

CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

THE UNIVERSITY OF MICHIGAN

Vol. 25, No. 1, p. 1-9 (2 text-figs.)

May 15, 1978

**NEW CONDYLRATHRA (MAMMALIA) FROM THE
PALEOCENE AND EARLY EOCENE OF NORTH AMERICA**

BY

PHILIP D. GINGERICH
MUSEUM OF PALEONTOLOGY
THE UNIVERSITY OF MICHIGAN



MUSEUM OF PALEONTOLOGY
THE UNIVERSITY OF MICHIGAN
ANN ARBOR

CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

Gerald R. Smith, Director

Robert V. Kesling, Editor

Diane Wurzinger, Editor for this number

The series of contributions from the Museum of Paleontology is a medium for the publication of papers based chiefly upon the collection in the Museum. When the number of pages issued is sufficient to make a volume, a title page and a table of contents will be sent to libraries on the mailing list, and to individuals upon request. A list of the separate papers may also be obtained. Correspondence should be directed to the Museum of Paleontology, The University of Michigan, Ann Arbor, Michigan, 48109.

VOLS. II—XXV. Parts of volumes may be obtained if available. Price lists available upon inquiry.

NEW CONDYLRARTHRA (MAMMALIA) FROM THE PALEOCENE AND EARLY EOCENE OF NORTH AMERICA

By

Philip D. Gingerich

Abstract.— Four relatively rare condylarths are described from localities in Montana, Wyoming, and Colorado. *Goniacodon levisanus* (Cope) is reported for the first time from the Rock Bench Quarry (Torrejonian) of the Big Horn Basin, Wyoming. *Stelocyon arctylos*, new genus and species, is described from a Torrejonian locality in the northern Big Horn Basin, Montana. Several specimens of *Thryptacodon* from the Clarkforkian of Buckman Hollow and the Big Horn Basin, Wyoming, are tentatively referred to *T. pseudarctos* Simpson, pending a detailed review of the genus. *Mimotricentes ischyryus*, new species, is described from two Clarkforkian localities near DeBeque, Colorado.

INTRODUCTION

Condylarthra are among the most abundant and most important early Tertiary mammals. Approximately a dozen different genera of condylarths are found in middle Paleocene through early Eocene local faunas in North America (Matthew, 1937; Simpson, 1937a; Sloan, 1970), and some of these, such as *Ectocion* and *Hyopsodus*, are among the dominant elements in many collections. European faunas from this interval are similarly rich in condylarths (Russell, 1964; Rich, 1971).

The classification of North American condylarths is presently divided into six families: Arctocyonidae, Mesonychidae, Hyopsodontidae, Meniscotheriidae, Periptychidae, and Phenacodontidae. Two of these have recently received detailed review, the Meniscotheriidae by Gazin (1965) and the Phenacodontidae by West (1976). The remaining four families offer a rich potential for detailed stratigraphical and morphological study — the radiation of each of these is poorly understood at present and much remains to be learned about their evolution. Such a broad review is, however, beyond the scope of this paper. My purpose here is to record several new and relatively rare forms that have been discovered in recent years.

Abbreviations used herein are as follows: AMNH, American Museum of Natural History (New York); FMNH, Field Museum of Natural History (Chicago); PU, Department of Geological and Geophysical Sciences, Princeton University (Princeton, New Jersey); UM, University of Michigan Museum of Paleontology (Ann Arbor); USNM, National Museum of Natural History (Washington).

SYSTEMATIC PALEONTOLOGY

Order CONDYLARTHRA

Family *Mesonychidae**Goniacodon levisanus* (Cope, 1883)

Text-fig. 1A, B

Type.— AMNH 3217, a right mandible with P_4M_{1-2} , from the Torrejonian of the San Juan Basin, New Mexico.

Discussion.— *Goniacodon levisanus* is the only species of the genus recognized by Matthew (1897, 1937). The species is reasonably common in middle Paleocene (Torrejonian) collections from the San Juan Basin, but it is unknown in the large collections of similar age from the Crazy Mountain Field, Montana. The only record of the genus outside of the San Juan Basin is Gazin's (1941) queried reference of an isolated upper molar from the Dragon fauna of Utah to *Goniacodon levisanus*.

