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MIOCENE AND PLIOCENE ARTIODACTYLS, TEXAS GULF COSTAL PLAIN

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MIOCENE AND PLIOCENE ARTIODACTYLS, TEXAS GULF COASTAL PLAIN

THOMAS HUDSON PATTON[1]

SYNOPSIS: Describes 27 species of fossil artiodactyls from a series of vertically successive mammalian assemblages in Miocene and Pliocene deposits of the Texas Gulf Coastal Plain and discusses their systematic positions. Among the new forms represented are two camel genera: *Australocamelus*, the probable *Aepycamelus* ancestor, and *Nothotylopus*, a very unusual member of the *Protolabis-Pliauchenia* lineage. The Floridagulinae are now seen to have had a trans-Coastal Plain distribution extending in time from the middle Hemingfordian Garvin Gully Fauna through the Barstovian Cold Spring Fauna. The Gulf Coast species of the Synthetoceratinae are discussed and the phylogeny of the subfamily outlined. Evidence from this study indicates that the Gulf Coastal Plain constituted a distinct faunal province throughout most of the Tertiary. Whereas many striking similarities exist between the faunas of the Texas Coastal Plain and those of the Great Plains, several groups are true Gulf Coast autochthons. Others, which are distributed in both regions, contain species endemic to the Gulf Coastal Plain. The ages of the Texas Gulf Coastal Plain faunas are revised and correlated with those from the Great Plains.

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INTRODUCTION

The Miocene sedimentary rocks along the Texas Coastal Plain provide a record of successive mammalian faunas unsurpassed anywhere in the Gulf and Atlantic coastal provinces of North America. This is the only such record outside of western North America, and consequently affords a basis for a detailed comparison of faunas from the Coastal Plain with those from the Miocene and Pliocene deposits of the High Plains.

A series of vertically successive mammalian assemblages of relatively short temporal span gives the paleontologist an opportunity to study and observe not only geographic changes or shifts in animal communities through time, but also to detect microevolutionary steps within the various groups represented. The combination of good stratigraphic control and increasingly clearer evolutionary lineages provides the basis for a more complete reconstruction of zoogeographical patterns, faunal interchange, and paleoecology than is usually realized in faunal studies. It also facilitates biostratigraphic correlations between faunas of the Texas Coastal Plain and those elsewhere especially from the more widely known Great Plains deposits. Whereas the Texas faunas show many similarities to those from the Great Plains region in individual taxa, they differ substantially in relative abundance of taxa and, partially, in their faunal associations. Some groups, for example the synthetocerines, which are only sparingly represented in the Great Plains deposits, are abundant in the Gulf Coastal Plain faunas and appear to have undergone most of their evolution in the Gulf region. As would be expected, some taxa appear earlier or persist longer in one area than in the other. Yet on the whole a similarity exists between the faunas of the two regions, which is fortunate for interregional biostratigraphic correlation, as most of the geochronologic framework of the North American Tertiary is based on the rocks and fossil vetebrate faunas of the Great Plains. Whereas the Great Plains and the Texas Coastal Plain faunas each evolved under their own particular set of environmental conditions, whatever ecological barriers existed between the two regions must have been slight enough to allow a relatively free interchange of forms between them. Still, enough isolation, geographic at least, existed between the faunas of the two regions to permit specific and greater differences to accumulate.

Although vertebrate fossils of Miocene and Pliocene age have been known from the Texas Coastal Plain for nearly a century, the area has only recently been investigated in detail. As fossil remains are for the most part fragmentary and widely dispersed throughout these deposits, the area has been generally uninviting from both the collecting and systematic standpoints. Only when the unique nature of the faunal elements and their associations was recognized and its importance understood were any significant studies undertaken.

Papers by Hay (1924) and Hesse (1943) included the first general faunal descriptions of fossil vertebrates from the Texas Coastal Plain. Quinn (1952, 1955) studied in detail the fossil horses from these faunas, and later Wilson (1957, 1960) described the entelodonts and the carnivores. Because of the unusually fortunate stratigraphic configuration of the Coastal Plain faunas and the relative abundance of remaining undescribed fossil vertebrate material available, the writer undertook a systematic investigation of various artiodactyl groups. It is hoped that data derived from the study of these taxa may serve as a basis for further systematic and biostratigraphic analysis of the Texas faunas and will provide a foundation for reconstructing a sequence of biological events through time and also perhaps the geological and climatic processes that determined these events.

ACKNOWLEDGMENTS

I am indebted to John A. Wilson of the Department of Geology, the University of Texas, for his suggestions and criticisms during the writing of this paper. The critical reading of the manuscript by W. Charles Bell, Ernest L. Lundelius, and W. Frank Blair, of the University of Texas, by Donald D. Savage of the University of California (Berkeley) and by Malcolm C. McKenna and Richard Tedford, American Museum of Natural History. is gratefully acknowledged.

I should also like to thank Malcolm C. McKenna, Morris F. Skinner, and my colleague S. David Webb of the Florida State Museum, the University of Florida, for numerous stimulating and enlightening discussions on the stratigraphy and fossil vertebrate faunas of the Tertiary of the western United States.

I am grateful to the Department of Geology of the University of Texas, the Coates Foundation of the University of Texas, The Society of the Sigma Xi and the Scientific Research Society of America, the Houston Geological Society, and to the Humble Oil and Refining Company for financial support during the course of this project.

I should like to express my appreciation to authorities at the American Museum of Natural History, the United States National Museum, the Museum of Comparative Zoology at Harvard University, Texas A & M University, the Shuler Museum of Paleontology at Southern Methodist University, the University of California Museum of Paleontology (Berkeley), the Florida State Museum, and the Frick Laboratory of the American Museum of Natural History, for permitting me to examine fossil material under their care.

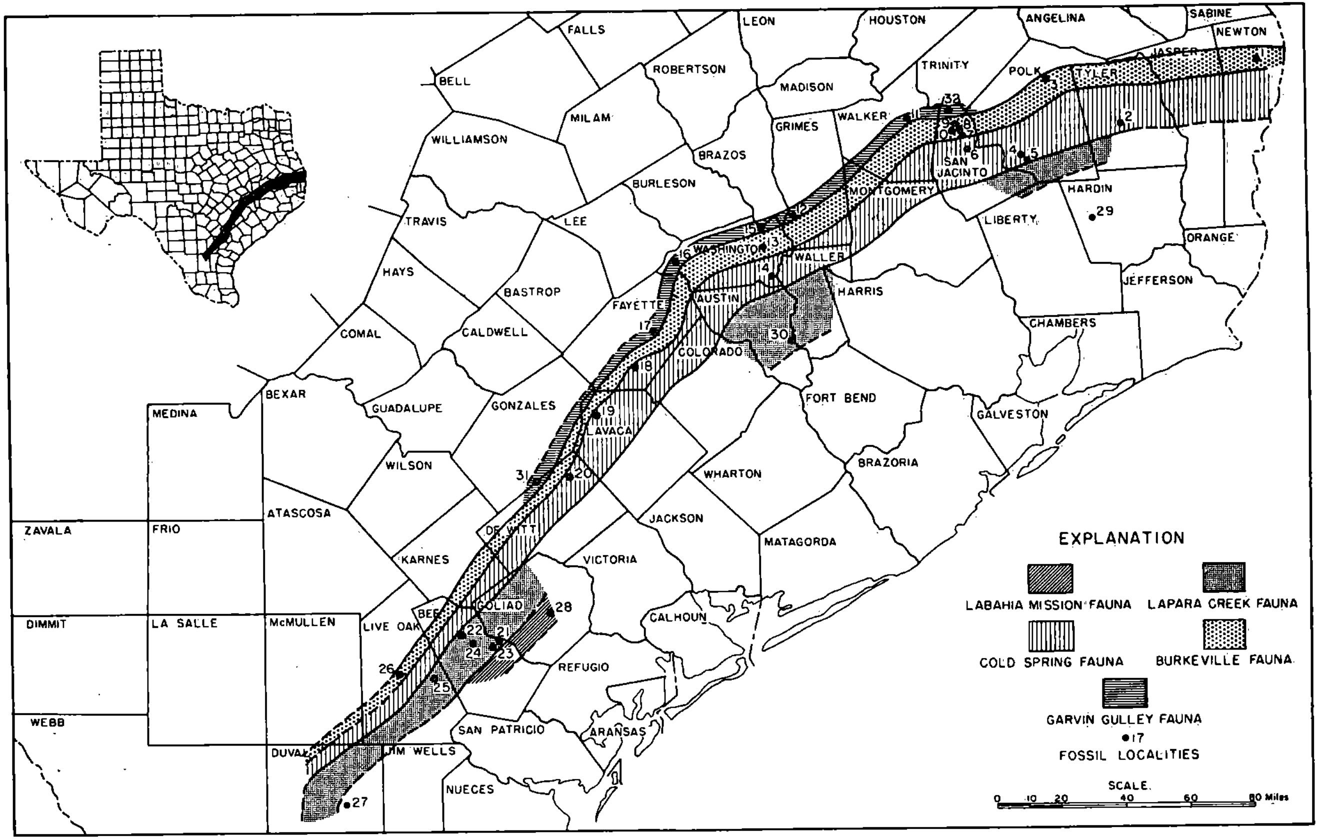
Finally, I wish to express my deepest thanks to my wife, Ellen Frederick Patton, for her constant encouragement and indispensable support throughout the course of this work. The illustrations were drawn by Mrs. Margaret Skeels Stevens.

ABBREVIATIONS

Materials belonging to various institutions are referred to in the text by their catalog numbers and the following abbreviations:

AMNH	American Museum of Natural History
FAM	Frick Collection, American Museum of Natural History
FSGS	Florida State Geological Survey
MCZ	Museum of Comparative Zoology, Harvard University
SMU	Southern Methodist University
TAMU	Texas A & M University
UCMP	University of California, Museum of Paleontology, Berkeley
UF/FSM	University of Florida, Florida State Museum
USNM	United States National Museum
UTBEG	University of Texas, Bureau of Economic Geology

FIGURE 1. Map of Miocene biostratigraphic units in the Texas Coastal Plain (from Wilson, 1962). Numbers refer to fossil localities listed in Table 1.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LEON
HOUSTON
ANGELINA
SABINE
NEWTON
JASPER
TYLER
POLK
TRINITY
BELL
ROBERTSON
MADISON
MILAM
WILLIAMSON
WALKER
GRIMES
BRAZOS
SAN JACINTO
MONTGOMERY
BURLESON
HARDIN
LIBERTY
ORANGE
JEFFERSON
TRAVIS
LEE
WASHINGTON
WALLER
HAYS
BASTROP
AUSTIN
HARRIS
FAYETTE
COMAL
CALDWELL
COLORADO
CHAMBERS
BEXAR
GUADALUPE
GONZALES
FORT BEND
GALVESTON
MEDINA
LAVACA
WILSON
WHARTON
BRAZORIA
ATASCOSA
JACKSON
ZAVALA
FRIO
DE WITT
KARNES
MATAGORDA
VICTORIA
DIMMIT
LA SALLE
McMULLEN
LIVE OAK
BEE
GOLIAD
CALHOUN
REFUGIO
WEBB
SAN PATRICIO
ARANSAS
DUVAL
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EXPLANATION
LABAHIA MISSION FAUNA
LAPARA CREEK FAUNA
COLD SPRING FAUNA
BURKEVILLE FAUNA
GARVIN GULLEY FAUNA
•17
FOSSIL LOCALITIES
SCALE
0 10 20 40 60 80 Miles

Table 1. AREAL DISTRIBUTION OF FOSSIL FAUNAS IN TEXAS[1]

Map no.	UTBEG no.	County	Location
1	31160	Newton	Near Burkville
2	31087	Tyler	Near Town Bluff
3	31057	Polk	Near Moscow
4	31183	Polk	Near Goodrich
5	31200	Polk	Near Goodrich
6	31219	San Jacinto	Near Cold Spring
7	31191	San Jacinto	Near Cold Spring
8	31243	San Jacinto	Near Point Blank[2]
9	31190	San Jacinto	Near Point Blank
10	31242	San Jacinto	Near Point Blank
11	30873	Walker	Aiken Hill
12	40071	Grimes	Near Navasota
13	40070	Grimes	Sommers Pit
14	31272	Washington	Near Chapel Hill
15	40067	Washington	Hidalgo Bluff
16	40068	Washington	Near Carmine
17	31259	Fayette	Near LaGrange
18	31278	Fayette	Near Amandsville
19	31273	Lavaca	Near Shiner
20	31262	DeWitt	Near Concrete
21	30896	Bee	Near Berclair
22	31132	Bee	Near Normanna
23	31080	Bee	Near Berclair
24	31170	Bee	Near Normanna
25	30936	Live Oak	Near George West
26	30904	Live Oak	Near George West
27	31089	Duval	Palangana dome
28	30895	Goliad	Goliad State Park
29		Hardin	Saratoga field
30	40539	Austin	S. F. Austin State Park
31	40193	DeWitt	Near Hocheim
32	40224	San Jacinto	Near Point Blank
33	40262	Gonzales	Near Shiner

[1] More detailed geographic information for each of the above localities is on file in the catalogue of the vertebrate fossil collection of the Bureau of Economic Geology, The University of Texas.

[2] This locality, on the basis of the fossils it contains, more likely falls within the Cold Spring rather than Burkeville Fauna. See also Quinn (1955).

STRATIGRAPHY

Stratigraphic nomenclature employed in this paper is that of Wilson (1956), who summarized the synonymy and revised the Miocene and Pliocene formations of the Texas Gulf Coastal Plain. Wilson divides these deposits into three lithostratigraphic units, the Oakville, Fleming, and Goliad Formations (in ascending order). Within these formations several vertebrate faunas can be recognized

(Quinn, 1955; Wilson, 1956). From oldest to youngest these are the Garvin Gully, Burkeville, Cold Spring, and Lapara Creek Faunas. According to Wilson, (1956):

> The Garvin Gully Fauna has known stratigraphic limits in Grimes, Washington, and Fayette counties. It coincides with the lower Oakville and the Moulton sandstone Members of Renick (1936). The stratigraphic limits of the higher faunas are not so well known, but the Burkeville and Cold Spring faunas are known to be within the outcrop limit faunas of the Fleming and Lagarto formations. It is hoped that future mapping and collecting will clarify the relation of the Goliad formation and its members to the faunas found within it.

Lithostratigraphic and biostratigraphic relationships are graphically represented in Figures 2 and 3. The age of these faunas is partially reinterpreted in this paper and is outlined under the section titled Age and Correlation.

The Miocene and Pliocene deposits of the Texas Gulf Coastal Plain are exposed in arcuate belts of varying width. They strike roughly parallel to the present shoreline of the Gulf of Mexico. The dip is characteristically small, seldom exceeding 2 to 4 feet per mile. Because the shoreline shifted progressively gulfward through successive geologic epochs since the Eocene, the younger outcrops are found south and east of the older ones. Topographically the Texas Coastal Plain varies from a nearly flat surface near the coast to a higher hilly region farther inland. The near-coast region consists of unconsolidated clay and sand deposits, whereas the inland belt is formed on differentially eroded alternating sandstone lenses and clay. In the hilly regions infacing cuestas, some with scarps more than 100 feet high, are supported by more resistant sandstone lenses; the intervening lowlands coincide with weaker, more easily eroded clay.

In this region the Cenozoic was a time of marine deposition on the fluctuating margins of the Gulf, and of continental deposition inland by meandering, anastomosing streams on the relatively flat, subsiding coastal plain. Because of its history of alternating marine transgressions and regressions, the region is characterized by a complicated intergrading of continental and marine sediments. Not only does one type of sediment replace another vertically, but some formational units grade laterally, or change abruptly, from one facies to another. This particular geologic configuration is the source of much of the confusion still present in the stratigraphic nomenclature of Gulf Coast Cenozoic deposits. The Lower Miocene strata present a continental facies at the outcrop, whereas downdip they change

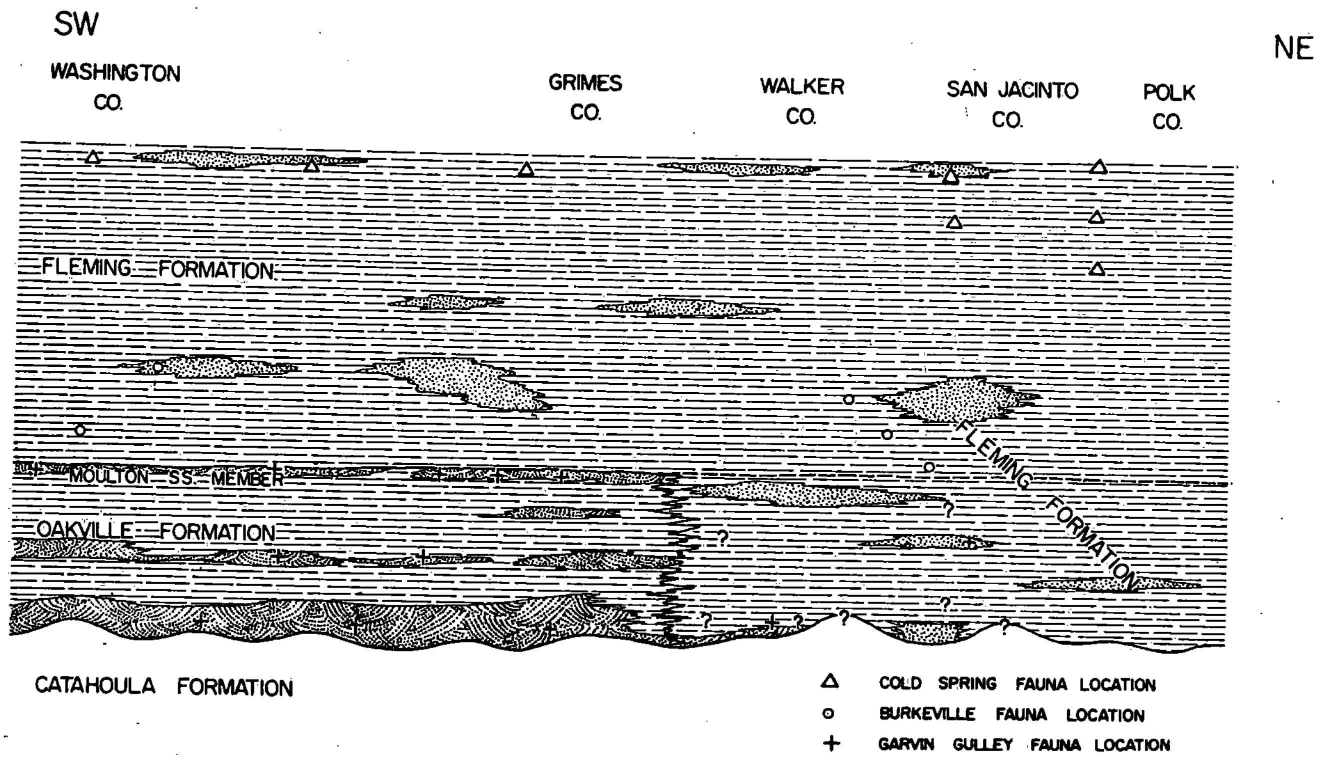

FIGURE 2. Stratigraphic framework of Texas Coastal Plain fossil vertebrate faunas.

to littoral deposits. Farther gulfward they assume a deeper-water marine aspect.

The continental Miocene deposits of this region are in themselves stratigraphically complex. Ragsdale (1960:7) describes the Oakville Formation (Fig. 2 & 3) as a . . . "sequence of interbedded, highly lenticular calcareous sandstones, claystones, conglomerates, and siltstones. The sandstones are moderately to poorly sorted. Conglomerates coarser than pebble size are uncommon but do exist."

The sandstone beds are intricately cross-bedded, are imbedded with small lentils of clay, and contain large quantities of bone, clay balls, calcareous nodules, and reworked Cretaceous invertebrates. Abraded bone fragments and some well-preserved teeth are recovered from sand units, particularly the coarser ones, in many places along the outcrop of the Oakville Formation. Fossil bones and teeth are also found in the surrounding clay. Identifiable vertebrate fossil remains have been found at at least a dozen localities (Table 1). Whereas the upper surfaces of clay units are at many places irregular, there is no evidence of deep channeling. All these features suggest conditions that must have favored rapid deposition of materials derived from a relatively near source area by aggrading streams on broad alluvial plains. These meandering, possibly braided streams deposited coarse material in channel and bar deposits, while the finer material accumulated in overbank and backwater environments.

Ragsdale (1960:11) describes the lithology of the clays and conglomerates of the Oakville Formation as follows:

> The clay units of the Oakville for the most part are gray, calcareous, silty, and indurated. They fracture conchoidally. Typically, there is no evidence of bedding. Commonly, the clays contain nodules of caliche. In places caliche is visible as irregular streaks or bands disseminated through the clay. In other places caliche nodules occur along a horizontal line. Schultz, Tanner, and Harvey (1953) found caliche in nodules and horizontal zones associated with ancient soil profiles in the Oligocene of Nebraska.
>
> Some conglomeratic beds in the Oakville calclithites contain caliche balls, apparently reworked from the clays. Caliche cobbles as large as 10 cm in diameter are present in some places. The presence of caliche pebbles in Oakville conglomerates is evidence that caliche formed in the associated clays during the Miocene. This strongly suggests at least semi-arid conditions during deposition of the calclithite lithosome.

The Oakville Formation is composed of two units: The Lower Oakville Member, and the Moulton Sandstone Member. In Central Texas the Oakville Formation forms a prominent cuesta which is capped by the Moulton Sandstone Member. The scarp is dissected and discontinuous, in part the result of the discontinuous nature of the Moulton itself (Ragsdale, 1960). Especially prominent bluffs rise along the Colorado River in Fayette County near LaGrange and on the Brazos River in Washington County opposite Navasota, Grimes County. According to Renick (1936) the Lower Oakville Member is 60 to 100 feet thick and the Moulton Sandstone Member 20 to 60 feet thick from Grimes to Gonzales Counties. (For detailed field relations of the Oakville Formation, see Plummer, 1933; Renick, 1936; Weeks, 1945; and Ragsdale, 1960).

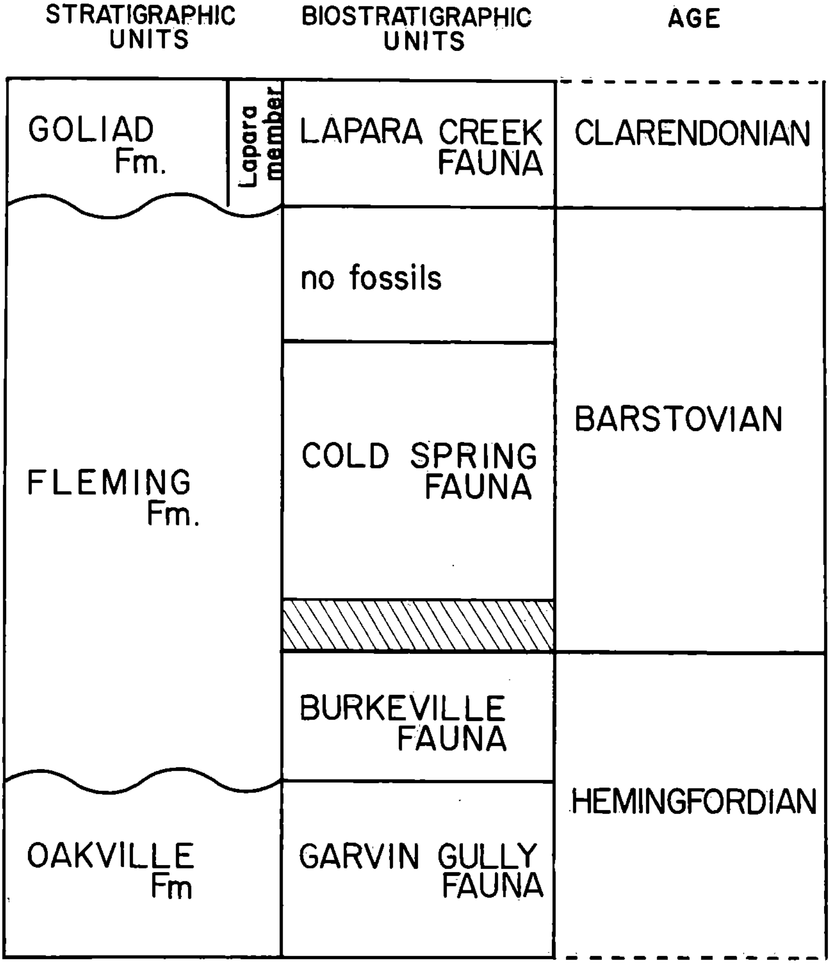

FIGURE 3. Diagrammatic east-west section from Washington County to Polk County to show distribution of vertebrate faunal localities in relation to present concept of stratigraphy (after Wilson, 1957).

The Fleming Formation is composed of approximately 75 per cent clay grading laterally and vertically into discontinuous interbeds of siltstone, sandstone, and conglomerate (Cassell, 1958). The Fleming Formation in Central Texas overlies the Moulton Sandstone Member. The Moulton is not recognized east of Grimes County (Wilson, 1957) and the Fleming Formation in that region lies on the greenish bentonitic clays of the Catahoula Formation (Fig. 3).

The basal unit of the Goliad Formation, the Lapara Member from which the Lapara Creek Fauna was collected, Plummer (1933) describes as follows:

> The member consists of conglomerate, cross-bedded sand, and limy clay. The conglomerate is composed of cobbles that range up to six inches in diameter, clay balls, sand, and much reworked material, such as bone fragments and bits of fossilized wood. The sand is coarse, friable, and contains clay pebbles, calcareous concretions, and lentils of red and green clay. The clay is irregularly bedded and contains pebbles and nodules similar to those in the conglomerate.

On the basis of a detailed petrographic study of the Oakville Formation, Ragsdale (1960:135) reconstructs a brief history of geologic events in the Texas Coastal Plain during the Miocene:

> Movements in the Balcones Fault Zone began to lift up the area now called the Edwards Plateau, increasing stream gradient. Under dry climatic conditions, fragments of Upper Cretaceous rock were carried down in the streams and deposited in channels. Volcanic ash was deposited through eolian action and by reworking older sediments. . . . The clays deposited in floodplains were almost entirely reworked from Upper Cretaceous rocks. The meandering, perhaps braided streams, choked with detritus, laid it down without cutting deep channels, thus building up a thick sequence of alluvial calclithites, the Oakville Formation.
>
> During the peak of calclithite deposition the landscape must have been flat across the coastal plain in the Texas region. The climate was that of savanna or steppe, alternating between wet and dry seasons . . . . During the dry seasons and in periods of drought, caliche formed in the clays. Occasionally, volcanic ash from the south may have fallen across the central part of this alluvial plain, but not far into the eastern part . . . . The detritus coming off the Edwards Plateau must have been deposited in a series of coalescing alluvial fans. Farther away from the uplifted calcareous highland, the proportion of calclithic material decreased . . . . To the east the drainage basins of streams bearing calclithic detritus were near streams from other regions which carried on calcareous sediment at all. At times, perhaps during wet cycles, streams from the calcareous highland deposited material farther to the east. During other periods, when less material came from the west, non-calcareous detritus spread westward.

Such a depositional history obviously creates a complex lithostratigraphic framework within which the relationships of the various vertebrate biostratigraphic units must be determined. This complexity is manifested in the various and often confused stratigraphic terminology applied to the rocks of this region (For a review of this problem, see Wilson, 1956).

Because of the above-mentioned close succession of fossil vertebrate assemblages contained in this rock sequence and its extreme importance in interregional correlation of the North American land mammal "stages," further, more detailed mapping and collecting in the Texas Coastal Plain section is certainly needed. Whereas the vertical and areal extent of the fossils presently known from this region already have been plotted grossly (Figs. 1 and 3), more precise determination should prove helpful in tracing more subtle evolutionary or zoogeographic events. Furthermore some areas and some parts of the section are at present inadequately sampled, as witnessed by the as yet undescribed Trinity River assemblage housed in the Frick Collection, which should fill part of the gap between the Burkeville and Cold Spring Faunas. (The protoceratids from this fauna are now being described by Patton and Taylor (MS).) Finally, several other groups of large mammals, e.g. peccaries, rhinoceroses, proboscidians, need to be studied carefully.

In addition to mentioning the work to be completed or refined, it should be emphasized that systematically (and ecologically) the Gulf Coast faunas are presently biased towards the larger mammals. Very few concerted attempts other than recent, reportedly successful ones by Bob Slaughter (pers. comm.) have been made to sample the smaller vertebrates in the Texas section. Better luck is reported from Tertiary deposits in Florida (Patton, 1969). It is hoped that future biostratigraphic studies in the Texas Coastal Plain will be directed towards gaining greater stratigraphic control for the existing assemblages and towards eliminating systematic and ecologic bias wherever possible.

DISTINGUISHING CHARACTERISTICS OF THE FAUNAS

GARVIN GULLY FAUNA (Table 2)

The oldest of the Texas coastal Plain vertebrate faunas, the Garvin Gully is characterized in part by the presence of several distinctive groups of artiodactyls that for the most part do not extend into any of the later faunas. *Oxydactylus benedentatus,* similar to the Upper Harrison (=Marsland) *O. longirostris,* is well-represented. *Nothokemas,* a camel that appears to be closely related to *Oxydactylus,* is represented by two species: *N. floridanus,* seemingly identical to

Table 2. FAUNAL LIST OF GARVIN GULLY MAMMALS

Taxon	Reference
LEPORIDAE	
Palaeolagus	Wood and Wood, 1937
CANIDAE	
Daphaenodon cf. *superbus*	Wilson, 1960
Amphicyon longiramus	" "
Cynodesmus iamonensis	" "
ENTELODONTIDAE	
Dinohyus hollandi	Wilson, 1957
MERYCOIDODONTIDAE	
?*Merychyus* sp.	This paper
TAYASSUIDAE	
Cynorca sociale	Woodburne (pers. comm.)
CAMELIDAE	
Oxydactylus benedentatus	This paper
Nothokemas floridanus	" "
Nothokemas hidalgensis n. sp.	" "
Australocamelus orarius n. gen. and n. sp.	" "
Floridatragulus nanus n. sp.	" "
PROTOCERATIDAE	
Prosynthetoceras texanus	This paper
CERVIDAE	
?*Longirostromeryx vigoratus*	This paper
RHINOCEROTIDAE	
Diceratherium	Quinn, 1955
EQUIDAE	
Hypohippus	Quinn, 1955
?*Merychippus*	" "
Anchitherium navasotae	" "
Parahippus blackbergi	" "
Hippodon vellicans	" "

Thomas Farm specimens, and a new species, *N. hidalgensis,* which is at present restricted to the Garvin Gully Fauna. Another camel also presently known only from the Texas Coastal Plain is referred to a new genus, *Australocamelus,* and is thought to lie at the base of an evolutionary series leading to *Aepycamelus* and *Hesperocamelus. Floridatragulus nanus* is the smallest and earliest known species of Floridatragulinae, now referred to the Camelidae. *Prosynthetoceras texanus* is the first member of an unusually well-documented evolutionary series extending from Garvin Gully to the Lapara Creek Fauna. An entelodont, *Dinohyus hollandi,* is also present. Carnivores are represented by *Daphaenodon, Amphicyon,* and *Cynodesmus.* Horses include several brachyodont genera described by Quinn (1955) and listed as *Anchitherium, Hypohippus, Archaeohippus,* ?*Merychippus,* and *Hippodon.*

BURKEVILLE FAUNA (Table 3)

Strata containing the Burkeville Fauna are the least productive of the Texas Coastal Plain sequence, and for that reason, the most poorly known.

