28. Camelidae

DONALD R. PROTHERO

ABSTRACT

Our understanding of the early evolution of the Camelidae has long been confused by poor specimens, bad taxonomy, and dubious methodology, but the excellent specimens in the Frick Collection have clarified much of the confusion. The earliest known camelid is *Poebrodon*, from the early and late Uintan of Utah, Wyoming, and California. *Hidrosotherium* is not a camel at all, but a leptomerycid. Four valid species of *Poebrotherium* are recognized: *P. chadronense*, n. sp., and *P. franki* from the Chadronian of Texas; *P. eximium* from the Chadronian and early Orellan of the High Plains; and *P. wilsoni*, from the Chadronian to Whitneyan of the High Plains. "*Poebrotherium*" *labiatum*, from the early Orellan, is transferred to *Paratylopus*, which previously included only the type species, the Whitneyan camel *Paratylopus primaevus*. The long misunderstood camels known as "*Protomeryx cedrensis*," "*Protomeryx campester*," and "*Paralabis matthewi*" are now combined as *Paralabis cedrensis*.

The highly specialized, extremely hypsodont, gazelle-like stenomyline camels of the late Arikareean-Barstovian have long been phylogenetically isolated, but Frick specimens show that *Pseudolabis dakotensis* (from the Whitneyan-Arikareean) and *Miotylopus* (from the Arikareean) are sister-taxa to the Stenomylini. *Miotylopus* includes three species: the small, *Stenomylus*-like *M. leonardi*; the medium-sized *M. gibbi* (including *Dyseotylopus*); and a large new species, *M. taylori*. *Gentilicamelus sternbergi* is the only valid species of this wastebasket genus, and is the sister-taxon of *Nothokemas*. The bizarre, long-snouted floridatragulines are closely related to higher camels.

INTRODUCTION

The first fossil vertebrate described from the western United States was the Oligocene camel *Poebrotherium wilsoni* (Leidy, 1847). Since that time, many more Eocene and Oligocene camels have been collected and described, particularly from the White River Group. Despite the abundance of specimens, early camel evolution remains poorly understood. Their taxonomy is one of the most confused among fossil mammals, with numerous invalid, misassigned, and "wastebasket" taxa (Table 1). This taxonomic confusion has made it necessary to reassign nearly every taxon in the group, and to resurrect several taxa that had been unjustly forgotten. Several new taxa are also named and described

below. Some of this taxonomic confusion can be attributed to the poor quality of the material, but much is due to inaccurate descriptions, incompetence, or bad methodology. The Oligocene Camelidae demonstrate how excessive reliance on stratigraphic sequence, "ancestor worship," and primitive characters can completely obscure an hierarchical pattern of relationships. The new material in the Frick Collection made it possible to incorporate characters of the facial region, the basicranium, the auditory bulla, and the skull sutures into a phylogenetic analysis, and reduce the over-reliance on teeth and metapodials.

Because the systematic papers in this book focus on the White River Chronofauna, this paper covers only the Camelidae (predominantly middle Eocene to late Oligocene) that are primitive sister-taxa to the clade that includes miolabines, protolabines, *Oxydactylus sensu stricto* and higher camels (Fig. 1). These higher camels first appear in the Harrison Formation, which is probably early Miocene in age (Honey et al., in press). This provides a convenient cut-off point at the base of a monophyletic group. The relationships of Miocene through Recent camels are also indicated in Figure 1, but their systematics will require much further work (currently under study by J. Honey; see Honey et al., in press).

ABBREVIATIONS

AC, Amherst College Museum, Amherst, Massachusetts; AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia, Pennsylvania; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; F:AM, Frick Collection, American Museum of Natural History, New York; KU, University of Kansas Museum of Natural History, Lawrence, Kansas; LACM(CIT), California Institute of Technology collection, now at the Los Angeles County Museum of Natural History; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; SDSM, South Dakota
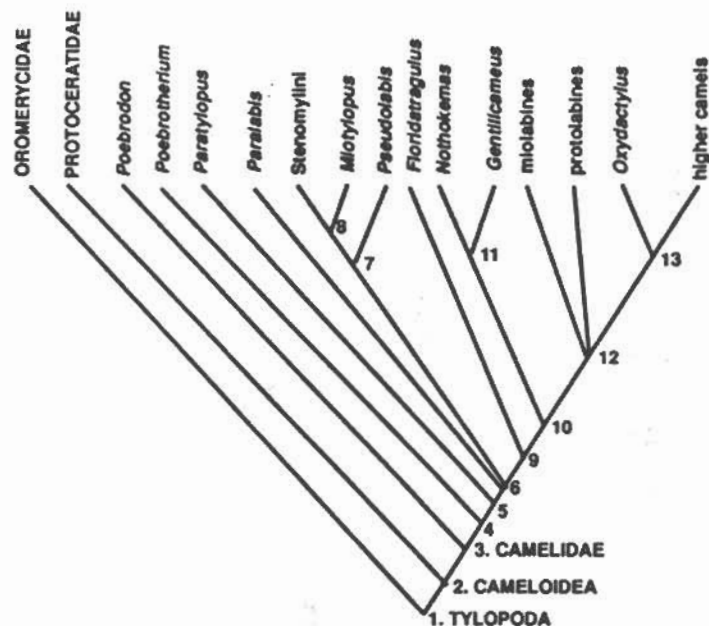
Figure 1. Phylogenetic relationships of the primitive Camelidae and their sister taxa (modified from Honey et al., in press). Character states as follows: 1) Tylopoda: camel condyle; metatarsals II, V reduced to nodules; 2) Cameloidea: long slender metapodials; fibula incomplete, becomes malleolar bone; wing-like basioccipital processes covering hypoglossal foramen; vertebrarterial canal passes through transverse processes of anterior cervical vertebrae; 3) Family Camelidae: highly hypsodont, dorsoventrally narrow upper molars, with straight ectolophs, and fossettes that close with wear; 4) higher-crowned teeth; increased size; M2 wide posteriorly; lingual hypoconulid lobe of m3 reduced; lingual entoconid and metaconid more flattened; hooked angular process; inflated auditory bulla with deep tympanohyal groove, filled with spongy bone; metacarpals II and V reduced to nodules; divergent distal metapodials; 5) reduced inner lobe of bulla; reduced premolars; 6) stronger sagittal crest; smaller lacrimal vacuity; posterior extension of inner portion of bulla; 7) Stenomylinae: premaxillary extended posteriorly; longer rostrum; deep, elongate maxillary fossa; elongated upper molars, which are laterally compressed and more hypsodont; weak mesostyles; partially fused metapodials; closed orbit; 8) highly reduced p2-3; 9) lower molars with metastylids, formed by overlap of metaconid on entoconid; heavier premaxilla; large postglenoid foramen; diastemal crest on mandible; 10) lower incisors more spatulate; P1 shortened; P3 internal cingulum stronger; orbits closed; 11) mandibular angle enlarged; p1 roots closely appressed; 12) medial plate of auditory bulla transversely compressed; rostrum lengthened; P2-3 reduced; molars more hypsodont; upper molars with weaker ribs; 13) cervical vertebrae elongate; metapodials slender, elongate, longer than basal length of skull; metatarsals and metacarpals approximately equal in length.

School of Mines Museum of Geology, Rapid City, South Dakota; TMM, Texas Memorial Museum, University of Texas, Austin, Texas; YPM, Yale Peabody Museum, New Haven, Connecticut; YPM-PU, Princeton University collection, now stored at the YPM.

SYSTEMATIC PALEONTOLOGY
Class MAMMALIA Linnaeus, 1758
Order ARTIODACTYLA Owen, 1848
Suborder TYLOPODA Illiger, 1811

Superfamily CAMELOIDEA Gill, 1872
Family CAMELIDAE Gray, 1821

Revised Diagnosis—The Family Camelidae is united by the following shared characters that distinguish it from the remaining Tylopoda, and all other artiodactyls: fully selenodont, transversely compressed upper molars that are relatively high-crowned (compared to other primitive Tylopoda), with straight ectolophs, and with fossettes that are closed

Table 1. Chronological list of camelid names discussed in this study.

NAME	AUTHOR	PRESENT REFERENCE	COMMENT/LAST REVISER
Poebrotherium wilsoni	Leidy, 1847	Poebrotherium wilsoni	Type species of genus
Protomeryx halli	Leidy, 1856	indeterminate	nomen dubium
Poebrotherium sternbergi	Cope, 1879	Gentilicamelus sternbergi	Only species of genus
Poebrotherium labiatum	Cope, 1881	Paratylopus labiatus	this paper
Gomphotherium	Cope, 1886	preoccupied	McKenna, 1966, note 1
Gomphotherium cameloides	Wortman, 1898	oxydactyline	McKenna, 1966
Gomphotherium serus	Douglass, 1900	oxydactyline	this paper
Protomeryx campester	Matthew, 1901	Paralabis cedrensis	lapsus calami
Protomeryx cedrensis	Matthew, 1901	Paralabis cedrensis	this paper
Poebrotherium eximium	Hay, 1902	Poebrotherium eximium	this paper
Oxydactylus longipes	Peterson, 1904	Oxydactylus longipes	Type species of genus
Miolabis (Paratylopus) primaevus	Matthew, 1904	Paratylopus primaevus	Type species of genus
Protomeryx leonardi	Loomis, 1911	Miotylopus leonardi	this paper
Oxydactylus gibbi	Loomis, 1911	Miotylopus gibbi	McKenna and Love, 1972
Poebrotherium andersoni	Troxell, 1917	Poebrotherium wilsoni	this paper
Pseudolabis (Paralabis) matthewi	Lull, 1921	Paralabis cedrensis	this paper
Paratylopus wortmani	Lull, 1921	oxydactyline	McKenna, 1966
Miotylopus bathygnathus	Schlaikjer, 1935	Miotylopus gibbi	McKenna and Love, 1972
Dyseotylopus migrans	Stock, 1935	Miotylopus gibbi	this paper
Gentilicamelus wyomingensis	Loomis, 1936	juvenile oxydactyline	McKenna, 1966
Gentilicamelus campestris	Loomis, 1936	Paralabis cedrensis	this paper
Gentilicamelus cederensis [sic]	Loomis, 1936	Paralabis cedrensis	lapsus calami
Miotylopus brachygnathus [sic]	McKenna, 1966	Miotylopus gibbi	lapsus calami
Paratylopus matthewi	McKenna and Love, 1972	Paralabis cedrensis	this paper
Miotylopus gibbi	McKenna and Love, 1972	Miotylopus leonardi	(in part)
Poebrotherium franki	Wilson, 1974	Poebrotherium franki	this paper
Hidrosotherium transpecosensis	Wilson, 1974	Hendryomeryx defordi	this paper
Miotylopus wilsoni	Dalquest and Mooser, 1974	floridatraguline	Stevens, 1977

anteriorly and posteriorly after moderate wear. Relatively long, narrow rostrum. Postorbital processes well developed, and nearly or completely closed. Inflated tympanic bulla filled with cancellous bone and indented by a deep tympanohyal groove. Angular process on mandible with a distinctive dorsal "hook." Long, unfused to fused, distally divergent middle metapodials with metacarpals II and IV and metatarsals II and V reduced to nodules. Metatarsals III and IV have flattened dorsal surfaces and their distal keels do not extend to the dorsal side. Fibular facet on the calcaneum has a proximal convexity and a dorsal concavity.

Poebrodon Gazin, 1955

Type Species—Poebrodon kayi Gazin, 1955
Included Species—The type and Poebrodon californicus Golz, 1976
Range—Washakie Formation, Adobe Town Member unit B, Washakie Basin, Wyoming (McCarroll et al., this volume, Chapter 2) (early Uintan); Myton Pocket, Uinta Formation C, Uinta Basin, Utah; Laguna Riviera

Quarry, Santiago Formation, San Diego Co., California (late Uintan).

Discussion—The known material of Poebrodon was described by Gazin (1955) and Golz (1976). No additional material of Poebrodon has since been reported, except for the specimens mentioned by McCarroll et al. (this volume, Chapter 2), which will be described by them.

Wilson (1974, p. 24) placed Poebrodon in its own subfamily, the Poebrodoninae, along with his new taxon, "Hidrosotherium," because he felt that Poebrodon could not be ancestral to Poebrotherium. He argued that some primitive Chadronian Poebrotherium had bifurcate protocones on their upper molars, and since it was not clear that Poebrodon did also (the relevant specimens are too worn to determine this), Poebrodon was considered too advanced to be ancestral to camels. However, I have examined all the relevant specimens discussed by Wilson (1974), and I find only one or two with bifurcate protocones that are clearly referable to Poebrotherium; many are not camels at all, but oromerycids. In fact, some of these reports are erroneous. Wilson

(1974, p. 25) says that TMM 40504-22 (here referred to *Poebrotherium chadronense*, new species, described below) has bifurcate protocones on M3, but the specimen is too worn to determine whether this is so. Besides, this single highly variable character does not invalidate the large number of unique synapomorphies that ally *Poebrodon* with the Camelidae. If *Poebrodon* lacks bifurcate protocones and some *Poebrotherium* have them (neither of which is established yet), this would make *Poebrodon* too autapomorphous to be an ancestor, but would not prevent it from being closest sister-taxon to *Poebrotherium*.

A Note on "*Hidrosotherium*"—Wilson (1974) described a skull, jaws, and additional specimens from the Porvenir l.f. (late Duchesnean) of Trans-Pecos Texas, and named it "*Hidrosotherium transpecosensis*." Wilson (1974, p. 29) commented that "the general appearance of the skull resembles a large *Leptomeryx* but the premolar and molar pattern in no way resembles that genus." Wilson compared the teeth with those of camels, and decided that the specimen was a primitive camelid related to *Poebrodon*, justifying the new genus.

As Wilson correctly noted, the skull is indeed leptomerycid, right down to the distinctive diamond shape of the prelacrimal vacuity, the reduced anterior dentition, and the lack of a camelid auditory bulla. However, I examined the cheek teeth closely, and they are leptomerycid in every feature. The upper molars are not as transversely narrow, high-crowned, or selenodont as true camelids, but they are a good match for many primitive leptomerycids in the Frick Collection. In fact, "*Hidrosotherium*" is only slightly larger than "*Leptomeryx*"(= ?*Hendryomeryx*) *defordi* from the same deposits, and I suspect that they are the same animal. Therefore, I remove "*Hidrosotherium*" from the Camelidae, and synonymize it with "*Leptomeryx*"(= ?*Hendryomeryx*) *defordi*.

Poebrotherium Leidy, 1847

Type Species—*Poebrotherium wilsoni* Leidy, 1847

Included Species—*P. chadronense*, new species; *P. eximium* Hay, 1902; *P. franki* Wilson, 1974.

Range— Early Chadronian to middle Whitneyan, High Plains and Texas.

Diagnosis— Small to medium-sized camels (M1-3 length = 28-37 mm), with anterior dentition becoming differentiated and developing diastemata. Relatively low-crowned molars with strong styles. Distinguished from *Poebrodon* by: larger size; greater hypsodonty; M2 wider posteriorly; lingual hypoconulid lobe of M3 reduced; lingual surface of metaconid and entoconid more flattened.

Discussion— The genus *Poebrotherium* is highly variable in both size and in the differentiation of its anterior dentition. The most primitive species, *P.*

franki, has a moderately long rostrum with undifferentiated anterior teeth and short diastemata. The typical Chadronian camels, *P. chadronense* and *P. eximium*, are considerably larger, but still retain the primitive condition in their anterior teeth. *P. wilsoni* is within the size range of *P. eximium*, but develops a large P1/P1-P2/P2 diastema and a smaller C-P1/P1 diastema. *P. wilsoni* frequently develops a caniniform I3. The size of the upper canine in *P. wilsoni* appears to be sexually dimorphic, with larger canines in males. The longer rostrum is also correlated with a larger, more attenuated mandibular symphysis, which is frequently ventrally deflected. The metapodials of *P. wilsoni* are shortened relative to the rest of the skeleton. In associated material of *P. eximium*, for example, the length of the metatarsals is equal to the distance from the foramen magnum to the canine on the skull. In comparably-sized *P. wilsoni*, however, the metatarsal length is equivalent to the distance from the foramen magnum to the anterior part of P2. This change in ratios is partly due to relative limb shortening, but due also to the lengthening of the rostrum. Although *P. wilsoni* is clearly more derived than *P. eximium* or more primitive species of the genus, the differences are too minor and too variable to justify erection of a separate genus for primitive *Poebrotherium*.

Poebrotherium franki Wilson, 1974
Figure 2, Tables 2-3

Type—TMM 40504-149, a skull with I1-M3, and lower jaw with p2-m1, and fragments of vertebrae (Fig. 2). Airstrip l.f. (early Chadronian), Vieja Group of Texas.

Referred Specimens—see Wilson (1974)

Range—Early-middle Chadronian (Airstrip and Ash Springs l.f.), Vieja Group of Texas.

Diagnosis—Smallest species of *Poebrotherium* (length M1-3 = 28-29 mm). Elongate rostrum with simple, equal-sized bladelike I1-3 and canine, and no diastema. P3 with no lingual cingulum or cusp.

Description—*P. franki* was fully described by Wilson (1974). No new material of *P. franki* has been reported.

Discussion—*P. franki* is the oldest known species that shows the skull features characteristic of camels (since *Poebrodon* is known only from teeth). *P. franki* has the elongate rostrum (derived for camels) with the primitive, undifferentiated anterior dentition. The premolars and molars are fully camelid, and the bulla is fully inflated. Most of these features are not yet known for *Poebrodon*, but they would be predicted to occur in more complete material. *Poebrotherium franki* (M1-3 length 28-29 mm) is considerably larger than *Poebrodon kayi* (M1-3 length 20.2 mm). *Poebrodon californicus* (consisting only of a dP4-M1 at present) is slightly larger than *Poebrodon kayi*, and much smaller than *P.*
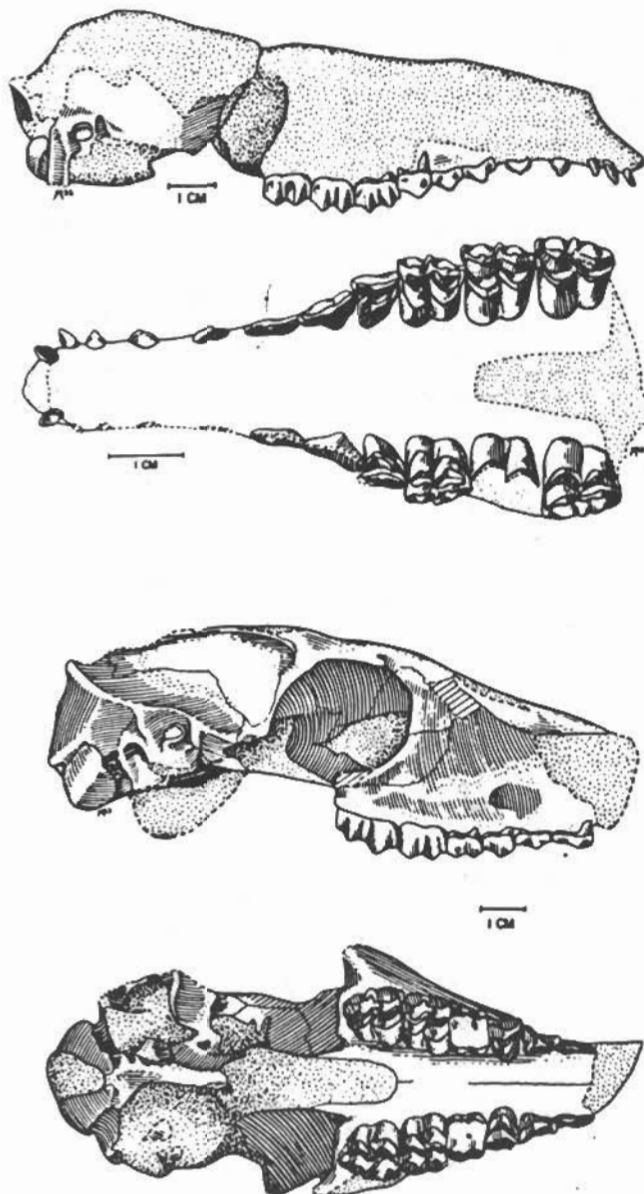

Figure 2. (Top). *Poebrotherium franki*, type specimen, TMM 40504-149 (after Wilson, 1974, p. 23). (Bottom) *Poebrotherium chadronense*, new species, TMM 40504-22 (after Wilson, 1974, p. 26).

Table 2. Camelid skull and upper teeth measurements (in mm)

CHARACTER	franki TMM 40504-149 (type)	chadro- nense TMM 40504-22 (type)	Poebrotherium eximium AMNH 632 (type)	F:AM 47118	F:AM 47091	wilsoni ANSP 1101 (type)	F:AM 47130	Paratylopus labiatus F:AM 42284	AMNH 6520 (type)	F:AM 42278	primaevus AMNH 9806 (type)	Paralabis cedrensis YPM 10167 (type)
Skull L (occ. cond>pmax)	131.5	—	163.6	161.5	161.4	—	187.5	189.0	—	182.3	188.0	—
I1-M3 L	78.4	—	100.2	97.0	97.8	—	109.1	108.1	—	106.0	103.0	—
L M3-occ. cond.	52.9	64.5	68.5	67.9	66.0	—	82.6	81.9	95.0	82.0	84.1	—
Skull W at M3	49.4	55.3	62.3	66.0	58.5	—	55.3	57.5	64.0	65.6	71.5	63.0
Rostral W at P1	13.4	17.0	23.2	20.7	15.8	—	17.7	18.0	—	22.0	21.4	18.0
P1-M3 L	57.8	—	74.7	70.3	72.5	—	77.8	76.7	—	88.3	81.5	84.8
P1-4 L	30.1	—	39.0	35.3	37.5	—	42.2	40.3	—	51.0	42.0	43.3
P1-2 diastema	2.6	—	2.0	1.5	3.3	—	10.8	8.3	—	6.0	9.0	10.5
P1L	5.1	—	7.9	6.8	7.8	—	8.5	7.5	—	7.5	8.1	—
P1W	1.9	—	2.5	3.1	2.0	—	3.0	2.2	—	3.0	—	—
P2L	7.3	10.4	10.4	9.5	8.3	—	8.8	8.8	9.1	9.0	9.7	8.7
P2W	27.	3.0	3.1	3.2	3.0	—	3.7	3.1	3.0	3.3	—	3.5
P3L	8.2	9.4	11.7	9.7	11.0	—	9.3	9.5	9.0	10.5	9.0	9.2
P3W	4.5	7.1	4.7	5.0	4.7	—	4.9	4.5	4.0	4.1	—	5.5
P4L	7.1	8.4	10.0	9.0	8.0	—	7.9	9.8	8.9	8.5	8.7	9.5
P4W	7.0	9.3	7.0	8.4	7.7	—	7.5	9.3	6.9	7.5	—	7.6
M1-3 L	29.1	34.4	36.8	36.3	37.5	39.5	35.7	36.3	39.0	37.8	39.5	43.5
M1L	9.5	10.2	10.6	11.4	11.0	11.5	10.8	10.3	11.5	11.8	11.6	12.6
M1W	9.1	10.9	11.3	10.2	10.3	10.3	10.5	10.2	10.1	10.7	10.8	12.5
M2L	10.5	12.7	12.7	12.7	14.3	13.5	12.8	12.9	14.0	13.0	13.4	15.9
M2W	10.6	12.6	12.0	10.5	11.2	11.5	11.5	12.1	12.1	11.7	12.8	14.6
M3L	10.6	13.3	14.7	14.1	15.0	14.5	14.9	16.0	16.1	15.0	17.0	18.0
M3W	11.0	13.4	10.9	11.2	10.5	12.5	12.2	12.1	11.8	12.8	14.6	15.0

Table 2 (continued).