A mandible in the Princeton collection from Rock Bench Quarry in the Big Horn Basin, Wyoming, is indistinguishable from specimens of *Goniacodon levisanus* collected in New Mexico. The fauna from the Rock Bench Quarry indicates a late Torrejonian age (Jepsen, 1930; Gingerich, 1976), hence the new find is at least broadly contemporaneous with other specimens of this species from New Mexico. This specimen extends the known range of *Goniacodon* to northwestern Wyoming.

The new specimen, PU 17497, is a left mandible with M_{2-3} preserved, and alveoli for P_4 and M_1 (text-fig. 1A, B). The mandibular ramus is very deep, measuring 20 mm in depth below M_2 . Measurements of the preserved molars are : M_2 length = 7.6 mm, width = 5.6 mm; M_3 length = 5.6 mm, width = 3.9 mm. The size of the teeth and mandible, relatively high trigonid on M_2 , and the relatively small M_3 compared to M_2 in this specimen are characteristic of *Goniacodon levisanus*. Direct comparison with specimens in the USNM and AMNH leaves little question that PU 17497 is conspecific with specimens of *G. levisanus* from New Mexico.

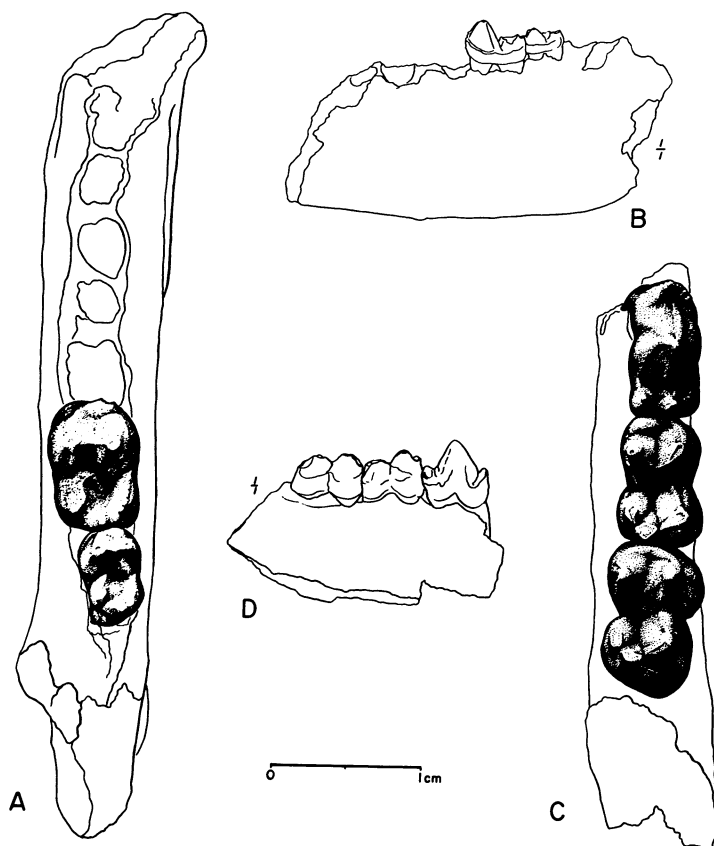
Family *Arctocyoniidae**Stelocyon*, new genus

Type species.— *Stelocyon arctylos*, new species.

Included species.— Type species only.

Diagnosis.— Differs markedly from *Colpoclaenus* and other Arctocyoniidae in having much narrower, higher-crowned lower molars. Resembles some triisodontine Mesonychidae (*Triisodon*, *Eoconodon*) but differs from them in the structure of the molar trigonids, especially on M_2 (see below).

Discussion.— *Stelocyon* resembles the mesonychids *Triisodon* and *Eoconodon* in having relatively narrow cheek teeth, with a very deep mandibular ramus. The structure of P_4 also suggests a possible relationship to triisodontine mesonychids. On the other hand, the form of the molar trigonids, especially on M_2 , is much more similar to that found in arctocyoniids. P_4 in *Stelocyon* is almost identical to P_3 and P_4 in *Claenodon montanensis* in size, in the position of the apical and accessory cusps, and in the form of the ridge of enamel running down the lingual side of the apical cusp. The molar trigonids of *Stelocyon* also resemble very closely the trigonids of similar-sized arctocyoniids, in particular those of *Colpoclaenus* (Patterson and McGrew, 1962). A distinct protoconid, paraconid, and metaconid are present on M_1 , with crests connecting the protoconid to the other two cusps. The paraconid on M_1 is smaller than the metaconid, but still well forward and distinct from it.



