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# SYSTEMATICS OF EARLY EOCENE MIACIDAE (MAMMALIA, CARNIVORA) IN THE CLARK'S FORK BASIN, WYOMING

By

Philip D. Gingerich

*Abstract.*—Four genera and six species of Miacidae are known from faunas representing the Clarkforkian through middle Wasatchian land-mammal ages in the Clark's Fork Basin, Wyoming. These are, in order of appearance, *Uintacyon rudis*, *Miacis winkleri* (n. sp.), *Miacis deutschii* (n. sp.), *Miacis exiguus*, *Vassacyon promicrodon*, and *Vulpavus* cf. *australis*. In addition, one new miacid, *Miacis petilus* (n. sp.), is described from middle Wasatchian strata of the central Bighorn Basin. It includes many middle to late Wasatchian specimens formerly referred to *M. exiguus*. The diversity of early Miacidae (excluding Viverravinae, classified as a distinct family) increased from a single lineage in the Clarkforkian to two lineages through the early Wasatchian, and three lineages in the middle Wasatchian. *Uintacyon* appears to be a Clarkforkian immigrant, possibly from Europe or eastern Asia. The first records of *Miacis* and *Vassacyon* coincide with intervals of significant faunal turnover (Clarkforkian-Wasatchian boundary and Schankler's "Biohorizon A", respectively), and these genera may be immigrants as well. Early representatives of *Vulpavus* are so similar to *Miacis* that they are easily confused, and it appears that *Vulpavus* originated from *Miacis exiguus* or a very similar structural ancestor in the early to middle Wasatchian.

## INTRODUCTION

Mammals of the order Carnivora are distinctive in having a single enlarged carnassial tooth in each jaw. In the maxilla this carnassial is  $P^4$ , and in the dentary it is  $M_1$ . Within Carnivora, Eocene genera of the family Miacidae are distinguished from Paleocene and Eocene Viverravidae by retention of three upper or lower molars in each jaw quadrant. Viverravids consistently lack upper and lower third molars. Viverravidae first appear in the North American stratigraphic record in the early Paleocene, and viverravids remain a common element in early and middle Eocene faunas as well. The earliest record of Miacidae is in the middle Clarkforkian Land-Mammal Age, which is generally considered to represent earliest Eocene time in North America (Rose, 1980). Miacids continued to diversify throughout the early and middle Eocene, gradually assuming dominance over viverravids in North American faunas.

Miacidae and Viverravidae have usually been considered to be closely related, and they are conventionally ranked as subfamilies in a single family Miacidae. Flynn and Galiano (1982) employed cladistic analysis to justify classification of viverravines and miacines in different suborders of Carnivora. The distinct radiations of these two groups documented in the fossil record and the lack of morphological intermediates between them suggest, in agreement with Flynn and Galiano, that each should be raised to full family rank. However, Viverravidae and

Miacidae are retained in a single superfamily Miacoidea that is probably broadly ancestral to all later superfamilies of Carnivora. Evidence available in the fossil record is insufficient to justify linking aeluroid families to Viverravidae and arctoid superfamilies to Miacidae, as implied by Flynn and Galiano (1982). Viverravidae probably represent an archaic radiation of Carnivora that acquired derived "aeluroid" characteristics (e.g., loss of third molars) independently of later aeluroid carnivorans. There is no evidence of evolutionary continuity between Viverravidae, which radiated in the Paleocene and early Eocene, and aeluroid families of carnivorans, which did not begin to radiate until the late Eocene.

In this paper the initial evolutionary diversification of North American Miacidae is outlined, based on a sequence of closely-spaced Clarkforkian and early Wasatchian faunas in the Clark's Fork Basin of northwestern Wyoming. Dental variation in extant carnivores is used as a guide for interpreting distributions of tooth size in fossils. The species-level systematics of early Eocene Miacidae are reviewed. Two new species of early Wasatchian *Miacis* are described from the Clark's Fork Basin, and one additional middle Wasatchian species of *Miacis* is named from the central Bighorn Basin. The morphology of the astragalus in *Uintacyon* is compared to that of *Miacis*. Finally, the radiation of North American early Eocene Miacidae documented in the Clark's Fork Basin is illustrated graphically, and brief comments are added on the possible origin and relationships of the family.

The stratigraphic setting and succession of Clark's Fork Basin faunas are discussed in Gingerich et al. (1980), Rose (1981), and Gingerich (1982, 1983). Zones of the Wasatchian Land-Mammal Age employed here are those developed by Granger (1914) and Schankler (1980), as reviewed in Gingerich (1983). "Sandcouleean" ( $Wa_1$ - $Wa_2$ ) is equivalent to early Wasatchian, "Graybullian" ( $Wa_3$ - $Wa_5$ ) is equivalent to middle Wasatchian, and "Lysitean" ( $Wa_6$ ) and "Lostcabinian" ( $Wa_7$ ) are equivalent to late Wasatchian. Dental and other anatomical nomenclature employed in this paper follows MacIntyre (1966) and Van Valen (1966). Measurements taken on upper and lower teeth are shown diagrammatically in Figure 1. Fossil localities prefaced by *SC* are University of Michigan localities in the Sand Coulee area of the Clark's Fork Basin. Localities prefaced by *YM* are Yale-Michigan localities in the central Bighorn Basin. The following museum acronyms are used in the text and figures: AMNH (American Museum of Natural History, New York), IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Peking), UCMP (University of California Museum of Paleontology, Berkeley), UM (University of Michigan Museum of Paleontology, Ann Arbor), and UW (University of Wyoming Museum of Geology, Laramie).

## DENTAL VARIATION AND SEXUAL DIMORPHISM

Dental variation in carnivorous mammals is not well studied. The only quantitative analysis of dental variation in a large homogeneous sample of a species with a well developed carnassial dentition is by Gingerich and Winkler (1979), who studied patterns of variation and correlation of tooth size in the extant red fox *Vulpes vulpes*. The principal conclusions of Gingerich and Winkler (1979) applicable to this study are that upper and lower first molars are the least variable cheek teeth in the dentition of carnivores (as they usually are in other mammals), and that the crown area of  $M_1$  has a total range of variation of about 0.35 units on a natural logarithmic scale. Coefficients of variation of tooth measurements in species of the Paleocene viverravid *Protictis* appear to be comparable to those in *Vulpes vulpes* (cf. MacIntyre, 1966).

The largest sample of a fossil species included in this study is the Clarkforkian and early Wasatchian sample of *Uintacyon rudis*. A total of 45 specimens of *U. rudis* are known to date

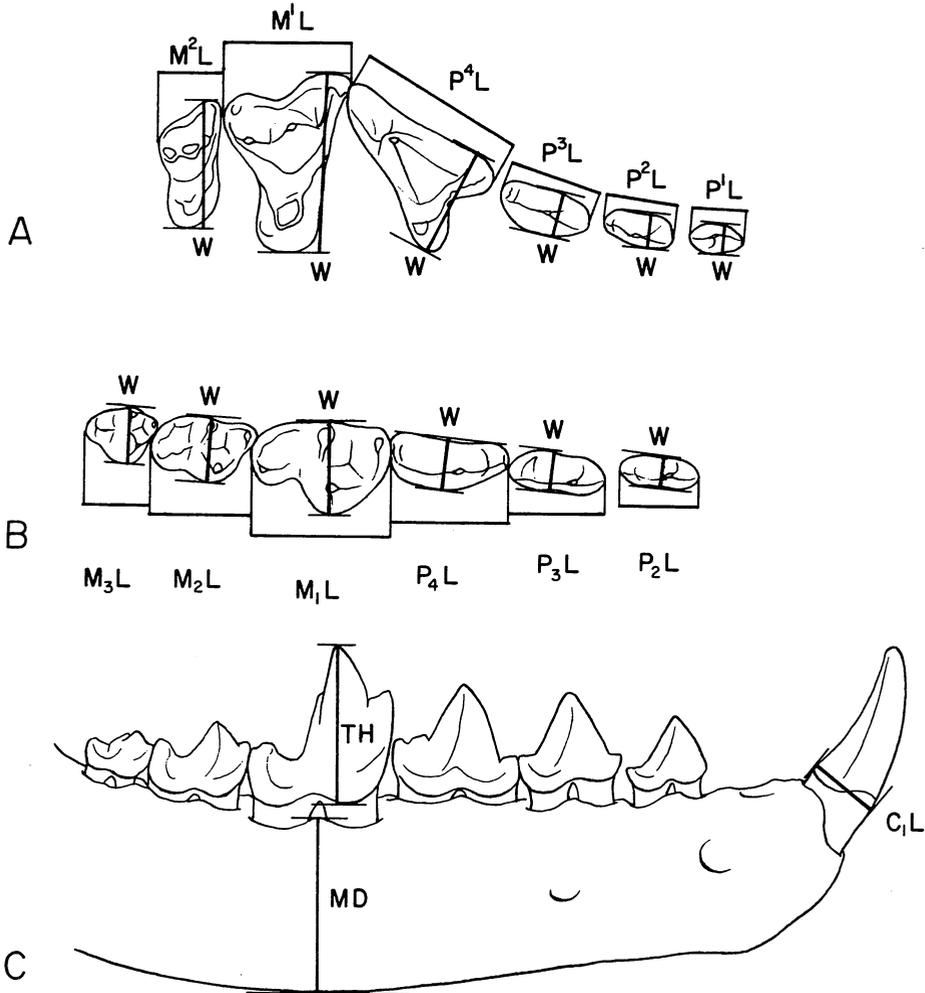


FIG. 1— Right maxillary and mandibular dentition of *Uintacyon rudis*, showing measurements used in this study. A, upper premolars and molars in occlusal view. B, lower premolars and molars in occlusal view. C, lower canine, premolars, and molars in lateral view. L = length, W = width, TH = trigonid height, and MD = mandibular depth. C<sub>1W</sub> was measured perpendicular to C<sub>1L</sub> at the same level on the tooth.

from the Clark's Fork Basin. This sample, spanning some two million years of geological time, is significantly more variable in most measurements (see Table 1) than the sample of extant *Vulpes vulpes* studied by Gingerich and Winkler (1979). *Uintacyon rudis* changed very little in size during this interval, and its increased variability clearly reflects more than a secular trend in body size averaged over time. Bown (1979, p.96) and Rose (1981, p.102) indicated that *Uintacyon* might be sexually dimorphic, and results presented here corroborate this suggestion.

Extant *Vulpes vulpes* exhibits very weak sexual dimorphism in both the cranium and dentition (including canines), and one might expect a dimorphic species to be more variable (research in progress on dental variation in extant *Martes* and *Mustela* confirms this; Bickart and Gingerich, in preparation). Canine dimensions and mandibular depth are usually the most strongly affected by sexual dimorphism. *Uintacyon rudis* is most variable in canine length, canine width, P<sub>3</sub>

length, and mandibular depth, a pattern consistent with this interpretation. The magnitude of canine and mandibular dimorphism in *Uintacyon rudis* is illustrated graphically in Figure 2.

The total range of variation of  $M_1$  crown area in twenty specimens of *U. rudis* preserving this tooth is 0.40 units on a natural logarithmic scale, which is only slightly greater than the range reported for weakly dimorphic *Vulpes vulpes* and it is within the range of variation expected for most mammalian species. Hence, all earliest Eocene specimens of *Uintacyon* are regarded as representing a single dimorphic species. *Miacis exiguus* (Table 4) is represented by one third as many specimens as *Uintacyon rudis*, and other species are represented by even fewer specimens. None of these species shows the high variability in tooth size or mandibular depth seen in *Uintacyon rudis*, suggesting that *Miacis*, *Vassacyon*, and *Vulpavus* were probably not as markedly dimorphic as *Uintacyon*.