The selenodont artiodactyl fauna of the Burkeville is characterized by the extreme rarity of specimens as well as taxa, a feature probably attributable to differential environmental sampling. The only camel present is the problematical genus, *Floridatragulus*. The absence of deer and hypertragulids we hope is only a temporary reflection of the paucity of material from this unit. *Prosynthetoceras texanus* from the Burkeville Fauna is larger and more advanced than *P. texanus* from Garvin Gully. I consider it to mark a recognizable step in the evolution of synthetocerines, and it may prove to be useful as a biostratigraphic and zoogeographic index. One canid, *Tomarctus canavus*, is recognized within this fauna (Wilson, 1960). Quinn (1955) characterizes the perissodactyls of the Burkeville Fauna by noting the lack of brachyodont horses, the appearance of hypsodont horses, and the presence of a large long-legged rhinoceros, *Aphelops meridianus*.

Table 3. FAUNAL LIST OF BURKEVILLE MAMMALS

Taxon	Reference
MYLAGAULIDAE	
Mylagulus	Quinn, 1955
CASTORIDAE	
Monosaulax	Quinn, 1955
PROCYONIDAE	
Edaphocyon pointblankensis	Wilson, 1960
CANIDAE	
Tomarctus canavus	Wilson, 1960
TAYASSUIDAE	
Dyseohyus	Quinn, 1955
FLORIDATRAGULIDAE	
Floridatragulus texanus	This paper
PROTOCERATIDAE	
Prosynthetoceras texanus	This paper
RHINOCEROTIDAE	
Aphelops meridianus	Quinn, 1955
EQUIDAE	
Hippodon gunteri	Quinn, 1955
?*Merychippus*	" "
Protohippus vetus	" "

COLD SPRING FAUNA (Table 4)

The Cold Spring Fauna is distinguished by the appearance of *Aepycamelus, Aelurodon, Teleoceras,* and *Gomphotherium* in the Coastal Plain. *Prosynthetoceras francisi* represents the most advanced species of that genus known to date. An oreodont from Cold Spring, *Ticholeptus rileyi,* Schultz and Falkenbach (1941a) described as resembling forms from the Lower Snake Creek. *Floridatragulus hesperus* n. sp. is larger and more advanced than the only other *Floridatragulus* species recognized, *F. texanus* n. sp. from the Burkeville Fauna.

Of the cervids *Barbouromeryx (Bouromeryx)* and *Longirostromeryx* appear most distinctive. *Longirostromeryx blicki* is identified

Table 4. FAUNAL LIST OF THE COLD SPRING MAMMALS

Taxon	Reference
MYLAGAULIDAE	
Mylagaulus	Quinn, 1955
CANIDAE	
Amphicyon longiramus	Wilson, 1960
Amphicyon pontoni	" "
Aelurodon francisi	" "
GOMPHOTHERIIDAE	
Gomphotherium	Quinn, 1955
MERYCOIDODONTIDAE	
Ticholeptus rileyi	Schultz & Falkenbach, 1941a
TAYASSUIDAE	
Hesperhys	Quinn, 1955
CAMELIDAE	
Aepycamelus sp.	This paper
Floridatragulus hesperus n. sp.	This paper
PROTOCERATIDAE	
Prosynthetoceras francisi	This paper
CERVIDAE	
Bouromeryx submilleri	This paper
Longirostromeryx blicki	" "
RHINOCEROTIDAE	
Diceratherium	Quinn, 1955
Teleoceras	" "
Peraceras	" "
EQUIDAE	
Hippodon sp.	Quinn, 1955
Merychippus	" "
Protohippus	" "
Pliohippus circulus	" "
Eoequus wilsoni	" "
Nannippus	" "
Hipparion or *Neohipparion*	" "
Calippus francisi	" "
Griphippus sp.	" "

on the basis of exceptionally well-preserved specimens and appears comparable to *L. blicki* material from New Mexico.

Wilson (1960) lists three carnivores from this unit: *Amphicyon longiramus, A. pontoni,* and *Aelurodon francisi.* Quinn (1955) believed that the Cold Spring horses are considerably more advanced than the Burkeville forms and recognizable by their more hypsodont teeth. He also lists three rhinoceroses: *Diceratherium, Teleoceras,* and a possible *Peraceras.*

LAPARA CREEK FAUNA (Table 5)

The youngest of the four Coastal Plains faunas, the Lapara Creek Fauna is also the richest in numbers and kinds of animals. The horses, camels, and deer are remarkably well-represented. *Protolabis* and *Megatylopus* make their first appearance in this fauna. They lived along with *Aepycamelus,* two species of *Procamelus,* and a new camel genus, *Nothotylopus.* Together they form one of the most abundant camel assemblages known to date. The oreodonts are represented by *Ustatochoerus profectus,* similar to *U. profectus* from the Lower Ash Hollow.

Isolated molars of *Synthetoceras tricornatus* are virtually identical to those of the type from the Clarendon beds and mark the last occurrence and culmination of that lineage in the Texas faunas. Among the cervids and antilocaprids, *Blastomeryx, Cranioceras, Ramoceros,* and an indeterminate merycodont are most distinctive. Carnivores include an amphicyonid, *Aelurodon taxoides, Leptocyon vafer,* and a canid (Wilson, 1960). Quinn (1955) describes the horses as all being fully hypsodont. *Gomphotherium, Prosthennops,* and *Teleoceras* are also present.

As Quinn (1955) and Wilson (pers. comm.) have stated, the Lapara Creek Fauna is separated from the Cold Spring Fauna by a relatively long lacuna. During the time represented by this lacuna immigrants, primarily from the High Plains, apparently arrived on the Texas Coastal Plain, while those forms already present advanced considerably over preceding forms. This is especially apparent among the artiodactyls. The assumption of migration into the Coastal Plain region is based on the first appearance of certain genera, e.g., *Protolabis* and *Megatylopus,* which appear to have undergone most of their evolution in the High Plains, and for which we have no evidence at present of any ancestors in any of the earlier Texas faunas. In the Lapara Creek 6 species of 5 genera of camels have replaced the 2 species of 2 genera known from the Cold Spring. The Lapara Creek *Synthetoceras tricornatus* is more advanced over

Prosynthetoceras francisi of the Cold Spring Fauna than *P. francisi* is over the preceding forms.

Table 5. FAUNAL LIST OF LAPARA CREEK MAMMALS

Taxon	Reference
LEPORIDAE	
?*Lepus*	Quinn, 1955
CANIDAE	
Amphicyonid	Wilson, 1960
Aelurodon taxoides	" "
Leptocyon vafer	" "
Canid	" "
GOMPHOTHERIIDAE	
Gomphotherium buckneri	Quinn, 1955
Gomphotherium cf. *productus*	" "
MERCOIDODONTIDAE	
Ustatochoerus profectus	Quinn, 1955
TAYASSUIDAE	
Prosthennops	Quinn, 1955
CAMELIDAE	
Procamelus occidentalis	This paper
Procamelus grandis	" "
Protolabis notiochorinos n. sp.	" "
Megatylopus primaevus n. sp.	" "
Nothotylopus camptognathus n. gen. et n. sp.	" "
Aepycamelus sp.	" "
PROTOCERATIDAE	
Synthetoceras tricornatus	This paper
CERVIDAE	
Blastomeryx elegans	This paper
Cranioceras clarendonensis	" "
ANTILOCAPRIDAE	
Ramoceras ramosus	This paper
Merycodont indet.	" "
RHINOCEROTIDAE	
Teleoceras proterus	Quinn, 1955
EQUIDAE	
Hypohippus	Quinn, 1955
Protohippus perditus	" "
Pliohippus supremus	" "
Dinohippus subvenus	" "
Hippotigris sellardsi	" "
Equus laparensis	" "
Equus sp.	" "
Neohipparion coloradense	" "
Hipparion	" "
Nannippus ingenuum	" "
Nannippus tehonensis	" "
Calippus anatinus	" "
Calippus optimus	" "
Calippus cf. *placidus*	" "
Astrohippus curtivalis	" "
Griphippus sp.	" "

Table 6. FAUNAL LIST OF TEXAS GULF COAST ARTIODACTYLS

	Garvin Gully Fauna	Burkeville Fauna	Cold Spring Fauna	Lapara Creek Fauna
ENTELODONTIDAE	*Dinohyus hollandi*			
MERYCOIDODONTIDAE	(?)*Merychyus benedentatus*		*Ticholeptus rileyi*	*Ustatochoerus profectus*
TAYASSUIDAE	*Cynorca sociale*	*Dyseohyus*	*Hesperhys*	*Prosthennops*
CAMELIDAE	*Oxydactylus* *Australocamelus orarius* n. gen. et n. sp. *Nothokemas floridanus* *Nothokemus hidalgensis* n. sp. *Floridatragulus nanus* n. sp.	*Floridatragulus texanus* n. sp.	*Aepycamelus* sp. *Floridatragulus hesperus* n. sp.	*Procamelus occidentalis* *Procamelus grandis* *Protolabis notiochorinos* n. sp. *Megatylopus primaevus* n. sp. *Nothotylopus camptognathus* n. gen. et n. sp. *Aepycamelus* sp.
PROTOCERATIDAE	*Prosynthetoceras texanus*	*Prosynthetoceras texanus*	*Prosynthetoceras francisi*	*Synthetoceras tricornatus*
CERVIDAE	(?)*Longirostromeryx vigoratus*		*Bouromeryx submilleri* *Longirostromeryx blicki*	*Blastomeryx elegans* *Cranioceras clarendonensis*
ANTILOCAPRIDAE				*Ramoceros ramosus* Merycodont indet.

SYSTEMATIC DESCRIPTIONS

TERMINOLOGY

Dental nomenclature used in this paper is a combination of that of Osborn (1907), of Loomis (1925), and of a topographic approach. Whenever cusp homologies are in doubt, the topographic method is employed, e.g. anterolingual cusp, posterolabial stylid. Multiple usages commonly encountered in artiodactyl tooth terminology are listed below.

Upper molars:
  paracone: paraselene = anterior crest
  metacone: metaselene = posterior crest
  protocone: protoselene = anterior crescent
  hypocone: hyposelene = posterior crescent = metaconule

Lower molars:
  metaconid: metaselenid = anterior crest
  entoconid: entoselenid = posterior crest
  protoconid: protoselenid = anterior crescent
  hypoconid: hyposelenid = posterior crescent

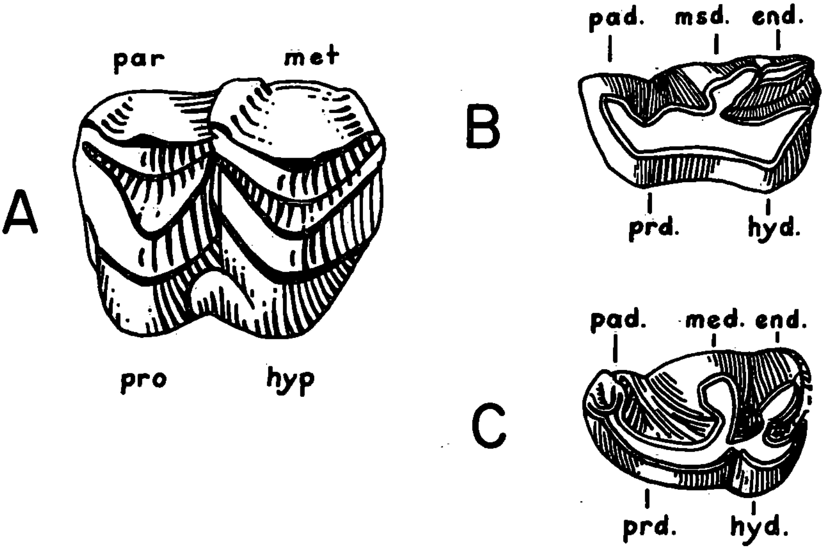

FIGURE 4. Artiodactyl tooth nomenclature. A. — Upper left molar, generalized. B. — Left P_4, camelid. C. — Left P_4, cervid. Abbreviations: par, paracone; met, metacone; pro, protocone; hyp, hypocone; pad, paraconid; end, entoconid; prd, protoconid; hyd, hypoconid; med, metaconid.

Nomenclature of molars and premolars is illustrated in Figure 4. All measurements, unless otherwise indicated, are given in millimeters.

Formal listing of synonyms in the systematic description is restricted to those species that are synonymized in this paper. The heading "Occurrence" refers only to distribution within the Texas Coastal Plain.

Order ARTIODACTYLA Owen, 1848

Suborder TYLOPODA Illiger, 1811

Family CAMELIDAE Gray, 1821

With the exception of the horses, the camels are the most abundantly represented group of fossil vertebrates in the Texas Coastal Plain both in terms of fossil specimens and in taxa. Their local abundance in Texas and their widespread distribution in fossil deposits of western North America make them useful for regional biostratigraphic correlation, for determining past zoogeographic patterns, and, in part, for reconstructing the paleoecology of the areas in which they occur. It is unfortunate that several of the North American Tertiary camel genera presently recognized are in need of major revision. Some, like *Oxydactylus*, are not unitary taxa but rather may prove to comprise several groups of possible generic rank. Others, like *Miolabis*, *Protolabis*, and *Pliauchenia*, require redefinition or revision in the light of new diagnostic material. In any event, the major part of the difficulty in fossil identification and in biostratigraphic correlation between the various fossil provinces lies in the uncertain and sometimes confused taxonomy of these "classical" Western genera. Six genera of the Gulf Coast camels are well-known from faunas of the Great Plains and Pacific Coast regions, while two, *Nothokemas* and *Floridatragulus*, are so far restricted to the Gulf Coastal Plain. In addition to these, two genera, *Australocamelus* and *Nothotylopus*, are described. The former genus appears to be closely related to the two advanced giraffe-camels, *Aepycamelus* and *Hesperocamelus*, whereas the latter belongs to the *Protalabis-Pliauchenia* lineage.

Subfamily AEPYCAMELINAE Webb, 1965

Oxydactylus Peterson, 1904

Simpson (1932: 36) points out that the genus *Oxydactylus* is based on, and confidently identifiable only by, a combination of tooth and limb characters. *Oxydactylus* is characterized by a slender, relatively deep mandible, unreduced premolars, short diastemata, and elongate, slender, uncoossified metapodials. Of all the recognizable camel material from the Garvin Gully Fauna, only five specimens do not fit this description, and they clearly belong to distinctly different taxa.

Two size groups of oxydactyline metapodials are present in the Garvin Gully Fauna. The large-sized group is assigned to *O. benedentatus* (Hay), and the smaller-sized uncoossified metapodials are tentatively referred to *Australocamelus orarius* n. gen. and sp. Until associated teeth and metapodials are confidently known for this new genus and also for the problematical genus *Nothokemas*, identification of camel metapodials from the Garvin Gully Fauna will remain at best uncertain.

Metapodials designed by Hay (1924) as the type of *Protolabis francisi* are herein referred to *Oxydactylus benedentatus* (see discussion of *O. benedentatus*).

Oxydactylus benedentatus (Hay) 1924
Figures 5, 6, 8B. Table 7

Procamelus benedentatus Hay, 1924, p. 12, pl. V, figs. 1, 2.
Procamelus concerptus Hay, 1924, p. 11, pl. IV, figs. 1, 2.
Protolabis francisi Hay, 1924, p. 13, pl. VI, figs. 1-3 (in part).

TYPE. – TAMU 2382, a right mandible with P_1-M_3.

TYPE LOCALITY. – Garvin Farm, near Navasota, Grimes County, Texas.

OCCURRENCE. – Garvin Gully Fauna.

REFERRED MATERIAL. – TAMU 2383, a juvenile left mandible (type of *O. concerptus*); TAMU 2464, right mandible with P_1-M_3 and alveoli for I_1-I_3 /C; TAMU unnumb., left mandible with M_1-M_3; TAMU 2465, right mandible with P_1-M_3; TAMU 2466, right mandible with P_1-M_3; TAMU 2526A, 2526B, B, C, D, 2391, all metapodials.

DESCRIPTION. – TAMU specimens listed above and assigned to *Oxydactylus benedentatus* agree closely in size and details of morphology with *O. longirostris* (Peterson, 1911) from the Upper Harrison, or Marsland, of Sioux County, Nebraska. The lower molars of *O. benedentatus* are brachyodont, and the lower premolars are unreduced. The stylids of the lower molars are only faintly visible. The mandible is characteristically thin and deep (Table 7), becoming more constricted anterior to P_2. No other known Gulf Coast camels exhibit this thinness and depth of mandible. The constriction anterior to P_2 fades below and just anterior to P_1 as the jaw deepens again at the symphysis. The diastema between P_2 and P_1 is slightly longer than that between P_1 and /C. In *O. longipes* the diastemata are equal in length, whereas in *O. brachyodontus* the diastema between P_2 and P_1 is longer than that between P_1 and /C. There is virtually no diastema between /C and I_3 in *O. benedentatus.* The posterior edge of the anterior mental foramen falls directly below the anterior border of P_1; the posterior mental foramen is situated below the middle of M_1. The posteroinferior border of the mandible projects slightly downward as it expands to accommodate the large masseter muscle. The ascending ramus projects up from the mandible at about a 60 degree angle with the alveolar border. This is a consistently lower angle than is found in any other genus of Gulf Coast camel. The pronounced but simple angular process is situated at a point on a line level with the mandibular foramen and the occlusal surface of the talonid of M_3. The condyloid process occurs roughly midway between the angular process and the tip of the tall and thin coronoid process.

Discussion. – The tooth row of *O. benedentatus* is 10-15 per cent longer than that of *O. brachyodontus* (Peterson, 1904) from the

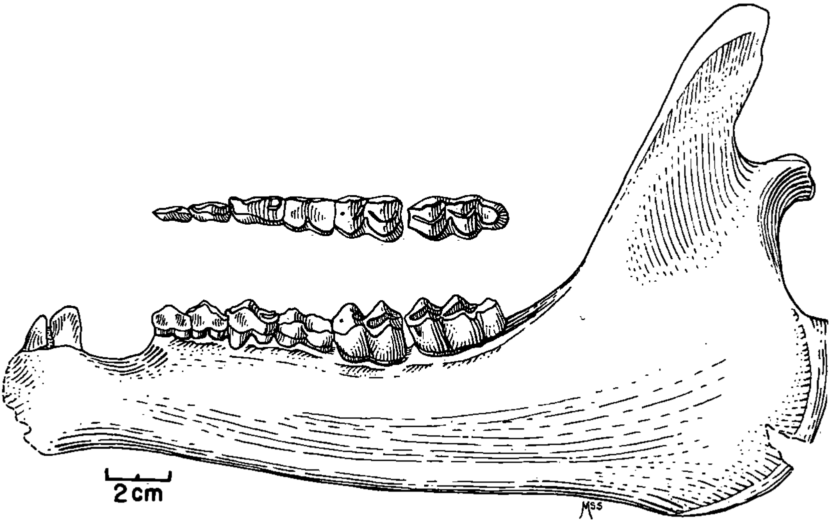

Figure 5. *Oxydactylus benedentatus* (TAMU 2465); left ramus, labial view I_1-M_3 and occlusal view P_2-M_3.

upper Harrison (=Marsland) beds of Nebraska, and although it approximates the size of *O. longipes* (Peterson, 1904), also from the upper Harrison, it differs from that species in having longer (6-15 per cent) premolars, as well as in the absence of a diastema between /C and I_3. *O. benedentatus* most closely resembles *O. longirostris* Peterson, but departs from it in having a more pronounced anterolingual fold in P_2 and P_3, and again in the absence of the /C-I_3 diastema. In dimensions of metapodials and radius-ulna, *O. benedentatus* occupies a position roughly intermediate between *O. longipes* and *O. longirostris*. Difficulty in comparison of the limb dimensions arises from lack of information on how Peterson took certain measurements.

Although the criteria for species differentiation enumerated above seem real enough now, the addition of more material may show these differences to be merely individual or sexual variation and not specific divergence.

Two specimens herein referred to *O. benedentatus* were originally designed by Hay (1924) as type specimens for two proposed species of *Procamelus*. TAMU 2382 served as the type of *P. benedentatus*

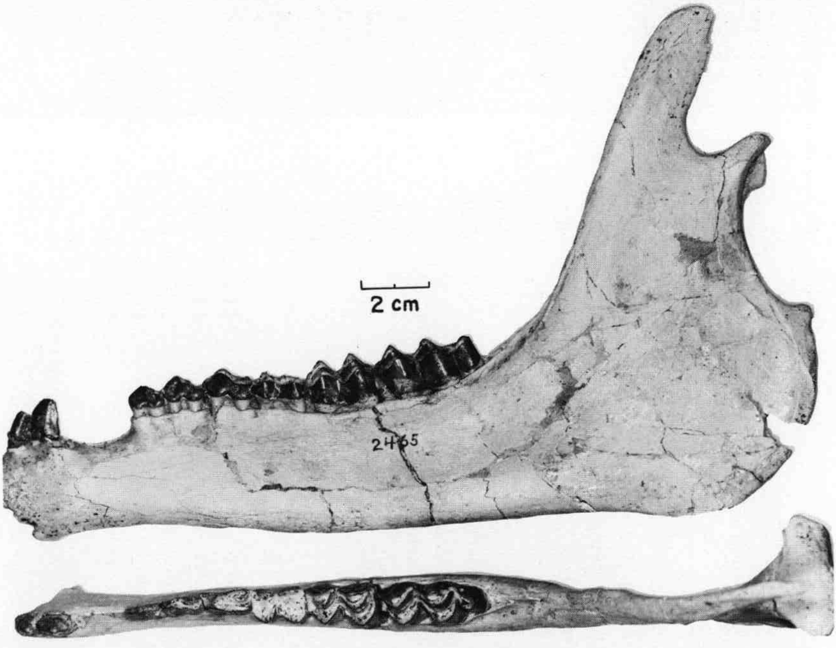

FIGURE 6. *Oxydactylus benedentatus* (TAMU 2465); left ramus, labial and occlusal views.

Table 7. MEASUREMENTS OF *Oxydactylus benedentatus*

Lower jaw	TAMU 2465	TAMU 2466	TAMU 2464	TAMU 2382 (Type)	TAMU 2383
Height vertical ramus	158.5	....	....	....	....
Condyle to ang. process	41.0	....	....	....	....
Condyle to cor. process	45.0	....	....	....	....
Depth jaw at M_3	42.2	39.5	45.0	....	....
Depth at M_2	38.3	36.5	41.9	42.5	....
Depth at M_1	39.0	36.1	41.1	38.5[1]	....
Depth at P_2-P_1 diastema	27.0	23.1	27.5	26.1	....
Length /C-P_1 diastema	....	....	22.1	16.4[1]	....
Length P_1-P_2 diastema	22.0	23.0	26.1	22.2	....
P_2-P_4	40.0	40.2	....	39.0	....
P_3-P_4	25.0	30.5	31.3	....	....
M_1-M_3	71.0	75.5	76.3	81.0[1]	....
P_2-M_3	110.5	114.2	119.0	119.5	....
P_3-M_3					
P_2, length × width	11.7 × 5.1	11.5 × 5.5[1]	....	11.5 × 5.4	....
P_3, length × width	14.2 × 6.0	15.0[1]	15.6 × 7.2	.... 7.0	....
P_4, length × width	16.6 × 8.0	16.5 × 9.0[1]	18.1 × 9.2	17.7 × 10.1	....
M_1, length × width	17.5 × 11.5	19.5 × 12.1[1]	19.1 × 13.5	21.0[1] × 14.2	22.3 × 13.6
M_2, length × width	22.0 × 14.0	23.2 × 14.5	23.7 × 15.7	24.1 × 17.1	24.9 × 14.5
M_3, length × width	21.7 × 13.1	32.4 × 15.5	35.3 × 15.9	36.1 × 15.7	....

[1] Approximate

while TAMU 2383, a juvenile, was designated the type of *P. concerptus*. *P. benedentatus* is clearly not assignable to *Procamelus*, but in fact, as the foregoing description indicates, should be included with the genus *Oxydactylus*. The size, depth of mandible, and the morphology of the premolars of *P. concerptus* corresponds with what would be expected in a juvenile *O. benedentatus* and *concerptus* is therefore included in that species. Because I believe the above-mentioned differences in P_2 and P_3 and in the /-I_3 diastema between *O. longirostris* and *O. benedentatus* are presently sufficient to justify separation at the species level, I have retained Hay's species, but include it in the genus *Oxydactylus* (Patton, 1967).

The relatively long, slender uncoossified metacarpals (TAMU 2391) from the Garvin Gully Fauna Hay (1924) designated as the type of *Protolabis francisi* I consider more properly placed in the genus *Oxydactylus*. *Protolabis* metacarpals, while generally uncoossifiied, are usually shorter and stouter than those of *Oxydactylus*. The only *Protolabis* metacarpals exhibiting a slenderness comparable to those of *Oxydactylus* belong to *P. angustidens* cope (description and measurements given by Matthew, 1901:434) from the Barstovian Pawnee Creek beds of Colorado. The length of the *P. angustidens* metacarpal (AMNH 9100) is given as 284 mm; the length of the Garvin Gully metacarpal is 312 mm. From both a morphological and stratigraphic standpoint I think it more reasonable to regard these metacarpals as belonging to *Oxydactylus* than to *Protolabis*. But as mentioned earlier, nothing is presently known of the metacarpals of the associated *Oxydactylus*-like genus, *Nothokemas*, and until such information is available, this designation will remain necessarily uncertain.

Nothokemas White, 1947

The systematic position of *Nothokemas* is poorly understood. White (1947) originally based this genus on characters of a crushed skull, a right maxilla with P^2-M^3, and several mandibles with partially preserved dentitions. This material was not definitely associated. The skull (MCZ 4322) of the type material I believe to belong rather to the genus *Floridatragulus*, hence those generic characters of *Nothokemas* based on the skull and upper dentition should be disregarded pending further study of confidently associated skulls and jaws. White (1947) tentatively referred *Nothokemas* to an uncertain position within the Hypertraguloidea and erected a new family, the Nothokemadidae, to contain it. From the characters of the mandible and lower dentition alone, I can see no reason for separating this genus from the camels. The previously described resemblance of *Nothokemas* and *Oxydactylus* seems too great to attribute entirely to convergence. Those characters of *Nothokemas* shared by members of the Hypertraguloidea, e.g. intercolumnar tubercles, are not exclusive to that group but may be considered archaic traits retained by several disparate artiodactyl phyla, including the camels. The increase in similarity between the tylopods and hypertraguloids as we look farther back into geologic time is well-documented (Matthew, 1905; Scott, 1940; Colbert, 1941; Simpson, 1945). These divergent groups are supposedly recognizable entities as far back as the Late Eocene, but here we find in the Early and Middle Miocene of the Gulf Coastal Plain at least two forms (*Nothokemas* and *Floridatragulus*) whose placement in either group involves some uncertainty. Perhaps *Nothokemas* represents a line not too distantly divergent from *Oxydactylus*, and which, while retaining a few relatively primitive characters, paralleled the course of evolution of one of the larger camel branches, the Aepycamelinae. The extent of the roles played by parallelism, convergence, and/or direct genetic relationship among these forms and the better known groups with which they are associated remains as yet unknown. Until such knowledge is forth-

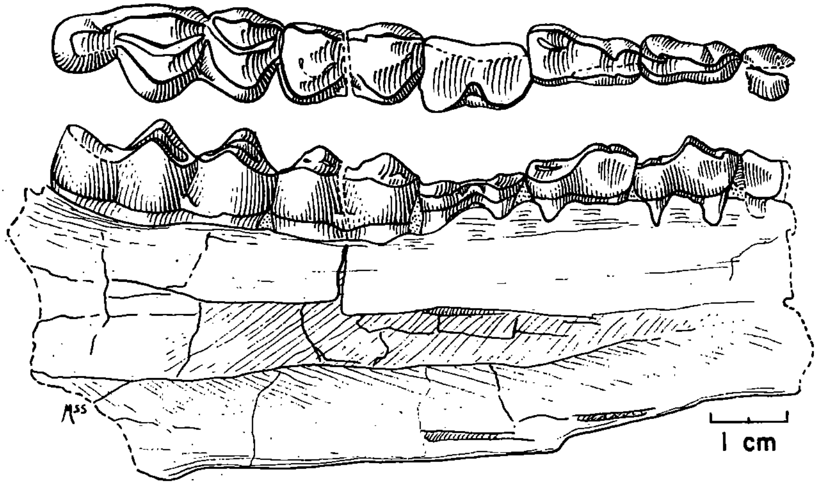

FIGURE 7. *Nothokemas floridanus* (TAMU unnumb.); right ramus, labial and occlusal views of P_2-M_3.

coming, the evidence now available seems to warrant the inclusion of *Nothokemas* in the Camelidae.

As the type species for *Nothokemas* White (1947) designated *Nothokemas grandis,* first described by him (1940) as *Paratylopus grandis. N. grandis* White and *Oxydactylus floridanus* Simpson (1932), also from the Thomas Farm, are inseparable and should be combined in a single species. For reasons described below [and earlier, Patton, 1966(67)] these specimens are assigned to *Nothokemas* and, by priority, assume the taxonomic designation *Nothokemas floridanus.*

Nothokemas floridanus (Simpson)

Figures 7, 8A, Table 8

Oxydactylus floridanus Simpson, 1932, p. 35, figs. 20, 21.
Paratylopus grandis White, 1940, p. 33, pl. V, figs. A, B.
Nothokemas grandis (White), White, 1947, p. 508, figs. 5, 6.

TYPE. — FSGS V-5247, part of a right maxilla with P^2-M^3; paratype-FSGS V-5238, a right ramus with P_3-M_3.

TYPE. — Thomas Farm, Gilchrist County, Florida.

OCCURRENCE. — Garvin Gully Fauna.

REFERRED MATERIAL. — TAMU unnumb., partial right ramus with P_2(broken)-M_3; UTBEG 40262-1, partial right ramus with P_3(roots)-M_3.

DESCRIPTION. — Among the camel remains from the Garvin Gully Fauna are two incomplete specimens that I consider belong to *Nothokemas.* The Texas specimens compare very closely with the Florida Thomas Farm material and are assigned to the same species.