TEXT-FIG. 1 — Torrejonian condylarths from the Big Horn Basin of Wyoming and southern Montana. A and B, left mandible of *Goniacodon levisanus*, PU 17497, with M_{2-3} in occlusal and lateral view. C and D, right mandible of *Stelocyon arctylos*, PU 17929 (type), with P_4M_{1-2} in occlusal and lateral view. Shaded occlusal views twice natural size (see scale). Outline drawings of lateral views are natural size.

The trigonid structure of M_2 is similar to that of M_1 , except that the paraconid is much smaller and joined to the metaconid. The rather bulbous protoconid and metaconid almost join in the center of the trigonid, giving the trigonid of *Stelocyon* a distinct resemblance to the "folded" trigonid of *Colpoclaenus*. For this reason *Stelocyon* almost certainly belongs in the Arctocyoniidae. The high-crowned, narrow molars of *Stelocyon* are, however, very different from those found in other arctocyoniids, and there is little question that it represents a distinct genus. *Stelocyon* is possibly related to the slightly later *Colpoclaenus keeferi*, but certainly differed from it in adaptation, and it clearly represents a very distinct evolutionary lineage.

Etymology.— *Stele* (Gr.), a column or pillar, and *cyon*, dog, in allusion to the pillar-like molars of this small and rather dog-like carnivorous mammal. The suffix parallels that in *Arctocyon*.

Stelocyon arctylos, new species

Text-fig. 1C, D

Type.— PU 17929, a right mandible with P_4M_{1-2} and associated left mandible with M_{1-2} .

Type locality.— Five miles southeast of Belfry, Montana, sometimes known as the "Simons' 1955 locality," in Section 29, T8S, R23E, Carbon County, Montana. This locality was revisited in 1977. It is in greenish sandy shale beds that resemble the Lebo Member of the Fort Union Formation, and have been so correlated by Rice (1976). The locality, part of which is in the adjacent SW $\frac{1}{4}$ of Section 28, is late Torrejonian in age (Gingerich, 1976, p. 19).

Age and Distribution.— Torrejonian *Stelocyon arctylos* is presently known only from the type locality in south-central Montana.

Diagnosis.— As for the genus, see above.

Etymology.— *arctylos* (Gr.), cub; named for the locality where the type was found, on Cub Creek.

Description.— The type and only specimen consists of right and left mandibular rami of a single individual. The right ramus, with P_4M_{1-2} , is better preserved than the left ramus with M_{1-2} . The left mandibular ramus has undergone some shearing deformation which has distorted the shape of the molars, however the left ramus is complete to the ventral border, having a depth of 15.6 mm measured below M_2 . The teeth of the right side have several cracks in their enamel surfaces due to compaction, but have not been distorted significantly (text-fig. 1C, D).

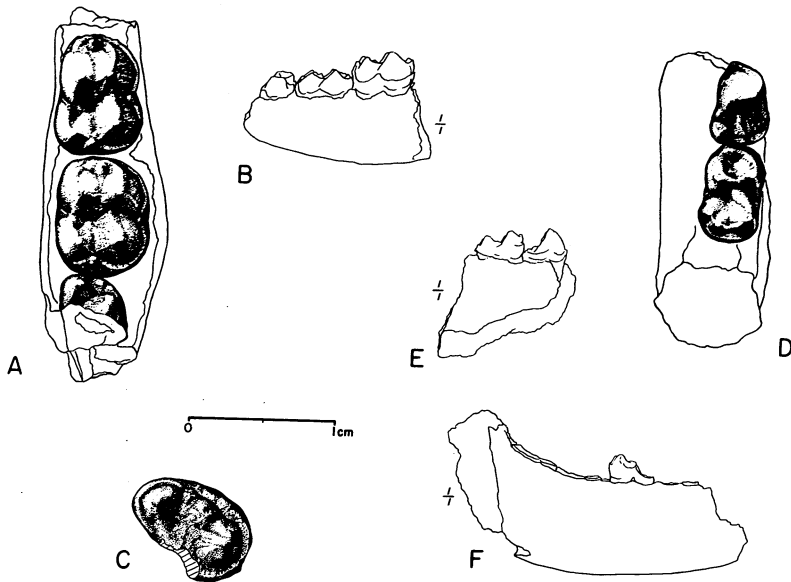
The preserved cheek teeth are all relatively long and narrow. P_4 has a single large pointed apical cusp, the protoconid, with an accessory paraconid at the base of the crown in front of it. A crest of enamel connects these two cusps. There is no trace of a metaconid, but a second enamel crest runs down the lingual side of the protoconid to near the base of the crown, where it turns posteriorly and joins the base of the small entoconid. A third crest runs posteriorly from the protoconid to join a distinct hypoconid on the heel of the tooth. The talonid itself is narrow and slightly basined.