### SYSTEMATIC PALEONTOLOGY

Species of Clarkforkian and early to middle Wasatchian Miacidae are discussed, by genus, in the order in which they appear stratigraphically in the Clark's Fork Basin.

Order CARNIVORA Bowdich, 1821  
 Family MIACIDAE Cope, 1880  
*Uintacyon* Leidy, 1872

*Uintacyon* Leidy, 1872, p. 277.

*Type species.*—*Uintacyon edax* Leidy, 1872.

*Included species.*—*Uintacyon rudis*, Matthew [middle Clarkforkian-early Wasatchian], *U. massetericus* (Cope) [middle-late Wasatchian], *U. asodes* Gazin [late Wasatchian], *U. edax* Leidy [Bridgerian], *U. vorax* Leidy [Bridgerian], *U. jugulans* Matthew [late Bridgerian], and *U. major* Matthew [Bridgerian].

*Diagnosis.*—"Dental formula 3.1.4.3/3.1.4.3. Premolars reduced, without accessory cusps, the second and third of equal size. Lower molars with trenchant heels, upper molars without hypocones. Protocone of  $P^4$  of moderate size. Upper molars moderately extended antero-externally with distinct parastyle crest; paraconule strong, metaconule weak, protocone subcrescentic with anterior and posterior horns equally developed. Paracone higher than metacone. Third upper molar small. Third lower molar small, one-rooted, flat-crowned. Lower jaw short, with robust and rather deep symphyseal region, somewhat reduced in depth and thickness under the premolars." (Quoted from Matthew, 1909b, p. 273). As one might expect, the oldest and most primitive species of the genus, *U. rudis*, differs from later species of *Uintacyon* in ways that make it more generalized, resembling early species of other contemporary genera:  $P_3$  is somewhat larger than  $P_2$ , talonids on lower molars are slightly basined,  $M_3$  retains distinct cusps, and  $M_3$  is occasionally double-rooted.

*Age and Distribution.*—*Uintacyon* is known from the Clarkforkian through Bridgerian land-mammal ages (early through middle Eocene) in North America, and it has also been reported (questionably) from the early Eocene of Europe (Rich, 1971).

*Uintacyon rudis* Matthew, 1915

Figs. 2, 3

*Uintacyon massetericus rudis* Matthew, 1915, p. 31, fig. 26.*Uintacyon massetericus*, Bown, 1979, p. 95, fig. 54c.*Uintacyon massetericus* (in part), Schankler, 1980, p. 105.*Uintacyon rudis*, Rose, 1981, p. 102, fig. 51, 52.

*Holotype*.—AMNH 16855, right dentary with  $M_{1-2}$  collected by W. Stein on September 2, 1913.

*Type locality*.—"Head of Big Sand Coulee" in the Clark's Fork Basin, Wyoming. Matthew (1915, p. 31) attributes a Sandcouleean (early Wasatchian) age to the holotype, but other fossils collected by Stein on the 3rd and 4th of September, 1913, from the Willwood Formation at the head of Big Sand Coulee include the holotypes of *Arctostylops steini* and *Probathyopsis praecursor* (see field catalogue for 1913 in the archives of the American Museum of Natural History). *A. steini* and *P. praecursor* have never been found in association with Wasatchian faunas. Most collecting levels at the head of Big Sand Coulee yield late Clarkforkian faunas, and the type specimen of *Uintacyon rudis* is almost certainly late Clarkforkian in age as well (Rose, 1981).

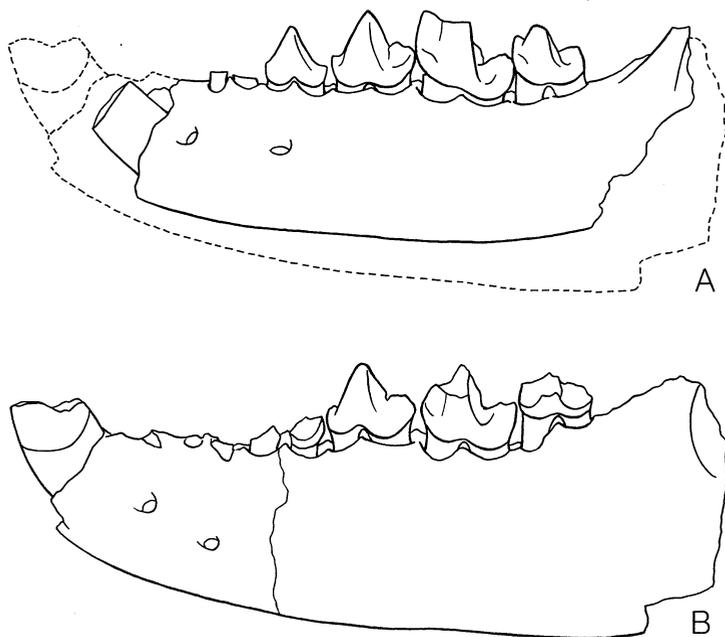


FIG. 2.— Sexual dimorphism in canine and mandibular morphology of *Uintacyon rudis*. A, left dentary of putative female (UM 80413) in lateral view. B, left dentary of putative male (composite of UM 64676 and 66349) in lateral view. Both drawn at the same scale. Outline of male dentary (dashed line) is superimposed over that of female, with teeth aligned to emphasize differences in canine size and mandibular depth. Enlarged 2x natural size.

*Age and Distribution.*—*Uintacyon rudis* is a common carnivore in early Eocene faunas of the middle-late Clarkforkian and early Wasatchian land-mammal ages in the Clark's Fork Basin. It is also represented in the early Wasatchian of the central Bighorn Basin (e.g., UM 63812) and the southern Bighorn Basin (Bown, 1979). An isolated  $M_3$  from the Powder River Basin described by Delson (1971, p. 343) as "Indeterminate genus and species" could represent *U. rudis*. If so, this is the only record of the species outside the Clark's Fork and Bighorn basins.

*Diagnosis.*—*Uintacyon rudis* differs from middle Wasatchian *U. massetericus* in being smaller, having relatively narrower lower molar talonids, and in having a relatively larger  $M_3$ . Talonids of *U. rudis* are slightly basined, whereas they are more trenchant and not at all basined in later *Uintacyon* (Rose, 1981).

*Description.*—A total of 45 specimens of *Uintacyon rudis* are known from the Clarkforkian and early Wasatchian of the Clark's Fork Basin. Upper premolars are preserved in UM 69385.  $P^{1-3}$  all have relatively small, simple crowns with no accessory cusps.  $P^4$  is a carnassial tooth constructed as in other miacids. The protocone and paracone are the largest cusps on  $M^1$ . The protocone is constricted anteroposteriorly, with small anterior and posterior lingual cingula at the base. There is no hypocone on the posterior lingual cingulum. There is a distinct paraconule but no metaconule on  $M^1$ . The metacone is much smaller than the paracone, and it is placed directly behind the paracone. These two cusps tend to be joined at the base, especially in Wasatchian *U. rudis*. There is a large parastyle. The metacrista and preprotocrista are the largest shearing crests.  $M^2$  is generally similar to  $M^1$  in form, although it is considerably smaller.  $M^3$  is not preserved in any of the available specimens and only one specimen (UM 64832) preserves any trace of an alveolus for  $M^3$ .

Part or all of the lower canine is preserved in five specimens. It is gracile in UM 68868, 69385, and 76846, and much more robust in UM 64676 and 76861. This marked difference in canine size, coupled with the high variability of other tooth measurements and mandibular depth, suggests that *Uintacyon rudis* was markedly dimorphic, and this dimorphism is plausibly attributed to sex differences (see previous section). Lower premolars are best preserved in UM 64677, 68868, 72196, and 80413. The crown of  $P_1$  is not preserved in any specimen, but its alveolus indicates that it was consistently single-rooted.  $P_2$  and  $P_3$  are double-rooted teeth with simple crowns. The only accessory cusp is a very small cuspid at the posterior margin of the crown. The crown of  $P_4$  is more complex, with distinct anterior and posterior accessory cuspids in addition to the large protoconid. There is no hypoconid or metaconid cusp on any of the premolars, and cingulids are also lacking. All of the premolars are closely spaced in the jaw.

Among the lower molars,  $M_1$  is the largest. It has a high and broad trigonid, the protoconid is the largest trigonid cusp, and the paraconid and metaconid are also prominent. The paraconid and metaconid are of equal height, but the metaconid is slightly more robust than the paraconid. The talonid of  $M_1$  is short and relatively narrow. It has a large hypoconid, a very small entoconid, and no hypoconulid. The presence of a small entoconid makes the talonid of *Uintacyon rudis* appear slightly more basined than in later species of *Uintacyon*, but it is much more trenchant than that of other early genera of Miacidae.  $M_2$  resembles  $M_1$ , but it is much smaller and lower crowned. The trigonid is not nearly so large relative to the talonid on  $M_2$  as it is on  $M_1$ .  $M_3$  is generally similar to  $M_2$ , but it is again smaller and lower crowned. There is a distinct talonid on  $M_2$  and  $M_3$ , and it is more trenchant and less basined than the talonid on  $M_1$ .  $M_3$  is double-rooted in the earliest specimen known (middle Clarkforkian UM 68868 from locality SC-188), but it is single-rooted in the remaining 17 specimens preserving roots or alveoli of  $M_3$  (about half of these appear to have had fused anterior and posterior roots).

Measurements (mm) of cheek teeth preserved in the holotype, AMNH 16855, are as follows:  $M_1$  L = 6.1, W = 4.2;  $M_2$  W = 3.2; mandibular depth below  $M_1$  = 11.0. Dental and mandibular measurements of Clarkforkian and early Wasatchian *Uintacyon rudis* are summarized in Table 1.

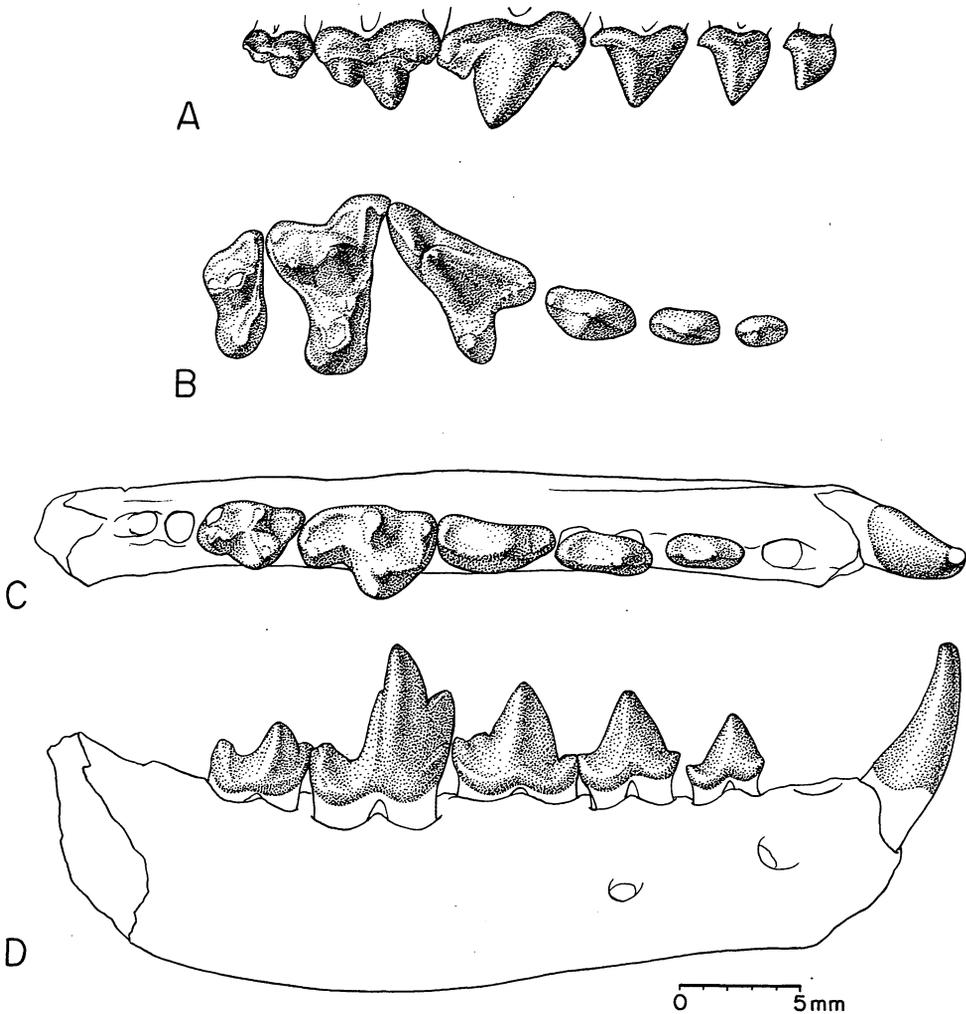


FIG. 3— Maxillary and mandibular dentition of middle Clarkforkian *Uintacyon rudis* Matthew (UM 68868) from Holly's Microsite, UM locality SC-188. Lower jaw is a composite based on left and right dentaries. P<sup>2-4</sup> restored from UM 69358 (SC-40, early Wasatchian). *A*, right maxilla with P<sup>1</sup>-M<sup>2</sup> in lateral view; *B*, same in occlusal view. *C*, right mandible with C<sub>1</sub>P<sub>2</sub>-M<sub>1-2</sub> in occlusal view; *D*, same in lateral view. Judging from differences illustrated in Figure 2, this specimen is a female. Enlarged 3x natural size.