CHARACTER	Pseudolabis dakotensis AMNH 9807 (type)	F:AM 36469 (male)	F:AM 41687 (female)	Miotylopus leonardi F:AM 36655	gibbi F:AM 36446	taylori F:AM 36459 (type)	Gentilicamelus sternbergi AMNH 7970 (type)
Skull L (occ. cond>pmax)	—	265.0	—	—	250.0	310.0	—
I1-M3 L	158.0	157.1	129.6	128.0	150.0	179.5	—
L M3-occ. cond.	—	110.3	90.0	—	106.5	136.6	99.5
Skull W at M3	—	86.6	66.5	—	81.5	74.0	87.4
Rostral W at P1	—	29.5	21.5	—	28.1	24.5	29.2
P1-M3 L	107.4	104.8	91.1	83.0	98.8	109.7	87.3
P1-4 L	61.4	57.8	45.0	41.6	52.3	60.4	47.7
P1-2 diastema	16.0	12.6	10.4	9.0	18.5	20.1	12.2
P1L	9.2	10.8	7.0	7.0	7.5	9.7	6.7
P1W	3.8	3.6	3.2	2.1	3.1	4.2	—
P2L	12.5	11.8	10.5	7.9	10.5	9.1	10.3
P2W	4.5	4.5	5.0	3.0	4.5	5.1	4.7
P3L	13.3	9.7	10.0	8.6	8.5	11.9	9.8
P3W	5.3	6.0	7.0	4.3	4.0	6.0	5.4
P4L	12.0	10.5	9.9	9.4	9.2	10.0	9.1
P4W	10.0	8.8	10.0	7.5	8.1	8.2	9.0
M1-3 L	50.9	48.0	47.2	42.2	46.8	51.4	40.4
M1L	16.0	12.9	14.6	12.5	13.1	14.2	11.9
M1W	14.2	13.1	13.5	10.5	12.8	12.5	11.2
M2L	17.5	15.3	16.7	14.5	15.7	16.3	13.5
M2W	15.3	15.3	15.4	12.5	13.7	14.0	12.1
M3L	20.1	20.3	18.6	16.3	20.3	21.1	16.4
M3W	16.9	17.1	14.0	13.1	15.5	16.0	13.5

franki, but it is intermediate in all its preserved features. The biggest morphologic gap is between *Poebrotherium franki* and *Poebrodon californicus*, so the generic distinction can still be justified.

Poebrotherium chadronense, new species
Figure 2, Table 2

Poebrotherium sp. Wilson, 1974

Type and only known specimen—TMM 40504-22, a skull and partial skeleton (Fig. 2). Airstrip l.f. (early Chadronian), Vieja Group of Texas.

Etymology—In reference to the Chadronian occurrence of this species.

Diagnosis—Medium-small sized *Poebrotherium* (M1-3 length = 33-35 mm) with a distinct posterolingual cusp on P3 and a wider P4 than *P. eximium*. Intermediate in size between *P. franki* and *P. eximium* or *P. wilsoni*.

Discussion—Wilson (1974) has adequately described and figured this species. He refrained from naming it "until more is known of the variation in species of *Poebrotherium*" (Wilson, 1974:26). It is clear from the presently known variation in *P. eximium* and

P. wilsoni that *P. chadronense* can be distinguished on the basis of size (Table 2). Although the size distinction is not obvious in the length of M1-3 (which I have used throughout as a convenient size measure), it is very noticeable in the rest of the skull measurements (Table 2). Since this species does not fit within the normal range of variation of *P. eximium*, and is much too large for *P. franki*, a new species is justified.

P. chadronense is known only from the early Chadronian Airstrip l.f. of Texas. It is very similar in overall morphology to *P. eximium* from the early and middle Chadronian of the High Plains, except that it is significantly smaller with a shorter rostrum.

Poebrotherium eximium Hay, 1902
Figure 3, Tables 2, 3, 5

Poebrotherium wilsoni Wortman, 1898
Poebrotherium eximium Hay, 1902

Type—AMNH 632, skull, mandible, parts of skeleton; supposedly from "Lower Oreodon Beds" (early Orellan), Big Badlands of South Dakota (Fig. 3), although all subsequently found specimens from South Dakota are known only from the Chadron Formation.

Referred Specimens—From 290 feet on zonation section, Ledge Creek, Natrona Co., Wyoming (early Chadronian): F:AM 47396, rami, limb elements. From McCarty's Mountain l.f., Madison Co., Montana (early Chadronian): F:AM 47446, mandible. From Flagstaff Rim, Natrona Co., Wyoming (local range—from 15 feet below Ash F—middle Chadronian): F:AM 47066; mandible. Chadron Formation, Shannon Co., South Dakota (late Chadronian): F:AM 42241, skull and jaws; F:AM 42240, skull and jaws; F:AM 42252, skull and jaws. From 2.5 miles north of Chadron, Dawes Co., Nebraska (Brecht Ranch, Morris Ranch—late Chadronian): F:AM 47116, skull and partial skeleton; F:AM 49119, skull and jaws; F:AM 17115, skull and jaws; F:AM 17143, left ramus; F:AM 17118, right ramus; F:AM 47105, skull and partial skeleton. From Geike Ranch, Sioux Co., Nebraska: F:AM 47427, mandible; F:AM 47426, skull and mandible; F:AM 47428, right ramus; F:AM 47429, skull, jaws, and partial skeleton. From the Douglas area, Converse Co., Wyoming (stratigraphic range 60 below to 100 feet above the 5 tuff of Evanoff et al., 1992): F:AM 47103, skull and complete, articulated skeleton; F:AM 47194, left and right rami; F:AM 47222, left and right rami; F:AM 63834, right ramus; F:AM 47194, palate; F:AM 47029, skull and jaws; F:AM 63832, mandible; F:AM 63836, left ramus; F:AM 63835, mandible; F:AM 63837, right ramus; F:AM 63833, right ramus; F:AM 47006, palate and mandible; F:AM 47001, skull and mandible; F:AM 47007, skull; AMNH 22467, skull and complete, articulated skeleton; F:AM 47002, skull and mandible; F:AM 47008, skull and jaws; F:AM 47023, skull and jaws; F:AM 47371, mandible; F:AM 47196, right ramus; F:AM 47009, juvenile palates, rami; F:AM 47197, mandible; F:AM 47104, juvenile skull; F:AM 42244 juvenile palate; F:AM 47191 partial skull; F:AM 47195, right ramus; F:AM 47319, skull and rami; F:AM 47318, juvenile skull and rami; F:AM 47192, skull; F:AM 47032, skull and jaws; F:AM 42242, skull and jaws; F:AM 47316, skull and partial skeleton; F:AM 47193, skull and partial skeleton; F:AM 47091, skull and partial skeleton; F:AM 42293, skull and partial skeleton; F:AM 42300, skull and jaws; F:AM 42298, juvenile skull; F:AM 47229, skull and jaws; F:AM 63830, skull and jaws; F:AM 42243, skull and jaws; F:AM 63831, skull and jaws; F:AM 47224, skull; F:AM 42297, skull and partial skeleton; F:AM 47021, skull. From the Lusk Area, Niobrara Co., Wyoming (stratigraphic range 0-40 feet above PWL): F:AM 63822, skull; F:AM 47092, skull and jaws; F:AM 63820, palate and partial skull; F:AM 63823, skull and rami; F:AM 47094, mandible;
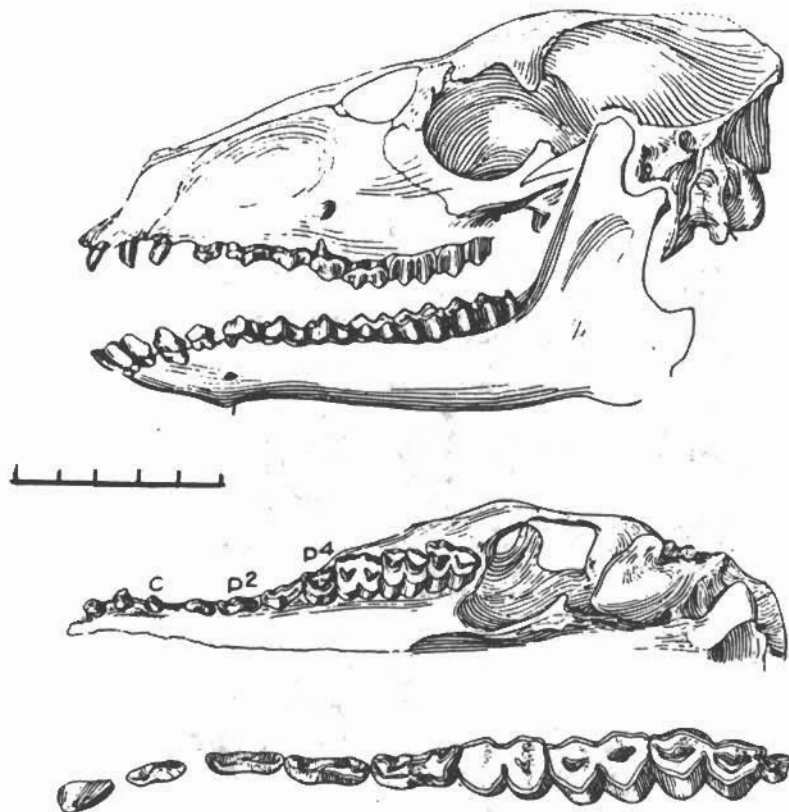
Figure 3. *Poebrotherium eximium*, type specimen, AMNH 632. Left lateral view of skull and mandible; palatal view; crown view of lower dentition. Scale in cm.

F:AM 47035, juvenile skull; F:AM 63821, mandibular and maxilliary fragments; F:AM 63824, left ramus; F:AM 47077, skull and complete skeleton; F:AM 47030, skull and mandible; F:AM 47036, skull; F:AM 47038, mandible; F:AM 47087, skull and partial skeleton.

Diagnosis — Medium-sized (M1-3 length 36-38 mm) camelid with undifferentiated anterior dentition and no diastemata. The m3 hypoconulid is a narrow crest, rather than a horn. Metapodials are longer than *P. wilsoni* or *Paratylopus labiatus*. Slightly larger than *P. chadronense*, with no posterolingual cusps on P3 and a narrower P4.

Description — The type skull was originally figured by Wortman (1898, figure 7), but never adequately described. The rest of the animal has never been described, since it was unknown until the Frick Collection became available.

Except for the anterior dentition, *P. eximium* differs very little from *P. wilsoni* or *Paratylopus labiatus*. As a consequence, some postcranial material of *P. eximium* very closely resembles that of *P. wilsoni*. Most specimens of *P. eximium* have primitive camelid skeletal morphology, also seen in *Paratylopus labiatus*

The skull of *P. eximium* (Fig. 3) differs from *P. wilsoni* in being slightly broader and shorter. The main differences between the two species are in the anterior dentition. Most specimens of *P. eximium* have equal sized, leaf-shaped upper incisors spaced evenly across the top of the rostrum. The canine is also incisiform and equal to the incisors in size, although some specimens (such as the type of *P. eximium*) have slightly more caniniform canines. P1 is usually a long, two-rooted blade which is separated from the canine by a short diastema. P2 is also a narrow, two-rooted blade with a distinct central cusp. In some advanced

specimens of *P. eximium*, the P1-2 diastema that characterizes *P. wilsoni* is beginning to develop. P3 is also bladelike, but there is usually a small discontinuous lingual cingulum such as on TMM 40504-22. P4 is completely selenodont. The molars are typically camelid, with distinct styles and moderate to weak ribs. Mesostyles are generally well developed on the upper molars, although they can be weak in some specimens. Otherwise, the skull and dentition differ little from *P. wilsoni*.

The mandible (Fig. 3) has equal-sized, leaf-shaped lower incisors. Unlike *P. wilsoni*, the incisors are not arranged in a closed "fan" at the tip of the symphysis. The lower canine is completely incisiform and continuous with the incisor row. The p1 is two-rooted, bladelike, and lies immediately behind the canine. There may be a small diastema between p1 and p2, although these teeth are normally not separated. The p2 and p3 are both two-rooted blades, with a distinct anterior cusp. The p4 has a small anterolingual spur. Of the two posterior crests on p4, the labial crest is longer than the lingual crest, and lingually inflated at its posterior end. The m1-3 show the typical selenodont camel condition. The hypoconulid of m3 in *P. eximium* is usually a single narrow crest, while in most *P. wilsoni* it is basin-like. There are some specimens that show exceptions in this feature, however. The posterior symphysis extends to the level of the p1-2 diastema. The symphysis in *P. eximium* is generally not as attenuated and ventrally deflected as it is in *P. wilsoni*, but has only a slight ventral curvature. The coronoid process is slender and straight. The condyle shows the typical camel condition, and is anteromedially inflected. The angular process has the typical camelid "hook" on the dorsal edge. This is below the level of the tooth row. The ventral portion of the angle extends slightly below the level of the ventral margin of the ramus.

The postcranial skeleton (Figs. 19-26) differs little from that of *Paratylopus labiatus* except in the limbs. Scott's (1940) descriptions apply to most of the known elements except the metapodials. As mentioned above, the metapodials in *P. eximium* are relatively longer than they are in *P. wilsoni* or *Paratylopus labiatus*. In length, they equal the distance from the foramen magnum to the canine in their associated skulls. Later individuals of *P. eximium* (for example, F:AM 47077) have a postcranial skeleton (including metapodials) that closely approaches the condition found in *P. wilsoni* although their skulls still have a dentition like *P. eximium*. Thus, the only really diagnostic elements of *P. eximium* are the skull and mandible.

Discussion — Wortman (1898, p. 111, fig. 7) first figured a lateral view of a skull of "*P. wilsoni*." He considered *P. wilsoni* to be the precursor of *Paratylopus labiatus* and stated that *P. wilsoni* lacked diastemata between its anterior teeth. However, Leidy's (1847) type specimen of *P. wilsoni* has diastemata between P1/1

and P2/2, so Wortman's characterization of *P. wilsoni* is incorrect. Hay (1902) apparently recognized this, and so gave the name *P. eximium* to the specimen figured by Wortman. Hay gave no further discussion, description, or characterization of the new species.

Matthew (1904) and Loomis (1928) subsequently adopted the name *P. eximium* for primitive poebrotheres with no caniniform teeth or diastemata. Scott (1940, p. 645) commented that: "This species, if really distinct, is of the sort that one would expect to find in the Chadron, for it much more nearly approximates *Protylopus*, of the Uinta Eocene [this was before *Protylopus* was recognized as an oromerycid by Gazin, 1955], than do the other species of *Poebrotherium*. In size, it about equals *P. wilsoni*, but the five anterior upper teeth (I1-P1) are almost equal in size and equally spaced apart, without distinct diastemata. If these characteristics should prove to be constant, the propriety of recognizing it as a separate species will be clear, especially if it should turn out to be a survivor from the Chadron substage."

Further material, particularly from the Chadronian, has confirmed Scott's suggestions. The skull morphology of *Poebrotherium eximium* does indeed seem to be remarkably consistent in the Chadronian. At the end of its range (early Orellan), *P. eximium* was apparently sympatric with *P. wilsoni* and *Paratylopus labiatus*. Although the latter two species intergrade with *P. eximium* in some features, the appearance of the characteristic anterior dentition of *P. wilsoni* and *Paratylopus labiatus* is quite sudden. Cranial material of all three species can be unambiguously distinguished where they occur together. *P. wilsoni* and *Paratylopus labiatus* both appear to have speciated from *P. eximium*, which persisted unchanged well into the Orellan. The youngest known specimen of *P. eximium* occurs 40 feet above the "Persistent White Layer" (PWL) in the Seaman Hills, near Lusk, Niobrara County, Wyoming (early Orellan) (see this volume, Chapter 14).

Poebrotherium wilsoni Leidy, 1847
Figure 4, Tables 2, 3, 5

Poebrotherium andersoni Troxell, 1917

Type — ANSP 11012, a skull and attached jaws of a juvenile individual (Fig. 4).

Referred Specimens — *P. wilsoni* is by far the most abundant camel from the Oligocene. Most smaller camel specimens in the many White River collections around the world can be referred to this species. Since there are over 500 catalogued specimens of *P. wilsoni* in the Frick Collection alone, and nearly as many uncatalogued specimens, it is clearly impractical to give a complete hypodigm here. The partial list given below includes specimens that had diagnostic portions of the skull or jaw preserved, and were identified to species.

Table 3. Camelid mandible and lower tooth measurements (in mm)

	Poebrotherium				wilsoni			Paratylopus		
	frunki	eximium						labiatus		primaevus
	TMM 40504-149 (type)	AMNH 632 (type)	F:AM 47118	F:AM 47002	ANSP 11012 (type)	F:AM 47130	F:AM 39086	AMNH 6520 (type)	F:AM 42278	AMNH 9806 (type)
CHARACTER										
Symphysis L	—	29.0	21.2	25.5	—	40.0	40.0	—	31.9	40.0
p1-m3 L	—	81.5	73.6	73.8	—	83.3	83.3	89.0	81.7	—
p1-4 L	—	41.5	35.0	38.0	—	40.1	44.5	42.7	42.4	—
p1-2 diastema	—	3.0	4.0	1.0	—	13.0	13.2	14.1	6.8	—
p1L	—	7.0	6.6	7.2	—	6.0	5.7	6.0	7.1	—
p1W	—	2.4	2.6	2.6	—	3.8	1.9	2.3	2.9	—
p2L	7.2	11.1	9.4	8.1	—	8.6	8.0	9.1	11.8	—
p2W	2.0	2.7	2.8	2.5	—	3.3	3.5	—	2.5	—
p3L	7.9	11.1	9.0	9.6	—	9.5	9.7	8.5	9.9	—
p3W	2.4	2.8	3.7	3.6	—	3.1	2.8	2.9	3.5	—
p4L	8.1	12.0	10.0	9.0	—	9.0	8.8	9.5	9.8	—
p4W	3.3	4.0	4.5	4.7	—	4.5	4.0	4.5	4.5	—
m1-3 L	—	42.0	3.70	37.2	39.5	39.1	38.8	43.3	42.2	44.2
m1L	9.7	11.3	10.6	10.7	10.0	10.3	11.0	11.8	11.8	11.3
m1W	6.5	6.4	7.0	6.4	—	6.5	7.0	6.6	6.6	—
m2L	—	13.4	11.8	11.4	13.5	11.9	11.3	12.5	12.7	13.2
m2W	—	8.1	7.0	7.5	—	8.3	7.7	8.4	7.4	8.9
m3L	—	18.1	16.8	16.5	18.0	18.0	17.0	20.1	17.9	19.0
m3W	—	8.6	7.1	7.4	—	8.2	8.1	8.6	8.2	8.8
jaw depth at p2	—	14.9	16.0	14.8	14.5	17.6	16.6	19.1	18.7	—
jaw depth at m2	11.0	18.0	20.3	17.8	14.5	20.7	19.5	19.8	25.7	—

Table 3 (continued).

	Paralabis cedrensis		Pseudolabis dakotensis		Miotylopus			Gentilicamelus sternbergi
					leonardi	gibbi	taylori	
	AMNH 8969 (type)	SDSM 4097	F:AM 36469 (male)	F:AM 41687 (female)	F:AM 36796 (female)	F:AM 36446 (male)	F:AM 36459 (male)	AMNH 7970 (type)
CHARACTER								
Symphysis L	—	39.3	51.0	33.2	31.5	38.4	58.1	40.0
p1-m3 L	92.0	90.1	107.2	99.4	88.1	108.2	127.3	99.1
p1-4 L	48.7	49.5	51.5	47.3	43.2	59.4	71.7	50.2
p1-2 diastema	20.3	16.2	13.8	10.7	16.7	26.7	31.8	16.0
p1L	6.3	—	8.2	6.7	6.0	6.3	7.9	6.7
p1W	2.7	—	2.6	3.3	2.6	2.5	2.7	—
p2L	7.5	6.3	11.2	9.4	5.1	8.4	10.3	9.0
p2W	2.9	2.4	3.9	3.2	2.0	2.6	2.8	3.3
p3L	8.6	8.5	11.3	10.2	8.2	9.3	12.0	11.8
p3W	2.9	3.2	4.5	3.7	3.0	2.9	4.2	4.2
p4L	9.1	9.1	12.1	11.5	10.5	10.5	12.9	11.6
p4W	4.1	4.7	5.2	3.5	3.5	3.5	4.5	5.0
m1-3 L	—	47.1	52.4	52.2	46.5	49.7	55.6	47.9
m1L	10.0	12.8	12.4	13.7	12.9	12.5	13.9	13.3
m1W	6.6	8.4	10.0	8.1	7.4	8.2	9.8	8.4
m2L	13.3	14.7	15.1	17.1	14.0	15.1	17.0	16.4
m2W	7.7	8.9	11.8	8.9	7.0	10.3	10.6	9.0
m3L	18.4	201.5	15.0	22.8	18.3	23.2	24.8	19.2
m3W	7.5	9.3	11.8	8.3	6.1	9.5	11.0	8.5
jaw depth at p2	15.5	18.1	24.0	16.6	15.6	23.8	34.5	21.0
jaw depth at m2	19.4	22.6	28.1	20.5	16.4	24.0	30.5	26.1

