American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK 24, N.Y.

NUMBER 2253 AUGUST 18, 1966

Synopsis of Whitneyan and Arikareean Camelid Phylogeny

By Malcolm C. McKenna[1]

INTRODUCTION

The present paper is an interim report on the phylogeny of camels during the early phases of their great evolutionary radiation during the mid-Tertiary. The manuscript was originally prepared as background information for the identification of a rare new form from the Miocene of the Bighorn Mountains, Wyoming, but, because of the complexity of the subject and because little has been published for many years other than brief descriptions, an equally brief synthesis is offered here.

Childs Frick's magnificent collection of mid-Tertiary camels was not seen while this paper was in preparation. Our knowledge will be very substantially enriched when that material can be published upon, but it will be some time before research based on the Frick collection reaches print. In the meantime an interim survey is needed.

I am indebted to Messrs. Thomas Patton, J. D. Love, P. O. McGrew, Beryl Taylor, C. A. Repenning, S. D. Webb, J. R. Macdonald, S. J. Olsen, and C. E. Ray for helpful comments.

WHITNEYAN CAMELS

Knowledge of Orellan and Whitneyan camels has been confined largely

[1] Frick Associate Curator, Department of Vertebrate Paleontology, the American Museum of Natural History.

to *Poebrotherium,* remains of which are encountered fairly frequently in Orellan sediments. Only a few specimens of Whitneyan camels have been described, but it is evident that various camelid lineages in addition to *Poebrotherium* were differentiating in North America during the late Oligocene and that these exhibited considerable parallelism in such features as the approximation of the metapodials, closure of the orbit, lengthening of the face, elongation of the cervicals, reduction of the upper incisors, and several other features. Several camelid lines appear to have existed in the Whitneyan: (1) *Pseudolabis dakotensis* Matthew, 1904; (2) *Paratylopus primaevus* (Matthew, 1904) and *"Paralabis" matthewi* Lull, 1921; (3) the unknown ancestors of stenomyline camels (possibly related distantly to *Pseudolabis*); and (4) a conservative *Poebrotherium*-like line.

Pseudolabis has long been recognized as a distinctive and precocious line, though Lull's (1921) retrogressive reference of *"Paralabis"* to *Pseudolabis* as a subgenus obscured the distinctiveness of *Pseudolabis. Pseudolabis* is characterized, among other features, by completely closed orbits, large size, a partly molarized P^4, and very weak mesostyles on the relatively elongate upper molars. Simpson (1945, p. 150) proposed a subfamily Pseudolabidinae for the reception of *Pseudolabis.*

The central camelid lineage, leading to such genera as *Gentilicamelus, Oxydactylus,* and *Miotylopus,* is represented in the Whitneyan by *Paratylopus primaevus* of the "upper Oreodon beds" (lower Poleslide Member of the Brule Formation) and by *"Paralabis" matthewi.* The latter species is perhaps referable to *Paratylopus,* though the species is more advanced than *Paratylopus primaevus* and is possibly from somewhat younger Whitneyan sediments. In known features *"Paralabis" matthewi* is closely similar to *Gentilicamelus sternbergi* of the upper John Day of Oregon and may be its ancestor. *Paratylopus* is intermediate in size between *Poebrotherium* and *Pseudolabis,* has open orbits, rather low-crowned teeth, enlarged I^3, rather square upper molars with prominent mesostyles, and short diastemata in front of and behind P^1. The genus was still closely similar to *Poebrotherium.*

"Protomeryx" is another Whitneyan camel, described by Leidy in 1856 and long a taxonomic dumping-ground for Whitneyan and Arikareean camels. Leidy's type of *Protomeryx halli* is a very poor specimen (see Leidy, 1869, pl. 15, figs. 8, 9), consisting of the damaged front end of a left lower jaw in which the incisor crowns are destroyed. The lower canine is more like that of Miocene non-stenomyline camels than like that of *Poebrotherium,* and there are diastemata on each side of P_1. *"Protomeryx"* may represent a large and advanced species of *Poebrotherium,* in which case that genus occurs in the Whitneyan, but it is also possible that *"Proto-*

meryx" is a prior synonym of *Paratylopus.* Unfortunately, the types of *Paratylopus primaevus* and *Protomeryx halli* cannot be compared directly with each other because of damage to comparable features. I prefer to regard *"Protomeryx"* as a *nomen dubium.*