*Referred specimens.*—Clarkforkian strata of the Clark's Fork Basin: UM 65066, 65234, 65473, 66298, 66918, 68868, 69314, 69872, 69896, 71482, 71582, 71583, 71584, 76861 and 76863. Wasatchian strata of the Clark's Fork Basin: UM 64599, 64676, 64677, 64832, 64853, 64967, 64990, 65340, 65573, 66349, 67070, 67072, 68487, 69385, 71267, 71287, 72118, 72196, 72852, 74108, 76495, 76571, 76846, 77513, 79029, 80179, 80413, 80496, 80527, and 80703. Wasatchian strata of the Foster Gulch area, northern Bighorn Basin: UM 63955, 75846, 75932, 77146, and 77216. Wasatchian strata of the central Bighorn Basin: UM 63812. Wasatchian strata of the Powder River Basin: questionably AMNH 56325 (Delson, 1971, p. 343, fig. 19).

TABLE 1 — Summary of measurements of upper and lower cheek teeth of *Uintacyon rudis* from the Willwood Formation of the Clark's Fork Basin, Wyoming. Specimens included here range from middle Clarkforkian to early Wasatchian in age (1280-1760 m levels in measured stratigraphic section). Measurements are defined in Figure 1.  $N$  = sample size,  $OR$  = observed range,  $\bar{x}$  = mean,  $S$  = standard deviation,  $V$  = coefficient of variation. All measurements in mm.

Tooth position		N	OR	$\bar{x}$	S	V
<i>Upper dentition</i>						
P <sup>2</sup>	L	1	3.3	-	-	-
	W	1	1.8	-	-	-
P <sup>3</sup>	L	1	4.6	-	-	-
	W	1	2.3	-	-	-
P <sup>4</sup>	L	5	6.8-7.3	7.02	0.19	2.7
	W	4	4.8-5.5	5.25	0.33	6.3
M <sup>1</sup>	L	8	4.6-5.6	5.14	0.40	7.7
	W	7	7.5-8.2	7.96	0.29	3.6
M <sup>2</sup>	L	4	3.0-3.4	3.20	0.23	7.2
	W	4	5.5-6.5	5.93	0.51	8.5
<i>Lower dentition</i>						
C <sub>1</sub>	L	5	3.3-5.2	4.28	0.74	17.3
	W	5	2.1-3.4	2.80	0.49	17.3
P <sub>1</sub>	L	-	-	-	-	-
	W	-	-	-	-	-
P <sub>2</sub>	L	4	3.1-4.0	3.40	0.41	12.0
	W	4	1.5-1.9	1.68	0.17	10.2
P <sub>3</sub>	L	8	3.6-5.9	4.34	0.74	16.9
	W	8	1.7-2.4	1.99	0.22	10.9
P <sub>4</sub>	L	15	5.0-6.4	5.38	0.39	7.2
	W	15	2.3-3.0	2.67	0.22	8.3
M <sub>1</sub>	L	21	5.4-6.3	5.79	0.31	5.3
	W	23	3.5-4.5	4.01	0.28	6.9
	TH	8	6.0-6.9	6.33	0.29	4.5
M <sub>2</sub>	L	23	3.6-5.3	4.30	0.39	9.0
	W	23	2.7-3.8	3.17	0.28	8.8
M <sub>3</sub>	L	4	2.6-3.1	2.90	0.22	7.4
	W	4	2.0-2.5	2.28	0.22	9.7
Mandibular depth		27	7.9-12.9	10.03	1.39	13.8

*Miacis* Cope, 1872

*Miacis* Cope, 1872, p. 2.

*Xinyuictis* Zheng, Tung, and Qi, 1975, p. 99.

*Oödetes* (in part), Bown, 1979, p. 97.

*Type species*.—*Miacis parvivorus* Cope, 1872.

*Included species*.—*Miacis winkleri* n. sp. [early Wasatchian], *M. deutschi* n. sp. [early Wasatchian], *M. exiguus* Matthew [early middle Wasatchian], *M. petilus* n. sp. [middle-late Wasatchian], *M. latidens* Matthew [late Wasatchian], *M. jepseni* Guthrie [late Wasatchian], *M. parvivorus* Cope [early Bridgerian], *M. sylvestris* (Marsh) [late Bridgerian], *M. hargeri* (Wortman) [late Bridgerian], *M. uintensis* Osborn [Uintan], *M. gracilis* Clark [Uintan], *M. hookwayi* Stock [Duchesnean], *M. tenuis* (Zheng, Tung, and Qi) [early Eocene, China], *M. invictis* Matthew and Granger [late Eocene, China and Mongolia], *M. lushiensis* Chow [late Eocene, China], *M. latouri* Quinet [early Eocene, Europe], and *M. exilis* (Filhol) [late Eocene, Europe].

*Diagnosis*.—Carnassial and tubercular dentition well differentiated, carnassials and premolars moderate to large, tubercular dentition small, lower molars with basined heels,  $M^1$  in early forms with small hypocone, slender or moderately deep jaw with the symphyseal region comparatively shallow and loosely sutured, and typically a full eutherian dentition, with  $M^3$  vestigial or absent in some species (after Matthew, 1909b, p. 345, 362). *Miacis* is the most generalized of early miacids, and it is, in practice, identified chiefly by the absence of characteristics distinguishing the other contemporary genera described here.

*Age and distribution*.—*Miacis* is known from the early Wasatchian through Duchesnean land-mammal ages (early through late Eocene) in North America. It is also known from the early to late Eocene of Europe and eastern Asia.

*Discussion*.—Study of the type specimen of *Xinyuictis tenuis* (IVPP 4785) described by Zheng et al. (1975) from the early Eocene of China indicates that it is very similar to early *Miacis*, especially *M. winkleri* and *M. deutschi*, and *Xinyuictis* is here synonymized with *Miacis*. Two specimens from the southern Bighorn Basin (UW 9774, 9775) were referred to *Oödetes* cf. *herpestoides* by Bown (1979). These almost certainly represent *Miacis*, probably *M. winkleri*, but both are fragmentary and the teeth heavily worn, precluding positive species identification.

*Miacis winkleri* n. sp.

Fig. 4

*Holotype*.—UM 75432, left dentary with alveoli for  $C_1$  and  $P_{1-2}$ , roots of  $P_3$ , intact crowns of  $P_4$ - $M_2$ , and part of an alveolus for  $M_3$ .

*Type locality*.—UM locality SC-210, Willwood Formation of the Clark's Fork Basin, east center of NE 1/4, Section 26, T56N, R102W, Park County, Wyoming.

*Age and distribution*.—*Miacis winkleri* is known from four earliest Wasatchian localities ranging from 1530-1665 m stratigraphically in the Clark's Fork Basin, Wyoming. It may also be present in the earliest Wasatchian of the southern Bighorn Basin (see below).

*Diagnosis*.—Smallest early Wasatchian species of *Miacis*. Differs from *M. deutschi*, *M. exiguus*, and later North American species of *Miacis* in having relatively higher trigonids and narrower, less basined talonids on  $M_1$  and  $M_2$ . Differs from European early Eocene *Miacis latouri*, as described by Quinet (1968) and to the extent that known specimens are comparable, in

being larger. Resembles *Miacis tenuis* from the early Eocene of China but differs from that species in having narrower, less medially placed paraconids and in having slightly more bulbous trigonid cusps on  $M_1$  and  $M_2$ .

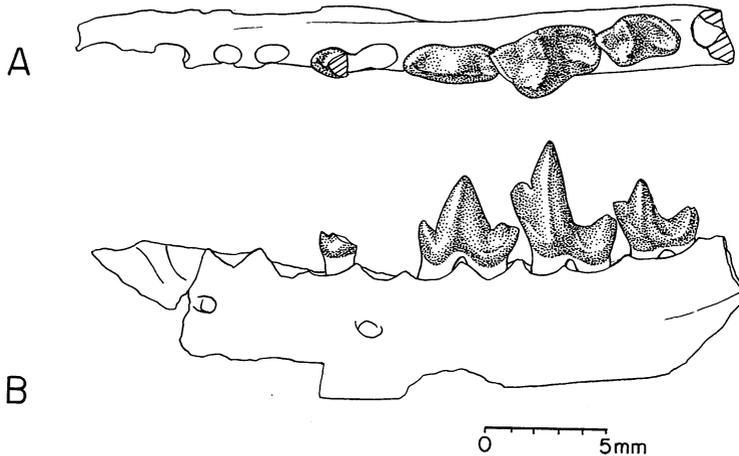


FIG. 4—Mandibular dentition of early Wasatchian *Miacis winkleri*, n. sp. *A*, left dentary with  $P_4M_{1-2}$  (UM 75432, holotype) from locality SC-210, in occlusal view; *B*, same in lateral view. Enlarged 3x natural size.

*Etymology.*—Named for Mr. Dale A. Winkler, who found the type specimen in 1980 while screen washing bulk sediment collected from SC-210.

*Description.*—Seven specimens of *Miacis winkleri* are known from the earliest Wasatchian of the Clark's Fork Basin. Upper teeth of this species have not yet been found. The holotype dentary (UM 75432) is the most complete specimen, and it preserves alveoli or intact crowns representing all teeth from the canine through  $M_3$ . Judging from alveoli, the lower canine was a moderately large tooth.  $P_1$  was single-rooted, and both  $P_2$  and  $P_3$  were double-rooted. There are small diastemata separating the three most anterior premolars.

The crowns of  $P_4$ - $M_2$  are intact in the holotype.  $P_4$  has a distinct anterior basal cusp (paraconid of MacIntyre, 1966) and a distinct posterior basal cusp (hypoconid or post-hypoconid of MacIntyre) but no trace of a metaconid or hypoconulid.  $M_1$  has a high protoconid and a lower paraconid and metaconid, the latter being more massive than the paraconid. The talonid is much narrower than the trigonid, and the hypoconid is the largest talonid cusp. There is a small hypoconulid and a very small entoconid, these cusps being connected by a lingual crest enclosing the talonid and making it basined as in other *Miacis*.  $M_2$  is similar to  $M_1$ , differing from it principally in being shorter anteroposteriorly and in being lower crowned. The talonid of  $M_2$  has about the same length and breadth as that of  $M_1$ , but the hypoconulid and entoconid are less distinct. The anterior border of an alveolus is the only evidence that remains of  $M_3$  in the holotype. The crown of  $M_3$  is preserved in several other specimens and it differs from  $M_2$  in being smaller and in being relatively lower crowned.  $M_3$  appears to be double-rooted in all specimens preserving this tooth, although, with the crown in place in the jaw, it is difficult to see the roots or alveoli very clearly and the roots may actually be fused in one or more specimens.