From Pipestone Springs, Jefferson Co., Montana (middle Chadronian): F:AM 47445, skull and partial skeleton; F:AM 47446, left ramus with p2-m3. From Flagstaff Rim, Natrona Co., Wyoming (local range—from 25 feet below Ash D to 15 feet below Ash G—middle Chadronian): F:AM 47065, maxilla and ramus; F:AM 47413, ramus with right m3; F:AM 47414, ramus with right p4-m3; F:AM 47070, maxilla, right ramus, partial skeleton; F:AM 47409, right ramus with m2-3; F:AM 47406, right M2-3; F:AM 47067, right maxilla; F:AM 47412, left ramus; F:AM 47411, right ramus with m2-3; F:AM 47407, left maxilla with M1-3; F:AM 47359, right ramus with p2-m3. There is much additional fragmentary uncatalogued material in the Frick Collection. From Devil's Gap, Beaver Divide, Fremont Co., Wyoming (Chadronian?): AMNH 14590, skull and jaws; AMNH 14592, mandible; AMNH 14593, right ramus. From the Lusk area, Niobrara Co., Wyoming (late Chadronian-early Orellan): F:AM 63719, left ramus and metapodial fragment; F:AM 47103, skull, mandible, and partial skeleton; F:AM 47077, associated male and female partial skeletons; F:AM 63704, partial skull, rami, partial skeleton; F:AM 63725, right and left rami; F:AM 63742, left partial ramus; F:AM 63724, right ramus; F:AM 47053, partial skull and mandible, vertebrae; F:AM 47059, right partial ramus; F:AM 63730, partial mandible; F:AM 47090, right and left rami; F:AM 47098, skull and mandible; F:AM 63723, left ramus; F:AM 47051, partial skull, left ramus, partial skeleton; F:AM 63741, right partial ramus; F:AM 63715, left ramus; F:AM 47335, partial skull and skeleton; F:AM 47097, partial skull and mandible, partial skeleton. From the Douglas area, Converse Co., Wyo. (late Chadronian-early Orellan): F:AM 47220, left maxilla and partial mandible; F:AM 47332, palate and partial mandible; F:AM 47370, partial skull and ramus, atlas; F:AM 47015, partial mandible; F:AM 47016, skull and mandible; F:AM 47022, partial skull and mandible; F:AM 47011, skull and mandible; F:AM 63761, right partial ramus; F:AM 47328, partial mandible; F:AM 47331, right ramus; F:AM 47373, anterior partial skull and mandible; F:AM 42248, right ramus. From the "lower nodular zone" (early Orellan), Cottonwood Pass area, Big Badlands, Shannon Co., S.D.: F:AM 42279, skull, mandible, partial skeleton; AMNH 39085, skull, cervicals; AMNH 28841, mandible, partial skeleton; AMNH 39086, skull and jaws; AMNH 38992, mandible; AMNH 38943, left ramus. From Geike Ranch, Sioux Co., Neb. (early Orellan): F:AM 47263, right ramus; F:AM 47271, right ramus; F:AM 47279, partial maxilla and femur; F:AM 47282, partial skull, right ramus; vertebrae; F:AM 47285, partial skull and mandible; F:AM 47276, right and left rami, articulated forelimb. From Munson Ranch, Sioux Co., Neb. (early Orellan): F:AM 47273, right ramus; F:AM 47262, partial skull and mandible; F:AM 47269, left partial ramus; F:AM 47284, partial skull and mandible; F:AM 47260, partial maxilla and rami; F:AM 47266, left ramus; F:AM 47264, left ramus; F:AM 47257, partial skull, left ramus, partial skeleton; F:AM 47259, right partial ramus; F:AM 47263, right ramus. From the area north and west of Chadron, Dawes Co., Neb. (late Chadronian-early Orellan): F:AM 47144, right ramus; F:AM 47145, right ramus; F:AM 47140, partial skull and mandible; F:AM 47125, partial palate and mandible; F:AM 47141, skull and mandible; F:AM 47235, right partial ramus; F:AM 47253, right ramus. From Kostelecky Ranch, Stark Co., N.D. (early Orellan): F:AM 47228, right P2-M2. From the Little Badlands, Stark Co., N.D. (early Orellan): F:AM 47229, M2; F:AM 47230, proximal metatarsal III-IV. From the "Middle Oreodon Beds" (late Orellan), Big Badlands, Shannon Co., S.D.: F:AM 42277, skull, jaws, partial skeleton; F:AM 47170, left ramus; F:AM 42265, right radius-ulna; F:AM 47185, partial skeleton; F:AM 47185, right ramus; F:AM 47173, left maxilla with M2-3; F:AM 47181, right ramus with p3-m3; F:AM 47176, left ramus with p3-m3; F:AM 47178, right ramus with m1-3; F:AM 47190, skull, jaws, partial skeleton; F:AM 47183, skull and jaws; F:AM 47177, right ramus with p4-m3; F:AM 47173, left ramus with m2-3; F:AM 47174, left maxilla with M1-3; F:AM 47172, right ramus with m1-3; F:AM 47169, left ramus with m1-3; F:AM 47171, right ramus with p2-m2. From the Leptauchenia nodules (Whitneyan), Big Badlands, S.D.: AMNH 39082, right M3 (tentatively referred). From the west end of Eagle Nest Butte, Scottsbluff Co., Neb. (middle Whitneyan): F:AM 47425, right ramus.

Diagnosis—Medium to small camels (length of M1-3 = 30-37 mm), with a long diastema between P1/1 and P2/2, and between the canine and P1/1. I3 enlarged. Lower incisors closely appressed in a fanlike arrangement. Lower canine larger, particularly in males. The m3 hypoconulid usually basined. Skeleton with relatively long and slender limbs, and short, arched back. Metapodials relatively shorter than in P. eximium.

Description—P. wilsoni was described by Scott (1940). Figures 19-26 shows the material referred to P. wilsoni in comparison with the other species. Measurements are given in Tables 2, 3, and 5.

Discussion—Poebrotherium wilsoni (Leidy, 1847) was based on an attached skull and mandible of a juvenile individual, with the rostrum anterior to P1 broken off (Fig. 4). The diagnostic diastemata between P1/1 and P2/2 can be clearly seen. The measurements of the specimen indicate that P. wilsoni is the smallest of the White River camels with long diastemata. Galbreath
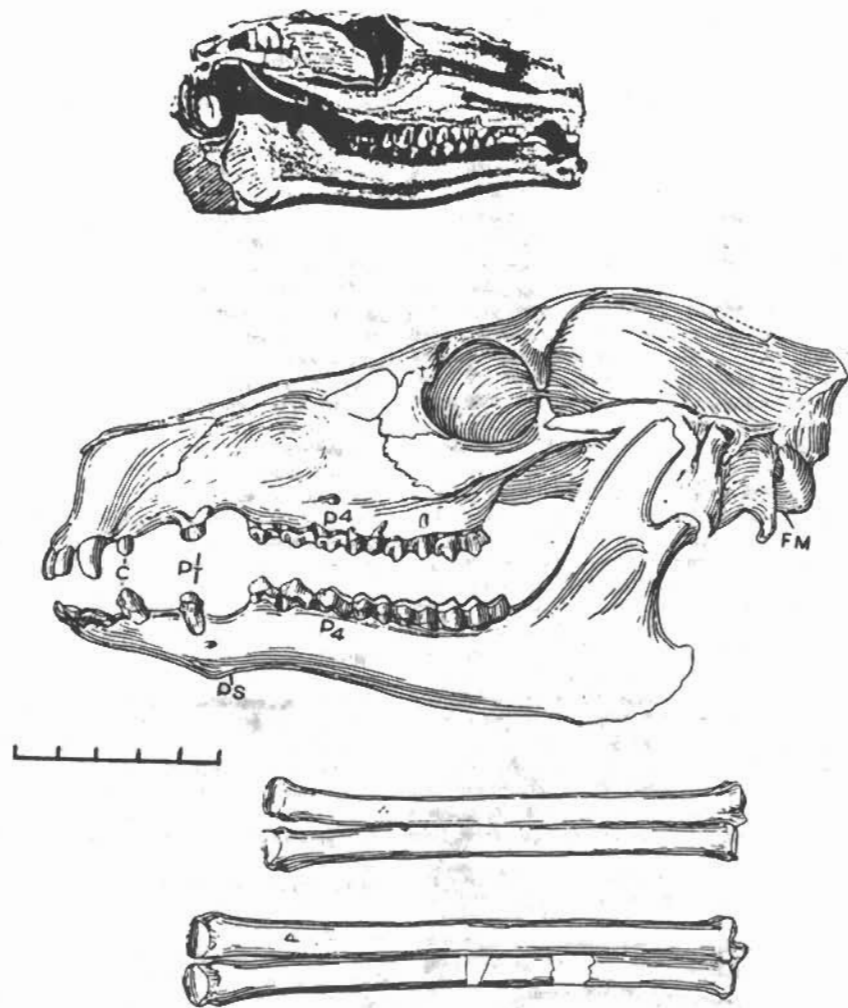
Figure 4. *Poebrotherium wilsoni.* (Top) Type specimen, ASNP 11012, as originally figured by Leidy. (Middle) Left lateral view of referred skull and mandible, F:AM 47130, with associated metacarpals and metatarsals (bottom). Scale in cm.

(1953, pp. 88-89) found that the Orellan camels of Colorado separated into two distinct clusters: the small, abundant, long-ranging *P. wilsoni*, and the larger, less abundant, and shorter-ranging *Paratylopus labiatus*. The camels in the Frick Collection show a similar pattern. *Poebrotherium wilsoni* is very abundant, and shows a moderately large range of size variation. It is similar in size to the contemporaneous specimens of *P. eximium*. Loomis (1928) thought that *P. wilsoni* could not be distinguished from *Paratylopus labiatus*, attributing the size differences to sexual dimorphism. As Scott (1940) and Galbreath (1953) have pointed out, there are several arguments against this idea:

1) Scott (1940) showed that *P. wilsoni* has a very derived, gazelle-like skeleton, very different from the primitive skeletal proportions of *Paratylopus labiatus* or *P. eximium*.

2) The relative scarcity of *Paratylopus labiatus* was
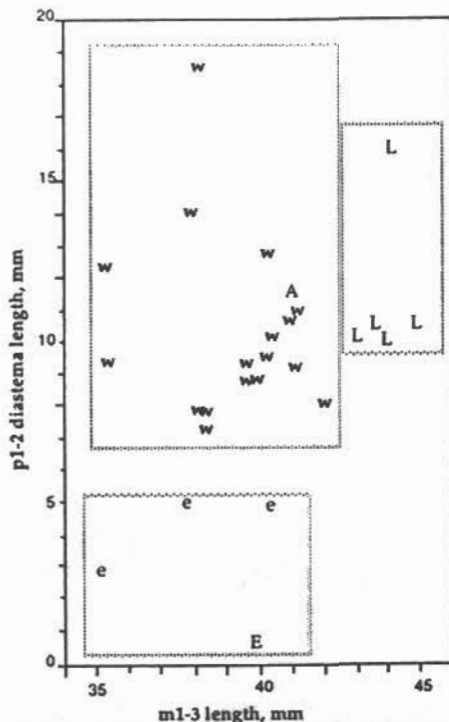
Figure 5. Bivariate plots of m1-3 length versus p1-2 diastema length in Orellan camels. A = type specimen of "*Poebrotherium andersoni*"; E = type specimen of *P. eximium*; e = referred specimens of *P. eximium*; L = specimens of *Paratylopus labiatus*; w = specimens of *Poebrotherium wilsoni*. *P. eximium* is clearly separated by its short diastema (less than 6 mm); *P. labiatus* by its larger size (m1-3 length greater than 42 mm). The type of *P. andersoni* falls within the range of variation of *P. wilsoni*.

used by Galbreath (1953) as evidence that *Paratylopus labiatus* was not the male of *P. wilsoni*. This argument is invalid, however, since some wild camelids have herds consisting of a single male and up to a dozen or more females (Koford, 1957; Franklin, 1983).

3) As Galbreath (1953) has shown, *Paratylopus labiatus* has a shorter stratigraphic range than *P. wilsoni*. There are no *Paratylopus labiatus* in rocks younger than the late early Orellan, whereas there are many examples of *P. wilsoni* in rocks correlated with the early and middle Whitneyan. In addition, *P. wilsoni* appears in the middle Chadronian, but *P. labiatus* is first known from the early Orellan.

4) There is sexual dimorphism in the upper canines of *P. wilsoni*, and several males showing this feature are distinctly smaller than *Paratylopus labiatus*.

5) "*Poebrotherium*" *labiatum*, but not *P. wilsoni*, share derived features with *Paratylopus primaevus*, and

thus I remove it from *Poebrotherium* entirely and place it with *Paratylopus* (see below).

Troxell (1917) erected the species *Poebrotherium andersoni* for a skull and mandible from the "Oreodon zone" near Harrison, Nebraska. Troxell compared this skull to *P. eximium* and *Paratylopus labiatus*, but not to *P. wilsoni*. The characters he cited as diagnostic are variable features of the anterior dentition that also occur in *P. wilsoni*. *Poebrotherium andersoni* fits entirely within the size range of *P. wilsoni* (Fig. 5). Loomis (1928) suggested that *P. andersoni* was a synonym of "*Poebrotherium*" *labiatum*, and Scott (1940) followed this synonymy. However, Loomis did not make adequate comparisons to *P. wilsoni*, either. The enlargement of the I3 and reduction of the canine cited by Loomis (1928) are typical of many specimens of *P. wilsoni*. The variability of the anterior dentition apparently confused many authors. *Paratylopus labiatus* and *P. wilsoni* are most easily distinguished by size, since they have similar development of the anterior dentition and diastemata.

P. wilsoni, with its unusual derived gazelle-like skeleton, is probably the terminal member of the *Poebrotherium* lineage. There seem to be no derived features which unite it with any later camel taxon. *P. wilsoni* persists into the mid-Whitneyan, but is relatively rare after the Orellan.

Poebrotherium wilsoni also shows a strong geographic gradient in abundance. It is extremely scarce in the Orellan deposits of North Dakota and northwest South Dakota, and also rare in the Big Badlands of South Dakota (less than 3% of the fauna, according to Clark et al., 1967). *Poebrotherium* is quite common in the samples collected along the Pine Ridge (particularly in eastern Wyoming and western Nebraska), and Galbreath (1953, p. 88) reports that they are more common than oreodonts in northeastern Colorado. There seems to be a clear north-south gradient in abundance of Orellan camels, which is paralleled by a similar gradient in abundance of *Hypertragulus* and *Miniochoerus* (Prothero, 1982). According to Clark et al. (1967), *Poebrotherium* samples were too small to determine if they showed a significant preference for near-stream versus more open habitat in the Big Badlands; they were found in both environments.

There is clearly sexual dimorphism in *Poebrotherium wilsoni*, as there is in *Pseudolabis*. The best evidence of this is a block containing two partially articulated skeletons (F:AM 47077 A and B) from 40 feet above the PWL ("Persistent White Layer"), Seaman Hills, Niobrara Co., Wyoming (earliest Orellan). The larger individual (F:AM 47077B) has a slightly longer and more pointed upper canine than the smaller individual (F:AM 47077A). The latter individual has a shorter, blunter upper canine with weak anterior and posterior cingula. Presumably, the larger specimen was a male. Sexual dimorphism may explain the large range in size

variation in *P. wilsoni*. Complete skulls with good upper canines are rare in the sample, but most show a rough correlation between larger body size and larger, more pointed upper canines. The number of skulls that can be sexed is too small to determine if the male/female ratios common in camelid harems (Koford, 1957; Wilson, 1975, p. 480; Franklin, 1983) occur in *Poebrotherium*.

Paratylopus Matthew, 1904

Poebrotherium Cope, 1881 (in part)
Protomeryx Hay, 1902 (in part)
Miolabis (Paratylopus) Matthew, 1904
Paratylopus Matthew, 1909
Gentilicamelus Loomis, 1936 (in part)

Type Species—*Paratylopus primaevus* (Matthew, 1904)

Included Species—*Paratylopus labiatus* (Cope, 1881), new combination.

Revised Diagnosis—Medium-sized camels (M1-3 length = 37-41 mm) with brachydont teeth, reduced premolars, and large skulls relative to their tooth size. Otherwise, skull and skeletal proportions remain primitive. Distinguished from *Poebrotherium* by larger size and reduced premolars. Distinguished from *Paralabis* by its smaller size, and slightly reduced premolars. Distinguished from other Whitneyan-Arikareean camels by its brachydont teeth, which are relatively small for their skull size.

Discussion—The nomenclature of Whitneyan and Arikareean camels is one of the most confused in the literature. McKenna (1966) cleared up much of this confusion, but did not attempt a formal revision. He also did not have access to the Frick Collection at the time, so many specimens that are now available for study were unknown to him.

The first name applied to a Whitneyan-Arikareean camel was *Protomeryx* (Leidy, 1856). The type specimen of *Protomeryx halli* (ANSP 11011) is a left mandibular fragment with the canine, p1-3, and the root of i3 (Fig. 6). In the size of the canine, the length of the p1-2 diastema, and in overall size, it could belong to *Paratylopus primaevus*, *Paratylopus labiatus* (for example, compare F:AM 42278 with ANSP 11011), and some specimens of *Poebrotherium wilsoni*. The type specimen of *Protomeryx halli* is clearly indeterminate, as McKenna (1966) showed, and the name *Protomeryx* is a *nomen dubium*.

As the first generic name applied to a Whitneyan camel, *Protomeryx* became a wastebasket taxon for many Whitneyan and Arikareean camels. Yet even the supposed Whitneyan age of the type specimen of *Protomeryx halli* is uncertain. Leidy (1856) states only that the type came from "Bear Creek, Nebraska Territory." Leidy (1869) wrote that the specimen came from Hayden's "Level D," which Matthew (1901)

Figure 6. ANSP 1101, anterior ramal fragment, type of "*Protomeryx halli*." Scale in cm.

interpreted as Whitneyan in age. Cope (1873) paid little attention to its stratigraphic position, but correctly noted that its morphology was nearly indistinguishable from *Poebrotherium wilsoni*. Scott (1891) and Wortman (1898) considered *Protomeryx halli* to be from the "Loup Fork" beds (late Miocene-Pliocene), contemporary with *Procamelus*, *Homocamelus*, *Pliauchenia*, and *Megalomeryx*. This confused many later paleontologists. Matthew's (1899, 1901) Whitneyan age assignment for *Protomeryx halli* influenced most subsequent authors. These age uncertainties are irrelevant, however, since the specimen is not diagnostic in the first place.

The next Whitneyan-Arikareean camel to be described was *Poebrotherium sternbergi* (Cope, 1879), from the ?upper John Day (?late Arikareean) of Oregon (Fig. 18). In 1886, Cope renamed this animal *Gomphotherium*. He was apparently unaware that the name was preoccupied by a proboscidean named by Burmeister in 1837. *Gomphotherium* then became another wastebasket taxon used by many authors for Arikareean and younger camels. Matthew (1901) placed *Gomphotherium* in synonymy with *Protomeryx*. Hay (1902) finally realized that *Gomphotherium* was preoccupied, and placed most Whitneyan-Arikareean camels in *Protomeryx*.

The third name to be applied to Whitneyan-Arikareean camels was *Paratylopus* (Matthew, 1904). It was originally proposed as a subgenus of *Miolabis* (a middle Miocene genus) and then raised to generic level by Matthew in 1909. *Paratylopus* was based on *P. primaevus* from the early Whitneyan of South Dakota. Matthew (1904) and Cope and Matthew (1915) referred "*Gomphotherium*" *sternbergi* to *Paratylopus*.

Since *Protomeryx* and *Gomphotherium* were both invalid, Loomis (1936) decided that no name was available for most Arikareean camels that were more derived than *Paratylopus primaevus*. He created the genus *Gentilicamelus*, based on "*Gomphotherium*"
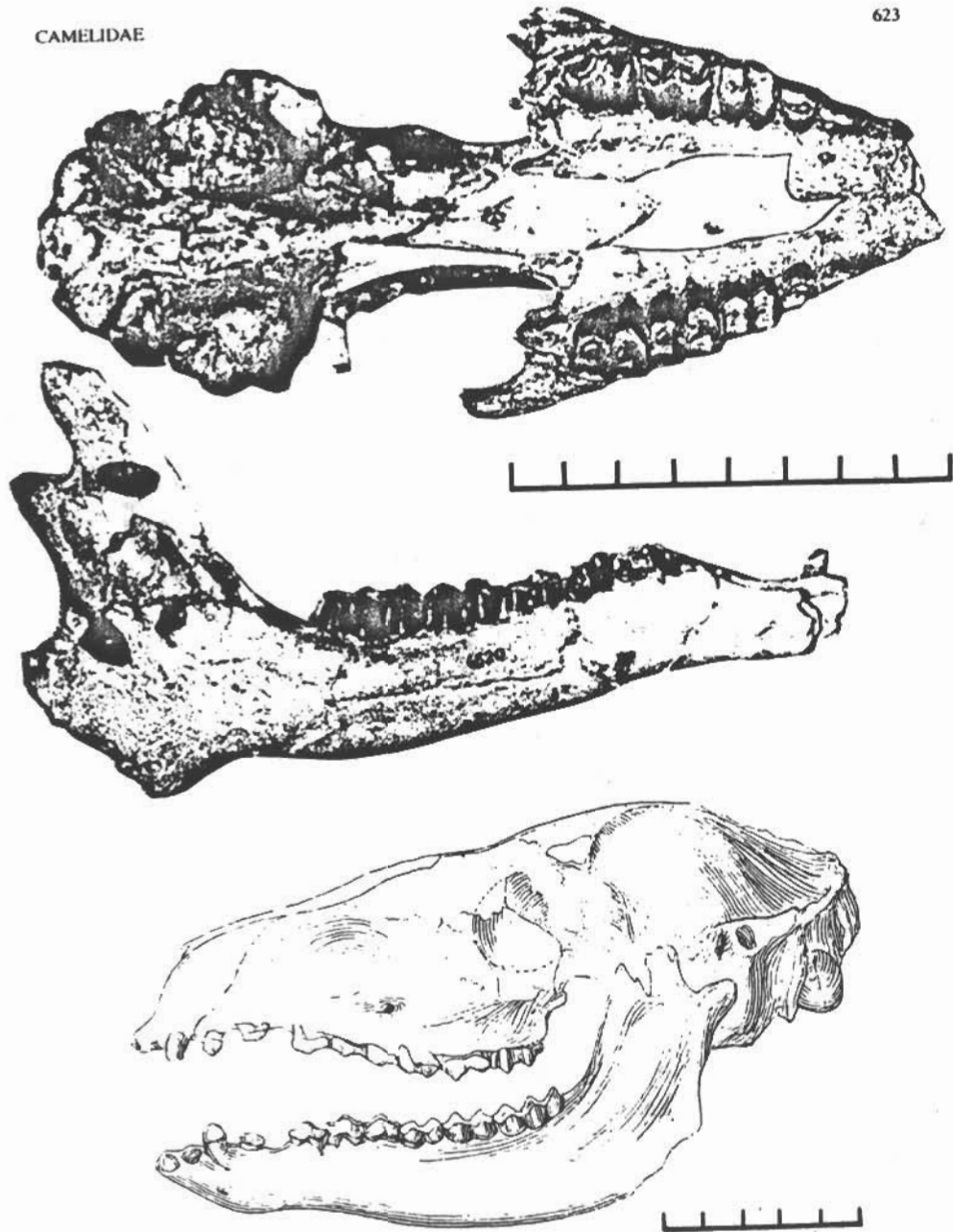

Figure 7. *Paratylopus labiatus*. (Top) Type specimen, AMNH 6250, in palatal view and right lateral view of ramus. Scale in cm. (Bottom) Referred specimen, F:AM 42278, in left lateral view. Scale bar in cm.

sternbergi. Unfortunately, he included within the genus a number of forms that have nothing to do with the type species, creating yet another taxonomic wastebasket. Gentilicamelus included such forms as the oxydactylines "Gomphotherium" cameloides, and "Gentilicamelus" wyomingensis (this taxon is based on an immature individual), and the enigmatic form "Protomeryx" campestris (here considered to be Paralabis), and "Protomeryx" leonardi (here considered to be a species of Miotylopus). Nothing unites this heterogeneous assemblage of camels except their supposed Arikareean age, and even that is open to question in some cases (McKenna, 1966). If Gentilicamelus is valid, it applies only to "Gomphotherium" sternbergi. As discussed below, G. sternbergi has a more derived dentition than Paratylopus or most of the other camels discussed here, so it appears to be a sister-taxon of the nothokematines (Honey et al., in press).