In the unreduced condition of the premolars and the configuration of both molars and premolars, the lower jaw of *Nothokemas* is remarkably similar to *Oxydactylus.* As in *Oxydactylus,* the body of the mandible is deep and thin, but the diastema anterior to P_2 is considerably longer. The mandible in this region is much more attenuated than in *Oxydactylus.* Both genera are brachyodont and both display a relative elongation of the molars. In a specimen (MCZ 4323) referred by White (1947) to *N. grandis,* just anterior to the mental foramen is what appears to be an alveolus for a large canine-like tooth. In a smaller and slightly dissimilar specimen (UTBEG 40067-10), assigned to *Nothokemas hidalgensis* n. sp., a large caniniform tooth is present. Because of its position well anterior to the anterior mental foramen and the posterior border of the

Table 8. MEASUREMENTS OF *Nothokemas floridanus*

Measurement	FSGS (Type) V-5238	UTBEG 40262-1	TAMU unnumb.
Depth jaw at M_1		31.6	30.2[1]
Depth jaw at P_4		28.4	
P_2-M_3	100.0		98.0[1]
P_2-P_4	36.0[1]	37.0[1]	39.0[1]
P_3-P_4		27.3	27.3
M_1-M_3	65.0	61.0	61.3
P_3-M_3		89.0	87.5
P_2, length × width	11.5[1] × 5.0[1]		
P_3, length × width	12.5 × 6.0	13.2 × 6.3	13.2 × 6.0
P_4, length × width	13.5 × 7.5	15.2 × 8.0	14.1 × 7.46
M_1, length × width	14.5 × 11.0	16.0 × 12.8	14.4 × 9.7
M_2, length × width	20.5 × 13.5	19.2 × 13.0	18.9 × 11.0
M_3, length × width	32.0 × 14.5	28.0 × 13.0	28.9 × 12.0

[1] Approximate

symphysis, I believe this tooth to be the true canine. Loss of P_1 therefore should be included in the generic diagnosis of *Nothokemas.*

The lower molars of *Nothokemas* differ from *Oxydactylus* in the presence of an intercolumnar tubercle between the protoconid and hypoconid. The posterior edge of the entoconid of M_3 overlaps the hypoconulid, giving the appearance of the beginning of an "outer lobe" on the talonid (White, 1947:511).

Parenthetically the division of the talonid described in *Floridatragulus* on page 000 of this paper appears to represent a greater development of this type of posterior extension of the entoconid.

The anterolingual fold of P_3 and P_4 is distinctly more pronounced in *Nothokemas* than in *Oxydactylus.* The posterolingual cusp (entoconid?) of P_2 and P_3 is rather strongly expressed in *Nothokemas;* in *Oxydactylus* it is distinct on three of the four specimens with P_3 intact, but it has virtually disappeared from P_2, the posterolabial cusp (hypoconid?) being the only posterior cusp remaining.

In summary, the long diastema anterior to P_2, loss of P_1, the posterior extension of the entoconid on M_3, the presence of intercolumnar tubercles on the lower molars, and the greater development of the posterolingual cusp on P_2 and P_3 all serve to separate *Nothokemas* from associated *Oxydactylus.*

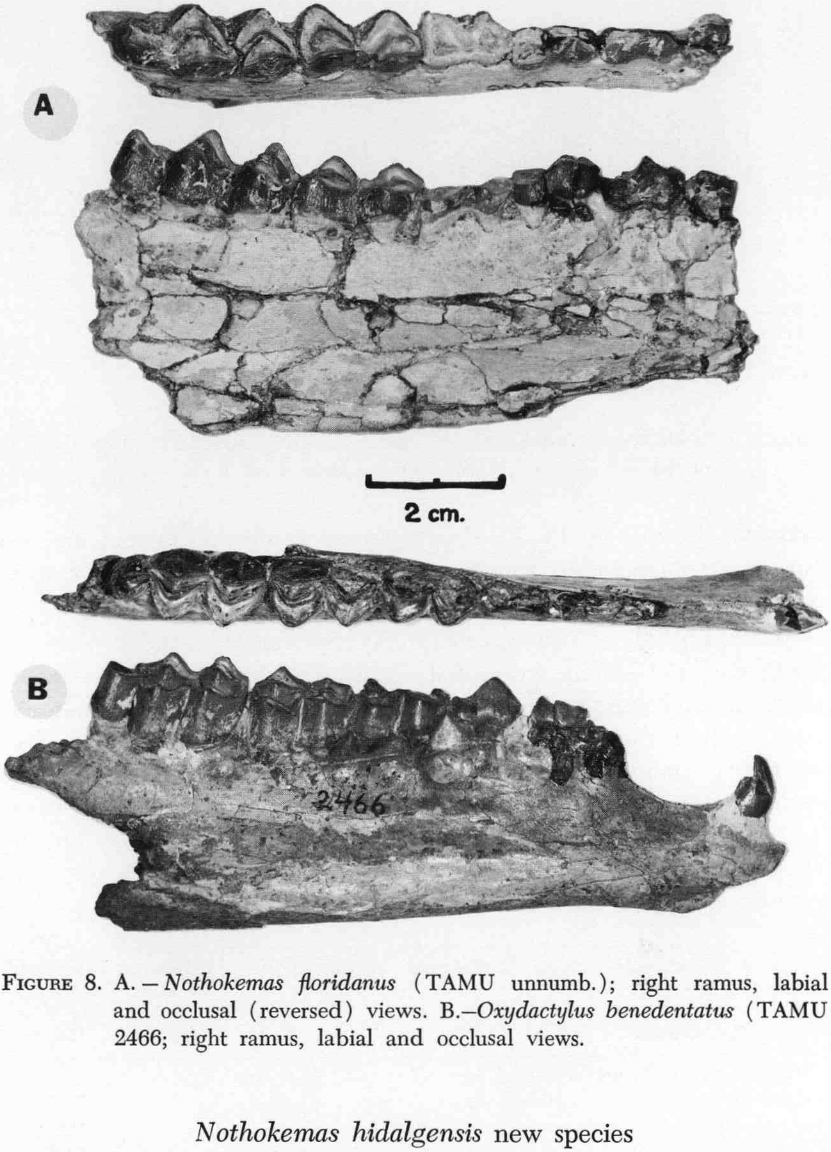

FIGURE 8. A. — *Nothokemas floridanus* (TAMU unnumb.); right ramus, labial and occlusal (reversed) views. B.—*Oxydactylus benedentatus* (TAMU 2466; right ramus, labial and occlusal views.

Nothokemas hidalgensis new species

Figures 9, 10, Table 9

TYPE. — UTBEG 40067-10, a partial right mandible with /C-M_3.

TYPE LOCALITY. — Hidalgo Bluff, Washington County, Texas.

OCCURRENCE. — Garvin Gully Fauna.

ETYMOLOGY. — Refers to Hidalgo Bluff, the type locality.

DIAGNOSIS. — About 20 per cent smaller than *N. floridanus;* long

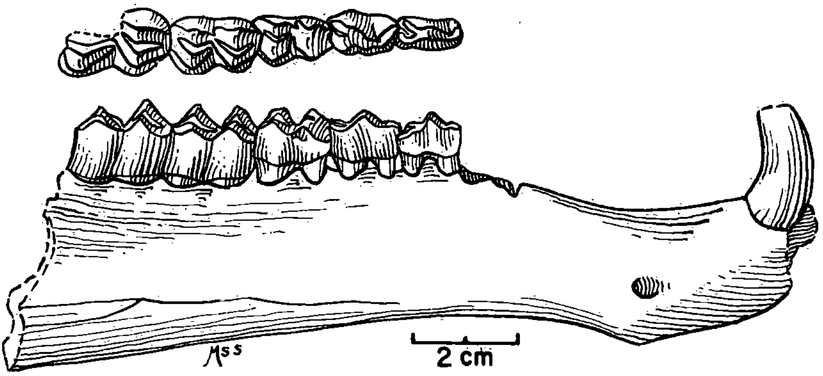

FIGURE 9. *Nothokemas hidalgensis* n. sp. (UTBEG 40067-10, Type); right ramus, labial view /C-M_3 and occlusal view P_3-M_3.

diastema anterior to P_2; P_1 absent, lower canine prominent and recurved; premolars more compressed anteroposteriorly than in *N. floridanus.*

DESCRIPTION. – This specimen is considerably smaller than *N. floridanus* and differs from that species in having a less slender diastema and symphysial region. The anterior mental foramen occurs at about the middle of the /C-P_2, diastema, whereas in *N. floridanus* the foramen is just posterior to the strongly recurved and oval canine. This tooth was apparently not so large in *N. floridanus.* P_3 and P_4 are proportionately as long as those in *N. floridanus,* but are of greater relative width; crests and crescents of molars are very regular and symmetrical.

Table 9. MEASUREMENTS ON TEETH AND MANDIBLE OF *Nothokemas hidalgensis*

Measurement	UTBEG 40067-10 (Type)
Depth of ramus below center of M_1	31.2
Depth of ramus below center of P_4	28.2
Length, P_2-M_3	90.0[1]
Length, P_3-P_4	24.3
Length, P_3-M_3	78.0[1]
Length, M_1-M_3	54.0[1]
P_3, length × width	12.2 × 6.0
P_4, length × width	13.0 × 7.2
M_1, length × width	15.0 × 10.0
M_2, length × width	17.0 × 10.9
M_3, length × width	25.0[1]

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[1] Approximate

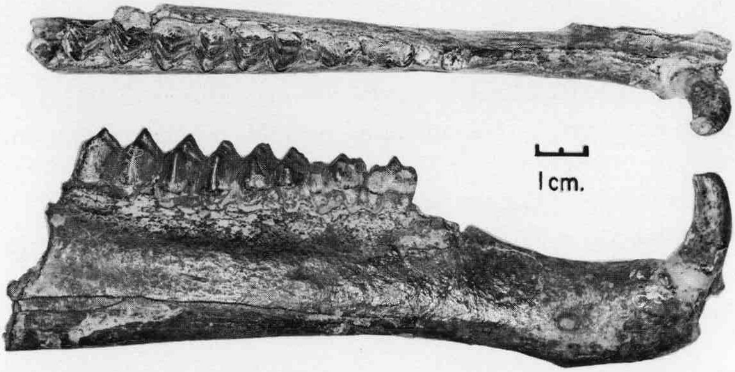

FIGURE 10. *Nothokemas hidalgensis* n. sp. (UTBEG 40067-10, Type); right ramus, labial and occlusal views.

Australocamelus new genus

A well-preserved but incomplete mandible from the type locality of the Garvin Gully Fauna is thought to represent an important link between *Oxydactylus* and the giraffe-camels of the Middle and Late Miocene and Early Pliocene of western North America. Although at present poorly known, the relatively primitive *Australocamelus* may provide a structural ancestor for the succeeding and more advanced genera, *Hesperocamelus* and *Aepycamelus.* Because this genus is now recognized on the basis of a single specimen, generic characteristics for the present correspond with those of the type species, *A. orarius.*

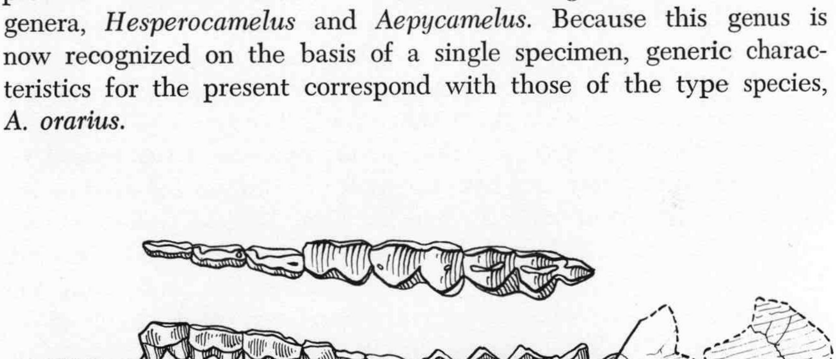

FIGURE 11. *Australocamelus orarius* n. gen. et sp. (TAMU 2466A, Type); left ramus, labial and occlusal views P_2-M_3.

Australocamelus orarius new species

Figures 11, 12, Table 10

TYPE. – TAMU 2466A, a partial left mandible with P_2-M_3.

TYPE LOCALITY. – Garvin Farm, near Navasota, Grimes County, Texas.

OCCURRENCE. – Garvin Gully Fauna.

REFERRED MATERIAL. – TAMU 2522, 2524, 2525, 2527E, and 2527F, all metapodials.

ETYMOLOGY. – *australis* = L. southern; *camelus* = L. camel; *orarius* = L. of the coast.

DIAGNOSIS. – A small species of camel, about the size of *Oxydactylus campestris* (Cook, 1909), but with a slender and vertically shallow mandible. Premolars unreduced, molars subhypsodont, and both molars and premolars laterally compressed and elongate all of which distinguish it from species of *Oxydactylus*.

DESCRIPTION. – This long, slender mandible is in striking contrast to the rather robust, deep-jawed camel it is associated with. While the body of the mandible is never deep, it becomes vertically constricted at the P_1-P_2 diastema. Just posterior to P_1 alveolus, the inferior border of the jaw deepens again, marking the posterior border of the symphsis. Because the anterior portion of the jaw is missing, the length of the symphysial region is impossible to estimate. Between the deepest part of the symphysis and P_1 alveolus occurs a large foramen, the anterior mental foramen. The posterior mental foramen is situated below the middle of M_1. The two small divergent alveoli at the P_1 position are thought to represent a two-rooted P_1. P_2 is long and narrow and has two small but distinct folds: anterointernal and posterointernal. P_3 and P_4 both have a well-developed anterointernal fold and a posterior enamel lake. P_4 is wedge-shaped; P_2 and P_3 tend to be rectangular. The molars are well worn, but still reveal a relative increase in hypsodonty over other camels of the same fauna. The lower molars are laterally compressed and elongated, and the external crescents (protoconid, hypoconid) form a rather wide V. The metaconid slightly overlaps the hypoconulid on M_3. There is no trace of an accessory pillar on any of the lower molars. A distinct film of cement covers the basal part of each tooth from P_3 to M_3, but is present to a greater extent on M_1 and M_2.

DISCUSSION. – *Australocamelus* differs markedly from other known groups of Early Miocene camels. It resembles *Oxydactylus* in

Table 10. MEASUREMENTS OF TEETH AND MANDIBLE OF THE TYPE OF *Australocamelus orarius*

Measurements	TAMU 2466A
Depth of ramus below center of M_3	26.1
Depth of ramus below center of M_1	21.1
Length of P_1-P_2 diastema	15.6
Length, P_2-M_3	113.2
Length, P_2-P_4	36.9
Length, M_1-M_3	67.3
P_2, length × width	11.1 × 4.0
P_3, length × width	12.8 × 4.8
P_4, length × width	14.6 × 6.3
M_1, length × width	17.5 × 9.6
M_2, length × width	21.7 × 10.6
M_3, length × width	30.0 × 10.7

the lack of reduction of lower premolars and in the short P_1-P_2 diastema, but differs from that genus in the more elongate, almost cervoid dimensions of the mandibles, as well as in the striking lateral compression of the molars and premolars. The characters that serve to distinguish *Australocamelus* from *Oxydactylus* are the very ones that suggest a relationship with the later giraffe-camels, including the Late Miocene and Early Pliocene genera *Aepycamelus* (= *Alticamelus*) and *Hesperocamelus*. Matthew (unpubl. MS) thus characterizes the giraffe-camels: "Compared with contemporary camels of the *Protolabis-Procamelus-Pliauchenia* series it is distinguishable by conservatism in premolar reduction, small head and much elongate limbs, and progressiveness in foot consolidation." Although no skull or metapodials of *Australocamelus* are known, the small and slender mandible, the short diastema, nonreduction of premolars, and lateral compression of molars and premolars, clearly indicate its affinity with the aepycamelines.

The discovery and description of the genus *Hesperocamelus* from the Chalk Spring beds of Nevada (MacDonald, 1949) led to the division of the later giraffe-camels into two groups (MacDonald, 1956): *Aepycamelus*, including the species *A. giraffinus*, *A. procerus*, *A. priscus*, *A. leptocolon*, *A. stocki*, and *A. bradyi*; and *Hesperocamelus*, including *H. stylodon* and *H. alexandrae*. The primary reason for this separation appears to be the small size and relative primitiveness (including the retention of two upper incisors) of *Hesperocamelus*, and the presumed contemporaneity (Clarendonian) of *Hesperocamelus* with more advanced species of *Aepycamelus*. Although MacDonald (1949) originally described *Hesperocamelus* from the

Clarendonian section of the Chalk Spring beds, he later (1964) extended the range of *Hesperocamelus* into the Barstovian on the basis of a specimen *(H. stylodon)* collected from the Raine Ranch Formation at Camp Creek, Nevada, and rejected the suggestion that the Chalk Spring specimen came from a level low enough in that section to warrant its inclusion in the Barstovian. In any event, the primitive condition of *Hesperocamelus,* its similarity to early *Aepycamelus,* and its stratigraphic position may justify its consideration as an evolutionary stage in the evolution of *Aepycamelus,* rather than as representing a separate lineage.

Matthew (unpubl. MS) considered *Oxydactylus longipes* Peterson from early Hemingfordian beds of Sioux County, Nebraska to be ancestral to the species of *Alticamelus* (now *Aepycamelus*). MacDonald (1949) envisioned *O. longipes* as the common ancestor of both *Alticamelus* and *Hesperocamelus.* A comparison of *O. longipes* with the earliest known species of *Aepycamelus,* i.e. *A. priscus,* from the Sheep Creek (this comparison is made with specimen AMNH 18869; the dentition of the type of *A. priscus* is limited to some broken premolars) suggests that *O. longipes* may be too conservative in most dental and mandibular characters to serve as a structural ancestor for *A. priscus,* whereas *Australocamelus orarius,* although much smaller, is very close in elongation and lateral compression of molars and premolars. Unfortunately there are no published records of the lower jaw of *Hesperocamelus.* Extrapolation of skull and mandible characters of *H. stylodon* and *H. alexandrae* suggest a rather close relationship between these species and *Australocamelus.* Structurally the three species can be arranged in a progressive series from *A.*

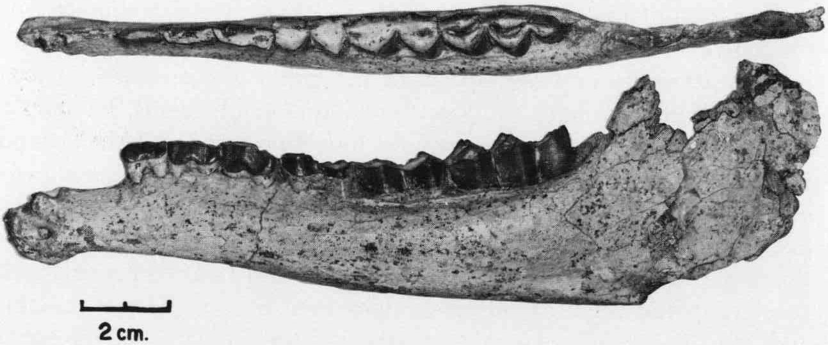

FIGURE 12. *Australocamelus orarius* n. gen. et sp. (TAMU 2466A, Type); left ramus, labial and occlusal views.

orarius through *H. stylodon* to *H. alexandrae.*

Until more is known of *Australocamelus*, its affinities with *Aepycamelus* and *Hesperocamelus* remain obscure. It apparently is closer to *Hesperocamelus*, but whether that genus is a structural antecendent of *Aepycamelus* or an early offshoot of that lineage is not yet known. However, because of its relative primitiveness and its low stratigraphic occurrence, *Australocamelus* clearly lies near the critical point of divergence between *Oxydactylus* on the one hand and *Aepycamelus* and *Hesperocamelus* on the other.

Aepycamelus MacDonald, 1956

Aepycamelus sp.

Figure 13

Occurrence. — Cold Spring and Lapara Creek Faunas.

Referred Material. — UTBEG 31183-46, metacarpus: 31183-33, radius-ulna; UTBEG 31081-561, metatarsus.

Description. — Several limb elements from the Texas Coastal Plain faunas are referred to the genus *Aepycamelus*. A right radius-ulna (UTBEG 31183-33) and a right metacarpus (UTBEG 31183-46) collected from the Smith Ranch, Polk County, Texas, and belonging to the Cold Spring Fauna, are about 15 per cent larger than *Aepycamelus alexandrae* (Davidson) from the Barstow beds and approximately 26 per cent smaller than *A. giraffinus* (Matthew) from the Pawnee Creeek. The radius-ulna, exclusive of the olecranon, measures 560 mm; the metacarpus measures 460 mm. Both dimensions fall within the range of variation for these elements of (?) *A. stocki* from the Late Barstovian Tonopah Fauna of Nevada (Henshaw, 1942).

A single metatarsus (UTBEG 31081-561) from the Lapara Creek Fauna reaches a length of 720 mm, 15 per cent longer than the metatarsus of *A. giraffinus* from the Pawnee Creek beds. The Lapara Creek specimen corresponds in size to *A. bradyi* from the Clarendonian Truckee Formation of Nevada (MacDonald, 1956). Although no metapodial measurements of *A. bradyi* are published, the Truckee species is consistently larger in all other known dimensions than *A. giraffinus* and represents the largest described species of *Aepycamelus* presently known.

Subfamily CAMELINAE Zittel, 1893

Protolabis Cope, 1876

The genus *Protolabis* is recognized in the Lapara Creek Fauna on the basis of a single mandible with both rami preserved and with

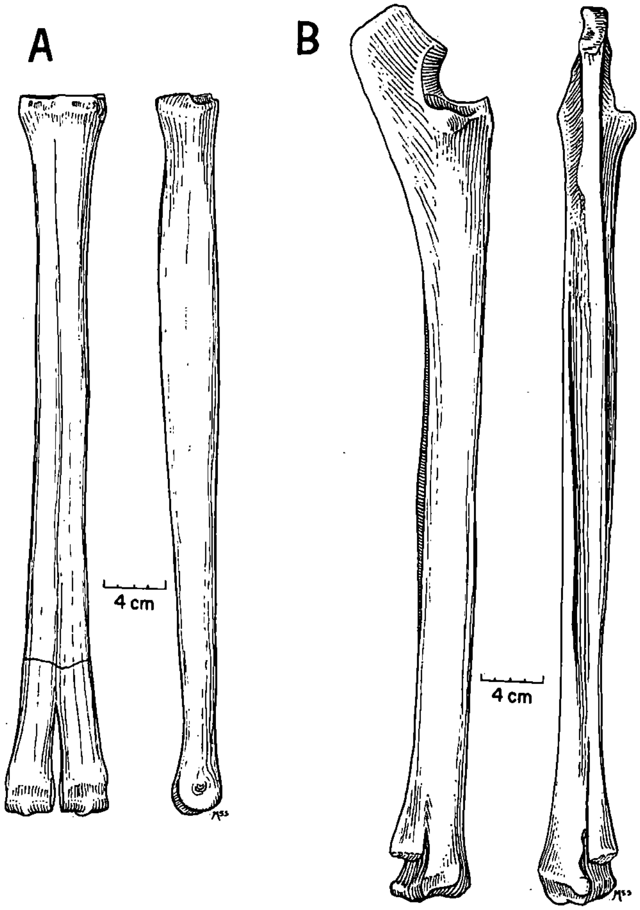

FIGURE 13. *Aepycamelus* sp. (UTBEG 31183-46, Type); A. – right metatarsal, front and lateral views. B. – right radius-ulna, rear and lateral views.

partial dentition. In the characters of the mandible and lower molars listed below, *Protolabis* closely resembles *Procamelus,* but is distinct from it in the configuration of the skull, upper incisors, lower premolars, and metapodials. In his paper on the Burge and Minnechaduza faunas, Webb (1969) revises the generic diagnosis of *Protolabis* as follows:

> Dentition unreduced with functional upper incisors in mature individuals. P$\frac{1}{1}$ double rooted. Cheek teeth proportionally narrower than in *Procamelus;* narrower and higher crowned than in *Miolabis.* Posterior cusps of P_3 narrower than middle cusps and lacking the lingual inflection or fossettes characteristic of

Procamelus. Deciduous cheek teeth proportionally much smaller and lower crowned than in *Procamelus;* dp_2 and dp_3 very slender and lacking lingual inflections. Deep cranium with flexed basicranial axis and S shaped zygomatic arch. Limbs about half as long as in *Procamelus grandis* and relatively lighter; metapodials unfused in mature individuals.

In a discussion of the confusion in the synonmy of the species of *Protolabis,* Webb (1969) suggests that two species should presently be recognized: "a smaller form which should probably be called *Protolabis fissidens* but is best represented by the material Matthew named *P. longiceps,* and a larger form represented by *Protolabis heterodontus* and its synonym *P. angustidens.*" I believe that other evidence indicates a necessity for continued separation of *P. fissidens* and *longiceps*: Cope's (1874 a: 327) unillustrated description of *Procamelus fissidens* points out that the reduction of the lower premolars approximates that of *Procamelus occidentalis,* and Matthew (1901) states that the premolars of *P. fissidens* are the least reduced of the procameline species. In comparison, the premolars of *Protolabis longiceps* (=*P. montanus*[1]) are quite reduced, P_1 and P_2 (although P_1 loss is probably rare) being absent. This suggests that although the genus *Protolabis* may contain two size groups, *P. longiceps* and *P. fissidens* should be considered distinct. In addition, Webb's gen-

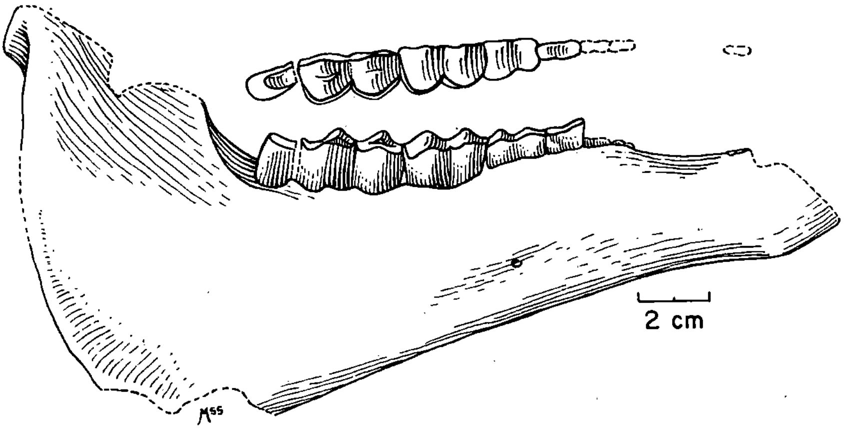

FIGURE 14. *Protolabis notiochorinos* n. sp. (UTBEG 31132-332, Type); right ramus, labial view of ramus and P_4-M_3, occlusal view of alveoli for P_1-P_3, and P_4-M_3.

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[1] In his statement on this synonymy, Matthew (1909: 115) refers to "*P montanus* Douglass" in Matthew, Mem. AMNH, v. 1, pt. 7, 1901, p. 435, figs. 31-33, not to *P. montanus* of Douglas (1900).

eric diagnosis should be augmented to include mention of this premolar reduction.

The molars of UTBEG 31132-332 from the Lapara Creek Fauna are 11-25 per cent smaller than those of *P. heterodontus* from the Burge and Minnechaduza Faunas. The Texas specimen is about 10 per cent larger than *P. longiceps*. Because of differences in overall size, shape, and proportions of the lower premolars, I am separating the Gulf Coast specimen from the Great Plains forms as a distinct species, *Protolabis notiochorinos*. This is the only species of *Protolabis* now known from the Gulf Coastal Plain, as I have referred *P. francisi* Hay to *Oxydactylus benedentatus* (page 135).

Protolabis notiochorinos new species

Figures 14, 15, Table 11

TYPE. – UTBEG 31132-332, mandible with P_4-M_3 intact; P_2-P_3 broken below crown. P_1 alveolus present.

TYPE LOCALITY. – Bridge Ranch; Site 17, Bee County, Texas.

OCCURRENCE. – Lapara Creek Fauna.

REFERRED MATERIAL.–UTBEG 31081-261, -293, -612, -525; UTBEG 31132-319, all metapodials.

ETYMOLOGY. – *notios* = Gr. southern; *choros* = Gr. land, country.

DIAGNOSIS. – A species of *Protolabis* intermediate in size between *P. longiceps* and *P. heterodontus*. Premolars more reduced than in *heterodontus*. P_1 two-rooted; P_2, P_3, and P_4 highly reduced. P_4 very narrow and with posterior lobe smaller than middle lobe, in contrast to *longiceps* and *heterodontus*. Masseteric region of mandible more greatly flared than in *longiceps*.

DESCRIPTION. – The shape of the mandible of *P. notiochorinos* appears to resemble closely *P. longiceps* from the Pawnee Creek, except that the masseteric region of the Texas specimen has a greater posteroinferior flare. The mandibular foramen is situated below the occlusal level, and its inferior border is interrupted by a wide, 4-6-mm groove extending down and forward for about 28 mm, probably serving to receive the mandibular artery and nerve. A smaller foramen appears toward the distal end of this groove on the left ramus. Only a hint of this foramen is present on the right ramus. A mental foramen occurs in the lower third of the ramus just below the posterior border of M_1. The rami are broken anterior to P_1. P_1 of the left ramus is only partially intact, but shows evidence of an alveolus from an anterior root, thus establishing the presence of a two-rooted P_1. P_1

Table 11. Measurements of the Type of *Protolabis notiochorinos*, New Species

Lower jaw	UTBEG 31132-332
Depth of ramus below center of M_3	51.5
Depth of ramus below center of M_1	40.2
Depth below center of P_1-P_2 diastema	30.0
Length, P_1-P_2 diastema	26.2
P_2-M_3	112.0[1]
P_4-M_3	95.0
P_2-P_4	27.0[1]
M_1-M_3	84.0[1]
P_3, length × width	8.0[1]
P_4, length × width	11.3 × 5.7
M_1, length × width	17.2 × 11.1
M_2, length × width	27.0 × 15.0
M_3, length × width	42.0 × 13.0

[1] Approximate

and P_2 are separated by a rather short (26 mm) diastema. Of the premolars, only the right P_4 is preserved. The roots of P_2 and P_3 are visible and reveal the highly reduced condition of these teeth. P_4 is short anteroposteriorly and extremely narrow (5.7 mm). In comparison to *Procamelus*, the anterolingual flexid of P_4 is only weakly expressed. A faint posterolabial fold is visible. The most notable feature of P_4 is that the posterior lobe is narrower than the anterior, in contrast to other camels, in which the wedge-shaped P_4 is much wider posteriorly than anteriorly. The absence of any elaboration of the posterior lobe precludes the formation of a posterior fossettid. The unusually narrow posterior lobe of P_4 of *P. notiochorinos* recalls a similar construction of P_3 in *P. heterodontus*. Also in *P. heterodontus* P_4 is marked by a weakly inflected anterior lobe. The molars of *P. notiochorinos* are quite narrow but simple, with only faint expression of lingual ribs or stylids. The only complete uncoossified camel metapodial (UTBEG 31132-319) from the Lapara Creek Fauna is only 194 mm long, but a broken specimen (UTBEG 31081-293) appears to be approximately 20 per cent larger.