At least one of the Whitneyan species referred to *"Protomeryx," P. campester* Matthew, 1901 (=*P. cedrensis* Matthew, 1901, as fixed by Stock, 1935, p. 122, and not to be confused with *Oxydactylus campestris*), apparently represents an advanced descendant of *Poebrotherium* in the Whitneyan in which the muzzle became elongated, P_{2-4} were shortened, and diastemata developed, especially between P_1 and P_2 where jaw depth is at a minimum. Possibly this group is ancestral to or congeneric with *Dyseotylopus,* as Stock suggested (*ibid.,* p. 123).

ARIKAREEAN CAMELS

Arikareean camels were first reported not from the High Plains, but rather from the upper John Day beds of Oregon, a part of the John Day approximately equivalent to the Harrison Formation of Nebraska and nearby states. The High Plains Arikareean became known at a later date. *Gentilicamelus sternbergi*[1] (Cope, 1879) and the *Oxydactylus*-like *"Paratylopus" cameloides* (Wortman, 1898) and *"Paratylopus" wortmani* Lull, 1921, were based on specimens from the upper John Day beds.

Gentilicamelus sternbergi appears to be a continuation into the Arikareean of the *"Paralabis" matthewi* morphology of the Whitneyan. In dental features *Gentilicamelus sternbergi* is similar to *"Paralabis"* and thus to *Paratylopus primaevus* of the late Orellan. *Gentilicamelus* may therefore be regarded as a primitive hold-over into the Oregon Miocene. Wortman's (1898, p. 114) figure of *G. sternbergi* is grossly inaccurate and indicates, among other things, a complete orbit, which can neither be confirmed nor denied on the basis of the specimen. The orbit may have been open. Cope's figure (Cope and Matthew, 1915, p. 116) of the same specimen is somewhat more accurate than Wortman's, but indicates vaguely that the orbit was closed.

A second group of Arikareean camels is represented in the Harrison Formation by *Stenomylus,* the progenitor of the remarkable late Tertiary

[1] This species was made the type species of *Gomphotherium* Cope, 1886, preoccupied, *non* Burmeister, 1837 (proboscidean), or Filhol, 1884 (talpid). It was also referred to *Protomeryx* by Hay (1902, p. 676), to *Paratylopus* by Matthew in 1904 (as a subgenus of *Miolabis*) and in 1915 (*in* Cope and Matthew, 1915, p. 116), and was later made the type species of *Gentilicamelus* Loomis, 1936. According to Dougherty (1940), the type specimen of *G. sternbergi* came from below the level of *"Paratylopus" cameloides* in the upper John Day beds.

genus *Rakomylus*. No remains of *Stenomylus* have been reported from the John Day beds or from California. *Stenomylus* is characterized, among many other distinctive features, by incisivization of the lower canine and P_1, resulting in a battery of 10 incisor-like teeth at the front of the mandible, by reduction of P^2, P^3, and P_3, by a diastema between P_2 and P_3, and by development of progressively elongate and very high-crowned molars of a unique type. The upper molars have lost the mesostyle. Because *Stenomylus* is such a distinctive genus, it is usually given a hypothetical separate ancestral line leading back to the early Oligocene or even into the Eocene, but it may be pointed out here that there are a number of dental similarities to *Dyseotylopus migrans* of the upper Sespe Formation of California and to certain other specimens from the Gering or Monroe Creek formations similar to *Dyseotylopus* and *Pseudolabis*. Unfortunately, adult specimens of pre-Harrison Arikareean camels are very poorly known at present, so the fascinating problem of stenomyline ancestry cannot be pursued further here.

