

## FOSSIL CAMELS FROM THE LATE OLIGOCENE EASTLAKE LOCAL FAUNA, OTAY FORMATION, SAN DIEGO COUNTY, CALIFORNIA

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**Abstract**—Fossil camel skulls and jaws recovered from the upper Oligocene Otay Formation (Eastlake local fauna) in southern San Diego County have never been fully described or identified. Re-examination of this material and comparison with camels described by Prothero in 1996 shows that the San Diego camel is referable to *Miotylopus leonardi*. This is the smallest of three species of the primitive stenomyline camel *Miotylopus* previously was known only from the early to middle Arikarean deposits (Gering-Monroe Creek equivalents) of eastern Wyoming. Both the small and medium-sized species from Wyoming include clear examples of male and female jaws with their distinctive canines, ruling out a size difference due to sexual dimorphism. The larger camel *Dyseotylopus migrans* from the upper Oligocene Sespe Formation in Ventura County is a junior synonym of the medium-sized stenomyline *Miotylopus gibbi* from the same Arikarean beds in Wyoming. These identifications extend the geographic range of these previously rare and poorly understood camels from a limited area of eastern Wyoming to the Pacific Coast.

### INTRODUCTION

Deméré (1986, 1988) and Walsh and Deméré (1991) described the geology and fossils recovered from salvage operations during the construction of housing projects in the Eastlake-Otay Mesa area of southern San Diego County. Preliminary assessment of the mammalian fossils (the Eastlake local fauna) suggested that the Otay Formation was early Arikarean in age (27–28.5 Ma), approximately equivalent in age to the Gering Formation of Nebraska (Tedford et al., 1996, 2004). This age assignment was refined by magnetic stratigraphy, because the Otay Formation is entirely reversed in polarity, correlating it with Chron C9r, which makes it 28.0–28.5 Ma in age (Prothero, 1991). Taxa known from the Eastlake local fauna include tortoises, lizards, birds, and at least 15 genera of mammals. The most common mammal is represented by abundant, well-preserved material of the tiny oreodont *Sespeia californica*, which was described in greater detail by Hoffman and Prothero (2004). Fossil camel material is also relatively abundant. Deméré (1988) suggested that the camel material might be referable to *Miotylopus* sp. and/or cf. *Dyseotylopus* sp. Walsh and Deméré (1991) assigned the camels to *Miotylopus*. No further mention of this camel collection has been published since 1991.

Prothero (1996) revised the taxonomy of all the earliest camels of North America, especially the primitive late Eocene and Oligocene genera *Poebrodon*, *Poebrotherium*, *Paralabis* (now *Matthewlabis*—Prothero, 2011), *Paratylopus*, *Gentilicamelus*, *Miotylopus*, and *Pseudolabis*. He recognized that *Pseudolabis* and *Miotylopus* shared derived features with the highly aberrant, extremely hypsodont gazelle-like stenomyline camels known from the early to middle Miocene of the High Plains. *Miotylopus* Schlaikjer, 1935 is a sister-taxon to the highly derived stenomylines *Stenomylus*, *Rakomylus*, and *Blickomylus* (Prothero, 1996). Some *Miotylopus* specimens match *Stenomylus hitchcocki* in size and most skull proportions, differing mostly in the extreme hypsodonty of *Stenomylus* teeth (Prothero, 1996, fig. 14C). Based on abundant undescribed material in the Frick Collection of the AMNH, Prothero (1996) recognized three different size clusters of *Miotylopus*, with male and female canines in each cluster to demonstrate that the size difference was not due to sexual dimorphism. The smallest size class was assigned to *Miotylopus leonardi* (Loomis, 1911); the intermediate-sized taxon to *M. gibbi* (Loomis, 1911); and a larger, new species was named *M. taylori*. Prothero (1996) suggested that *Dyseotylopus* Stock, 1935 from the Oligocene portion of the Sespe Formation in California was a junior synonym (by only a few months' priority) of *Miotylopus* Schlaikjer, 1935, although it was not possible to examine the type material of *Dyseotylopus* at that time.

The existence of all this new camelid material from the SDNHM collections, plus additional material in the AMNH, F:AM, YPM, ACM and MCZ collections that was never seen or fully described, provided an opportunity to re-examine the systematic hypotheses of Prothero (1996). Those hypotheses were based on research done over 30 years

ago. Back in 1982, Prothero had not measured every specimen of *Miotylopus* in the AMNH collections. This paper will re-evaluate the old conclusions and hypotheses in light of new material and see if the results are corroborated.

### METHODS

Tom Deméré provided an opportunity for Lubar to study the unpublished SDNHM camel fossils from the Eastlake l.f. as her senior research project. We made two separate visits to San Diego, as well as two separate visits to see the material in the AMNH collections, and two visits to the LACM to see the holotype of *Dyseotylopus migrans*. We also visited the type material in the ACM, YPM, and MCZ collections. Specimens were measured with a digital calipers and data recorded on Excel spreadsheets. All graphs and statistics were created in Excel as well. We used common statistical calculations (mean, standard deviation, coefficient of variation). Specimens were photographed with a Nikon 5700 camera, and then edited in Photoshop by Pat Linse.

**Institutional Abbreviations:** ACM, Beneski Museum of Natural History, Amherst College, Amherst, MA; AMNH, Division of Paleontology, the American Museum of Natural History, New York, NY; F:AM, Frick American Mammals, Division of Paleontology, the American Museum of Natural History, New York, NY; LACM(CIT), Caltech collection, now housed at the Museum of Natural History, Los Angeles, CA; MCZ, Harvard Museum of Natural History, Harvard University, Cambridge, MA; SDNHM, San Diego Natural History Museum, San Diego, CA; YPM, Yale Peabody Museum, Yale University, New Haven, CT.

### SYSTEMATIC PALEONTOLOGY

**Class Mammalia Linnaeus, 1758**  
**Order Artiodactyla Owen, 1848**  
**Family Camelidae Gray, 1821**  
**Subfamily Stenomylinae Matthew, 1910**  
***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:** *M. leonardi* (Loomis, 1911); *M. taylori* Prothero, 1996.

**Diagnosis:** (after Prothero, 1996, p. 632, and Honey et al., 1998) 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 the P4 lingual selene. Differs from the Stenomyliini in having less hypsodont teeth; P1/p1 to C1/c1 diastemata still present; and no diastemata between P2/p2 and P3/p3. Differs

from all other camels in having hypsodont teeth with very weak or no mesostyles, and dorsal premaxilla extended posterior to the level of P1.

**Discussion:** Prothero (1996, p. 632-636) discussed the complex taxonomic history of the early-middle Arikareean stenomyline camels (i.e., those bearing mesodont teeth with weak mesostyles, and dorsal premaxillae posterior to the level of P1). Loomis (1911) described the first two known specimens from the “Upper Harrison beds” (later determined to be from the Muddy Creek beds, an early-middle Arikareean unit, *fide* McKenna and Love, 1972, p. 26). Loomis (1911) named the smaller camel *Protomeryx leonardi*, based on an isolated ramus, ACM 2004 (Fig. 1).

