542, left m2 fragment; V-2543, left m3; V-2544, talonid of right m3; V-2545, lower tooth fragments; V-2546,

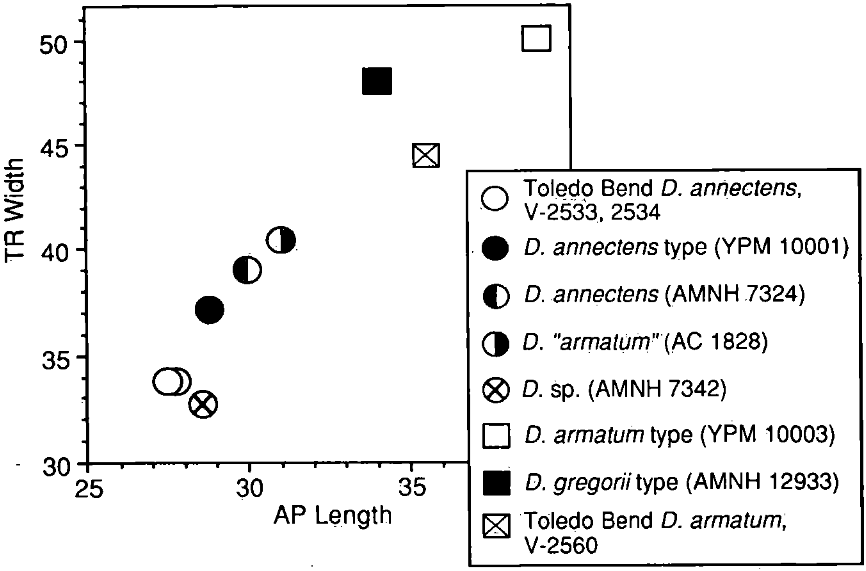

Figure 6. Bivariate scatter plot of various *Diceratherium* P4s (mm).

mandibular symphysis fragment; V-2547, fragment of post-glenoid process; V-2548, fragments of atlas vertebra; V-2549, two proximal right scapulae fragments; V-2550, proximal right humerus; V-2551, distal left humerus; V-2552, distal right humerus; V-2553, proximal right ulna; V-2554, proximal right Mc III; V-2555, distal left Mc IV; V-2556, magnum; V-2557, left astragalus; V-2558, distal right calcaneum; V-2559, right periotic.

Description and Discussion.—Table 5 and Figure 6 compare the size of upper cheek teeth of various species of *Diceratherium*, including the Toledo Bend specimens. Dental terminology follows that of Prothero et al. (1986:354, fig. 6). Incisors from Toledo Bend compare closest with those of AMNH 7312 and 7346 from "Turtle Cove." The crown of the I1 is short anteroposteriorly and narrow transversely (Fig. 7E).

Premolars from Toledo Bend also most closely resemble those from various John Day specimens. The P1 (Fig. 8A) compares best with AMNH 7346 and 7324 (type of *D. nanum*). P1 of *D. annectens* is more anteroposteriorly compressed and transversely broader than that of *Menoceras*, and it has a labial cingulum continuous with the parastyle and metastyle not seen in *Menoceras*. There is also a lingual cingular segment between the parastyle and protocone and between the protocone and the hypocone. P2-3 compare well with AC 1828 and AC 4509. Although labeled "*Diceratherium armatum* from the Lower Harrison near Agate, Nebraska,"

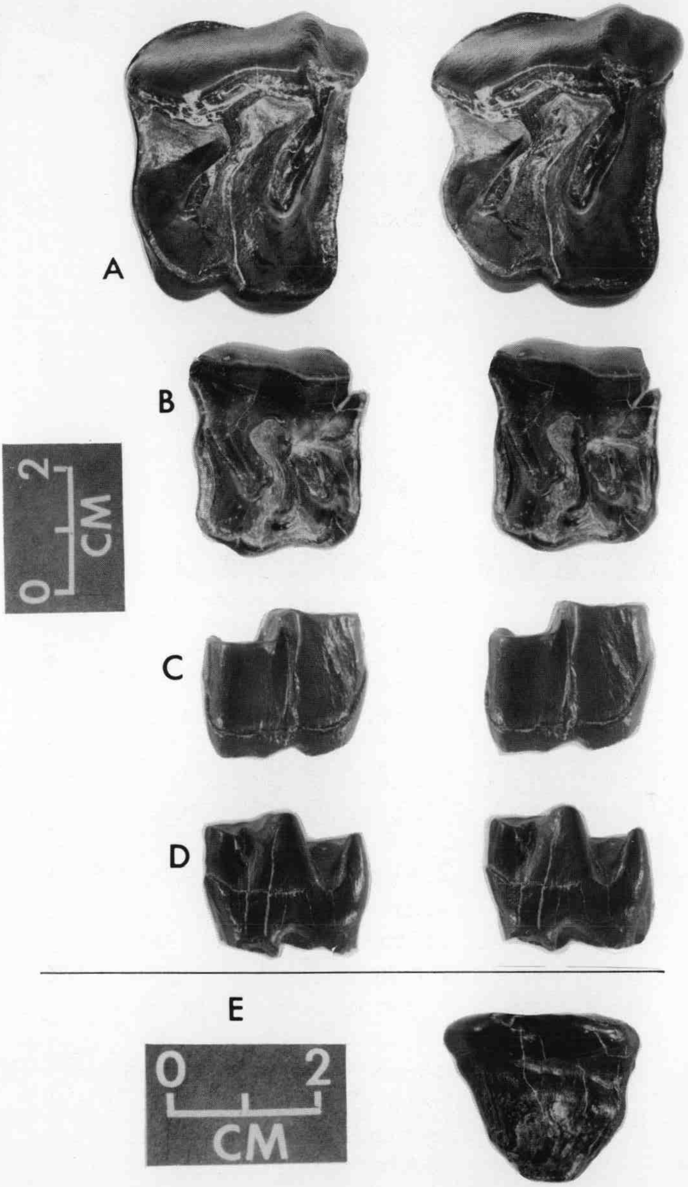

Figure 7. **(A)** *Diceratherium armatum*, stereo view of right P4, LSUMG V-2560; **(B)** *D. annectens*, stereo view of left P4, V-2533; **(C)** *D. annectens*, stereo view of labial surface of right p3, V-2763; **(D)** Same specimen, lingual surface; **(E)** *D. annectens*, left I1, V-2250.

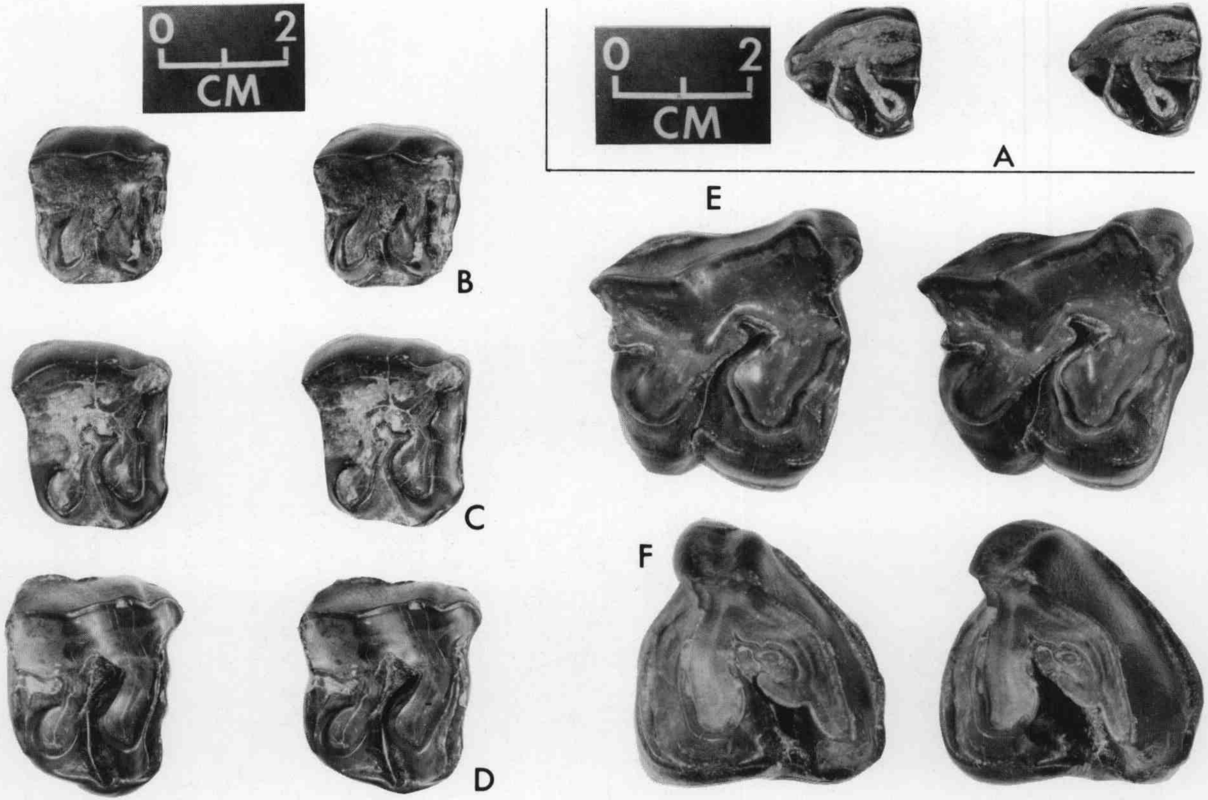

Figure 8. *Diceratherium annectens*, upper dentition. **(A)** Stereo view of left P1, LSUMG V-2527; **(B)** Stereo view of right P2, V-2529; **(C)** Stereo view of right P3, V-2530; **(D)** Stereo view of right P4, V-2534; **(E)** Stereo view of right M2, V-2265; **(F)** Stereo view of left M3, V-2266.

AC 1828 and 4509 are of size more suggestive of *D. annectens* (Table 5). Premolars and molars in the two skulls match those from John Day and Toledo Bend in size and in the weak to nonexistant crochets and cristae. P2s from Toledo Bend are nearly square in occlusal outline with a cingulum that is continuous around the tooth, although weak at the hypocone (Fig. 8B). There is also a "mure" connecting the metaloph to the protoloph (see Green, 1958:592) and an incipient crista. P3 (V-2530) has a continuous anterior, lingual, and posterior cingulum and a small crochet and crista (Fig. 8C). The labial surface is too water worn to determine if there was a labial cingulum. A fragment of the lingual part of another P3 shows no crochet or cristae, but, like P2, it has a tiny "mure."

P4 (V-2534) has a strong labial cingulum that ascends the posterolabial corner of the crown (Fig. 8D). The anterior, lingual, and posterior cingula are nearly continuous, broken only at the posterolingual corner of the hypocone. The transverse median valley is narrow and there is no crochet or crista. V-2533 is similar with only a slight hint of a crochet. There is a prominent cusp at the lingual entrance of the transverse median valley, immediately labial to the lingual cingulum (Fig. 7B).

That V-2533 has a lingual tubercle, whereas V-2534 does not, leads one to question the validity of *D. cuspidatum*. This John Day species is so named because the type specimen (YPM 12007) shows a prominent cusp from the floor of the lingual part of the median valley in the molars. Furthermore, the premolars of *D. cuspidatum* each show a "mure" joining the metaloph to the protoloph which is one of the features that Green (1958) used to synonymize *D. lobatum* with *D. armatum*. *Diceratherium annectens* and the Toledo Bend species also show this small "mure" and *D. cuspidatum* is of similar size to *D. annectens*. For these reasons, *D. cuspidatum* is here placed in synonymy with *D. annectens*. Except for the cusp of V-2533, the two P4s from Toledo Bend closely resemble the type specimen of *D. nanum* (AMNH 7342) from Turtle Cove.

Upper molars (Fig. 8E, F) also compare well with the type and referred specimens of *D. annectens* in their simple morphology and size. They are considerably smaller than molars of the type specimen of *D. armatum* (YPM 10003). Those from Toledo Bend have no crista and the crochet is small compared with the strong crochets so diagnostic of *Menoceras*. The M3 (V-2266) has a strong anterior and posterior cingulum, the latter of which continues lingually until ending at the posterolingual surface of the protocone. There is a prominent, non-plicated crochet that arcs anterolabially and a weak crista. M3 of *Menoceras* differs in having a distinct ridge that ascends the posterolabial surface of the hypocone which is probably a reduced, posterior extension of the ectoloph such as that seen in *Hyracodon*. No such ridge is seen in *Diceratherium* or on the M3 from Toledo Bend.

Lower premolars from Toledo Bend also compare closest to those of AMNH 7346 from the John Day Formation. Like all other *Diceratherium* premolars examined from both the John Day Formation and from the High Plains, those from Toledo Bend have a lingual cingulum that remains low on the crown and extends around the anterior surface of the tooth to connect with the labial cingulum. This differs from the condition that appears to be characteristic of *Menoceras* in which the lingual cingulum ascends the lingual surface of the paraconid. This character is particularly comparable in p3s (Fig. 7C, D). Lower molars of *D. annectens* and the Toledo Bend species are also relatively less hypsodont than those of *Menoceras*.

Scapula fragments include only the proximal ends. The glenoid surface measures about 44 mm AP in both fragments and about 35 mm TR. There is no coracoid process and the scapular spine does not extend distally to the glenoid surface. Only a slight indication of the spine is apparent about 45 mm from the glenoid.

The magnum from Toledo Bend referred to *D. annectens* (Fig. 9A) is virtually identical to those in the Frick collection from the 77 Hill Quarry and also quite similar but slightly smaller than that referred to *D. niobrarense* (AMNH 14212). The Toledo Bend specimen measures 63.0 mm AP; 27.3 mm of this length includes the anteroposteriorly concave Mc III facet which is also about 22 mm wide. Compared with the magnum of *Menoceras*, the posterior tuber of *Diceratherium* is longer and the Mc III facet more concave.

On the proximal Mc III fragment, the strongly convex facet for articulation with the magnum measures about 38 mm AP by 32 mm TR. Maximum transverse width of this element is about 44 mm. The lateral surface has two prominent facets, one dorsally (or anteriorly) and one ventrally (or posteriorly). The anterior facet is divided into a large, slightly convex, proximolaterally facing facet for articulation with the unciform and a smaller anteroposteriorly-expanded, distolaterally facing facet for articulation with the Mc IV. The former is separated from the facet for the magnum by a prominent ridge. A deep, rugosely-textured sulcus separates the anterior Mc IV-unciform facets from the posterior Mc IV facet. The latter is slightly concave and oval-shaped with its long axis extending proximodistally. This element compares well with F:AM 132057 from 77 Hill Quarry. It is larger than that of *Menoceras barbouri* (MCZ 7449). Also, the lateral volar facet in the Toledo Bend specimen is proximodistally oval, whereas in *M. barbouri* this facet is dorsoventrally oval.

The astragalus measures 62.0 mm TR across the trochlea and 53.0 mm TR across the navicular and cuboid facets. The medial trochlea meets the navicular facet. The cuboid facet is separated from the navicular facet by a distinct ridge. The large size of this element and the distal calcaneum fragment suggests that they may belong to the larger Toledo Bend rhino.

Wood and Wood (1937) described a maxillary fragment with highly worn teeth (USNM 6573) from the Cedar Run locality in Washington County, Texas, and referred it to *Caenopus* cf. *premitis* (the "Derrick Farm rhino"). Prothero and Manning (1987) considered the specimen representative of *Menoceras arikarense*.

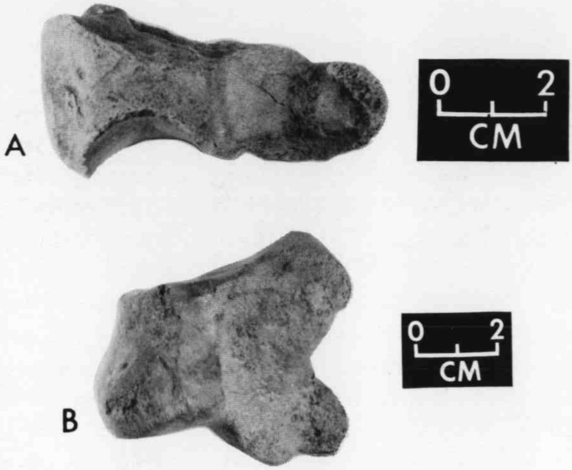

Figure 9. **(A)** *Diceratherium annectens,* magnum, LSUMG V-2556; **(B)** *Diceratherium armatum*, left magnum, V-2567.