TABLE 2 — Summary of measurements of the lower cheek teeth of *Miacis winkleri* n. sp. from the Willwood Formation of the Clark's Fork Basin, Wyoming. Specimens included here are all early Wasatchian in age (1590-1665 m levels in measured stratigraphic section). Measurements are defined in Figure 1. Abbreviations as in Table 1. All measurements in mm.

Tooth position		N	OR	$\bar{x}$	S	V
P <sub>4</sub>	L	1	4.4	-	-	-
	W	1	1.8	-	-	-
M <sub>1</sub>	L	4	4.3-4.6	4.43	0.13	2.8
	W	4	2.9-3.1	3.00	0.08	2.7
	TH	2	5.1-5.8	5.45	0.50	9.1
M <sub>2</sub>	L	3	3.4-3.9	3.63	0.25	6.9
	W	4	2.2-2.6	2.43	0.17	7.0
M <sub>3</sub>	L	3	2.7-3.1	2.90	0.20	6.9
	W	3	1.7-2.1	1.70	0.20	11.8
Mandibular depth		2	6.8-6.9	6.85	0.07	1.0

Measurements (mm) of cheek teeth preserved in the holotype are as follows: P<sub>4</sub> L = 4.4, W = 1.8; M<sub>1</sub> L = 4.4, W = 3.1, TH = 5.1; M<sub>2</sub> L = 3.6, W = 2.4. Measurements of the entire Clark's Fork Basin sample of *M. winkleri* are summarized in Table 2.

*Hypodigm.*—Early Wasatchian of Clark's Fork Basin: UM 67076, 69440, 72265 (topotype), 75432 (holotype), 77504, 77517, and 79412.

*Miacis deutschii* n. sp.

Fig. 5

*Holotype.*—UM 71387, right dentary with M<sub>1-2</sub>.

*Type locality.*—UM locality SC-213, Willwood Formation of the Clark's Fork Basin, SE 1/4, section 26, T56N, R102W, Park County, Wyoming.

*Age and distribution.*—*Miacis deutschii* is known from six earliest Wasatchian localities ranging from 1720 to 1760 m stratigraphically in the Clark's Fork Basin, Wyoming. It is also known from one locality in the Foster Gulch area of the northern Bighorn Basin, Wyoming.

*Diagnosis.*—Intermediate in size between earliest Wasatchian *Miacis winkleri* and *M. exiguus*. Also differs from the former in having lower trigonids and broader, more basined talonids on M<sub>1</sub> and M<sub>2</sub>. Differs from the latter principally in being smaller (about 10% smaller in linear dimensions), and also in having slightly narrower lower molars, and relatively broader upper molars.

*Etymology.*—Named for Mr. Harvey Deutsch, who found the holotype in 1978.

*Description.*—Ten specimens of *Miacis deutschii* are known from the Clark's Fork Basin. One of these, UM 80449, is an isolated, virtually unworn right M<sup>1</sup> (Fig. 5C,D). This upper molar has a broad protocone and a prominent paracone. The metacone is a smaller cusp joined to the paracone and positioned directly behind it. There is a prominent parastylar shelf and the

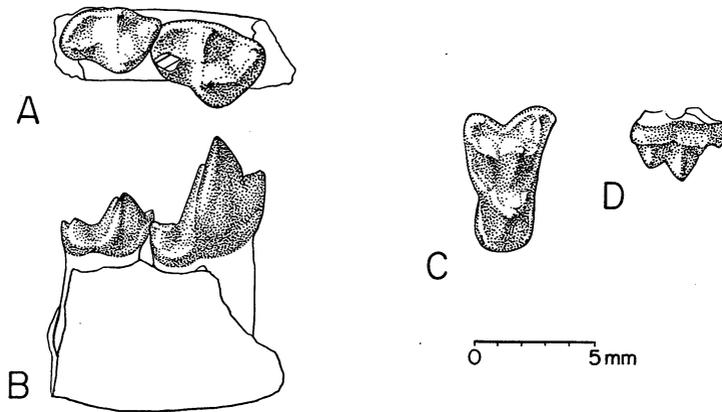


FIG. 5—Mandibular and maxillary dentition of early Wasatchian *Miacis deutschi* n. sp. A, right dentary with  $M_{1-2}$  (UM 71387, holotype) from locality SC-213, in occlusal view; B, same in lateral view. C, isolated right  $M^1$  (UM 80452) from locality SC-2, in occlusal view; D, same in lateral view. Enlarged 3x natural size.

parastyle itself is a moderately large, labiolingually oriented crest-shaped cusp. There is a relatively large paraconule on the postprotocrista, and a second smaller accessory conule on the postprotocrista labial to this. There are several very small cusplules in the position of the metaconule, but none of these is large enough to regard as a real conule.  $M^1$  has prominent anterior and posterior lingual cingula. There is a cusplule on the posterior cingulum that might be identified as a hypocone, but this is very small, and it would be obscured by the slightest wear.

None of the specimens at hand preserves any part of the dentary anterior to  $P_4$ . The crown of  $P_4$  is preserved in UM 77141. It is similar to that of *M. winkleri*, but differs in having a larger posterior basal cusp (posthypoconid of MacIntyre, 1966) and a small crest-like entoconid giving the talonid a slightly basined appearance.  $M_1$  and  $M_2$  resemble these teeth in *M. winkleri*, but differ in being relatively lower crowned. The hypoconid on  $M_1$  and  $M_2$  is relatively larger and the talonid broader than in *M. winkleri*. The crown of  $M_3$  is not preserved in any specimen but, judging from alveoli, it was double-rooted in the one specimen preserving this part of the lower jaw.

Measurements (mm) of cheek teeth preserved in the holotype are as follows:  $M_1$  L = 4.7, W = 3.2, TH = 5.1;  $M_2$  L = 3.8, W = 2.6. Measurements of the entire Clark's Fork Basin sample of *M. deutschi* are summarized in Table 3.

*Hypodigm.*—Early Wasatchian of Clark's Fork Basin: UM 68076, 69489, 69513, 71387 (holotype), 75065, 76584, 79548, 79676, 79762, 79777, and 80452. Early Wasatchian of Foster Gulch area, northern Bighorn Basin: UM 77141. Some specimens from the Sand Wash Basin of northern Colorado referred to *Miacis exiguus* by McKenna (1960, p. 96) may also represent *M. deutschi*.

TABLE 3 — Summary of measurements of the upper and lower cheek teeth of *Miacis deutchi* n. sp. from the Willwood Formation of the Clark's Fork Basin, Wyoming. Specimens included here are all early Wasatchian in age (1720-1760 m levels in measured stratigraphic section). Measurements are defined in Figure 1. Abbreviations as in Table 1. All measurements in mm.

Tooth position		N	OR	$\bar{x}$	S	V
<i>Upper dentition</i>						
M <sup>1</sup>	L	1	4.3	-	-	-
	W	1	6.6	-	-	-
<i>Lower dentition</i>						
P <sub>4</sub>	L	1	4.6	-	-	-
	W	1	2.1	-	-	-
M <sub>1</sub>	L	6	4.7-5.1	4.92	0.18	3.7
	W	6	3.0-3.6	3.28	0.19	5.9
	TH	2	5.1	-	-	-
M <sub>2</sub>	L	4	3.4-4.0	3.80	0.28	7.4
	W	4	2.6-3.1	2.78	0.22	8.0
M <sub>3</sub>	L	-	-	-	-	-
	W	-	-	-	-	-
Mandibular depth		2	6.2-7.5	6.85	0.92	13.4

*Miacis exiguus* Matthew, 1915  
Figs. 6, 8F-J

*Miacis exiguus* Matthew, 1915, p. 33, fig. 28.

*Miacis latidens* mut. prim., Matthew, 1915, p. 36, fig. 27 (part).

*Holotype*.—AMNH 15176, palate, part of dentary, and fragmentary skeleton collected by W. Granger on September 7, 1910.

*Type locality*.—Gray Bull beds in the central Bighorn Basin, Wyoming (Matthew, 1915). According to field records in the archives of the American Museum of Natural History, the type specimen was found by Granger on the "lower forks of Dorsey Creek." Thus, on faunal grounds, it is early or middle Graybullian in age (corresponding to middle Wasatchian faunal zones Wa<sub>3</sub> or Wa<sub>4</sub>).

*Age and distribution*.—*Miacis exiguus* is known from seven middle Wasatchian localities ranging from 1815 to 2050 m stratigraphically in the Clark's Fork Basin. The holotype is from the early or middle Graybullian (middle Wasatchian) of the central Bighorn Basin. In addition, *M.*

*exiguus* may be present in the middle Wasatchian of the Sand Wash Basin in Colorado (McKenna, 1960).

*Diagnosis.*—*Miacis exiguus* differs from *M. winkleri* and *M. deuschi* in being larger and in having relatively lower and broader crowns on mandibular molars. It differs from *M. jepseni* in being considerably larger. It differs from *M. petilus* and *M. latidens* in having distinctly broader talonids on  $P_3$  and  $P_4$ , with a large posterior basal cusp (post-hypoconid of MacIntyre, 1966) on the latter. *M. exiguus* is also distinctive in having higher, sharper cusps and crests on  $M_2$ . It apparently always has a double-rooted  $M_3$ .

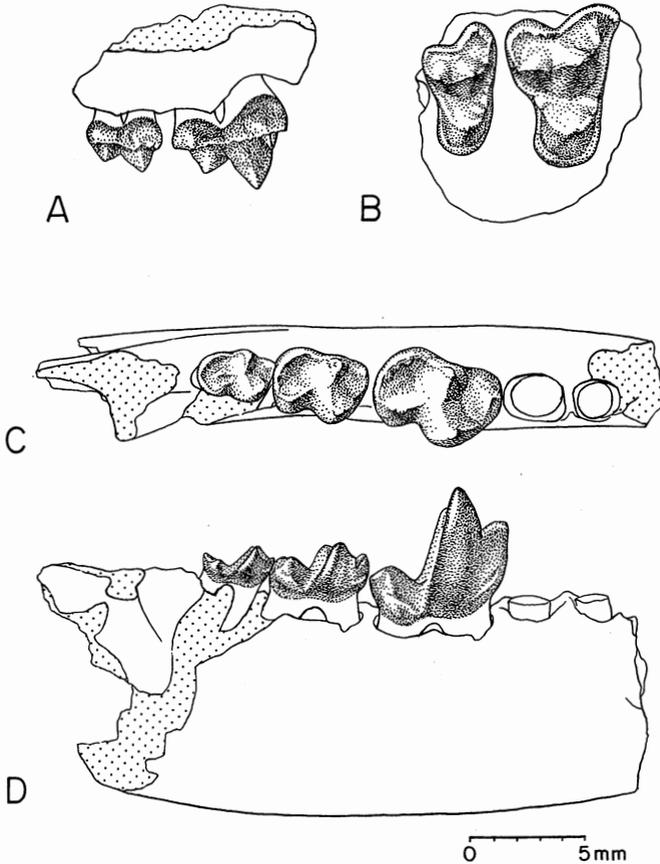


FIG. 6.—Maxillary and mandibular dentition of middle Wasatchian *Miacis exiguus* Matthew. A, right maxilla with  $M^{1-2}$  (UM 69127) from locality SC-192, in lateral view; B, same in occlusal view. C, right dentary with  $M_{1-3}$  (UM 80138) from locality SC-255, in occlusal view; D, same in lateral view. Enlarged 3x natural size.