However, Prothero (1996) showed the genus *Protomeryx* to be invalid because the type specimen is indeterminate and inadequate. By the early twentieth century, *Protomeryx* had become a taxonomic wastebasket for many poorly understood camelids. Loomis (1911, p. 67) named the larger camel *Oxydactylus gibbi*, based on a fragmentary specimen with upper and lower jaws, YPM 10328 (Fig. 2). Further study, however, showed that *Oxydactylus s.s.* is a much larger and more derived long-necked and long-limbed camel with mesostyles on the upper molars, not closely related to *O. gibbi* (Honey et al., 1998).

The first valid generic name applied to these camels was *Miotylopus bathygnathus*, described by Schlaikjer in May 1935 (Schlaikjer, 1935, p. 174-176, pl. 39) (Figs. 4-5). In July of that same year, Stock (1935) described *Dyseotylopus migrans* from the early Arikareean assemblage recovered from the Kew Quarry in the upper part of the Sespe Formation, Ventura County, California (Prothero et al., 1996). This taxon was based on a fragmentary skull, LACM (CIT) 1721, which has since undergone much breakage and lost its rostrum. Schlaikjer (1935, p. 176) mentioned that Stock was about to name this new camel, but later research (Prothero, 1996; see below) suggested that they could not be distinguished, so Schlaikjer’s *Miotylopus* becomes the senior synonym of Stock’s *Dyseotylopus* by two months.

The systematics of Arikareean camels continued to be confused for many years. Loomis (1936) transferred “*Protomeryx leonardi*” to his wastebasket genus *Gentilicamelus*, but Prothero (1996) showed that “*P. leonardi*” is very different from the holotype specimen of the type species of the genus, *G. sternbergi*, from the Arikareean of the John Day beds. McKenna (1966) resolved much of the taxonomic confusion about Arikareean camels. He transferred “*Oxydactylus gibbi*” to *Miotylopus*, but did not synonymize “*O. gibbi*” with the very similar junior taxon *Miotylopus bathygnathus* (consistently misspelled “*brachygnathus*” by McKenna, 1966, and McKenna and Love, 1972). However, McKenna

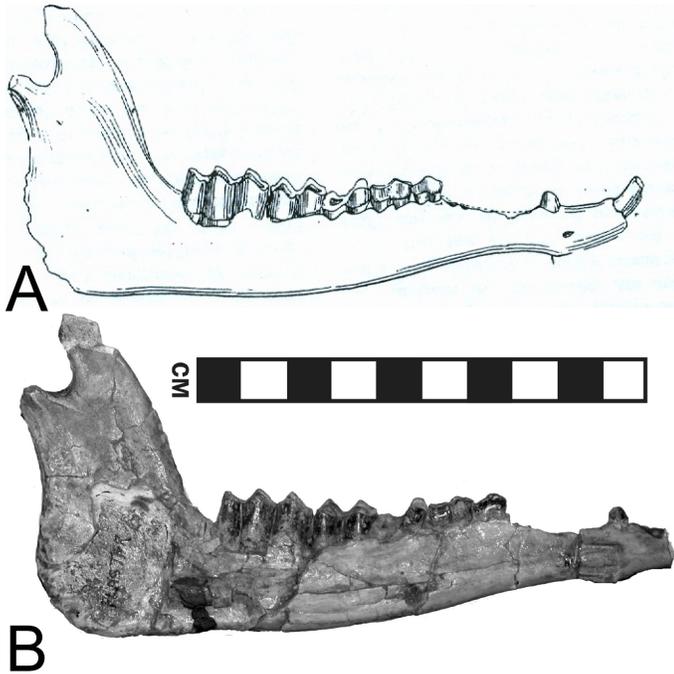


FIGURE 1. *Miotylopus leonardi*. A, drawing of holotype (ACM 2004) (F:AM 36796) (from Prothero, 1996, fig. 13); and B, lateral view of holotype left ramus. Scale bar in cm.

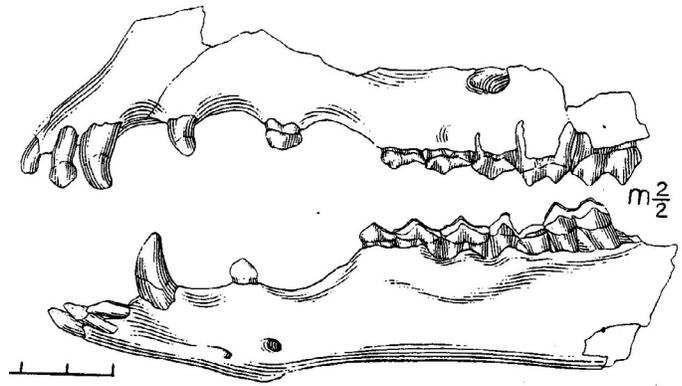


FIGURE 2. *Miotylopus gibbi*. YPM 10328, holotype rostrum and mandible (from Prothero, 1996, fig. 15).

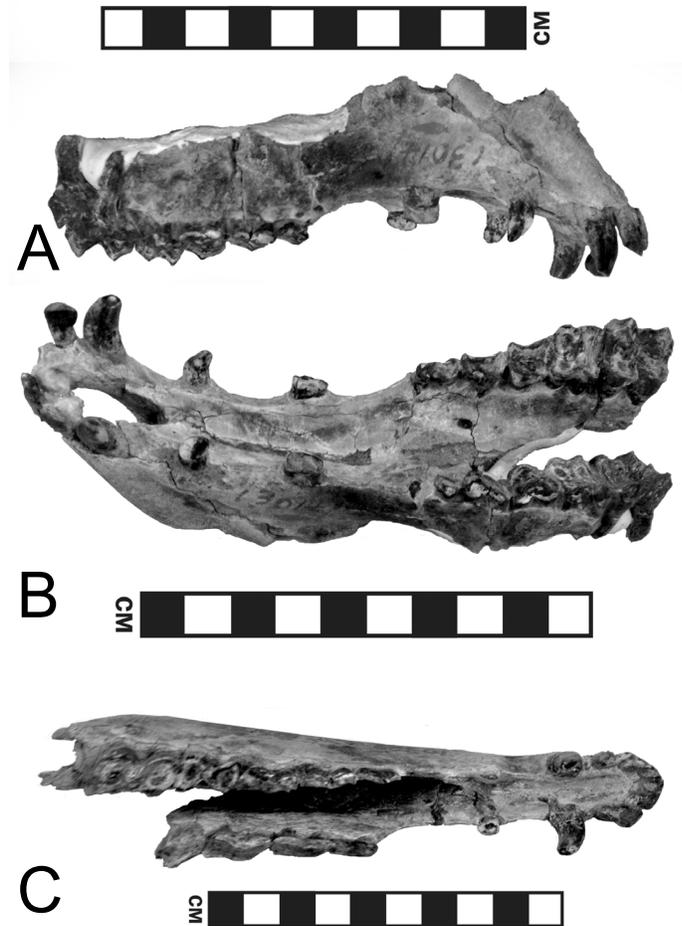


FIGURE 3. *Miotylopus gibbi*, YPM 10328 (holotype). A, lateral view of rostrum; B, palatal view of rostrum; and C, occlusal view of mandible. A-C. (Photographs courtesy D. McCoy).

and Love (1972) formally established that *M. “brachygnathus”* [*sic*] was a junior synonym of *M. gibbi*. McKenna (1966) indicated that *Dyseotylopus* was extremely similar to *Miotylopus*, but did not regard them as synonyms.