The specimen was originally reported from the Catahoula Formation, but a personal communication from J. A. Wilson to Prothero and Manning (1987:391) indicated that it "could easily be derived from a channel from the overlying Oakville Formation." Although USNM 6573 is similar in size to *M. arikarense*, it is also quite similar to *D. annectens* and even shares with the latter species the close proximity of the metaloph and protoloph, unlike the more separated condition found in *M. arikarense*. In fact, Loomis (1908:54-55), referring to *D. annectens*, noted that "this small species is readily distinguished by the fact that on the molars the protoconule and the hypocone are so closely placed that on a partly worn tooth they actually join and the intervening valley between the protoloph and metaloph is interrupted." Similarities between the Cedar Run and Toledo Bend local faunas, in addition to the similar size and morphology of the Derrick Farm rhino with *D. annectens*, suggests the possibility that the former represents *D. annectens* rather than *M. arikarense*.

Diceratherium armatum Marsh, 1875
Figures 7, 9

Diceratherium armatum Marsh. Peterson, 1920
Diceratherium lobatum Troxell, 1921
Diceratherium armatum Marsh. Green, 1958
Diceratherium armatum Marsh. Macdonald, 1963
Diceratherium armatum Marsh. Macdonald, 1970

Holotype.—YPM 10003, complete skull with associated foot bones, "lower John Day Formation" (Peterson, 1920:414).

Referred Specimens.—LSUMG V-2560, right P4; V-2561, skull fragment (frontal); V-2562, posterior right zygoma fragment; V-2563, left lateral cranium fragment with post-glenoid process; V-2564, right post-glenoid process fragment; V-2565, proximal right radius; V-2566, left cuboid fragment; V-2567, left magnum; V-2569, lateral proximal phalanx; V-2570, distal right femur; V-2571, distal right femur.

Description.—P4 (V-2560) has a cingulum that completely surrounds the tooth except at the anterolabial corner. It begins weakly on the anterolabial surface but is prominent and shelf-like anteriorly. There is no crochet, crista, or connecting mure, but the metaloph shows four plicae on its anterior surface. V-2560 measures 35.5 mm AP by 44.5 mm TR (Fig. 7A).

A large, abraded, nearly flat skull fragment, undoubtedly part of the frontal of a large animal, is referred to *D. armatum* primarily because no other animal of this time had a skull with enough flat surface area to produce such a fragment. Interiorly, the fragment shows a honey-combed pattern reminiscent of that seen internally in elephant skulls in order to reduce weight without compromising strength.

V-2563 is a fragment of the left lateral portion of the skull with a large post-glenoid process and the internal continuation of the glenoid surface. The post-glenoid process is directed strongly medially. A fragment of the right posterior zygoma (V-2562) is dorsoventrally broadest above the glenoid surface (about 48 mm) and tapers anteriorly. The external surface is highly textured.

The partial cuboid (V-2566) consists only of the dorsal portion and measures 34.6 mm proximodistally at its anterior surface. The magnum (V-2567) measures 50 mm transversely and about 36 mm proximodistally at its anterior-most point. Its maximum proximodistal height is about 58 mm. The articular surface for the Mc III measures 44 mm anteroposteriorly and has a maximum transverse width of 42 mm. The posterior tuber is reduced (Fig. 9B).

The lateral proximal phalanx measures 36.5 mm long, 29 mm transversely across the proximal end, and 24 mm across the distal end. The proximal articulating surface is a nearly round depression with a small notch ventrally for the keel of the distal metapodial. The distal articulating surface is smooth, flat, and asymmetrical.

The two distal femur fragments are large and show a round, slender shaft. Maximum transverse width measures about 102 mm across the distal condyles.

Discussion.—This material is referred to *D. armatum* because of its similarity to material referred to this species from the 77 Hill Quarry. The P4 is virtually identical to the larger specimens from 77 Hill (e. g., F:AM 132056) in size, degree of hypsodonty, and in morphology, including the occurrence of plications on the anterior surface of the metaloph and the prominent lingual cingulum. Absence of the long, anteriorly extending crochet and presence of a prominent lingual cingulum are features that distinguish it from large species of *Menoceras*.

The zygoma and post-glenoid fragments match those of *D. armatum* (F:AM 112176) from north of Keeline, Niobrara County, Wyoming, and those of AC 1828 and AC 4509, which are labeled *D. armatum* but, as noted previously, are more similar to *D. annectens* in teeth size. The Toledo Bend elements also compare well with those of the type specimen of *D. armatum*, YPM 10003, and with AMNH 7321, another specimen from the John Day Formation. The zygoma of the male *Menoceras*, unlike that of *Diceratherium*, ends in a bulbous, blunt knob, which is only textured at its posterior-most point. That of the female *Menoceras* tapers posteriorly as in *Diceratherium*, but is considerably smaller, more gracile, and non-textured.

The cuboid and magnum from Toledo Bend are larger than those referred to *D. annectens* (e. g., YPM 12493). The cuboid is similar morphologically, but slightly larger than that of *D. niobrarense*. The magnum is substantially larger than any referred to *Menoceras* and slightly larger than many referred to *D. armatum*.

Order ARTIODACTYLA Owen, 1848

Family ENTELODONTIDAE Lydecker, 1883

?*Dinohyus* sp.

Figure 10

Type Species.—*Dinohyus hollandi* Peterson, 1905a (also see Peterson, 1905b).

Holotype.—AMNH 7387, symphysis of lower jaw with roots of incisors and canine, John Day Formation, Bridge Creek, Wasco County, Oregon (Peterson, 1909).

Referred Specimens.—LSUMG V-2415, incisor fragment; V-2417, left M2 fragment; V-2268, left M3; V-2416, left p4 fragment; V-2418, edentulous anterior right maxillary fragment with C, P1, and partial P2 alveoli; V-2578, right periotic; V-2419, right m3 fragment; V-2579, ramal fragment; V-2420, premolar fragments; V-2575, partial atlas; V-2576, cervical vertebra fragment; V-2577, distal humerus; V-2426, distal right humerus; V-2421, left magnum; V-2422, distal metatarsal; V-2423, distal right tibia; V-2424, right astragalus; V-2425, left astragalus.

Description.—The edentulous maxillary fragment (LSUMG V-2418) is broken, exposing the medial surface of the large canine alveolus. The two alveoli of P1 are situated medial to the posteromedial corner of the canine alveolus. A short (29 mm) diastema separates the posterior edge of the posterior P1 alveolus from the anterior edge of the anterior P2 alveolus. The M2 fragment (V-2417) shows a broad anterior cingulum that ends at the anterolabial corner of the paracone. This fragment also shows a small portion of the protoconule. The M3 (V-2268) measures 49.3 mm anteroposteriorly, and would have measured greater than 44 mm

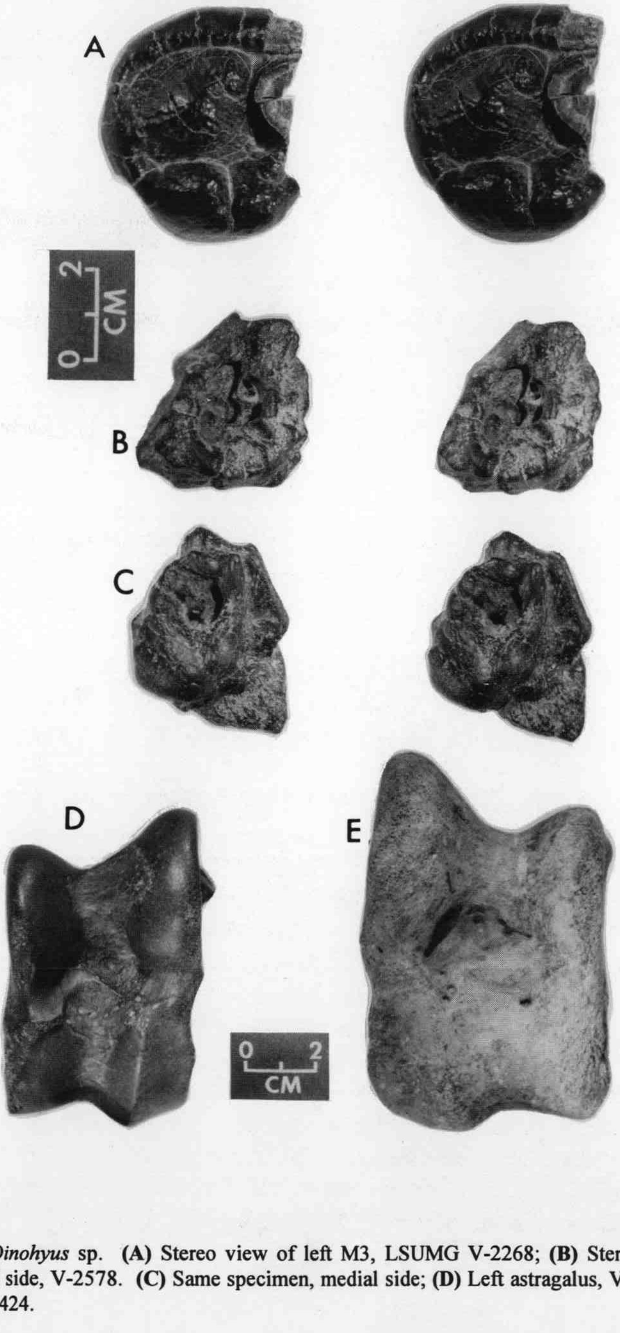

Figure 10. ?*Dinohyus* sp. **(A)** Stereo view of left M3, LSUMG V-2268; **(B)** Stereo view of right periotic, lateral side, V-2578. **(C)** Same specimen, medial side; **(D)** Left astragalus, V-2425; **(E)** Right astragalus, V-2424.

transversely were the labial surface intact (Fig. 10A). The unworn crown is nearly complete, missing only the labial half of the paracone, and has a textured surface. The protocone is the largest cusp. A thick, robust cingulum extends continuously from the anterolabial corner lingually to the metaconule.

The p4 fragment (V-2416) includes the posterior half of the crown and shows a thick, highly pustulose-textured posterior heel. From the point where the posterolabial cingulum begins, there is a ridge that ascends the crown, forming a "corner" effectively separating the labial surface of the tooth from the posterior surface. The m3 fragment (V-2419) consists of only a single worn cusp.

The periotic is large and massively constructed (Fig. 10B, C). A detailed description is provided in Albright (1991). Fragments of the atlas (V-2575) and cervical vertebrae (V-2576) compare closely in size and morphology with those of *Dinohyus hollandi* in the F:AM collection.

The distal metapodial III or IV fragment is convex on the anterior surface and flat to concave on the posterior surface. The metapodial keel is placed somewhat asymmetrically on the distal articular surface and, as in *D. hollandi*, does not extend onto the anterior face of that surface. The distal articular surface measures 47.5 mm transversely.

The proximal surface of the magnum (V-2421) is dominated by the facet for the scaphoid. The scaphoid facet is separated from the posterolaterally facing lunar facet by an oblique ridge. On the medial side of the magnum is a rugosely textured depression where the trapezoid articulates. The lateral side has a deep, rhomb-shaped excavation centrally located between the two facets for the unciform. The anterior facet for the unciform is flat and the posteror one concave. The distal surface for articulation with Mc III is concave anteroposteriorly and convex transversely. The magnum from Toledo Bend is smaller than that figured by Peterson (1909:120, fig. 72) for *D. hollandi* (maximum AP diameter = 52.8 mm vs. 70 mm).

The distal tibia (V-2423) is flat anteriorly with a small, but prominent medial malleolus. The astragalar facets are aligned parallel to the sagittal plane. The medial facet is slightly narrower than the lateral. The distal fibula was not coossified with the tibia. The astragalar facet measures about 90 mm TR and about 79 mm AP. The smaller of the two astragali (V-2425) measures 92 mm long by 62.5 mm wide. The larger, heavily worn specimen (V-2424) measures 110 mm long by 66 mm wide (Fig. 10D, E).

Discussion.—The only described late Oligocene-early Miocene North American artiodactyls to which material of this size can be referred are the entelodonts *Daeodon shoshonensis* Cope (1878), *Ammodon leidyanum* Marsh (1893), *Dinohyus hollandi* Peterson (1905a) (see also Peterson, 1905b), *Dinohyus* (?) *mento* Allen (1926), or *Archaeotherium trippensis* Skinner et al. (1968). In describing the poor type specimen of *Daeodon*, *D. shoshonensis*, from the John Day Formation, Cope (1878) referred to it as one of the largest species of North American perissodactyls. Studying additional material published by Sinclair (1905), Peterson (1909) removed it from the Perissodactyla and placed it into the artiodactyl family Entelodontidae. In the same publication, Peterson listed additional traits that distinguished *Daeodon* from *Dinohyus hollandi*, another large entelodont that he had previously described.

Peterson (1909) also considered *Dinohyus hollandi*, from the Agate fossil beds, distinct from *Ammodon leidyanum*, as did Troxell (1920:441) who considered "*A. leidyanus*" generically separate "from all the specimens found on the Great Plains." Wilson (1957), on the other hand, felt that the generic distinction of *Ammodon* was probably dubious, adding that its relationship to *Dinohyus* or *Daeodon* would have to await the recovery of more material. Brunet (1975) similarly noted that additional material was needed for validation of the various purported species because many type specimens were undiagnostic. He cited the following examples: the type specimens of *Daeodon shoshonensis* and *Dinohyus* (?) *mento* are both mandibular symphyses, and *Boochoerus* Cope (1879) from the John Day Formation is only known from post-crania (see Foss and Fremd, 1998). Brunet (1975) noted that because *Boochoerus* and *Daeodon* are both from the John Day Formation, and because *Boochoerus* and *Dinohyus* share a magnum and unciform separated by a semi-lunar and both lack the trapezium, the four genera (including *Ammodon* based on tooth similarities to *D. hollandi*) could probably be grouped into one genus. He preferred *Dinohyus* to *Daeodon* because *Dinohyus hollandi* is known from a complete skeleton, whereas the others (*Daeodon*, *Ammodon*, *Boochoerus*) are known from much less complete material. He concluded, however, that specific relationships between them would be nearly impossible to determine. Similarly, Parris and Green (1969:1278), in their description of *Dinohyus* sp. from the Sharps Formation, South Dakota, refrained from naming a new species "because of the uncertain state of entelodont taxonomy." Lucas et al. (1997, 1998) recently reached a conclusion similar to that of Brunet (although they did not mention *Boochoerus*), but placed the above named species in *Daeodon*, rather than *Dinohyus*, based on nomenclatural priority. Brunet (1975) listed numerous traits suggesting that these large earliest Miocene forms are of Asiatic origin unrelated to the older, smaller, North American Oligocene forms.

The other large entelodont of slightly older age is *Archaeotherium trippensis*. The type specimen, F:AM 42937, includes a complete skull of an immature individual from the Wewela Local Fauna, South Dakota, which Tedford et al. (1987:171) considered "of Monroe Creek age." Similar in size to *Dinohyus hollandi*, *A. trippensis* is considerably larger than other species of *Archaeotherium*. Skinner et al. (1968) cited numerous characters that distinguish it from *D. hollandi*.

The Toledo Bend entelodont is questionably referred to *Dinohyus*, because, in my opinion, the type specimen of *Daeodon* is "inadequate for definitive diagnosis" and the genus, therefore, should be considered a *nomen vanum* (see Mones, 1989:232). Specific distinction of the Toledo Bend species is also ambiguous due to the paucity of material. The questionable referral is also based on some major morphological differences seen in the Toledo Bend specimen; these are discussed below.

The Toledo Bend species and *D. hollandi* share M3s that are similar in size, that lack a metaconule, and that have a broad anterior cingulum and no posterior cingulum. The Toledo Bend p4 fragment resembles that described of *Ammodon leidyanum* in its large size and in having the broad, posteriorly extending, pustulose textured posterior margin. In this character, the Toledo Bend species also resembles *A. trippensis*.