A third group of Arikareean camels is represented by *Dyseotylopus* Stock, 1935, a small camel first described from the upper Sespe Formation of California.[1] In this group the upper molars are somewhat elongate and have weak mesostyles, but P^4 is simple in contrast to P^4 of *Pseudolabis*. *Dyseotylopus* differs from *Miotylopus* in that the mesostyles of *Dyseotylopus* become weaker toward the occlusal surface as in stenomylines and *Pseudolabis,* and the molars are more elongate and high-crowned (even when wear in available specimens is taken into account). The foot structure of *Dyseotylopus* is at present unknown, but from the crushed type skull of *Dyseotylopus migrans* it can be seen that the orbit was closed. Additional specimens of *Dyseotylopus* from Kew Quarry would be most welcome, for both the affinities and the age of *Dyseotylopus migrans* are uncertain. Certainly Kew Quarry is older than the upper John Day or the Harrison Formation, but in Nebraska and South Dakota several formations and disconformities representing a significant interval of time separate the Harrison from the Whitney. The faunas of these intervening formations are still poorly known and may be equivalent to the upper part of the Sespe containing Kew Quarry (see Macdonald, 1963). Durham, Jahns, and Savage (1954) regarded Kew Quarry as Miocene on the marine microfossil time scale and as latest Oligocene on the marine megafossil and terrestrial vertebrate scales.

---

[1] Unless, as seems possible, *"Protomeryx" leonardi* Loomis, 1911, belongs to this species or is congeneric. Both the affinities and supposed "upper Harrison" occurrence of the type specimen of Loomis' species are puzzling.

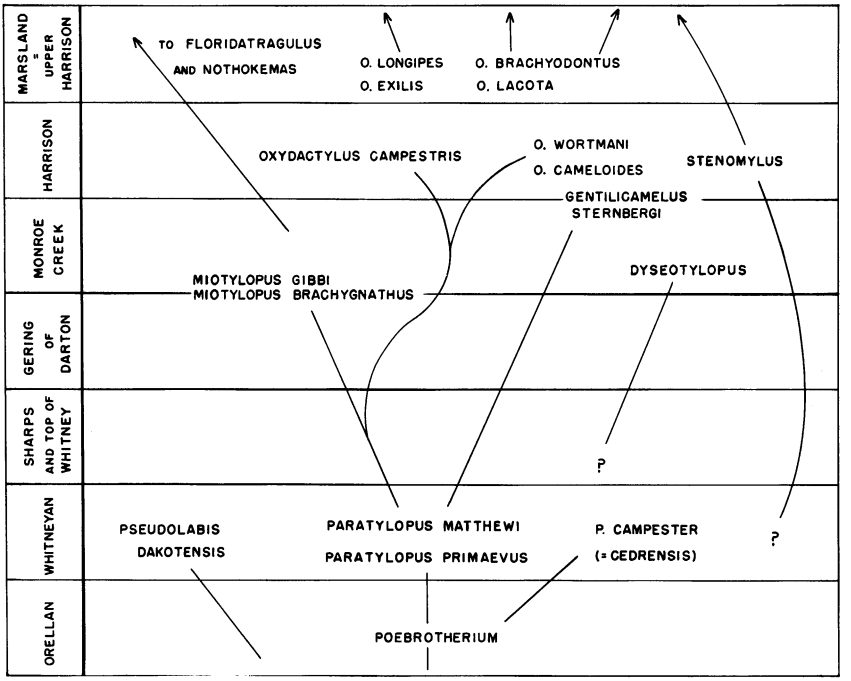

FIG. 1. Suggested generalized phylogeny of mid-Tertiary Camelidae. The time scale is crude and is in terms of North American land mammal ages and of geochrons of High Plains rock units.