Prothero (1996) used the much larger sample of camels from the Frick Collection to resolve many of these taxonomic problems. After analysis of this large collection, three distinct size clusters of early-middle Arikareean camels emerged, with specimens preserving both male and female canines in each size cluster. The smallest group of the three camels is referable to *Miotylopus leonardi*, transferring Loomis’

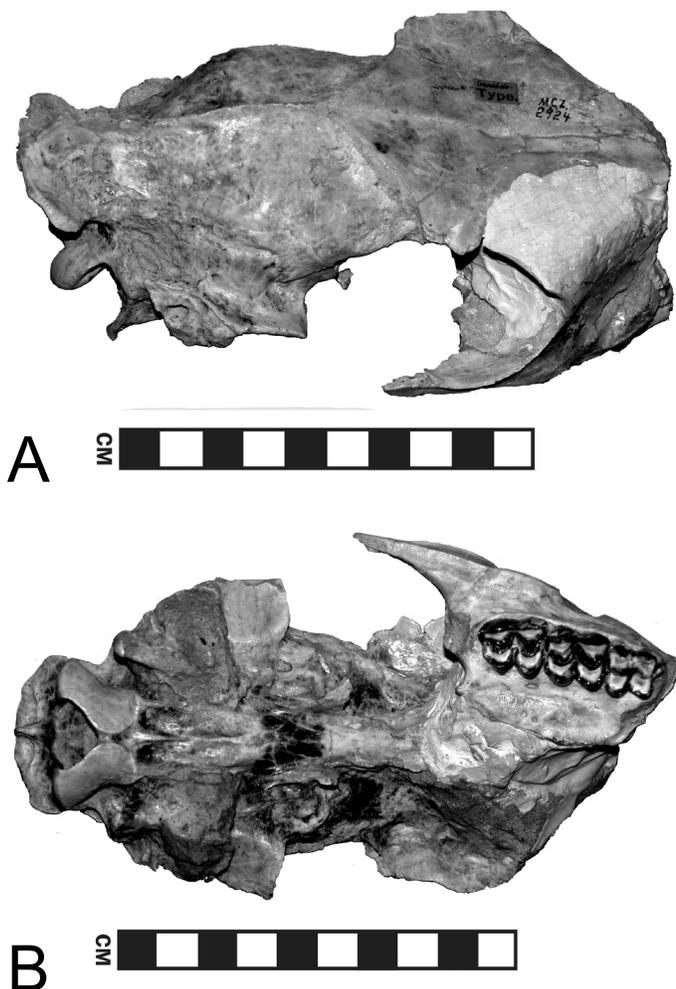


FIGURE 4. *Miotylopus gibbi* (=holotype of *M. bathygnathus*) MCZ 2924 (holotype) skull. **A**, dorsal and **B**, ventral views.

(1911) species from invalid generic assignments such as “*Protomeryx*” or “*Gentilicamelus*” to the correct genus. The senior name for the medium-sized *Miotylopus* is *M. gibbi*, with *M. bathygnathus* and *M. brachygnathus* [sic] as junior synonyms. Finally, the Frick Collection contains a much larger unnamed new species, named *Miotylopus taylora* by Prothero (1996). All three of these species seem to be distinct in morphology and size (Prothero, 1996, fig. 12). Both the *M. leonardi* and *M. gibbi* samples contained both upper and lower jaws with male and female canines.

#### *Miotylopus leonardi* (Loomis, 1911)

*Protomeryx leonardi* Loomis, 1911

*Gentilicamelus leonardi* Loomis, 1936

“*Protomeryx leonardi*” Skinner, Skinner and Gooris, 1968

*Miotylopus gibbi* McKenna and Love, 1972 (in part)

**Type specimen:** ACM 2004, left ramus (Fig. 1)

**Type Locality:** Muddy Creek area, “3 miles below Spanish Diggings Spring” (Loomis, 1911, p. 68), Goshen County, Wyoming.

**Age:** Late Oligocene, early-middle Arikareean (Monroe Creek or Harrison Formation equivalents), about 26-28 Ma (Tedford et al., 1996, 2004).

**Referred Material:** Specimens previously listed by Prothero (1996, p. 634-635) from the Little Muddy Creek-Muddy Creek-Goshen Hole area, Goshen County, Wyoming; plus the new specimens from the Eastlake local fauna: Locality 3280, Eastlake Shores: SDNHM 28594, right ramus fragment with m2-m3; 31083, left astragalus; 31084, right tibial epiphysis; 31087, left m3; 31088, left ramus with p2-m2; 31091, left M2-3; 31094, right humerus, distal fragment; 31095, right P3-M2; 31200, left maxilla with dP2-4, M1; 31252, right M1-2; 31253, right

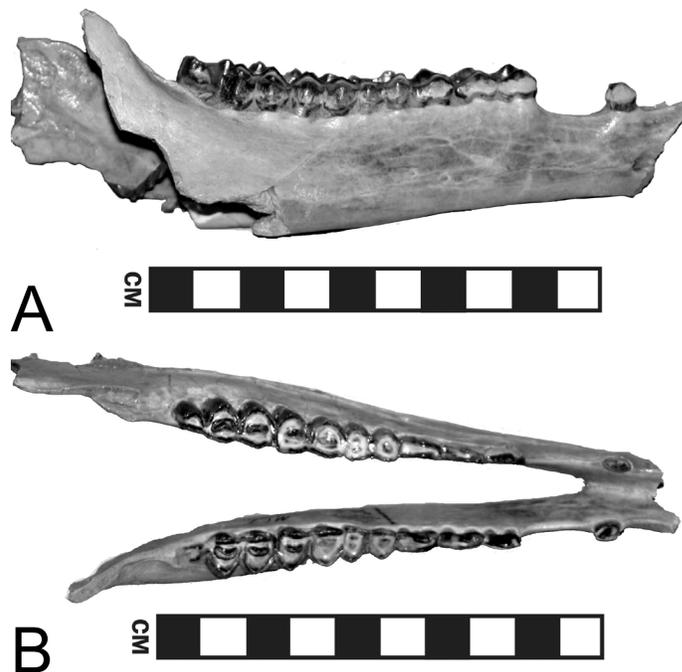


FIGURE 5. *Miotylopus gibbi* (=holotype of *M. bathygnathus*) MCZ 2924, holotype mandible. **A**, right lateral; and **B**, occlusal views.