Paratylopus labiatus (Cope, 1881), new combination
Figure 7, Tables 2, 3, 5

Poebrotherium labiatum Cope, 1881
Poebrotherium wilsoni Loomis, 1928 (in part)

Type—AMNH 6520, a partial skull, associated mandible, and partial skeleton (Fig. 7).

Referred Specimens—Paratylopus labiatus is not as common as the contemporary form Poebrotherium wilsoni, but it is still quite abundant. Most large Orellan camels can be referred to P. labiatus. A partial listing of specimens in the Frick Collection includes the following: From the Lusk area, Niobrara Co., Wyoming (stratigraphic range = 40-80 feet above the PWL): F:AM 63743, right ramus; F:AM 63711, skull and jaws; F:AM 47334, partial skull and skeleton; F:AM 53733, right ramus; F:AM 63731, right ramus. From the Douglas area, Converse Co., Wyoming (stratigraphic range = 30-100 feet above the 5 tuff—Evanoff et al., 1992); F:AM 63837, juvenile right ramus; F:AM 63831, skull, jaws, and partial skeleton. From Geike Ranch, Sioux Co., Neb. (stratigraphic range = 0-30 feet above the PWL): F:AM 47436, skull and partial skeleton; F:AM 47283, skull and jaws. From Munson Ranch, Sioux Co., Neb. (stratigraphic range = 30-90 feet above PWL): F:AM 47274, left ramus; F:AM 47261, skull and jaws. From the Chadron area (Morris, Brecht, Bartlett, Schmechel Ranches), Dawes Co., Neb.: F:AM 47235A, quarry block of associated skulls, jaws and partial skeletons; F:AM 47147, right ramus; F:AM 47146, mandible; F:AM 47142, palate and mandible. From the "lower Oreodon beds," Sheep Mountain Table, Big Badlands, Shannon Co., S.D.: F:AM 42278, skull and jaws.

Diagnosis—Medium-sized camel (length M1-3 = 37.5-40 mm). Distinguished from Poebrotherium by its slightly reduced premolars (P2-4/M1-3 ratio is

approximately 0.65—see Table 4) and its larger size. Distinguished from Paratylopus primaevus by its slightly smaller size, and its teeth, which are primitively large in relation to skull size.

Description—Paratylopus labiatus was described by Scott (1940), and figured by Cope and Matthew (1915, plate 115). In most skeletal features, Paratylopus labiatus resembles Poebrotherium eximium, except that it is slightly larger (Figs. 19-26). It has essentially primitive poebrotherine skeletal proportions (Scott, 1940, p. 640, fig. 131), which differs greatly from the gazelle-like proportions of Poebrotherium wilsoni. The most diagnostic features are size and the anterior part of the cranium. Paratylopus labiatus has many of the derived features found in Poebrotherium wilsoni: a large p1-2 diastema, large canines in males, enlarged I3, and i1-3 arranged in a closed "fan."

Discussion—I transfer "Poebrotherium" labiatum to the genus Paratylopus because it shares the following derived features with Paratylopus primaevus: larger size, more reduced premolars, and larger, more robust skull in relation to its tooth size (Tables 2, 3). Paratylopus labiatus seems to be clearly part of the monophyletic lineage that includes Paratylopus primaevus, so it is best referred to Paratylopus. It is not as hypsodont as the Paralabis-Oxydactylus lineages, or the stenomylines. If P. labiatus were retained in Poebrotherium, the latter genus would become paraphyletic.

Figure 8. Paratylopus primaevus. Type specimen, AMNH 9806, in left lateral view of skull and mandible. Scale in cm.

Paratylopus primaevus (Matthew, 1904)
Figure 8, Tables 2, 3, 5

Miolabis (Paratylopus) primaevus Matthew, 1904
Paratylopus primaevus Matthew, 1909

Type—AMNH 9806, a skull with right ramus, partial skeleton (Fig. 8); Whitneyan (upper Oreodon beds), South Dakota.

Referred Specimens—From the Whitneyan (upper Oreodon beds), South Dakota: AMNH 17358, skull and jaws; USNM 14763, skull and jaws; AMNH 9803, skull, jaws, and partial skeleton. From Wetzel Ranch, 6 miles north of Mitchell, Sioux Co., Neb. (early Whitneyan): F:AM 47248, right ramus; F:AM 47247, right ramus. From the east side of Chimney Rock, 25 feet above lower Whitney Ash, Morrill Co., Neb. (early Whitneyan): F:AM 47237, fragmentary palate, right ramus, badly distorted partial skeleton. From H. A. Blackburn Ranch, 7 miles north of Mitchell, Sioux Co., Neb. (early Whitneyan): F:AM 47249, right ramus. From the Sherrill Hills, Niobrara Co., Wyoming (210 feet above PWL, ?early Whitneyan): F:AM 47076, left ramus.

Diagnosis—Medium-sized camel (M1-3 length = 39-41 mm, P3-M3 length = 64-65 mm), slightly larger than Paratylopus labiatus, but with more robust skull and more reduced premolars. Differs from Gentilicamelus sternbergi in that it is slightly smaller with less reduced premolars and less robust skull. Differs from species of Paralabis and Pseudolabis in having much lower-crowned teeth which are small relative to the size of the skull.

Description—Matthew (1904) and Scott (1940) thoroughly described this species. Measurements are given in Table 2, 3 and 5. Postcranial elements are shown in Figures 19-26.

Discussion—Very little new material of Paratylopus primaevus has appeared since its original description. If a larger sample of this species were known, it would probably overlap considerably with Paratylopus labiatus; the differences between the two are very slight.

Several authors (for example, Matthew, 1904; McKenna, 1966) have considered Paratylopus to represent the "central camelid lineage" which gave rise to Oxydactylus, Miotylopus, and Gentilicamelus. Although Paratylopus primaevus is a very primitive camel, it has autapomorphies (such as the skull which is large relative to the dentition) which exclude it from close relationship with Paralabis, Oxydactylus, or with the stenomylines.

Paralabis (Lull, 1921), new rank

Protomeryx Matthew, 1901 (in part)
Pseudolabis (Paralabis) Lull, 1921
Pseudolabis Hay, 1902 (in part)
Protomeryx Hay, 1930 (in part)
Gentilicamelus Loomis, 1936 (in part)
Paratylopus (="Paralabis") McKenna, 1966

Type and only species—Paralabis cedrensis (Matthew, 1901)

Diagnosis—Medium-sized camel (length of M1-3 = 43-45 mm) with moderately hypsodont teeth and highly reduced premolars (P2-4/M1-3 ratio = 0.506—see Table 4). Distinguished from Poebrotherium, Paratylopus, and Gentilicamelus by its larger size, more hypsodont teeth, and more reduced premolars. Distinguished from
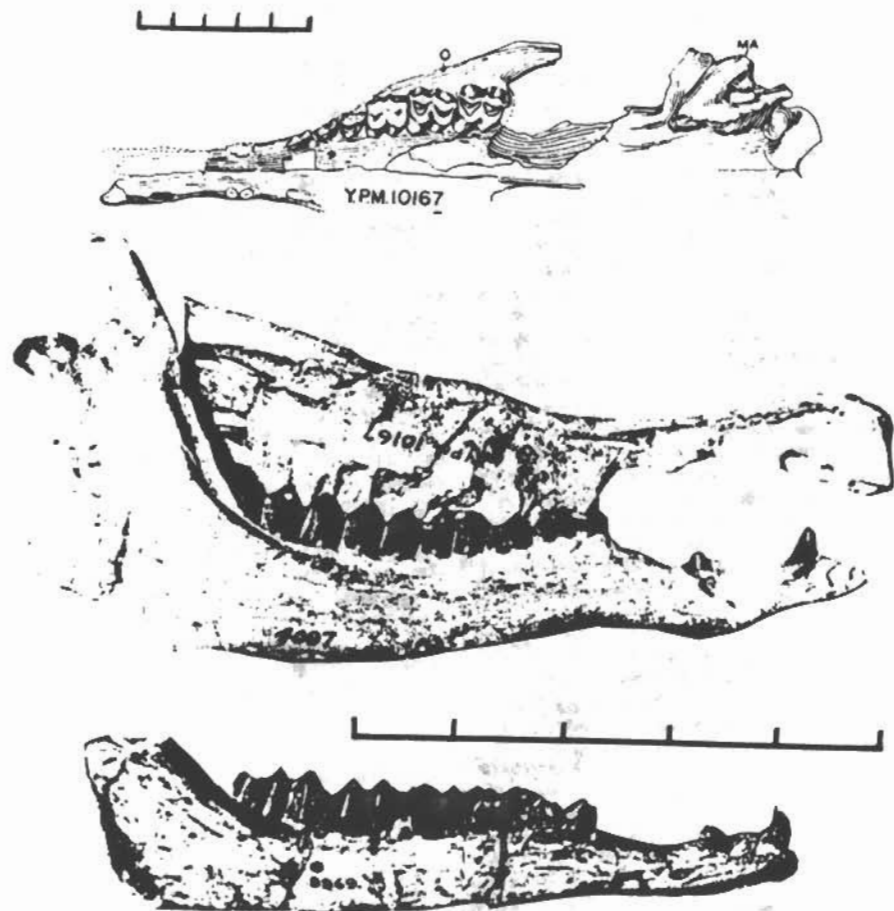
Figure 9. *Paralabis cedrensis* (Top). YPM 10167, type of "*Paralabis matthewi*." Scale in cm. (Middle) Occlusion of YPM 101067 with SDSM 4097, a lower jaw referred to "*Protomeryx cedrensis*," showing their close match in occlusion and premolar reduction. (Bottom) AMNH 8969, type of "*Protomeryx cedrensis*" (= "*P. campester*"). Scale: 1 bar = 2 cm.

Pseudolabis or *Miotylopus* by less hypsodont teeth and presence of mesostyle. Smaller than *Oxydactylus*, but otherwise quite similar.

Discussion—Whitneyan camels with extremely reduced premolars were first referred to the wastebasket taxon *Protomeryx cedrensis* by Matthew (1901). At that time, the species was known from a single lower jaw (AMNH 8969) from Colorado (Fig. 9). In 1921, Lull described a skull (YPM 10167) from the Whitneyan "*Protoceras* beds" of South Dakota, which showed a

similar extreme reduction of the premolars. Lull compared it to *Pseudolabis* and *Poebrotherium*, but not to "*Protomeryx cedrensis*." On this basis, he concluded that it was referable to *Pseudolabis*, and created a new subgenus, *Paralabis*. Apparently, no one has noticed that the skull and jaw seem to match in size and morphology. As a result, the lower jaw taxon ("*Protomeryx cedrensis*") was placed in one wastebasket genus after another, and the skull has languished in obscurity, incorrectly referred to *Pseudolabis*.

McKenna (1966) did not associate the skull and jaw, but he did realize that they were both placed in the wrong genera. He recognized that "*Protomeryx campester*" was a taxon completely distinct from other Whitneyan camels, but he considered *Paralabis matthewi* to be an advanced form of *Paratylopus* that might be ancestral to *Gentilicamelus sternbergi*. Apparently he did not realize how extreme the premolar reduction was in *Paralabis*, or he would not have associated it with *Paratylopus* and *Gentilicamelus*.

In comparing the types of "*Protomeryx*" *cedrensis* and *Paralabis matthewi*, it seems clear that they belong to the same genus and species. Both specimens have more extreme premolar reduction than any other Whitneyan or Arikareean camel. The P2-4/M1-3 ratio of *Paralabis matthewi* is 0.506, the lowest of any camel in this study (Table 4). The type lower jaw of "*Protomeryx*" *cedrensis* is too broken to measure accurately, but a referred lower jaw (SDSM 4097) from the *Protoceras* channels of South Dakota has a p2-4/m1-3 ratio of 0.540, lower than any other camel. *Paralabis matthewi* and "*Protomeryx*" *cedrensis* are the same size, and, allowing for post-mortem distortion, they even occlude quite well (Fig. 9). The type of "*Protomeryx*" *cedrensis* comes from Colorado, but the referred specimen (SDSM 4097) comes from the same beds as the type of *Paralabis matthewi*. Although we still do not have very complete material, it is clear from the present evidence that they are the same taxon, and I synonymize them. Since *Paralabis* is the first valid genus-rank name applied to this taxon, I raise it from subgeneric rank to generic rank (since it is clearly not a subgenus of *Pseudolabis*).

The relationships of *Paralabis* are somewhat ambiguous. The extreme reduction of premolars seems to be an autapomorphy, and thus does not clarify relationships. The increased hypsodonty strongly argues against *Paralabis* having affinities to *Paratylopus* or *Gentilicamelus* (contra McKenna, 1966). Instead, the hypsodonty suggests that *Paralabis* is an advanced camel, related to either the stenomyline group or to the higher camels (Fig. 1). Unfortunately, *Paralabis* is too poorly known at present to resolve its relationships further.

Paralabis cedrensis (Matthew, 1901), new combination
Figure 9, Tables 2, 3, 4

Protomeryx cedrensis Matthew, 1901: 358, fig. 29
Protomeryx campester Matthew, 1901: 422
Protomeryx campester Matthew, 1904
Protomeryx cedrensis Matthew, 1909
Pseudolabis (Paralabis) matthewi Lull, 1921
Pseudolabis matthewi Hay, 1930
Protomeryx campester Hay, 1930
Protomeryx cedrensis Hay, 1930
Protomeryx campester Stock, 1935

Gentilicamelus (Protomeryx) cederensis [sic] Loomis, 1936
Gentilicamelus (Protomeryx) campestris Loomis, 1936
Paratylopus (= "*Paralabis*") *matthewi* McKenna, 1966
Protomeryx campester (= *cedrensis*) McKenna, 1966

Type—AMNH 8969 (Fig. 9), a lower mandible from the Whitneyan (Vista Member) of northern Colorado (Galbreath, 1953, p. 89).

Referred Specimens—KU 133, mandible from the Vista Member, Colorado; YPM 10167, skull, Whitneyan, *Protoceras* beds, South Dakota (Fig. 9, type of *Paralabis matthewi*); SDSM 4097, right ramus, *Protoceras* beds, South Dakota (Fig 9); F:AM 47310, skull, middle Whitney Member (5 feet below Upper Whitney Ash), 1 mile northwest of Pussy Springs, Ruby Ranch, Morrill Co., Nebraska. The postcranial skeleton of *Paralabis cedrensis* is presently unknown.

Diagnosis—Same as for genus.

Description—Since the only new specimen (F:AM 47310) is less well preserved than the type of *P. matthewi* (YPM 10167), nothing new can be added to Lull's (1921) original description of the skull. The referred lower jaws are all very similar to the type, so Matthew's (1901) original description is sufficient. In most features, *Paralabis* is very similar to *Paratylopus*, except that it is much more hypsodont and has much more reduced premolars.

Discussion—The correct species name of this taxon has been greatly confused in the literature. Matthew (1901) gave two different names to the same specimen. In the text, the name *Protomeryx cedrensis* appears first on p. 358 and in fig. 29 (p. 422), and in a subsequent table (p. 423). But at the bottom of p. 422, below fig. 29, is the formal description under the heading "*Protomeryx campester* n. sp." This mistake misled several authors (including Hay, 1930, and Loomis, 1936), who thought that the two names represented different specimens. In his next mention of the species, Matthew (1904) used *Protomeryx campester*. However, in the subsequent literature, Matthew (1909) went back to using the name *cedrensis*. In a manuscript in the American Museum archives that was unpublished at the time of his death, Matthew continued to use *cedrensis*.

Stock (1935, p. 122, footnote 1) decided that Matthew originally intended to use the name *campester*, even though the name *cedrensis* appears many times, and *campester* is used only once. McKenna (1966) followed Stock's determination. However, the name *campester* cannot be used. First, it is clear that Matthew intended to use *cedrensis*, since the name *campester* appears only once, and must have been a *lapsus calami*. Secondly, as first reviser, Matthew (1909, MS) persisted in using *cedrensis* in all other publications (except Matthew, 1904). This was apparently his final intent, since he had referred the species "*Protomeryx cedrensis*" to *Oxydactylus*, which already had a species named

Table 5. Camelid postcranial measurements (in mm)

CHARACTER	Poebrotherium eximium	Poebrotherium wilsoni	Poebrotherium wilsoni	Paratylopus labiatus	Paratylopus primaevus	Pseudolabis dakotensis	Pseudolabis dakotensis	leonardi	Miotylopus gibbi	Miotylopus taylori	Gentilicamelus camelus
	F:AM 47118	F:AM 47130 (female)	AMNH 1364 (male)	AMNH 6520 (type)	AMNH 9806 (type)	F:AM 41687 (female)	F:AM 41942 (male)	F:AM 36655 (female)	F:AM 36446 (male)	F:AM 41829 (male)	AMNH 7910 (type)
Axis centrum L	—	49	—	61	56	58	—	—	67	73	—
Axis centrum dors/vent ht	—	37	—	41	48	—	—	—	45	50	—
Atlas W, at transv. proc.	49	40	—	55	54	37	—	—	53	68	—
Atlas L, dorsal centrum	25	30	—	25	31	25	—	—	30	39	—
Scapula, length	—	140	—	—	127	—	163	—	170	167	—
W of neck	—	18	—	18	18	19	22	—	28	23	—
W of scapula	—	98	—	—	77	88	88	—	103	90	—
Humerus length	150	147	150	—	—	—	—	—	195	—	177
Midshaft W	14	16	15	19	—	18	—	—	14	18	22
Radius-ulna L	177	188	182	214	—	258	310	—	309	—	259
Midshaft radial W	15	14	13	16	—	22	23	—	20	21	21
Metacarpus L	—	117	127	120	—	183	214	180	238	298	178
MCIII-IV W	—	15	13	15	—	19	22	13	13	17	29
Femur L	185	182	161	—	—	—	264	—	250	—	223
Midshaft W	18	12	14	29	—	—	21	—	19	—	20
Tibia L	193	—	180	222	—	254	292	—	289	335	256
Midshaft W	16	15	13	16	—	20	21	—	29	22	20
Metatarsus L	142	133	129	152	—	185	216	—	244	—	186
MTIII-IV W	16	16	13	18	—	18	22	—	13	—	28
Astragalus L	27	25	28	28	—	29	38	—	30	—	34
Astragalus W	16	15	18	17	—	20	21	—	17	—	20
Calcaneum L	52	—	55	55	57	63	54	—	76	82	74
Calcaneal tuber L	34	—	31	35	48	37	54	—	51	61	52

campestris. Although I do not agree that this taxon is synonymous with *Oxydactylus*, a serious problem arises if the name *campester* is used for *Paralabis*. The feminine form of the adjective, *campestris*, is required when it modifies the suffix *-labis* (Latin, feminine, "forceps"). (The ending of *cedrensis* is correct for either masculine or feminine nouns.) If the name became *Paralabis campestris*, it could be easily confused with a similar camel, *Oxydactylus campestris* Cook, 1909, from the late Arikareean of Nebraska. Since the author's original intent and later revisions favored *cedrensis*, and reviving the name *campester* could create a rare case of secondary homonymy (and certainly a lot of confusion), I designate *cedrensis* as the valid species name for the only species of *Paralabis*.

Subfamily STENOMYLINAE Matthew, 1910
(= Pseudolabidinae Simpson, 1945)

Known Distribution—Whitneyan-early Barstovian (early Oligocene to middle Miocene) of the North American High Plains; early Arikareean (late Oligocene) of California.

Diagnosis— Medium to large camels (P2-M3 length = 65-82 mm) with long rostra and a deep, anteroposteriorly elongate maxillary fossa. Teeth are more hypsodont and transversely narrow than *Poebrotherium*, *Paratylopus*, *Paralabis*, or oxydactylines. Very weak or no mesostyle on the upper teeth, or metastylid on the lower teeth. The premaxilla is extended posteriorly at least to the level of P1.

Included Taxa—*Pseudolabis* Matthew, 1909; *Miotylopus* Schlaikjer, 1936; and the Stenomylini Matthew, 1910 [here reduced to tribe rank], which include *Stenomylus* Peterson, 1906; *Blickomylus* Frick and Taylor, 1968; *Rakomylus* Frick, 1937.

Discussion—As listed above, there are a number of unique shared derived characters that unite a clade consisting of *Pseudolabis*, *Miotylopus*, and the stenomylines. Despite the striking similarities between these taxa, most authors have postulated that these similarities arose independently. Since the Stenomylini appear suddenly in the late Arikareean with all their bizarre specializations, several authors (for example, Peterson, 1906; Frick and Taylor, 1968) postulated that they diverged very early in camel evolution, possibly as early as the Eocene. McKenna (1966, p. 4) was the first
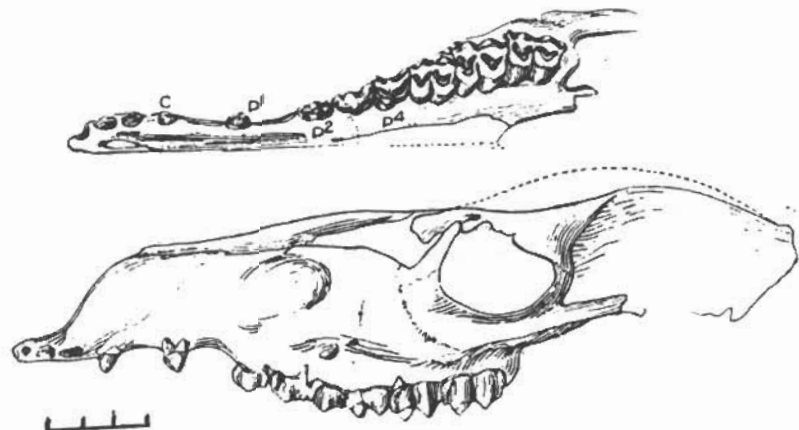
to note the similarities between stenomylines, *Pseudolabis*, and *Miotylopus* (= *Dyseotylopus*), but he did not pursue these questions further. Honey and Taylor (1978, p. 419) pointed out that *Stenomylus*, *Pseudolabis*, and *Miotylopus* share the derived character of a weak or absent mesostyle. In addition to this feature, the peculiar maxillary fossa, the precocious elongation and hypsodonty of the teeth, and the posterior extension of the premaxillary are all good synapomorphies which corroborate this hypothesis of relationships. Therefore, I expand the subfamily Stenomylinae to include not only the traditional stenomylines of Frick and Taylor (1968), but also their primitive sister-taxa, *Pseudolabis* and *Miotylopus*. As a consequence, the traditional taxa of the Subfamily Stenomylinae are grouped under the Tribe Stenomylini, to reflect this hierarchical relationship (Fig. 1).

The expanded taxon Stenomylinae is an important, previously unrecognized monophyletic group that was the dominant group of camels during the Whitneyan and Arikareean. By contrast, the *Paratylopus* lineage was relatively rare in the Whitneyan, and extinct by the Arikareean. The oxydactylines, paralabines, and miolabines did not diverge until the late Arikareean, when the more primitive stenomylines, such as *Pseudolabis* and *Miotylopus*, declined and only the hyperspecialized Stenomylini remained.

Pseudolabis Matthew, 1904

Pseudolabis Matthew, 1904
non *Pseudolabis* Lull, 1921
  Type and only species—*Pseudolabis dakotensis* Matthew, 1904

Figure 10. *Pseudolabis dakotensis*. AMNH 9807, type specimen in left lateral and palatal view. Scale in cm.