Discussion. — The Lapara Creek specimen resembles *P. heterodontus* from the Burge and Minnechaduza Faunas in many respects, and could well be a close relative of it. The relatively more advanced stage of evolution represented by *P. notiochorinos* as compared to *P. heterodontus* suggests an ancestor-descendent phylogenetic relationship, but the inference is refuted by the presence of these two forms in contemporaneous deposits (Clarendonian). More probably, *P. notiochorinos* represents a branch off an early *P. heterodontus* stock and

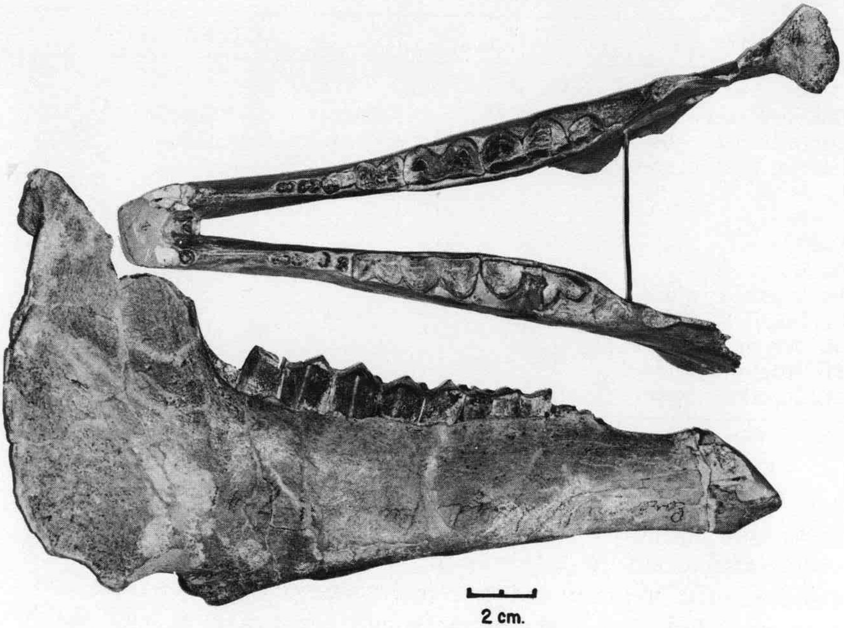

FIGURE 15. *Protolabis notiochorinos* n. sp. (UTBEG 31132-332, Type); mandible, labial view of right ramus, occlusal view of both rami.

one that evolved separately at a more accelerated rate than the Great Plains species, but the synonymy and systematic relationships of the various species will remain uncertain until this genus is thoroughly reviewed.

Procamelus Leidy, 1858

Procamelus is among the most abundantly represented artiodactyl groups recovered from the faunas described in this paper. Although absent from the Garvin Gully and Burkeville Faunas and only sparingly represented in the Cold Spring, it is the most numerous form in the Lapara Creek Fauna. Whereas *Oxydactylus* is the commonest camel in the Garvin Gully Fauna, *Procamelus* assumes this position in the Lapara Creek Fauna.

The type species is *Procamelus occidentalis,* described by Leidy (1858) from the late Miocene deposits of the Niobrara River Valley in Nebraska. *Procamelus* is represented in the Texas faunas by 12 well-preserved mandibles, 12 metapodials, 1 humerus, and 3 radius-ulnae. Many of the nominal species formerly assigned to the genus

Procamelus are now regarded as *nomina nuda* or *nomina dubia* (Gregory, 1942; Webb, 1969). In general, three species groups of *Procamelus* are currently recognized (Gregory, 1942; Webb, 1969): *P. occidentalis* and its probable descendant *P. grandis;* the wide-toothed, short-jawed *P. robustus*; and the group of small procamelines composed of *P. gracilis, P. leptognathus,* and *P. coartatus. Procamelus* specimens from the Lapara Creek Fauna are assignable to two distinct species: *P. occidentalis* Leidy and *P. grandis* Gregory. This bipartite division of *Procamelus* in the Lapara Creek Fauna is discernible in the size distribution and morphology of the mandibles and the metapodials.

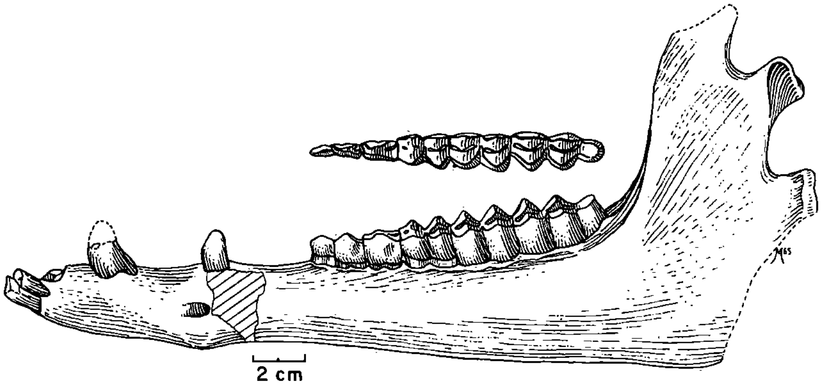

FIGURE 16. *Procamelus occidentalis* (UTBEG 31081-665); left ramus, labial view I_1-M_3, occlusal view P_2-M_3.

Procamelus occidentalis Leidy, 1858
Figure 16, Table 12

TYPE. – USNM 797, right P_3-M_3 (broken), fig. Leidy, 1869, Pl.V, fig. 5.

OCCURRENCE. – Lapara Creek Fauna.

REFERRED MATERIAL. – Mandibles: UTBEG 31081-665, 31081-738, 31081-49, 31081-313, 31081-241, 30896-475, 31170-6; humerus: UTBEG 31081-509; radius-ulnae; UTBEG 31081-562, -451, 31132-18; metacarpals: UTBEG 31081-418, -503, -666, -840, -1080, -1085; metatarsals: UTBEG 31081-407, -408, -417, -438, -490, -159.

DESCRIPTION. – The smaller of the two *Procamelus* species from the Lapara Creek Fauna, *P. occidentalis* is the best represented of all the camels in numbers of specimens. UTBEG 31081-665 (Fig. 4B) consists of both rami of the mandible with one ascending ramus virtually complete and the dental series intact, except for the incisors, which are present but broken on the left side and missing on the right. The lower jaw and lower dental series show few or no qualitative differences between the Lapara Creek specimens and either *P. occidentalis* or *P. grandis*. The lower incisors are too fragmentary for detailed description. The ventral surface of the mandible shows no deep sulcus along the symphysial plane between left I_1 and right I_1, as occurs in *Pliauchenia* and *Nothotylopus*. A short diastema (10 mm between alveolar borders) is present between I_3 and /C. The anterior surface of /C is marked by a very thin, bladelike flange which is pinched off sharply from the body of the tooth. A similar flange is present, but much less developed in P_1. Less defined flanges occur along the posterior edges of /C and P_1. The prominent single-rooted P_1 lies roughly midway between /C and P_2. The P_1-P_2 diastema, as mentioned, is almost equal to that between /C and P_1, a condition characteristic also of *Protolabis*, but in *Nothotylopus* the P_1-P_3 diastema is more than twice the distance between /C and P_1. P_2 of *P. occidentalis* is thin, sharp, and considerably reduced in comparison to P_3 and P_4. The two posterior premolars resemble one another closely

Table 12. MEASUREMENTS OF *Procamelus occidentalis*

Lower jaw	UTBEG 31081-665	UTBEG 30896-475	UTBEG 31081-241
Condyle to angular process	26.4	....	....
Length of /C-P_1 diastema	22.8	....	....
Length of P_1-P_2 diastema	30.1	....	....
Depth of ramus below center of M_3	43.2	39.1	43.5
Depth below center of M_1	35.2	30.0	....
Depth below center of P_1-P_2 diastema	27.6	24.2	....
P_2-M_3	115.7	112.0[1]	118.4[1]
P_3-M_3	108.0	102.0[1]	109.5
P_2-P_4	33.6	34.8[1]	37.0[1]
P_3-P_4	26.2	26.2[1]	28.4
M_1-M_3	83.1	77.0	81.0
P_2, length × width	9.4 × 5.0	....	....
P_3, length × width	12.7 × 6.0	....	13.5 × 5.8
P_4, length × width	14.0 × 8.5	15.0 × 7.4	15.9 × 8.0
M_1, length × width	20.1 × 12.3	20.6 × 12.0	21.0 × 12.5
M_2, length × width	26.0 × 15.0	23.7 × 12.3	25.6 × 13.7
M_3, length × width	38.1 × 15.0	34.6 × 13.8	36.6 × 14.2

[1] Approximate

in cusp morphology. They are marked by a pronounced anterolingual fold (flexid) between the anterior (paraconid?) and middle metastylid?) lobes. The lingually flexed paraconid makes a slight dogleg anteriorly, a feature also observable in some species of *Protolabis,* though less well-expressed in that genus. The posterior lobe of P_3 and P_4 is divided into two distinct cusps: a broad labial hypoconid and a narrow, less pronounced lingual entoconid. The entoconid attains much greater development in P_4, so that with continued wear the entoconid and hypoconid join posteriorly to form a posterior lake; in P_3 the entoconid is so weakly expressed that at no stage of wear does a posterior lake form. This condition obtains also in *Protolabis.* P_3 tends to be rectangular, the anterior and posterior widths being approximately the same, whereas P_4 has the wedge shape characteristic of most camels. The molar teeth are high-crowned and very simple. In *P. grandis* the stylids are much more prominent.

The body of the ramus is slender and graceful, its depth being not so great as in *Oxydactylus* or so variable anteroposteriorly as in *Pliauchenia.* A large mental foramen occurs below and anterior to P_1; a second, much smaller foramen is situated directly below the posterior edge of P_4. The dorsal border of the mandibular foramen is approximately level with the occlusal surface of M_3. In contrast to *Oxydactylus* and *Nothotylopus,* there is no downward expansion of the posteroinferior border of the mandible; the ascending ramus makes a steeper angle with the body of the mandible in this and other species of *Procamelus* than in *Oxydactylus.* The angular process is quite prominent and is canted lingually. The condyloid process resembles that of *Oxydactylus.* The long, slender coronoid process of *P. occidentalis* specimens from other areas extends well back over the condyle, in marked contrast to the short, stubby coronoid in *Nothotylopus.*

Metacarpals of *P. occidentalis* average 336.3 mm in length, metatarsals 330.0 mm. The average length of the radius-ulnae, exclusive of the olecranon, is 368 mm.

Procamelus grandis Gregory, 1942
Table 13

TYPE. — UCMP 32864; skull and jaws.

OCCURRENCE. — Lapara Creek Fauna.

REFERRED MATERIAL. — UTBEG 31081-429, 30896-531.

DESCRIPTION. — The identification of *P. grandis* is based on two

Table 13. MEASUREMENTS OF *Procamelus grandis*

Mandible	Fence Line Loc.[1] UCMP 33473	Big Spring Canyon[2] UCMP 32301	Bee County UTBEG 31081-429	Bee County UTBEG 30896-531
Distance betwen angle and condyle	34.0	45.0	28.0	
Depth of jaw posterior end of M_3	69.1	64.0	64.0	69.0
Depth of jaw at anterior end of M_1	47.9	37.0	43.0	38.0
Depth below /C	28.3	20.4		
/C-P_1	21.4	19.0		
P_1-P_2	19.1	29.4		
P_2-P_4	43.9	41.0	45.0[3]	105.0
M_1-M_3	96.8	102.0	104.0[3]	
P_2-M_3	137.8	144.0	150.0[3]	
C, length × width	13.2 × 9.6			
P_1, length × width	10.4 × 7.0			
P_2, length × width	13.1 × 6.3			
P_3, length × width	13.5 × 8.2	14.5 × 5.8		
P_4, length × width	16.9 × 10.5			20.2 × 8.8
M_1, length × width	22.9 × 17.1		14.3	26.6 × 16.0[3]
M_2, length × width	29.3 × 18.9		30.8 × 14.9	34.0 × 16.5
M_3, length × width	45.8 × 19.2		45.3 × 14.9	46.0 × 16.6

[1] In Webb (1969) after Gregory (1942)

[2] After Webb (1969)

[3] Approximate

partial lower jaws: UTBEG 31081-429, a left mandible possessing a broken M_1 and M_2-M_3 and alveoli for P_2-P_4, and a virtually complete ascending ramus; and UTBEG 30896-531, a right mandible with P_4-M_3. In general morphology the Lapara Creek specimens closely resemble the holotype of *P. grandis* described by Gregory (1942) and *P. grandis* specimens from the Burge Fauna figured by Webb (1969). With the exception of a single P_4 preserved on UTBEG 31081-429, the Texas specimens lack the diagnostically valuable premolars. Some minor differences in the molars and in mandible configuration are observable, but whether or not these differences are geographically consistent, or even diagnostically reliable, is uncertain. If the mandible (UCMP 33473) from the Fence Line Locality (Webb, 1969) is representative of the Burge *P. grandis,* then the lower molars of members of that population appear to be shorter and wider than those from the Lapara Creek Fauna (Table 13). The molars of both the Burge and Lapara Creek specimens are narrower than those of *P. robustus.* No important differences between the Burge and Lapara Creek specimens are discernible in characters of P_4. Although the tips of the coronoid processes of the holotype (UCMP 32864) and paratype (UCMP 32589) of *P. grandis* from Big Spring Canyon and of UTBEG 31081-429 are broken off, they appear to lack the pronounced posterior sweep of the Burge specimen (UCMP 32286). Other minor differences, and perhaps those listed above as well, are apparently attributable to normal individual variation. On the

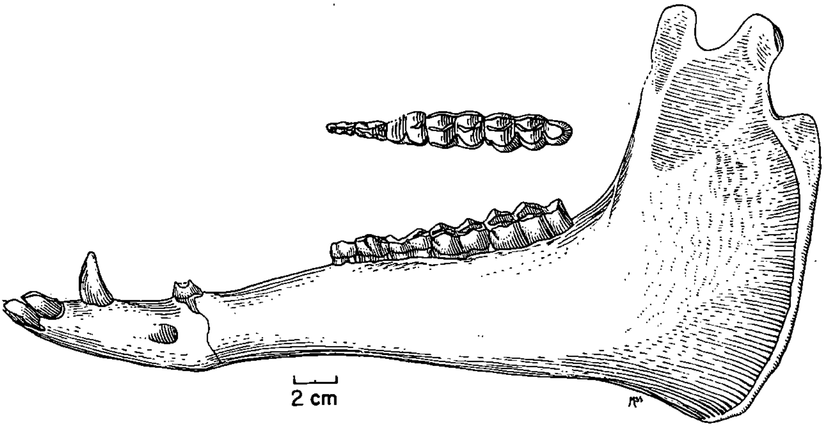

FIGURE 17. *Nothotylopus camptognathus* n. gen. et sp. (UTBEG 31081-26, Type); left ramus, labial view I_1-M_3, occlusal view P_3-M_3.

basis of presently inadequate material there seems to be no way to separate or recognize geographic variants in this species.

Because nothing is definitely known of the metapodials of the new Lapara Creek genus, *Nothotylopus*, the large (average length = 460 mm) *Procamelus*-like metapodials from the same Lapara Creek quarry from which both *P. grandis* and *Nothotylopus* were recovered are not confidently assignable to either taxon.

Nothotylopus new genus

A virtually complete mandible of a medium-sized camel from the Lapara Creek Fauna of Bee County, Texas, is believed to represent a lineage distinct from previously recorded extinct camels and whose origins may be found within the *Protolabis* stock. Until further material is forthcoming, generic characters will correspond to those of the type species, *Nothotylopus camptognathus*.

Nothotylopus camptognathus new species

Figures 17, 18, Table 14

TYPE. — UTBEG 31081-26, a left mandible with I_1-M_3.

TYPE LOCALITY. — Farish Ranch, Site 15, Bee County, Texas.

OCCURRENCE. — Lapara Creek Fauna.

ETYMOLOGY. — *nothos* = Gr. spurious, bastard, in reference to its uncertain origins; *tylopus* = Gr. camel; *kamptos* = Gr. curved, bent; *gnathos* = Gr. jaw.

DIAGNOSIS. — A medium-sized camel with widely flared and curved masseteric region; short, weak coronoid process; long P_1-P_3 diastema; P_2 absent; lower premolars anteroposteriorly compressed but complex; molars robust and low-crowned with pronounced anterolabial ribs.

DESCRIPTION. — Identification and systematic placement of this species is based on a well-preserved left mandible with complete dentition. Dental formula: $I_3C_1P_3M_3$. Shape and proportions of the lower jaw of *N. camptognathus* are very distinctive. The masseteric region is widely expanded and broadly curved labially (Figs. 17, 18). The prominent angular process occurs high on the ascending ramus well above the occlusal level and lacks the strong inflection seen in *Procamelus*. The condylar process is thick and broad. In contrast to the broader, backsweeping coronoid process of *Procamelus* and *Pliauchenia*, the coronoid process of *N. camptognathus* is thin, narrow, and extends vertically to a level only slightly above that of the condyle. The masseteric fossa is deep and ovate. On the lingual side of the ascending ramus the large mandibular foramen occurs at a level approximately halfway between that of the occlusal surface and the angular process. The inferior border of the body of the ramus rises obliquely with respect to the superior border until just anterior to P_3 it becomes parallel to the horizontal axis of the mandible. The ramus deepens again at the posterior end of the symphysis, forming a lump on the inferior border at that point. There is a large mental foramen below the anterior border of P_1 and a small one below P_3. From a point just anterior to P_1 the symphsis widens towards the anterior tip. This widening is further emphasized by the outward flare of the lateral incisors. A deep groove about 15 mm long occurs on the inferior side of the symphysis along the symphysial suture between the first lower incisors.

The incisors are procumbent and slightly spatulate. A short, 9 mm diastema occurs between I_3 and /C. The canine is strong and slightly recurved, but lacks the sharp anterior blade present in *Procamelus*. P_1 is small, two-rooted, and only mildly caniniform, differing in each respect from P_1 of *Procamelus*. P_2 is absent. The diastema between P_1 and P_3 is more than twice as long as that between /C and P_1. P_3 and P_4 are more compressed anteroposteriorly than in *Procamelus* or *Pliauchenia*. Although small, P_3 has three well-developed lobes with easily discernible minor cusps, a condition contrasting with that of *Procamelus, Pliauchenia,* or *Protolabis*. It is also shorter crowned than *Procamelus* or *Pliauchenia*. The lobes are separated by two small labial folds and a more pronounced anterolingual flexid. The posterior lobe is composed of a major labial cusp (hypoconid?) and a minor lingual one (entoconid?). Continued wear should result in the formation of a small posterior lake between these cusps. The middle lobe (metastylid?) is high but blunt. The anterior lobe (paraconid?) is flexed anterolingually and exhibits a slight anterior bifurcation. P_4 is characteristically wedge-shaped, but is shorter than in other contemporaneous camels. A deep posterolabial flexid lies between the middle and posterior lobes and a wider, more prominent one between the middle and anterior lobes. Smaller folds occur anterolabially and posterolingually. A distinct posterior lake has formed between entoconid and hypoconid. The lower molars of *N. camptognathus* are relatively wider and less hypsodont than those of *Procamelus* and *Pliauchenia* (Tables 12-14). M_2 and M_3 have well-developed anterolabial ribs, a character that may be found in some other camels, e.g., *Miolabis,* although it does not appear in *Protolabis, Procamelus,* or *Pliauchenia*. Extreme wear prevents the determination of this character on M_1. A

Table 14. MEASUREMENTS OF THE TYPE OF *Nothotylopus camptognathus*

Lower jaw	UTBEG 31081-26
Height vertical ramus	186.0[1]
Condyle to angular process	31.5
Condyle to coronoid process	21.0
Depth of ramus below center of M_3	60.7
Depth below center of M_1	49.7
Depth below center of P_1-P_3 diastema	35.8
Length P_3-P_1 diastema	61.5
Length P_1-C diastema	28.1
P_1-M_3	184.0
P_3-M_3	108.4
P_4-M_3	97.7
P_3-M_4	24.3
M_1-M_3	84.4
P_3, length × width	11.8 × 5.8
P_4, length × width	13.8 × 8.5
M_1, length × width	19.2 × 14.0
M_2, length × width	27.4 × 16.5
M_3, length × width	39.7 × 18.0

[1] Approximate

tiny accessory tubercle is visible at the base of the crown between the anterior and posterior crescents of M_1 and M_2. This feature is not characteristic of the other advanced camels with which *Nothotylopus* is contemporary.

DISCUSSION. — In view of the incomplete material available for comparison, derivation of *Nothotylopus* from any of the currently known groups of camels is difficult and precise systematic placement tenuous. *Nothotylopus* exhibits a strange mixture of advanced and conservative features: long diastemata; reduced but complex P_3 and P_4; P_2 absent but P_1 two-rooted; and robust, buttressed molars.

Reduction and loss of lower premolars has been one of the most consistently employed and reliable characters in differentiating Late Tertiary camels. With the possible exception of *Aepycamelus* (= *Alticamelus*), all of the major taxa, i.e.: *Protolabis, Procamelus, Pliauchenia, Megatylopus,* and *Miolabis* exhibit some degree of premolar reduction, including the loss of P_2 and/or P_1. Heretofore loss of P_2 has been a diagnostic character restricted, at least among the large Tertiary camels, to *Pliauchenia* (Cope, 1874a) and *Megatylopus* (Matthew and Cook, 1909) although individuals in some species of *Protolabis*, e.g. *P. longiceps*, may lose P_2. Whereas reduction may be a parallel convergent character acquired separately by each of these genera, it is more likely a progressive character peculiar to the *Proto-*

labis lineage. For example, there has been reduction and occasional loss of P_2 in *Protolabis,* reduction in *Procamelus,* and loss in *Pliauchenia* and *Megatylopus. Nothotylopus* possesses this and other, separately acquired, progressive characters, but retains enough conservative features to preclude its derivation from any but the *Protolabis* stock. This conclusion is based primarily on short, two-rooted P_1 and reduced P_3 and P_4 of *Protolabis.* These features are also present in the small *gracilis* group of procamelines and in *Miolabis.* However, the former is a separate, early offshoot of the procamelines, whereas *Miolabis,* as it is now known, is taxonomically uncertain, perhaps ultimately to be placed in synonymy with *Protolabis.* The *Oxydactylus, Aepycamelus,* and *Hesperocamelus* lineage is far too conservative in premolar reduction, and too advanced in upper incisor reduction and dimensions of skull to provide a possible direct ancestor for *Nothotylopus,* while the *Procamelus-Pliauchenia-Megatylopus* groups are too specialized, especially in degree of hypsodonty. The probable ancestral stock, therefore, should be found among the early members of the genus *Protolabis,* or perhaps some form intermediate between *Protolabis* and that line of oxydactylines which presumably gave rise to it.

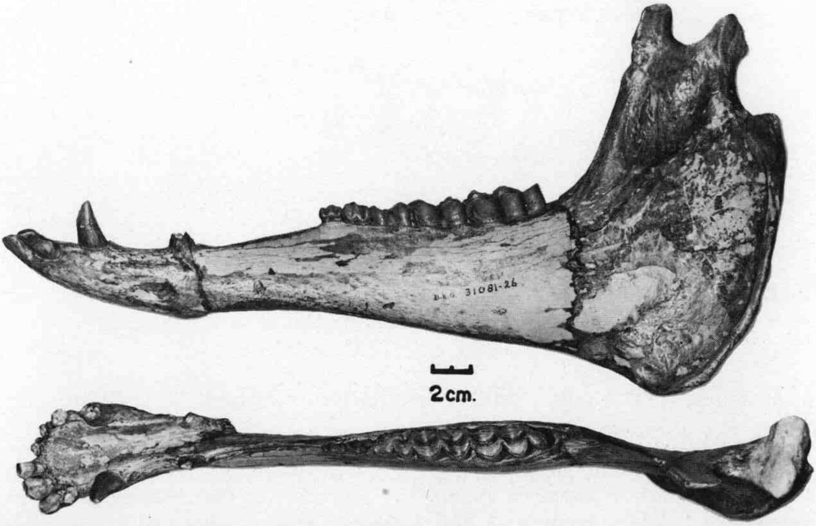

FIGURE 18. *Nothotylopus camptognathus* n. gen. et sp. (UTBEG 31081-26, Type); left ramus, labial and occlusal views.

Megatylopus Matthew and Cook, 1909

In 1875 Cope proposed the genus *Pliauchenia* to include those camels lacking the second premolar of the lower jaw. In addition to the type species, *P. humpreysiana,* he described another species, *P. vulcanorum,* from an upper dentition in which P_2 was present. The dental formula for the new genus was therefore given as "premolars $\frac{4}{3}$". *P. vulcanorum* has subsequently been assigned by Gregory (1942) to *Procamelus* on the basis of retained P^2, but lack of P_2 has been used as a diagnostic character for all later additions to the genus. Included in this taxon are various presumably related forms which, while sharing P_2 loss and succeeding premolar reduction, are clearly distinct on other grounds. Therefore, as Matthew (unpubl. MS) suggested, it appears that P_2 loss marks a stage in the evolution of the protolabine camels and is not characteristic of a group of nearly related species. In an attempt to rectify part of this confusion, Matthew and Cook (1909) restricted the very large species of *Pliauchenia* to a separate subgenus, *Megatylopus,* which has since been elevated to generic rank (Gregory, 1937).

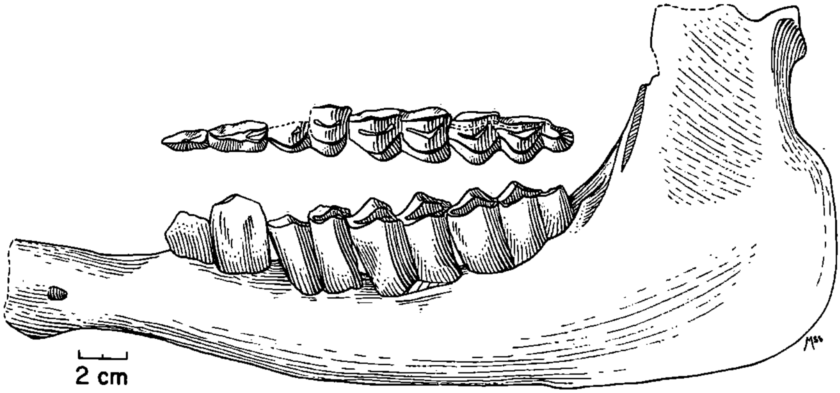

FIGURE 19. *Megatylopus primaevus* n. sp. (UTBEG 31081-460, Type); left ramus, labial and occlusal views P_3-M_3.

Matthew and Cook (1909) originally described *Megatylopus* as having the following characteristics:

> Gigantic camels with dentition $I\frac{1}{1}$ $C\frac{1}{1}$ $P\frac{2-3}{2-3}$ $M\frac{3}{3}$, the second premolar absent in both jaws, the first retarded or absent, the reduction of the posterior premolars intermediate between *Procamelus* and *Camelus.* Upper molars with prominent external ribs and styles, as in *Auchenia.* Limbs and feet moderately elongate and very massive, large in proportion to size of skull.

Although additional knowledge of *Megatylopus* has accumulated since its original description, the genus is still imperfectly understood and, therefore, any comparisons and/or systematic conclusions regarding it and related forms are necessarily tentative.

Species that have been included in *Megatylopus* are the type species, *M. gigas* Matthew and Cook (1909), *M. spatula* (Cope, 1893), *M. merriami* (Frick, 1921), *M. major* (Leidy, 1886) and *M. cochrani* (Hibbard and Riggs, 1949). *M. spatula* and *M. merriami* are regarded by Webb (1965) to be properly placed in *Titanotylopus* Barbour and Schlutz (1934). Webb (1965) bases his conclusion in part, on the lack of a cranial flexure, the broad anterior lobe of P_4, and the nonreduced P_3, features that these two species share in common with *Titanotylopus*, but which serve to distinguish them from *Megatylopus*. To the remaining species of *Megatylopus* must be added two new forms: *M. matthewi* from the Hemphillian Coffee Ranch Quarry, a distinct species which Matthew (unpubl. MS) recognized as *Paracamelus arenicola*, which is listed but not described by Reed and Longnecker (1932) and which Webb (1965) described and a rather primitive form from the Lapara Creek Fauna, *M. primaevus*, which is described below.

Megatylopus primaevus new species

Figures 19, 20, Table 15

Type. — UTBEG 31081-460, a left mandible, with P_2 alveolus, P_3-M_3.

Type Locality. — Farish Ranch, Bee County, Texas.

Occurrence. — Lapara Creek Fauna.

Referred Material. — UTBEG 31081-18A, a partial right ramus with P_3-M_3; 31081-18B, a metapodial.

Etymology. — *primaevus* = L. early, young.

Diagnosis. — An early species of *Megatylopus*, similar to *M. major*, but with a small P_2 and a larger and more complex P_3; mandible slender and vertically shallow.

Description. — The type mandible of *M. primaevus* is long and slender, the depth of the ramus being consistently shallower than *Nothotylopus* or *Protolabis* (Tables 11, 14, 15). Characters of the ascending ramus are mostly indeterminate because of poor preservation. A small mental foramen occurs just below the center of the anterior half of M_1; the anterior mental foramen is situated above the posteroinferior border of the symphysis where it deepens ventrally. The alveolus anterior to this foramen contained the lower canine.

Above the foramen and just below the surface of the bone is the unerupted P_1. Two small alveoli for P_2 occur anterior to P_3. This tooth was obviously quite small and probably nonfunctional. In view of the fact that the more advanced species of *Megatylopus* are characterized by loss of P_2, the retention of a small P_2 in *M. primaevus* is regarded as representing the last stage of reduction of that tooth in the *Megatylopus* lineage.

The diastema between /C and P_3 is approximately 62 mm long. P_3 is two-rooted and has well-developed anterior and posterior cuspids. The central cuspid (metastylid) is unworn and attains a height of 16 mm above the base of the crown. The crown flares from the base to reach its greatest anteroposterior length (17.8 mm) at about two-thirds its vertical height. The anterior lobe or cuspid is rather deeply grooved but only weakly inflected lingually. The posterior lobe has a large posterolabial cuspid (hypoconid) that is strongly inflected lingually, its lower slope extending farther lingually than the weakly expressed posterolingual cuspid, or entoconid. These two cuspids do not join towards the base, thus continued wear would not produce a posterior lake.