M1-2; 31254, right M3?; 31255, 31255, left maxilla, I3, C1; 31256, left M3; 31257, right ischium; 31258, right astragalus; 31259, left fibula, distal end; 31260, right astragalus; 31263, right navicular; 31269, left fibula, distal end; 31331, left cuboid; 86098, right ramus with p4-m3; locality 3286, Eastlake Hills and Shores Site 10: SDNHM 31089, left m3; 31266, left astragalus; 31330, right cuboid; locality 3288, Eastlake Hills and Shores, Site 8: SDNHM 70255, left astragalus fragment; locality 3295, Eastlake Hills and Shores, Site 26: SDNHM 31090, left humerus, distal end, with fragments; 31199, left ramus fragment with p3-m2; 31264, left m3, left P4; locality 3331, Eastlake Business Center, Site 35: SDNHM 31085, mandibular symphysis with left p1,rc1,p1-2; 31096, left humerus, distal end; 31261, right calcaneum; 31270, right radius-ulna, fused; 42911, left ramus fragment with p4,m1-2; 42913, left humerus, distal end; 42914, right tibia, distal end; 88921, right ulna-radius; 88922, humerus, distal end; locality 3332, Eastlake Business Center, Site 47: SDNHM 42916, right scapula fragment, proximal end; 42917, left humerus, distal end; locality 3334, Eastlake Business Center: SDNHM 31082, right ramus, fragment with p2-m3; 31086, left ramus fragment with p1-m2; 31241, left ramus with p4-m2; 31262, left calcaneum; 42949, palate, with right P2-M3; left P2-M3; 70683, left tibia fragment; locality 3335, Eastlake Business Center: SDNHM 31192, left humerus, distal fragment; 71839, vertebrae, articulated cervicals 3-6; locality 3336, Eastlake Business Center, Site 63: SDNHM 31249, skull, anterior region with palate; 43436, right calcaneum; 71789, vertebrae, articulated cervicals, 3-6; 88934, left maxilla with p4-m3; locality 3372, Eastlake Business Center, General #8: SDNHM 31092, left distal humerus; 31093, right ramus with m2-3; 31193, left distal humerus; 31198, left ramus with p2-m3; 31251, maxilla with P3-M3; 31265, left calcaneum; 31267, left distal humerus; 31268, distal right tibia; 31273, palate and partial mandible with dentition; 31274, dentary with right p4, left p4-m2, 2 vertebrae; 31308, skeleton with associated left scapula, pelvis; locality 3461, McMillin Bonita Long Canyon, Site 1: SDNHM 74301, left ramus with p4-m2; locality 3492, Eastlake Business Center, Site 75: SDNHM 38638, mandible, partial with right complete dentition; 43423, right M2; 43424, tibia, right distal; locality 3499, Eastlake Business Center, Site 77: SDNHM 38637, left mandible with i1-3,c1,p1-m2,rt i1-3; locality 3579, Eastlake Salt Creek 1: SDNHM 42880, humerus, right distal; 42881, humerus, left distal; 42882, humerus, left distal; locality 3602, Eastlake Greens: SDNHM 43443, right ramus with p4-m3; locality 3606, Eastlake Greens: SDNHM 75070, left partial mandible with i2,p3-4,m1,rti1,ci1; locality 5608, McMillin Rolling Hills Ranch, Neigh. 9-12: SDNHM 104312, right ulna-radius, proximal end and shaft; locality 5609, McMillin Rolling Hills Ranch, Neigh. 9-12: SDNHM 104313, left ramus, with

dp2-dp4, m1; 104314, maxilla; locality 5697, Otay Ranch Village 7 – Micro Site: SDNHM 111011, metatarsal, proximal end; 111012, left ramus, with p2, p4, m1, m3 fragments and m2; 111013, 1 dent w p2-m3, r dent w p3-m3; locality 5942, SR 125 Toll Road: SDNHM 113374, left ramus, with p2-m3, broken c1; locality 6015, Otay Ranch Village 2 East: SDNHM 114661, mold of foot print; 114662, foot print; 114663, foot print.

**Diagnosis:** Smallest known species of *Miotylopus* (P2-M3 length = 65-70 mm), with relatively gracile skull and limbs.

**Description of new material:** The most complete camel skull in the Eastlake collection is SDNHM 31249 (Fig. 6A-B), the front half of a skull that is broken anterior to the back of the tooth row. In right lateral view (Fig. 6A), the sutures of the major skull bones are fairly well preserved, although there is some breakage. Long, splint-like nasals and frontals extend along the dorsal surface of the skull. The maxillary is broken in numerous places, so its sutures cannot be clearly delineated. Portions of the lacrimal and jugal bones are also preserved. The premaxilla is long and slender, and, in lateral view, it has a sharp ventral inflection from the dorsal profile of the rostrum to the anterior portion of the nasal opening; the same inflection and general configuration of the rostrum can be seen on less distorted F:AM specimens of *M. leonardi* from Wyoming (Fig. 7). The tip of the premaxilla has a slight dorsal inflection and flattening above I1-2. Although sutures of the facial region are partially obscured by breakage, it does appear that the skull has the dorsal portion of the premaxilla above P1, a diagnostic character of this genus.

In palatal view (Fig. 6B), SDNHM 31249 shows highly spatulate and procumbent first and second upper incisors, and a large caniniform I3, suggesting that this specimen is from a male. The caniniform I3 in SDNHM 31249 is conical and slightly recurved, with considerable apical wear. The canine is bladelike, short, blunt and laterally compressed, very similar to the condition in the anterior premolars. As in other species of *Miotylopus*, the rostrum is elongate and parallel-sided with a rounded incisive margin in ventral view. The rostrum is particularly narrow in the region between the simple triangular, blade-like P1 and P2, which are separated from the canine and from each other by long diastemata.



FIGURE 6. *Miotylopus leonardi*, SDNHM 31249. A, right lateral and B, palatal views.

The remaining cheek teeth in SDNHM 31249 are highly worn, so only minimal crown patterns remain. P3 is antero-posteriorly elongate, with a bladelike shape and deeply worn crown, with slight swellings in the area of the paracone and metacone. P4 is almost molariform, with a large arcuate selene connecting the protocone-metaconule lingually, and a broad arcuate paracone-metacone selene labially. As can be seen in lateral view (Fig. 6A), there is no mesostyle on the upper molars, a diagnostic feature of the stenomylines. M1 is so deeply worn that only a rectangular crown remains, with two lingual bulges where the bases of the protocone and hypocone once were. M2 is square in occlusal outline, and slightly less worn, with the deep fossettes separating the paracone and metacone from the lingual part of the tooth. M3 has a much less worn paracones and metacones, with some remnant of the high triangular labial point on the meeting of the paracrista and metacrista. The protocone and hypocone are only slightly worn and form large arcuate buttresses on the lingual side of the tooth. The palate is moderately well preserved, and the anterior edge of the internal nares forms a broad arc that terminates at the level of M2.