Range—Whitneyan (*Protoceras* beds) to late Arikareean (Harrison Formation), High Plains of Nebraska, Wyoming, and South Dakota.

Diagnosis—Medium to large camels (length of M1-3 = 47-59 mm) with a slight flexure of the P4 lingual selene. Like all stenomylines, *Pseudolabis* has a posteriorly elongated deeply depressed maxillary fossa, a posteriorly elongated premaxilla, and relatively high-crowned teeth. It is further distinguished from *Miotylopus* in having a slightly shorter rostrum and less reduced premolars. *Pseudolabis* can be distinguished from all non-stenomyline camels by its weak mesostyles, deep maxillary fossa, and posteriorly extended premaxilla.

Discussion—From his initial descriptions, Matthew (1904) recognized that *Pseudolabis* was a precociously specialized form in having hypsodont teeth and a closed orbit. However, *Pseudolabis* has always been relegated to a "side branch" of the Camelidae, since it is clearly too specialized to be ancestral to any other camel. McKenna (1966, p. 4) was the first to point out dental similarities between *Pseudolabis*, *Dyseotylopus*, and the stenomylines. In addition to these dental similarities, several other unique features of the skull strongly corroborate the hypothesis that *Pseudolabis* is part of a monophyletic group including *Miotylopus* and the stenomylines (see above).

Pseudolabis dakotensis Matthew, 1904
Figures 10-11, Tables 2, 3, 5

Type—AMNH 9807, badly crushed female skull lacking basicranium (Fig. 10), and an associated atlas from the Whitneyan "*Protoceras* beds" of South Dakota.
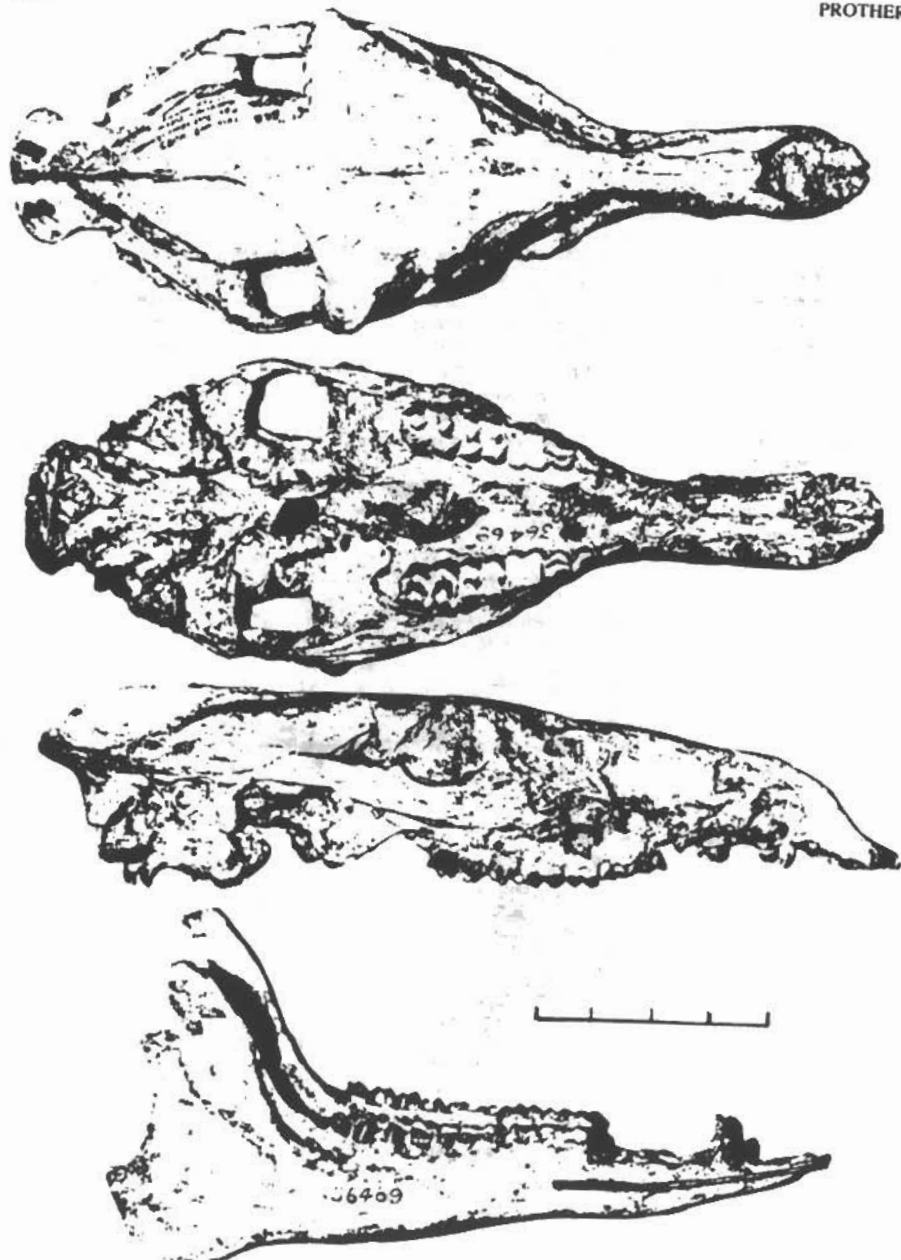**Referred Specimens**—From the Whitneyan

Figure 11. *Pseudolabis dakotensis*. F:AM 36469, an undistorted skull and associated mandible, showing the normal morphology of the species. Scale: 1 bar = 2 cm.

Nebraska (5 feet below the base of the Gering Formation, 155 feet above the Upper Whitney Ash, northeast corner of Castle Rock, southeast of Bayard, Scottsbluff Co., Nebraska): F:AM 41687, female skull and jaws, three partial skeletons. From the Sharps Formation, Shannon Co., S.D. (latest Whitneyan or Arikareean, *fide* Tedford et al., 1985): F:AM 47188, male skull. Gering Formation and equivalents (early Arikareean): From south side of 66 Mountain, 15 feet below white layer, Goshen Co., Wyoming: F:AM 31867, left male maxilla; F:AM 36793, tibia and calcaneum; From Horse Creek, Willow Creek area, Goshen Co., Wyoming: F:AM 36798, femur, tibia, tarsals and metatarsals; F:AM 36795, metacarpals and metatarsals; F:AM 36802, metatarsals and phalanges; F:AM 41800, female skull and jaws; Little Muddy Creek area, Goshen Co., Wyoming: F:AM 41807, partial male skull and jaws; F:AM 41815, partial skull and jaws; F:AM 36432, right ramus; F:AM 36469, male skull and jaws (Fig. 9B); F:AM 41942, male skull, jaws, partial skeleton. Monroe Creek Formation and equivalents (middle Arikareean): Muddy Creek area, Goshen Co., Wyoming: F:AM 41700, female mandible; F:AM 36642, male mandible and partial skeleton; F:AM 36791, juvenile left ramus; F:AM 41814, juvenile skull and partial skeleton; F:AM 41948, complete forelimb; F:AM 36470, male palate; F:AM 41943, female left ramus; F:AM 41811, palate and partial skeleton; F:AM 36475, male right ramus. Harrison Formation, Niobrara Co., Wyoming (late Arikareean): F:AM 36487, female mandible; F:AM 41845, humerus and ulna, metacarpals; F:AM 36547, humerus, metacarpals; F:AM 36812, metacarpals and phalanges. Harrison Formation, Sioux Co., Nebraska: F:AM 41844, femur, tibia, metatarsals, phalanges; F:AM 36647, femur, tibia, metatarsals, tarsals, phalanx.

Diagnosis—Same as for genus.

Description—A beautifully uncrushed skull and mandible (F:AM 36469) gives a much better conception of *Pseudolabis* than does the badly crushed and distorted type specimen (Fig. 11). The rostrum is more elongate than *Paratylopus*, but not as narrow as seen in *Miotylopus*. The posterodorsal extension of the premaxilla terminates above the diastema between P1 and P2. There is a deep, anteroposteriorly elongated maxillary fossa. The lacrimal vacuity is small and slit-like, contrary to the condition in the type specimen (which is badly crushed and distorted). Between the supraorbital canals is a slight midline concavity on the frontals. The postorbital processes are very broad and fused to the zygomatic arch. They form a definite "hood" around the posterodorsal rim of the orbit. The braincase is relatively small, but the sagittal crest and lambdoid crests are very large, sharp, and prominent. The zygomatic arches are slender; their maximum lateral width is at the level of the orbit.

The basicranium is well preserved, and shows the typical camelid condition. The wing-like basioccipital processes are present, although weak. The postero-internal (paroccipital) extension of the tympanic bulla is very prominent because the lateral portion of the bulla is broken. The glenoid surfaces are broad and slightly dorsolaterally inclined (as is typical for camels). The external auditory meatus is strong, but the postglenoid foramen is nearly absent. The well preserved pterygoids do not show the peculiar bifurcate tips unique to *Pseudolabis*. The secondary palate terminates at the level of M2. The infraorbital foramen lies above P4, as is typical of camels.

The anterior dentition of F:AM 36469 is poorly preserved (as is the anterior dentition of the type), but F:AM 41942 has a good anterior dentition. I1-2 are small, chisel-shaped teeth spaced out along the tip of the premaxilla. I3 is greatly enlarged, conical, and recurved, as in most primitive camels, including *P. wilsoni* (but not *P. eximium* or *P. franki*), *Paratylopus*, *Miotylopus*, and *Oxydactylus*. There is a large I3-canine diastema. The canines in males are also large, conical and recurved, although not so large as I3. The canines of females are much smaller, and in many cases barely protrude from the maxilla. There is a larger canine-P1 diastema, and a slightly smaller P1-P2 diastema. P1 is a narrow, two-rooted blade. P2 is also bladelike, but P3 is more triangular, with a strong parastyle and weak lingual cusps and cingula. The P3 ectoloph is concave. This condition is primitive for camels, and differs markedly from the condition seen in higher camels. P4 shows the diagnostic *Pseudolabis* flexure of the lingual selene that was a part of Matthew's (1904) definition of the genus. However, only the type shows the extreme development of two lingual crests. Most other specimens have just a slight kink in the posterior half of the lingual selene.

M1-3 show the typical camelid selenodont condition, but are higher crowned than the upper molars of *Poebrotherium*, *Paratylopus*, or *Oxydactylus*. All of the styles are relatively weak, but the mesostyle is completely absent or weakly developed near the base of the tooth. The ribs are stronger than the styles, but not as marked as in most other camels. There are no lingual cingula or cusps on the molars.

The mandible is unknown in the type specimen, but F:AM 36469 is nearly complete and undistorted (Figure 9B). I1-3 are leaf-shaped and arranged into a continuous fan-like pattern. These teeth wear flat at the tips in older individuals. The lower canines follow the incisors without a diastema, and show sexual dimorphism (as do the uppers). Males have canines which are large, conical and recurved, but females have smaller, laterally flattened canines about the size of p1. The c-p1 and p1-p2 diastemata are of about equal length. p1 is a small, simple blade. p2 is also bladelike, but with a parastylid. p3 has a weak parastylid, and two posterior crests which

are closely appressed. As usual, the labial crest is lingually recurved, and longer than the lingual crest. p4 has a strong parastylid and a short posterolingual crest.

The lower molars are high crowned, anteroposteriorly elongate, and transversely compressed. Their lingual borders are smooth, with no metastylids. m3 is particularly narrow, with a basined hypoconulid.

The symphysis is unusually long and narrow, and fused to the level of posterior p1. It shows relatively little ventral deflection. The coronoid process is long and slender, rising from the tooth row at the typical camelid angle. There is a deep elongate fossa running along the dorsolateral edge of the coronoid process immediately posterior to m3. It is deeper in *Pseudolabis* than in any other camelid; this fossa condition seems to be unique to this genus. The condyle shows the typical camelid condition, with a straight posterior border. The angular hook is on the level of the crowns of the lower molars. The angular process protrudes very slightly ventrally.

Most of the best preserved elements described below are from a nearly complete skeleton, F:AM 41942. Of the axial skeleton, only the cervical vertebrae are known. They are similar in proportion to those of *Paratylopus*, except for their larger size (Fig. 19). The neck of *Pseudolabis* was apparently no longer than that of any other primitive camel.

The scapula is best known from F:AM 41942 (Fig. 20). It is narrower dorsally than *Paratylopus*, with a smaller infraspinous fossa. The spine is very prominent and posteroventrally recurved at its margin. There is a small acromion process, but it does not extend as far as the glenoid. The coracoid process is a distinct knob.

The humerus (Fig. 21) is relatively short and slender compared to *Paratylopus*. It is otherwise very similar except for a distally extended entepicondyle. The fused radius-ulna is also relatively long and slender, with a less pronounced olecranon (Fig. 22). No carpals are known for *Pseudolabis*.

Metacarpals III-IV are unfused, and slightly shorter than the metatarsals (Fig. 23). Absolute metapodial length seems quite variable, probably because of the strong sexual size dimorphism. The metacarpal length is usually equal to the distance between the foramen magnum and the P2 on a male skull.

The poorly preserved pelves are similar to those of other camels in parts that remain. The femur has a deep digital fossa and a prominent greater trochanter that is slightly above the level of the head (Fig. 24). The lesser trochanter is a distinct process on the plantar side, as in *Paratylopus* and most tylopods. The tibia (Fig. 25) is relatively long and slender compared to *Paratylopus*, with a very strong cnemial crest. The tarsals are typically camelid (Fig. 26). Metatarsals III and IV are fused (unlike the metacarpals), and equal in length to the distance between the occipital condyle and P1. The phalanges are unremarkable.

In general, *Pseudolabis* is a slightly longer-limbed, more gracile animal than *Paratylopus*, but its proportions are very similar to those of *Oxydactylus*. The metacarpals are slightly shorter than the metatarsals; the former are still unfused, but the latter are completely fused.

Discussion—Although the sample of *Pseudolabis* is still small, there seems to be an unusually large variation in size. This size variation persists throughout the history of *Pseudolabis*, since both small and large individuals can be found at each level in the Whitneyan and Arikareean. I suspect that this size difference is due to sexual dimorphism, since the larger forms invariably have much larger canines than the smaller forms. Both large and small morphs have the same stratigraphic range, which also suggests that they are sexual dimorphs, rather than two species.

Miotylopus Schlaikjer, 1935

Oxydactylus Loomis, 1911 (in part)
Protomeryx Loomis, 1911 (in part)
Miotylopus Schlaikjer, 1935
Dyseotylopus Stock, 1935
Gentilicamelus Loomis, 1936 (in part)

Type Species—*Miotylopus gibbi* (Loomis, 1911)
Included Species—*Miotylopus leonardi* (Loomis, 1911), new combination; *Miotylopus taylori*, new species.

Range—Arikareean (Gering to Harrison formations), Wyoming, Nebraska, and South Dakota; early Arikareean, southern California.

Revised Diagnosis—Stenomyline camels with highly reduced premolars and elongate rostra. Differs from *Pseudolabis* in these two features and in the lack of a pseudolabine flexure on P4 lingual selene. Differs from the Stenomylini in having lower-crowned teeth; P1/1-C1/1 diastemata still present; and no diastemata between P2/2 and P3/3. Differs from all other camels in having high-crowned teeth with very weak or no mesostyles, and dorsal premaxilla extended posterior to the level of P1. Size quite variable. P2-M3 length ranges from 65 to 84 mm.

Discussion—Two small, primitive oxydactyline-like camel jaws were described by Loomis (1911). The larger jaw was named *Oxydactylus gibbi* (p. 67) and the smaller jaw was called *Protomeryx leonardi* (p. 68). Loomis thought that these specimens were from the "Upper Harrison Formation" in the Muddy Creek area. Goshen County, Wyoming, but McKenna and Love (1972, p. 26) believed that they were from much lower in the Arikaree Group. In the Frick Collection, camels from the Muddy Creek area are from sediments equivalent to the Gering and Monroe Creek formations, and occasionally equivalent to the Harrison Formation—but none are equivalent to the "Upper Harrison" rocks of Nebraska. Apparently, Loomis's Muddy Creek
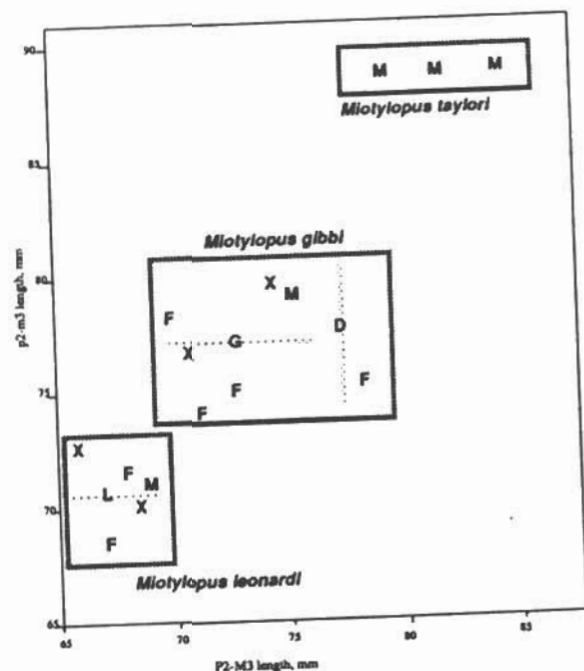

Figure 12. Plot of p2-m3 vs. P2-M3 of selected specimens of *Miotylopus*, showing the size clusters here recognized as *M. leonardi* (small species), *M. gibbi* (medium species), and *M. taylori* (large species). "M" and "F" indicate specimens that can be sexed as male or female; "X" indicates a specimen whose sex is indeterminate. "L" = type of "*Protomeryx*" *leonardi* (a lower jaw, so P2-M3 length is unknown); "G" = type of "*Oxydactylus*" *gibbi* (a lower jaw, so P2-M3 length is unknown); "D" = type of "*Dyseotylopus migrans*" (a partial skull, so p2-m3 length is unknown).

specimens are early or middle Arikareean in age.

In May, 1935, Schlaikjer described the skull and jaws of a camel from the "Lower Harrison" on the south side of 66 Mountain, Goshen County, Wyoming. According to McKenna and Love (1972, p. 28), this specimen was actually from Monroe Creek Formation or older rocks. Schlaikjer named this form *Miotylopus bathygnathus*, and compared it only to "*Paratylopus*" *sternbergi*, *Poebrotherium*, and "*Protomeryx*." He recognized that the mesodont molars without a mesostyle were a new combination for camels, and this was part of his diagnosis for the genus. In July of the same year, Stock (1935) described a camel, *Dyseotylopus migrans*, from the early Arikareean Kew Quarry in the Sespe Formation, Las Posas Hills, Ventura County, California (see this volume, Chapter 8). It also had mesodont teeth and weak mesostyles on the upper molars. Schlaikjer (1935, p. 176) briefly discussed this specimen, and considered it distinct from his *Miotylopus*, or possibly intermediate between *Miotylopus* and *Poebrotherium*.

Loomis (1936) placed the enigmatic *Protomeryx leonardi* in his new genus *Gentilicamelus*. As discussed

above, nothing united the different species that Loomis assigned to *Gentilicamelus* except their Whitneyan-Arikareean age. Most of the contents of *Gentilicamelus* are here referred to *Paralabis*, *Oxydactylus*, and *Miotylopus*, except for the type species, *G. sternbergi*.

McKenna (1966) straightened out much of the confusion regarding small Arikareean camels with weak mesostyles. He transferred "*Oxydactylus*" *gibbi* to *Miotylopus*, although he did not formally synonymize it with *M. bathygnathus* (consistently misspelled "*brachygnathus*" by McKenna, 1966, and McKenna and Love, 1972). McKenna (1966) also noted the similarities of *Miotylopus* with *Dyseotylopus*, although he felt they represented separate lineages. In his 1966 paper, McKenna suggested that "*Protomeryx*" *leonardi* might be referable to *Dyseotylopus*. But in 1972, McKenna and Love formally synonymized *leonardi*, "*brachygnathus*" [sic], and some other specimens with *M. gibbi* (new combination). They also described a new specimen from the Arikareean of Darton's Bluff, Johnson County, Wyoming, which was considerably smaller than other specimens of *M. gibbi*.

McKenna and Love (1972) referred specimens from the Castolon l.f. of Texas described by Stevens et al. (1969) to *M. gibbi*. Stevens (1977, p. 48) has since referred these camels to *Michenia*, based on more complete material, including upper molars with strong mesostyles. Frick and Taylor (1971) suggested that *Dyseotylopus* might be related to *Michenia* and the protolabidines, but Taylor (cited in Stevens, 1977, p. 51) later rejected this idea.

In my studies of the large samples of Arikareean camelids with weak mesostyles in the Frick Collection, I found considerable variation in size. Specimens with relatively broad rostra, unreduced premolars, and the typical *Pseudolabis* P4 were all referred to *Pseudolabis* (see above). The remaining specimens were all united by the derived condition of reduced premolars and relatively slender rostra. All had weak or absent mesostyles, and their dorsal premaxillae are always extended posterior to the level of P1, so they are clearly stenomylines. Most specimens have the deep, elongate premaxillary fossa characteristic of stenomylines, although there is some variation in this feature (see *M. taylori* below). After sorting specimens by size and canine development (which seem to be the best indicator of sexual dimorphism in camels), I found no strong size dimorphism in most *Miotylopus* (unlike in *Poebrotherium* or *Pseudolabis*). For example, one of the smallest jaws, F:AM 36427, has male-shaped canines, yet is the same size as a jaw with presumed female canines, F:AM 36806, from the same deposits (Fig. 13D). In sorting the sample, there seemed to be three distinct size clusters (Fig. 12) with both males and females represented. The small form includes the type of "*Protomeryx*" *leonardi*. The medium-sized form includes the types of "*Oxydactylus*" *gibbi*, *Miotylopus bathygnathus*, and *Dyseotylopus migrans*. A very large form was also found that has never been named or described, and must be a new species. These size clusters are much more apparent in overall proportions of skull and mandible than they are in tooth dimensions (Fig. 12).

The largest forms are a new species, described as *Miotylopus taylori* below. The medium- and small-sized forms are more difficult to separate. McKenna and Love (1972) lumped them together as *Miotylopus gibbi*. However, I am not comfortable with such a wide difference in size and morphology (not attributable to sexual dimorphism) in a single species. The differences are clearly not due to ontogeny, either. F:AM 36441 (a small male) and F:AM 36446 (a medium-sized female) are strikingly different in size, yet their M3's are fully erupted and show comparable wear. I find that the specimens can easily be sorted by size into small and medium-sized *Miotylopus*. Therefore, I recognize two species: the medium-sized *M. gibbi* and the smaller *M. leonardi* (new combination).

Miotylopus is the first valid generic name for this group of camels. It is the senior synonym of *Dyseotylopus* by two months. The name *Miotylopus* was originally chosen because these camels are typical of the Arikareean, which was then considered early Miocene. Ironically, nearly all of the early and middle Arikareean (and thus nearly all *Miotylopus*) are now considered late Oligocene (Tedford et al., 1987; Prothero and Rensberger, 1985), so the name *Miotylopus* has become a misnomer.