Two specimens (M.C.Z. Nos. 2068 and 17763) from the Arikareean (probably upper Gering or Monroe Creek) of the south side of 66 Mountain, Laramie County, Wyoming, were referred to *Protomeryx* by Schlaikjer (1935, p. 177), who believed the locality to be in the (lower) Harrison Formation (*sensu* Schlaikjer). Schlaikjer stated that a probably conspecific skeleton collected in 1927 was to be described by Loomis, but this specimen is not to be confused with the specimen Loomis (1936) selected as the type of *Gentilicamelus wyomingensis.* The latter was collected several miles southwest of the Harding Ranch on Bear Creek, Platte County, Wyoming, in 1933 (J. D. Love, personal communication). The two early Arikareean specimens in the Harvard collection from 66 Mountain are immature and therefore possess dP^3 and dP^4 rather than P^3 and P^4, but M^1 and M^2 are present and are similar to those of *Dyseotylopus* and *Pseudolabis,* even though their elongate shape is somewhat exaggerated by lack of wear. The mesostyles are quite weak, and the unworn pattern

is suggestive of a hypothetical early stage through which the ancestors of *Stenomylus* must have passed. The milk dentition is not adequately comparable yet with that of various pertinent camelid lineages, but it does not seem to me out of the question that the deciduous dentition of *Stenomylus* could be a modification of the general kind displayed by these early Arikareean specimens.

A fourth group of Arikareean camels, *Miotylopus,* is evidently related to *Oxydactylus* of the Harrison and Marsland formations and their equivalents, but is smaller and has very low-crowned cheek teeth and apparently open orbits. It is possible that *Oxydactylus* is descended from *Paratylopus* via early Arikareean species of *Miotylopus,* but unfortunately details of the foot structure have not been reported. Schlaikjer (1935, p. 174) provided a generic name for these camels when he described *Miotylopus brachygnathus* from early Arikareean sediments (lower Harrison sediments, *sensu* Schlaikjer; Gering or Monroe Creek formations of other authors) on the south side of 66 Mountain, Laramie County, Wyoming. Schlaikjer's evidence for an open orbit in *Miotylopus* is not altogether certain, as Schlaikjer himself was aware (1935, p. 165), but if the orbit was closed the postorbital bar was only a very weak structure. In addition to the type species, Loomis' (1911, p. 67) "upper Harrison" *Oxydactylus gibbi* appears to belong to *Miotylopus,* and, if this reference is correct, *Miotylopus gibbi* demonstrates that *Miotylopus* retained a large I^3 relative to the upper canine. *Oxydactylus campestris* of the Harrison Formation is intermediate in this regard between *Miotylopus* and Marsland species of *Oxydactylus.*

A fifth group of Arikareean camels, *Oxydactylus,* appears to be confined to the Harrison and Marsland formations (mainly the latter) and their equivalents, though at one time or another most non-stenomyline camels from the Marsland and older Miocene formations of the High Plains have been referred to it. *Oxydactylus* was originally based on *O. longipes* Peterson, 1904, from the Marsland, but many additional species have been referred to the genus, stretching its morphological boundaries past the breaking point. The reader is referred to Peterson's excellent description for details of the skeletal anatomy of *Oxydactylus, sensu stricto. Oxydactylus, sensu lato,* probably represents several closely related genera descended from *Paratylopus, sensu lato,* perhaps via early members of the genus *Miotylopus.* In the same sense, *Oxydactylus* gave rise to other later Miocene lineages in addition to the one leading to *"Alticamelus." Oxydactylus* is a larger camel than *Miotylopus,* and the orbits are fully closed. The upper incisors are somewhat reduced, I^3 is never markedly larger than the upper canine and may be somewhat smaller, and the molars are still fairly low-crowned and possess strong mesostyles.