Most of the dentaries and rami in the SDNHM collections are fragmentary, and show few features not already described by Prothero (1996). The most complete specimen is a partial mandible, SDNHM 38638, which preserves the fused symphysis, right ramus, and the anterior portion of the left ramus (Fig. 8). Although the specimen is cracked and laterally compressed due to post-mortem compaction, much of the original morphology is still well preserved. The symphysis is flaring with a pinched base near the lower canine and p1. All the lower incisors are present and well preserved, and form a fan-like arrangement in dorsal view. The lower first incisors are compressed cylinders with spatulate apices. In SDNHM 38638, the i1 crowns have fossettes at the apex due to wear. Closely appressed to each side of the lower first incisors are the lower second incisors. They are roughly triangular in cross-section, with a flat enamel face on the posterior side, and are strongly procumbent. The i3 is much larger than the i1 or i2, and has a roughly bladelike shape and rounded tip, with some apical wear. The i3s are ovoid in cross-section, and there is a small diastema between the anteriorly inclined i2 and the vertically oriented i3. Another short diastema separates the i3 from the lower canine, which is a large, robust bladelike tooth with a slight curvature in the postero-dorsal direction. The canine in SDNHM 38638 seems quite large, suggesting the specimen was probably from a male. Smaller lower canines are found in a number of specimens in the SDNHM collections, and probably represent female individuals.

There is a short diastema behind the lower canine, separating that tooth from the p1, which is elongate and bladelike with a blunt, rounded lateral profile. The largest diastema is between p1 and p2. The p2 is also elongate and bladelike, with an even flatter rounded lateral profile. The least worn specimens show some remnant of a cusp on the p2 representing the trigonid, but most specimens have too much apical wear to delineate any cusp pattern. There is a short diastema between the p2 and p3. The p3 is antero-posteriorly elongate and bladelike with a blunt, rounded lateral profile. However, on unworn specimens two separate cusps with a fold between them marks the position of the trigonid. A short ridge and cusp posterior to the trigonid represents the talonid. The p4 is also antero-posteriorly elongate, but much larger than p1-3, and less bladelike. The p4 trigonid is represented by a large, rounded ridge with a labial fold between the paraconid and metaconid ridges. The talonid on p4 is a much lower elongate heel. In most specimens, these ridges are deeply worn, so there are no cusps preserved.

The molars on SDNHM 38638 (Fig. 8) are highly worn, but



FIGURE 7. Comparable specimen (F:AM 36451) of *M. leonardi* from Muddy Creek, Wyoming, showing the similarity in the front half of the skull with SDNHM 31249.

TABLE 1. Statistics of upper tooth dimensions in samples of *Miotylopus*. N = number of samples; SD = standard deviation. Measurements of holotypes of named species are also given. All measurements in mm.

DIM.	F:AM <i>M. leonardi</i>			SDNHM			F:AM <i>M. gibbi</i>			<i>M. gibbi</i> (type)	<i>D. migrans</i> (type)
	N	MEAN	SD	N	MEAN	SD	N	MEAN	SD	YPM 10328	LACM 1721
P2L	5	7.6	1.4	4	6.7	0.5	9	8.4	1.3	8.0	—
P2W	5	3.6	0.4	4	2.2	0.3	9	4.1	0.8	3.0	—
P3L	7	8.9	1.0	6	9.5	1.2	10	9.7	1.1	9.0	—
P3W	7	4.0	1.0	6	3.6	0.2	10	5.2	0.7	4.0	—
P4L	7	9.0	1.0	6	8.8	1.2	10	10.1	0.8	10.0	10.0
P4W	7	7.1	0.9	6	7.0	0.6	10	8.3	1.0	6.0	11.4
M1L	7	11.1	1.9	12	11.6	0.1	10	12.5	0.8	10.0	12.0
M1W	7	10.7	1.2	12	11.1	1.2	10	12.3	0.5	9.0	9.7
M2L	7	13.9	1.5	13	14.5	1.0	10	15.3	2.1	12.0	18.1
M2W	7	11.9	0.9	13	11.3	1.5	10	14.1	0.9	12.0	11.4
M3L	7	16.5	2.1	10	17.5	1.2	10	18.3	0.7	16.0	18.8
M3W	7	11.2	1.8	10	11.4	2.1	10	13.9	1.5	13.0	11.2
M1-3	7	39.0	3.1	4	41.4	1.8	9	53.1	2.4	47.0	45.0
P2-4	7	23.7	1.7	3	22.8	0.8	8	27.5	1.2	36.0	—
P2-M3	5	60.6	5.9	3	64.1	2.8	9	70.6	5.4	84.0	—

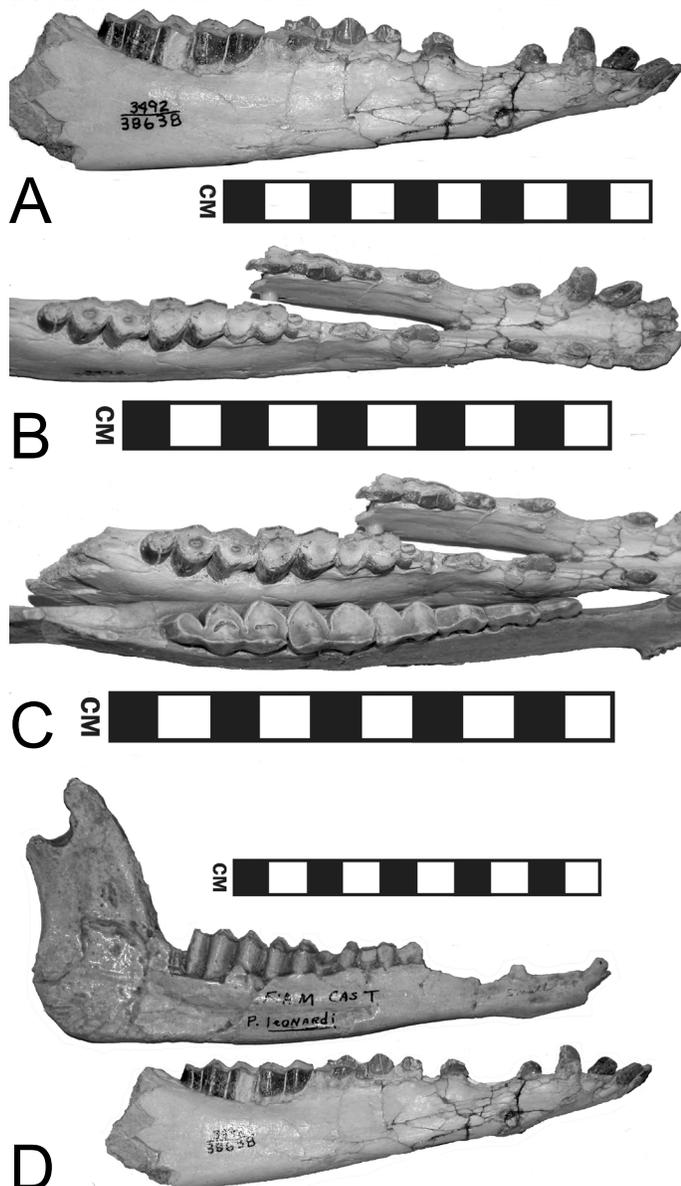


FIGURE 8. *Miotylopus leonardi*, SDNHM 38638, partial lower mandible in **A**, lateral; and **B**, dorsal views; **C**, comparison of dorsal view of SDNHM 38638 (top) with cast of the holotype of *M. leonardi*, ACM 2004 (bottom); and **D**, comparison of lateral view of SDNHM 38638 (bottom) with cast of the holotype of *M. leonardi*, ACM 2004 (top).