*Description.*—Seventeen specimens of *Miacis exiguus* are known from the middle Wasatchian of the Clark's Fork Basin. Crowns of maxillary P<sup>4</sup>-M<sup>2</sup> are preserved in UM 73812 and unworn M<sup>1-2</sup> are preserved in UM 69127. P<sup>4</sup> in *Miacis* resembles this tooth in *Uintacyon rudis*. The paracone is the largest cusp. There is a prominent protocone positioned anterolingually with respect to the paracone. There is a distinct parastylar shelf anterior to the paracone (this shelf is not well developed in *Uintacyon rudis*). The metastyle is crest-like in form, extending posterolingually from the paracone. The metacone forms a distinct carnassial notch with the crest-like posterior margin of the paracone. M<sup>1</sup> in *M. exiguus* differs from this tooth in *M. deutschii* in being longer anteroposteriorly relative to crown width, especially in the protocone region, and in having a small but distinct metaconule. The posterior lingual cingulum is more prominent, with a small hypocone cusp present in some specimens. The crown of M<sup>2</sup> resembles that of M<sup>1</sup>, but it is smaller and lacks the anterior deflection of the parastylar shelf seen in M<sup>1</sup>. The metaconule is also less prominent on M<sup>2</sup>. Impressions of two alveoli are preserved posterior to M<sup>2</sup> in UM 69127, but the crown of M<sup>3</sup> is not preserved in any of the specimens at hand.

The most complete dentary of *M. exiguus* from the Clark's Fork Basin is UM 66837, which has roots and fragments of crown representing P<sub>2</sub>-P<sub>4</sub>. All three of these teeth are double-rooted, and there is a distinct diastema between P<sub>2</sub> and P<sub>3</sub>. The crown of P<sub>4</sub> in *M. exiguus* resembles that in *M. deutschii*, and the talonid is perhaps even more basined. Crowns of M<sub>1-3</sub> also resemble those of *M. deutschii*, but they are relatively lower and broader. M<sub>3</sub> is consistently double-rooted.

Measurements of cheek teeth preserved in the holotype, AMNH 15176, are as follows: P<sup>3</sup> L = 4.5, W = 2.4; P<sup>4</sup> L = 6.6, W = 5.0; M<sup>1</sup> L = 5.0, W = 7.9; M<sup>2</sup> L = 3.4, W = 6.0. Measurements of the Clark's Fork Basin sample of *Miacis exiguus* are summarized in Table 4.

*Discussion.*—All specimens of medium-sized *Miacis* from the middle and late Wasatchian are currently lumped together under the name *M. exiguus*, in spite of a considerable amount of variation in the form of P<sub>4</sub>-M<sub>3</sub> and in the number of roots on M<sub>3</sub>. It is desirable to distinguish early and late forms of "*Miacis exiguus*." The holotype, coming from the "lower forks of Dorsey Creek" in the central Bighorn Basin, is an early-middle Graybullian representative. Thus the name *M. exiguus* is appropriately restricted to early and middle Graybullian specimens of *Miacis* distinguished by characteristics listed in the diagnosis above. The late Graybullian and Lysitean form is described as a new species *M. petilus*.

The earliest representatives of *Vulpavus* in the Clark's Fork and Bighorn basins are difficult to distinguish from *M. exiguus* (as restricted here). This suggests that *Vulpavus* may be a direct descendant of *Miacis exiguus*, and *M. petilus* may be a conservative form of *Miacis* that reappeared after *Vulpavus* diverged.

*Hypodigm.*—Middle Wasatchian of Clark's Fork Basin: UM 65289, 65343, 66795, 66837, 67048, 69127, 69137, 69627, 69632, 71514, 73215, 73258, 73812, 75702, 78993, 79911, and 80138. Middle Wasatchian of the central Bighorn Basin: holotype, AMNH 2517, 2521, 15177, 15182, and UM 64275.

### *Miacis petilus* n. sp.

Figs. 7, 8A-C

*Miacis exiguus* (in part), Matthew, 1915, p. 33, fig. 29. Guthrie, 1967, p.30, fig. 20b. Schankler, 1980, p. 105.  
*Miacis latidens* (in part), Guthrie, 1967, p. 29.

*Holotype.*—UM 64124, left and right dentaries preserving the roots of C<sub>1</sub>-P<sub>2</sub>, crowns of P<sub>3</sub>-M<sub>2</sub>, and part of an alveolus for M<sub>3</sub>. The holotype was collected by E.L. Simons in 1974.

TABLE 4 — Summary of measurements of the upper and lower cheek teeth of *Miacis exiguus* from the Willwood Formation of the Clark's Fork Basin, Wyoming. Specimens included here are all middle Wasatchian in age (1815 to 2050 m levels in measured stratigraphic section). Measurements are defined in Figure 1. Abbreviations as in Table 1. All measurements in mm.

Tooth position		N	OR	$\bar{x}$	S	V
<i>Upper dentition</i>						
P <sup>4</sup>	L	1	6.0	-	-	-
	W	1	4.7	-	-	-
M <sub>1</sub>	L	3	4.8-5.2	5.00	0.20	4.0
	W	3	6.7-8.1	7.30	0.72	9.9
M <sub>2</sub>	L	3	3.4-3.7	3.50	0.17	4.9
	W	2	5.6-6.7	6.15	0.78	12.6
<i>Lower dentition</i>						
P <sub>3</sub>	L	1	4.2	-	-	-
	W	1	1.7	-	-	-
P <sub>4</sub>	L	5	4.6-5.2	4.88	0.26	5.3
	W	5	2.1-2.5	2.30	0.16	6.9
M <sub>1</sub>	L	11	5.2-5.8	5.45	0.20	3.7
	W	11	3.5-4.0	3.76	0.20	5.4
	TH	6	5.3-6.0	5.65	0.35	6.2
M <sub>2</sub>	L	7	4.0-4.3	4.13	0.13	3.0
	W	7	2.8-3.3	3.09	0.19	6.0
M <sub>3</sub>	L	1	3.3	-	-	-
	W	1	2.5	-	-	-
Mandibular depth		7	7.6-9.8	8.89	0.73	8.2

*Type locality.*—Yale-Michigan locality 421, on the upper forks of Dorsey Creek in the south center of Section 6, T50N, R95W, Bighorn County, Wyoming. This locality is at the 390 m level in the central Bighorn Basin, just above Schankler's "Biohorizon B" (Schankler, 1980).

*Age and distribution.*—*M. petilus* is known from the middle and late Wasatchian (late Graybullian and Lysitean faunal zones) in the central Bighorn Basin and in the Wind River Basin, Wyoming.

*Diagnosis.*—Differs from *M. winkleri*, *M. deutschii*, and *M. jepseni* in being significantly larger. Same size as *M. exiguus*, but differs from that species in having narrower crowns on lower premolars, lacking a prominent posterior basal cusp (hypoconid or post-hypoconid of MacIntyre, 1966; see Fig. 8). Further differs from *M. exiguus* in having M<sub>2</sub> and M<sub>3</sub> relatively smaller, with lower and more rounded cusps. M<sub>3</sub> single-rooted in some specimens. Resembles later *M. latidens* but differs from that species in being significantly smaller (*vide* Guthrie, 1971, p. 76).

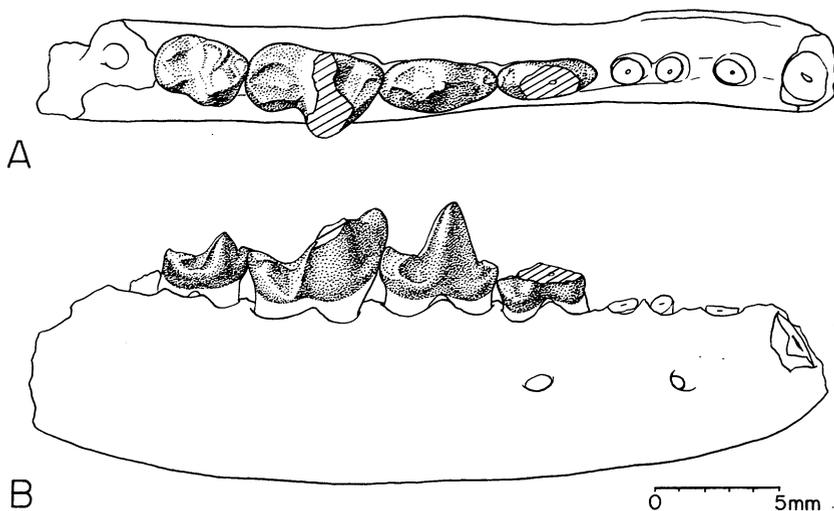


FIG. 7.— Mandibular dentition of middle-late Wasatchian *Miacis petilus* n. sp. *A*, right dentary with P<sub>3</sub>-M<sub>2</sub> (UM 64124, composite drawing of holotype based on left and right dentaries) from locality YM-421, in occlusal view; *B*, same in lateral view. Enlarged 3x natural size.

*Etymology*.—*petilus*, Latin, thin or slender, in reference to the narrow premolars helping to distinguish this species from *Miacis exiguus*.

*Description*.—Three specimens of *Miacis petilus*, all dentaries, are known from the type locality. The holotype, UM 64124, is the most complete. The crown of the canine is missing, but judging from the preserved root it was of moderate size. P<sub>1</sub> is single-rooted. P<sub>2</sub> is double-rooted and separated from P<sub>1</sub> and P<sub>3</sub> by small diastemata. The base of the crown of P<sub>3</sub> is preserved in the left dentary of the holotype. It is relatively narrow and has very small anterior and posterior basal cusps in addition to a large protoconid (broken). P<sub>4</sub> is preserved in all three specimens from the type locality. The crown is large but otherwise resembles that of P<sub>3</sub>. There is a distinct paraconid cuspule and a small posterior basal cusp (hypoconid), but the latter is not as prominent as the hypoconid of *Miacis exiguus*. There is no real entoconid and the talonid is more trenchant than basined. M<sub>1</sub> is similar to that in *M. exiguus*, differing only in having a slightly longer and narrower talonid. The crown of M<sub>2</sub> is smaller and relatively narrower than that of *M. exiguus*, and its cusps are lower and more rounded. The crown of M<sub>3</sub> is not preserved in the holotype or either toptype. The number of roots on M<sub>3</sub> cannot be determined in the holotype or in UM 64489, but it is clearly single-rooted in UM 64093. It is double-rooted in UM 64351.

Measurements of *M. petilus* are recorded in Table 5.

*Discussion*.—See discussion under *Miacis exiguus* above.

*Hypodigm*.—Middle to late Wasatchian of the central Bighorn Basin: AMNH 4245, 15717, 15718, 16831b, UM 64124 (holotype), 64093 (topotype), 64351, 64489 (topotype), 65967, and 75201.