The type specimen of *"Gentilicamelus" wyomingensis* Loomis, 1936, is not closely related to the type species of *Gentilicamelus,* but is an immature, *Oxydactylus*-like camel with dI^{1-3}, dC^{1}, P^{1}, dP^{2-4}, M^{1-2}. The mesostyles are strong on all teeth from dP^{3} to M^{2}. M^{3} was not yet in place. The orbit was closed. Loomis' failure to identify the milk teeth correctly and his designation of *G. sternbergi* as the type of the genus to which he supposed the Wyoming species to belong have led to considerable confusion. Harksen, Macdonald, and Sevon (1961, p. 678) and Macdonald (1963) have correctly deciphered the true affinities of *"G." wyomingensis* and referred it to *Oxydactylus.* If it does not belong in *Oxydactylus,* it is at least closely related to that genus.

The larger upper John Day camels usually referred to *"Paratylopus"* may also belong in *Oxydactylus,*[1] though they are perhaps best placed in a new genus. Even the names *Gentilicamelus* or *Paralabis* (as recombinations) might be applicable, if those generic concepts were to be given that much latitude, but the name *Paratylopus* is certainly a poor choice. *"Paratylopus" cameloides* and *"Paratylopus" wortmani* were regarded as synonymous by Dougherty (1940, p. 58). Dougherty (1940) has also shown that the orbit is closed in a referred skull of *"Paratylopus" cameloides.* The various real and supposed species of *Oxydactylus* have been inadequately compared with the John Day camels, but such studies should be made because of their bearing on the correlation of various parts of the John Day sequence with the Oligocene and Arikareean sequence of the High Plains.

The Thomas Farm Miocene locality in Florida has yielded camelid remains that have generally been interpreted as those of peculiar hypertraguloids, though recently their camelid affinities have been recognized (Ray, 1957; Olsen, 1959; and others). Two principal kinds of camels are represented at Thomas Farm, though both are adapted to the same mode of feeding, which resulted in elongated snouts that carried the dentitions anterior to the level of the orbits and resulted in prominent diastemata between the anterior teeth. The genera represented are *Floridatragulus* White, 1940 (=*Hypermekops* White, 1942), and *Nothokemas* White, 1947.

Floridatragulus is known from two species at the Thomas Farm locality: *Floridatragulus dolichanthereus* White, 1940 (=*Hypermekops olseni* White, 1942), and *Floridatragulus barbouri* White, 1947. *Nothokemas* is apparently represented by a single species, *Nothokemas floridanus* (Simpson, 1932), variously called *Oxydactylus floridanus* Simpson, 1932, and *Paratylopus grandis* White, 1940.

---

[1] Suggested by Repenning and Vedder (1961, p. C-237), who regarded the synonymy of *Paratylopus cameloides* and *Oxydactylus brachyodontus* as possible.

Floridatragulus was placed in the Hypertragulidae by White (1940, 1941, 1942) and in the Hypertragulidae, *incertae sedis,* by Simpson (1945). In 1947, White placed *Nothokemas* in the Hypertraguloidea, *incertae sedis,* and a new hypertraguloid family, Nothokemadidae, was proposed to receive it. Romer (1948) listed the Nothokemadidae merely as an artiodactyl family without reference to a superfamily, and he continued to regard *Floridatragulus* and *Hypermekops* as members of the Hypertragulidae. Ray

TABLE 1

CHARACTERS OF *Floridatragulus* AND *Nothokemas*

Floridatragulus	*Nothokemas*
Extremely elongate snout in *F. dolichanthereus* but shorter in *F. barbouri.*	Moderately elongate snout
Orbit open	Orbit closed
Diastema between P_2 and P_3	No diastema between P_2^2 and P_3^3
M_3 with divided hypoconulid	M_3 with poorly divided hypoconulid (seen only in unworn condition)
Cheek teeth lower-crowned, upper molars squared (partly from wear)	Cheek teeth higher-crowned, upper molars not so square
P_2 and P_3 with cusps essentially in line	P_2 and P_3 with camelid pattern essentially unmodified

(1957, p. 18) listed both *Floridatragulus* and *Nothokemas* as questionable camelids, and did not list *Hypermekops,* presumably because he was aware that it was a synonym. Ray's listing was based on unpublished work by Bryan Patterson and on Ray's own unpublished studies (Ray, 1957, p. 2). The family-group name Nothokemadidae was not utilized in Ray's classification. Olsen (1959) exactly followed Ray (1957), but in 1962 Olsen listed *Floridatragulus* and *Nothokemas* as camels without a query. Patton (1964) listed *Floridatragulus* as a camel-like artiodactyl and *Nothokemas* as a camel.