P^4 is a much larger and more robust tooth than P_3, and is quite hypsodont. The maximum height of the tooth, only slightly worn, is about 27 mm. The anterior cuspid is lingually inflected and set off from the primary cuspid by a prominent groove. A faint posterolabial groove is present between the principal and two posterior cuspids. The posterior cuspids are equally prominent and join posteriorly. In medium stages of wear they will form a posterior lake.

Table 15. Measurements of *Megatylopus primaevus*

Lower jaw	UTBEG 31081-460 (Type)
Condyle to angular process	37.0
Depth of jaw below M_3	51.0
Depth of jaw below M_1	33.0
Depth of jaw below P_1-P_3 diastema	30.0
P_3-M_3	159.0
P_4-M_3	142.0
P_3-P_4	39.0
M_1-M_3	120.0
P_3, length × width	17.8 × 8.2
P_4, length × width	22.2 × 12.0
M_1, length × width	34.0 × 18.8
M_2, length × width	43.0 × 21.0
M_3, length × width	50.8 × 20.0

The lower molars are hypsodont and are characterized by strongly developed stylids. Mesostylid and metastylid are especially prominent in the holotype. In the only other ramus referred to *M. primaevus* (UTBEG 31081-18A), these stylids are virtually absent. This jaw differs also in its smaller size and more reduced premolars. Whether or not the differences between the two specimens now assigned to *M. primaevus* are significant is for the present indeterminate.

A large, massive metapodial (UTBEG 31081-18B) is tentatively assigned to this species.

DISCUSSION. — Of the species of *Megatylopus* accepted in this paper (*M. gigas, M. major, M. matthewi, M. cochrani,* and *M. primaevus*), *M. primaevus* is the most primitive form yet recognized. In a clearly discernible evolutionary trend towards the condition reached by the genus *Camelops* (Webb, 1965), the premolars show a continuous reduction in size and number. P_2 having already been lost in all species but *M. primaevus,* this involves the reduction and eventual loss of P_1 and P_3. The absence of P_3 (and the usual absence of P_1) represents the taxonomic line of demarcation between *Megatylopus* and *Camelops*. *M. cochrani* from the Rexroad Fauna of Kansas has been demonstrated by Hibbard and Riggs (1949) to be very similar to *Camelops* and probably represents the most advanced species of the *Megatylopus* lineage. Unaware of the Lapara Creek specimens, Webb (1965) considered *M. major* from Mixson's Bone Bed in Florida to occupy the earliest level of *Megatylopus* evolution and placed the species *M. matthewi* from the Hemphillian of Texas between those stages represented by *M. gigas* and *M. cochrani.* This arrangement is based primarily on the condition of P_3. In all species but *M. major* and *M. primaevus,* the roots of P_3 are fused. These species also exhibit greater reduction in size and complexity of P_3 than is attained by *M. major* and *M. primaevus.* On these grounds, *M. primaevus* and *M. major* are clearly more primitive than *M. matthewi* and the two succeeding species. *M. major* and *M. primaevus* are similar and probably closely related, but because of the retention of a small P_2 and the greater complexity and size of P_3 in *M. primaevus,* I consider it to be a more primitive species than *M. major.* The differences are not great, but because the characters employed in taxonomic differentiation of these forms also reflect relative advances or stages in their evolution, it is useful to recognize and emphasize such distinctions. This is most apparent when considering these species from the standpoint of their stratigraphic occurrence. The evolutionary series beginning with *M. primaevus* and continuing

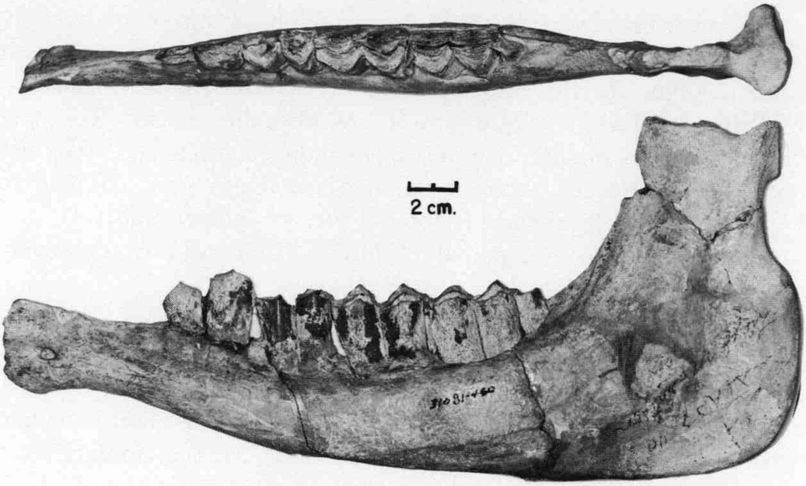

FIGURE 20. *Megatylopus primaevus* n. sp. (UTBEG 31081-460, Type); left ramus, labial and occlusal views.

through *M. major*, *M. matthewi*, *M. gigas*, and *M. cochrani* corresponds with their relative stratigraphic position. Complications in this evolutionary-stratigraphic sequence arising from different rates of evolution in different geographic regions, intermigrations, etc., are not as yet apparent.

Subfamily *Floridatragulinae* Maglio, 1966

Floridatragulus White, 1940

The exact systematic position of these puzzling artiodactyls is uncertain. The fragmentary nature of floridatraguline material from Texas and Florida deposits has prevented much speculation on phyletic affinities, but it is hoped that study of skull and jaw material now available from the Thomas Farm will lead to a better understanding of the group. As I have previously commented (Patton, 1966(67): 184):

> *Floridatragulus* bears considerable resemblance to members of two families of artiodactyls, the Hypertragulidae and the Camelidae. *Floridatragulus* resembles members of the Hypertragulidae in the presence of the intercolumnar pillars, a double enamel loop of the heel of M_3, rather prominent cingula, and in the occurrence of a diastema between P_2 and P_3. In the hypertragulids the detached P_2 tends to be unicuspid; in *Floridatragulus* this tooth is bicuspid, though weakly so. The anterior lower premolars of *Floridatragulus* are laterally compressed as in camels, and P_4, although more foreshortened than in most camels, retains the

general features of that group. In the skull and jaws of *Floridatragulus* from the Thomas Farm, now in the Frick Laboratory, the extremely elongated muzzle has four caniniform teeth (or alveoli) on each side, probably representing modifications of the incisors, C/, and P^1. This is a characteristic feature of the Tylopoda, in which the upper incisors and anterior premolars may undergo reduction, but in which there is never a complete loss of the upper incisors. In contrast, the hypertragulids are marked by either extreme reduction or complete suppression of the upper incisors, although they may be retained in some of the very primitive types.

Because of its overall resemblance to the camels, in the same paper I referred *Floridatragulus* to the Camelidae as a new subfamily[1]. I felt that those features that distinguish it from the Camelinae are certainly equal in taxonomic weight to those of the other camel subfamilies. Apparently for similar reasons, White (1947) tentatively placed *Nothokemas* as the type genus of a new family in the Hypertraguloidea. *Nothokemas'* affinities with the Camelinae are rather substantially documented, but similar assurance cannot be claimed for *Floridatragulus.*

Clearly while *Floridatragulus* has several distinctive camelid features such as the "hook" on the angle of the lower jaw, the caniniform condition of the upper anterior dentition, and the relatively swollen bullae, other traits are characteristically "ruminant" (*fide* Simpson, 1945). For example the enclosed orbit, the presence on the molars of intercolumnar tubercles, cingula, strong ribs and styles, and the double lobe on the hypoconulid of M_3 are all quite primitive features not fully shared by any of the camels, especially the later ones. That the similarity between the various artiodactyl group increases back through geologic time is indisputable (Matthew, 1905; Scott, 1940; Colbert, 1941; Simpson, 1945). However, although the camels and ruminants are supposedly recognizable as distinct groups as early as the late Eocene, *Floridatragulus* shares relatively few features in common with contemporary representatives of its basal stock. Whether or not the morphological similarity between it and the Camelidae is the result of direct evolution, parallelism, or convergence is not immediately determinable. For the present, available evidence suggests that *Floridatragulus* descends from an early and distinct offshoot of the basal tylopod stock and that it (and *Nothokemas*) subsequently occupied an adaptive zone in the Coastal Plain similar to that occupied by some camels in the Great Plains. With the invasion of the Gulf Coast by several diversified artiodactyl genera

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[1] A similar conclusion was reached by Maglio (1966) as the quoted paper was in press.

(including other camels) during the late Miocene and early Pliocene, the autochthonous Gulf Coast genera became extinct.

The known species of *Floridatragulus,* so far restricted to the Gulf Coastal Plain Miocene, are separable into three size groups that correspond with their stratigraphic occurrence. The smallest group is represented by *F. nanus* n. sp. from the Garvin Gully and *F. barbouri,* known only from Thomas Farm. The medium-sized *F. texanus* n. sp. and *F. dolichanthereus* have been recovered from the Burkeville Fauna of Texas and the uppermost strata of the Thomas Farm quarry, respectively. The stratigraphically higher Cold Spring Fauna of Texas has yielded a still larger form, *F. hesperus* n. sp., which is 12 per cent larger than F. *dolichanthereus* and 20 per cent larger than *F. barbouri.*

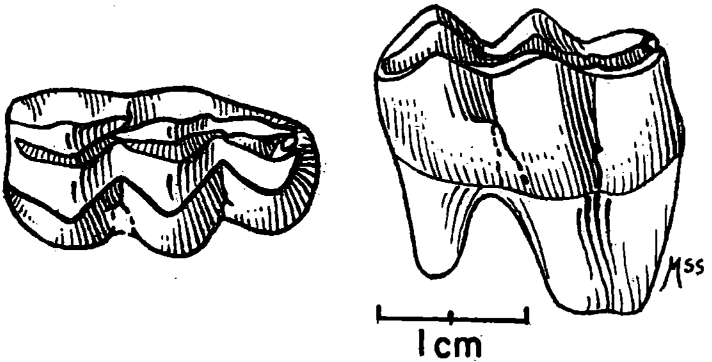

Figure 21. *Floridatragulus nanus* n. sp. (UTBEG 40067-194, Type); left M_3, occlusal and labial views.

Floridatragulus nanus new species
Figure 21

Type. – UTBEG 40067-194, a left M_3.

Type Locality. – Hidalgo Bluff, Washington County, Texas.

Occurrence. – Garvin Gully Fauna.

Etymology. – *nanos* = Gr. small, dwarf.

Diagnosis. – The smallest known species of *Floridatragulus;* intercolumnar tubercle strongly developed between protoconid and hypoconid of M_3, weakly developed between hypoconid and hypoconulid, talonid of M_3 divided, but differs from that of other species of *Floridatragulus* in having a posterior cingulum and two small tubercular cusps developed posteriorly between the two grinding surfaces.

DESCRIPTION. — This species is recognized in the Garvin Gully Fauna by a single tooth collected from the Oakville Formation exposed at Hidalgo Bluff, Washington County, Texas. This specimen differs from those representing later occurring species of *Floridatragulus* not only in its small size (20.0 mm × 10.0 mm vs. 24 mm × 12 mm for *F. barbouri*), but in the nature of the talonid of M_3. Whereas all known species of *Floridatragulus* have an invaginated talonid on M_3, none but *F. nanus* exhibits any cusp development between the two resultant grinding surfaces. Rising between the division of the talonid at its posterior border are two small cuspules, apparently developed from infoldings of the posterior wall of the hypoconulid. Both labial and lingual cuspules show wear. In addition to the above mentioned minor cusps, a small but distinct cingulum appears on the talonid of M_3, a feature also unique to this species of *Floridatragulus*.

Floridatragulus texanus new species

Figures 22, 24B, 24C, Table 16

TYPE. — UTBEG 31190-28, a pair of lower jaws with right P_2-M_3 and left P_2-P_3 and M_1-M_3.

TYPE LOCALITY. — Near Point Blank, San Jacinto County, Texas.

OCCURRENCE. — Burkeville Fauna.

DIAGNOSIS. — A medium-sized artiodactyl with brachyodont molars and a very long mandibular symphysial region; diastema between P_2 and P_3 equal to two thirds of that between P_1 and P_2; intercolumnar tubercles occur between protoconid and hypoconid in M_1 and M_3; talonid of M_3 divided into two separate grinding surfaces. Differs from *F. dolichanthereus* in having larger premolars, and in the less invaginated talonid of M_3.

DESCRIPTION. — Although the lower molars of *Floridatragulus* resemble those of *Prosynthetoceras*, they are separable from that genus on the basis of lower crown height, a larger and divided hypoconulid on M_3, and the presence of an intercolumnar tubercle between the protoconid and hypoconid on M_3. The lower premolars are generally narrower and less reduced anteroposteriorly than those of *Prosynthetoceras*. When the complete mandible and dentition are preserved, the two genera are easily separated by the presence of diastemata separating the anterior premolars of *Floridatragulus*.

DISCUSSION. — The Texas specimens of *F. texanus* are very closely similar to the one White (1940) described from the Thomas Farm

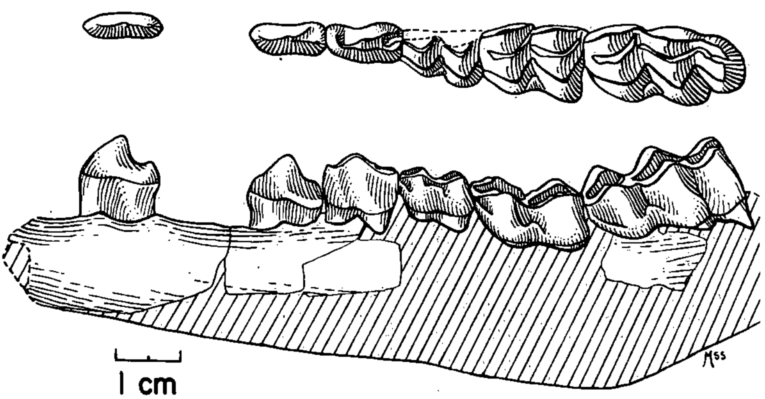

FIGURE 22. *Floridatragulus texanus* n. sp. (UTBEG 31190-28, Type); left ramus, labial and occlusal views P_2-M_3.

deposits of Florida as *F. dolichanthereus*. The Burkeville specimens, not known to White, differ from the Florida type specimen (MCZ 3635) and material subsequently assigned to the same taxon in the slightly larger premolars and in the lesser development of the division of the talonid of M_3, a feature White emphasized in the original description. In the Thomas Farm specimen the invagination of the posterior border of the talonid of M_3, a reflection of this division, is pronounced and extends from the occlusal surface down to the dorsal edge of the basal cingulum. The Burkeville specimens, which exhibit approximately the same amount of wear, show only a very slight infolding of the posterior border of the talonid, which extends no farther down than 1.0 mm from the occlusal surface. Although the Texas and Florida specimens are very similar, the above-mentioned differences may be real and may possibly reflect a minor genetic divergence resulting from geographic isolation of indefinite, but probably small extent and duration. If these differences prove to be consistent, then they assume not only taxonomic, but also zoogeographic importance. For these reasons, I feel that they warrant specific separation.

Floridatragulus barbouri White differs from *F. dolichanthereus* in being slightly smaller and in the shorter diastema between P_3 and P_2. The anterior half, metaconid and protoconid, of M_1 of the holotype (MCZ 4086) of *F. barbouri* is extremely foreshortened, but judging from the way it is crowded between M_2 and P_4, this is probably a pathologic condition. No such foreshortening appears in any other of the known specimens of *Floridatragulus.* Whether *F. dolichanthereus* and *F. barbouri* lived contemporaneously, or whether they represent an actual ancestor-descendent lineage is uncertain. The nature of the Thomas Farm deposit and the history of its excavation (White, 1942; Bader, 1956) suggest that those forms as they are known so far were separated temporally. The largest species, *F. dolichanthereus,* was recovered from the uppermost layers of the deposit and has not been found in any of the deeper sediments (White, 1942: 30). The smaller, less advanced *F. barbouri* was recovered from a deeper portion of the quarry. Hence there is a reason to accept the second alternative, that *F. barbouri* represents an earlier group that evolved (no evidence suggests replacement) into *F. dolichanthereus.* Such an interpretation has obvious chronologic implications (see Age and Correlation).

Table 16. MEASUREMENTS OF *Floridatragulus dolichanthereus* AND *texanus* n. sp.

Lower jaw	MCZ 3635 (Type of *F. dol.*)	UTBEG 31190-28 (Type of *F. tex.*)
Length P_3-P_2 diastema	33.4	
Length P_2-P_1 diastema	29.5	
P_3-M_3		76.7
P_3-P_4		22.7
M_1-M_3		55.0
P_2, length × width		12.1 × 3.9
P_3, length × width		11.6 × 4.9
P_4, length × width		11.0 × 6.5
M_1, length × width	13.0 × 8.5	13.2 × 9.1
M_2, length × width	16.3 × 11.0	18.1 × 11.4
M_3, length × width	25.6 × 12.6	25.2 × 12.0

Floridatragulus hesperus new species

Figures 23, 24a, Table 17

TYPE. – UTBEG 31219-266, an incomplete right mandible with M_1-M_3.

TYPE LOCALITY. – Donahoe Farm, near Cold Spring, San Jacinto County, Texas.

OCCURRENCE. – Cold Spring Fauna.

ETYMOLOGY. – *hesperos* = Gr. west.

DIAGNOSIS. – A large species of *Floridatragulus,* some 12 per cent larger than *F. dolichanthereus.* It is characterized by a rather large, recurved metastylid on M_3, and an intercolumnar tubercle between

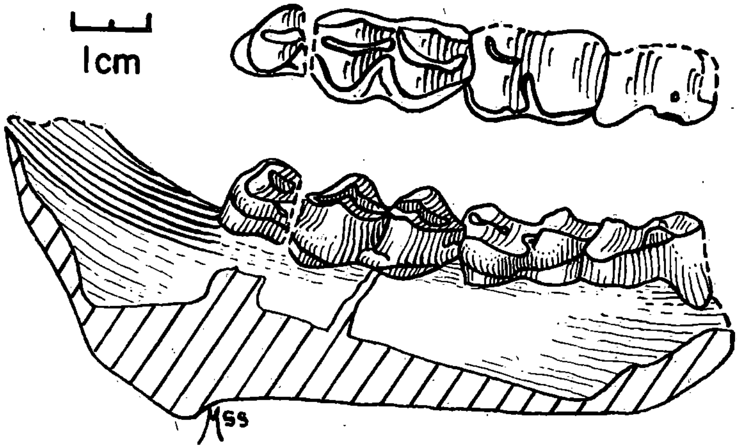

FIGURE 23. *Floridatragulus hesperus* n. sp. (UTBEG 31219-266, Type); right ramus, labial and occlusal views.

Table 17. MEASUREMENTS OF *Floridatragulus hesperus*

Lower jaw	UTBEG 31219-266 (Type)
M_1-M_3	63.0[1]
M_1, length × width	15.1 × 11.0[1]
M_2, length × width	19.2 × 12.6
M_3, length × width	29.5 × 12.8

[1] Approximate

the hypoconid and hypoconulid, in addition to the one between the hypoconid and protoconid of M_3.

DISCUSSION. – This larger form from the Cold Spring Fauna occurs highest stratigraphically of all the *Floridatragulus* species and represents the most advanced stage the genus reached. In addition to its large size, the presence of the intercolumnar tubercle on the talonid of M_3, the pronounced metastylid, and the better developed anterior cingulum of M_3 serve to distinguish it.

Suborder RUMINATA Scopoli, 1777
Infraorder TRAGULINA Flower, 1883
Family PROTOCERATIDAE Marsh, 1891
Subfamily SYNTHETOCERATINAE Frick, 1937

The peculiarly horned synthetocerines comprise the most abundantly represented group of artiodactyls recovered from the Miocene

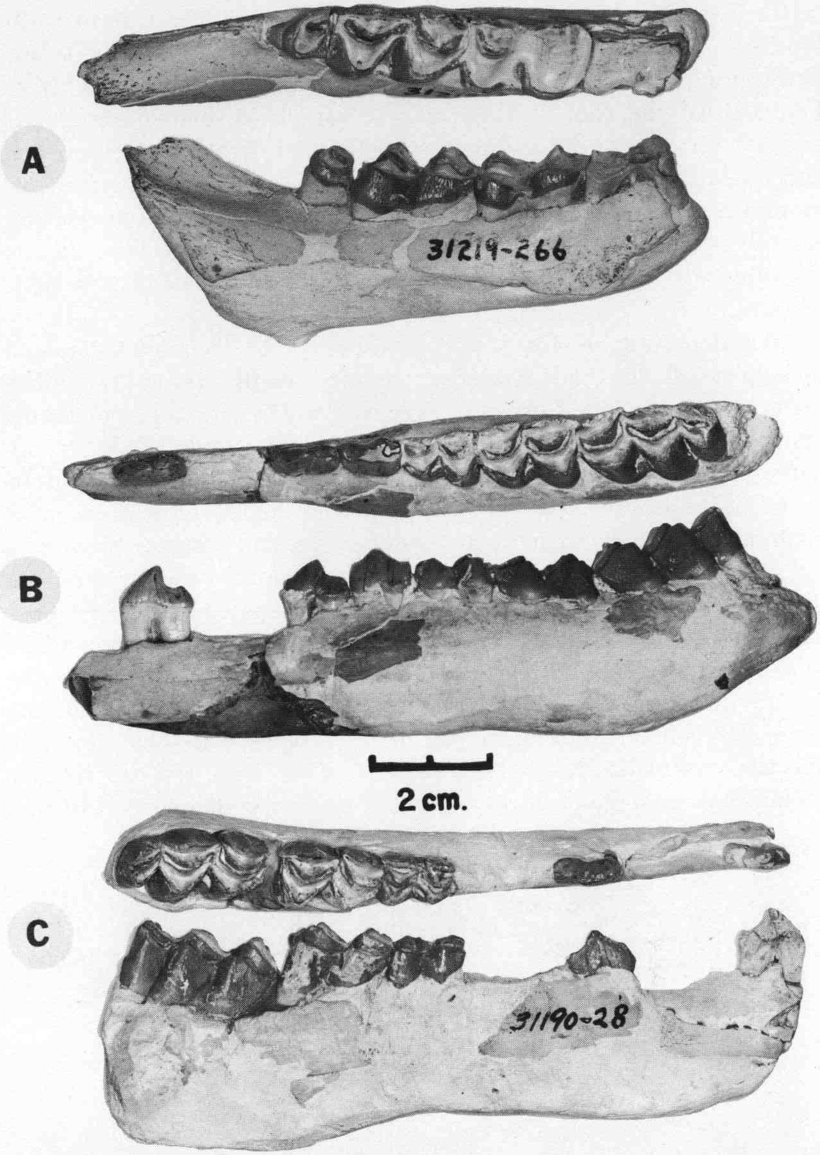

FIGURE 24. A. – *Floridatragulus hesperus* n. sp. (UTBEG 3121919-266, Type); right ramus, labial and occlusal views. B. – *Floridatragulus texanus* n. sp. (UTBEG 31190-28, Type); left ramus, labial and occlusal views. C. – *Floridatragulus texanus* n. sp. (UTBEG 31190-28, Type); right ramus, labial and occlusal views.

of the Texas Coastal Plain. They appear earliest in the Garvin Gully Fauna in moderate numbers, become dominant in the Burkeville and Cold Spring faunas, and are reduced in numbers in the Lapara Creek Fauna. Like the camels, they were a rapidly evolving group, and because they occur in a direct succession of stratigraphic units of only slightly differing chronologic age, they are particularly amenable to studies of microevolutionary change. Total numbers of specimens, as well as relative numbers of comparable anatomical elements, are unfortunately too few to justify a quantitative treatment of taxonomic features.

Material available for study consisted of 10 incomplete jaws, 3 incomplete skulls, and numerous isolated teeth. Several complete rostral and postorbital horns were recovered. The paucity of definitely assignable synthetocerine postcranial elements soon made it apparent that useful taxonomic criteria would necessarily have to be based on tooth and skull morphology. The degree of expression of anatomical features such as accessory cusps and cingula proved to be most consistently diagnostic, and consequently the greatest reliance was placed on them. The primary cusps showed very little variability in form, either within any one fauna or from one fauna to the next. Where vertically successive faunas were closely similar in age, taxonomic characters usually were not separable in absolute terms, but differed only in degree of their expression. Thus throughout the systematic description, separation is made on the relative prominence, or stage of development, of particular diagnostic features.

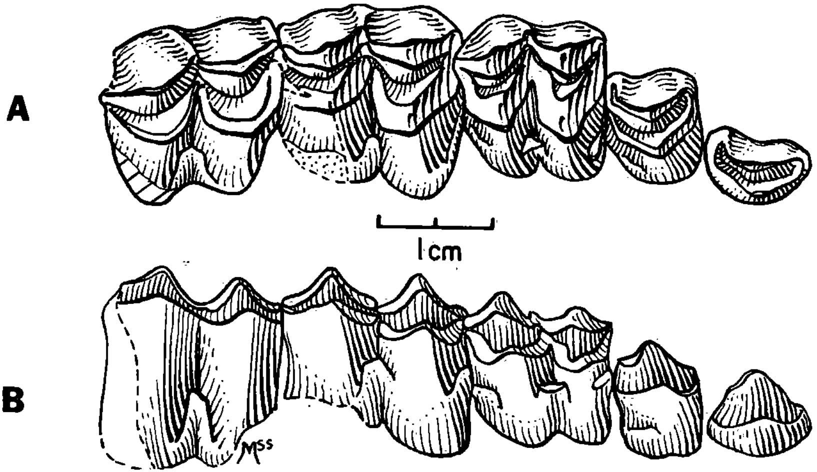

FIGURE 25. *Prosynthetoceras texanus* (TAMU unnumb.); right upper dentition, occlusal view P_3-M_3, lingual view P_3-M_3.

The synonymy of *Prosynthetoceras* species has been treated previously (Patton, 1966(67); 1967).

Since completing this manuscript, I have had the opportunity to begin a new study with Beryl Taylor of the American Museum of Natural History (Patton and Taylor, MS) on synthetocerines in the Frick Collection which were not available at the time this was written.

Prosynthetoceras Frick 1937

Prosynthetoceras texanus (Hay)

Figures 25, 26, 27, Tables 18, 19

Dromomeryx texanus Hay, 1924, p. 15, pl. II, figs. 8-12.
Dromomeryx angustidens Hay, 1924, p. 16, pl. II, figs. 6, 7.
Merycodus grandis Hay, 1924, p. 17, pl. III, figs. 9-11.
Protolabis francisi Hay, 1924, p. 14, pl. III, figs. 5-8.
cf. *Miolabis* sp. indet., Simpson, 1932, p. 37.
?*Cranioceras texanus* (Hay); Frick, 1937, p. 82, 97.
?*Synthetoceras rileyi* Frick, 1937, p. 603. 605, fig. 66.
Blastomeryx texanus (Hay); Wood and Wood, 1937, p. 137, pl. I, figs. 5, 6.
Syndyoceras australis White, 1941, p. 97, pl. XV, figs. 1, 1a, 2, 2a.
?*Syndyoceras texanus* (Hay); Hesse, 1942, p. 163 (?*Syndeoceras texanus*, p. 167, *lapsus*).
Synthetoceras (Prosynthetoceras) douglasi White, 1947, p. 504, fig. 3a.
Nothokemas grandis White, 1947, p. 508 (in part).
cf. *Miolabis tenuis* Ray, 1957, p. 18.

TYPE. — TAMU 2387, a right M^3.

TYPE LOCALITY. — Garvin Farm, near Navasota, Grimes County, Texas.

OCCURRENCE. — Garvin Gully Fauna, Burkeville Fauna.

REFERRED MATERIAL. — UTBEG 31190-61, maxilla with P^3-M^3; TAMU unnumb., partial right maxilla with alveolus for P^2, and P^3-M^3; UTBEG 31190-31, partial skull; 31190-75, partial rostral horn core; 31084-81, anterior portion of left ramus with P_4-M_1; 31190-95, left P_4-M_3; 31190-102, left M_1-M_3; SMU 60898, left P_2-M_3; and numerous isolated teeth.

DIAGNOSIS. — A relatively small synthetocerine with short-shafted rostral horn and subhypsodont teeth. P_2 retained. Upper molars are short, broad, and strongly tapered toward occlusal surface; they are characterized by prominent medial V-shaped pillars and bladelike cingula, anteriorly and posteriorly. There is a pronounced development of styles, especially the mesostyle. P_1 present. P_2 is reduced, but two-rooted.

DESCRIPTION. – *P. texanus* was originally described by Hay (1924) as *Dromomeryx texanus* on the basis of a right M^3 and two right M^1's. Frick (1937) described *Synthetoceras rileyi* (= *P. texanus*) on the basis of a partial mandible and left M_1-M_3. Specimens described by Patton (1967) and in this paper provide the only knowledge to date of the cranial armament of this species.

Because no anterior portions of the *texanus* jaws were recovered, P_1 is not available for description. However, because it is present in *Syndyoceras cooki* and *P. francisi*, it doubtless occurred in *P. texanus*. P_2 is represented only by two alveoli in the single specimen of *P. texanus* with that portion of the maxilla preserved (TAMU unnumb.). P_3 is elongated anteroposteriorly; the paracone is high and sharp, and the recurved metastyle forms a small cusp posteriorly. The paracone has no rib. A large cingulum extends from the parastyle lingually to join the metastyle at the posterior border of the tooth. P^4 has both parastyle and metastyle well developed. The metastyle is more prominent and more strongly recurved than the parastyle. The paracone is separated from the protocone by a deep valley. A relatively large accessory cusp extends up from the base of the posterior limb of the protocone, and a smaller cusp is apparent at the base of the anterior limb.