The first molar, M_1 , has three trigonid cusps, with the protoconid and metaconid being subequal. A distinct but smaller paraconid is present. The protocristid curves posteriorly before joining the metaconid, and the paracristid curves forward, bending sharply to join the paraconid. The talonid is slightly wider than the trigonid, and a distinct hypoconid, hypoconulid, and entoconid are present, the latter two cusps being separated by a small notch. M_2 is very similarly constructed, except that the paraconid is reduced to a small cusp on the front of the metaconid, and the paracristid thus curves back to join the front of the metaconid. This gives the trigonid of M_2 a form resembling that of *Colpoclaenus* (Patterson and McGrew, 1962). Both molars are very high-crowned, with the talonid almost as high as the trigonid. Unworn enamel surfaces on the teeth are very slightly crenulated.

Length (L) and width (W) measurements of the teeth in the holotype of *Stelocyon arctylos*, PU 17929, are as follows (in mm):

	L	W
P_4	8.9	4.3
M_1	7.5	5.4
M_2	8.0	6.0

Typodigm.— Type specimen only.



TEXT-FIG. 2 – Clarkforkian condylarths from western Wyoming and western Colorado. A and B, right mandible of *Thryptacodon pseudarctos*, UM 68355, with M_{1-2} in occlusal and lateral view. C, isolated right M^3 of same specimen of *T. pseudarctos*, UM 68355, in occlusal view. D and E, right mandible of *Mimotricentes ischyrys*, FMNH 15016 (type), with P_4M_1 in occlusal and lateral view. F, right mandible of *M. ischyrys*, FMNH 15556, with broken M_1 in lateral view. Shaded occlusal views twice natural size (see scale). Outline drawings of lateral views are natural size.

Thryptacodon pseudarctos Simpson, 1928

Text-fig. 2A, B, C

Type.— AMNH 22176, a right M^2 (or possibly M^1), from the Bear Creek fauna in southern Montana (actually in the northern part of the Big Horn Basin, *s.l.*).

Discussion.— Simpson (1928) described the species *Thryptacodon pseudarctos* from Bear Creek, Montana, based on an isolated upper molar. At the time, he regarded the Bear Creek fauna as either Torrejonian, Tiffanian, or Clarkforkian in age. Subsequent study of this fauna by Van Valen and Sloan (1966) led them to suggest that it is Clarkforkian in age, a suggestion further substantiated by studies on Carpolestidae (Rose, 1975) and Plesiadapidae (Gingerich, 1976).

The first two species of *Thryptacodon* were described by Matthew (1915) from the early Wasatchian of the Big Horn Basin. He described *Thryptacodon antiquus* and *T. olseni*. The type species of the genus, *T. antiquus*, was based on a specimen collected 5 miles southeast of the mouth of Pat O'Hara Creek in the Clark's Fork drainage; this area yields *Pelycodus mckennai*, and is in "lower Gray Bull" beds. The type specimen of *T. olseni* was collected "a few miles east of St. Joe" in the central Big Horn Basin; this area yields *Pelycodus trigonodus*, and is in "upper Gray Bull" beds. Hence both of Matthew's species are somewhat younger in age than Simpson's *T. pseudarctos*.

Simpson (1935) described another new species, *Thryptacodon australis*, from the late Tiffanian Mason Pocket locality. He also identified all of the Clarkforkian *Thryptacodon* from the Clark's Fork drainage as *T. antiquus* (without mentioning the Bear Creek species *T. pseudarctos*; see Simpson, 1937b). Subsequently, Kelley and Wood (1954) described the small *Thryptacodon loisi* from

Lysite beds of the Wind River Basin. Thus a total of five species of *Thryptacodon* have been described from late Tiffanian, Clarkforkian, and Wasatchian sediments.