otherwise show the stereotypical selenodont dentition of most mesodont camelids. The m1 is worn down to two distinct, equal-sized selenes representing the trigonid and talonid. The condition in the m2 is very similar to that of the m1, although m2 is a bit larger. The m3 is the least worn of all the molars, so there are tiny rounded fossettes in the worn surface of the trigonid and talonid selenes, and a large looping hypoconulid on the posterior end of the m3. In lateral view, the rami are slender, with a slight ventral “chin” where the symphysis ends just below the long p1-p2 diastema. Most specimens do not preserve the posterior part of the dentary. However, the holotype ramus of *Miotylopus leonardi* (Fig. 1) has the typical long hooked coronoid process and the dorsally elevated articular process typical of all camels (Prothero, 1996).

**Discussion:** When Prothero (1996) first described and sorted out the various species of *Miotylopus*, the sample size was small. Now, with the larger sample of specimens from the Eastlake local fauna, plus the additional identifiable specimens from the F:AM and AMNH collections, it is worthwhile looking at the data to see whether they support the earlier conclusions that there are three distinct size classes.

Plotting the tooth data in the much larger sample still supports the separation of a larger taxon (*M. gibbi*) and a smaller taxon (*M. leonardi*). Some representative plots are shown in Figure 9A-E, although we do not have space to show every plot. The larger sample makes the distinction less clear from individual teeth (Fig. 9C), but the measurements along tooth rows are consistent with the original analysis (Prothero, 1996, fig. 12) and show the distinction much better. Almost all of the SDNHM Eastlake camel specimens (Fig. 9, Tables 1-2) fall within the smaller size cluster, making them referable to *Miotylopus leonardi*.

How do the new data support the previous conclusion that the size differences are attributable to different species, and are not just due to sexual dimorphism? Several arguments support this hypothesis even more strongly than they did back in 1996:

1. The most striking evidence of the size classes and distinct taxa is not as apparent in the individual tooth dimensions (e.g., Fig. 9C), as in measurements of tooth row lengths (Figs. 9A-B, D-E), and overall skull size and proportions (Figs. 10-11). The *M. gibbi* skulls are dramatically larger and more robust than the small gracile *M. leonardi* skulls. Although the number of unbroken skulls has not increased since Prothero (1996, fig. 12) first plotted them, the limited number of complete skulls showed discrete size clusters. These dramatic size differences are clearly evident (Figs. 10-11).

2. The two size classes each contain specimens with both large (male) and small (female) caniniform I3's and lower canines (Figs. 10-11). Thus, it is clear that the size difference is not due to sexual dimorphism, because there are *M. gibbi* specimens with small female canines and caniniform I3's, and *M. leonardi* specimens with large male canines and caniniform I3's.

3. If all the specimens were one highly variable species, there should be the same degree of variability from smallest to largest specimens in the SDNHM sample as in the F:AM sample. Instead, the SDNHM sample (Fig. 8) plots only in the smaller size cluster, suggesting that only one species (*Miotylopus leonardi*) was present in the Eastlake local fauna.

4. Another way of determining whether a variable population

TABLE 2. Statistics of lower tooth dimensions in samples of *Miotylopus*. N = number of samples; SD = standard deviation. Measurements of holotypes of named species are also given. All measurements in mm.

DIM.	F:AM <i>M. leonardi</i>			SDNHM			F:AM <i>M. gibbi</i>			<i>gibbi</i>	<i>bathygnathus</i>	<i>leonardi</i>
	N	MEAN	SD	N	MEAN	SD	N	MEAN	SD	(type) YPM 10328	(type) MCZ 2424	(type) ACM 2004
p2L	24	7.1	1.2	6	7.6	1.0	11	8.5	0.9	6.0	8.6	—
p2W	24	2.7	0.4	6	2.6	0.2	9	2.8	0.6	4.0	2.5	—
p3L	27	8.7	1.0	9	8.2	1.4	11	9.4	1.2	8.0	9.8	7.4
p3W	27	3.2	0.4	9	3.4	0.8	9	3.5	0.6	3.0	2.4	2.9
p4L	28	9.0	1.8	10	9.5	1.8	11	10.4	1.3	10.0	9.5	11.3
p4W	28	4.4	0.8	10	4.7	1.6	11	4.9	1.2	4.0	4.1	3.7
m1L	28	11.8	1.3	14	12.0	1.2	11	12.5	1.1	11.0	10.4	12.2
m1W	28	7.3	1.1	14	6.9	0.8	11	8.2	1.5	7.0	8.2	7.8
m2L	28	14.3	1.5	13	14.9	1.5	11	15.4	1.4	13.0	14.2	14.2
m2W	28	8.4	1.2	13	7.3	0.6	11	9.1	1.4	8.0	9.1	8.1
m3L	28	20.4	2.9	8	19.7	2.5	11	22.9	2.2	15.0	20.3	18.7
m3W	28	8.6	1.4	8	7.6	0.7	11	9.2	2.1	9.0	9.5	8.3
m1-3	27	44.7	3.2	9	44.9	2.2	11	52.3	1.8	46.0	59.7	47.0
p2-4	26	24.3	1.9	9	29.5	2.2	11	29.0	2.5	38.0	27.6	24.0
p2-m3	25	67.9	7.1	6	71.5	4.9	11	77.4	6.1	84.0	75.8	70.0

is one species or two is to use the coefficient of variation, which is 100 x Standard Deviation/Mean (Kurtén, 1953; Simpson et al., 1960; Yablokov, 1974; Plavcan and Cope, 2001). In Table 3, the samples of teeth of each size class have CV values typically less than 10. However, the pooled sample of large and small morphs have CV values much greater than 10, which are thought to be too high to belong to a single species (Kurtén, 1953; Simpson et al., 1960; Yablokov, 1974; Plavcan and Cope, 2001).