All upper molars display strong stylar cusps on the anterior and posterior crests. The entire anterior half of each molar is set farther lingually than the posterior half. This has resulted in a very prominent mesostyle and a rather deep recess anterior to it at the junction of the paracone and metacone crests. A strong rib extends up each crest from the base of the crown to the tip of both paracone and metacone. The shape of the crescents varies from an open V in M^3 to a more closed, slightly recurved V in M^1. Highly developed median pillars occur between the anterior and posterior crescents and extend half the height of the crescents in unworn teeth. This relationship is generally maintained with wear; the pillars are worn at virtually the same rate as the crescents. The pillars form an inverted V as both limbs hug closely their respective crescents. On most of the molars these pillars exhibit some wear. On the anterior margin of each molar is a narrow winglike cingulum which projects from just above the crown near the apex of the protocone and extends labially along the side, becoming fainter as it approaches the anterior crest. This feature is present but not so strongly developed along the posterior side of the tooth. The M^1 and M^2 are broader

Table 18. MEASUREMENTS OF THE LOWER DENTITION OF SPECIES OF *Prosynthetoceras*

	P_2		P_3		P_4		M_1		M_2		M_3					$/C$-P_2
UTBEG no.	L	W	L	W	L	W	L	W	L	W	L	W	P_3-M_3	P_4-M_3	M_1-M_3	diastema
P. texanus																
(G. Gully)																
SMU 60898	8.4	3.9	9.8	5.0	10.2	6.7	14.1	9.8	16.1	11.3	27.6	11.6	71.5	62.2	54.9	37.8
P. texanus																
(Burkeville)																
31190-95					10.5	6.1	14.1	10.1	17.4	11.4	26.1	10.8			56.1	
31190-102							14.9	10.2	17.1	11.8	26.8	12.1			56.0[1]	
P. francisi																
(Cold Spring)																
31219-213			9.9	5.2	10.5	7.0	16.4	11.1	22.0	12.7	29.2	12.7	85.0	74.6	66.0	
31219-214					11.1	7.8	16.2	12.1	21.6	14.0	29.8	13.1	85.6[1]	76.2	66.0	66.1
31219-219					11.3	8.1		12.5	21.5	14.5	33.0	13.0		76.5	68.0	
31243-5			10.0	5.1	10.5	6.8	15.6	11.3	20.6	13.7	30.0	13.4	83.6	74.5	65.1	
31182-47							17.4	10.7[1]	21.8	12.0	31.2	11.6			69.4	

[1] Approximate

Table 19. MEASUREMENTS OF UPPER DENTITION OF SPECIES OF *Prosynthetoceras*

UTBEG no.	P^2 L	P^2 W	P^3 L	P^3 W	P^4 L	P^4 W	M^1 L	M^1 W	M^2 L	M^2 W	M^3 L	M^3 W	P^2-P^4	P^3-P^4	M^1-M^3	P^2-M^3	P^3-M^3
P. texanus (G. Gully)																	
TAMU unnumb.			9.7	7.2	8.7	11.5	13.8	16.4	17.5	17.9	17.6	15.4		19.5	46.7		64.7
40067-54					8.9	10.0											
P. texanus (Burkeville)																	
31190-61			6.4	7.0	9.7	11.0	14.6	15.5	18.2	18.3	19.8	18.7		20.6	51.0		68.5
31190-31									17.2	19.9	20.0	22.0					
31190-62							16.7	17.0	17.5	17.6							
31190-55					9.6	12.0			18.6	19.6							
31190-39									17.8	18.2							
P. francisi (Cold Spring)																	
31219-241	9.5	5.6	11.1	6.8	11.0	13.1	18.5	18.6	22.5	20.2	22.1	16.6	30.7	22.1	63.0	94.6	84.4
31219-257									23.3	20.8							
31219-254									23.1	20.1							
31219-264							20.8[1]	19.6	21.6	20.4							
TAMU unnumb.	9.1	5.5	10.2	7.2	11.0	13.0	16.1	16.8	21.2	19.8	22.8	20.8	27.8	19.5	58.3	84.0	76.3

[1] Approximate

than they are long, while all three molars show strong tapering toward the occlusal surface.

The lower premolars are all reduced, especially P_2. P_2 is two-rooted and is similar to but smaller than P_3. The primary differences between P_2 and P_3 are the greater expression of the anterolingual flexid and the greater separation of hypoconid and entoconid in the latter. P_3 is elongate and is but slightly broader posteriorly than anteriorly. The hypoconid and protoconid are more distinct from the metaconid than in P_4. As in P_4 swellings at the base of the hypoconid and protoconid are noticeable. P_4 is slightly wedge-shaped. Most of the reduction in this tooth has occurred in the region of the protoconid. The metaconid is high and sharp; the entoconid is narrow and bladelike. The hypoconid extends posteriorly and lingually to join the entoconid. On worn specimens the metaconid, entoconid, and hypoconid join to form a small enamel islet. The base of the hypoconid is swollen to form a bulge at the posterolabial edge of the tooth. There is a less distinct swelling at the base of the protoconid.

The lower molars of *P. texanus* are subhypsodont. The crescents (protoconid, hypoconid) are symmetrical and show little tendency towards recurving. Stylids are reduced in comparison with those on the upper molars; only the metastylid is pronounced. The anterior crescent (metaconid) overlaps the posterior crescent (entoconid) slightly to form a faint stylid. A small median pillar occurs at the base of the crown between the anterior (protoconid) and posterior (hypoconid) crests of M_1 and M_2. No accesory pillars appear on M_3. In contrast to the median pillars on the upper molars, the lower ones would not show wear until the teeth were worn almost to the base of the crown. No cingula are present on the lower molars. Perhaps the most significant characteristics of the lower molars is the presence of a double enamel loop on the hypoconid of M_3 which, with wear, encloses a fossettid. This feature occurs in all protoceratids (and other ruminants) but never is found in camels. In this regard, M_3 of *Prosynthetoceras* resembles that of *Floridatragulus,* which is often found in association, but is distinguishable from it on the basis on the strong anterior cingulum, the accessory pillar between the protoconid and hypoconid, and the lower crown height of the latter. Another contemporary genus, *Nothokemas,* has a similar M_3, but in this instance, the formation of the double enamel loop is accomplished by the posterior extension of the metaconid.

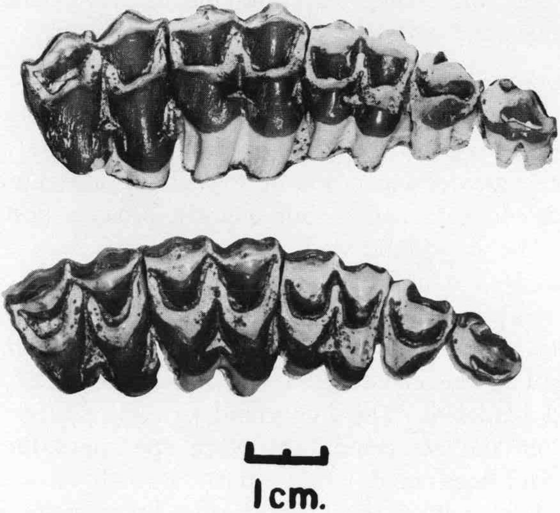

FIGURE 26. *Prosynthetoceras texanus* (UTBEG 31190-61); occlusal and oblique occlusal views.

DISCUSSION. – The lengths of the type specimens of *P. texanus* and the specimens from the Garvin Gully Fauna referred to it are within the range of published measurements of *Syndyoceras cooki* (Barbour, 1905; Frick, 1937). Specimens from the Burkeville Fauna are clearly larger. Unfortunately the teeth of the only available specimen of *S. cooki* are very badly worn, but as far as can be determined they approach closely those of *P. texanus.* Equally lamentable is the fact that to date no complete synthetocerine horns are known from the Garvin Gully Fauna, and this appears to be the most useful taxonomic character in the separation of the two genera. Three horn fragments (TAMU 2395) from Garvin Gully described by Hay (1924) as the type of *Merycodus grandis* appear to be fragments of the rostral horn of *P. texanus.* The largest fragment consists of a part of the main beam and one of the two branches, the other branch having been broken off. As is true of synthetocerines, the horn is convex on one side and concave on the other, with the branch leaning posteriorly. The size of this horn corresponds with that expected for the rostral horn of an early *P. texanus.* If the horn does belong to *P. texanus,* it can be used to demonstratate a definite advance over the rostral armament of *Syndyoceras,* for the point of branching is considerably higher on the beam than in *Syndyoceras.* Rostral horns of *P. texanus* from the Burkeville Fauna (UTBEG

31190-31, -72) are demonstrably much more advanced than those of either *Syndyoceras* or those specimens of *P. texanus* from the Garvin Gully Fauna. In addition the premolars of *P. texanus* appear to have undergone approximately 10 per cent greater reduction than those of *Syndyoceras*, indicating that the former had developed further along the lines characterizing the later synthetocerines.

Frick (1937: 605) originally separated the subgenus *Prosynthetoceras* from the genus *Synthtoceras* on the basis of "smaller size, the smaller and shorter-crowned dentition and retained P^2" in *Prosynthetoceras*. It has been demonstrated above that specimens confidently assigned to *P. texanus* (=(?) *Synthetoceras rileyi* Frick) have the alveoli for P^2; thus *P. texanus* now can be included in his subgenus *Prosynthetoceras*. Because I believe the retention or loss of P^2 in this linage to be an important and useful taxonomic character most applicable above the species level, I elevated the subgenus *Prosynthetoceras* Frick to the rank of genus (Patton, 1967).

The protoceratids White (1941, 1947) described from the Thomas Farm of Florida as *Prosynthetoceras douglasi* (MCZ 4065, White, 1947) and *Syndyoceras australis* (MCZ 3654 and 3642, White, 1941) are indistinguishable from *P. texanus* on the basis of the material presently available. For this reason, I have referred these species to synonomy with *P. texanus* (Hay) (Patton, 1966(67).).

The Burkeville specimens (UTBEG 31190-31, a partial skull with horns, left M^3, and right M^2-M^3; UTBEG 31190-61, maxilla with left M^1-M^3, and right P^3-M^3) are intermediate in size, crown height, and complexity of molars between *P. texanus* from the Garvin Gully Fauna and *P. francisi* from the Cold Spring Fauna. The metastyle of P^4 of the Burkeville *P. texanus* is large and strongly recurved; the parastyle is small. A tiny tubercle is present at the base of the anterior limb of the protocone. This tooth is more elongate and appears slightly more wedge-shaped than that of the Garvin Gully *P. texanus*. The metastyle on P^3 is also large and recurved. Cingula and intercolumnar pillars are less strongly developed than in the Garvin Gully *P. texanus*, more so than in *P. francisi*. The shape of crests and crescents of the molars of the Burkeville form are similar to those of the Garvin Gully. The posterior cingulum, when present, is tight against the side of the tooth, is relatively pronounced lingually, and becomes faint as it approaches the anterior edge of the metastyle; these cingula are only faintly visible on M^1-M^2 of UTBEG 31190-61. The anterior cingula are strongly pronounced lingually and rise over half the length of the anterior limb of the protocone for approximately one-third the width of the tooth, then dip down close to the base of the crown, becoming increasingly faint towards the parastyle. The median pillars are strong and folded into limbs that abut closely on their respective crescents. Wear on the pillars is proportional to the degree of wear on the primary cusps. The styles are very well-developed, especially the mesostyle. The postorbital horns are laterally directed. The shaft of the rostral horns of the Burkeville *P. texanus* is longer than that of the Garvin Gully form, attaining a length of approximately 135 mm from the base to the point of bifurcation.

P. texanus specimens from the Burkeville Fauna mark an intermediate stage in the evolution of this group of synthetocerines between that of earlier *P. texanus* and *P. francisi* of the Cold Spring Fauna. An analysis of all the features in the teeth, skulls, and jaws, excepting those whose comparison was prevented by lack of material, indicates a remarkably close relationship between the Garvin Gully and Burkeville populations. This affinity is witnessed in the intergradation of every comparable diagnostic character available in the two series of specimens. Although *P. texanus* from the Burkeville Fauna more closely approximates *P. texanus* from the Garvin Gully Fauna than *P. francisi* in size as well as in evolutionary development, separation of these two forms nevertheless involves in part an arbitrary taxonomic decision. For example, Figure 30 illustrates the distribution of lengths of left M_3 of synthetocerines from the four biostratigraphic units included in this study. The separation of *P. francisi* from the Burkeville *P. texanus* is apparently consistent and reliable. However, there is a moderate overlap in the observed ranges of M_3 lengths of the Garvin Gully *P. texanus* and the Burkeville *P. texanus*, with the Burkeville form showing a definite size increase over the one from Garvin Gully. But although the mean lengths (Garvin Gully 22.2 mm, Burkeville 23.9 mm) of M_3 in the two forms are distinct, the degree of distinction is less than that between the succeeding forms. This same pattern is observed in other synthetocerine characters.

Though characters are not necessarily of equivalent value in different species or subspecies, in a relatively uninterrupted lineage such as this one they are almost equally diagnostic. A single changing lineage of successive species, "chronocline" of Simpson (1961), offers few nonarbitrary ways to arrive at taxonomic subdivision. Yet because of the general biostratigraphic, zoogeographic, and evolutionary utility derived from segmenting a continuous linage, it is often desirable to do so. It has been possible to recognize certain shifts in the patterns of synthetocerine characters from the Garvin Gully Fauna to the Burkeville Fauna, and because these shifts may be important in interpreting the evolution of this group of artiodactyls, they may eventually warrant separate taxonomic status for the two forms. The Burkeville specimens may represent a temporal or successional

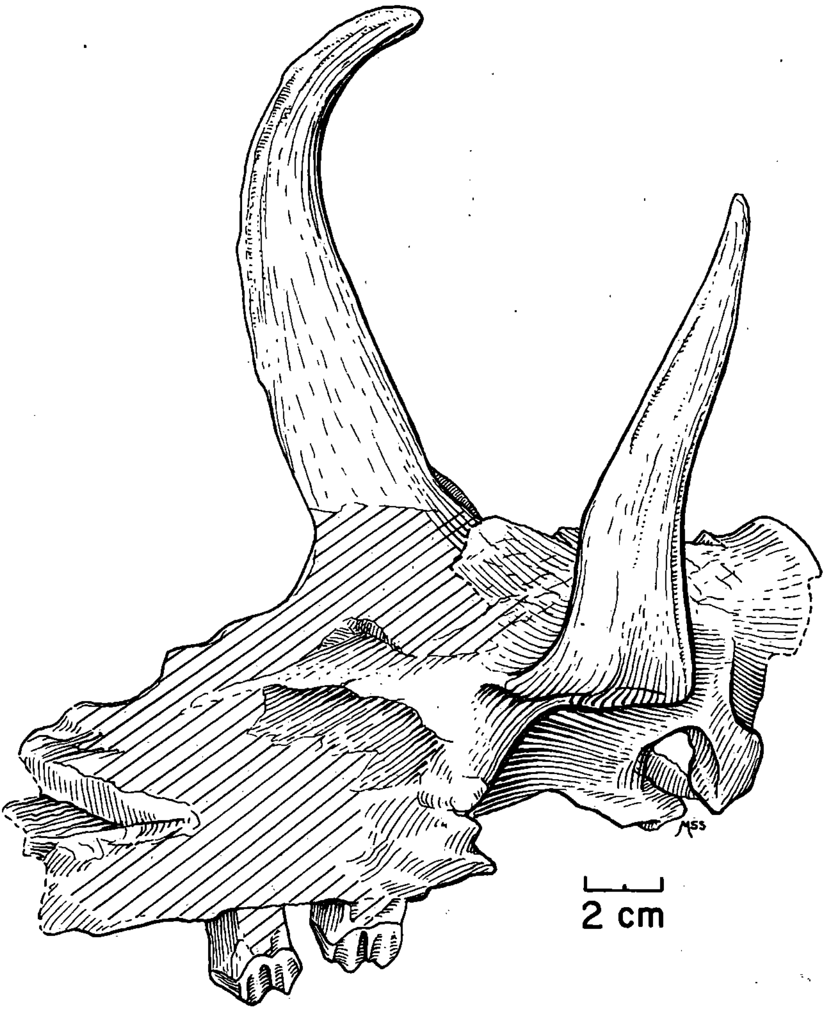

FIGURE 27. *Prosynthetoceras texanus* (UTBEG 31190-31); partial skull and postorbital horns.

subspecies of *P. texanus*. This is based on the range of variation of morphological characters and because the degree of their differentiation is significantly smaller than the sequential differences observed in other synthetocerine species. However the limited sample of specimens now available for study does not justify separate nomenclatorial status for the Burkeville specimens at this time.

Prosynthetoceras francisi Frick, 1937

Figure 28, Tables 18, 19.

TYPE. – TAMU unnumb., a skull with canine alveolus, P^2-M^3, rostral horn and bases of paired horns.

TYPE LOCALITY. – near Cold Spring, San Jacinto County, Texas.

REFERRED MATERIAL. – UTBEG 31219-214, partial left mandible with /C and P_4-M_3; 31219-213, partial left mandible with P_3-M_3; 31243-5, partial right mandible with P_3-M_3; 31183-47, partial left mandible with M_1-M_3; 31219-236, rostral horn; 31219-219, partial right mandible with P_4-M_3.

OCCURRENCE. – Cold Spring Fauna.

DIAGNOSIS. – A relatively large synthetocerine with hypsodont molars. P_2 highly reduced. The rostral horns are heavy and long; shaft longer than that of *P. texanus;* the paired postorbital horns are directed laterally and to the rear (posterolaterad). Other characters are described by Frick (1937: 605) as follows:

> The type cranium (Figures 2, 2A, 60-63), as noted above differs from (*Synthetoceras tricornatus*) in its considerably smaller size and notably smaller and shorter crowned dentition and retained P^2. What evidently is the alveolus of an enlarged canine occurs at the anterior base of the rostral horn. The cranial characters are better shown than in several of the (*Synthetoceras tricornatus*) skulls. Lacrimal vacuities, as in the case of *Protoceras*, are absent. The inverted U-shaped supra-occipital area, the peculiar paraoccipital processes and peculiarly constructed bullae are well shown. The paired postorbital horns are broken; the rostral horn is proportionately heavy and long-forked.

DESCRIPTION. – Other than size, the most striking differences in the skull and horns between *texanus* and *francisi* is the backward sweep of the frontal horns and the proportionately longer shaft of the rostral horn in the latter. Other skull comparisons are precluded by lack of diagnostic specimens of *texanus*. The upper molars of *P. francisi* are approximately 20 per cent larger than those of the earlier Burkeville *P. texanus*. Although the teeth of both the type and the most complete specimen (UTBEG 31219-213) in the University of Texas collection are worn, they appear to have been more hypsodont than forms lower in the section. The greatest changes have affected the accessory cusps; the posterior cingula are no longer visable and the anterior ones are considerably reduced. The median pillars, which are especially prominent in the molars of *P. texanus*, have undergone reduction. The second and fourth premolars of *P. francisi* are proportionately smaller than those of the Garvin Gully and Burkeville forms. This is equally true of the third premolar of the type of *P. francisi*. However, in other specimens confidently assigned to *P. francisi* and also in the large *Synthetoceras tricornatus*, the P^3 is anomalously robust.

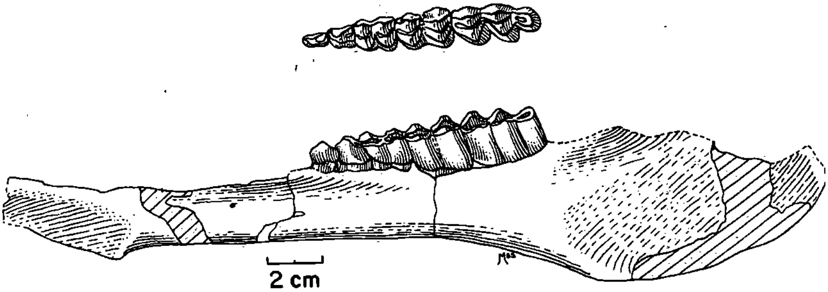

FIGURE 28. *Prosynthetoceras francisi* (UTBEG 31219-213); left ramus, occlusal view P_3-M_3, labial view of ramus and P_3-M_3.

Five rather well preserved lower jaws (UTBEG 31219-213, 31219-214, 31183-47, 31243-5, 31219-219) known from the Cold Spring Fauna provide an adequate basis for specific identification. In four of the five specimens the complete cheek dentition is present or indicated, and consists of three premolars and three molars. The caniniform P_1 and the base of the incisiform canine are preserved on UTBEG 31219-214, a left mandible, P_1 is seldom present. On UTBEG 31219-213, also a left mandible, most of the diastema and symphysis remains intact. The mandibular diastema of *P. francisi* is considerably longer than that of *P. texanus*, corresponding to a similar increase in diastema length of the upper jaw. Because the type specimen of *P. texanus* is broken anterior to P_2, the length of the diastema cannot be determined precisely, but judging from symmetry alone, it appears to be relatively shorter than the later forms. The diastemata of *Protoceras* and *Syndyoceras* are much shorter than any of the succeeding forms. Each ramus of *P. francisi*, except the type described by Frick (1937), has a P_2 or an alveolus for P_2, but this tooth, when present, is highly reduced. In UTBEG 31219-213 are two small alveoli for P_2 whereas UTBEG 31219-214 has only one alveolus. In all other respects the specimens are virtually identical and afford no reason for taxonomic separation. In view of the gradual reduction of the P_2 in earlier protoceratids and its complete loss in *Synthetoceras tricornatus* (based on FAM 32468 from the Clarendon beds), variation in occurrence of this tooth (and P_1) among individuals within any one population is not surprising, indeed is to be expected. P_3 of *P. francisi* is virtually indistinguishable from the earlier forms. With the exception of the greater recurving of the protoconid, which forms a distinct recess lingually between it and the metaconid, no significant difference in morphology is noted in P_4. M_2 has a small accessory tubercle at the base of the posterior limb of the protoconid. The M_3 of *P. francisi* is high-crowned and lacks any trace of accessory cusps.

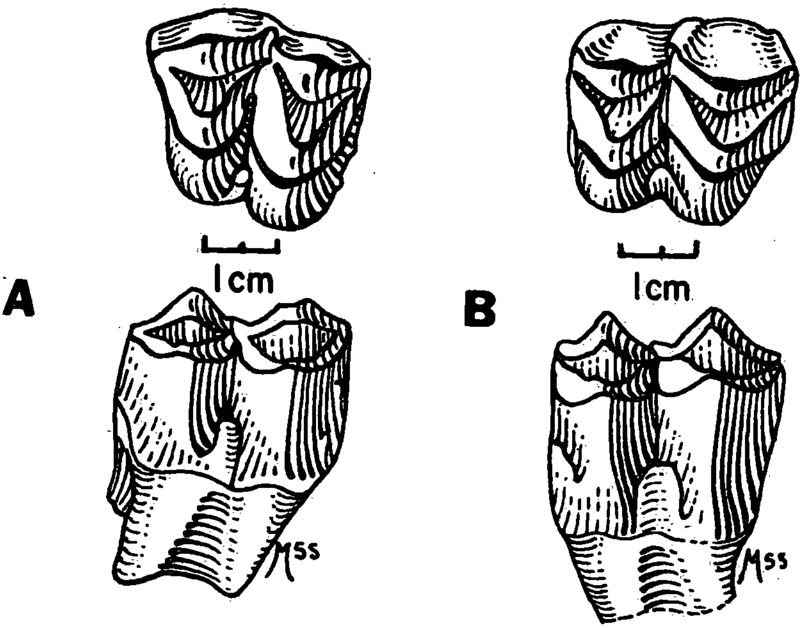

FIGURE 29. *Synthetoceras tricornatus* (UTBEG 31132-563); right M_2, occlusal and lingual views.

Synthetoceras Stirton, 1932
Synthetoceras tricornatus Stirton, 1932
Figure 11B, 11C, Table 20

Type. — Skull, UCMP 31520.

Occurrence. — Lapara Creek Fauna.

Referred Specimens. — UTBEG 30936-214, 31152-563.

Discussion. — Stirton (1932) described a new genus and species of artiodactyl from the Clarendon beds of the Texas Panhandle that subsequently became the type genus of a new subfamily of Protoceratidae, the Synthetoceratinae (Frick, 1937). This nearly complete skull represents the most advanced stage of synthetocerine evolution now known.

This species is recognized on the basis of a right M^3 (UTBEG 30936-214) from Live Oak County, and a right M^2 (UTBEG 31132-563) from Bee County. To date no other synthetocerine remains are known from the Pliocene of the Texas Coastal Plain. Younger Hemphillian McGehee deposits of Florida have so far yielded only two teeth, both of which are inseparable from Clarendonian specimens. The molars from the Lapara Creek Fauna are also inseparable from those of the Clarendon beds. Unfortunately, no better comparisons of the forms from these two areas can be made without additional material, especially that involving skull and cranial armament.

The Lapara Creek specimens are virtually identical in size and morphology with the previously mentioned two molars (UF 10044, 10045) recovered from the McGehee deposit (Hemphillian) of north central Florida. Until more material is forthcoming from the McGehee quarry, it is probably safe to include that form also in *S. tricornatus*.

Table 20. Measurements of Upper Molars of *Synthetoceras tricornatus*

Specimen no.	Length	Width
UTBEG 30936-214, RM^3	29.3	26.4
UTBEG 31132-563, RM^2	29.2	25.2
UCMP 31520, RM^3	29.3	25.6
UCMP 31520, LM^3	29.6	25.5
UF 10044, RM^2	27.0	25.6
UF 10045, RM^3	30.0	25.5

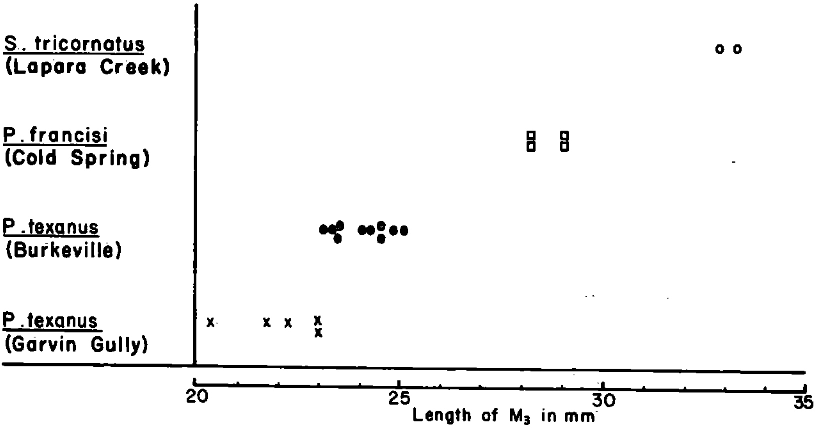

FIGURE 30. Distribution of measurements of M_3 lengths in Gulf Coast synthetocerines.

PHYLOGENY OF THE SYNTHETOCERATINAE

The series of protoceratids collected from successive biostratigraphic units in the Texas Coastal Plain Miocene exhibit characters that occur in a steplike progression thought to represent their actual phylogeny.

Remarkable uniformity in this group exists within each fauna; although sample size is small, the degree of variability found among specimens from widely separated localities is comparable to that expected in a single modern population of ruminant artiodactyls. No extreme variants have been recovered to indicate the presence of divergent geographically separated populations. Thus it appears that these animals at any one time were either members of one large interbreeding population, or perhaps were distributed in very closely related allopatric populations with occasional opportunity for contact, preventing the accumulation of isolating mechanisms. All evidence suggests that the sequence of synthetocerines from the Garvin Gully, Burkeville, Cold Spring, and Lapara Creek Faunas represents a continuously evolving lineage of successive ancestral-descendant populations, with evolution proceeding *in situ* by direct, sustained inheritance from one generation to the next, involving a slow shift of the adaptive optimum.

Dispersal, with the obvious exception of the initial immigration into the Coastal Plain, apparently entailed only emigration from this region, as no discontinuities ascribable to replacement by adaptively superior allochthons are evident.

The earliest protoceratids are known from the Great Plains of North America. The genus *Protoceras* is generally thought to be the ancestral group from which the later forms were derived. Among these, *Protoceras nasutus* of the White River appears to be the most likely progenitor of the early Miocene *Syndyoceras*. The skull of the genus *Protoceras* is characterized by the development of bony protuberances rising from the temporal crests of the parietals, from the supraorbital borders of the frontals, and from the upper margins of the maxillaries. These processes are represented in each *Protoceras* species, although suppressed to a greater extent in what are believed to be females. In *P. celer* the maxillary protuberances are broad and platelike, curve outward, and are widely separated at the base. In *P. nasutus* they are much narrower, more rodlike, and unite suturally over the nasal canal (Scott, 1940: 577). It is in this character especially that *P. nasutus* appears to anticipate *Syndyoceras*. The genus *Syndyoceras* has four prominent horns: the rostral or maxillary pair join over the nasal canal to form a common trunk, then bifurcate just above the juncture into two outwardly curving branches; the two frontal horns rise from a point above and behind the orbits and curve gently towards the midline. The kind of rostral horn seen in *Syndyoceras* appears to have evolved from the union of the two maxillary protuberances of the type seen in *Protoceras nasutus*. The frontal horns, on the other hand, were probably derived from the union of the bony processes on the supraorbital borders of the frontals and those on the temporal crests of the parietals, forming a single beam. *P. nasutus* satisfies those requirements necessary for being placed in a morphologically ancestral position to *Syndyoceras* and the later synthetocerines.

The lack of a significant number of frontal (postorbital) and nasal (rostral) horns in any of the availible collections makes difficult the detection of any evolutionary trends in these parts. It is difficult to determine the constancy of anatomical details observed in contemporaneous specimens because of the very small samples available from any one fauna, it is especially difficult when comparing specimens collected from each of the successive faunas. It becomes easy to confuse variability with phylogeny. Notwithstanding this complication, the ancestral horn condition for this lineage seems discernible in *Syndyoceras*. The postorbital horns of *Syndyoceras* extend laterally at nearly right angles to the long axis of the skull and curve up and towards the midline in a wide semicircle. At the base, these horns tend to be slightly flared and flattened, but become more rounded toward the middle. No bony protuberances occur along their edges. The only recovered postorbital horns of *P. texanus* share several characters of *Syndyoceras.* The horns are directed laterally from the skull and recurve rather sharply toward each other. They differ from those of *Syndyoceras* in the slightly greater flare near the base and in the increase in irregularity or roughness of the anterior and posterior edges at the flare. *P. francisi* shows considerable change from the preceding forms; the horns sweep out from the skull at a low angle and in a posterior direction, have greater flattening towards the base, and the anterior and posterior edges are marked by more prominent irregularity. This progression in characters of the horn continues into *Synthetoceras.*

The evolution of the rostral horn of the synthetocerines has involved primarily the lengthening of the main shaft, resulting in an increase of the distance from the base of the rostral horn to the point of bifurcation. There also seems to have been a gradual increase in backward growth of the distal, or forked, end of the rostral horn. This is perhaps a counterbalancing adaption serving partially to overcome the disadvantage of having such a heavy weight towards the tip of the snout.

Thus from the preceding discussion and from the data included in the systematic description of these forms, a morphologic, and presumably phylogenetic, series representing the steps in protoceratid evolution from late Oligocene through early Pliocene can be established. On the generic level this series is as follows:

Protoceras-Syndyoceras-Prosynthetoceras-Synthetoceras.[1]

Several morphologic trends from *Syndyoceras* of the early Miocene to *Synthetoceras* of the early Pliocene can be discerned.

(1) increase in size
(2) reduction of premolars
(3) reduction of intercolumnar tubercles and cingula in molars
(4) increase in crown height
(5) increase in diastema length

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[1] As this paper was going into press, Stirton's (1967) description of a new genus, *Lambdoceras,* was published. This genus from the middle Hemingfordian Flint Hill fauna of South Dakota, is in my opinion very difficult to separate from *Prosynthetoceras.* I have not had the opportunity to study Stirton's specimens; however, the new taxon is discussed in Patton and Taylor (MS).