Miotylopus leonardi new combination
Figures 13-14, Tables 2, 3, 5

Protomeryx leonardi Loomis, 1911
Gentilicamelus leonardi Loomis, 1936
"*Protomeryx leonardi*" Skinner et al., 1968
Miotylopus gibbi McKenna and Love, 1972 (in part)

Type—AC 2004, a complete right ramus (Fig. 13), from the early Arikareean (Monroe Creek or Harrison formations), Muddy Creek area, "3 miles below Spanish Diggings Spring" (Loomis, 1911, p. 68), Goshen County, Wyoming.

Referred Specimens—The listing below includes catalogued specimens which have the necessary diagnostic elements (usually skulls or jaws). Much catalogued and uncatalogued material in the Frick Collection is referable to this species based on size, but is too incomplete or fragmentary to be certain of this.

From the Gering Formation and equivalents, early Arikareean, Horse Creek-Tremaine area, Sioux County, Nebraska: F:AM 36486, left ramus, right maxilla; F:AM 36463, left and right rami; F:AM 36660, left female ramus; F:AM 36658, male skull and mandible; F:AM 41819, skull; F:AM 36797, juvenile skull, mandible, partial skeleton. Little Muddy Creek area, Niobrara County, Wyoming: F:AM 36806, female mandible; F:AM 36665, female rostrum and mandible; F:AM 36464 partial skull, left ramus; F:AM 36820, female right ramus; F:AM 36442, right ramus; F:AM 36427, female right ramus; F:AM 41944, male left ramus, partial skeleton; F:AM 36441, male mandible; F:AM 36450, partial skull; F:AM 36806, female rostrum; F:AM 36443, female palate; F:AM 36807, female left ramus; F:AM 36473, left ramus; F:AM 41810, palate; F:AM 36825, left ramus; F:AM 41946, female left ramus; F:AM 36452, left ramus; F:AM 36440, left ramus; F:AM 36451, female skull, tarsus; F:AM 36448, juvenile skull; F:AM 36435, left ramus; F:AM 41945, right ramus, partial skeleton; F:AM 36425, skull; F:AM 36655, male skull, mandible, partial skeleton; F:AM 36796, female skull, mandible, partial skeleton (Fig. 13B-C); F:AM 36441, mandible; F:AM 36810, female partial skull and skeleton; F:AM 36846, female skull and partial mandible; F:AM 36447, female skull, mandible, and partial skeleton. From the Monroe Creek Formation and equivalents, Muddy Creek area, Niobrara County, Wyoming (middle Arikareean):
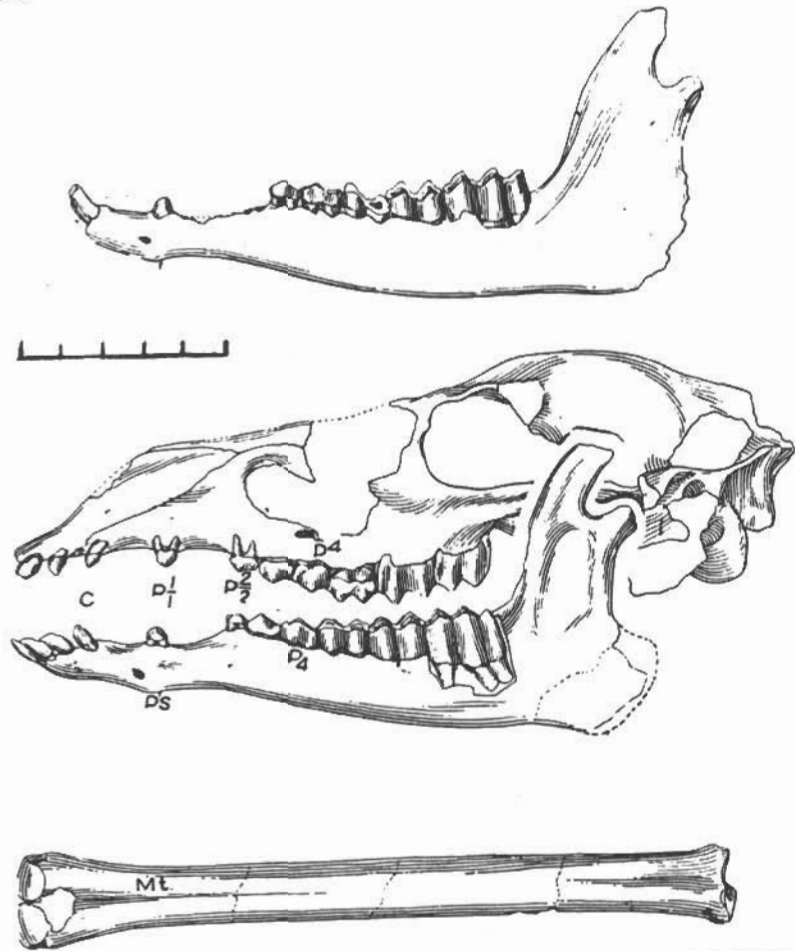

Figure 13. *Miotylopus leonardi*. (Top) AC 2004, type of "*Protomeryx*" *leonardi* (reversed for comparison) (Middle) F:AM 36796, skull and jaws referred to *M. leonardi*. (Bottom) F:AM 36796, associated metatarsals. Scale in cm.

F:AM 36821, partial skeleton; F:AM 36823, female skull, mandible, and partial skeleton; F:AM 41995, partial skeleton; F:AM 36436, right maxilla, partial skeleton; F:AM 41949, female right ramus; F:AM 41950, palate; F:AM 36445, male skull; F:AM 36483, left ramus; F:AM 36484, left ramus; F:AM 36434, female left ramus, partial skeleton; F:AM 41953, female mandible; F:AM 41831, male mandible. From the Harrison Formation and equivalents, near Node, Niobrara County, Wyoming (late Arikareean): F:AM 36785, female mandible; F:AM 36826, female left ramus; F:AM 36437, left ramus; F:AM 36426, male right ramus.

Diagnosis—Smallest species of *Miotylopus* (P2-M3 length = 65-70 mm).

Description—The type specimen (Fig. 13) of *M. leonardi* is a right ramus. Much more complete material of the species is represented in the Frick Collection. The skull (as shown by F:AM 36425, F:AM 36796, and F:AM 36655) has a rather delicate premaxilla similar to that seen in *Stenomylus*. The nasal process of the premaxilla extends well posterior to P1. There is a deep, elongate maxillary fossa. The lacrimal vacuity was apparently small and slit-like, although most specimens are damaged in this area. The postorbital bar is complete. The frontal portion of the postorbital bar

has an almost pedicellate contact with the braincase, since the orbits project laterally from the side of the head. The cranium is small and bulbous, as in *Stenomylus*, with very small sagittal and lambdoid crests. The basicranium is very poorly preserved in most specimens, but what can be seen is typically camelid. The bulla is relatively small for the size of the skull.

The upper incisors are small and chisel-like. They are arranged continuously around the tip of the rostrum. I3 is not enlarged. A small incisiform canine (slightly larger in males) lies immediately posterior to I3. There is a short C-P1 diastema and the P1-P2 diastema is about the same length. P1 is incisiform, but P2 is a narrow blade. P3 is blade-like, with a weak postero-lingual cingulum. P4 is fully selenodont, with no flexure of the lingual selene (contrary to the condition in *Pseudolabis*). P2-4 are considerably reduced in comparison to the molars. The molars are relatively elongate, narrow, and subhypsodont, with very weak mesostyles. However, they do not show the extreme elongation and hypsodonty seen in *Stenomylus*.

The mandible (as seen in F:AM 36796 or F:AM 36441) is slender and gracile, with a very narrow symphysis. The i1-3 are leaf-shaped, with a strong lingual rib. They are arranged in a continuous "fan" around the symphysis. The lower canine shows marked sexual dimorphism. In presumed females, it is almost incisiform, and only slightly separated from the incisors. In presumed males, however, it is a much larger, more robust caniniform tooth, lying much further posterior from the rostrum. The c-p1 and p1-p2 diastemata are of about equal length. The symphysis terminates at the level of p1, which is a small, simple, bladelike tooth, as is p2. The p3 has a lingually inflected parastyle, but is otherwise bladelike. The p4 has a strong parastyle, but is so severely compressed that the posterior ridges are fused. The p2-4 are noticeably reduced in size relative to the size of the molar row, a feature of *Miotylopus* that distinguishes it from many other camels. The lower molars are transversely narrow, subhypsodont, and m3 is particularly elongated. There is a bladelike hypoconulid on m3. The posterior ramus shows the typical slender recurved coronoid, high condyle, and distinct hooked angle. The dorsal edge of the angular "hook" is well above the tooth row.

Although there is much postcranial material from the localities that produce *M. leonardi*, little of it is associated with cranial material that can be identified with *M. leonardi*. The metapodials associated with F:AM 36655 and F:AM 36796 are long and slender, and both metacarpals and metatarsals are fused. The metacarpals are approximately equal in length to the metatarsals, and both are equal to the total length of the skull. The smaller unassociated postcranial elements which may belong to *M. leonardi* are similarly long and slender compared to other camels.

Discussion—As discussed above, *Miotylopus* can be divided into three distinct size groups. The smallest species includes the ramus that was originally named *Protomeryx leonardi* (Loomis, 1911). This ramus best matches the small species of *Miotylopus*, although it shows few uniquely derived features of that genus. It is clear, however, that it can be referred to no other taxon, because: 1) it is too large and too hypsodont for *Poebrotherium*; 2) it is too small, too hypsodont, and its premolars are too reduced for *Paratylopus*; 3) it is similar in size and premolar reduction to *Paralabis*, but the ramus is much shallower dorsoventrally; 4) it is too small for *Pseudolabis*, *Oxydactylus*, or any other species of *Miotylopus*; and 5) it does not have the extremely hypsodont teeth of *Stenomylus*. "*Protomeryx*" *leonardi* also comes from the same deposits as the Frick Collection samples which are here referred to *M. leonardi*.

Miotylopus leonardi shows some striking resemblances to *Stenomylus* (Fig. 14A-C). It is nearly identical in size, and has similarly slender premaxillae, flaring pedicellate postorbital processes, bulbous braincase with weak sagittal crests, and relatively short basicranium. The anterior dentitions are very similar, particularly in females, with their small canines (male *Stenomylus* show no noticeable dimorphism in the canines). The major difference between the two taxa is that *Stenomylus* has shifted an incisiform p1 into the anterior cropping battery, and developed a p2-p3 diastema. The cheek teeth of *Stenomylus*, of course, are much more derived, with their extreme anteroposterior lengthening and hypsodonty of M1-3/1-3 (particularly M3/3), and their highly reduced premolars. *Stenomylus* also has a smooth, rounded angular process, and short coronoid process not seen in most other camels.

Nevertheless, the similarities between the two are very impressive, although there are few features which are unique to these two taxa. Both taxa are similar-sized members of the Stenomylinae. The skull similarities are partly related to their similarity in size, and most of the dental similarities are primitive for the Steno-mylinae. The reduction of I3 may unite the two (other species of *Miotylopus* have a larger I3). However, this same reduction occurs independently in several other camelids, and may not be very reliable. No unique synapomorphies unite *Miotylopus leonardi* and *Stenomylus*, so the species *leonardi* cannot be referred to *Stenomylus*. In non-cladistic terms, *Stenomylus* more closely approaches *M. leonardi* than any other known camel, and *M. leonardi* has no known features which would rule out ancestry of the Stenomylini. It is also of the right age to represent the lineage which gave rise to the Stenomylini. Such hypotheses, however, are speculative.

However, there is certainly no reason to believe (as did Peterson, 1908, and Frick and Taylor, 1968) that the
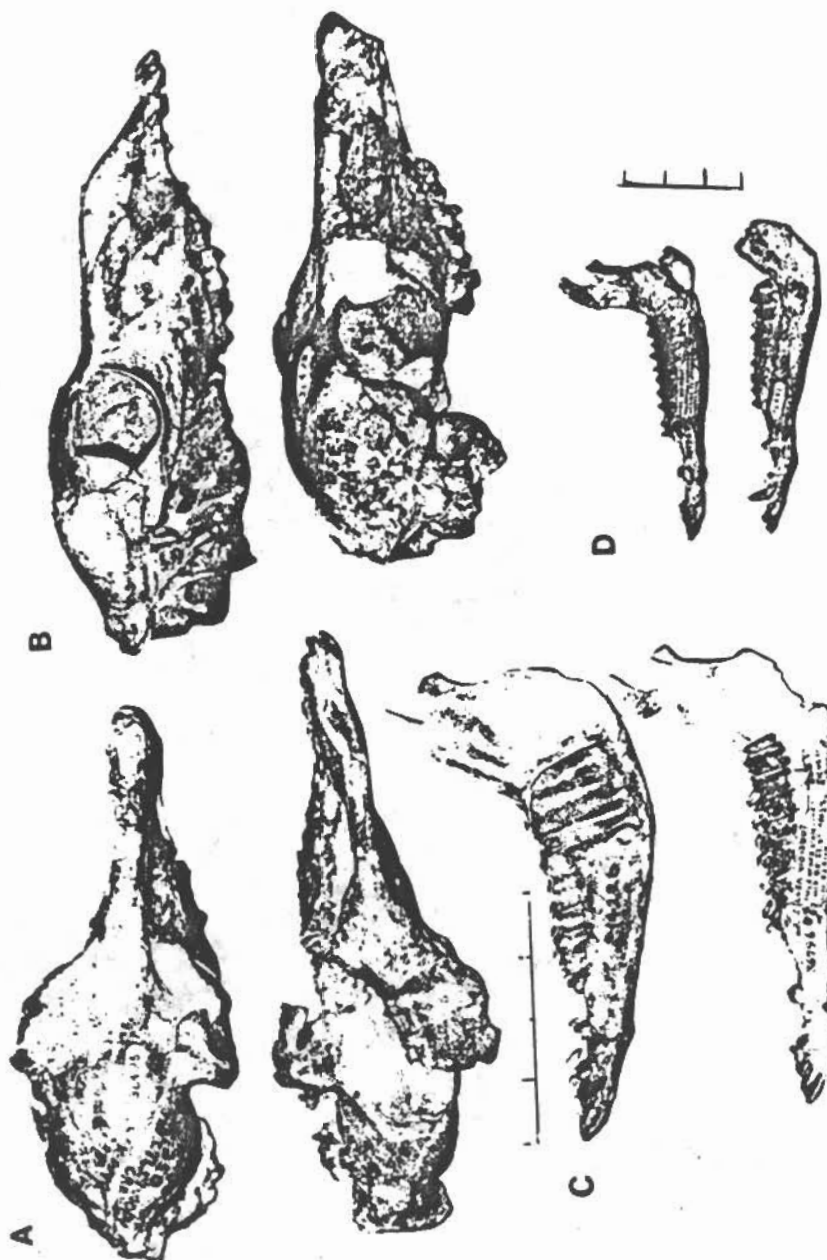

Figure 14. A-C. Comparison of *Miotylopus leonardi* (F:AM 36425) with *Stenomylus gracilis* (F:AM 16226), showing their extreme similarity in most features except hypsodonty and size of the molars in *Stenomylus*. D. Sexual dimorphism in lower jaws of *M. leonardi*, showing a male ramus (F:AM 36441, bottom specimen) with enlarged canine and a female ramus (F:AM 36796, top specimen), with a smaller canine. Scale bar in 2 cm increments.
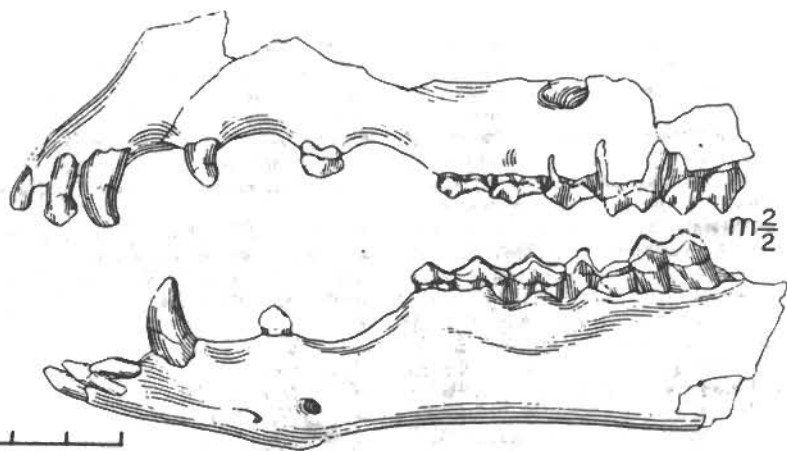
Figure 15. *Miotylopus gibbi.* YPM 10328, type specimen of *"Oxydactylus" gibbi,* including partial upper and lower jaws. Scale in cm.

ancestry of stenomylines must go back to the Eocene. Although stenomylines are very specialized, relatively little change (increased hypsodonty and the anterior shift of p1 and p2) is required to make a *Stenomylus* out of *M. leonardi.* Frick and Taylor (1968, pp. 6-7) argued against the relationship of stenomylines with other Oligocene camelids because "it would require a more rapid rate of evolution for *Stenomylus* to be derived from *Poebrotherium* between Whitneyan and Arikareean time than is known to occur elsewhere in the Camelidae." It is fallacious to argue that because some camelids show relatively slow, stereotyped evolution, all of them must. Stenomylines were highly specialized for an ecological niche very different from their contemporaries. In occupying this new niche, they could have evolved very rapidly.

Miotylopus gibbi (Loomis, 1911)
Figures 15-16, Tables 2, 3, 5

Oxydactylus gibbi Loomis, 1911
Miotylopus bathygnathus Schlaikjer, 1935
Dyseotylopus migrans Stock, 1935
Miotylopus gibbi McKenna, 1966
Miotylopus brachygnathus [sic] McKenna, 1966
Miotylopus gibbi McKenna and Love, 1972 (in part)

Type—YPM 10328, palate and lower jaws missing M3/3 (Fig. 13A); from the Gering or Monroe Creek formations ("Upper Harrison" according to Loomis, 1911), "on Muddy Creek, about opposite to the spring associated with the 'Spanish Diggings'" (Loomis, 1911, p. 67).

Referred Specimens—As was the case with *M. gibbi,* the list below includes only a part of the Frick Collection that bears the diagnostic features of this species (mainly skulls and jaws). Many more catalogued and uncatalogued specimens are probably referable to this species, but will not be listed below.

From Gering Formation and equivalents, Little Muddy Creek, Niobrara County, Wyoming (early Arikareean): F:AM 36477, left ramus; F:AM 36454, skull, mandible, partial skeleton; F:AM 41803, male partial skull, mandible; F:AM 36446, male skull, mandible, partial skeleton (Fig. 16); F:AM 41826, male rostrum. From the Monroe Creek Formation and equivalents, Muddy Creek, Niobrara County, Wyoming (middle Arikareean): F:AM 41689, skull; F:AM 41695, female left ramus; F:AM 41805, partial skeleton; F:AM 41830, partial mandible and skeleton; F:AM 36457, partial skeleton; F:AM 36453, male rostrum; F:AM 41808, male mandible; F:AM 48133, female mandible; F:AM 41809, skull and ramus; F:AM 41831, partial skull; F:AM 41812, male mandible; F:AM 41854, right ramus. Head of Warbonnet Creek, Sioux County, Nebraska: CM 1329, mandible, right maxillary fragment. From the Harrison Formation and equivalents (late Arikareean), near Node, Niobrara County, Wyoming: F:AM 36436, female mandible and humerus; F:AM 36431, female left ramus and symphysis. From the early-middle Arikareean, 150 feet
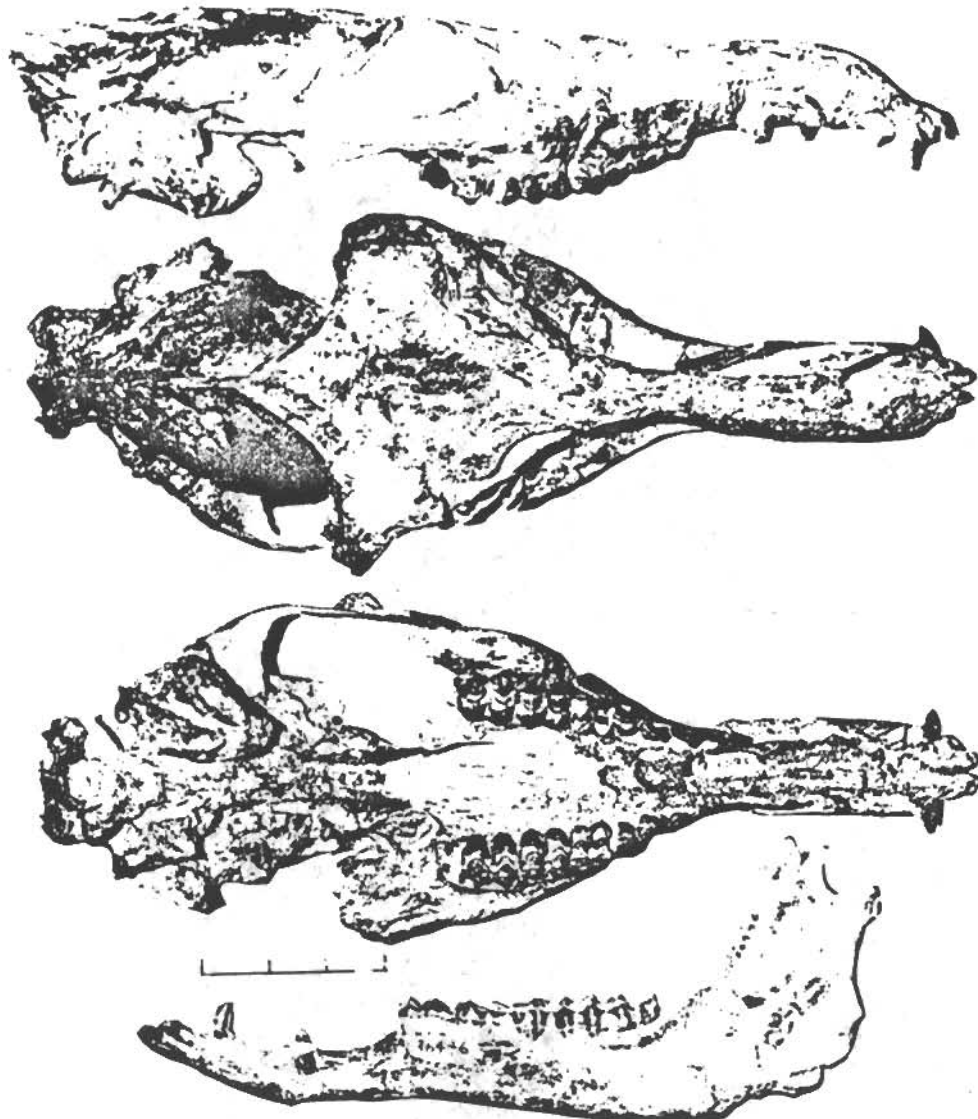

Figure 16. *Miotylopus gibbi.* F:AM 36446, referred male specimen of *M. gibbi,* showing complete skull and mandible. Scale in 2 cm increments.

above the top of the Brule Formation, Goshen Hole, Goshen County, Wyoming: MCZ 2924, partial skull and jaws, pelvis (type of *Miotylopus bathygnathus*). From the ?early Arikareean Kew Quarry, Sespe Formation, Las Posas Hills, Ventura County, Califor-

nia: LACM(CIT) 1721 (type of *Dyseotylopus migrans*).