The most diagnostic feature of the Toledo Bend species, and the most obvious difference between it and other large entelodonts, is the position of P1 relative to the canine. In the Toledo Bend form, the P1, as shown by its two alveoli, is situated nearly medial to the canine rather than posterior to it. Only the posterior-most margin of the posterior alveolus extends slightly posterior to the canine alveolus. In *Dinohyus hollandi*, the P1 is directly posterior to the canine and separated from it by a very short diastema. *Dinohyus* sp. from the Sharps Formation, which Parris and Green (1969) noted more closely resembled the Whitneyan *Pelonax lemleyi* Macdonald (1951), also has a P1 posterior to the canine alveolus. In the type specimen of *A. trippensis*, the P1 is also clearly posterior to the canine. However, in comparing *A. trippensis* with *Dinohyus*, Skinner et al. (1968) noted that the former had a long, slender rostrum that was "not greatly expanded in the area of the incisors and canines as in *Dinohyus hollandi* ... ." The canine of *A. trippensis*, therefore, had to curve abruptly in a posterior direction because of its slender rostrum (Skinner et al., 1968:421, fig. 15). If the lateral side of the alveolus for the canine was broken away, it might appear that the P1 alveoli were somewhat medial to the canine alveolus.

The other major difference between the Toledo Bend species and *D. hollandi* concerns the distal ankylosis of the fibula to the tibia. In *D. hollandi* the tibia and fibula are fused. The Toledo Bend form appears to lack the fused condition. The postcranial anatomy of *A. trippensis* is unknown.

Entelodont material from the Gulf Coastal Plain, in addition to that from Toledo Bend, includes two specimens (TMM 40223-1 and TMM 40224-1) from the Garvin Gully Fauna that Wilson (1957) referred to *Dinohyus hollandi*. Although he pointed out several differences between the Texas specimens and the type specimen of *D. hollandi*, he did not cite any specific reasons for referral of these specimens to that species. The lower jaw, TMM 40224-1, from "beds close to the base of the Fleming formation" in San Jacinto County, Texas, does not show the tuberosities on the chin supposedly diagnostic of *Dinohyus*, although there are prominent tuberosities located more posteriorly (Wilson, 1957:644). Degree of tuberosity expression may be a function of sexual dimorphism. TMM 40223-1 was found near the base of the Oakville Formation in Washington County, Texas. A direct comparison is not possible as the TMM specimen includes only the P4 and M1. Unfortunately, there is no postcranial material from Garvin Gully faunas that might provide important comparisons. Another specimen that includes a left mandibular ramus with p1-m3 was recently reported by Westgate (1993) as having been found in the Catahoula Formation of Fayette County, Texas. With a molar row length of 102 mm, this entelodont may have been slightly smaller than that from Toledo Bend. Elsewhere in the Gulf Coastal Plain, two broken teeth and a radio-ulna fragment from the Franklin Phosphate Pit No. 2 Local Fauna, Florida, were referred to *Dinohyus* (Simpson, 1930).

The position of P1 relative to the canine and the lack of an ankylosed distal tibia-fibula are features that would seem to indicate distinctiveness for the Toledo Bend entelodont. But definitive taxonomic referral is declined pending recovery of additional material and a more thorough understanding of the relationships between these large, earliest Miocene "genera" and "species."

Family TAYASSUIDAE Palmer, 1897

?*Floridachoerus olseni* White, 1941

Figure 11A

Floridachoerus olseni White, 1941
Desmathyus olseni (White). MacFadden and Webb, 1982.

Holotype.—MCZ 3657, partial skull with right P3-M3 and left P4-M3, from Thomas Farm, Gilchrist County, Florida.

Referred Specimens.—LSUMG V-2504, right I1; V-2505, right upper C; V-2267, left ramal fragment with m1-3; V-2506, distal left and right tibia fragments; V-2507, astragalus.

Description.—I1 is relatively large and bulbous with a weak labial cingulum. It is somewhat excavated lingually with a small, centrally situated ridge that runs from the base of the crown to slightly less than half the distance to the apex. The dagger-like upper canine has a crown length of 36.1 mm and measures 18.5 mm AP by 11.5 mm TR. It is nearly flat lingually and convex labially. The anterior surface is worn flat from contact with the posterior surface of the lower canine while the posterior surface is sharp and straight-edged. Wright and Eshelman (1987:609) stated that "identification of tayassuid species based on canine size [is] practically impossible."

The m1 is highly worn. The m2 is also quite worn; the transverse median valley is blocked internally by a transversely expanded conulid. There is also a small tubercle at the labial entrance of the transverse median valley that is continuous with an anterior cingulum. This cingulum weakly wraps around the labial surface of the protoconid and joins it (Fig. 11A). The m3 has an anterior and a labial cingulum which may have been barely continuous before the tooth was worn. A paracristid extends lingually from the protoconid and joins with the anterior cingulum. At the entrance to the valleys between the protoconid and hypoconid and between the hypoconid and hypoconulid, the labial cingulum

Table 6. Lower molar measurments for various species of early Miocene peccaries.

	m1		m2		m3	
	AP	TR	AP	TR	AP	TR
Toledo Bend						
LSUMG V-2346					20.0	11.0
LSUMG V-2267	15.8	12.3	17.9	14.0	22.3	13.1
Floridachoerus olseni						
MCZ 7302	15.9	12.7				
MCZ 7304					21.5	13.6
Thinohyus decedens						
UCMP 1989	13.0	9.0			22.0	12.0
Van Tassell species						
ACM 7035	16.3	12.6	18.5	14.3	25.2	14.4
"Thinohyus" siouxensis						
CM 1423 (type)			18.9	15.9	26.8	16.2
Hesperhys pinensis						
AMNH 12936 (type)	17.8	13.6	22.6	16.4		
H. cf. H. pinensis						
UNSM 62604	17.0	13.3	20.2	16.1	25.5	16.7

thickens to form tubercle-like structures. The hypoconulid is asymmetrically bilobate with the labial lobe being larger. There is a transversely expanded conulid centrally located within the tranverse median valley and another one between the hypoconulid and the hypoconid-entoconid lophid. Although the protoconid, metaconid, hypoconid, and entoconid are separate and distinct, the two anterior cusps and the two posterior cusps, respectively, would have united to form transverse lophids once the tooth was worn.

Discussion.—Although lower molars and postcrania are not particularly diagnostic, late Oligocene-early Miocene North American tayassuids of similar size to the larger Toledo Bend species include *Thinohyus decedens* (Cope, 1879) from the "*Diceratherium* beds, Middle John Day" (Sinclair, 1905:134), *Hesperhys pinensis* (Matthew, 1907), "*Thinohyus*" *siouxensis* (Peterson, 1905c; see Wright, 1998:395), and the "Van Tassell species" (Wright, 1991:80) from the late Arikareean of the Great Plains, and *Floridachoerus olseni* White (1941) from Thomas Farm (Table 6). All of the above except *T. decedens* are members of Wright's (1991, 1998) *Hesperhys*-"*Cynorca*" *sociale* clade of peccaries.

The Toledo Bend species is closest in size to *Floridachoerus olseni*. Although White (1941, 1942) reported no lower molars for *F. olseni*, Wright's (1991:100) more recent analysis does include some. The Toledo Bend m3 resembles that described by Wright in having a large and bilobed hypoconulid. There is no mention, however, of interloph structures such as those seen in the Toledo Bend tooth, nor is the cingulum morphology described. Wright (pers. comm., 1990) found the labial cingulum to be variable within the same species and therefore generally undiagnostic. Although the anterior half of a worn tooth from the Cedar Run Local Fauna labeled *Floridachoerus* (TMM 40068-14) is of similar size to the m2 in the Toledo Bend jaw fragment, the specimen is in poor, taxonomically undiagnostic condition.

The lack of more diagnostic material, such as premolars, hinders an unequivocal identification. Referral to *F. olseni* would extend the temporal range of that taxon from the early Hemingfordian to the late Arikareean, whereas *Hesperhys pinensis*, "*Thinohyus*" *siouxensis*, and the Van Tassell species are likely of similar age to the Toledo Bend species.

?*Hesperhys* sp.
Figure 11B

Type Species.—*Hesperhys vagrans* Douglass, 1903

Referred Specimens.—LSUMG V-2346, right m3.

Description.—This isolated m3 has an anterior cingulum and small cingular segments between the protoconid and hypoconid and between the hypoconid and hypoconulid (Fig. 11B). There is no continuous labial cingulum in contrast to the m3 of the larger species described above. A paracristid extends lingually from the protoconid and joins with the anterior cingulum. The hypoconulid is asymmetrically bilobate; the labial lobe is larger. The lingual lobe appears to have been made up of three different cuspules before wear reduced them. There is a transversely expanded conulid centrally located within the tranverse median valley and another one between the hypoconulid and the hypoconid-entoconid loph. The tooth measures 20.0 mm AP by 11.0 mm TR.

Discussion.—As noted previously, lower molars are not particularly diagnostic in the hesperhyine group of peccaries. Although this tooth may represent the smaller end of any variation that may have existed in the large Toledo Bend species, it is about 10% shorter and more gracile than that of the latter. As sexual dimorphism is not detectable, except in the canines, of these early peccaries (D. Wright, pers. comm., 1990), taxonomic referral is questionable at this time.

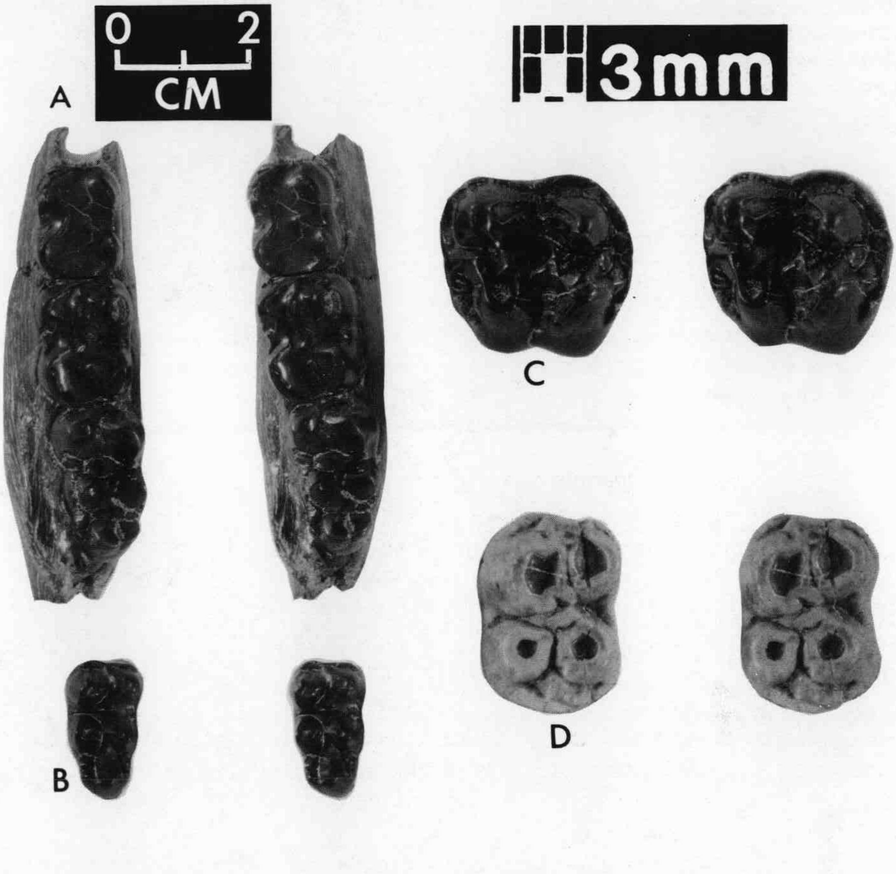

Figure 11. **(A)** ?*Floridachoerus olseni*, stereo view of left ramal fragment with m1-3, LSUMG V-2267; **(B)** ?*Hesperhys* sp., stereo view of right m3, V-2346; **(C)** "*Cynorca*" *sociale*, stereo view of left M1, V-2617; **(D)** "*Cynorca*" *sociale*, stereo view of right m1, V-2271.

Genus *Cynorca* Cope, 1867

"*Cynorca*" *sociale* (Marsh, 1875)

Figure 11C, D

Thinohyus socialis Marsh, 1875
Palaeochoerus socialis (Marsh). Cope, 1879
Thinohyus socialis Marsh. Stehlin, 1899
Thinohyus socialis Marsh. Sinclair, 1905
Thinohyus (*Bothrolabis*) *socialis* (Marsh). Merriam and Sinclair, 1907
Perchoerus socialis (Marsh). Matthew, 1909
Cynorca sociale (Marsh). Woodburne, 1969
"*Cynorca*" *sociale* (Marsh). Wright and Eshelman, 1987

Holotype.—YPM 11785, associated right and left M2-M3, John Day Formation, Oregon (Woodburne, 1969:289).

Referred Specimens.—LSUMG V-2617, left M1; V-2271, right m1.

Description.—M1 has a nearly square occlusal outline with a continuous anterior, labial, and posterior cingulum (Fig. 11C). There is no lingual cingulum. All four cusps are similar in size and there is a metaconule located slightly anterior to the metacone and hypocone, but still posterior to the transverse median valley. The tooth measures 9.4 mm AP by 9.2 mm TR.

The m1 is anteroposteriorly elongate (Fig. 11D). The metaconid is the largest cusp, the protoconid is only slightly larger than the hypoconid, and the entoconid is the smallest. The protoconid is situated slightly anterior to the metaconid and is separated by a larger distance from the hypoconid than the metaconid is from the entoconid. A paralophid originates from the anterior surface of the protoconid and extends lingually a short distance across the anterior surface of the metaconid. There is both an anterior and posterior cingulum and a prominent hypoconulid. There is also a prominent entoconulid (see Wright, 1991:41) in the center of the four cusps, blocking the transverse median valley, and a tiny cingular shelf at the labial entrance of that valley. The tooth is in an early stage of wear and measures 9.4 mm AP by 6.9 mm TR.

Discussion.—Wright and Eshelman (1987) and Wright (1991, 1998) regard *Cynorca* a *nomen dubium* because of the inadequacy of the genoholotype (*C. proterva*) to distinguish the taxon; hence the quotation marks in the systematic heading above.

M1 clearly belongs to a species in Wright's (1991, 1998) *Hesperhys-Tayassu* clade because the paraconule lies slightly anterior to the paracone and protocone, and similarly, the metaconule is slightly anterior to the metacone and hypocone. In less derived taxa, the paraconule and metaconule "lie between the bases of the labial and lingual principal cusps ... " (Wright, 1991:271). That the four principal cusps of the tooth form the vertices of a square further indicates that this species can be placed within Wright's (1991:271, 282-283) *Hesperhys*-"*Cynorca*" *sociale* clade. In Wright's "*Prosthennops*" *xiphodonticus-Tayassu* clade, the four principal cusps form the vertices of an anteroposteriorly elongate rectangle. The Toledo Bend tooth is similar in size to Wright and Eshelman's (1987:606) "Tayassuid sp. A" (the "Pope's Creek species" of Wright, 1991) from "bed 2 of the Calvert Formation," Maryland, and to specimens reported by Woodburne (1969:294) from Wheeler County, Oregon (e.g., UCMP 66861).

The lower first molar from Toledo Bend resembles that of MCZ 17744, referred by Woodburne (1969:297) to *Cynorca* cf. *C. sociale*, from the "?Early Miocene (?Arikareean), 'Loup Fork Tertiary,' Nebraska." TMM-TAMU 2894, from the Garvin Gully Fauna and also listed in Woodburne's (1969:289) hypodigm for *C. sociale*, is somewhat larger than LSUMG V-2271. Wright (pers. comm., 1990) considered this specimen insufficiently diagnostic to be unambiguously referred to "*Cynorca*" *sociale*.

Family ANTHRACOTHERIIDAE Gill, 1872
Subfamily BOTHRIODONTINAE Scott, 1940
Genus *Arretotherium* Douglass, 1901

Arretotherium, the last of the North American anthracotheres, is characterized by the loss of the paraconule in upper molars and a shortened face. The type species, *A. acridens*, was recovered from the Blacktail Deer Creek beds in the upper Renova Formation, western Montana (Douglass, 1901), considered lower Miocene by Hibbard and Keenmon (1950:198) and possibly equivalent to the Harrison Formation by Tedford et al. (1987:164). The type specimen, CM 704, includes parts of the skull with most of the upper dentition and various post-cranial elements.