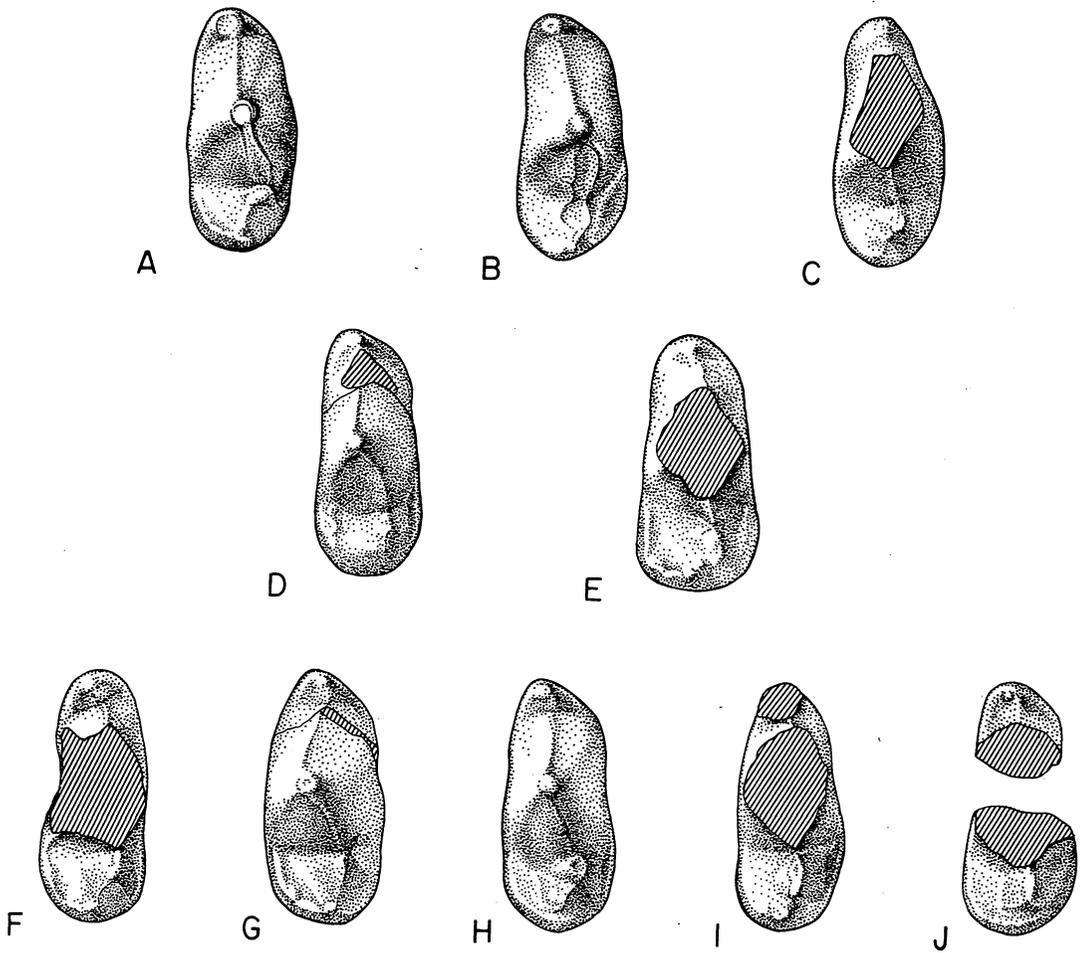


FIG. 8— Right premolars of *Miacis petilus* (top row), *Vulpavus australis* (middle row), and *Miacis exiguus* (bottom row). All in occlusal view and brought to the same crown length for comparison. Note that the crown of P<sub>4</sub> tends to be broader and the posterior basal cusp (hypoconid or post-hypoconid of MacIntyre, 1966) is usually more labially positioned on the talonid in *M. exiguus* than it is in *M. petilus*, a resemblance to *Vulpavus australis*. These and other similarities suggest that *Vulpavus australis* may be a direct descendant of *Miacis exiguus*. A, UM 64124 (holotype); B, UM 64093; and C, UM 64489, all *M. petilus* from the late Graybullian (Wa<sub>5</sub>). D, UM 64064 (reversed), and E, UM 64303, both *V. australis* from the late Graybullian (Wa<sub>5</sub>). F, UM 73215; G, UM 69627 (rev.); H, UM 75702 (rev.); I, UM 69632 (rev.), and J, UM 66837; all *M. exiguus* from the early to middle Graybullian (Wa<sub>3-4</sub>).

TABLE 5 — Measurement of lower cheek teeth of *Miacis petilus* n. sp. from the Willwood Formation of the central Bighorn Basin, Wyoming. Specimens included here range in age from middle to late Wasatchian (late Graybullian to early Lysitean; 390 to 490 m levels in Schankler's, 1980, measured stratigraphic section). Measurements are defined in Figure 1. Abbreviations as in Table 1. All measurements in mm.

Tooth position		UM 64124 YM-421 (holotype)	UM 64093 YM-421 (topotype)	UM 64489 YM-421 (topotype)	UM 75201 GR-7 (Graybullian)	UM 65967 YM-45 (Lysitean)
P <sub>3</sub>	L	3.9	-	-	-	-
	W	1.8	-	-	-	-
P <sub>4</sub>	L	4.8	4.8	5.0	-	-
	W	2.2	2.2	2.4	-	-
M <sub>1</sub>	L	5.6	-	6.1	-	-
	W	3.5	-	3.7	-	-
M <sub>2</sub>	L	3.9	3.8	-	3.9	3.7
	W	2.8	2.5	-	2.8	2.8
M <sub>3</sub>	L	-	-	-	2.8	2.3
	W	-	-	-	2.1	2.0
Mandibular depth		7.9	10.9	8.9	9.0	8.2

*Vassacyon* Matthew, 1909

*Uintacyon* (in part), Wortman and Matthew, 1899, p. 110.

*Prodaphaenus* (in part), Wortman, 1901, p. 449.

*Vassacyon* Matthew, 1909a, p. 93.

*Type species.*—*Uintacyon promicrodon* Wortman and Matthew, 1899.

*Included species.*—Type species only.

*Diagnosis.*—Premolars increase in size posteriorly, upper molars with short parastyle, well developed hypocone, M<sub>1</sub> carnassiform with a large, broadly basined heel, M<sub>2</sub> tubercular and large with low trenchant heel (from Matthew, 1909b, 1915).

*Age and distribution.*—*Vassacyon* is known only from the middle Wasatchian in North America.

*Vassacyon promicrodon* (Wortman and Matthew)

Fig. 9

*Uintacyon promicrodon* Wortman and Matthew, 1899, p. 111.

*Prodaphaenus promicrodon*, Wortman, 1901, p. 30.

*Vassacyon promicrodon*, Matthew, 1909a, p. 93; 1909b, p. 376, Pl. 43, fig. 4; 1915, p. 41, figs. 34-40.

*Vassacyon* cf. *promicrodon*, Gazin, 1962, p. 61.

Cf. *Vassacyon* sp., Bown, 1979, p. 96.

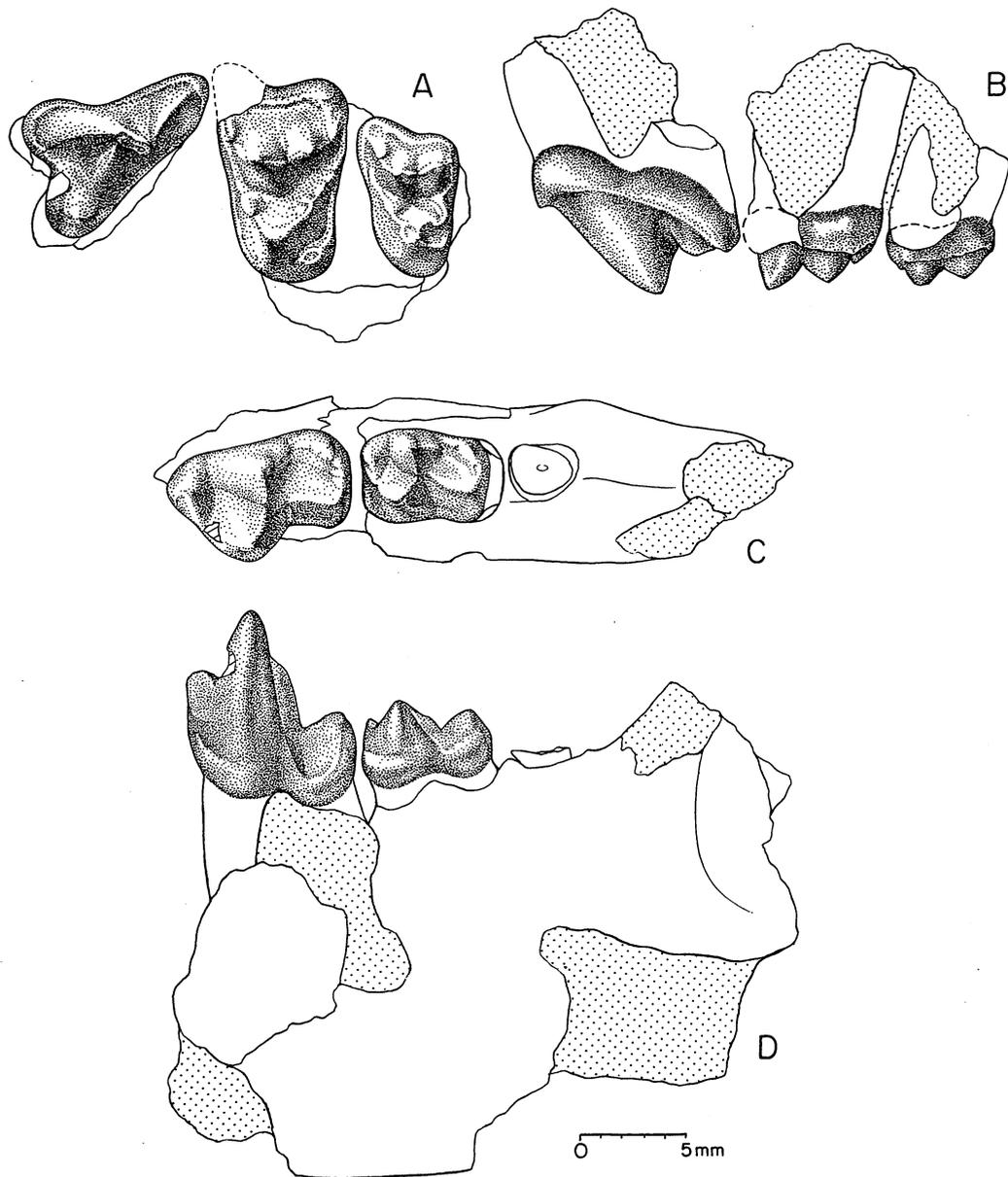


FIG. 9— Associated maxillary and mandibular dentition of middle Wasatchian *Vassacyon promicrodon* Wortman and Matthew (UM 74527), from locality SC-255. A, left maxilla with P<sup>4</sup>-M<sup>2</sup> (molars reversed from right side), in occlusal view; B, same in lateral view. C, left dentary with M<sub>1-2</sub> (single root for M<sub>3</sub> preserved in right ramus), in occlusal view; D, same in lateral view. Enlarged 3x natural size.

*Holotype*.—AMNH 83, dentary with P<sub>4</sub>-M<sub>1</sub>, collected by J. Wortman in 1891.

*Type locality*.—"Coryphodon beds" of the central Bighorn Basin.

*Age and distribution*.—All well dated remains of *Vassacyon promicrodon* are from the Graybullian (middle Wasatchian) of the Clark's Fork and Bighorn Basins. Gazin (1962, p. 61) has reported this species from a "Graybull" horizon in the Fossil Basin of southwestern Wyoming. In a summary report, Schankler (1980, p. 105) shows *V. promicrodon* ranging from the early through late Wasatchian of the central Bighorn Basin, but these records cannot be evaluated until the specimens on which they are based are described.

*Diagnosis*.—As for the genus (see above). *Vassacyon promicrodon* is easily distinguished from other early and middle Wasatchian Miacidae by its much larger size.