Diagnosis—Medium-sized species of *Miotylopus.* Length of P2-M3 = 71-79 mm. M3 more elongate relative to the size of the animal than in any other species of *Miotylopus.*

Description—The type of *M. gibbi* consists of a palate and jaws, and the types of *M. bathygnathus* and *Dyseotylopus migrans* are poorly preserved. A skull and jaw, F:AM 36446 (referred to *M. gibbi*) shows all the known features of these three type specimens and is much better preserved, with only slight dorsoventral flattening (Fig. 16). The rostrum is longer and narrower than in *Pseudolabis* or *Oxydactylus*. The nasal process of the premaxilla extends almost to the level of the P2. There is a deep, elongate maxillary fossa, slightly exaggerated by the crushing. The frontals are very broad, with almost no medial depression between the supraorbital canals. The lacrimal vacuity is narrow and slit-like. The postorbital processes are broad and flaring, with a prominent lateral flange. They are well sutured to the zygomatic arch, closing the orbit. The braincase is relatively small, with moderately weak sagittal and lambdoid crests. The basicranium is of the normal camelid type, with moderately large bullae. The pterygoids flare widely. The secondary palate terminates at the level of M2, and the internal nares are broadly open.

I1-2 are small, chisel-like, and evenly spaced around the tip of the rostrum. I3 is very large and caniniform. There is a long I3-C diastema, and shorter C-P1 diastema, and a moderately long P1-P2 diastema. The upper canine is small and incisiform. P1 is a small, blunt blade. P2 is bladelike, but with a weak lingual cingulum. P3 has a strongly convex ectoloph and a weak lingual cingulum. P4 is fully selenodont, with a faint cusp on the posterolabial rim of the lingual selene. M1-3 are fully selenodont, with weak mesostyles and moderately strong ribs. M3 is more elongate relative to the size of the animal than is found on other species of *Miotylopus*.

The lower i1-3 are chisel-like, with faint lingual ribs. The lower canine follows after a short diastema. It is large, upright, and caniniform in males, but nearly incisiform in females. The lower c-p1 and p1-p2 diastemata are quite large, with sharp diastematal crests on the dorsal edge of the ramus. The p1 is a small, blunt crest. p2-4 are blade-like, very narrow, and small relative to the size of the molars. m1-3 are mesodont with a basined m3 hypoconulid. The posterior ramus is typically camelid in all its preserved parts.

The postcranial skeleton of F:AM 36446 is relatively complete. The scapula (Fig. 20) is slender, with a relatively small supraspinous fossa. The acromion is long and delicate, and the coracoid process is unusually thick, partly because the neck above the glenoid is so narrow. The humerus (Fig. 21) has a very shallow bicipital groove and a relatively weak lateral tuberosity. The condyles are quite narrow, and the epicondyles are very weak. The radius-ulna (Fig. 22) is long and slender, with a prominent olecranon. The metacarpals are fused and approximately the same length as the skull. They are only slightly shorter than the fused

metatarsals. The femur (Fig. 24) is remarkably long and slender, with a pronounced curvature that is convex dorsally. The greater trochanter is less robust than in *Paratylopus*, but the lesser trochanter is in the typical plantar position. The tibia (Fig. 25) is as long as the ulna. It is unusually slender at midshaft, but quite robust at the proximal end, with a prominent cnemial crest. The calcaneum has an unusually long tuber, and a very prominent convex proximal fibular facet. The phalanges are long and slender.

Discussion—Medium-sized *Miotylopus* have been referred to two different genera and three species, but there seems no justification for more than one species. The first name applied to this group was *Oxydactylus gibbi* (Loomis, 1911). Although this specimen consists only of a palate and mandible, the teeth are typical of *Miotylopus*, including the weak mesostyles and large I3.

Schlaikjer's (1935) *Miotylopus bathygnathus* is a camel of the same size and morphology as "*Oxydactylus*" *gibbi*, and this provides the first valid generic name for the group. In all of its preserved features, it falls within the normal range of variation of medium-sized *Miotylopus*. Schlaikjer considered the orbits open, but the specimen is too fragmentary to determine this. The only anomalous feature is the slightly smaller bullae with a shallow tympanohyal groove, but this is within the range of variation seen in the Frick Collection sample.

Dyseotylopus migrans (Stock, 1935) is a camel similar in size, age, and preserved morphology to those referred here to *M. gibbi*. The only significant difference between *Dyseotylopus* and the other specimens of *M. gibbi* is that the mesostyles are stronger at the base of the molars of *Dyseotylopus* than they are in most stenomylines. However, I have seen a similar condition in some Frick Collection *M. gibbi*. This feature is not of generic or specific significance, so I place *Dyseotylopus migrans* in synonymy with *Miotylopus gibbi*. Deméré (1988) reports specimens of both cf. *Dyseotylopus* and *Miotylopus* from the early Arikareean Eastlake l.f. in southern San Diego County. However, based on more extensive collections, Deméré (personal communication) now recognizes only a single camelid taxon at Eastlake. It is neither *Dyseotylopus* nor *Miotylopus*, but a new stenomyline, which will be described by Deméré in the near future.

McKenna (1966) suggested that *Miotylopus* was an intermediate between *Paratylopus* and *Oxydactylus*. However, the anatomy and relationships of *Miotylopus* are much better known now. It is clear that *Miotylopus* is a highly derived camel closely related to *Pseudolabis* and the Stenomylini. If one seeks a sister-taxon for the oxydactylines, *Paralabis* makes a much better candidate than does *Miotylopus*.

Miotylopus taylori, new species
Figure 17, Tables 2, 3, 5

Type—F:AM 36459, male skull, mandible (Fig. 17), atlas, and axis. From the early Arikareean (Gering Formation correlative) rocks of the Willow Creek area, Goshen County, Wyoming.

Referred Specimens—From the Muddy Creek area (middle Arikareean, Monroe Creek equivalent), Niobrara County, Wyoming: F:AM 36824, male skull and mandible; F:AM 41855, partial skeleton; F:AM 41829, partial skeleton; F:AM 36461, male palate, mandible, and partial skeleton; F:AM 34460, skull, mandible, partial skeleton.

Etymology—In honor of Beryl Taylor, who devoted most of his career to the study of the Frick Collection camels, and whose hard work and insights made this research possible.

Diagnosis—Largest species of *Miotylopus*. P2-M3 length = 81-85 mm. The p4 posterior crests are separate, unlike other species in the genus.

Description—The type specimen (Fig. 17) is a nearly complete skull and jaws missing only the jugal portion of the zygomatic arches. The skull is unusually large and narrow for *Miotylopus*, although this may be partly due to lateral crushing. The nasal process of the premaxilla extends to the level of the center of the P1-P2 diastema. The maxillary fossa is relatively shallow in the type specimen, although it shows the more typical condition in another referred specimen, F:AM 36824. The rostrum is long and slender, but the palate is not as wide as is typical of other *Miotylopus*. This, too, may be an artifact of crushing, since F:AM 36824 shows more normal *Miotylopus* proportions. It shows the lacrimal vacuity is ovoid in shape, with a tapered anterior end. There is a marked midline depression in the frontals between the supraorbital canals. The postorbital processes of the zygomatic arches are broken, so it is impossible to determine if the orbits were closed in the type. They are closed in F:AM 36824, however. The braincase in the type is relatively narrow, again due to deformation, since the braincase in F:AM 36824 looks more normal in proportions. There is a very high, thin sagittal crest, and a long lambdoid crest which flares laterally from a narrow base.

The basicranium is well preserved, although it has not been sufficiently prepared to see many foramina or other fine details. It does show the typical higher camelid bulla, posteriorly projecting paroccipitals, wing-like basioccipital processes anterior to the occipital condyles, and broad shelf-like glenoids. The glenoid foramen was apparently quite small. The pterygoids are long and slender, and slightly pinched posterior to the palate. The secondary palate terminates at the posterior end of M2.

I1-2 are leaf-shaped, without a lingual rib, and spaced evenly across the front of the rostrum. I3 is very large

and caniniform. The upper canine is also fairly large and caniniform, although smaller than I3; apparently the type specimen was a male (as is evident from the lower canine as well). There are long diastemata between the I3-C, the C-P1, and the P1-P2. P1 is a two-rooted, pointed blade. P2 is blade-like and simple. P3 has a convex ectoloph, but no lingual cingula or cusps. P4 is selenodont with a small labial space in the posterior selene (as in *M. gibbi*). The molars are lingual selene (as in *M. gibbi*). The molars are mesodont, with strong ribs and weak styles. The mesostyles are completely absent. M2 and M3 are also relatively elongate anteroposteriorly.

The mandible is slender, particularly anterior to the cheek teeth. The lower incisors are leaf-shaped and arranged in the typical "fan." The lower canine in the type is large and caniniform, so this specimen appears ✦ to be a male. There is a short i3-c diastema, and long, convex c-p1 and p1-p2 diastemata. p1 is a small, single-rooted triangular blade. p2 and p3 are also bladelike and rooted triangular blade. p4 is unlike that in *M. gibbi* transversely compressed. p4 is unlike that in *M. gibbi* in that the posterior crests are still separate, although short and nearly connected. m1-3 are mesodont and anteroposteriorly elongate. The m3 hypoconulid is only partially basined.

The coronoid process slopes backward much more than is typical for camels, and the tip is shorter and less slender. This is in part due to the unusually high condyle, which resembles the condition seen in some higher camelids. The angular process is badly broken, but its ventral extension projects sharply below the ventral border of the ramus.

Two cervical vertebrae were associated with F:AM 364591. The transverse processes of the atlas (Fig. 19) are unlike most other camels because they have long posterior extensions that are sharply separated from the posterior face of the centrum. The intervertebral and alar foramina were apparently quite large, although this has been exaggerated by breakage of the lateral part of the transverse processes. The axis is long with a short odontoid process and a long dorsal spine. The spine has a nearly horizontal dorsal border, and a much broader anterior end than *Oxydactylus campestris*. It is also laterally narrower than the condition seen in *O. campestris*, but otherwise similar in size and proportion.

No other postcranial remains are associated with the type specimen, but parts of the skeleton are found in association with other fragmentary referred dentitions. A scapula (F:AM 36461) is very similar to that of *M. gibbi*, except that it is proportionally larger (Fig. 20). It has a relatively small supraspinous fossa, a long curved acromion, and a thick blunt coracoid process. The humerus (based on F:AM 41829) is relatively short and slender, with a posteriorly extended entepicondyle (Fig. 21). It is articulated with the proximal end of the radius-ulna, which has a relatively short, robust olecranon. The fused metacarpals are equal to the skull in length,
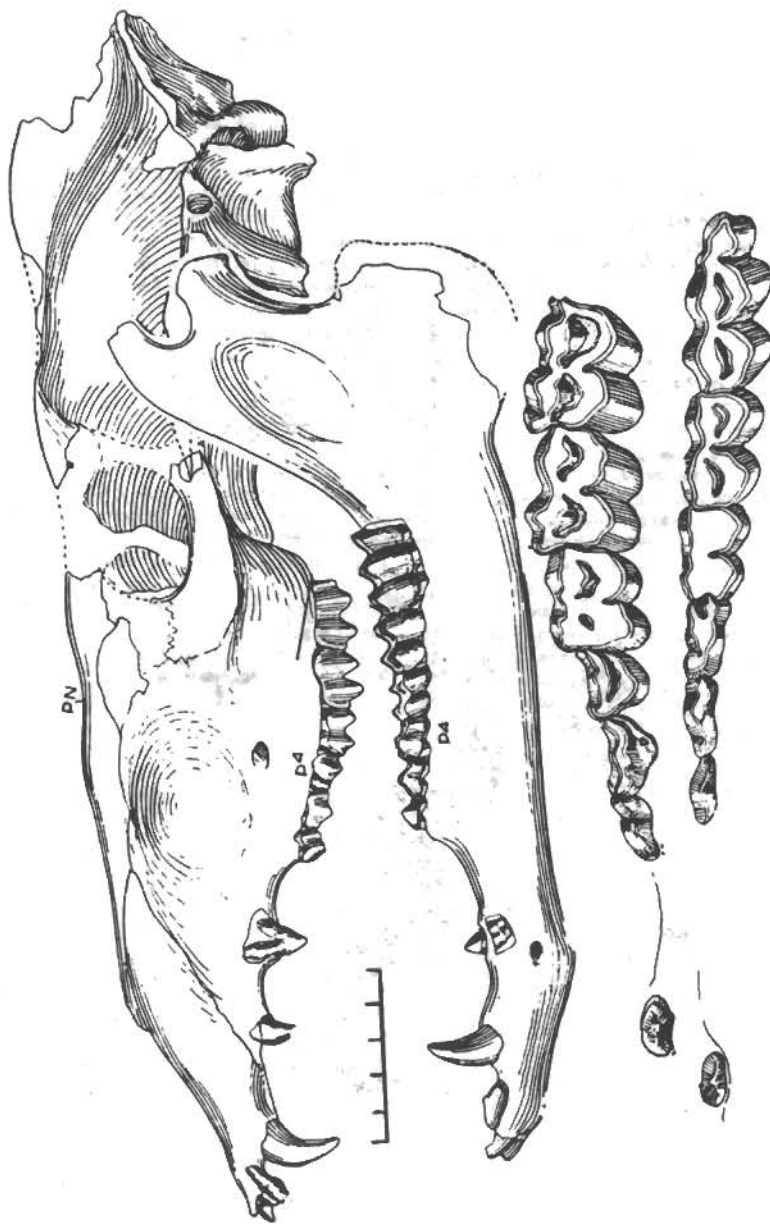
Figure 17. *Miotylopus taylori*, new species. F:AM 36459, type specimen, showing left lateral view of skull and mandible, and crown views of upper and lower dentitions. Scale in cm.

and approximately as long as the metatarsals.

The pelvis (F:AM 46829) is known from a fragment, which shows that it was relatively small and gracile, with a deep acetabulum. The femur is unknown. The tibia (F:AM 41829) is exceptionally long and slender, with a weaker cnemial crest and proximal end than *M. gibbi*. It does show a similar dorsal curvature. This specimen of a tibia is articulated with the tarsals and metatarsals (Fig. 26). Although poorly preserved, the striking feature of these specimens is the length of the calcaneal tuber, which has a knob-like, rugose end, and a plantar keel.

Discussion—The striking feature of the skull and skeleton of *M. taylori* is its more giraffe-like proportions, with elongate cervical vertebrae and distal limb elements. In this respect, it converges on many of the oxydactylines and aepycamelines. However, the diagnostic *Miotylopus* skull features clearly show that these features are convergent (as happens many times in camels).

The difference in overall proportions may also explain why three closely related species of *Miotylopus* could live sympatrically through most of the Arikareean in Wyoming and Nebraska (Fig. 12). Apparently, they were ecologically differentiated. *M. gibbi* maintains the more primitive proportions seen in many camelids. *M. leonardi* has the gazelle-like size and build that eventually was the niche of the stenomylines. *M. taylori* had the longer neck and legs of the giraffe-camel niche, which was later occupied by *Oxydactylus*, the aepycamelines, and other later camels.

Although sparse material referable to *M. gibbi* and *M. leonardi* is known from the upper Arikareean Harrison Formation and equivalents, it appears that the heyday of *Miotylopus* was over by the late Arikareean. Instead, the Harrison and younger formations are characterized by the oxydactylines (which were also highly differentiated in size and ecological adaptations) and by the highly specialized stenomylines.

Subfamily "NOTHOKEMATINAE" Honey et al.
(in press)
Gentilicamelus Loomis, 1936

Poebrotherium Cope, 1879 (in part)
Gomphotherium Cope, 1886 (*non* Burmeister, 1837)
Protomeryx Hay, 1902 (in part)
Miolabis (Paratylopus) Matthew, 1904 (in part)
Paratylopus Cope and Matthew, 1915 (in part)
Type and Only Species—*Gentilicamelus sternbergi* (Cope, 1879).
Revised Diagnosis—Large camel (P2–M3 length = 70.0 mm), distinguished from contemporary *P. primaevus* by its larger size, and by the presence of metastylids on the lower molars. Distinguished from all other Eocene/Oligocene camels by its advanced features, including lower molar metastylids, strong P3 lingual

cingulum, more spatulate lower incisors, and shortened P1. Distinguished from Miocene camels by its primitive skull proportions and by its brachydont teeth which are small relative to the skull size (Table 2).

Discussion—As described above, the generic affinities of this specimen have been disputed ever since it was first described. Although it shares many primitive similarities with *Paratylopus*, the presence of many derived oxydactyline features, such as the lower molar metastylids, high angular process, strong P3 lingual cingulum, shortened P1, and more spatulate lower incisors show that it is probably a sister-taxon of the later Arikareean oxydactylines. Since its stratigraphic position within the John Day Formation is unknown, it is possible that it comes from the late Arikareean, early Miocene portion of the section.

Honey et al. (in press) presented evidence that *G. sternbergi* is a much more advanced camel than the primitive poebrotheres and stenomylines discussed so far. In particular, it shares the enlarged mandibular angle and closely appressed P1 roots of *Nothokemas*, so it is tentatively placed in the "Nothokematinae." This clade of camels is also closely related to the bizarre floridatragulines, although in the cladogram (Fig. 1) of Honey et al. (in press), the "Nothokematinae" are slightly closer to the advanced camelids.

Gentilicamelus sternbergi (Cope, 1879)
Figure 18, Tables 2, 3, 5

Poebrotherium sternbergi Cope, 1879
Gomphotherium sternbergi Cope, 1886
Protomeryx sternbergi Hay, 1902
Miolabis (Paratylopus) sternbergi Matthew, 1904
Paratylopus sternbergi Cope and Matthew, 1915
Paratylopus sternbergi Lull, 1921
Gentilicamelus sternbergi Loomis, 1936
Type—AMNH 7910, skull, mandible, and partial skeleton (Fig. 18); from the ?Upper John Day beds (?late Arikareean), Oregon.
Referred Specimens—AMNH 7913, mandible and limb bones; AMNH 7911, mandible; both from the type locality.
Diagnosis—Same as for genus.
Description—Cope's (1879, 1886) and Wortman's (1898) descriptions of *P. sternbergi* are very sketchy, and also inaccurate. The skull of *P. sternbergi* has a very robust appearance seen in no other camel (Fig. 18). This is due to the relatively short, broad rostrum and the disproportionately small teeth. The rostrum is broken anterior to the canine alveolus, so the condition of the upper incisors and canines is unknown. The maxilla has a broad, shallow, ovoid fossa, characteristic of primitive camels. There is a slight concavity along the anterior midline of the frontals, just anterior to the supraorbital canals. The skull is broken in the region of the lacrimals on both sides, so it is impossible to determine
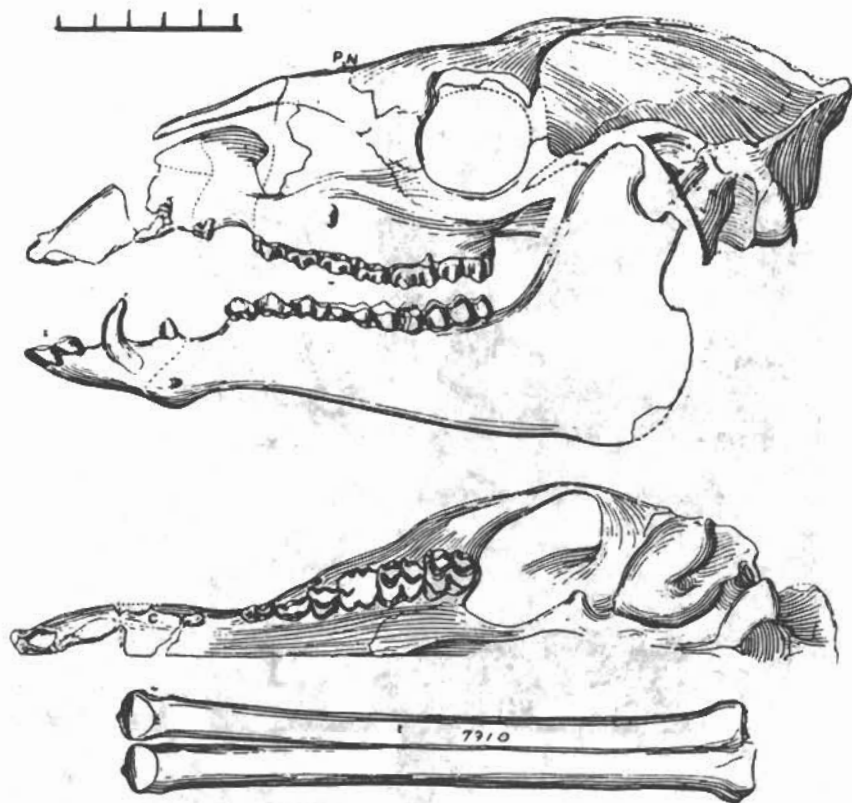
Figure 18. *Gentilicamelus sternbergi*. AMNH 7910, type specimen, showing left lateral view of skull, mandible, palatal view of skull, and associated metatarsals. Scale in cm.

the original size and shape of the lacrimal vacuity. As McKenna (1966) noted, the postorbital region is badly broken, so the original continuity of the postorbital bar is impossible to determine. Neither Wortman's (1898, p. 114) nor Cope's (Cope and Matthew, 1915, p. 116) figures are accurate in this respect. The braincase is disproportionately large by comparison with *P. primaevus*. The sagittal and lambdoid crests are weaker than in *P. primaevus*, but they are partially broken.

The zygomatic arches are poorly preserved, but the left side is more complete and shows that the arch flares much less than in most other camels. The basicranium is only crudely prepared, so few details of the basicranial structure can be determined. However, the bullae are even more inflated and bulbous than would be expected for the skull size, and the portion of the bulla medial to the tympanohyal groove is considerably smaller than

the lateral portion. The pterygoids are poorly prepared, but show the primitive, broadly separated condition (in contrast to the pinched condition seen in stenomylines). The secondary palate terminates at the level of M2 (the primitive condition).

The upper dentition is well worn, but reasonably well preserved. I1-3 and the canines are missing, as mentioned above. Both first upper premolars are broken, although from their remnants, it appears that they have the shape of double-rooted blades. They appear to be disproportionately small in comparison to the first upper premolars of *P. primaevus* and other camels. There is a large diastema between P1 and P2, which is a bladelike tooth with a strong parastyle and lingual cingulum. P3 is more triangular, with an even stronger parastyle and a labially-inflected metastyle. A distinct lingual cingulum with a small cusp is present on P3.

P4 shows the typical camelid selenodont condition, although with a stronger parastyle. M1-3 are fully selenodont, with strong styles and even stronger ribs. The overall impression of the teeth is that they are unusually brachydont for a camel, and disproportionately small in comparison to the size of the skull.

The mandible is complete but poorly preserved and not very well prepared. The ramus is relatively robust, yet has a more ventrally deflected symphysis than does *P. primaevus*. Lower i1-3 are wedgelike and closely associated, fanning out from the symphysis. The lower canine is an unusually large, posterolabially-curved tusk. Apparently this individual was a male, since the canine seems to be sexually dimorphic in many camels. There are short diastemata before and after the canine, and a longer diastema between p1 and p2. The p1 is a small, narrow wedge with two roots. p2 is bladelike, but broader and less compressed than is typical for camels. The same is true of p3, which also has a strong, lingually-inflected parastylid. The parastylid of p4 is even larger and more lingually inflected. The posterolabial crest of p4 is much larger than the posterolingual crest, and both are connected to form a small fossette. Lower m1-2 are too badly worn and broken to describe, other than that they are low-crowned and selenodont. The m3, however, shows a faint metastylid, a derived character seen only in higher camels. The hypoconulid of m3 is broad and basined.