A second species, *Arretotherium leptodus* (Matthew, 1909), was recovered from the "Lower Rosebud beds" on the Pine Ridge Reservation, Shannon County, South Dakota, now considered equivalent to the early to "medial" Arikareean Sharps, Monroe Creek, and Harrison formations (Tedford et al., 1987:171; see Skinner et al., 1968, for a discussion of problems pertaining to the "Rosebud beds"). The type specimen of *A. leptodus* (AMNH 13005), originally described as *Ancodon* (*?=Bothriodon*) *leptodus*, consists of a skull with lower jaws and some post-cranial elements. Macdonald (1956:616) considered *Ancodon leptodus* a *nomen vanum* because he claimed so little information could be gained from the poor condition of the type. Later, however, Macdonald (1963:229) placed *Ancodon leptodus* in the genus *Arretotherium* based primarily on its age, and additionally noted "upper molars with reduced mesostyle, transverse groove not prominent labially, short diastema between upper canine and P1, [and] canine moderately compressed." A shortened snout was previously noted by Matthew (1909).

Macdonald's *nomen vanum* designation was due partly to the molars of AMNH 13005 being too worn to determine presence or absence of the paraconule. However, another skull, F:AM 132055, closely resembling the type of *A. leptodus* and collected in the same area, clearly shows the absence of the paraconule leaving little doubt as to the generic status of the type. The *nomen vanum* status of *Arretotherium leptodus* should therefore be disregarded. Furthermore, *A. acridens* and *A. leptodus* may represent the same species, although further study is required to confirm this.

A third species, *Arretotherium fricki* Macdonald and Schultz (1956), was described from a badly crushed female skull, UNSM 5764, from the "Upper Marsland" Formation, Box Butte County, Nebraska. The upper part of the Marsland Formation in Box Butte County is equivalent to the early Hemingfordian Runningwater Formation. These rocks are not equivalent to strata in Sioux County, Nebraska, and Goshen and Niobrara counties, Wyoming, that Schultz (1938) termed the Marsland Formation and considered equivalent to those in Box Butte County. The latter strata are equivalent to Peterson's (1907) Upper Harrison beds (for a discussion on the above, see McKenna, 1965, and Tedford et al., 1987:166, 167, 186).

Macdonald (1956) noted another possible species based on a lower molar, SDSM 53440, from the Flint Hill quarry in the Batesland Formation of Bennett County, South Dakota, but Stirton (pers. comm. with Macdonald and Schultz, 1956) subsequently referred that specimen to *A. fricki* (Harksen and Macdonald, 1967:7). Recently, Macdonald and Martin (1987) described additional material of *A. fricki* from Flint Hill, including a well preserved skull (UCMP 32369).

Arretotherium acridens and *A. leptodus* are distinguished from *A. fricki* by their heavier, deeper, more robust jaw morphology in contrast to the slender, more gracile rami of the latter. Although the anterior portion of the mandible is spatulate in all species, it is much more so in *A. fricki*. In general, the upper molars of *A. acridens* are larger than those of *A. fricki*. A broadly separated M3 mesostyle supposedly distinguishes *A. acridens* from *A. fricki* (Macdonald and Schultz, 1956), but the M3 mesostyle of the latter species is also well divided.

Arretotherium acridens Douglass, 1901
Figures 12, 13

Arretotherium acridens Douglass, 1901
Arretotherium acridens Douglass. Macdonald, 1956

Holotype.—CM 704, partial skull with upper dentition and associated postcrania, Blacktail Deer Creek beds, Renova Formation, Montana (Douglass, 1901).

Referred Specimens.—**Toledo Bend**: LSUMG V-2351, left upper C; V-2352, dP1?; V-2353, P1; V- 2354, two right, one left P2; V-2355, left P3; V-2356, right P4; V-2357, right P4; V-2358, right P4; V-2359, left P4; V-2360, right dP4; V-2361, left dP4; V-2362, two left M1s; V-2363, right M1; V-2487, right M1 or dP4; V-2364, two right M2s; V-2365, two left M2s; V-2366, right M3; V-2367, left M3; V-2368, left upper molar "ghost"; V-2269, right maxilla fragment with M2-M3; V-2474, left lateral basicranial fragment; V-2370, three incisors (I3/3?); V-2371, lower left C, male; V-2372, lower left C, female; V-2373, two right p4s; V-2374, two left m2s; V-2375, right m3; V-2376, m3 fragments; V-2377, lower tooth fragments; V-2378, tooth fragments; V-2379, right mandibular symphysis with canine fragment, adult male; V-2380, left mandibular symphysis with canine, adult male; V-2381, left mandibular symphysis with canine and p1 fragment, adult male; V-2382, right mandibular symphysis fragment with canine root; V-2383, right mandibular symphysis, edentulous, juvenile male; V-2384, left mandibular symphysis, edentulous, juvenile female; V-2347, left ramal fragment with p4-m2; V-2270, right ramal fragment with m1-m3; V-2348, left ramal fragment with m3; V-2349, right ramal fragment with partial m3 root; V-2350, mandibular angle fragments; V-2385, proximal right scapula; V-2386, proximal left humerus; V-2387, proximal right radioulna; V-2458, proximal right radius fragment; V-2388, right lunar; V-2389, left lunar; V-2476, left Mc I; V-2390, proximal metacarpal III; V-2391, three left, one right proximal Mc IV; V-2392, two proximal Mc IV fragments; V-2477, one right, one left Mc V; V-2478, left proximal Mc V; V-2393, distal metapodial; V-2394, distal metapodial; V-2395, four proximal phalanges plus fragments; V-2396, medial phalanges; V-2397, lateral digit distal phalanx; V-2699, medial digit distal phalanx; V-2480, sacrum fragment; V-2481, patella; V-2482, tibia shaft fragments; V-2398, one left, two right distal tibia fragments; V-2475, juvenile right distal tibia; V-2399, five calcanea; V-2400, four astragali; V-2401, five naviculars; V-2402, left cuboid; V-2403, right cuboid; V-2479, proximal left Mt II; V-2404, three proximal Mt III; V-2405, proximal Mt IV; V-2483, distal metapodial fragments; **Garvin Gully**: TMM 31084-168, protocone of upper left molar; TMM 31084-60, anterior half of lower molar; **Mann Place**: TMM-TAMU 3065, left M3.

Description.—Dentition: Measurements of teeth are provided in Table 7. Incisors are spatulate with a well developed internal cingulum on some specimens (Fig. 12A, B). The male upper canine (V-2351) is laterally compressed, nearly flat on the lingual surface, convex on the labial surface, with a prominent wear facet on the anterior surface. Canines of female *Arretotherium* are more rounded than laterally compressed (Macdonald and Martin, 1987).

P2 is triangular in occlusal outline with a cingulum, heavy and rounded at the posterior lingual angle, that completely surrounds the base of the tooth. The apex of the laterally compressed blade is anterior of center. P3 is similar to P2 but larger, higher crowned, and the apex of the thin blade is more centrally placed. P4 has a lingual and labial cusp with prominent anterior and posterior cingula. A lingual cingulum is prominent on one specimen, reduced on another, and nonexistent on two other specimens.

The upper molars have a deep transverse median valley with strong, shelf-like anterior and posterior cingula (Fig. 13A). There is a short, prominent lingual cingular segment between the protocone and metaconule that extends from the internal surface of the protocone toward, but not abutting, the interior surface of the metaconule. There is no internal blockage of the transverse median valley between the lingual cingular segment and the mesostyle. The median buttresses of the

Table 7A. Comparative measurements of upper cheek teeth of various species and specimens of *Arretotherium* (* type specimens).

	Toledo Bend		*A. acridens* CM 704*		*A .leptodus** AMNH 13005		*A. leptodus* F:AM 132055		*A. fricki* * UNSM 5764		*A. fricki* UCMP 32369		*A. fricki* UCMP 37440		*A. fricki* F:AM 132053	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W
P2	15.9	11.9	13.5	7.9					7.9	---						
	15.1	12.4														
	16.3	11.9														
P3	19.2	---	17.0	14.3	18.5	13.6			16.1	12.7	15.4	11.9				
											15.9	11.8				
P4	13.5	19.7	15.5	18.8	13.6	17.0	14.6	16.2	12.6	15.3	12.3	15.9			11.7	16.8
	13.4	17.1			14.0	17.1	13.0	16.5			12.2	15.5				
	13.7	20.3														
	13.3	17.6														
M1	22.5	20.0	18.3	20.0	18.0	----	18.1	20.4	19.6	20.7	19.5	20.2	19.25	18.25		
	24.4	23.3			18.0	20.0+	20.1	20.0	18.7	20.4	20.2	20.1				
	22.1	22.9														
M2	24.6	26.9	24.7	26.4	22.9	24.5	26.0	24.1	24.4	23.3	23.9	22.8			24.4	25.3
	27.1	25.0	25.8	26.8	22.3	23.7	24.7	24.2	24.6	24.4	23.7	22.9			23.8	25.1
	25.4	25.6														
	25.4	---														
	25.0	23.5														
	26.4	24.6														
M3	28.1	26.8	28.3	29.4	24.9	26.6	27.6	27.0	25.7	24.9	25.9	26.1			25.5	27.0
	26.5	26.2			25.8	28.7	27.4	27.0			25.3	24.75			25.5	26.9
	27.5	26.5														

Table 7B. Comparative measurements of lower cheek teeth of various species and specimens of *Arretotherium*.

	Toledo Bend		UCMP 32373		SDSM 53440		SDSM 6826	
	L	W	L	W	L	W	L	W
p4	16.8	10.5	15.6	9.4				
	17.4	11.4						
	18.0	11.5						
m1	19.6	12.5	18.2	10.5	19.8	11.3	20.3	10.3
m2	24.0	14.4	23.5	12.7				
	24.3	14.5						
m3	35.1	15.7						
	35.0	14.6						

paracone and metacone meet very low, near the base of the crown, and just barely block the labial entrance to the transverse median valley. M1s are heavily worn and slightly smaller than M2-3s. The interior surface of the paracone and metacone is highly crenulated.

The deciduous P4s are molariform and smaller than the molars. V-2360 measures 19.4 mm AP by 17.8 mm TR; V-2361 measures 18.3 by 16.3 mm.

Lower dentition: From the size and shape of alveoli in a mandibular symphysis fragment (V-2380), i2 was larger than i1, which in turn was larger than i3. The canine in V-2380 is round in cross-section at the crown-root junction. Its anterior edge is pinched into a carina that, beginning at the apex of the tooth, descends the anterior edge, curving medially as it approaches the base of the crown where it formsan anterolingual cingulum. This cingulum has numerous protuberances giving it a rough, almost serrated texture (Fig. 12C). There is a prominent wear facet on the posterior edge. Between the canine and p1 is a short diastema. In the adult male specimen (V-2380) there is a long diastema (32.5 mm) between p1 and p2 (Fig. 12C). Juvenile and female mandibular symphysis specimens maintain similar c-p1 diastemata, but that between p1-p2 is reduced (Table 8). Males also possess a larger alveolus for the canine. All mandibular symphysis fragments show a laterally directed flare at the anterior end that begins just posterior to the p1 alveolus. Alveoli show that p1 was single rooted; p2-3 were double rooted.

The single-cusped p4 has an anterior, posterolabial, and lingual cingulum. The labial surface is convex, the lingual surface slightly concave. There is a tiny paraconid and a ridge, the protocristid, that extends down the lingual side of the main cusp, the protoconid, to the lingual cingulum.

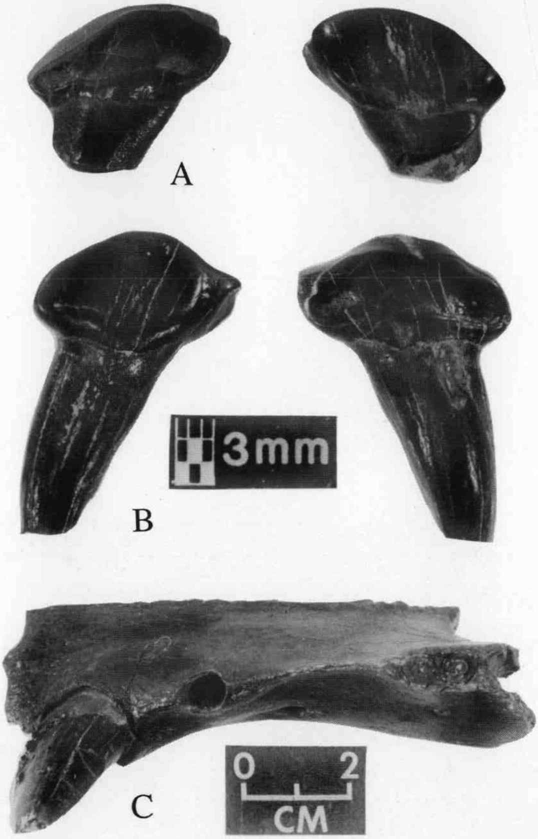

Figure 12. *Arretotherium acridens.* **(A)** Incisor, lingual view (left), labial view (right), LSUMG V-2370; **(B)** Incisor, labial view (left), lingual view (right), V-2370; **(C)** Left anterior ramus with canine, V-2380.

Lower molars are simple with a high, pointed protoconid and hypoconid that are V-shaped at their apex and rounded at their base (Fig. 13B, C). Lingual to the protoconid and hypoconid, respectively, are the similarly high and pointed, slightly anteriorly curving, metaconid and entoconid. The m1s are highly worn with a small labial cingular segment between the protoconid and the hypoconid. The m1-2 have a prominent, rugosely textured anterolabial cingulum and an even more robust posterior cingulum. Between the protoconid and hypoconid, within the median valley, is a single, small, cone-like tubercle, and the labial entrance to the median

Table 8. Mandibular diastema measurements for *Arretotherium*.

Specimen	age/sex	c - p1	p1 - p2
LSUMG-V 2380	adult male	10.3	32.5
LSUMG-V 2381	adult male	7.1	-----
LSUMG-V 2379	adult male	15.0	-----
LSUMG-V 2383	juvenile male	8.0	17.3
LSUMG-V 2384	juvenile female	10.4	14.0

valley is blocked by a small cingular segment. The m3 has a prominent hypoconulid and a strong, rugosely textured cingular segment between the hypoconid and hypoconulid labially and between the entoconid and hypoconulid lingually.

Post-crania: Table 9 provides measurements of the more complete post-cranial elements. The radius and ulna are solidly fused except for a short (approx. 1 cm) portion about 25 to 30 mm distal to the humeral facet of the radius. Other proximal radii fragments indicate that degree of fusion to the ulna may be age dependent.

On the distal tibia, facets for the astragalus are parallel to the sagittal plane with the medial facet being longer and narrower than the lateral. This morphology contrasts with the description of *A. acridens* given by Douglass (1901:274) who described the same facets as being "very oblique." The anterior surface of this element is flattened and separated from the lateral surface by a thin ridge. The distal-most part of this ridge forms the anterior surface of the concavity into which the fibula articulated. The posterior surface of the distal tibia is rounded. The tip of the anterior tuberosity is bifurcated.

The distal articulating surface of the metapodials is asymmetrical with a strong keel that does not extend onto the anterior face. The proximal articulating surface of the proximal phalanx is slightly dished with a strong notch on its posterior edge into which articulates the keel of the distal metapodial. The distal end of the phalanx has two slightly asymmetrical condyles for articulation with the medial phalanx.