The purpose of this extended discussion is to call attention to a complex but potentially very interesting problem. Van Valen and Sloan (1966, p. 273) synonymized *Thryptacodon pseudarctos* with *T. antiquus*, and *T. olseni* has never been very clearly distinguished from *T. antiquus*. Thus there could possibly be only a single lineage of *Thryptacodon* in western North America in the late Paleocene and early Eocene. On the other hand, one *Thryptacodon* specimen described here, UM 68355 (text-fig. 2A, B, C), seems too large to belong to the lineage of smaller specimens comprising *T. australis*, *T. antiquus*, and *T. loisi*.

UM 68355 was collected in 1977 from Buckman Hollow in west-central Wyoming, and it is the first record of *Thryptacodon* from this locality (see Gazin, 1956b, for a discussion of the Buckman Hollow fauna). The new specimen, a right mandible with unworn M_{1-2} and isolated M^3 , has relatively broad lower molars with bulbous cusps and crenulated enamel. In these characteristics it compares well with the holotype of *T. pseudarctos*, although the latter is an upper molar. Measurements of the two lower molars of UM 68355 are: M_1 length = 7.4 mm, width = 5.9 mm; M_2 length = 7.1 mm, width = 6.2 mm.

It is not clear at present, (1) what the relationships of the large Clarkforkian specimens of *Thryptacodon* (e.g., UM 68355, and others) are to other smaller late Paleocene and early Eocene representatives of the genus, (2) whether these specimens represent a distinct species and, if so, if the correct name for this species is really *T. pseudarctos*, (3) whether the larger specimens even belong in the genus *Thryptacodon*. Answers to these questions can only come from very detailed biometrical and stratigraphical studies of all of the known specimens, especially those from Bear Creek and the Clark's Fork Basin. Based on a preliminary study of UM 68355, 68256, PU 19026, and other specimens in the UM and PU collections, I suspect that the large Clarkforkian *Thryptacodon* represents a distinct species (and possibly genus) distinguished from the partly contemporaneous *T. antiquus* by its larger size, metaconid on P_4 , larger pericones on the upper molars, and less labiolingually compressed canine teeth. *Thryptacodon pseudarctos* appears to be the only name available for the large Clarkforkian *Thryptacodon* and it is used here provisionally, pending a detailed systematic revision of the genus. *Thryptacodon pseudarctos* also appears to be remarkably similar to the European *Arctocyonides arenae* described by Russell (1964) from Berru.

Mimotricentes ischyros, new species

Text-fig. 2D, E, F

Type.— FMNH 15016, a right mandible with P_4 and M_1 .

Type locality.— Hell's Half Acre locality, Plateau Valley, Mesa County, Colorado. FMNH 26112 is a mandible of *Plesiadapis dubius* from this locality, indicating a Clarkforkian age (Gingerich, 1976).

Age and Distribution.— Clarkforkian. This species is known only from two Plateau Valley localities at present.

Diagnosis.— Approximately the same size as *Mimotricentes latidens* and *M. fremontensis*, but differs from them in having relatively narrower molars, longer M_3 , and a more complex, wedge-shaped P_4 with a distinct metaconid forming a high, sharp protocristid.

Etymology.— *ischyros* (Gr.), obstinate, stubborn — in reference to this species' documentation of survival of the genus *Mimotricentes* into the Clarkforkian.

Description.— The type specimen of *Mimotricentes ischyros* is a right mandibular fragment with P_4 and M_1 intact (text-fig. 2D, E). P_4 is a wedge-shaped tooth with a broad base and a high proto-

TABLE 1 — Measurements of the teeth of *Mimotricentes ischyurus* compared with those of *M. latidens* (Gidley), *M. fremontensis* (Gazin), and an unnamed species in the Princeton collection. Locality where each specimen was found is also listed. All measurements in mm. Data for *M. latidens* and *M. fremontensis* from Simpson (1937a) and Gazin (1956a).