#### *Miotylopus gibbi* (Loomis, 1911)

*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)

*Miotylopus gibbi* Prothero, 1996

**Type Specimen:** YPM 10328 (Figs. 2-3), partial upper and lower jaws.

**Type Locality:** From the Muddy Creek beds (Monroe Creek equivalent beds *vide* McKenna and Love, 1972, but "Upper Harrison" beds according to Loomis, 1911), "on Muddy Creek, about opposite to the spring associated with the 'Spanish diggings'" (Loomis, 1911, p. 67).

**Age:** Early Arikareean, Little Muddy Creek (Gering Formation equivalent, about 27-29 Ma) and Muddy Creek beds (Monroe Creek Formation equivalent, about 25-27 Ma, *vide* Tedford et al., 1996, 2004).

**Referred Material:** Fossils from Little Muddy Creek (Gering equivalent) and Muddy Creek beds (Monroe Creek beds) in the F:AM collection, Goshen County, Wyoming, listed by Prothero (1996, p. 638-640).

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

**Description:** *M. gibbi* was described by Schlaikjer (1935) (as *Miotylopus "bathygnathus"*), and additional material was described by Prothero (1996).

**Discussion:** As discussed above, multiple names have been proposed for the medium-sized species of *Miotylopus*. By the rules of priority, "*Oxydactylus*" *gibbi* Loomis 1911 is the senior synonym for this size cluster (Fig. 9). The holotype material (YPM 10328) falls within the size cluster (Fig. 9, Tables 1-2) of medium-sized *Miotylopus* from the Frick Collection. The holotype material (MCZ 2424; Figs. 4-5) of *Miotylopus bathygnathus* Schlaikjer, 1935 also falls within the size dimensions of Frick Collection *M. gibbi* (Fig. 9, Tables 1-2), so it is a junior synonym of *M. gibbi*. None of the specimens from the Eastlake local fauna closely match the excellent unbroken skulls and jaws of *M. gibbi* described by Prothero (1996, fig. 16).

Another question is whether Stock's *Dyseotylopus migrans* is a junior synonym of *Miotylopus gibbi*. McKenna (1966) was reluctant to synonymize them, even though he admitted they were extremely similar. Prothero (1996, p. 640) suggested they were synonyms, because some of Stock's diagnostic features (e.g., mesostyles on upper molars stronger than typical for stenomylines) are encompassed within the range of morphological variation in the Frick sample of *Miotylopus*. The measurable teeth are also within the range of *M. gibbi* (Table 1). Stock (1935, p. 122-123) made no comparisons to *Miotylopus*. The description of *Miotylopus* by Schlaikjer was not available to Stock because it published just months before his paper, so there is no way to know how Stock would have distinguished the two taxa; he never commented on them in future publications. Stock (1935) only compared *Dyseotylopus* to much more primitive camels such as *Poebrotherium*, "*Protomeryx*," and *Pseudolabis*, so there are no comparisons relevant to distinguish *Dyseotylopus* from *Miotylopus*. Deméré (1988) suggested the presence of *Dyseotylopus* in the Eastlake local fauna, but Walsh and Deméré (1991) only mentioned *Miotylopus* in the Eastlake local fauna. Deméré (pers. commun. to Prothero) later told Prothero (noted in Prothero, 1996, p. 640) he thought that the Eastlake camel was neither

TABLE 3. Coefficient of variation of tooth dimensions in samples of *Miotylopus*. The P2/p2 and P3/p3 consistently have high CV values, probably because their shape is not constrained by adjacent teeth since they have diastemata on both sides. But the sample of *M. gibbi* from Wyoming and *M. leonardi* from San Diego have normal CV values (<10 on most teeth), while the pooled sample has CV > 10 for all teeth, too high for a single population.

DIM.	Pooled Sample		F:AM <i>M. gibbi</i>		SDNHM <i>M. leonardi</i>	
	UPPERS	LOWERS	UPPERS	LOWERS	UPPERS	LOWERS
P2L	17.05	17.21	16.15	10.60	8.09	13.06
P2W	28.56	17.86	20.36	21.93	15.40	8.62
P3L	17.36	12.48	11.52	12.85	12.59	16.95
P3W	22.74	15.72	14.27	19.19	6.98	24.76
P4L	11.85	18.34	8.49	22.67	13.71	19.40
P4W	14.90	20.66	13.07	4.66	9.35	33.21
M1L	11.41	10.56	6.65	8.45	8.63	10.76
M1W	10.35	17.22	4.19	18.27	11.01	11.78
M2L	14.54	10.67	13.96	8.96	7.06	10.07
M2W	9.78	16.30	6.67	16.09	13.32	9.14
M3L	18.11	13.61	9.28	9.60	6.89	12.67
M3W	8.94	19.01	10.58	23.66	19.02	9.40
M1-3	7.30	11.51	4.52	8.44	3.50	7.55
P2-4	9.82	9.63	5.56	3.49	4.53	4.99
P2-M3	36.33	11.35	7.76	7.93	4.38	6.42