The medial phalanges are shorter and more "stubby" than the proximal ones. They can be divided into two groups. The proximal articular surface of the group with the larger elements is transversely broader than it is anteroposteriorly deep and it shows two slightly asymmetrical, very shallow facets matching the distal articular surfaces of the proximal phalanges. Elements of the second group are smaller and have a proximal surface that is equally as broad as it is deep. The distal articular

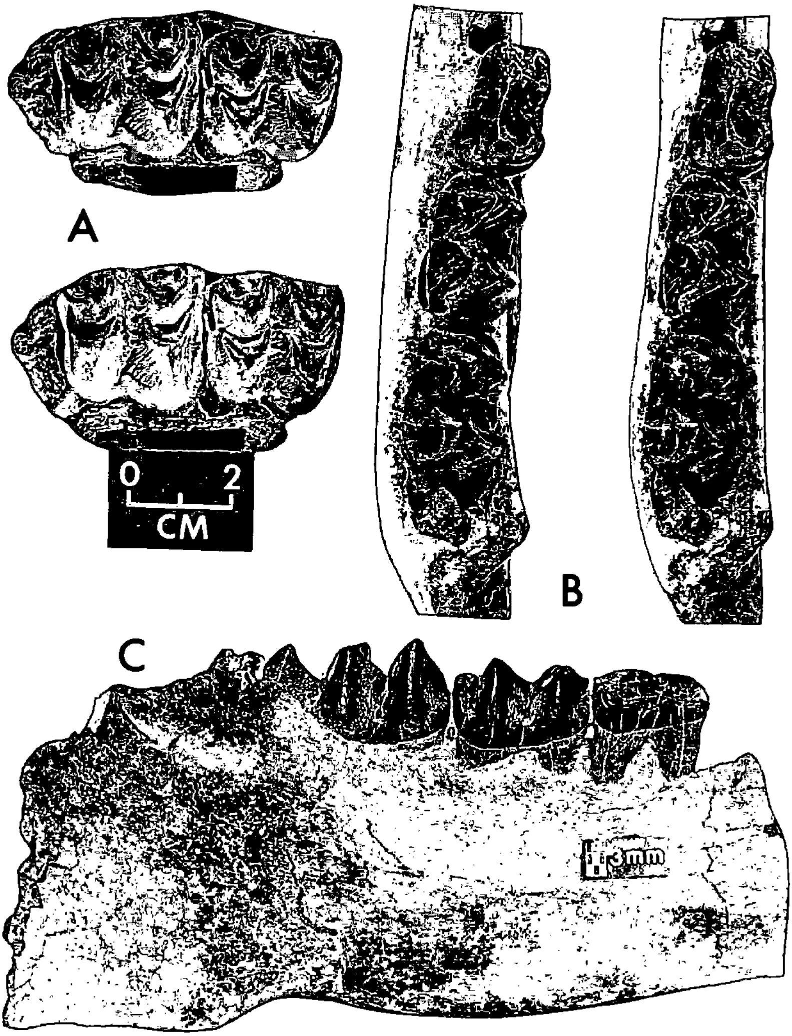

Figure 13. *Arretotherium acridens*. **(A)** Stereo view of right M2-3 in maxillary fragment, LSUMG V-2269; **(B)** Stereo view of right m1-3 in ramal fragment, V-2270; **(C)** Labial view of same.

Table 9. Measurements of various post-cranial elements of *Arretotherium* from Toledo Bend. (Number of elements).

Distal tibia (3)					
AP diameter	35.8	33.0	36.5		
Transverse diameter	40.1	41.1	44.1		
Metacarpal I (1)					
Length	51.1				
Metacarpal V (1)					
Length	85.5				
Proximal phalanx (3)					
Length	32.3	35.2	41.1		
Width, proximal end	17.1	18.5	18.6		
Lunar (2)					
Dorsoventral diameter	28.0	23.5			
Calcaneum (5)					
Length, end of tuber to astragalar fac	66.9	49.2	68.7	59.7	66.0
Anterior-posterior diameter of tuber	27.4	22.7	28.2	27.8	28.7
Transverse diameter of tuber	14.9	13.2	14.1	15.0	15.0
Astragalus (4)					
Length	52.6	56.5	49.0	54.8	
Width, distal end	27.6	30.5	27.2	29.0	
Cuboid (2)					
Dorso-ventrally	26.1	27.0			
Width across astragalar facet	13.4	13.5			
Navicular (3)					
Length	30.4	30.0	30.3		
Width	19.8	19.4	19.3		
Dorso-plantar thicknes	20.5	19.0	18.8		

surface in both groups, as in the proximal phalanges, is divided into two slightly asymmetrical condyles. The larger elements are probably associated with digits III and IV while the smaller ones likely represent lateral digits. Two distal phalanges (claw cores) mirror the situation above. One (V-2397) is small with a highly asymmetrical articular surface, whereas the other (V-2699) is large and symmetrical.

Discussion.—Absence of a paraconule in the upper molars clearly places the Toledo Bend species in the genus *Arretotherium*. Although there is some degree of overlap in molar measurements between *A. acridens* and *A. fricki*, particularly in M1s, Table 7 and Fig. 14 A-D show that the Toledo Bend species, the type specimen of *A. acridens*, the type specimen of *A. leptodus* (AMNH 13005), and F:AM 132055 (= *A. leptodus*), are generally larger than specimens referred to *A. fricki*. They also have a deeper, more robust mandible than the gracile morphology of the Batesland and Runningwater specimens assigned to *A. fricki*. The latter include Batesland specimen UCMP 32373 (see Macdonald and Martin, 1987) and

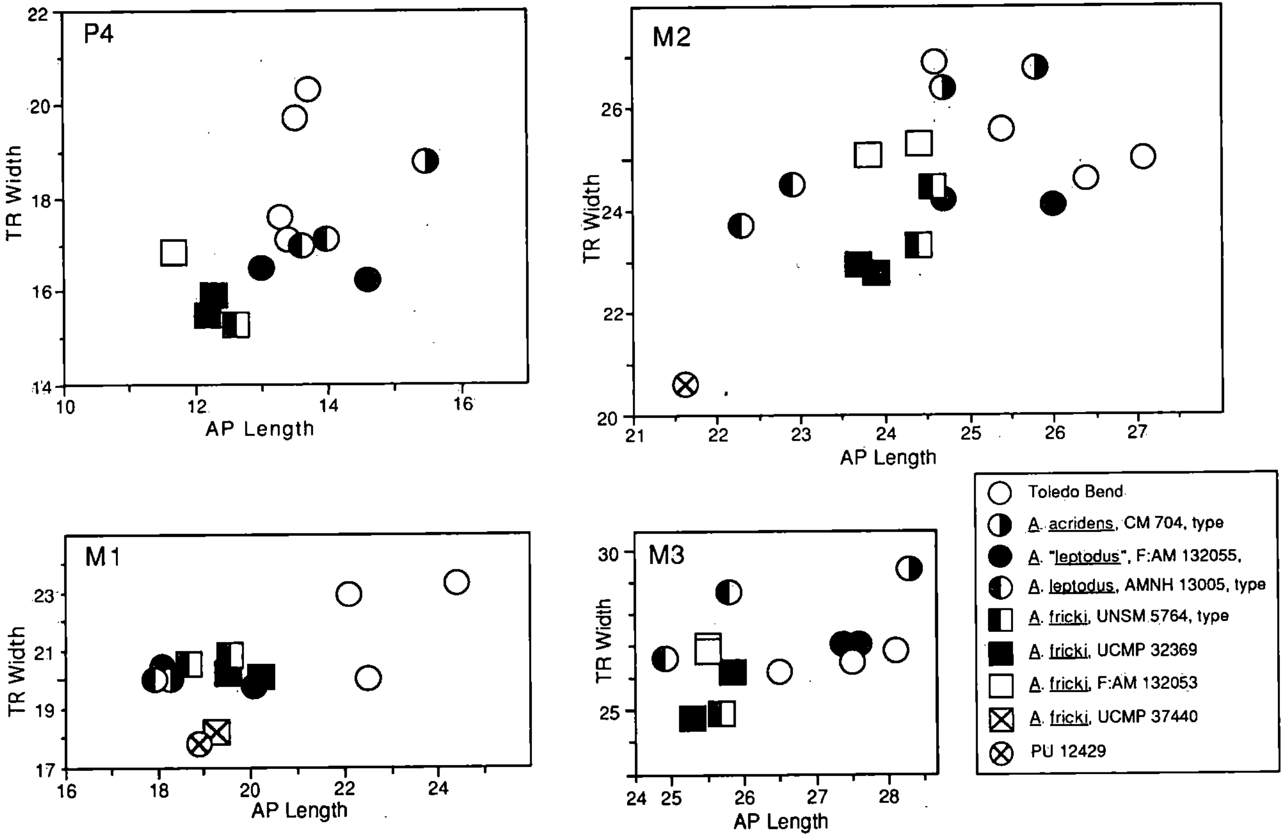

Figure 14. Bivariate scatter plot of dentition of various specimens of *Arretotherium* (mm).

Runningwater specimens F:AM 132053 and F:AM field number (AINS) 475-287. Although sexual dimorphism occurs in *Arretotherium* (Macdonald and Martin, 1987), this is not the cause of the difference in robustness reported here. The small, round, lower canine alveoli and the short p1-2 diastema indicate that the type specimen of *A. leptodus* is a female, yet this specimen is considerably more robust than UCMP 32369, a male *A. fricki*.

P4 of the type specimen of *A. acridens* has a small tubercle, or style, at the labial end of the preprotocrista. This feature is probably variable, as it is also seen in the left P4 of the type specimen of *A. fricki*, but not in any other specimens examined. No P4s from Toledo Bend have this feature.

In the type specimen of *A. acridens*, the paracone and metacone of M3 are completely separated such that the two median buttresses of these cusps that make up the mesostyle do not join. As a result, there is a labial entrance to the transverse median valley. This character was previously used to distinguish *A. acridens* from *A. fricki* (Macdonald, 1956; Macdonald and Shultz, 1956). However, in upper molars of all other specimens examined, the median buttresses of the paracone and metacone abut against one another very low such that a labial entrance to the transverse median valley is just barely blocked. These specimens include: the type of *A. leptodus* and F:AM 132055 from Shannon County, South Dakota; the Batesland specimens UCMP 32369 and 37440 referred to *A. fricki* (Macdonald and Martin, 1987); another specimen reported here for the first time and referred to *A. fricki*, F:AM 132053, from the Runningwater Formation; and the Toledo Bend specimens.

Macdonald and Schultz (1956), in describing M1-3 of *A. fricki*, noted a reduced anterior and posterior cingulum. Although personal observation of the type agrees with their description, the Batesland and Runningwater specimens 'referred to *A. fricki* have strong, shelf-like anterior and posterior cingula similar to those of *A. acridens*. Macdonald and Schultz (1956) also described M1 as having a lingual cingular segment between the protocone and metaconule, but they made no note of this feature on M2 or M3 and their fig. 2 does not show it. Macdonald and Martin (1987), on the other hand, noted "a small cuspule" at the lingual opening of the medial valley of each molar. The anterior and posterior cingula of the Toledo Bend upper molars are quite prominent and all three molars have a lingual cingular segment between the protocone and metaconule.

Plate IX, fig. 2 of Douglass (1901) and text fig. 13 of Macdonald (1956), shows the M3 anterior cingulum of *A. acridens* wrapping around the lingual surface of the protocone, then strengthening between the protocone and metaconule before terminating against the anterior surface of the metaconule. Two of four Toledo Bend M2s (but none of the M3s) possess a weak remnant of a lingual protocone cingulum, but it is not nearly as prominent as that illustrated in the figures noted above. Examination of a cast of the illustrated specimen showed that the lingual cingulum does not continue unbroken around the protocone to the extent the illustrations suggest.

Referring to M3 of the type specimen of *A. fricki*, Macdonald and Schultz (1956) noted that the transverse median valley was blocked by spurs from the protocone and "hypocone" (= metaconule). Macdonald and Martin (1987:58) also noted that "the medial ends of the selene of the protocone and hypocone barely meet in the medial valley." In the Toledo Bend upper molars, the medial ends of the protocone and metaconule selenes are broadly separated and the transverse median valley shows no tendency toward being blocked internally.

The Toledo Bend lower molars are of similar size and of virtually the same morphology as both the Shannon County specimens and the more recent Runningwater specimens. However, lower molars from Batesland show some complexities not found in the others. Slightly smaller than those from Toledo Bend, they differ from the rest in having a strong, posteriorly-directed spur that originates on the posterior surface of the protoconid and effectively blocks the median valley. In m3, this posteriorly-directed spur is met by an anteriorly-directed one originating from the anterior surface of the hypoconid. Additionally, the Batesland m2s have a strong, conical style on the posterolingual corner.

Arretotherium has not been previously reported from the Texas Coastal Plain or from Florida. The only other specimens of the genus currently known from the Gulf Coastal Plain include a fragmented M3 from the Mann Place site in San Jacinto County, Texas, of early Hemingfordian age, and two molar fragments from the similarly aged Garvin Farm Local Fauna in Grimes County. The Mann Place M3 (TMM-TAMU 3065) is only slightly smaller in size than those from Toledo Bend. It measures 25.1 mm AP by about 27 mm TR. The Garvin Farm specimens consist of a protocone of a left upper molar (TMM 31084-168) and the anterior half of a lower molar (TMM 31084-60).

Also noteworthy is a report by C. D. Frailey (pers. comm., 1992; unpubl. ms) of the older (Chadronian to Orellan) anthracothere *Bothriodon* from a site stratigraphically below the Suwannee Limestone in Pasco County, Florida. Although not yet published, this record is particularly important with respect to the earliest land mammal faunas in Florida and the timing of the subaerial emergence of the Florida Platform. It is with anticipation, therefore, that we await further confirmation of this report.

Suborder TYLOPODA Illiger, 1811
Family CAMELIDAE Gray, 1821
Subfamily "NOTHOKEMATINAE" Honey et al., 1998
Genus *Nothokemas* White, 1947
Nothokemas sp.
Figure 15A

Type Species.—*Nothokemas floridanus* (Simpson, 1932; see Patton, 1969:141)

Referred Specimens.—LSUMG V-2406, left ramal fragment with m2-3; V-2407, right m1.

Description.— The broken m2 measures 10.9 mm AP by 8.0 mm TR. Actual measurements would be somewhat larger, as the ectoloph and the posterior edge are missing. Both m2 and m3 have an intercolumnar tubercle between the protoconid and hypoconid. The m3 measures 17.5 mm AP by 8.9 mm TR. The entoconid of m3 extends posteriorly and overlaps about one-half the length of the labial surface of the hypoconulid. The hypoconulid is not the "double enamel loop" type of protoceratids; it consists of a single cusp. In occlusal view, the hypoconid and hypoconulid appear separated from the rest of the tooth (Fig. 15A). The enamel is distinctly crenulated.

Discussion.—In the master's thesis from which this report originates (Albright, 1991), LSUMG V-2406 was referred to *Floridatragulus* sp. This specimen is also responsible for placement of "*Floridatragulus* sp." on the faunal lists of Albright (1998a) and Manning (1990), and it is the latter citation that likely resulted in the report of "*Floridatragulus* sp." at the Toledo Bend site (as locality GCS) in Honey et al. (1998:446). However, more recent study of the specimen has led to the conclusion that V-2406 resembles *Nothokemas* and *Delahomeryx browni* Stevens (in Stevens et al., 1969) more closely than any of the Floridatragulinae, i.e., *Aguascalientia* and *Floridatragulus*. The basis for this revision rests primarily on the morphology of the m3. Although *Nothokemas*, *Delahomeryx*, the Toledo Bend species, and the floridatragulines have intercolumnar tubercles between the protoconid and hypoconid and an entoconid that overlaps the hypoconulid, the entoconid overlap in the former three taxa is not nearly as pronounced as in *Aguascalientia* and *Floridatragulus*, where even greater posterior extension of the entoconid, together with transverse inflation, has resulted in the distinctive, divided m3 hypoconulid so diagnostic of the Floridatragulinae.

Because ancestors of the Floridatragulinae would have likely gone through a stage similar in morphology to that of *Nothokemas*, *Delahomeryx*, and the Toledo Bend species, one might argue that the latter is a primitive member of the former family. Unfortunately, the ancestry of this group of putative camelids is unknown and lack of additional material of the Toledo Bend species, such as premolars, precludes comparisons that might otherwise provide refined insights into the relationship of this taxon with either the "Nothokematinae" or the Floridatragulinae.