(6) more posteriorly directed postorbital horns
(7) increase in irregularity of lateral edge of postorbital horns towards the base
(8) increase in distance from base of rostral horn to point of bifurcation
(9) gradual development of bony covering of canal for nerves and blood vessels supplying rostral horns

Infraorder Pecora Linnaeus, 1758
Family Cervidae Gray, 1821
Subfamily Palaeomerycinae Matthew, 1904
Blastomeryx Cope, 1877
Blastomeryx elegans Matthew and Cook, 1909
Table 21

Type. — AMNH 1401, a partial left ramus, with P_3-M_3.

Occurrence. — Lapara Creek Fauna.

Referred Specimens. — UTBEG 31132-331, partial left ramus with M_2-M_3; 31132-4, dP_4; 30896-326, partial right ramus with P_3-M_2 and broken M_3; 30896-496, partial right ramus with P_3-M_3.

Description. — The four referred specimens from Bee County, Texas, are indistinguishable from a series (AMNH 17345, 17341, 17347, 17348, 17349) collected from the Snake Creek beds of Sioux County, Nebraska, and designed by Matthew and Cook (1909) as *Blastomeryx elegans*. Frick (1937) separates the genera *Blastomeryx* and *Longirostromeryx* on the basis of the latter's elongate diastema and greatly reduced P_2-P_3. No symphysis is preserved in any of the Lapara Creek specimens, but the premolars are not markedly reduced as in species of *Longirostromeryx*. P_2 is represented by two alveoli.

Table 21. Measurements of *Blastomeryx elegans*

Measurement	AMNH 14101 (Type)	UTBEG 30896-496	UTBEG 30896-326	UTBEG 31132-321
Length P_3-P_4	14.3[1]	14.5	13.8	....
Length P_3-M_3	45.0[1]	43.4	....	....
Length M_1-M_3	32.0	30.7	....	....
P_3, length × width	6.2 × 3.0	6.5 × 3.2	6.8 × 3.0	....
P_4, length × width	7.3 × 4.0	8.2 × 3.5	8.0 × 2.8	....
M_1, length × width	9.0 × 5.2	8.8 × 4.7	8.4 × 4.3	....
M_2, length × width	10.3 × 5.9	9.0 × 5.9	8.6 × 5.3	9.5 × 5.7
M_3, length × width	13.9 × 5.6	14.0 × 5.5	....	12.4[2] × 5.5

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[1] From illustration (Matthew and Cook, 1909: 410, fig. 23)

[2] Approximate

Longirostromeryx Frick, 1937

Longirostromeryx blicki Frick, 1937

Figure 31, Table 22.

Type. – FAM 31734, a right ramus with symphysis and P_2-M_3.

Occurrence. – Cold Spring Fauna.

Referred Material. – UTBEG 31183-35, a partial skull with P^3-M^3, a right ramus with P^4-M^3, and two upper canines.

Discussion. – The Cold Spring specimens compare closely to specimens Frick (1937) assigned to (?)*Longirostromeryx blicki* from North Santa Clara River, New Mexico. In addition to the elongate diastema of *Longirostromeryx*, the genus is also characterized by reduction of P_2-P_3. (?)*L. blicki* is known to have an elongate diastema, but apparently because it has comparatively large premolars, Frick (1937) assigned it questionably to *Longirostromeryx*.

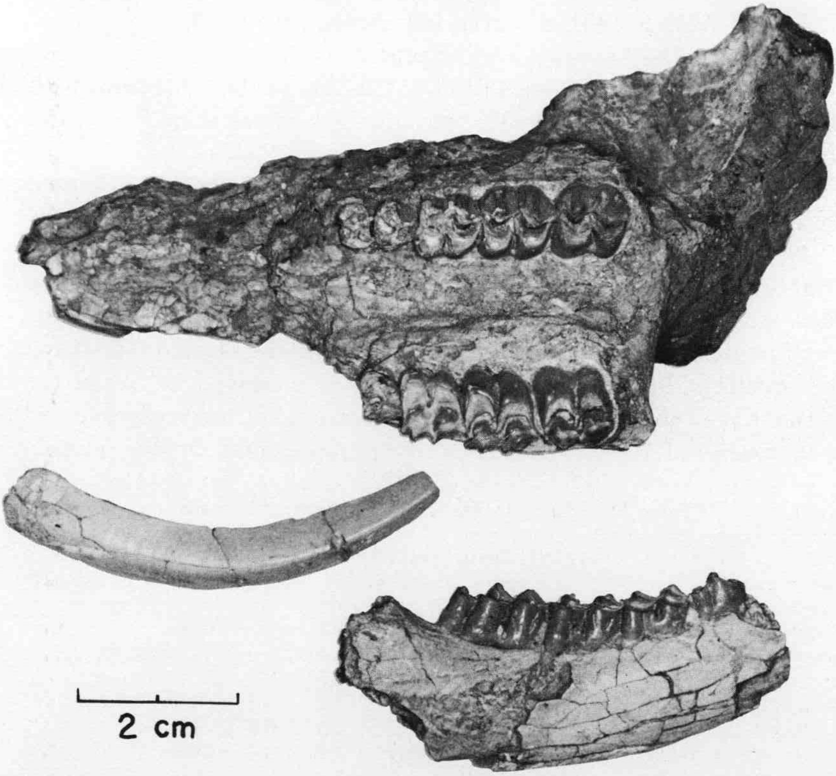

Figure 31. *Longirostromeryx blicki* (UTBEG 31183-35); occlusal view of partial skull with upper dentition, lateral view of left C/, labial view of right ramus.

The genus *Longirostromeryx* as defined by Frick (1937) includes seven species (two questionably assigned): *L. wellsi* (*Matthew*); *L. merriami* Frick, the type species of *Longirostromeryx; L. serpentis* Frick; *L. clarendonensis* Frick; *L. novomexicanus* Frick; (?)*L. vigoratus* (Hay); and (?) *L. blicki* Frick. I can see no substantial difference between *L. wellsi* and *L. merriami* in size or morphology and believe the two species should be synonomized under *L. wellsi.* The teeth of *L. serpentis* are very worn so that litle cusp morphology remains visible, but the shape and dimensions of the teeth and jaws are comparable to *L. wellsi* and also should probably be synonymized with that species.

L. novomexicanus from the Santa Cruz beds of New Mexico is based on a partial left ramus with P_2-P_3 alveoli and P_4-M_3. Because neither of the two diagnostic characters of *Longirostromeryx,* reduction of P_2-P_3 and elongate symphysis are present on the type and only specimen, no clear reason exists for including it in this genus. (?)*L. vigoratus* was originally described as *Blastomeryx vigoratus* by Hay (1924) on the basis of a left M_2 and left M_3. Again no conclusive evidence exists for assigning it to either genus.

Faced with a similar dilemma in constructing a tenative arrangement of New World testudinines and supposed testudinines, Williams (1950) states:

> Dr. Paulo Vanzolini of the Department of Zoology, State of San Paulo, Brazil, has suggested to the author that specific names of this nature to be designated *species inquirendae.* This nomenclatorial category seems to be unusual or unknown in North American taxonomy. It would, the author believes, serve a useful purpose. Certainly names of possible but presently indemonstrable validity cannot properly be treated as of equivalent value with adequately based, well-known taxonomic categories, nor is it at all reasonable to place such names in synonymy, since this could be done only arbitrarily and doubtfully. There is evident need for a purgatory in which such names may reside until proper disposition can be made for them.

The International Code of Zoological Nomenclature (1961) authorized such a procedure, and under the category *species inquirendae* I prefer to include the taxa *L. novomexicanus* and (?)*L. vigoratus.*

L. clarendonensis represents the most advanced stage of *Longirostromeryx* development in premolar reduction. P_2 tends to be lost and P_3-P_4 are greatly reduced. (?)*L. blicki,* on the other hand, was only questionably assigned to *Longirostromeryx* by Frick (1937) apparently because of its comparatively unreduced premolars. The

Table 22. MEASUREMENTS OF *Longirostromeryx blicki*

Measurement	UTBEG 31183-35
P^3-M^3	36.4
P^4-M^3	31.9
M^1-M^3	26.2
P^3, length × width	4.6[1] × 5.7[1]
P^4, length × width	6.0 × 6.6
M^1, length × width	8.7 × 9.1
M^2, length × width	10.0 × 10.2
M^3, length × width	9.2 × 9.9
P_4-M_3	39.0
M_1-M_3	31.6
P_4, length × width	7.8 × 4.0
M_1, length × width	8.7 × 5.6
M_2, length × width	9.6 × 6.2
M_3, length × width	14.0 × 6.1

[1] Approximate

elongate diastema in this species is well established. Because premolar reduction appears to be a progressive character in this genus, it is not surprising to find Barstovian specimens with less premolar reduction than those from Clarendonian deposits. Nor would it be unexpected to find forms conservative in premolar reduction contemporaneous with the more progressive species in this regard. *Longirostromeryx* is probably better defined on the basis of the great length of the mandibular symphysis although, as Gregory (1942) points out, the extent of variation of this character is as yet undetermined. For this reason I prefer to consider the Cold Spring specimens and those Frick (1937) referred to (?)*L. blicki* as belonging to *Longirostromeryx* and remove them from their questionable status within that genus.

(?)*Longirostromeryx vigoratus* (Hay)

Blastomeryx vigoratus Hay, 1924, p. 16, pl. II, figs. 13, 14.

TYPE. — TAMU 2378, left M_2-M_3.

OCCURRENCE. — Garvin Gully Fauna.

DISCUSSION. — Hay (1924) described *Blastomeryx vigoratus* on the basis of six teeth collected from the Garvin Farm quarry. He characterized the species as being of nearly the same size as *B. wellsi* Matthew (Now *Longirostromeryx wellsi*) from the late Miocene of South Dakota, although M_1 of *wellsi* is no longer and wider (11 × 8 mm) than that of *vigoratus*, which is 10 mm long and 6.3 mm wide.

L. wellsi differs from *vigoratus* also in having more hypsodont teeth. Frick (1937) has since listed this species as (?)*Longirostromeryx vigoratus* (Hay), although the length of its symphysis and proportions of its premolars are still unknown. Perhaps this decision was based on the presumed affinity of (?)*L. vigoratus* to *L. wellsi*, whose assignment to *Longirostromeryx* is more confidently founded. In any event, I believe (?)*L. vigoratus* should be considered a *species inquirenda* for the same reasons as outlined in the discussion of *L. blicki.*

Subfamily Dromomerycinae Frick, 1937

Barbouromeryx Frick, 1937

Barbouromeryx (Bouromeryx) submilleri Frick, 1937

Figure 32C.

Type. — FAM 33729, a right ramus.

Occurrence. — Cold Spring Fauna.

Referred Material. — UTBEG 40622-26, a partial right ramus with M_2 and M_3.

Description. — This specimen is from Belt's Creek, Tyler County, Texas. The molars are comparable to and about the size of those of *Bouromeryx submilleri* from Aphelops Draw, Sioux County, Nebraska, except for a less prominent metastylid on the anterior lobe of M_3. M_2 measures 12.7 mm × 10.9 mm; M_3, 18.0 × 11.1 mm.

Discussion. — The systematic position of this subgenus is rather unclear. Frick (1937) includes it in his subfamily Barbouromerycinae, apparently in the type genus *Barbouromeryx*. As with other groups, he does not discuss the type subgenus; presumably it would assume the characteristics of *Barbouromeryx*, but in Frick's treatment of these forms, subgeneric characters seem to bear equal taxonomic weight with generic characters. Under this arrangement the utility of the subgeneric grade is lost by the lack of hierarchical ranking, and as a result systematic relationships within and among the closely allied taxa become obscured. That these taxonomic assignments are not regarded by Frick to reflect presumed genetic relationships is further evidenced by his phylogenetic considerations of the Barbouromerycinae, in which subgenera are sometimes treated separately from the genera in which they are included (Frick, 1937: 49, 127). The validity of the subgeneric grade in taxonomy is not denied (for pertinent remarks on Frick's usage of subgenera see Simpson, 1945: 267), but its utility in a paleontological series such as this one is questionable.

I do not suggest that *Bouromeryx* or any other subgenus of the Barbouromerycinae be elevated or reduced in rank at this time. The group is still poorly understood, and a rearrangement of any one of its parts without detailed study and consideration of its relationship to the others is obviously premature. Clearly this genus and the rest of the Dromomerycinae comprise a closely related group of artiodactyls that differ substantially (and, I think fundamentally) from the rest of the Cervoidea with which they are usually classified (Simpson, 1945). I agree with the observations of some others (Matthew, 1915, 1918; Schlosser, 1924; Pilgrim, 1941a, 1941b; Crusafont Pairo, 1952) that the dromomerycines share many features of the giraffoids and may actually share common ancestry as well. In a later paper Crusafont Pairo (1953) concluded that this resemblance results rather from convergence. The issue obviously is not settled.

Cranioceras Matthew, 1918

Frick (1937: 47) recognizes two groups within the genus *Cranioceras*: a subgenus *Procranioceras*, distinguished by distinctly brachyodont molars and large-proportioned premolars, and *Cranioceras* "proper" (sensu Frick, 1937) which is characterized by a larger size, slightly more hypsodont molars, proportionately smaller premolars, and an occipital horn which in the male is rounder, more posteriorly directed, and longer.

The skull of *Procranioceras* is roughly suggestive of *Dromomeryx*, but is separated from that genus "in the more anterior position of the orbits, the erectness of the paired horn cores, the absence of any trace of a postorbital flange, and in the characters of the sagittal area, with its remarkable, backwardly directed, forwardly curved median-occipital horn" (Frick, 1937: 75). The lower incisors and canines of *Cranioceras clarendonensis* also closely resemble those of *Dromomeryx*. The premolars of *C. clarendonensis* are "notably brachyodont. Compared to [*Dromomeryx*], the premolars tend to be proportionately larger, the P_4 anterior fossette is unformed, and . . . there is no dP_1 (P_1)" (Frick, 1937: 76).

Two specimens from the Lapara Creek Fauna appear referable to *Cranioceras* "proper": a right immature dentition (UTBEG 31081-1480), and a left postorbital horn (UTBEG 31132-455). Although material is admittedly meager, these specimens are assigned to *Cranioceras clarendonensis* Frick.

Specimens from the Garvin Gully Fauna Hay (1924) described as *Dromomeryx texanus* and Frick (1937) lists as ?*Cranioceras texanus* (Hay) are referred to *Prosynthetoceras* Frick.

Cranioceras clarendonesis Frick, 1937

Figure 32a

TYPE. — FAM 32454, a right ramus with symphysis and P$_2$-M$_3$.

REFERRED MATERIAL. — UTBEG 31081-1480, an immature dentition; and UTBEG 31132-455, partial horn.

OCCURRENCE. — Lapara Creek Fauna.

DESCRIPTION. — An immature dentition (UTBEG 31081-1480) from Bee County, Texas, agrees very closely in size and cusp morphology with a similar dentition (FAM 32216A) from the MacAdams Quarry, Clarendon, Texas. Other immature dentitions of similar size (FAM 32491, *Subdromomeryx scotti,* and FAM 31199, *Bouromeryx nebrascensis*) differ from the Lapara and Clarendon specimens primarily in size of tubercles of dP$_4$ and in the presence of a "*Palaeomeryx* fold" on M$_1$.

The left postorbital horn, UTBEG 31132-455, from this fauna is broken distally, but on the basis of the proximal cross-sectional shape and the direction and taper of the preserved part of the shaft, it more closely approaches the postorbital horns of *Cranioceras* than *Dromomeryx, Bouromeryx,* or any other similar form. For this reason,

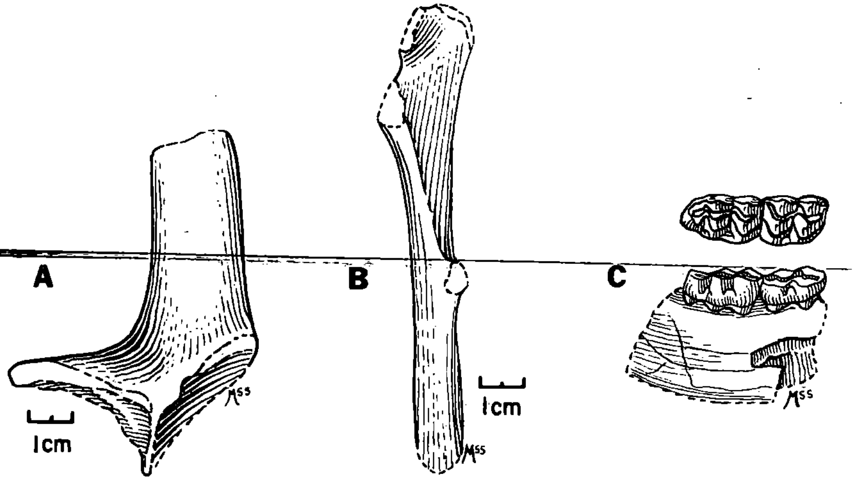

FIGURE 32. A. — *Cranioceras clarendonensis* (UTBEG 31132-455); partial horn. B. — *Ramoceros ramosus* (UTBEG 311-73); partial horn. C. — *Barbouromeryx (Bouromeryx) submilleri* (UTBEG 40622-26); labial and occlusal views of right M$_2$-M$_3$.

I tentatively refer this specimen to *C. clarendonensis*, the only *Cranioceras* species presently recognized in the Lapara Creek Fauna.

Family *Antilocapridae* Gray, 1866
Ramoceros Frick, 1937
Ramoceros ramosus (Cope), 1874c
Figure 32B

TYPE. – USNM 1144, a three-pronged "antler."

OCCURRENCE. – Lapara Creek Fauna.

REFERRED MATERIAL. – This species is recognized on the basis of a partial four-pointed "antler," or horn, recovered from the Santa Fe Marls of New Mexico. The Lapara Creek specimen is inseparable from horn material assigned by Frick to *Ramoceros ramosus* from New Mexico, Colorado and Nebraska.

DISCUSSION. – Frick (1937: 290) defines the genus *Ramoceros* as: "characterized by the depressed postorbital position of the three-to-four-pointed 'antlers,' which are of remarkably Cervine appearance; the basal 'pedicle' is depressed and directed outwardly and posteriorly; the tips (not always symmetrical) flare widely; the shafts are slender with circular-tending cross section and are deeply curved anteriorly."

This genus, included in Frick's Division Merycodontini (Merycodontinae of Simpson, 1945), is divided into two subgenera, *Paramoceros* and *Merriamoceros*, from which *Ramoceros* "Proper" (sensu Frick) is excluded. These subgenera, presently monotypic, are separated from each other by the shape and length of the shaft, and the shape, number, and distribution of terminal prongs of the postorbital horns. *Paramoceros* is based on *R. (P.) brevicornis* from Barstow, California, whereas the type species of *Merriamoceros* is *R. (M.) coronatus* (Merriam), also from Barstow. If subgenera are retained, the type subgenus, *Ramoceros,* must be recognized for the type species of the genus, *R. ramosus* (Cope). The three groups are decidedly different in appearance. *Ramoceros* "Proper" (should read *Ramoceros (Ramoceros)*) is characterized by Frick (1937: 290) thusly: "The shaft is long, with a forwardly directed prong ('brow tine') at two-thirds distance above the base, and distally is bi- or tri-forked."

Frick (1937: 291) recognizes the subgenus *Paramoceros* on the following grounds: "The main shaft is short (in the California subgenotype) to long (in Rocky Mountain variation) and the secondary shaft is reduced, the lower and two terminal prongs simulating a tripointed crotch."

The third subgenus, *Merriamoceros,* Frick (1937: 291) describes as having the following features: "The 'horns' are remarkable for their small size, tendency to palmation and mutitubercular pointing. They recall, in minor measure, miniature moose antlers."

Merycodont indet.

OCCURRENCE. – Lapara Creek Fauna.

REFERRED MATERIAL. – UTBEG 31170-28, a right M_3; and UTBEG 31170-68, left M_3.

DESCRIPTION. – Two small hypsodont M_3's from Bee County, Texas, are referred to the Merycodontinae. Reliable generic designation of these isolated molars is virtually impossible and is not attempted. Whether they are referable to recognized merycodonts in the Lapara Creek Fauna, e.g., *Ramoceros,* or represent an otherwise unrecognized group is equally uncertain.

Infraorder OREODONTA Osborn, 1910

Although the presence of oreodont material in the Texas Coastal Plain fauna was previously reported by Quinn (1955) and by Schultz and Falkenbach (1941a), the former distribution of these animals in the Gulf Coast region has remained largely unknown. In addition to the three genera from Texas described in this paper, oreodonts now are known to occur in Florida deposits as well. Maglio (1966) describes *Merychyus* from Thomas Farm, while Patton (1967, 1966[67]) reports oreodonts from several different Florida localities ranging in age from Late Oligocene to Middle Miocene. Aside from their local importance, these occurrences demonstrate a greater accessibility of the Gulf Coastal Plain to immigration from the Great Plains than previously had been considered probable.

Family MERYCOIDODONTIDAE Thorpe, 1923
Subfamily TICHOLEPTINAE Schultz and Falkenbach, 1941a
Ticholeptus Cope, 1878
Ticholeptus rileyi Schultz and Falkenbach, 1941a

Table 23

TYPE. – FAM 42329, a left mandible with I_1 (alv.)-M_3 and partial femur.

Table 23. MEASUREMENTS OF *Ticholeptus rileyi*[1]

Ramus	FAM 42329
Length (max., including incisors)	165.5
Length, /C to condyle incl.	150.0
Depth of jaw below coronoid	77.0
Depth of jaw below anterior edge of M_3	26.5
Length, /C-M_3 incl.	103.5
Length, P_1-M_3 incl.	96.5
Length, P_1-P_4 incl.	39.5
Length, M_1-M_3 incl.	57.0

[1] After Schultz and Falkenbach (1941a)

TYPE LOCALITY. – near Cold Spring, San Jacinto County, Texas.

OCCURRENCE. – Cold Spring Fauna.

DISCUSSION. – This species is currently recognized in the Cold Spring Fauna only on the basis of material in the Frick Collection. No material other than the type was reported.

Schultz and Falkenbach (1941a: 83-84) describe this species as being very close to *T. hypsodus* Loomis (1924) from Sioux County, Nebraska. Their specific description follows:

> SKULL.– Unknown.
>
> MANDIBLE. – Approximate size of that of *T. hypsodus;* ramus shallow (even shallower than in *T. obliquidens* and *T. tooheyi*); ascending ramus shallow and narrow anteroposteriorly; condyle light.
>
> DENTITION. – Superior series unknown; inferior series approximate size of those of *T. zygomaticus* and *T. hypsodus.*
>
> LIMBS. – Unknown only from a partial femur; lighter than examples of *T. hypsodus.*

Ustatochoerus Schultz and Falkenbach 1941a

Ustatochoerus profectus (Matthew and Cook), 1909

Figure 33, Table 24

TYPE. – AMNH 14055, incomplete left ramus with I_2-M_3 (/C broken and P_4 represented by alveolus).

OCCURRENCE. – Lapara Creek Fauna.

REFERRED SPECIMENS. – UTBEG 31081-685, a right maxillary with /C-M^3, UTBEG 31081-1157, a right maxillary with M^2-M^3 and alveoli for P^1-M^1.

DISCUSSION. – The Lapara Creek specimens are morphologically inseparable from specimens from the Lower Ash Hollow Formation of Nebraska referred to *U. profectus* (Matthew and Cook) by Schultz and Falkenbach (1941a: 36). The Coastal Plain specimens fall within

Table 24. MEASUREMENTS OF CERTAIN SPECIES OF *Ustatochoerus*[1]

	Lapara Creek 31081-685	*U. profectus* FAM 33621	*U. profectus studeri* FAM 43031	*U. medius* FAM 4303OB	*U. medius mohavensis* FAM 34464	*U. medius novomexicanus* FAM 43258A
Length, C/-M^3	134.0	142.5	127.0	122.0	130.0	136.0
Length, P^1-M^3	118.0	128.5	113.0	109.0	113.0	121.0
Length, P^1-P^4	47.6	55.5	50.0	45.5	46.5	52.5
Length, M^1-M^3	75.3	74.0	70.0	67.0	70.5	71.5

[1] Mostly after Schultz and Falkenbach (1941a, Table 1)

the lower limits of the range of variation of *U. profectus*, represented by *U. profectus studeri* from the Texas Panhandle, and the upper limits of the range of *U. medius* (Leidy), represented by two subspecies, *U. medius mohavensis* and *U. medius nomomexicanus* (Table 24). At present there seems to be no way to separate the jaws of large "varieties" (sensu Schultz and Falkenbach, 1941a) of *U. medius* from those of the smaller varieties of *U. profectus*. The Lapara Creek specimens more closely approach *U. profectus profectus* (not so designated by Schultz and Falkenbach (1941a) but provided for under Article 61(a) of the International Code of Zoological Nomenclature (1961: 59)) than they do *U. medius*.

Subfamily MERYCHYINAE Simpson, 1945

Merychyus Leidy, 1858

Merychyus sp.

Figure 33

OCCURRENCE. – Garvin Gully Fauna.

REFERRED MATERIAL. – UTBEG 40105-5, a fragment of left mandible lacking dentition.

DESCRIPTION. – The nature and number of alveoli present in the fragmentary mandible indicate that it represents a juvenile individual. The specimen measure 60 mm from the anterior of P_1 alveolus to the posterior of M_3 alveolus, falling just below the minimum range of

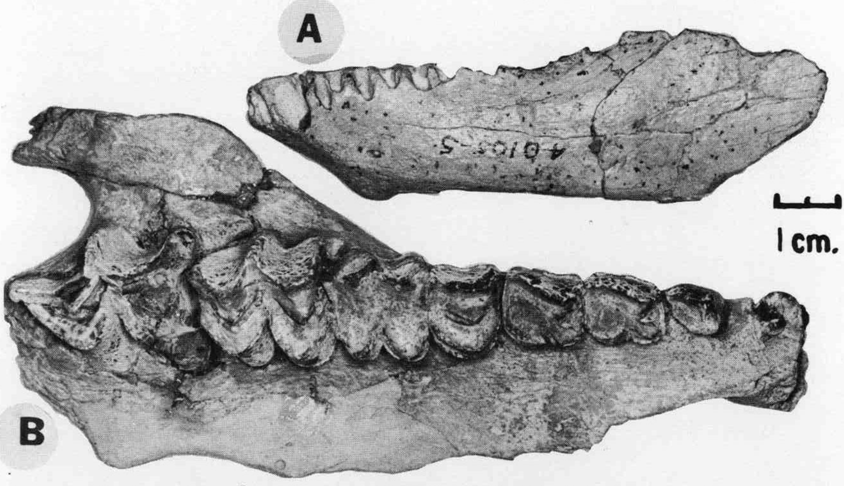

FIGURE 33. A. – *Merychyus* sp. (UTBEG 40105-5); labial view of edentulous left ramus. B. – *Ustatochoerus profectus* (UTBEG 31081-685); occlusal view of right maxillary with C/-M_3.

Merychyus minimus Peterson from the Lower Marsland (Schultz and Falkenbach, 1947)[1].

AGE AND CORRELATION

This paper, as one of a series of taxonomic and stratigraphic studies of the fossil vertebrate faunas of Tertiary age in the Texas Gulf Coastal Plain (Hay, 1924; Hesse, 1943; Quinn, 1952, 1955; Wilson, 1956, 1957, 1959, 1960), provides additional information useful in making biostratigraphic correlations between the Texas faunas and those elsewhere. As each major taxonomic study is completed, and the systematic relationships of the various groups become better known, increasing information on which to base studies of biostratigraphy, zoogeography, and paleoecology is made available. Because the faunas (sensu Wilson, 1959) in question correspond to what many biostratigraphers call assemblage zones, new information on previously poorly known components serves to broaden the foundation upon which the assemblage zone rests and alleviate overdependence on a few taxa for correlation purposes. Evidence presented in this study indicates that the ages assigned to some of the Texas Coastal Plain faunas can be modified (Fig. 34).

GARVIN GULLY FAUNA

Studies by Quinn (1955) and Wilson (1956, 1957, 1960) established the first clear outline of the general stratigraphic framework within which these faunas occur. Quinn (1955) and Wilson (1960) considered the Garvin Gully Fauna to be of late Arikareean age. This view was based primarily on the close similarity of the Garvin Gully taxa to those from the Florida Thomas Farm deposit. The Thomas Farm at that time was included in the Hawthorne Formation, of middle Miocene age. Apparently because Simpson (1932) believed material from the Hawthorne Formation at Quincy and Midway, Florida to be somewhat younger than that from the Thomas Farm Quarry, Quinn suggested that the Thomas Farm fossils were prob-

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[1] The Marsland Formation of Schultz and Falkenbach (1947) includes more than Peterson's (1906) "Upper Harrison," as that unit is interpreted by Cook (1960, 1965), McKenna (1965), and Skinner (pers. comm.). The "Lower Marsland" of Schultz and Falkenbach is equivalent to Peterson's Upper Harrison and the restricted Marsland of Cook (1965) and McKenna (1965). The "Upper Marsland" includes Cook's Runningwater Formation (See McKenna, 1965, for review of this problem).

ably of "Tampa", or early Miocene age. The ages of both the Hawthorne and Tampa Formations were determined on the basis of marine invertebrates fossils (Cooke and Mossom, 1929; Puri and Vernon, 1964), which in the Gulf Coast region have not yet been tied into the terrestial vertebrate faunas. Thus, there is no wide agreement on the equivalence of these sections, nor much information available on the magnitude of the geochronologic "offset" between the two.

In his section on Age and Correlation, Quinn (1955: 72-76) states that "there is nothing in the Garvin Gully fauna indicative of an age later than lower Miocene." The Thomas Farm deposit definitely is not correlative with the Tampa Formation, nor can it be placed with any certainty even in the Hawthorne Formation, a more commonly accepted correlation. (Vernon (1951) traces the Hawthorne only to within 25 miles of Thomas Farm.) The Florida Geological Survey includes the Thomas Farm sediments in the "Alachua Formation," which they regard as the continental equivalent of the Hawthorne. According to Puri and Vernon (1964):

> The placement of the bone-bearing sediments at the Thomas Farm excavation presents a very perplexing geologic problem. Beds of at least two ages are represented: Upper Eocene, Crystal River Formation; and middle to upper Miocene, Alachua Formation. Limestone of the Crystal River Formation occurs as a pinnacle on the north side of the quarry . . . and around it, and also overlapping it are clays, boulder bars composed of Suwannee Limestone fragments . . . and cross-bedded lime and quart sands of the Alachua Formation . . .