Floridatragulus and *Nothokemas* seem to me to be derived from the ancestry of *Oxydactylus,* perhaps as late in time as the *Miotylopus-Oxydactylus* transition in the early Arikareean but perhaps earlier if parallelism is postulated. *Nothokemas* could well be a highly modified descendant of *Oxydactylus campestris* Cook, from the Harrison Formation, but *Floridatragulus* suggests affinities with earlier camels in that the orbit is still open. What amount of time was involved in the development of the elongate snout of these peculiar Florida camels after they branched off from the ancestry of *Oxydactylus* remains a question until the age of the

Thomas Farm deposit in terms of the High Plains Arikareean and Hemingfordian sequence becomes better known.

REFERENCES

BURMEISTER, K. H. K.
1837. Handbuch der Naturgeschichte. Berlin, Abt. I and II. [Not seen.]

COPE, E. D.
1879. Observations on the faunae of the Miocene Tertiaries of Oregon. Bull. U. S. Geol. and Geogr. Surv. Terr., vol. 5, pp. 55–69.
1886. The phylogeny of the Camelidae. Amer. Nat., vol. 20, pp. 611–624, 12 figs.

COPE, E. D., AND W. D. MATTHEW
1915. Hitherto unpublished plates of Tertiary Mammalia and Permian Vertebrata. Monogr. Amer. Mus. Nat. Hist., no. 2, 154 pls.

DOUGHERTY, J. F.
1940. Skull and skeletal remains of the camel *Paratylopus cameloides* (Wortman) from the John Day deposits, Oregon. Publ. Carnegie Inst. Washington, no. 514, pp. 49–58, 1 pl.

DURHAM, J. W., R. H. JAHNS, AND D. E. SAVAGE
1954. Marine-nonmarine relationships in the Cenozoic section of California. Bull. California Div. Mines, no. 170, chap. 3, pp. 59–71, figs. 1–4.

HARKSEN, J. C., J. R. MACDONALD, AND W. D. SEVON
1961. New Miocene formation in South Dakota. Bull. Amer. Assoc. Petrol. Geol., vol. 45, no. 5, pp. 674–678, figs. 1–3.

HAY, O. P.
1902. Bibliography and catalogue of the fossil Vertebrata of North America. Bull. U. S. Geol. Surv., no. 179, pp. 1–868.

LEIDY, J.
1856. Notice of some remains of extinct vertebrated animals. Proc. Acad. Nat. Sci. Philadelphia, vol. 8, pp. 163–165.
1869. The extinct mammalian fauna of Dakota and Nebraska, including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America. Jour. Acad. Nat. Sci. Philadelphia, vol. 7, pp. i–vii, 1–472, 30 pls.

LOOMIS, F. B.
1911. The camels of the Harrison Beds, with three new species. Amer. Jour. Sci., vol. 31, pp. 65–70, 3 figs.
1936. The skeleton of a new fossil camel from Wyoming. Univ. Wyoming Publ., vol. 2, no. 5, pp. 59–64, figs. 1–4.

LULL, R. S.
1921. New camels in the Marsh collection. Amer. Jour. Sci., vol. 1, pp. 392–404, figs. 1–5.

MACDONALD, J. R.
1963. The Miocene faunas from the Wounded Knee area of western South Dakota. Bull. Amer. Mus. Nat. Hist., vol. 125, pp. 139–238, figs. 1–30, 2 maps.