The oldest floridatragulid, *Aguascalientia* sp., is known only from the early late Arikareean Castolon Local Fauna, Trans-Pecos Texas (Stevens, 1977). *Aguascalientia* sp. is smaller than the late Hemingfordian *A. wilsoni*, which, likewise, is known only from the Zoyatal Local Fauna, Mexico (Dalquest and Mooser, 1974; Stevens, 1977). *Floridatragulus* ranges from the early Hemingfordian (*F. nanus*, *F. dolichanthereus*, and *F. barbouri*) through the Barstovian (*F. texanus* [early], *F. hesperus* [late]) of the Gulf Coastal Plain (Patton, 1969; Honey et al., 1998). Differences that Stevens (1977) noted between *Aguascalientia* and *Floridatragulus* involve characteristics of the anterior portion of the mandible and premolars which, as noted above, cannot be directly compared with the Toledo Bend specimen. The Toledo Bend species is slightly larger than *Aguascalientia* sp., but smaller than all species of *Floridatragulus*.

Nothokemas and *Delahomeryx browni* are also first recorded in the early late Arikareean. *Nothokemas waldropi* Frailey (1978) occurs in at least two of Florida's Arikareean sites (SB-1A and Franklin Phosphate Pit no. 2), and another even smaller species that appears closely related to *N. waldropi* is abundantly represented at several sites (Albright, 1998a); *Delahomeryx*, like *Aguascalientia* sp., is known only from the Castolon Local Fauna. *Nothokemas* also occurs in the early Hemingfordian Thomas Farm and Garvin Gully faunas as *N. floridanus* and *N. hidalgensis* (Patton, 1969). The Toledo Bend species is larger than *N. waldropi* and smaller and lower crowned than *N. floridanus* and *N. hidalgensis*.

The rare appearance of what is likely a new species of *Nothokemas* at Toledo Bend, together with the abundance of the small, undescribed species noted above found at several Florida localities (yet entirely absent at Toledo Bend), re-emphasizes the restricted, low latitude distribution of these morphologically primitive camelids.

Family PROTOCERATIDAE Marsh, 1891

Although Wilson (1974) described a number of very early protoceratids from the late Eocene of southwest Texas, the Toledo Bend Local Fauna records the first appearance of protoceratids in the Gulf Coastal Plain prior to the early Hemingfordian. Moreover, at Toledo Bend are two different size classes of teeth indicating the presence of two different protoceratids: (1) a small form similar in size to *Protoceras* from the Whitneyan to late Arikareean of the northern Great Plains, and to *Paratoceras wardi* from the early Barstovian Trinity River Pit 1 Local Fauna, Texas, and (2) a larger species indistinguishable from the Coastal Plain endemic *Prosynthetoceras texanus*. (Note: Patton and Taylor [1971] considered *Lambdoceras* a subgenus of *Prosynthetoceras* which would then place the latter in the northern Great Plains. Following Webb [1981] and Prothero [1998:436], *Lambdoceras* is here considered a valid genus, thus restricting *Prosynthetoceras* to the Gulf and Atlantic Coastal Plains.) The small species is the most common mammal in the fauna, accounting for nearly 22% of all mammalian remains recovered (second to anthracotheres). The larger species, represented by only three molars, is rare.

Complicating matters are three small horn fragments representing three distinct morphologies. Two are clearly attributable to frontal, or orbital, horns. The morphology of the third is suggestive of a rostral tine, but close examination reveals that it, too, is likely that of an orbital horn. The fragments belonged to an animal substantially smaller than previously described species of *Prosynthetoceras*, or of

Table 10. Comparative measurements of various species of Protoceratidae. All measurements except Toledo Bend from Patton and Taylor (1973).

	Protoceras celer			*P. skinneri*			*P. neatodelpha*			*Paratoceras wardi*			*Prosynthetoceras orthrionanus*		
	N	L	W	N	L	W	N	L	W	N	L	W	N	L	W
M1	16	11.0-14.5	12.0-15.3	1	13.5	14.5	1	14.0	15.5	5	11.1-12.5	13.0-14.0	3	12.0-13.0	14.1-15.0
M2	16	11.8-15.4	13.8-17.0	1	15.5+	16.7	1	16.2	16.8	4	12.2-13.3	15.2-16.0	2	13.3-14.0	15.3-16.5
M3	11	12.6-15.5	13.3-17.5		--	--	1	15.0	16.5	3	12.5-12.8	15.2-16.6	2	14.4-14.5	16.2-16.6
m1	16	11.0-14.0	8.9-11.5	1	12.0+	--		--	--	11	10.7-11.8	--	4	11.0-11.3	7.8-8.5
m2	16	11.0-14.2	9.6-12.0	2	14.5+	--		--	--	12	11.5-12.5	--	1	13.1	10.5
m3	15	16.0-20.3	9.9-11.1	2	20.5-21.0	11.0		--	--	12	16.2-18.0	--	7	18.0-21.8	10.1-11.7

the earliest synthetoceratine, *Syndyoceras cooki* from the Harrison Formation (Barbour, 1905), and likely represent the same species as that to which the small teeth belong. It is also likely that all three morphologies represent only one species, but vary, perhaps, as a function of ontogenetic stage.

Because post-cranial material from Toledo Bend compares closest to the Whitneyan *Protoceras celer*, which had only small, bony knobs rather than well developed horns, it is possible that these horns belonged to one of the two Arikareean species of that genus, *Protoceras skinneri* or *P. neatodelpha*. However, it is not known if the latter two species had horns because only skulls of females have been recovered (Patton and Taylor, 1973). The small early Barstovian Texas Coastal Plain endemic, *Paratoceras wardi*, on the other hand, had prominent orbital horns as did the synthetoceratines *Prosynthetoceras* and *Syndyoceras*. But, again, the Toledo Bend horn fragments belonged to an animal much smaller than previously described species of the latter two taxa. Evidence provided below suggests that this material belongs to a small, primitive new species of *Prosynthetoceras* that lived alongside early *P. texanus*. Measurements of the dentition of several species of protoceratids, including the small Toledo Bend species, are provided in Table 10.

Subfamily SYNTHETOCERATINAE Frick, 1937

Genus *Prosynthetoceras* Frick, 1937

Prosynthetoceras orthrionanus sp. nov.

Figure 15 B-H

Blastomeryx texanus: Wood and Wood, 1937, p. 137, pl. 1, figs. 5-6.

Holotype.—LSUMG V- V-2619, right orbital horn tip

Paratypes.—LSUMG V-2630, orbital horn tip; V-2631, orbital horn tip

Type Locality.—Toledo Bend Site, Newton County, Texas

Etymology.—Named for the early temporal occurrence (Gr., *orthrios*, early, dawn) and its small size (Gr., *nanos*, little) relative to *Prosynthetoceras texanus*.

Referred Specimens.—LSUMG V-2623, three upper canine fragments; V-2624, two dP4s; V-2625, left P4; V-2626, one left, two right M1s; V-2627, right M2; V-2770, left M2; V-2628, one left M3 and one left M3 fragment; V-2771, left M3; V-2629, upper molar fragments; V-2632, i1?; V-2633, left i2?; V-2634, anterior right ?p2; V-2635, right ramal fragment with m1; V-2636, one right, two left m1s; V-2637, right m2; V-2638, six m3s; V-2772, right m3; V-2639, m3 fragments; V-2640, two edentulous anterior right ramal fragments; V-2641, two axis fragments; V-2642, four distal scapula fragments; V-2643, distal humerus fragments; V-2644, proximal and distal radius fragment; V-2645, right scaphoid; V-2646, one right, two left lunars; V-2647, left cuneiform; V-2648, femur head fragment; V-2649, distal tibia fragments; V-2650, thirteen astragali; V-2651, four calcanea; V-2652, calcanea fragments; V-2653, six naviculars; V-2654, cuboid; V-

2655, two proximal right Mt III; V-2656, proximal right and left Mt IV; V-2657, distal metapodial fragments; V-2658, proximal phalanx fragments; V-2659, medial phalanges; V-2660, ungual phalanx.

Diagnosis.—Differs from *Prosynthetoceras texanus* in smaller size, lower crowned teeth, and in retaining unfused distal radius and ulna; lower m3s differ from *P. texanus* in retaining stylids between protoconid and hypoconid and between hypoconid and hypoconulid; similar in size to *Paratoceras wardi* but differs in lacking a continuous lingual cingulum on upper molars and in retaining unfused distal radius and ulna; similar in size to *Protoceras celer* but differs in having orbital horns and in lacking a continuous lingual cingulum on upper molars; similar in size and tooth morphology to *Protoceras skinneri* and *Protoceras neatodelpha*, but postcrania and cranial armament unknown for latter two taxa.

Description.—Horns: V-2619, a fragment consisting of only the distal part, is about 42 mm long, transversely compressed, and weakly curved toward the sagittal plane (Fig. 15B). It is anteroposteriorly broad proximally, tapers distally, and the forward edge is rounded while the posterior edge is pinched. As in *Paratoceras* and the synthetoceratines, it shows longitudinal vascular grooving. It most closely resembles the distal part of a *Paratoceras wardi* orbital horn, but lacks the bulbous knob at the tip. Whether this horn had the medial strut described for that of *P. wardi* (Patton and Taylor, 1973) is indeterminable from this fragment. It is not yet known if *Protoceras skinneri* or *P. neatodelpha* had orbital horns.

In contrast to V-2619, specimen V-2631, also a fragment representing only the distal part, is not transversely compressed. It is slightly more recurved than V-2619 and has a bulbous tip. A prominent sulcus ascends the posterior edge. On the anterior surface is another, less prominent, sulcus. Several minor grooves additionally sculpt the surface, particularly medially. The length of this fragment along the outside curvature is about 39 mm; both the anteroposterior and transverse diameters measure about 8.5 mm. With the grooves and bulbous tip, V-2631 most closely resembles the orbital horns of *Prosynthetoceras texanus* and *Syndyoceras cooki* except for its tiny size (Fig. 15C).

The third horn fragment, V-2630, is neither transversely compressed like V-2619, nor does it show the bulbous tip and prominent posterior sulcus of V-2631. V-2630 is relatively long and slender, not as strongly recurved as the others, and tapers to a blunt, rounded point. It measures 55 mm long, is rounded labially, and flattened medially (Fig. 15D).

Upper dentition: Terminology follows Patton and Taylor (1973:355). Three small fragments represent the long, recurved upper canine typical of protoceratids. The P4 is triangular in occlusal outline and wider labially than lingually. It has a well developed parastyle and metastyle and a lingual cingulum that extends a short distance labially on both the anterior and posterior surface. The dP4 is molariform and smaller than M1. Upper molars are low crowned with strong styles and cingula (Fig. 15E, F). They are broader transversely than long anteroposteriorly and the

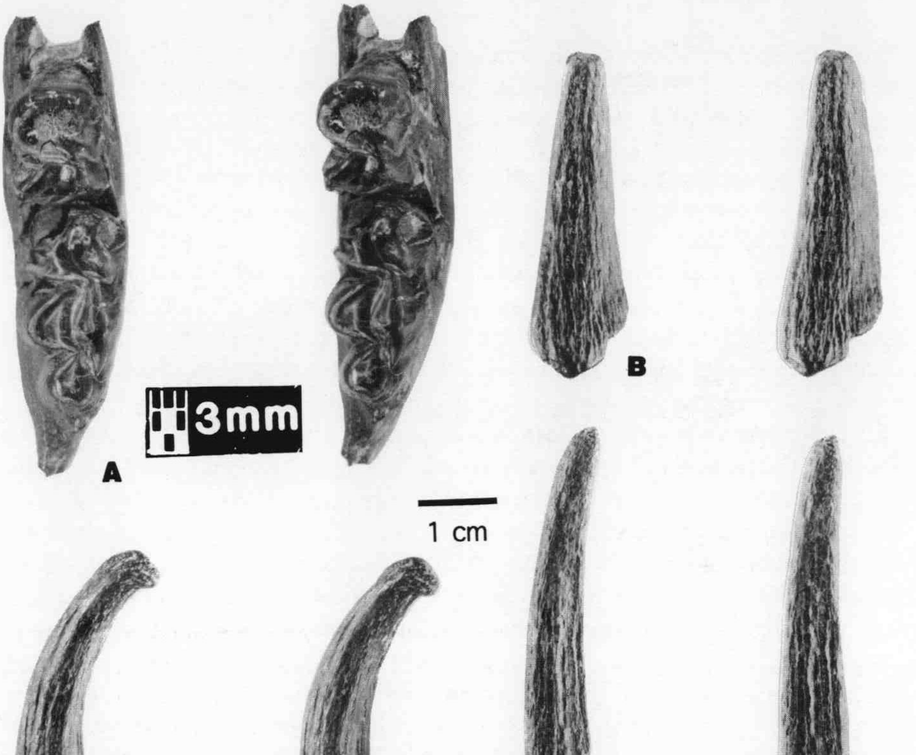

Figure 15. **(A)** *Nothokemas* sp., left ramal fragment with m2-3, LSUMG V-2406; **(B)** *Prosynthetoceras orthrionanus* n. sp., frontal horn fragment, V-2619; **(C)** *P. orthrionanus*, frontal horn fragment, V-2631; **(D)** *P. orthrionanus*, frontal horn fragment, V-2630; **(E)** *P. orthrionanus,* left M2, V-2770; **(F)** *P. orthrionanus*, left M3, V-2771; **(G)** *P. orthrionanus*, right m3, V-2772; **(F)** *Prosynthetoceras texanus*, left M3, V-2662; **(G)** *P. orthrionanus*, right m3, V-2772, occlusal view; **(H)** Same specimen, labial view. 3 mm scale bar for **A** only; 1 cm scale bar for **B-H**..

anterior half is set farther lingually than the posterior half, particularly on M3. Both the paracone and metacone have a strong labial rib and there is a prominent mesostyle. The crescents are generally V-shaped. Between the protocone and metaconule is a well developed blade-like style characteristic of protoceratids. There is an anterior and posterior cingulum; the former large and blade-like lingually. In some molars the posterior cingulum continues lingually around the metaconule to connect with the blade-like intercolumnar style.

Lower dentition: The crown of an incisor tentatively referred to this species is believed to be an i1. It is smooth, relatively symmetrical, and convex labially. There is a cingulum that extends upward from the base of the crown along both lateral edges. The ventral edge of the crown of i2? is convex while the dorsal edge is concave. The lingual surface is slightly excavated. The i3 is asymmetrically spoon-shaped. Like i2, the ventral edge of the crown is convex while the dorsal edge is concave. The anterior ?p2 fragment shows a distinct notch between the paraconid and protoconid, but is otherwise undiagnostic. The m1 and m2 show a variably small to prominent intercolumnar tubercle between the protoconid and the hypoconid. In one specimen the tubercle is blade-like as in upper molars. The posterior edge of the metaconid barely overlaps the anterior edge of the entoconid forming only a slight metastylid. The parastylid, however, is relatively prominent. The metaconid and entoconid are both ribbed and there are no cingula. The m3s also have a prominent parastylid and similar metaconid-entoconid overlap (Fig. 15G). Characteristic of protoceratids, the hypoconulid of m3s shows the double enamel loop which encloses a fossettid with wear (Patton, 1969). Five of eight complete m3s and one anterior fragment have an anterolabial cingular segment. Some also have an intercolumnar stylid between the protoconid and hypoconid and also between the hypoconid and hypoconulid.

Mandible: Two small, worn, anterior ramal fragments (V-2640) have a p1 alveolus, the anterior margin of which lies directly above the distinct, downwardly directed "hook" on the ventral edge of the ramus that marks the posterior-most position of the symphysis. Posterior to the p1 alveolus is a relatively long, sharp-ridged diastema. Both specimens are broken anterior to the p2.

Vertebrae: The axis fragments consist primarily of the odontoid process. Although slightly smaller, they closely resemble those of *Protoceras celer* from the Poleside Member of the Brule Formation (F:AM 53527).

Forelimb: All postcranial elements compared were nearly identical to those of *Protoceras celer* and only slightly different from those of *Paratoceras wardi*. The scapula fragments consist only of the glenoid surface and part of the neck, and compare well with F:AM 53521, a scapula of *P. celer*. The neck is narrow and there is no indication that the scapular spine extended onto it. The coracoid process is short but prominent.