*Description*.—Eight specimens of *Vassacyon promicrodon* are known from the middle Wasatchian of the Clark's Fork Basin. UM 74527 and 79021 preserve associated upper and lower cheek teeth. P<sup>4</sup> in *Vassacyon* is larger but otherwise similar to that in *Uintacyon* in the arrangement of cusps and crests. As in *Uintacyon*, there is no real parastylar shelf on P<sup>4</sup>. M<sup>1</sup> in *V. promicrodon* is distinctive among early Eocene Miacidae in having a much more quadrate outline. The crown is relatively long and narrow. The parastyle is much less projecting than in other species, there is a distinct metaconule, and the hypocone is well developed on the posterior lingual cingulum. M<sup>2</sup> is similar to M<sup>1</sup>, but differs in being smaller and in having lower, more rounded cusps. One root of M<sup>3</sup> is preserved and there is an alveolus for another root in UM 69215, but the crown of M<sup>3</sup> is not preserved in any of the available specimens.

The lower canine is preserved in place in the dentary in UM 79021. It is a stout, projecting tooth with a somewhat compressed crown. P<sub>1</sub> is a small, single-rooted tooth with a simple crown. Judging from alveoli, P<sub>2</sub> was relatively small, double-rooted, and separated from both P<sub>1</sub> and P<sub>3</sub> by diastemata. P<sub>3</sub> is also relatively small, with a simple crown and a very small, almost flat posterior shelf near the base of the crown. Judging from several badly broken crowns, P<sub>4</sub> was much longer than P<sub>3</sub> and it has a broad, wedge-shaped posterior cusp (post-hypoconid of MacIntyre, 1966). M<sub>1</sub> resembles M<sub>1</sub> in *Uintacyon rudis* in having a highly trenchant hypoconid, but there is also a well developed entoconid crest making the heel distinctly basined. M<sub>2</sub> is rather high-crowned, but the trigonid is little higher than the talonid. M<sub>2</sub> has a prominent anterolabial cingulid and a relatively open trigonid as in *U. rudis*, although the talonid of this tooth is also basined. M<sub>3</sub> is not preserved in any specimen at hand; judging from alveoli it was single-rooted in one specimen and double-rooted in another.

Measurements (mm) of cheek teeth preserved in the holotype, AMNH 83, are as follows: P<sub>3</sub> W = 2.4; P<sub>4</sub> L = 7.4, W = 4.1; M<sub>1</sub> L = 8.1, W = 5.8; M<sub>2</sub> W = 4.9; mandibular depth below M<sub>1</sub> = 16.9. Dental and mandibular measurements of the Clark's Fork Basin sample of *Vassacyon promicrodon* are summarized in Table 6.

*Hypodigm*.—Middle Wasatchian of Clark's Fork Basin: UM 69215, 71217, 73102, 74527, 79021, 79971, 80853, and 80854.

### *Vulpavus* Marsh, 1871

*Vulpavus* Marsh, 1871, p. 124.

*Type species*.—*Vulpavus palustris* Marsh, 1871.

*Included species*.—*Vulpavus australis* Matthew [middle-late Wasatchian], *V. canavus* (Cope) [late Wasatchian], *V. palustris* Marsh [Bridgerian], *V. profectus* Matthew [Bridgerian], *V. ovatus* Matthew [Bridgerian].

TABLE 6 — Summary of measurements of the upper and lower cheek teeth of *Vassacyon promicrodon* from the Willwood Formation of the Clark's Fork Basin, Wyoming. Specimens included here are all middle Wasatchian in age (1840 to 2050 m levels in measured stratigraphic section). Measurements are defined in Figure 1. Abbreviations as in Table 1. All measurements in mm.

Tooth position		N	OR	$\bar{x}$	S	V
<i>Upper dentition</i>						
P <sup>4</sup>	L	1	9.4	-	-	-
	W	1	6.7	-	-	-
M <sup>1</sup>	L	3	6.2-6.6	6.43	0.21	3.2
	W	3	9.3-9.7	9.50	0.20	2.1
M <sup>2</sup>	L	2	4.1-5.0	4.55	0.64	14.0
	W	2	7.2-7.3	7.25	0.07	1.0
<i>Lower dentition</i>						
C <sub>1</sub>	L	2	5.4-6.2	5.80	0.57	9.8
	W	2	3.6-4.2	3.90	0.42	10.9
P <sub>1</sub>	L	1	1.9	-	-	-
	W	1	1.4	-	-	-
P <sub>2</sub>	L	-	-	-	-	-
	W	-	-	-	-	-
P <sub>3</sub>	L	1	4.4	-	-	-
	W	1	2.1	-	-	-
P <sub>4</sub>	L	-	-	-	-	-
	W	-	-	-	-	-
M <sub>1</sub>	L	4	7.8-8.1	7.93	0.15	1.9
	W	4	5.2-5.6	5.38	0.17	3.2
	TH	1	9.3	-	-	-
M <sub>2</sub>	L	4	5.5-6.4	5.90	0.39	6.6
	W	5	4.1-4.8	4.38	0.28	6.3
M <sub>3</sub>	L	-	-	-	-	-
	W	-	-	-	-	-
Mandibular depth		3	13.7-17.8	15.37	2.16	14.0

*Diagnosis*.—"Upper molars rounded, quadrate with low cusps and no shear. P<sup>4</sup> not carnassiform; lower molars with low trigonids and broadly basined heels" (quoted from Matthew, 1909b, p. 379). The Wasatchian species of *Vulpavus* are more generalized and resemble other early miacid genera more closely than Bridgerian species do. One of the most distinctive characteristics of early *Vulpavus* is the presence of a talonid basin on the lower molars as broad or broader than the trigonid.

*Age and distribution*.—*Vulpavus* is known from the middle Wasatchian through Bridgerian land-mammal ages (early to middle Eocene) in North America.

TABLE 7 — Measurements of the lower cheek teeth of *Vulpavus australis* and *V. cf. australis*. The holotype, AMNH 16226, is from the middle to late Wasatchian San Jose Formation of New Mexico. UM 64064 is from the late Graybullian (middle Wasatchian) of the central Bighorn Basin. UM 73534 is from the middle Graybullian (middle Wasatchian) of the Clark's Fork Basin. Measurements are defined in Figure 1. Abbreviations as in Table 1. All measurements in mm.

Tooth position		AMNH 16226 San Juan Basin (holotype)	UM 64064 YM-421 <i>V. australis</i>	UM 73534 SC-256 <i>V. cf. australis</i>
P <sub>4</sub>	L	4.8	4.7	-
	W	2.3	2.3	-
M <sub>1</sub>	L	5.9	5.5	-
	W	3.9	4.0	-
M <sub>2</sub>	L	4.3	4.6	4.6
	W	3.7	3.8	3.6
M <sub>3</sub>	L	3.5	-	3.6
	W	2.9	-	2.9
Mandibular depth		9.5	8.5	-

*Vulpavus cf. australis*  
Figs. 8D-E, 10

*Discussion*.—One specimen from the Clark's Fork Basin (UM 73534, with part of M<sub>1</sub> and intact M<sub>2</sub> and M<sub>3</sub>, not certainly associated) is referred to *Vulpavus* as *V. cf. australis* (Fig. 10). It differs in some ways from typical *V. australis*: the anterior cingulid on M<sub>2</sub> is less complete, the paraconid is well separated from the metaconid, and the entoconid crest is high and curved but not serrated like that in *V. australis* (Fig. 11). UM 73534 is so similar to contemporary and slightly older *Miacis* that it could possibly represent *M. exiguus*. On the other hand, UM 73534 has a much broader talonid on M<sub>2</sub> and M<sub>3</sub> than is seen in *Miacis*, a characteristic diagnostic of *Vulpavus*. Measurements of the holotype and referred specimens of *V. australis* are listed with those of UM 73534 in Table 7.

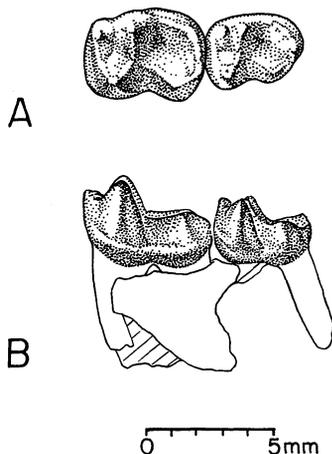


FIG. 10— Mandibular dentition of *Vulpavus* cf. *australis* from the middle Graybullian ( $W_{a4}$ ) in the Clark's Fork Basin. A, left dentary with  $M_{2-3}$  (UM 73534) from locality SC-256, in occlusal view; B, same in lateral view. Enlarged 3x natural size.

#### POSTCRANIAL ANATOMY

Postcranial elements of Miacidae are rarely preserved in association with jaws and teeth in the Clark's Fork Basin. Two exceptional specimens are UM 76861, a partial skeleton of *Uintacyon rudis*, and UM 73812, a partial skeleton of *Miacis exiguus*. Neither is very complete, but both are associated with dentitions permitting positive reference to these species. In order to facilitate identification of isolated tarsal elements, astragali of each are illustrated in four standard views (Fig. 12). Astragali of miacids are distinctive in having a relatively flat capitulum, an arched, shallowly grooved trochlear tibial facet with a confluent, smoothly curved maleolar tibial facet, a broad lateral tibial facet, an astragalar canal perforating the body of the astragalus, and a deep, slightly oblique posterior trochlear groove for the flexor hallucis longus tendon.

The astragalus of *Miacis exiguus* is similar to that of *Uintacyon rudis*, but differs in being smaller (14.2 mm in total length as compared with 16.5 mm), in having a flatter capitulum, and in having a less strongly arched trochlear tibial facet. The maximum height of the astragalar body is 6.7 mm in *M. exiguus* and 8.2 mm in *U. rudis*. Judging from the anterior position of the trochlear tibial facet, both species were plantigrade. They may have resembled modern palm civets in gait, locomotor habits, and habitat.

#### DISCUSSION

The stratigraphic record of Miacidae in the Clark's Fork Basin is the most complete known anywhere documenting the early radiation of this group. Tooth size is plotted against stratigraphic level in Figure 13 for all miacids from the Clark's Fork Basin preserving first lower molars. Figure 13 summarizes what is known about the relative body sizes and stratigraphic ranges of each of the species. The only miacid lineage present during the Clarkforkian is *Uintacyon rudis*. It appears abruptly in the middle Clarkforkian. No plausible ancestors are

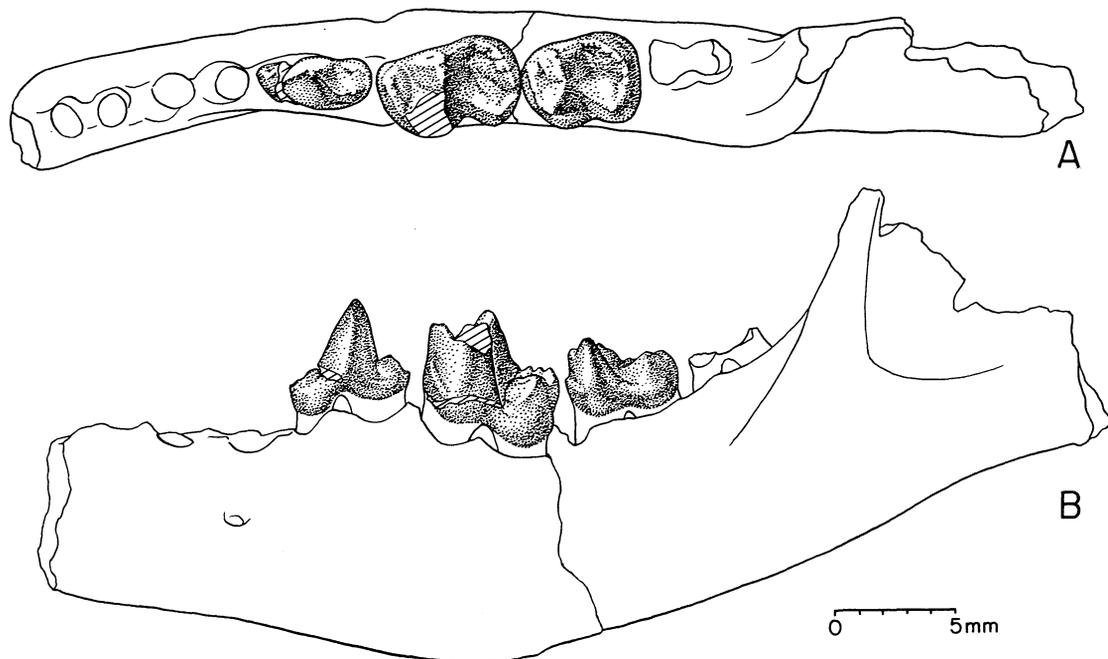


FIG. 11— Mandibular dentition of *Vulpavus australis* Matthew from the late Graybullian (W<sub>3</sub>) of the central Bighorn Basin. A, left dentary with P<sub>4</sub>-M<sub>2</sub> (UM 64064) from locality YM-421, in occlusal view; B, same in lateral view. Enlarged 3x natural size.

known in North America, and it is possible, even probable, that *U. rudis* was an early or middle Clarkforkian immigrant from elsewhere. *Miacis* first appears abruptly at the beginning of the Wasatchian, and it too lacks a plausible precursor in earlier North American strata. Three species, *M. winkleri*, *M. deuschi*, and *M. exiguus*, appear to form a single evolutionary lineage.