Sediments of the "Alachua Formation" occur in fissures, depressions, and sinkholes in the underlying Ocala Limestone and are related only in that they are derived primarily from the same source (the Hawthorne Formation) and in that they accumulated in the same kind of karst-controlled catchment basin. Because this process has been operative since late Oligocene time,[1] the deposits are usually totally disjunct and quite varied geochronologically, and in no sense can they be considered to comprise a formation in the generally accepted use of the term (Code Strat. Nomen., 1961). In any event, because of the peculiar geologic configuration of the Thomas Farm deposit, it is fruitless to attempt to achieve accurate age determination for it using evidence based on lithostratigraphic data.

The age of the Thomas Farm fauna generally has been con-

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[1] Based on the discovery of a late Oligocene land vertebrate fauna in central Florida (Patton, 1967, 1969)

sidered to be late Arikareean. White (1942) believed it to be somewhat older, but based his thesis on paleogeographical arguments (concerned with the extent, depth, and length of existence of the so-called Okefenokee Trough) that many workers dispute. Bader (1956), in a study of the Thomas Farm horses, regarded the fauna as being late Arikareean, but based this conclusion in part on Quinn's (1955) estimation of the age of the Thomas Farm in relation to the Garvin Gully Fauna. In a more recent paper, H. E. Wood (1964) states that a Thomas Farm rhinoceros, *Diceratherium barbouri*, is progressive over the classic early Miocene index fossil from the Harrison beds, *D. cooki,* and indicates a late Arikareean or early Hemingfordian age for the deposit. On the basis of their closer proximity to and greater number of taxa shared with the geochronologically more accurately placed Great Plains faunas, seemingly a more logical approach is to place greater reliance on the Texas Coastal Plain faunas in dating the Thomas Farm, rather than the other way around. Irrespective of the larger argument, there is general agreement that the Thomas Farm fauna is slightly younger than the Garvin Gully.

Wilson (1957, 1959, 1960) assigned the Garvin Gully Fauna to the Arikareean on the basis of *Daphaenodon* cf. *superbus, Dinohyus hollandi,* and the abundance of *Parahippus.* He pointed out that the association of *Daphaenodon, Dinohyus,* and *Parahippus* is characteristically Arikareean, as designated by the Wood Committee (Wood et al., 1941). Wilson (1959) further stated that of the horse material of *Parahippus* size and proportions from the Garvin Gully Fauna, 10 per cent possess *Merychippus* characters, which is similar to the

Table 25. AGE RANGE OF GARVIN GULLY GENERA

Taxon	Arikareean	Hemingfordian	Barstovian	Clarendonian
Palaeolagus	x			
Daphaenodon	x			
Amphicyon		x	x	x
Cynodesmus		x		
Dinohyus	x			
Merychyus	x	x	x	
Oxydactylus	x	x		
Diceratherium	x	x		
Hypohippus		x	x	x
Merychippus		x	x	x
Anchitherium	x	x		
Parahippus	x	x	x	
Archaeohippus;	x	x	x	
Hippodon			x	

finding of Bader (1956) for the Thomas Farm horses. Among individual skulls of these horses from the Thomas Farm, several have dentitions exhibiting both *Parahippus* and *Merychippus* features (White, 1942; Bader, 1956). Wilson (1959: 773), following White (1942) and Bader (1956), concluded that:

> Since *Parahippus* is absent in the Burkeville Fauna it seems obvious that it became extinct by evolution into *Merychippus*. Once *Merychippus* had evolved it migrated northward and lived alongside surviving parahippines in Nebraska.
>
> The appearance of *Merychippus* then at the type section in Nebraska is one of migration from the Gulf Coast northward. The appearance of *Merychippus* on the Gulf Coast is by evolution and must be earlier.

Continuing, since the appearance of unquestioned *Merychippus*, or that stage of horse evolution represented by "*Merychippus*," i.e. presence of cement, connected crotchet, etc., marks the base of the Hemingfordian, the aforementioned evolutionary transition leading to it must logically precede it also in time, and therefore should be regarded as an Arikareean event. Thus the presence of *Daphaenodon* and *Dinohyus*, neither of which is known above the Arikareean, and the *Parahippus-Merychippus* transition with its attendant evolutionary-zoogeographical implications, led Wilson to place the Garvin Gully Fauna in the late Arikareean.

Although the first appearance of *Merychippus* has been used by some to recognize the base of the Hemingfordian in North American Tertiary deposits, no evidence shows this single criterion to be valid. In the generally accepted guide to the nomenclature and correlation of the North American continental Tertiary, Wood et al. (1941) make no claim for *Merychippus* as marking the base of the Hemingfordian, but rather simply list its first occurrence as being in the Hemingfordian. Further, *Merychippus* does not occur at the base of the Hemingfordian in the type area, but actually replaces *Parahippus* well up in the Hemingford section. In an early work Osborn (1918: 98-99), in his section on the generic diagnosis of *Merychippus*, lists the first occurrence of that genus in the Great Plains as being in the Sheep Creek. Morris Skinner (pers. comm.), in his study of the Tertiary horses of the Great Plains, also contends that *Merychippus* is not found in beds older than Sheep Creek. Cook (1960) however recognizes *Merychippus* in the underlying Runningwater Formation. (M.C. McKenna (pers. comm.) claims that Cook misidentified a younger channel cut into the Runningwater as the Runningwater itself.) In a preliminary paper describing the ecologic factors affecting horse evolution in the Great Plains, Cook (1960: 203) states:

> In the beds representing the earlier stages of what is currently being called the Marsland formation, all known horses had simple patterned, brachydont molars. After Marsland times, and before Sheep Creek times of late middle Miocene, events occurred including another massive regional elevation to the west, with marked erosional effects, and a new series of deposits was laid down across western Nebraska. In these new deposits, now included in the upper half of the Marsland formation, the most astonishing degree of evolution occurred in the horses. The crowns of the molars rapidly became more hypsodont, and more complicated in pattern, and as they grew longer, they deposited, for the first time cement in the enamel valleys in the teeth, reinforcing and strengthening them. Now, with three degrees of hardness in the crowns, exposed, as they wore down, as being enamel, dentine, and cement, the molars maintained an efficient millstone grinding surface. Correspondingly, through the time represented by these few hundred feet of new deposits, the molars rapidly increased in length, so that by Sheep Creek time the dominant, complicated, hypsodont, *Merychippus* pattern had replaced the brachydont, simple, *Parahippus* present at the beginning of Marsland sedimentation. Space here prevents a discussion of other related faunal changes also present. For this series of deposits above the lower stages of the Marsland (which were originally named Upper Harrison Beds) and are below the Sheep Creek beds of Matthew and Cook, we are proposing the name Runningwater Formation, after an old, local name of the river which they occur. More evolution is recorded in the teeth of fossil horses in the Runningwater Formation than in all the preceding millions of years in which their fossil record is known. Another paper, going into essential details on the occurrence of this formation and its fossils, is under preparation.

Whereas the *Parahippus-Merychippus* transition as described above is not as yet substantiated, Cook's paper does serve to point out that *Merychippus* does not appear in the Great Plains sequence below the Runningwater Formation. Schultz (1938), Lugn (1938), Elias (1942), Cady (1940), Schultz and Stout (1941), Schultz and Falkenbach (1941b), and McKenna (1965) all consider the Marsland Formation to be the basal formation of the Hemingford Group in western Nebraska. Thus, if the concept of the Hemingfordian Stage/Age is based on the rocks and fossils comprising the Hemingford Group, its lower limit should generally be recognized out of the type area on the basis of fossils that appear in the lowest beds of the Marsland Formation. *Merychippus* on the other hand does not appear in the section until at least as high in the section as the Runningwater Formation, which is younger than the Marsland.[1] If the criteria Osborn (1918) and Cook (1960) use for recognizing *Merychippus* are valid, then evidence from the stratigraphic occurrence of these

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[1] Cook and Cook (1933) list the fauna from the "Upper Harrison" (=Marsland) of Nebraska. Their "Upper Rosebud" may be in part equivalent to the Runningwater.

fossils indicates that the practice of employing the first occurrence of *Merychippus* to mark the base of the Hemingfordian, insofar as it is based on the rocks and fossils of the Hemingford Group, (and this is the stated intention of Wood et al., 1941: 12) is of negative value. Although the *Merychippus,* if it actually is *Merychippus,* from the Garvin Gully Fauna may represent a less advanced stage of evolution than *Merychippus* occurring in the late Hemingfordian of the Great Plains, it is demonstrably more advanced than the parahippines known from late Arikareean deposits in that region. In point of fact it compares most closely with forms occurring in deposits of much younger age, i.e. the Runningwater and later.

Until the faunas of the Marsland and Runningwater Formations (and those from the even lesser known Red Fill and Box Butte deposits) become better known, the most definite statement I can make about the placement of the Garvin Gully Fauna is that, in terms of their respective faunas, it is post-"Lower Harrison" and pre-"Sheep Creek." On the basis of correspondence of taxa and relative stage of evolution of its faunal components, I believe that of the two the Garvin Gully Fauna is considerably younger than the Lower Harrison and is probably best correlated with the fauna from Runningwater. The same may be said of the Florida Thomas Farm fauna, except that it appears to be slightly younger than the Garvin Gully.

BURKEVILLE FAUNA

Quinn (1955) suggested a close correlation between the Burkeville Fauna and the presumably advanced components of the Thomas Farm, and an even closer correlation with the Quincy and Midway Faunas of Florida. This appears to be valid. The Burkeville *Prosynthetoceras texanus,* which is more advanced than the Garvin Gully form, closely resembles the Thomas Farm *P. texanus* (=*Prosynthetoceras douglasi* White and *Syndyoceras australis* White). *Floridatragulus* specimens from the Burkeville Fauna are similar to *F. dolichanthereus* from the Thomas Farm, but are assigned to a new species, *F. texanus. Tomarctus canavus* occurs in both faunas, as does *Merychippus gunteri* (=*Hippodon gunteri* of Quinn, 1955).

Its stratigraphic occurrence above the Hemingfordian Garvin Gully Fauna and the association and relative stage of evolution of its fauna (Table 26) indicates that the Burkeville Fauna also should be assigned to the middle Hemingfordian. The small steps observed in the phyletic sequences of both *Prosynthetoceras* and *Floridatra-*

gulus between the Garvin Gully and Burkeville Faunas indicates that the time separating the two faunas is of relatively short duration.

Of the four biostratigraphic units considered in this paper, only the Burkeville Fauna lacks camel material. This seemingly anomalous situation may be in part a reflection of the comparatively poorer state of knowledge of this fauna, suggesting that specimens may yet be found; or it may be attributed to differential environmental sampling, whereby only certain habitats, apparently unfavorable to camels, were near enough to the environment of deposition to contribute samples of their fauna. In any event, it is difficult to conceive of entire camel populations emigrating from the Texas Coast during the time the Burkeville deposits were accumulating only to return shortly thereafter. Possibly local differential extinction was followed by a new spread, although we have no evidence for this.

The absence in the Burkeville Fauna of other grasslands or savannah dwelling forms such as *Amphicyon* and the oreodonts, and the comparatively diminished horse fauna is significant. It is noteworthy that these forms are present in relatively plentiful numbers in the faunas that bracket the Burkeville Fauna in time. If the lack of camels is a result of limited habitat sampling, it is a most unfortunate circumstance with regard to comprehending camel evolution in the Coastal Plain faunas, for without such information it is virtually impossible to speculate on the nature of the relationship between the camels of the Garvin Gully Fauna and those of the Cold Spring. This

Table 26. Age Range of Cold Spring Genera

Taxon	Arikareean	Hemingfordian	Barstovian	Clarendonian
Mylagaulus			x	
Amphicyon		x	x	x
Aelurodon		?	x	x
Gomphotherium			x	x
Ticholeptus		x	x	
Hesperhys	x	x	?	
Aepycamelus			x	x
Bouromeryx		x	x	
Longirostromeryx			x	x
Diceratherium	x	x		
Teleoceras			x	x
Peraceras			x	x
Merychippus		x	x	x
Pliohippus				x
Nannippus				x
Neohipparion				x
Calippus			x	x

becomes especially critical, for example, in the attempt to establish the possible phylogenetic relationship of *Australocamelus* to *Aepycamelus.*

COLD SPRING FAUNA

The Cold Spring Fauna is considered by Quinn (1955) to be approximately of late Hemingfordian age: "The horses of the Cold Spring seem unrelated to any forms other than those from the Calvert formation. The age of the Cold Spring fauna must therefore be evaluated by the relative evolutionary position of the fauna with regard to the Burkeville fauna, which is certainly older, and with regard to the Lapara Creek fauna, which is certainly younger. In this respect the Cold Spring fauna is clearly much closer to the Burkeville fauna than to the Lapara Creek fauna and seems to be approximately late middle Miocene age."

Quinn (1955: 74) further states that "the indigenous components (of the Cold Spring Fauna) appear to have no counterparts elsewhere except for the Calvert material (Gazin and Collins, 1950), which corresponds with the Cold Spring insofar as the proboscideans are concerned." Several Cold Spring forms, some of which were not fully known to Quinn, are virtually inseparable from forms occurring in western faunas. *Ticholeptus rileyi* is reported by Schultz and Falkenbach (1941a) to resemble Lower Snake Creek material. Measurements of the radius-ulna and metatarsus of Cold Spring *Aepycamelus* correspond to those of *A. alexandrae* from the Barstow fauna of California (Davidson, 1923). Cold Spring specimens assigned to *Longirostromeryx blicki* correspond to the type specimens of that species from the "uppermost" Santa Fe beds (Mio-Pliocene) of New Mexico (Frick, 1937; Simpson, 1950).

None of the allocthonous Cold Spring genera except *Diceratherium* are restricted to the Hemingfordian or below but range either into the Barstovian or the Clarendonian. The camels and the deer of the Cold Spring are advanced over related late Hemingfordian forms in the Great Plains. *Gomphotherium* is not confidently known to appear in North American faunas earlier than the Barstovian. Mastodon remains have not been recovered from the lower Snake Creek deposits, but in the Great Plains appear for the first time in the Pawnee Creek beds, which are generally regarded as late Barstovian. *Gomphotherium* from the Calvert Formation of Maryland is discussed by Gazin and Collins (1950) as being significant in either of two ways: "If the presence of mastodon is to be regarded as placing an early limit on the possible age assignment, then a lower Barstovian age would likely be indicated. On the other hand, there is always the possibility that the Calvert represents the first appearance of mastodons in North America, a conclusion not out of keeping with its geographic remoteness from the western occurrences."

In a preceding paragraph, Gazin and Collins (1950) conclude that the age of the Calvert is either latest Hemingfordian or early Barstovian. Thus here again exists a situation where the fauna in question lies relatively near an age boundary, as Quinn (1955) also recognized. However, on the basis of evidence deriving from this study that was not available to Quinn, the Cold Spring Fauna assumes a geologically younger aspect than was previously recognized and warrants its inclusion in the Barstovian, probably representing the early to middle part of this age.

LAPARA CREEK FAUNA

As the most extensive of the Texas Tertiary Gulf Coastal Plain faunas, the Lapara Creek Fauna provides a broad and reliable foundation for interregional correlation. The fauna is systematically well-balanced and the material fortunately has been amenable to greater precision in taxonomic determination, as the greater number of specific identifications (Table 27) witnesses. This relative profusion of taxa is thought not to be merely a result of accidents of preservation, but rather to reflect the great amount of taxonomic differentiation or radiation that occurred in this region in the late Miocene and early Pliocene.

Quinn (1955: 75) correlates the Lapara Creek Fauna with the "Alachua (Bone Valley) fauna" of Florida. He subscribes to the age Kellogg (1924) assigns to the Bone Valley fauna from his study of its marine mammals. However, his "Alachua (Bone Valley) fauna" is not a unitary one and attempts to correlate one aspect of the fauna without regard to the lack of isochroneity of the whole are destined to lead to confusion. In a summary of the Alachua problem, Webb (1964) states:

> "Much of the confusion as to the age of the "Alachua Fauna" stemmed from the failure on the part of these early workers to consider the possibility that the Alachua Formation was heterochronic. Leidy unknowingly included fossils from the Pliocene and Pleistocene localities in his studies. Hay recognized that the "Alachua Fauna" included species of Pliocene and Miocene aspect along with typical Pleistocene forms, but he assumed that this indicated the survival of archaic types in the Pleistocene of Florida. This situation was largely remedied by Simpson's (1930) revision of the Pliocene part of the "Alachua Fauna." He

Table 27. Age Range of Lapara Creek Species

Taxon	Barstovian	Clarendonian	Hemphillian
Aelurodon taxoides	x	x	
Leptocyon vefer	x	x	
Ustatochoerus profectus		x	
Procamelus occidentalis	x		
Procamelus grandis		x	
Synthetoceras tricornatus		x	
Blastomeryx elegans		x	
Cranioceras clarendonensis		x	
Ramoceros ramosus	x	x	
Teleoceras proterus		x	
Protohippus perditus	x		
Pliohippus supremus		x	
Nannippus ingenuus			x
Nannippus tehonensis		x	
Neohipparion coloradense		x	
Calippus placidus		x	

demonstrated, using exact locality data, that certain sites produced only Miocene, others only Pliocene, and still others only Pleistocene terrestrial fossil vertebrates.

Thus, whereas Kellogg (1924), on evidence derived from marine mammals, considers the "Alachua fauna" to be not older than late Miocene, Simpson (1930) shows that most of Leidy's original "Alachua fauna" came from Mixson's Bone Bed near Williston, Florida, which is clearly Hemphillian (Webb, 1964).

Quinn (1955: 75) regards the Lapara Creek Fauna to be older than the Burge Fauna of Nebraska as indicated by

> . . . direct comparison of specimens of *Protohippus, Hippotigris,* and *Calippus.* The amount of time separation is difficult to determine because the available Burge sample is inadequate for statistical comparison. In general, the North Texas-Clarendon and Nebraska-Lower Ash Hollow horses are readily distinguishable from their Lapara Creek relatives by virtue of the much greater degree of hypsodonty in the northern forms, but the Lapara Creek horse, *Calippus anatinus,* is barely distinguishable from *C. regulus* of the Clarendon fauna. At the same time the Burge *Hippotigris* is closer to *H. clarendonensis* than to *H. sellardsi* of the Lapara Creek.

Quinn (1955: 75) observes that species can exist sufficiently long to transcend provincial age boundaries and concludes:

> In consideration of this factor (that species may transcend time boundaries), and because exact comparisons of Burge and Lapara Creek forms could not generally be made, several of the Lapara Creek forms are, in this paper, referred to the Burge species. In spite of this, the conclusion that the Burge and Lapara Creek are exactly synchronous is not warranted. Some of the forms referred to

Burge species will, no doubt, with better comparative materials, be separable; others undoubtably will not.

Of the 8 specifically identified artiodactyls with the same or related species occurring in High Plains faunas, 6 are conspecific with forms from the Clarendonian or later, 1 occurs in both the Barstovian and Clarendonian, and only 1 is previously undescribed above the Barstovian (Table 27). A direct comparison of the Lapara Creek species with those from the Great Plains and elsewhere also strongly suggests a Clarendonian assignment for the fauna. The Lapara Creek oreodont, *Ustatochoerus profectus,* is very similar to specimens representing that species from the Burge Fauna and from the overlying Minnechaduza Fauna (both Clarendonian). *Synthetoceras tricornatus* and *Cranioceras clarendonensis* are indistinguishable from their types from the Clarendon beds of the Texas Panhandle, while *Blastomeryx elegans* is previously described only from the Hemphillian Upper Snake Creek beds. *Ramoceros ramosus* is found in both Barstovian and Clarendonian deposits in New Mexico (Frick, 1937) and California (James, 1963). The Lapara Creek specimens of *Procamelus occidentalis,* a species heretofore restricted to the Barstovian, are higher crowned and probably more advanced than the Barstovian species. *Procamelus grandis* from the Lapara Creek is advanced over its Burge equivalent, while *Protalabis notiochorinos,* a new species from the Lapara Creek Fauna, is advanced over similar forms from both the Burge and the Minnechaduza Faunas. *Megatylopus primaevus,* also a new species, is very similar to, but slightly more primitive than, *M. major* from the Burge.

It seems clear, then, that the age assignment Quinn (1955) gives to the Lapara Creek Fauna should be reinterpreted in the light of evidence and information unavailable to him at the time of his study. As Quinn recognized, some forms in the Lapara Creek Fauna are commonly found in Barstovian deposits, and some formerly even restricted to beds of that age. Still others were previously thought to occur in beds no older than Hemphillian. The majority of Lapara Creek artiodactyls, however, are characteristic Clarendonian forms, and indicate that those disparities existing between the Lapara Creek Fauna and the Pliocene faunas of the High Plains have not resulted simply from temporal isolation of the faunas in the two regions, but rather from differing rates and directions of dispersal of some of the taxa in question. Thus consideration of the correspondence of fossil taxa between the Lapara Creek Fauna and late Tertiary faunas of the High Plains, as well as evidence derived from the evaluation of the relative stage of evolution of forms shared by the Lapara Creek and other faunas, indicates that the Lapara Creek Fauna is younger than faunas from the Lower Valentine Formation of Nebraska and the Pawnee Creek beds of Colorado but older than the Clarendon and Minnechaduza faunas of Texas and Nebraska. It is most closely cor-

EPOCH	N.A. PROVINCIAL AGES	GREAT PLAINS	TEXAS COASTAL PLAIN	FLORIDA
PLIOCENE	HEMPHILLIAN	UPPER UPPER SNAKE CREEK UPPER SNAKE CREEK	LABAHIA MISSION	BONE VALLEY Mc GEHEE
	CLARENDONIAN	MINNECHADUZA BURGE	LAPARA CREEK	
MIOCENE	BARSTOVIAN	LOWER VALENTINE PAWNEE BUTTES LOWER SNAKE CREEK	COLD SPRING	ASHVILLE
	HEMINGFORDIAN	SHEEP CREEK BOX BUTTE RUNNINGWATER MARSLAND	BURKEVILLE GARVIN GULLY	QUINCY-MIDWAY THOMAS FARM BUDA
	ARIKAREEAN	HARRISON MONROE CREEK GERING		BROOKSVILLE

FIGURE 34. Biostratigraphic correlation of Texas Gulf Coastal Plain faunas.

related with the early Clarendonian Burge Local Fauna of Nebraska (Fig. 34).

SUMMARY AND CONCLUSIONS

From a series of vertically successive mammalian assemblages in Miocene and Pliocene deposits of the Texas Gulf Coastal Plain 27 species of fossil artiodactyls are described and their systematic positions discussed. These include 10 species (5 new) of Camelidae, 3 new species of Floridatragulinae, 3 species of Synthetoceratinae, 5 species of Cervidae, 2 antilocaprids, and 3 oreodonts. Among the new forms recognized are two camel genera: *Australocamelus*, the probable *Aepycamelus* ancestor, and *Nothotylopus*, a member of the *Protolabis-Pliauchenia* lineage.

The camels are the most numerous group of fossil artiodactyls from the Texas Coastal Plain. Of the 9 genera represented, 5 (*Oxydactylus, Aepycamelus, Protolabis, Procamelus,* and *Megatylopus*) are well-known from faunas of the Great Plains and Pacific Coast regions, while 4 (*Nothokemas, Floridatragulus, Australocamelus,* and *Nothotylopus*) are so far restricted to the Gulf Coastal Plain. The former genera are geographically widespread and are apparently allocthonous elements contributed by the Great Plains faunas. *Oxydactylus benedentatus* is closely similar to species of *Oxydactylus* well established in the Great Plains faunas, and the Texas Gulf Coast representative of *Procamelus* are cospecific with Great Plains forms. *Procamelus* species from the Florida Pliocene are based on astragali and are indeterminate, but like *Megatylopus* are probably derived from Texas forms. *Protolabis notiochorinos* appears to represent an advanced branch from an early *P. heterodontus* stock, whereas *Megatylopus primaevus* is closely related to, but is more primitive than, *M. major* from the Nebraska Burge and Minnechaduza Faunas. Apparently *M. primaevus* gave rise to the *M. major* from the Florida McGehee deposit (Hemphillian), but whether it is the actual ancestor of *M. major* from the Burge and Minnechaduza faunas or owes its origin to a Great Plains form ancestral to both the Texas and Nebraska forms, is not known. In any event, it is morphologically the most primitive of the *Megatylopus* species. Specimens from the Cold Spring and Lapara Creek Faunas assigned to *Aepycamelus* sp. are comparable to Great Plains forms, but *Australocamelus* from the Garvin Gully Fauna qualifies as a structural ancestor to *Aepycamelus* and *Hesperocamelus* and may represent the earliest member of a phylogenetic series that evolved in the Gulf Coastal Plain and provided the basal stock for the Great Plains and Pacific Coast members of the lineage. The lamentable lack of camel material from the Burkeville Fauna unfortunately precludes verification of this possibility.

The three late Tertiary camel genera endemic to the Gulf Coastal Plain are *Nothokemas*, *Australocamelus*, and *Nothotylopus*. Only *Nothokemas* is found in Florida (Thomas Farm) *Nothokemas* is morphologically similar to early *Oxydactylus*, but does not seem derivable from any presently known species of that genus. As it occurs in the earliest Miocene Coastal Plain vertebrate faunas (Garvin Gully and Thomas Farm), its origins must be sought elsewhere. The Floridatragulinae are known only from Miocene deposits in the Gulf Coastal Plain. They occur in the Burkeville and Cold Spring Faunas of Texas and in the Thomas Farm Fauna of Florida. The exact systematic placement of this group is presently uncertain, but for reasons outlined on page 000, I have included them in the Camelidae. They have apparently evolved entirely in the Gulf Coastal Plain, but their phyletic origin is poorly understood. *Australocamelus* and its probable relationships have been mentioned above. The origins of *Nothotylopus* are unclear. This strangely conservative yet in some ways progressive camel seems too specialized to be derived from the *Procamelus*, *Pliauchenia*, and *Megatylopus* groups, but probably evolved from an early member of the genus *Protolabis* or some form intermediate between *Protolabis* and the line of oxydactylines that presumably gave rise to it. Whether or not *Nothotylopus* is a true Gulf Coast autochthon is presently unanswerable.

The Synthetoceratinae are represented in the Gulf Coastal Plain by the genera *Prosynthetoceras* and *Synthetoceras*. From *P. texanus* of the Garvin Gully and Burkeville Faunas to *S. tricornatus* of the Lapara Creek Fauna, these forms exhibit characters that occur in a step-like progression thought to represent their actual phylogeny. Although ultimately derived from Great Plains protoceratids, most of their later evolution occurred in the Gulf Coastal Plain. The Florida Thomas Farm and McGehee synthetocerines are conspecific with their Texas correlatives, suggesting that few, if any, lasting barriers existed for this species between Texas and Florida. The Claredon *Synthetoceras tricornatus* from the Texas High Plains probably represents an emigrant population from the Coastal Plain.

The cervids and antilocaprids from Texas show their greatest affinities to the Great Plains forms, as witnessed in the identity of taxa shared by the two regions. Only one species, *Blastomeryx vigoratus* from the Garvin Gully Fauna, is restricted to the Gulf Coastal Plain; another, *Cranioceras clarendonensis*, is known from the Lapara Creek Fauna and from the Clarendon beds of the Texas Panhandle. The correspondence of Great Plains and Texas Coastal Plain taxa may be only illusory but the insufficient preserved material from the Texas deposits prevents more accurately founded comparisons. The identification of Thomas Farm cervids suffers from similar defects; a revision by the writer of these and other Thomas Farm artiodactyls has recently been completed (Patton, 1966[67]).

Three oreodonts, *Merychyus* sp., *Ticholeptus rileyi*, and *Ustatochoerus profectus*, have been identified in the Texas Coastal Plain faunas, in the Garvin Gully, Cold Spring, and Lapara Creek Faunas, respectively. No evolutionary sequences are apparent in the Texas Coastal Plain oreodonts. They all seem to be derivable from Great Plains forms, apparently having been introduced to the Coastal Plain as occasional migrants. Until the Oligocene and early Miocene oreodonts from the Serra Vieja and Big Bend regions of west Texas are known (now being studied by J. A. Wilson, University of Texas), this will remain conjectural.

The fossil artiodactyls from Miocene and Pliocene deposits in the Texas Coastal Plain fill an important gap in completing the understanding of the terrestrial mammalian faunas existing at that time in the Gulf Coastal Plain of North America. As Bader (1956) and Quinn (1955) recognized, the Gulf Coastal Plain was essentially a distinct faunal province. The elements of this province, while greatly influenced by immigrants from the Great Plains of the western United States, underwent much of their evolution *in situ* under the influences of their own peculiar geography and ecology. This is evident not only in the presence of taxonomically distinct forms at the species level and above, but also in the detection of microevolutionary sequences in some of the groups represented.

As established by Quinn (1955) and Wilson (1960), the Miocene and Pliocene deposits on the Texas Coastal Plain contain four fossil land mammal assemblages. The earliest of these is the Garvin Gully Fauna. It is here considered to be of approximately middle Hemingfordian age and correlative with the older portion of the Thomas Farm fauna of Florida. Characteristic taxa are *Daphaenodon, Dinohyus, Parahippus, Oxydactylus benedentatus, Australocamelus orarius,* *Nothokemas hidalgensis, Floridatragulus nanus,* and *Prosynthetoceras texanus.*

The Burkeville Fauna is of middle Hemingfordian age and corresponds to the Quincy-Midway faunas of Florida and to the younger portions of the Thomas Farm fauna. Its distinguishing taxa are *Tomarctus canavas, Merychippus gunteri, Floridatragulus texanus,* and *Aphelops meridianus.* No camels have yet been found in the Burkeville Fauna.

The age of the Cold Spring Fauna is reinterpreted in this paper and is considered to be of middle Barstovian age. The camels and the deer of the Cold Spring are advanced over related late Hemingfordian forms, while the presence of *Mylagaulus, Gomphotherium, Teleoceras, Peraceras, Pliohippus, Nannippus, Neohipparion* and *Calippus* warrants an age assignment for the Cold Spring Fauna later than previously designated. The Cold Spring Fauna is probably best correlated with the interval between the Lower Snake Creek of Nebraska and the Pawnee Buttes of northeastern Colorado, the late Miocene portion of the Barstow "fauna" from California, and the Calvert fauna of Maryland.

The Lapara Creek Fauna is the most extensive of the Texas Tertiary Coastal Plain faunas and provides a broader basis for interregional correlation than the preceding faunas. Comparison of the Lapara Creek species with those from the Great Plains (outlined in section on Age and Correlation strongly suggests a Clarendonian assignment for the fauna. A comparison of these taxa and a consideration of their relative stage of evolution indicates that the Lapara Creek Fauna is younger than faunas from the Lower Valentine Formation of Nebraska and the Pawnee Creek beds of Colorado but older than the Clarendon and Minnechaduza faunas of Texas and Nebraska. It appears to be most closely correlative with the Burge Local Fauna of Nebraska.

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