The posterior ramus shows the typical slender camel coronoid, with small "pillow"-shaped condyles which are relatively high on the jaw. The dorsal "hook" of the angular process is very high—well above the level of the tooth row, and much higher than in primitive camels. This, too, appears to be a derived feature that unites it with oxydactylines. There is a slight ventral extension of the angular process below the level of the ventral margin of the ramus. The whole posterior portion of the jaw appears to be more robust than is typical, but this may be an artifact of preservation.

Except for the larger size, the postcranial skeleton (Figs. 19-26) is very similar to *P. primaevus*, and requires no additional description.

Camelidae *incertae sedis*
(sister taxon to the Aepycamelinae and higher camels)
Oxydactylus Peterson, 1904

Discussion—The genus *Oxydactylus* has long been a taxonomic wastebasket for a variety of Arikareean camels (McKenna, 1966; Honey et al., in press). Most do not belong to the genus, and some have been reassigned in Table 1. In addition, the genus *Oxydactylus* as presently constituted is probably a paraphyletic assemblage that includes the sister-taxa of aepycamelines, protolabines, miolabines, and other higher camels (Fig. 1). Honey and Taylor (1978) have already shown that some specimens referred to *Oxydactylus* are

actually primitive protolabines. The same may also be true for primitive aepycamelines labeled "*Oxydactylus*." Honey (personal communication) is currently revising the taxonomy of oxydactyline camels, some of which is summarized in Honey et al. (in press). Since *Oxydactylus s.s.* first appears in the early Miocene (latest Arikareean, Harrison Formation and younger beds), it is beyond the scope of the present study. When comparisons to *Oxydactylus* are made in this document, I am referring to the type species, *O. longipes*, and to the most primitive species, *O. campestris*.

A NOTE ON THE FLORIDATRAGULINES

The affinities of the bizarre, long-snouted floridatragulines (*Floridatragulus*, *Aguascalientia*) from the early Hemingfordian of Florida and Texas have mystified many scientists (for example, White, 1940, 1941, 1942; Simpson, 1945; Romer, 1948; Ray, 1957; Olsen, 1959, 1962; Patton, 1964, 1966, 1969; Maglio, 1966; McKenna, 1966). They were originally placed in the hypertragulines by White (1940), but Ray (1957) and most subsequent workers have realized that they were camels. Their peculiar, crocodile-like rostrum, strong intervallic cingular cusps on the upper molars, and divided hypoconulids on m3 are autapomorphic and do not clarify their relationships. However, the rest of their anatomy is clearly camelid, as several recent workers (Patton, 1966, 1969; Maglio, 1966) have shown in detail. Some (for example, Patton, 1969; Maglio, 1966) thought that floridatragulines were an early side branch of the Camelidae, with no apparent close relatives. Stevens (1977, p. 56) states that the floridatragulines are descended from oromerycids, but she cites no derived oromerycid characters in support of this contention. All of the characters she does mention are primitive for tylopods, or autapomorphic, and she ignores the great number of camelid synapomorphies seen in floridatragulines. Apparently, she has changed her mind, because in her contribution to Honey et al. (in press) she agrees floridatragulines belong in the Camelidae.

Honey et al. (in press) cited a number of derived characters to show that floridatragulines are camelids, more derived than the stenomyline-pseudolabine clade, but more primitive than miolabines, protolabines, or oxydactylines (Fig. 1). An undescribed specimen of *Floridatragulus* (F:AM 31864) shows an apparently continuous postorbital bar, so it may be even more derived than postulated by Honey et al. (in press). Stevens (in Honey et al., in press) argues that *Poebrotherium franki* is the sister-taxon of the floridatragulines, since it has a slightly elongate rostrum with diastemata between some of the anterior teeth. Elongated rostra and diastemata between the anterior teeth occur several times in the Camelidae, and this feature is so prone to parallelism that I see no reason for attempting to push the ancestry of floridatragulines back
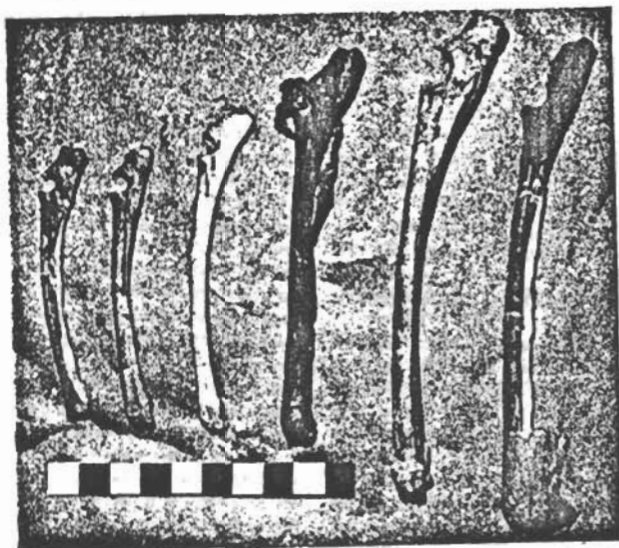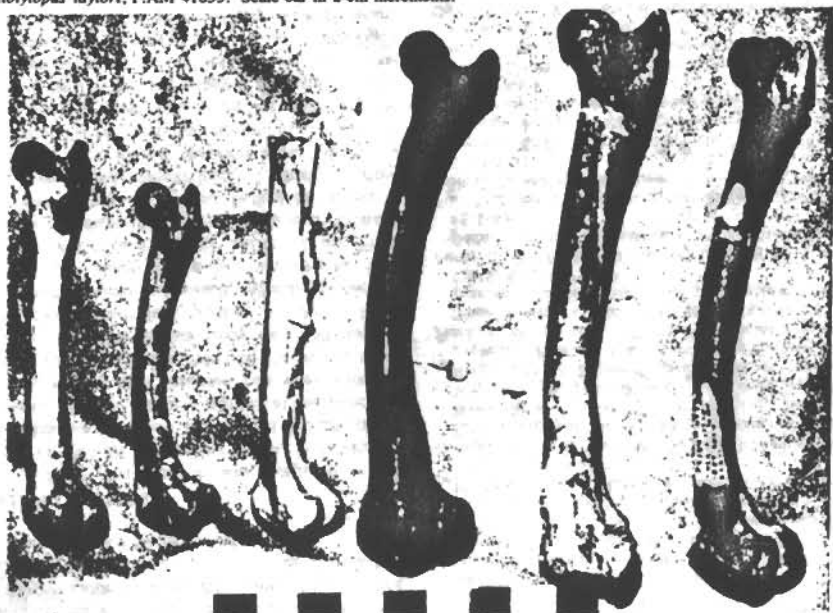
Figure 19. Atlas vertebrae. From left to right: *Poebrotherium eximium*, F:AM 47118; *Poebrotherium wilsoni*, F:AM 47130; *Paratylopus labiatus*, AMNH 6520; *Paratylopus primaevus*, AMNH 9806; *Miotylopus taylori*, F:AM 36459. Scale bar in 2 cm increments.

Figure 20. Scapulae. On left (from top to bottom): *Paratylopus primaevus*, AMNH 9806; *Paratylopus labiatus*, AMNH 6520; *Poebrotherium wilsoni*, F:AM 47077. On right (from top to bottom): *Miotylopus taylori*, F:AM 41829; *Miotylopus gibbi*, F:AM 36446; *Pseudolabis dakotensis*, F:AM 41942. Scale bar in 2 cm increments.
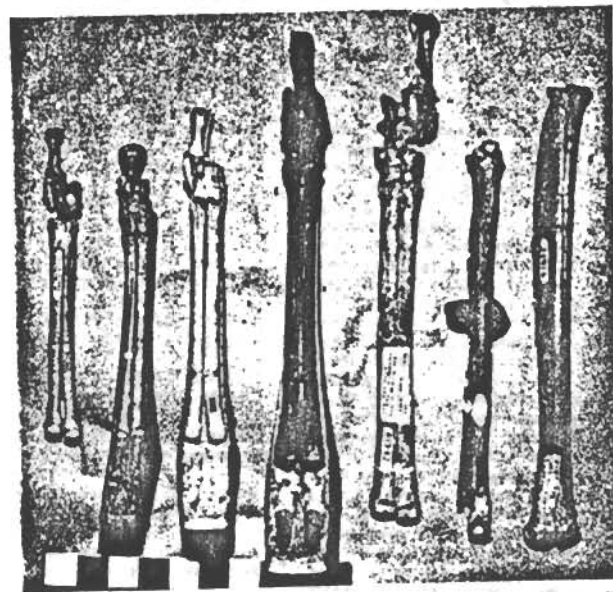

Figure 21. Humeri. From left to right: *Poebrotherium eximium*, F:AM 47118; *Poebrotherium wilsoni*, AMNH 1364; *Paratylopus labiatus*, AMNH 6520; *Gentilicamelus sternbergi*, AMNH 7910; *Miotylopus gibbi*, F:AM 36446; *Pseudolabis dakotensis*, F:AM 41942; *Miotylopus taylori*, F:AM 41855. Scale bar in 2 cm increments.

Figure 22. Radii and ulnae. From left to right: *Poebrotherium eximium*, F:AM 47118; *Poebrotherium wilsoni*, AMNH 1364; *Paratylopus labiatus*, AMNH 6520; *Gentilicamelus sternbergi*, AMNH 7910; *Pseudolabis dakotensis*, F:AM 41942; *Miotylopus gibbi*, F:AM 36446. Scale bar in 2 cm increments.

Figure 23. Metacarpals. From left to right: *Poebrotherium wilsoni*, AMNH 1364; *Paratylopus labiatus*, AMNH 6520; *Gentilicamelus sternbergi*, AMNH 7910; *Pseudolabis dakotensis*, F:AM 41942; *Miotylopus gibbi*, F:AM 36446; *Miotylopus taylori*, F:AM 41855. Scale bar in 2 cm increments.

Figure 25. Tibiae. From top to bottom: *Poebrotherium eximium*, F:AM 47118; *Poebrotherium wilsoni*, AMNH 1364; *Paratylopus labiatus*, AMNH 6520; *Gentilicamelus sternbergi*, AMNH 7910; *Pseudolabis dakotensis*, F:AM 41942. Scale bar in 2 cm increments.

Figure 24. Femora. From left to right: *Poebrotherium eximium*, F:AM 47118; *Poebrotherium wilsoni*, AMNH 1364; *Paratylopus labiatus*, AMNH 6520; *Gentilicamelus sternbergi*, AMNH 7910; *Pseudolabis dakotensis*, F:AM 41942; *Miotylopus gibbi*, F:AM 36446. Scale bar in 2 cm increments.

Figure 26. Tarsals and metatarsals. From left to right: *Poebrotherium eximium*, F:AM 47118; *Poebrotherium wilsoni*, AMNH 1364; *Paratylopus labiatus*, AMNH 6520; *Gentilicamelus sternbergi*, AMNH 7910; *Pseudolabis dakotensis*, F:AM 41942; *Miotylopus gibbi*, F:AM 36446 (laterally crushed); *Miotylopus taylori*, F:AM 41855. Scale bar in 2 cm increments.

to the Chadronian. Instead, I suspect that it has more to do with the gradualistic bias of many mammalian paleontologists, who, when they find something bizarre that appears suddenly, insist that it must have diverged from some unknown ancestor back in the Eocene (see discussion of stenomylines above).

ACKNOWLEDGMENTS

LITERATURE CITED

Burmeister, K. H. K. 1837. Handbuch der Naturgeschichte. Berlin, Abteilung I and II.

Clark, J., J. R. Beerbower, and K. K. Kietzke. 1967. Oligocene sedimentation, stratigraphy, paleoecology and paleoclimatology of the Big Badlands of South Dakota. Fieldiana: Geology Memoir 5:1-158.

Cope, E. D. 1873. [On *Menotherium lemurinum, Hypisodus minimus, Hypertragulus calcaratus, H. tricostatus, Protohippus,* and *Procamelus heterodontus.*] Proceedings of the Academy of Natural Sciences of Philadelphia 25:419-420.

Cope, E. D. 1879. Observations on the faunae of the Miocene Tertiaries of Oregon. Bulletin of the U. S. Geological and Geographical Survey of the Territories 5:55-69.

Cope, E. D. 1881. On the origin of foot structures of the ungulates. American Naturalist 15:269-273.

Cope, E. D. 1886. The phylogeny of the Camelidae. American Naturalist 20:611-624.

Cope, E. D., and W. D. Matthew. 1915. Hitherto unpublished plates of Tertiary Mammalia and Permian Vertebrata. Monographs of the American Museum of Natural History 2:1-154.

Dalquest, W. W., and O. Mooser. 1974. Miocene vertebrates from Aguascalientes, Mexico. The Pearce-Sellards

Series, Texas Memorial Museum 31:1-10.

Deméré, T. A. 1988. Early Arikareean (late Oligocene) vertebrate fossils and biostratigraphic correlations of the Otay Formation at Eastlake, San Diego County, California; pp. 35-44 *in* M. V. Filewicz and R. L. Squires (eds.), Paleogene Stratigraphy, West Coast of North America. Pacific Section SEPM Publication 58.

Eldredge, N., and S. J. Gould. 1972. Punctuated equilibria: an alternative to phyletic gradualism; pp. 82-115 *in* T. J. M. Schopf (ed.), Models in Paleobiology. Freeman Cooper, San Francisco.

Evanoff, E., D. R. Prothero, and R. H. Lander. 1992. Eocene-Oligocene climatic change in North America: the White River Formation near Douglas, east-central Wyoming; pp. 116-130 *in* D. R. Prothero and W. A. Berggren (eds.), Eocene-Oligocene Climatic and Biotic Evolution, Princeton University Press, Princeton, N.J.

Franklin, W. L. 1983. Contrasting socioecologies of South America's wild camelids: the vicuña and the guanaco. American Society of Mammalogists Special Publication 7:573-629.

Frick, C. 1937. Horned ruminants of North America. Bulletin of the American Museum of Natural History 69:1-669.

Frick, C., and B. E. Taylor. 1968. A generic review of stenomyline camels. American Museum Novitates 2353:1-51.

Galbreath, E. C. 1953. A contribution to the Tertiary geology and paleontology of northeastern Colorado. University of Kansas Paleontological Contributions, Vertebrata 4.

Gazin, C. L. 1955. A review of the upper Eocene Artiodactyla of North America. Smithsonian Miscellaneous Collections 128(8):1-96.

Golz, D. J. 1976. Eocene Artiodactyla of southern California. Los Angeles County Natural History Museum Bulletin 26, 85 pp.

Hay, O. P. 1902. Bibliography and catalogue of the fossil Vertebrata of North America. Bulletin of the U.S. Geological Survey 179:1-868.

Hay, O. P. 1930. Second bibliography and catalogue of the fossil Vertebrata of North America. Carnegie Institute of Washington Publication 390(2):1-1074.

Honey, J. G., and B. E. Taylor. 1978. A generic revision of the Protolabidini (Mammalia, Camelidae) with a description of two new protolabidines. Bulletin of the American Museum of Natural History 161:371-425.

Honey, J., J. A. Harrison, D. R. Prothero, and M. S. Stevens. In press. Camelidae; *in* C. Janis, K. M. Scott, and L. Jacobs (eds.), Tertiary Mammals of North America, Cambridge University Press, Cambridge (in press).

Koford, C. B. 1957. The vicuña and the puna. Ecological Monographs 27:153-219.

Leidy, J. 1847. On a new genus and species of fossil Ruminantia. Proceedings of the Academy of Natural Sciences of Philadelphia 3:322-326.

Leidy, J. 1856. Notice of some remains of extinct vertebrated animals. Proceedings of the Academy of Natural Sciences of Philadelphia 8:163-165.

Leidy, J. 1869. The extinct mammalian fauna of Dakota and Nebraska. Journal of the Academy of Natural Sciences of Philadelphia 7:1-472.

Loomis, F. B. 1911. The camels of the Harrison beds, with three new species. American Journal of Science 31:65-70.

Loomis, F. B. 1928. *Poebrotherium.* American Journal of Science 16:137-142

Loomis, F. B. 1936. The skeleton of a new fossil camel from Wyoming. University of Wyoming Publications 2(5):59-64.

Lull, R. S. 1921. New camels in the Marsh collection. American Journal of Science 1:392-404.

Maglio, V. J. 1966. A revision of the fossil selenodont artiodactyls from the middle Miocene Thomas Farm, Gilchrist County, Florida. Breviora 255:1-27.

Matthew, W. D. 1899. A provisional classification of the freshwater Tertiary of the west. Bulletin of the American Museum of Natural History 12(3):19-75.

Matthew, W. D. 1901. Fossil mammals of the Tertiary of northeastern Colorado. Memoirs of the American Museum of Natural History 1:355-447.

Matthew, W. D. 1904. Notice of two new Oligocene camels. Bulletin of the American Museum of Natural History 20:211-215.

Matthew, W. D. 1909. Faunal lists of the Tertiary Mammalia of the West. U. S. Geological Survey Bulletin 361:91-138.

Matthew, W. D. 1910. On the skull of *Apternodus* and the skeleton of a new artiodactyl. Bulletin of the American Museum of Natural History 28:33-42.

McKenna, M. C. 1966. Synopsis of Whitneyan and Arikareean camel phylogeny. American Museum Novitates 2253:1-11.

McKenna, M. C., and J. D. Love. 1972. High-level strata containing early Miocene mammals on the Bighorn Mountains, Wyoming. American Museum Novitates 2490:1-31.

Olsen, S. J. 1959. Fossil mammals of Florida. Special Publications of the Florida Geological Survey 6:1-74.

Olsen, S. J. 1962. The Thomas Farm fossil quarry. Quarterly Journal of the Florida Academy of Sciences 25(2):142-146.

Patton, T. H. 1964. The Thomas Farm fossil vertebrate locality; pp. 12-20 *in* W. Auffenberg, W. T. Neill, T. H. Patton, and S. D. Webb, Guidebook to the 1965 field trip, Society of Vertebrate Paleontology, central Florida. Gainesville, Florida.

Patton, T. H. 1966. Revision of the selenodont artiodactyls from Thomas Farm. Quarterly Journal, Florida Academy of Sciences 29:179-190.

Patton, T. H. 1969. Miocene and Pliocene artiodactyls, Texas Gulf Coastal Plain. Bulletin of the Florida State Museum 14:115-227.

Peterson, O. A. 1904. Osteology of *Oxydactylus,* a new genus of camels from the Loup Fork of Nebraska, with descriptions of two new species. Annals of the Carnegie Museum of Natural History 2(3):434-476.

Peterson, O. A. 1906. The Miocene beds of western Nebraska and eastern Wyoming and their vertebrate faunas. Annals of the Carnegie Museum 4:21-72.

Peterson, O. A. 1908. Description of the type specimen of *Stenomylus gracilis* Peterson. Annals of the Carnegie Museum 4:286-300.

Prothero, D. R. 1982. Medial Oligocene magnetostratigraphy and mammalian biostratigraphy: testing the isochroneity of mammalian biostratigraphic events. Ph.D. dissertation, Columbia University, New York.

Prothero, D. R. 1994. Mammalian evolution; pp. 238-270 *in* D. R. Prothero and R. M. Schoch (eds.), Major Features of Vertebrate Evolution. Paleontological Society Short Courses in Paleontology 7.

Prothero, D. R., and J. M. Rensberger. 1985. Magnetostratigraphy of the John Day Formation, Oregon, and the North American Oligocene-Miocene boundary. Newsletters in Stratigraphy 15(2):59-70.

Ray, C. E. 1957. A list, bibliography, and index of fossil vertebrates of Florida. Special Publication of the Florida Geological Survey 3:1-175.

Romer, A. S. 1948. The fossil mammals of Thomas Farm, Gilchrist County, Florida. Quarterly Journal of the Florida Academy of Sciences 10(1):1-11.

Schlaikjer, E. M. 1935. Contributions to the stratigraphy and paleontology of the Goshen Hole area, Wyoming. IV. New vertebrates and the stratigraphy of the Oligocene and early Miocene. Bulletin of the Museum of Comparative Zoology, Harvard, 76(4):97-189.

Scott, W. B. 1940. The mammalian fauna of the White River Oligocene. Part 4. Artiodactyla. Transactions of the American Philosophical Society 28(4):363-746.

Simpson, G. G. 1945. The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History 85:1-350.

Skinner, M. F., S. M. Skinner, and R. J. Gooris. 1968. Cenozoic rocks and faunas of Turtle Butte, south-central South Dakota. Bulletin of the American Museum of Natural History 138(7):381-436.

Stevens, M. S. 1977. Further study of the Castolon local fauna (early Miocene), Big Bend National Park, Texas. The Pearce-Sellards Series, Texas Memorial Museum 28:1-69.

Stevens, M. S., J. B. Stevens, and M. R. Dawson. 1969. New early Miocene formation and vertebrate local fauna, Big Bend National Park, Brewster County, Texas. The Pearce-Sellards Series, Texas Memorial Museum 15:3-52.

Stock, C. 1935. Artiodactyla from the Sespe of Las Posas Hills, California. Publications of the Carnegie Institute of Washington 453:119-125.

Tedford, R. H., J. B. Swinehart, R. M. Hunt, Jr., and M. R. Voorhies. 1985. Uppermost White River and lowermost Arikaree rocks and faunas, White River Valley, north western Nebraska and their correlation with South Dakota. Dakoterra 2:335-352.

Tedford, R. H., T. Galusha, M. F. Skinner, B. E. Taylor, R. W. Fields, J. R. Macdonald, J. M. Rensberger, S. D. Webb, and D. P. Whistler. 1987. Faunal succession and biochronology of the Arikareean through Hemphillian interval (late Oligocene through earliest Pliocene Epochs) in North America; pp. 152-210 *in* M. O. Woodburne (ed.), Cenozoic Mammals of North America, Geochronology and Biostratigraphy, Univ. Calif. Press, Berkeley.

Troxell, E. L. 1917. An Oligocene camel, *Poebrotherium andersoni,* n. sp. American Journal of Science 43:381-389.

White, T. E. 1940. New Miocene vertebrates from Florida. Proceedings of the New England Zoological Club 18:31-38.

White, T. E. 1941. Additions to the Miocene fauna of Florida. Proceedings of the New England Zoological Club 18:91-98.

White, T. E. 1942. The lower Miocene mammal faunas of Florida. Bulletin of the Museum of Comparative Zoology, Harvard, 92(1):1-49.

Wilson, J. A. 1974. Early Tertiary vertebrate faunas, Vieja Group and Buck Hill Group, Trans-Pecos Texas: Protoceratidae, Camelidae, Hypertragulidae. Bulletin of the Texas Memorial Museum 23:1-34.

Wilson, E. O. 1975. Sociobiology: a synthesis. Harvard University Press, Cambridge, Massachusetts.

Wortman, J. D. 1898. The extinct Camelidae of North America and some associated forms. Bulletin of the American Museum of Natural History 10:93-142.