*Vassacyon*, appearing abruptly in the middle Wasatchian after the faunal turnover at Schankler's (1980) "Biohorizon A," represents a third lineage of early Miacidae. *Vassacyon* is most similar to *Uintacyon*, and it probably evolved from this genus or a closely related form in North America or elsewhere. *Vulpavus* also makes its first appearance in the middle Wasatchian. *Vulpavus* is most similar to early *Miacis*, and *V. australis* may be a direct descendant of the *Miacis winkleri* - *M. exiguus* lineage. Alternatively, *Vulpavus* may conceivably represent immigration of a fourth lineage closely related to *Miacis*. *Miacis* and *Vulpavus* are first known to occur in the same stratigraphic interval at locality YM-421, just above Schankler's "Biohorizon B." If *Vulpavus* is a direct descendant of *Miacis exiguus*, then *M. petilus* must represent a sister lineage retaining primitive *Miacis* morphology and immigrating into the central Bighorn Basin at the beginning of the late Graybullian.

A single miacid lineage is present in the Clarkforkian, two lineages are present in the early Wasatchian, and a third lineage is present in the middle Wasatchian. Within individual lineages, the amount of evolution recorded varies from little change (in *Vassacyon*) to moderate change (in *Miacis*). The maximum rate of evolution observed at the scale of resolution illustrated in Figure 13 is about 0.40 darwins (in the *Miacis winkleri* - *M. exiguus* lineage), indicating that significant evolutionary change was occurring *in situ* in the Clark's Fork Basin and surrounding area. On the other hand, the first appearances of all new lineages coincide with well known faunal

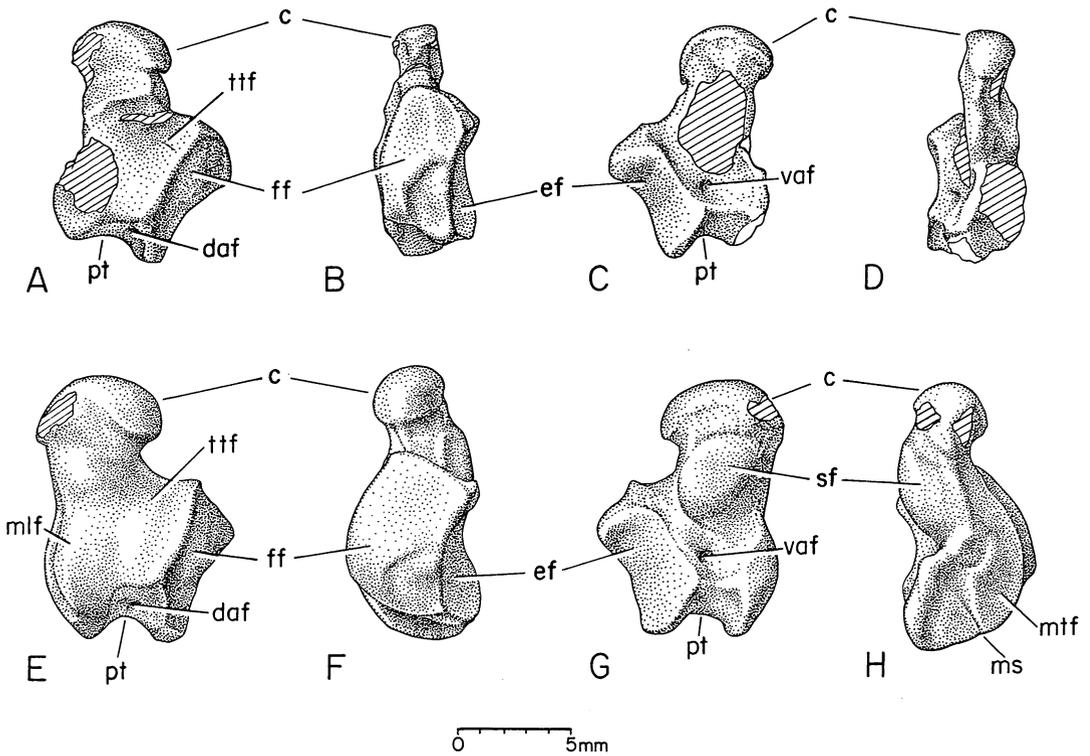


FIG. 12— Left astragali of *Miacis exiguus* (UM 73812, top: A-D) and *Uintacyon rudis* (UM 76861, bottom: E-H), in dorsal, lateral, ventral, and medial views, respectively. Abbreviations are as follows: *c*, capitulum with navicular facet; *daf*, dorsal astragalar foramen; *ef*, ectal facet; *ff*, fibular facet; *ms*, medial or maleolar sulcus; *mlf*, maleolar tibial facet; *pt*, posterior trochlear groove for flexor hallucis longus; *sf*, sustentacular facet; *ttf*, trochlear tibial facet; *vaf*, ventral astragalar foramen.

turnover events, indicating that important evolutionary change was taking place outside the Clark's Fork Basin as well.

Little is known about the origin of North American Miacidae. Viverravidae, the only true Carnivora present in the Paleocene of North America, resemble Miacidae in ways that identify both as true carnivorans. However, derivation of Miacidae from known Viverravidae is improbable because Viverravidae lack upper and lower third molars, present in Miacidae, and because the earliest miacids, *Uintacyon* and *Miacis*, are markedly distinct from viverravids when they make their first appearance in the fossil record (MacIntyre, 1966). Consequently, it seems plausible that Miacidae originated in an area not yet well sampled paleontologically.

The oldest representative of *Uintacyon*, *U. rudis*, is first known from the middle Clarkforkian in North America. The oldest specimens of *Miacis* are the type sample of *M. latouri* from the early Sparnacian locality of Dormaal in Belgium (Quinet, 1968; Godinot et al., 1978). Dormaal may be correlative with late Clarkforkian localities in North America (Godinot, 1981), indicating that middle Clarkforkian *Uintacyon rudis* is the oldest record of Miacidae known to date. Actually, the first appearance of these two genera, *Miacis* in Europe and *Uintacyon* in North America, is so nearly synchronous and the two genera are sufficiently similar morphologically that either one could be an ancestor of the other. Rose (1981) has suggested that *Miacis* is the

## CLARK'S FORK BASIN MIACINAE

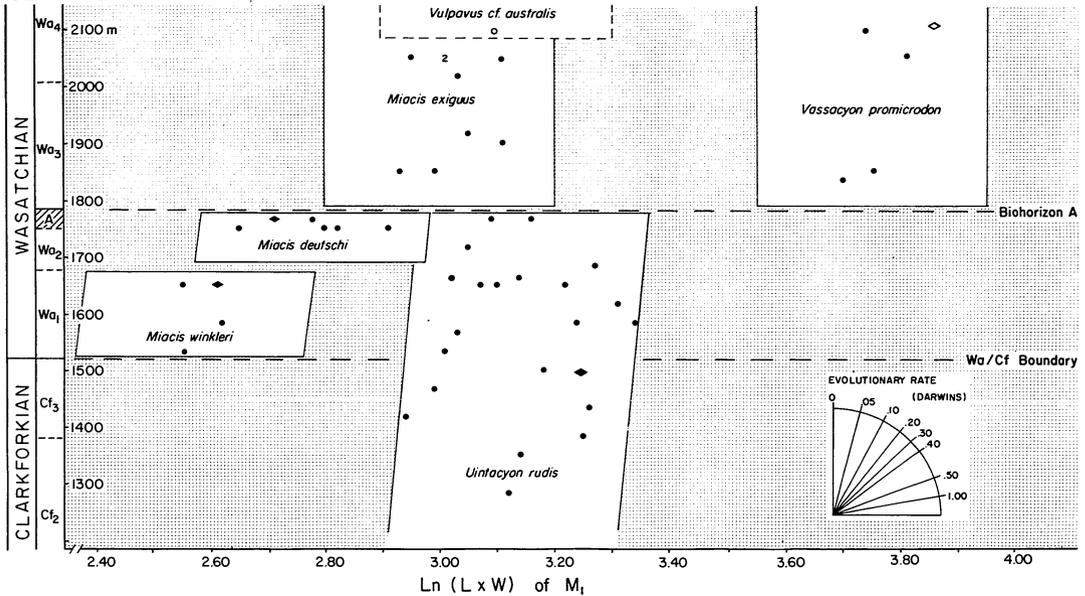


FIG. 13— Relative body sizes (judged from tooth size) and stratigraphic ranges of early Eocene Miacidae in the Clark's Fork Basin, Wyoming. Abscissa is the natural logarithm of  $M_1$  crown area, measured as shown in Figure 1. Ordinate is stratigraphic level in meters, measured from the base of the Paleocene Fort Union Formation on Polecat Bench.  $Cf_2$  and  $Cf_3$  are middle and late Clarkforkian, respectively.  $Wa_{1-2}$  (Sandcouleean) and  $Wa_{3-4}$  (early and middle Graybullian) represent the early Wasatchian and part of the middle Wasatchian, respectively. Solid circles represent individual specimens of known stratigraphic level. Solid triangles are type specimens. Open circle is an approximation of  $M_1$  size in *Vulpavus cf. australis* of known stratigraphic level. Open triangle reflects imprecisely known stratigraphic level of holotype of *Vassacyon promicrodon* in the central Bighorn Basin. Note that maximum rate of change in the *Miacis winkleri* - *M. exiguus* lineage, at this scale of resolution, is about 0.40 darwins. Note also the abrupt appearances of *Uintacyon rudis*, *Miacis winkleri*, and *Vassacyon promicrodon* indicating that they are probably immigrants in the early or middle Clarkforkian, at the beginning of the early Wasatchian, and at the beginning of the middle Wasatchian, respectively. *Vulpavus australis* may be a direct descendant of *Miacis exiguus*.

more generalized of the two, and it is probably more likely to represent primitive miacid morphology.

*M. latouri* differs from early Wasatchian *Miacis* in North America, to the extent that available materials can be compared, only in being older and in being smaller. Hence, European *M. latouri* is a plausible ancestor of North American *M. winkleri* and later species. One might conclude from this that miacids originated in Europe, but recent discovery of a very primitive *Miacis winkleri*-like miacid, *Miacis* ("Xinyuictis") *tenuis*, in the early Eocene of China (Zheng et al., 1975), confuses the issue by raising the possibility that miacids originated in eastern Asia and dispersed to North America and Europe. A better understanding of the stratigraphic record of miacids in early Eocene faunas of Asia and Europe will be required to clarify the early biogeographic history of this radiation.

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