		<i>M. latidens</i> USNM 9269 (type) Gidley Quarry	<i>M. fremontensis</i> USNM 20583 (type) Saddle Locality	<i>M. sp.</i> PU 19576 Coon Creek	<i>M. ischyurus</i> FMNH 15016 (type) Plateau Valley	FMNH 15556 Plateau Valley
P ₂	L	3.6	—	4.9	—	—
	W	2.8	—	3.7	—	—
P ₃	L	4.6	—	5.5	—	—
	W	3.3	—	4.1	—	—
P ₄	L	5.4	—	5.4	5.5	—
	W	4.0	—	4.6	3.9	—
M ₁	L	5.5	6.2	6.7	6.0	5.9*
	W	4.7	4.5	5.2	4.0	4.0
M ₂	L	6.0	6.4	7.5	—	6.5*
	W	5.5	4.9	6.3	—	—
M ₃	L	6.1	6.6	8.5	—	8.2*
	W	4.7	4.3	5.5	—	—

* estimated

conid cusp. A long paracristid curves forward and down from the protoconid to the anterolingual corner of the base of the crown. A small but distinct metaconid is present directly lingual to the protoconid. These two cusps are connected by a high protocristid, sloping lingually at an angle of about 45 degrees. A very weak cristid obliqua is present running to the hypoconid, and the talonid has a slightly basined shape.

The first lower molar, M₁, has a distinct protoconid, paraconid, and metaconid, with the paraconid centered on the anterior edge of the trigonid, reminiscent of its position in *Thryptacodon*. The trigonid is raised somewhat above the talonid, and the cristid obliqua on M₁ runs up the back of the trigonid toward the metaconid. A distinct hypoconid, hypoconulid, and entoconid are present, with the latter two being paired on the posterolingual corner of the talonid. Measurements of the holotype are given in Table 1.

A second specimen of *Mimotricentes ischyurus* is also known from Plateau Valley. FMNH 15556 is a right mandibular ramus with a broken M₁ and the roots of P₄ and M₂₋₃ (text-fig. 2F). The M₁ in this specimen is very nearly the same size and shape as M₁ in the holotype, and it has the twinned entoconid-hypoconulid seen in the type. The preserved roots of P₄ indicate a relatively short and broad tooth, but none of the crown is preserved. The length of M₂ and M₃ can be estimated from their preserved roots and alveoli. M₃ in *M. ischyurus* was clearly a much longer and relatively narrower tooth than in *M. latidens* or *M. fremontensis*. In this respect it is similar to a specimen, PU 19579,

representing a new and undescribed late Tiffanian species of *Mimotricentes*. The mandibular ramus is relatively thick but not particularly deep in FMNH 15556, measuring 12.4 mm in depth under M_1 . Other measurements of this specimen are given in Table 1. It appears from FMNH 15556 that the mandibular symphysis began as far back as P_4 , indicating a much shorter mandible than in other species of the genus.

Discussion.— Description of *M. ischyurus* extends the range of *Mimotricentes* into the Clarkforkian for the first time. If I have correctly interpreted the phylogeny of this genus, there are four or five species that form a single lineage. *Mimotricentes subtrigonus* (Cope, 1881) and/or *M. latidens* in the Torrejonian gave rise to early Tiffanian *M. fremontensis*, which in turn gave rise to a larger middle and late Tiffanian species (undescribed). The latter is represented by a very complete specimen collected by Russell Lambert from Coon Creek in the Big Horn Basin, PU 19579, with both upper and lower jaws. Also belonging to this undescribed species are two mandibles from Croc Tooth and Divide Quarries in the Big Horn Basin, PU 14970 and 17758, respectively, as well as UM 68376 and USNM 214539, isolated teeth from a mid-Tiffanian locality (Chappo-17) near LaBarge, Wyoming.

Mimotricentes is a relatively rare element in Torrejonian-Clarkforkian faunas, being represented by a single specimen in most localities. Thus it is difficult to gain a real understanding of possible variation in premolar numbers, relative size of M_3 , and so forth. It is clear, however, that there was also a separate lineage of small forms related to *Mimotricentes*. These, represented by specimens like PU 13943 from Princeton Quarry, were formerly placed in *Tricentes*, but that name properly belongs to the group usually called "*Metachriacus*" (Van Valen, 1971). A detailed biostratigraphical study will be required to clarify the phylogenetic relationships of the small forms to the larger *Mimotricentes* lineage.

ACKNOWLEDGMENTS

I thank Drs. D. Baird, Princeton University, and W. D. Turnbull, Field Museum of Natural History, for the loan of specimens described here. In addition, Drs. M. C. McKenna, American Museum of Natural History and R. E. Emry, National Museum of Natural History, permitted me to study related specimens in their care. Drs. L. Van Valen, R. T. Bakker, and Mr. E. Manning examined several of the specimens described here, and their comments were helpful in classifying *Stelocyon*. Mr. David Krause read and improved the manuscript. Karen Payne drew the figures, Karna Steelquist assisted with photography, and Mrs. Gladys Newton typed the manuscript. This research was supported in part by a Faculty Research Grant from the Rackham School of Graduate Studies, University of Michigan; and in part by a grant from the National Science Foundation (DEB77-13465).