MATTHEW, W. D.
1901. Fossil mammals of the Tertiary of northeastern Colorado. Mem.

Amer. Mus. Nat. Hist., vol. 1, pp. 355–447, figs. 1–34, pls. 37–39.

1904. Notice of two new Oligocene camels. Bull. Amer. Mus. Nat. Hist., vol. 20, pp. 211–215.

OLSEN, S. J.

1959. Fossil mammals of Florida. Spec. Publ. Florida Geol. Surv., no. 6, pp. i–iv, 1–74, figs. 1–13, pls. 1–14.

1961. Has anyone seen our camel? News Bull. Soc. Vert. Paleont., no. 63, p. 38, 1 fig.

1962. The Thomas Farm fossil quarry. Quart. Jour. Florida Acad. Sci., vol. 25, no. 2, pp. 142–146.

1964. The stratigraphic importance of a lower Miocene vertebrate fauna from north Florida. Jour. Paleont., vol. 38, no. 3, pp. 477–482, figs. 1, 2, pls. 68–70.

PATTON, T. H.

1964. The Thomas Farm fossil vertebrate locality. *In* Auffenberg, W., W. T. Neill, T. H. Patton, and S. D. Webb, Guidebook 1964 field trip Society of Vertebrate Paleontology in central Florida. Gainesville, Florida, pp. 12–20, 1 fig.

PETERSON, O. A.

1904. Osteology of *Oxydactylus,* a new genus of camels from the Loup Fork of Nebraska, with descriptions of two new species. Ann. Carnegie Mus. Nat. Hist., vol. 2, no. 3, pp. 434–476, figs. 1–3, pls. 4–15.

RAY, C. E.

1957. A list, bibliography, and index of the fossil vertebrates of Florida. Special Publ. Florida Geol. Surv., no. 3, pp. i–iv, 1–175.

REPENNING, C. A., AND J. G. VEDDER

1961. Continental vertebrates and their stratigraphic correlation with marine mollusks, eastern Caliente Range, California. Prof. Paper U. S. Geol. Surv., no. 424, pp. C-235–C-239, figs. 235-1, 235-2, 1 table.

ROMER, A. S.

1948. The fossil mammals of Thomas Farm, Gilchrist County, Florida. Quart. Jour. Florida Acad. Sci., vol. 10, no. 1, pp. 1–11.

SCHLAIKJER, E. M.

1935 (May). Contributions to the stratigraphy and paleontology of the Goshen Hole area, Wyoming. IV. New vertebrates and the stratigraphy of the Oligocene and early Miocene. Bull. Mus. Comp. Zool., Harvard, vol. 76, no. 4, pp. 97–189, figs. 1–13, pls. 1–41.

SIMPSON, G. G.

1932. Miocene land mammals from Florida. Bull. Florida State Geol. Surv., no. 10, pp. 9–41, figs. 1–23.

1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., vol. 85, pp. i–xvi, 1–350.

STOCK, C.

1935 (July). Artiodactyla from the Sespe of the Las Posas Hills, California. Publ. Carnegie Inst. Washington, no. 453, pp. 119–125, 1 pl.

WHITE, T. E.

1940. New Miocene vertebrates from Florida. Proc. New England Zool. Club, vol. 18, pp. 31–38, pls. 3–7.

1941. Additions to the Miocene fauna of Florida. *Ibid.,* vol. 18, pp. 91–98, pls. 14, 15.
1942. The lower Miocene mammal fauna of Florida. Bull. Mus. Comp. Zool., Harvard, vol. 92, no. 1, pp. 1–49, figs. 1–10, pls. 1–14.
1947. Additions to the Miocene fauna of North Florida. *Ibid.,* vol. 99, no. 4, pp. 497–515, figs. 1–6.

WORTMAN, J. D.
1898. The extinct Camelidae of North America and some associated forms. Bull. Amer. Mus. Nat. Hist., vol. 10, pp. 93–142, figs. 1–23, 1 pl.