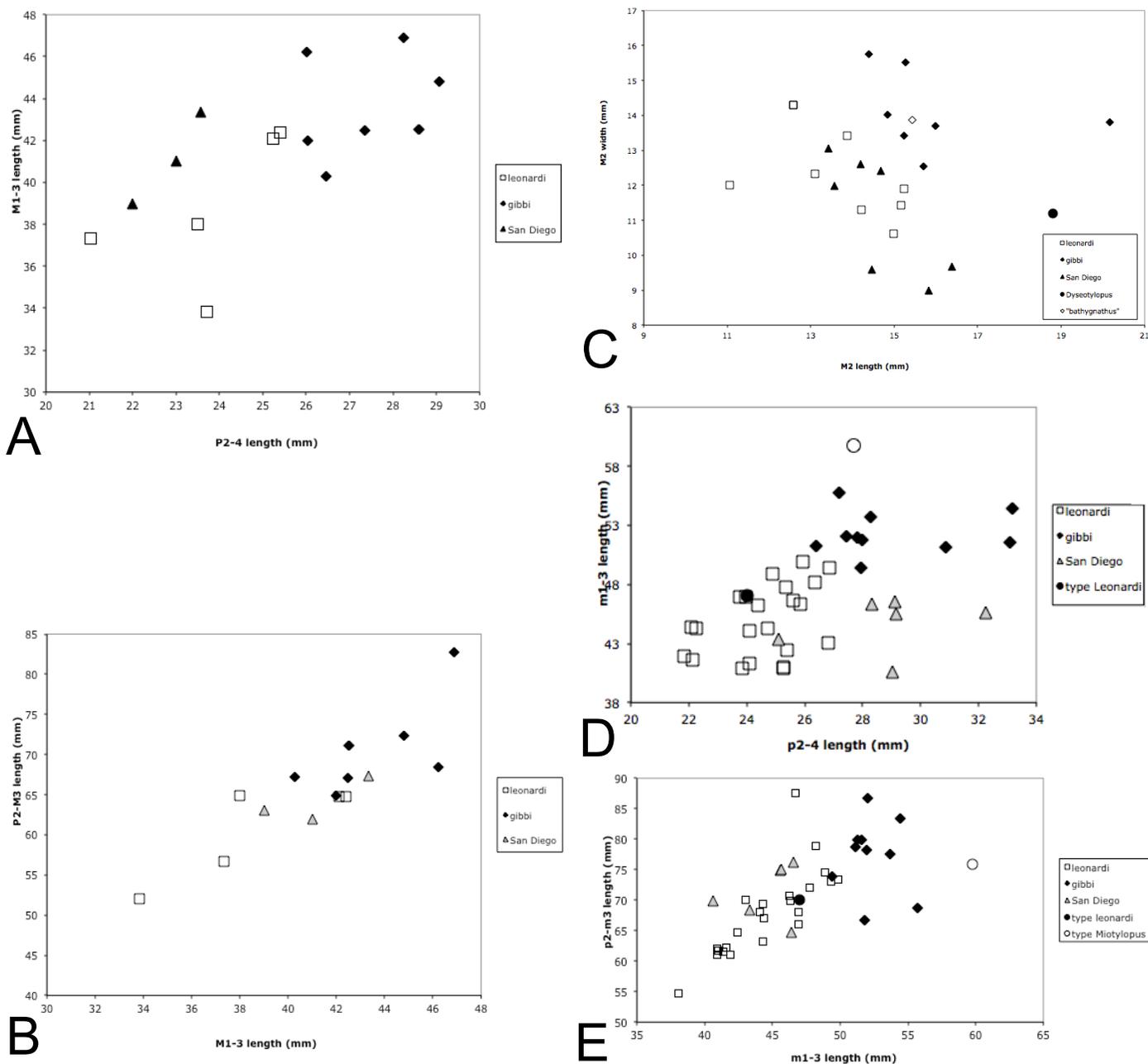


FIGURE 9. Plot of tooth dimensions of samples of *M. leonardi* from Wyoming (open squares), *M. gibbi* from Wyoming (solid diamonds), and *M. leonardi* from San Diego (gray triangles). **A**, M1-3 length vs. P2-4 length. **B**, M1-3 length vs. P2-M3 length. Both of these plots clearly separate *M. gibbi* from *M. leonardi*, and most San Diego specimens fall in the *M. leonardi* field, as does the holotype of *Miotylopus bathygnathus* (open diamond). **C**, plots of individual teeth, such as M2 length vs. width, do not separate the taxa as well as the longer tooth-row measurements, but do demonstrate that *Dyseotylopus* (solid circle) falls within the *M. gibbi* field, as does the holotype of *Miotylopus bathygnathus* (open diamond). **D**, lower p2-4 vs. m1-3, and **E**, lower m1-3 vs. p2-m3. Both of these plots clearly separate the Wyoming samples of *M. gibbi* and *M. leonardi*. The holotype of *M. leonardi* (solid circle) falls within the range of the F:AM specimens of *M. leonardi*, and the holotype of *Miotylopus bathygnathus* (open circle) falls within the range of *M. gibbi*.

*Dyseotylopus* nor *Miotylopus*, but a distinct genus.

The taxonomic status of *Dyseotylopus* has remained unresolved for the over 81 years since it was first described. We re-examined the type material on two different trips to the LACM to resolve this question. The first thing we found is that the type specimen, LACM(CIT) 1721, has suffered much breakage since it was first described by Stock in 1935 (Figs. 12-13). In the original figure, a long rostrum and preorbital-maxillary region is present, but today the specimen (Fig. 13B-C) lacks those portions of the skull. The Caltech specimens probably suffered considerable wear and tear after Stock died in 1950. They were apparently moved from one place to another, and probably were damaged even more when they were packed up and moved to the LACM. What remains of the skull is badly crushed

and broken into small pieces, which is not apparent in Stock's (1935, pl. 1) figure, so that only the orbit and other parts of the cranium can be distinguished. The skull is too fractured to recognize sutures. The teeth have remained relatively undistorted (Fig. 13B-C), so we were able to obtain measurements from them, although measurements along the tooth row were difficult to obtain due to their displacement and distortion. Re-examination of the teeth and the surviving features of the skull show no features that would distinguish it from *Miotylopus gibbi*. As mentioned above, the condition of the mesostyles on the upper molars is within the range of Frick *Miotylopus*, and the size entirely encompassed within the range of Wyoming *M. gibbi*. Thus, we find no evidence that *Dyseotylopus migrans* can be objectively diagnosed as distinct from *Miotylopus gibbi*, and formally place them in synonymy.



FIGURE 10. **A**, comparison of skull of male *M. gibbi*, F:AM 36446 (top), with female *M. leonardi*, F:AM 37806, showing the striking difference in size and skull proportions that is not reflected in the size of individual cheek teeth. **B**, comparison of skull of male *M. gibbi*, F:AM 36446 (largest specimen), with female of *M. gibbi* (F:AM 36451) and female of *M. leonardi* (F:AM 36425).

#### CONCLUSIONS

The camel fossils from the late Oligocene Eastlake local fauna, Otay Formation, San Diego County, California, belong to a single taxon, *Miotylopus leonardi* (Loomis, 1911). Re-examination of the material from Wyoming as well as the newer San Diego collections confirms the original conclusions of Prothero (1996) that there are three distinct species of *Miotylopus*, each with specimens that have male and female canines: the small-sized *M. leonardi* (Loomis, 1911), the medium-sized *M. gibbi* (Loomis, 1911), and the large-sized *M. taylori* Prothero, 1996. Restudy of the type material of *Dyseotylopus migrans* Stock, 1935, from the late Oligocene Kew Quarry, Sespe Formation, Ventura County, California, confirms earlier suggestions that this taxon is a junior synonym of *Miotylopus gibbi*.

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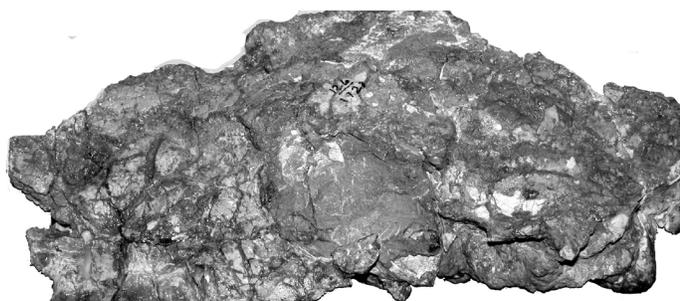


FIGURE 11. Comparison of mandibles of a male *M. gibbi* (F:AM 36446, largest specimen) vs. male (F:AM 36441) and female (F:AM 36806) specimens of *M. leonardi* **A**, crown and **B**, lateral views, showing the clear sexual dimorphism of lower canines in each size cluster.

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FIGURE 12. *Dyseotylopus migrans*, LACM (CIT) 1721. Stock's (1935, Plate I) original figure of the specimen as it was described.



A



B

FIGURE 13. *Dyseotylopus migrans*, LACM (CIT) 1721. A, lateral and B, palatal views of the specimen today, showing the loss of the rostrum since its original description.

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