LITERATURE CITED

- COPE, E. D. 1881. On some Mammalia of the lowest Eocene beds of New Mexico. *Paleont. Bull.*, 33: 1-12.
 ——— 1883. First addition to the fauna of the Puerco Eocene. *Proc. Amer. Phil. Soc.*, 20: 545-563.
 GAZIN, C. L. 1941. The mammalian faunas of the Paleocene of central Utah, with notes on the geology. *Proc. U. S. Nat. Mus.*, 91: 1-53.
 ——— 1956a. Paleocene mammalian faunas of the Bison Basin in south-central Wyoming. *Smithsonian Misc. Coll.*, 131(6): 1-57.
 ——— 1956b. The upper Paleocene Mammalia from the Almy Formation in western Wyoming. *Smithsonian Misc. Coll.*, 131(7): 1-18.
 ——— 1965. A study of the early Tertiary condylarthran mammal *Meniscotherium*. *Smithsonian Misc. Coll.*, 149(2): 1-98.

- GINGERICH, P. D. 1976. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). Univ. Michigan Pap. Paleont., 15: 1-140.
- JEPSEN, G. L. 1930. Stratigraphy and paleontology of the Paleocene of northeastern Park County, Wyoming. Proc. Amer. Phil. Soc., 69: 463-582.
- KELLEY, D. R. and A. E. WOOD. 1954. The Eocene mammals from the Lysite member, Wind River Formation of Wyoming. Jour. Paleont., 28: 337-366.
- MATTHEW, W. D. 1897. A revision of the Puerco fauna. Bull. Amer. Mus. Nat. Hist., 9: 259-323.
- . 1915. A revision of the lower Eocene Wasatch and Wind River faunas. Part I. — Ferae (Carnivora). Bull. Amer. Mus. Nat. Hist., 34: 4-103.
- . 1937. Paleocene faunas of the San Juan Basin, New Mexico. Trans. Amer. Phil. Soc., 30: 1-510.
- PATTERSON, B. and P. O. MCGREW. 1962. A new arctocyonid from the Paleocene of Wyoming. Breviora, 174: 1-10.
- RICE, D. D. 1976. Correlation chart of Cretaceous and Paleocene rocks of the northern Great Plains. U. S. Geological Survey, Oil and Gas Investig. Charts, OC-70: 1 sheet.
- RICH, T. H. V. 1971. Deltatheridia, Carnivora, and Condylarthra (Mammalia) of the early Eocene, Paris Basin, France. Univ. Calif. Publ. Geol. Sci., 88: 1-72.
- ROSE, K. D. 1975. The Carpolestidae, early Tertiary primates from North America. Bull. Mus. Comp. Zool., 147: 1-74.
- RUSSELL, D. E. 1964. Les mammifères paléocènes d'Europe. Mém. Mus. Nat. d'Hist. Natur., Ser. C, 13: 1-324.
- SIMPSON, G. G. 1928. A new mammalian fauna from the Fort Union of southern Montana. Amer. Mus. Novitates, 297: 1-15.
- . 1935. The Tiffany fauna, Upper Paleocene. III. Primates, Carnivora, Condylarthra, and Amblypoda. Amer. Mus. Novitates, 817: 1-28.
- . 1937a. The Fort Union of the Crazy Mountain Field, Montana and its mammalian faunas. Bull. U. S. Nat. Mus., 169: 1-287.
- . 1937b. Notes on the Clark Fork, Upper Paleocene fauna. Amer. Mus. Novitates, 954: 1-24.
- SLOAN, R. E. 1970. Cretaceous and Paleocene terrestrial communities of western North America. Proc. N. Amer. Paleont. Conv., 1: 427-453.
- VAN VALEN, L. 1971. Toward the origin of artiodactyls. Evolution, 25: 523-529.
- and R. E. SLOAN. 1966. The extinction of the multituberculates. Syst. Zool., 15: 261-278.
- WEST, R. M. 1976. The North American Phenacodontidae (Mammalia, Condylarthra). Milwaukee Publ. Mus. Contrib. Biol. Geol., 6: 1-78.