The distal humeri fragments range from 21.5 to 27.0 mm transversely across the distal trochlea. These measurements would be slightly greater if the specimens were unworn. There is no entepicondylar foramen. The proximal end of the radius measures 22.0 mm transversely (vs. 23.2 mm in *P. celer*, F:AM 53521) and, as in *P. celer* specimens F:AM 53521 and 40879, is not fused to the ulna. As a result, the distal end of the radius has only a scaphoid and lunar facet; the cuneiform facet is on the distal end of the ulna. In *Paratoceras wardi* and the Synthetoceratinae, the distal ulna is strongly fused to the distal radius. The scaphoid, lunar, and cuneiform are virtually indistinguishable from those of F:AM 40879. These elements have been adequately described by Osborn and Wortman (1892) and Scott (1940). Measurements taken in the proximodistal aspect are 11.0 mm for the scaphoid, 12.0 mm for the lunar, and 11.0 mm for the cuneiform; much smaller than the same elements of *Prosynthetoceras texanus*.

Hindlimb: The head of the femur is indistinguishable from that of both *Protoceras celer* and *Paratoceras wardi*. Distal tibia fragments range from about 18 to 20 mm transversely. The prominence of the medial malleolus and intercondylar ridge result in a deep, narrow, dorsal notch (the medial astragalar condylar groove), as well as a deep and narrow medial facet for the astragalus. The lateral facet for the astragalus is broad and shallow. Astragali vary in size from 19.8 mm to 30.5 mm long. The astragalus of *P. celer* (F:AM 53521) and *Paratoceras wardi* (F:AM 40870) are virtually identical in size and morphology to those from Toledo Bend and measure 30.0 and 29.0 mm, respectively. The calcanea from Toledo Bend vary from relatively robust specimens at 55.3 mm long to gracile ones at 50.6 mm. Astragali referred to *Paratoceras wardi* (F:AM 40868 and 40869) measure 56.5 to 59.2 mm, respectively, and differ from *P. celer* and the Toledo Bend specimens only in a slightly narrower sustentacular facet. The naviculars, which range from approximately 15 to 19 mm anteroposteriorly, are not fused to the cuboid as they are in ruminants, and are indistinguishable from the same elements in *P. celer*. Metatarsals III and IV are not coossified. The width of the proximal Mt III from Toledo Bend is 9.4 mm, and 9.7 mm for Mt IV, compared with 10.8 and 10.2 for the same elements, respectively, of *P. wardi* (F:AM 40872 and 40874). More detailed descriptions of the postcrania of *Protoceras celer* and *Paratoceras wardi* can be found in Osborn and Wortman (1892) and Patton and Taylor (1973), respectively.

Discussion.—Were it not for the recovery of the orbital horn fragments described above, the size and morphology of the teeth and, particularly, the primitive morphology of the postcrania of this small protoceratid would suggest referral to *Protoceras*, two species of which occurred in the Arikareean: *P. skinneri* from the early Arikareean Sharps and Gering formations of South Dakota and Nebraska, and *P. neatodelpha* from beds equivalent in age to the Harrison Formation, north of Keeline, Niobrara County, Wyoming (Patton and Taylor, 1973:367; **Note**: recent work by R. Hunt [pers. comm., 1998] indicates that Arikaree deposits north of Keeline may be slightly older than the stratotype Harrison Formation in Sioux County, Nebraska). In fact, it was to *P. neatodelpha* that I originally assigned this material in the Master's thesis from which this report is derived (Albright, 1991), because post-cranial material from Toledo Bend compares closest to the Whitneyan *Protoceras celer*, the upper molars closely resemble those of *P. skinneri* and *P. neatodelpha* in lacking the prominent continuous lingual cingulum seen in *P. celer*, and *P. neatodelpha* is likely of similar age to the Toledo Bend species. However, *P. celer* had only small, bony knobs rather than well developed horns. On the other hand, the early Barstovian *Paratoceras wardi* had prominent orbital horns. Considering the sister taxon relationship of *Protoceras* with *Paratoceras* (Patton and Taylor, 1973) one might argue that prominent orbital horns likely developed in *Protoceras neatodelpha* as well, given its approximately 9-10 million year occurrence following *Protoceras celer*. Currently, however, the cranial armaments of *P. neatodelpha* and *P. skinneri* are unknown because only skulls of females have been recovered (Patton and Taylor, 1973).

Although Patton and Taylor (1973:397) found *Paratoceras wardi* more closely related to *Protoceras* than to any of the synthetoceratines, they considered the origin of *Paratoceras* to be "the greatest gap in our knowledge of protoceratine evolution." Temporally the Toledo Bend species falls within that gap and biogeographic data would also support the idea that the Toledo Bend species might be an evolutionary precursor of *P. wardi*. (Interestingly, Whitmore and Stewart [1965] referred a primitive protoceratid from the Hemingfordian of Panama to *Protoceras*. Patton and Taylor [1973], however, later assigned the specimens to *Paratoceras*.) One significant morphological argument against this interpretation, however, rests on the prominent lingual cingulum retained in upper molars of *Paratoceras wardi* (as in *P. celer*). This condition in an early Barstovian taxon would require an evolutionary reversal from that in the late Arikareean Toledo Bend species where the lingual cingulum is weak to absent.

It is unfortunate that only a single worn P4 represents the premolar dentition of the small Toledo Bend protocertid, because the primary means of distinguishing *P. skinneri* from *P. neatodelpha*, and both of those species from *P. celer* and *Paratoceras*, relies on premolar morphology and size relative to the molars (Patton and Taylor, 1973). Lower premolars are also helpful in distinguishing *Protoceras* from *Paratoceras*, but none were recovered. Lower molars from Toledo Bend, as in *P. skinneri* and *P. neatodelpha*, have a less prominent anterior cingulum than those of *P. celer*. *Paratoceras wardi* lower molars also have a weak anterior cingulum.

The Toledo Bend species is substantially smaller than the first synthetoceratines recorded, *Syndyoceras cooki* and *Prosynthetoceras texanus*, although upper molars are similar in lacking lingual cingula. Lower molars are also smaller and lower crowned than those of *P. texanus* and, as in *Protoceras* and *Paratoceras*, they show weak intercolumnar stylids between the protoconid and hypoconid (and between the hypoconid and hypoconulid in the m3s), and they have a weak anterior cingular segment. Lower molars of *P. texanus* generally lack intercolumnar stylids and an anterior cingulum (Patton, 1969:181; Patton and Taylor, 1973:382). Recovered postcranial elements lack derived features found in *Prosynthetoceras texanus*, and in *Paratoceras wardi*, such as a distally fused radius and ulna, and are virtually identical to those of *Protoceras celer*. Horn fragments, however, although much smaller than those of *Prosynthetoceras texanus* and *Paratoceras wardi*, closely resemble those of the latter two taxa in morphology.

The most reasonable hypothesis therefore, given the evidence currently available, is to consider the Toledo Bend form a small, new, primitive species of *Prosynthetoceras* that lived alongside early *P. texanus*. Although the post-crania most closely resemble those of *Protoceras celer*, this resemblance is likely the retention of primitive traits that carry, in a cladistic sense, no phylogentic significance. The similarity in morphology of the teeth with those of *P. skinneri* and *P. neatodelpha*, whereby the continous lingual cingulum in upper molars is lost, may, likewise, be a convergent trait. The possibility that the species represents an evolutionary precursor to *Paratoceras wardi* based on similar size and horn morphology is also dismissed because of the retention of prominent lingual cingula in upper molars of *P. wardi*—a character absent in the older Toledo Bend species. It is important, however, to consider the possibility that *Protoceras neatodelpha* made its way to the Texas Coastal Plain from the northern Great Plains in the early late Arikareean, as both *Arretotherium acridens* and *Nexuotapirus marslandensis*, two taxa previously known only from the northern mid-continent, are abundant at Toledo Bend. But this hypothesis cannot be tested until a male skull of *Protoceras neatodelpha* and/or *P. skinneri* is recovered. Such a find would shed considerable light on the evolution of frontal horns in this lineage and obviously help clarify the relationship of the small Toledo Bend protoceratid with both the protoceratinae and the synthetoceratinae.

In light of the above, the report by Tedford et al. (1987:176) of "early *Prosynthetoceras*" in the Cedar Run Local Fauna is likely attributable to *P. orthrionanus*, particularly considering the revised age of the Cedar Run Local Fauna as equivalent with Toledo Bend (Albright, 1998a). The two Cedar Run teeth (AMNH 30084) were referred to "*Blastomeryx texanus*" by Wood and Wood (1937), a taxon later synonymized with *P. texanus* by Patton and Taylor (1971). Patton and Taylor (1971) did not, however, include AMNH 30084 in their hypodigm of material referred to *P. texanus*, possibly because the teeth are considerably smaller than specimens they referred to the latter. This conclusion is made in consideration of Patton and Taylor's (1971) findings through measurements of lower third molars that *P. texanus* increased in size through the progressively younger Aiken Hill, Garvin Farm, and Burkeville local faunas.

One final note should be included regarding the biogeography of this group. It is particularly intriguing, given the abundance of *Prosynthetoceras orthrionanus* at Toledo Bend, that protoceratids are absent prior to the early Hemingfordian in Florida where the Arikareean is much better represented than in Texas. Furthermore, *Paratoceras* is known only from the early Barstovian and Clarendonian of Texas and the Hemingfordian of Panama (Whitmore and Stewart, 1965; Patton and Taylor, 1973:367) and *Prosynthetoceras*, which ranges from the late Arikareean to the late Barstovian, is also known only from the Gulf and Atlantic Coastal Plains. The scarcity of protoceratids in the extensivley sampled Arikareean deposits of the northern Great Plains, their absence in the thick Arikareean and Hemingfordian deposits of the John Day Valley, Oregon, together with an abundance of endemic forms from the Arikareean through Clarendonian along the Gulf Coastal Plain supports ideas that evolution of the group was largely centered in the tropical to subtropical regions of Central America and southern North America.

Prosynthetoceras texanus (Hay, 1924)
Figure 16A

See Patton and Taylor (1973) for synonymy.

Holotype.—TAMU 2387, right M3, Garvin Gully Fauna, Grimes County, Texas.

Referred Specimens.—LSUMG V-2661, left M2; V-2662, left M3; V-2663, right i3; V-2664, partial right m3.

Description.—M2 and M3 are typically protoceratid in their prominent parastyle and mesostyle, ribbed paracone and metacone, and intercolumnar blade between the V-shaped protocone and metaconule (more prominent on the posterior side of the median valley than on the anterior side). M2 measures 18.7 mm AP by 21.7 mm TR; M3 measures 17.0 mm AP by 19.0 mm TR (Fig. 16A).

The m3 fragment is high crowned with a prominent parastylid. The posterior edge of the metaconid strongly overlaps the anterior edge of the entoconid. Both the labial and the lingual surface of the metaconid and entoconid are ribbed. There is no anterior cingulum and there is no intercolumnar tubercle between the protoconid and the hypoconid. Because the hypoconulid is broken off and missing, the 18.8 mm AP length is about 4.5 to 5 mm less than its total length would have been were the hypoconulid intact.

Discussion.—The teeth referred here to *Prosynthetoceras texanus* are larger and higher crowned than those of *P. orthrionanus* sp. nov. discussed above, and the m3 lacks an anterior cingulum and stylids between the labial cusps.

It is interesting that *P. texanus*, which is common in early Hemingfordian faunas of the Coastal Plain such as Garvin Gully and Thomas Farm, is absent from Arikareean sites in Florida such as the Buda, SB-1A, Franklin Phosphate Pit No. 2, and Brooksville local faunas. The rare occurrence of *P. texanus* at Toledo Bend, therefore, which is considered nearly age equivalent to the Florida Arikareean sites (Albright, 1998a), provides one of the oldest records of the species, in turn suggesting an earlier arrival in Texas than in Florida.

Suborder RUMINANTIA Scopoli, 1777
Family HYPERTRAGULIDAE Cope, 1879
Genus *Nanotragulus* Lull, 1922
Nanotragulus sp.
Figure 16 B, C

Type Species.—*Nanotragulus loomisi* Lull, 1922

Referred Specimens.—LSUMG V-2492, right m1; V-2493, right m2; V-2254, right m2; V-2494, proximal right scapula fragment; V-2495, two distal humeri; V-2496, distal tibia-fibula; V-2497, three astragali; V-2498, two right cubonaviculars; V-2499, one left, one right ectocuneiform; V-2500, two distal metapodials; V-2501, proximal phalanx.

Description.—In lower molars the labial surface of the metaconid and entoconid are weakly ribbed, there is a small anterior cingulum situated high on the crown; there is a stylid at the labial entrance of the valley between the protoconid and the hypoconid; and the labial surface of the labial cusps form narrow, sharp Vs (Fig. 16B). There is no metastylid and no overlap of the entoconid by the metaconid. V-2254 measures 7.0 mm AP by 4.4 mm TR with a slightly worn crown height of 7.1 mm. V-2492 measures 7.0 mm AP by 3.9 mm TR with a worn crown height of 6.9 mm. V-2493 measures 7.4 mm AP by 4.9 mm TR with a worn crown height of 4.4 mm.

The scapula (V-2494) has a strong coracoid process and no coracoscapular notch. The distal tibia shows three prominent projections formed by the medial malleolus, the intercondylar ridge, and a strongly fused distal fibula (Fig. 16C) which Scott (1940:519) noted was "highly characteristic" of *Hypertragulus*. The astragular facets of the distal tibia are both deep and narrow. The astragali (V-2497) are narrow and elongate with no distal keel on the lower ginglymi. The ectocuneiforms (V-2499) measure about 10 mm AP, are about 6 mm deep dorsoventrally, and about 8 mm TR. The dorsal articular surface is concave anteriorly and convex posteriorly. Ventrally, the opposite is true. The cubonavicular (V-2498) is fused and the central metapodials (V-2500) are unfused. The metapodial keel is strong but confined to the ventral surface.

Discussion.—The "triple projection" morphology due to fusion of the distal tibia and fibula clearly places this small species within the Hypertragulidae, as this feature is not present in other ruminants (Webb and Taylor, 1980). Unfused metapodials preclude referral to the Leptomerycidae or Blastomerycinae. *Hypertragulus* retains an "extremely reduced but apparently continuous" fibula (Webb and Taylor, 1980:144; Scott, 1940). A continuous fibula is evidently lost in *Nanotragulus*, leaving only the fused proximal and distal remnants. Hence referral of the Toledo Bend species to *Nanotragulus*.

The Toledo Bend species is slightly smaller than *N. albanensis* Frick (1937) and similar in size to *N. ordinatus* (Matthew, 1907) and *N. matthewi* Cook (1934)

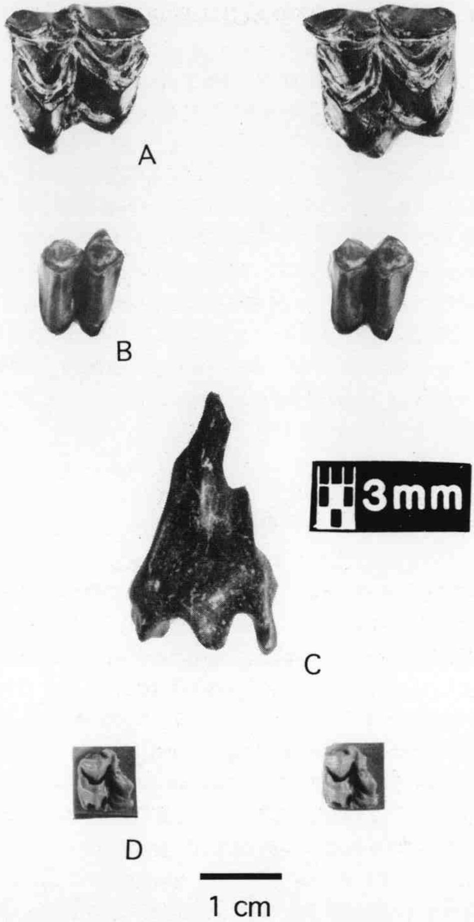

Figure 16. **(A)** ***Prosynthetoceras texanus***, LSUMG V-2662, left M3; **(B)** ***Nanotragulus*** sp., stereo view of right m2, LSUMG V-2254; **(C)** ***Nanotragulus*** sp., fused distal tibiofibula, V-2496; **(D)** Small artiodactyl, undet., left partial upper molar, V-2253. 3 mm scale bar for **B** and **C**; 1 cm scale bar for **A** and **D**.

from the Harrison Formation. The latter two species have more rounded labial cusps than the sharp, distinctly V-shaped labial cusps of the Toledo Bend species. *Nanotragulus loomisi* Lull (1922) is smaller and also has more rounded labial cusps. Although hinted at by Voorhies (1973), Frailey (1979) showed that material representing *N. loomisi*, *N. intermedius* Schlaikjer (1935), and *N. lulli* Frick (1937) should be referred to the single species *N. loomisi*, abundant in Arikareean faunas of the Great Plains (e.g., Macdonald, 1963) and in the Buda Local Fauna, Florida (Frailey, 1979).

Stevens et al. (1969) and Stevens (1977) reported *N. ordinatus* from the Castolon Local Fauna of Big Bend National Park, Texas. This fauna is of similar age to the Toledo Bend Local Fauna and the size of *N. ordinatus* and the Toledo Bend hypertragulid is similar. But the figures of the Castolon specimens (1969, fig. 13; 1977, fig. 17B) showing cut-away sections of the mandible indicate that m2 and m3 were considerably more hypsodont than in the Toledo Bend species.

In his discussion of hornless ruminants, Webb (1998:473) listed the blastomerycine *Machaeromeryx gilchristensis* as occurring in the Toledo Bend Local Fauna, evidently following the preliminary faunal list of Manning (1990). More detailed study revealed that this material represented *Nanotragulus*. Thus, the record of *M. gilchristensis* at Toledo Bend is in error.

Artiodactyla, undet.

Figure 16D

Referred Specimen.—LSUMG V-2253, partial left upper molar.

Description and Discussion.—This very low crowned tooth was compared with nearly all small artiodactyls in the F:AM collection, but eludes identification. It is missing most of its two posterior cusps (Fig. 16D). There is a thin but prominent anterior cingulum at the base of the crown extending from the anterolabial surface of the ectoloph to a point where the protocone is broken lingually. It cannot, therefore, be determined whether this cingulum continued around the protocone to connect with a prominent, transversely elongate style between the two lingual cusps, although it appears to have done so. The labial surface of the paracone has a median rib and there is an anteriorly-directed mesostyle. There does not appear to have been a parastyle. The posterior crescent of the protocone does not join the anterior crescent of the metaconule. The anterior crescent of the metaconule is strongly connected to the mesostyle. Most peculiar are the greatly offset lingual cusps and the robust lingual cingulum protecting the metaconule. This cingulum abuts the transversely elongate style mentioned above. The length of the tooth cannot be determined but its transverse width would have been only slightly greater than 8 mm.

Nanotragulus and *Hypertragulus* generally lack a mesostyle in upper molars. *Leptomeryx*, *Pronodens*, *Pseudoparablastomeryx*, *Blastomeryx*, *Machaeromeryx*, and *Longirostromeryx* do not have lingual cingula. *Dremotherium* has a continuous anterior and lingual cingulum, but the posterior lingual cingulum is not nearly as developed as in the Toledo Bend tooth. Upper molars of *Heteromeryx* show a lingual cingulum, but this species is larger, with heavier enamel and a more labially rounded paracone and metacone. *Barbouromeryx* has no lingual cingula, is larger, and has crista-like structures on the anterior limb of the metaconule. *Bouromeryx* is also larger and has complicated cristae. *Archaeomeryx* is smaller. *Paracosoryx* has hypsodont upper molars. The tooth is reminiscent of Eocene forms such as *Leptoreodon*, *Leptotragulus*, and *Poabromylus*, but these taxa have a more prominent lingual cingulum on the protocone than on the metaconule and they have a prominent parastyle. The tooth does not resemble deciduous P4s of hypertragulids or leptomerycids. On the other hand, the presence of distinct ribs on the paracone and metacone, a prominent mesostyle, a prominent style between the protocone and metaconule, and what appear to be prominent lingual cingula suggest the possibility that the tooth may be a dP4 of the small Toledo Bend protoceratid or *Nothokemas*. However, the dP4 of *Paratoceras wardi* figured by Patton and Taylor (1973:380) differs from V-2253 in its larger size, prominent parastyle, and absence of strong lingual cingula.

It is unfortunate that only this single partial tooth has been recovered. Although it may represent a new Gulf Coastal Plain taxon, additional material is required before an unambiguous taxonomic designation is forthcoming.

AGE AND CORRELATION

The heterogeneous nature of the deposit from which the Toledo Bend assemblage was recovered implies that nearly all fossils found are at least to some extent reworked. Fossils from the Paleozoic through the earliest Miocene have been recovered (Manning, 1990). Nevertheless, those mammals that comprise the Toledo Bend Local Fauna are considered contemporaneous primarily because all have overlapping ranges with similar taxa in comparably aged faunas elsewhere, because few vertebrate fossils are known from the underlying Catahoula Formation (considered Oligocene in age), and because early Oligocene marine strata of the Vicksburg Group underlie the latter. In other words, only older strata lie upstream from the Toledo Bend locality, and there is no evidence that those older strata could have contributed the mammalian taxa that accumulated in the paleochannel deposit. Taxa from a younger age are also unlikely to have been reworked into the deposit because the fossil bearing conglomerate appears to have been "encapsulated" within the Carnahan Bayou Member siltstones shortly after the high energy event that formed the deposit subsided.

Although Albright (1998a) discussed several problems that discourage high resolution geochronology for Arikareean assemblages of the Gulf Coastal Plain, the age of the Toledo Bend Local Fauna can be relatively well constrained by a number of biochronologically diagnostic taxa. As Manning (1990) noted, the presence of an entelodont and an anthracothere indicates that the site can be no younger than early Hemingfordian, as that is their last occurrence in the North American fossil record (Tedford et al., 1987). On the other hand, the site can be no older than early Arikareean because that is when *Diceratherium*, *Moropus*, and *Nanotragulus* make their first appearance (Tedford et al., 1987, 1996). *Diceratherium*, *Nanotragulus*, and *Daphoenodon* also last occur in the late Arikareean (Tedford et al., 1987, 1996), although *Miohippus* last occurs in the early Arikareean. The presence of *Prosynthetoceras*, however, provides a later Arikareean aspect to the fauna as does *Nothokemas*.

Although material representing the same tapir as that from Toledo Bend is also found in the early Arikareean Monroe Creek Formation, the type specimen of *Nexuotapirus marslandensis* is thought to have come from the early Hemingfordian Runningwater Formation. *Arretotherium*, too, ranges from the early Arikareean to early Hemingfordian in the High Plains, although the Toledo Bend species resembles most closely the older *Arretotherium acridens*.

The mutual occurrence of *Daphoenodon notionastes*, *Moropus* sp., and *Texomys* sp. in both the Toledo Bend and Buda local faunas suggests age equivalence. Both faunas also have the characteristic Arikareean hypertragulid *Nanotragulus*. As shown in Figure 17, the Buda Local Fauna is considered "medial" Arikareean in age (see Albright, 1998a, for a summary of Arikareean faunas in Florida).

Noticeably absent from Toledo Bend are taxa found in the Gulf Coastal Plain during the early Hemingfordian such as the amphicyonid *Amphicyon longiramus*, the canid *Tomarctus*, the horses *Parahippus leonensis* and *Anchitherium clarencei*, and the rhino *Menoceras barbouri*. Instead, at Toledo Bend the amphicyonid is *Daphoenodon*, the common horse is *Anchippus texanus*, and two of the three rhinoceroses are species of *Diceratherium*. Although oreodonts are present in the Texas Coastal Plain during the early Hemingfordian, and camels are both diverse and abundant, the absence of oreodonts and rarity of camels at Toledo Bend, in contrast to their presence in Florida during the Arikareean and Hemingfordian, is likely due to ecological factors rather than temporal (see below). Figure 17 shows the chronostratigraphic position of the Toledo Bend Local Fauna relative to some of the other Arikareean and Hemingfordian faunas of North America with which it has been compared.

One final mention should be made regarding the reports of *Machaeromeryx gilchristensis* in the Toledo Bend Local Fauna by Webb, of *Floridatragulus* sp. by Honey et al., and of *Menoceras barbouri* and *Floridaceras whitei* by Prothero in the recently published volume on Tertiary mammals of North America edited by Janis et al. (1998). These records are evidently based on a preliminary faunal list published by Manning (1990) prior to the completion of the present author's more detailed studies. More recent study determined that these identifications were erroneous and that the material referred to *Machaeromeryx* actually represents *Nanotragulus*, that material referred to *Floridatragulus* more likely belongs to a new species of *Nothokemas*, and that the material referred to *Menoceras* and *Floridaceras* belongs to *Diceratherium*.

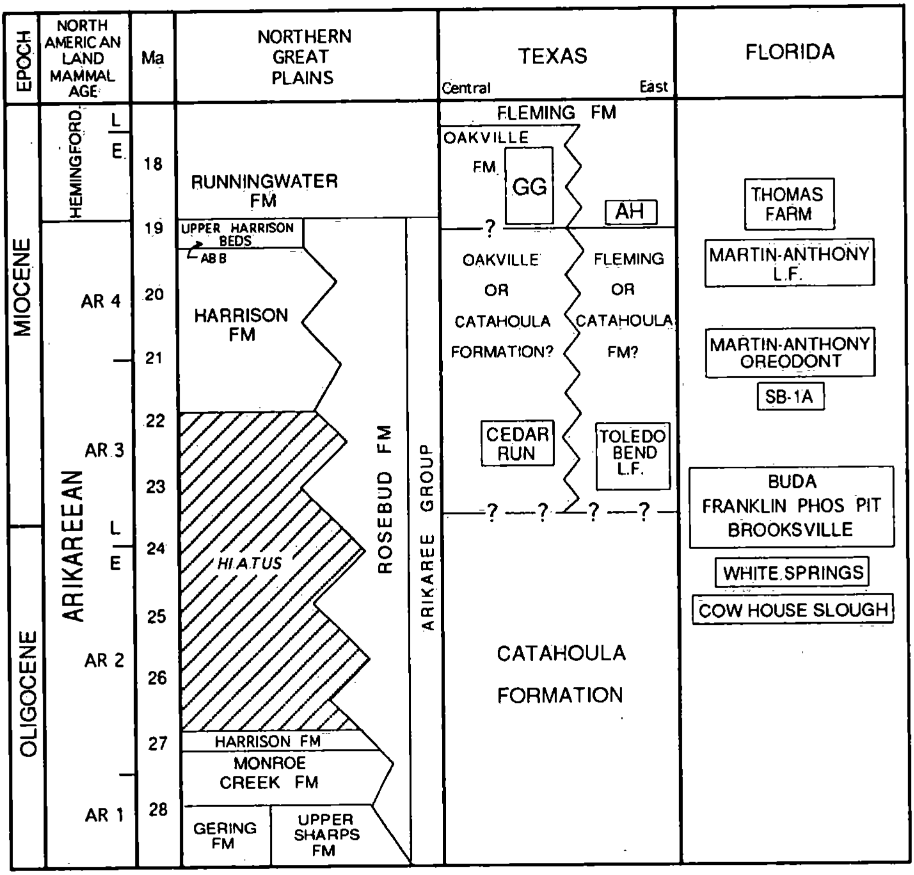

Figure 17. Correlation chart of early Miocene faunas of the Gulf Coastal Plain and northern Great Plains. Chronostratigraphy of northern Great Plains follows MacFadden and Hunt (1998); ABB = Agate Bone Bed, Agate Fossil Beds National Monument, Nebraska; AH = Aikin Hill Local Fauna; GG = Garvin Gully Local Fauna.

SUMMARY

The Toledo Bend Local Fauna includes the most diverse representation of Arikareean mammals yet reported from the Gulf Coastal Plain. This assemblage of at least 25 mammalian taxa differs from other early Miocene coastal plain faunas in the unusual abundance of otherwise rare, riparian species. Exceptional is the fact that three riparian forms, the "hippo-like" anthracothere *Arretotherium acridens*, the tapir *Nexuotapirus marslandensis*, and the small new protoceratid, *Prosynthetoceras orthrionanus*, account for the majority of mammalian remains recovered—a likely result of these animals living in or near a riverine environment conducive to the preservation of their remains.

It has long been recognized that early Miocene faunas of the Gulf Coastal Plain represented a distinct biogeographic province from the better known assemblages of similar age in the northern Great Plains. This is particularly evident in the Arikareean faunas of Florida and further emphasized at Toledo Bend with records of such new, apparently endemic, forms as the small protoceratid, camelid, and rhinoceros. In contrast to Florida, however, there is also at Toledo Bend the added element of several taxa previously known only from the Great Plains, such as *Arretotherium*, *Nexuotapirus*, and *Diceratherium*, resulting in an unusual and diverse mixture of taxa that reflects an environment able to sustain overlapping ranges from adjacent biomes; so called "ecotone" conditions.

There are additional differences between Toledo Bend and Florida's Arikareean assemblages, as well. Oreodonts, for example, are present in Florida during this interval, yet they are entirely absent at Toledo Bend—a particularly interesting point considering that the late Arikareean was their time of maximum diversity. Camelids, too, are relatively common in Florida's Arikareean sites, yet they are extremely rare at Toledo Bend. In contrast, the three most abundantly represented mammals at Toledo Bend, noted above, are entirely unknown in Florida, and rhinos, also common at Toledo Bend, are exceptionally rare in Florida until the Hemingfordian..

These differences may be due to physiographic factors, as the east Texas region of the Gulf Coastal Plain would certainly have been influenced by a west-to-east migrating Mississippi River system during the early Miocene (Galloway et al., 1991) in contrast to what may have been a somewhat less fluvially influenced environment in Florida. Furthermore, prior to the late Oligocene the Florida Platform persisted as a marine shallow-water carbonate bank that was separated from the continental mainland by the Suwannee Strait, which flowed from the northeastern Gulf of Mexico to the Atlantic Ocean (Huddlestun, 1993). Within the Suwannee Strait was the deeper-water Gulf Trough which extended from the Gulf of Mexico northeasterly across the eastern part of the Florida panhandle region far into southern Georgia. During the Late Oligocene, according to Huddlestun (1993), there began a series of progressively lower low stands punctuated by lower high stands which finally culminated in the extreme low stand at the beginning of depositional cycle TB1.1 of Haq et al. (1987). Not until then, during the early part of the Chattian Stage, did the Florida Platform finally become subaerially continuous with the continental mainland, at least in eastern Georgia beyond the easternmost extent of the Gulf Trough. During the latest Oligocene, Huddlestun (1993:140-142) speculates that the Suwannee Straits region would have been "a vast, low-elevation karst plain" and that the Gulf Trough would have been a large river valley during low stands and a "vast estuary" during high stands. Subsequent early Miocene sea-level high stands and low stands would result in further episodes of Florida peninsula isolation and continental connection until the connection was permanently established upon burial of the Gulf Trough during the early Middle Miocene (Huddlestun, 1993). Such a scenario provides ample opportunity for filtered dispersal into northern Florida, south of the Suwannee Strait, as well as for insular isolation and the consequent affects including endemism and dwarfism.

Another probable cause for differences between the western and eastern Gulf Coastal Plain is the location of the Toledo Bend site nearer to the Great Plains than is Florida, particularly considering the environmental corridor between the Great Plains and the Texas Coastal Plain likely provided by a paleo-Mississippi River system. Temporal inequivalencies that are difficult to resolve due to the lack of accurate geochronological control over this interval in the region may also have contributed, as well as inadequate knowledge regarding truly contemporaneous faunas elsewhere due to circumstances such as the temporal gap noted in the Arikaree Group of northwestern Nebraska from about 22-27 Ma. It is with anticipation, therefore, that we await the results of new geochronological studies currently underway in fossil-bearing strata of the John Day Formation, Oregon, that span this important interval.

Nevertheless, the identification of at least three, and perhaps more, new endemic ungulates in the Toledo Bend Local Fauna, in addition to the presence of other species apparently restricted to the Gulf Coastal Plain, such as the small chalicothere (it has yet to be determined if this and the John Day species are the same) and amphicyonid (see Albright, 1996, 1998a), serves to reinforce the previously espoused concept of faunal provinciality of this southeastern region during the earliest Miocene (see Webb, 1977; Prothero and Sereno, 1982; Tedford et al., 1987; and Webb et al., 1995). Further study of the mammals noted in this report, in addition to continued paleontological work in the Gulf Coastal Plain in general, can only add to our understanding of this region as a unique biogeographic province during the early phase of large herbivore diversification in North America.

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