

EARLIEST EOCENE MIACIDAE (MAMMALIA: CARNIVORA) FROM NORTHWESTERN WYOMING

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ABSTRACT—Fossil carnivorans are described from earliest Eocene localities in the Clarks Fork and southern Bighorn basins of Wyoming. Three new species, *Miacis rosei*, *Uintacyon gingerichi*, and *Vassacyon bowni*, collected from the base of the Wasatchian North American Land Mammal Age (Wa-0), are the smallest and possibly most basal members of their respective genera, and increase from one to four the number of miacids known from this faunal zone. An upper dentition of *Miacis deuschi* from slightly younger (Wa-2) deposits is also described. Previously known only from lower teeth and a single M1, the specimen of *M. deuschi* includes the left P3-M2, alveoli for the canine, first two premolars and the last molar, as well as most of the maxilla. The new material helps fill gaps in our knowledge of the dental morphology of basal Miacidae and provides insight into the functional differences of the carnassial teeth in the diverging *Uintacyon* and *Miacis* lineages. It also provides an opportunity to further assess the hypothesis that climactic warming in the earliest Eocene resulted in evolutionary dwarfing of mammalian species; based on three criteria for identifying dwarfed species at least one of the new taxa, *U. gingerichi*, is consistent with this hypothesis.

INTRODUCTION

THERE IS increasing evidence that all living members of the order Carnivora trace their origin to the family Miacidae (Wesley and Flynn, 2005; Polly et al., 2006), a paraphyletic taxon of early carnivorans that are best known from the Eocene of North America. The earliest North American miacids are all described from the Clarks Fork and Bighorn basins of northwestern Wyoming where mammalian biostratigraphy over the Paleocene–Eocene boundary is well documented and reasonably well correlated between the two basins (Bown et al., 1994; Gingerich, 2001; Gingerich and Clyde, 2001). *Uintacyon rudis* Matthew, 1915 is the oldest miacid, ranging from the middle Clarkforkian (latest Paleocene) to the middle Wasatchian North American Land Mammal Ages, with *Miacis winkleri* Gingerich, 1983 appearing next in the earliest Eocene at the very base of the Wasatchian North American Land Mammal Age (Gingerich, 1983). Unlike *Uintacyon* Leidy, 1872, specimens attributed to the genus *Miacis* Cope, 1872 are also known from the early Eocene of Europe and possibly Asia, supporting a contention that the morphology exhibited by early *Miacis* is more generalized than *U. rudis* and closer to that of the ancestral miacid condition (Rose, 1981). A phylogenetic analysis of the basalmost species of the North American early Eocene genera *Uintacyon*, *Miacis*, *Vassacyon* Matthew, 1909a, *Vulpavus* Marsh, 1871, and *Oödetes* Wortman, 1901 using viverravid carnivorans as the outgroup (Heinrich, 1997), however, did little to clarify the basal miacid morphology, and the geographical origin of the family has yet to be resolved.

We describe here recently collected fossils including new species of *Uintacyon*, *Miacis*, and *Vassacyon* from Wa-0 localities in the southern Bighorn Basin, and the previously all but unknown upper dentition of *Miacis deuschi* Gingerich, 1983 from the Clarks Fork Basin. The new species are the smallest known, and possibly basalmost members of their respective genera. Previous studies on mammals from Wa-0 localities have found that many species from this faunal zone are of smaller size than closely-related taxa from earlier and later sediments (Gingerich, 1989; Strait, 2004), and it has been suggested that this smaller size is a response to climactic change that occurred in the earliest Eocene (Gingerich, 2003; Strait, 2004). The new species are considered in light of this evolutionary dwarfing hypothesis. The new material considerably increases our knowledge of miacid species diversity in the earliest Eocene and, along with reconsideration of the early Eocene Asian miacid, suggests that much of the initial diversity within the family may considerably predate the Paleocene–Eocene boundary. Although specimens of the new *Miacis*

and *Vassacyon* species are rare and of limited use for phylogenetic analysis, comparisons of the upper dentitions of *Miacis deuschi* and the new species of *Uintacyon* shed some light on functional differences in mastication that may have contributed to the evolutionary divergence of *Miacis* and *Uintacyon*, and provide some additional circumstantial evidence that the morphology of early *Miacis* is primitive for Miacidae.

ABBREVIATIONS

Institutions.—IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; UCMP, University of California Museum of Paleontology, Berkeley; UM, University of Michigan Museum of Paleontology, Ann Arbor; USGS, United States Geological Survey, Denver, Colorado; USNM, National Museum of Natural History, Washington DC.

Measurements.—CL, maximum length of the upper canine, similarly defined for P1–P3; CW, maximum width of the upper canine, similarly defined for P1–P3; P4L, length of labial aspect of P4 between anterior border of parastyle and posterior border of metacone blade; P4Ln, length of lingual aspect of fourth upper premolar between anterior border of protocone and posterior border of metacone blade; P4W, width of P4 between labial border of parastylar shelf and lingual border of protocone; M1L, length of first upper molar between anterior border of parastyle and posteriormost margin of tooth perpendicular to the transversely oriented long axis of the tooth, similarly defined for M2; M1Wa, anterior width of M1 between labial border of parastylar shelf and lingual border of protocone parallel to the transversely oriented long axis of the tooth, similarly defined for M2; M1Wp, posterior width of M1 between labial border of metastylar shelf and lingual border of protocone parallel to the transversely oriented long axis of the tooth, similarly defined for M2; m1L, maximum length of lower first molar between anterior border of trigonid and posterior border of talonid, similarly defined for m2 and m3; m1W, maximum width of m1 between labial and lingual borders of trigonid perpendicular to the anteroposterior axis of the tooth, similarly defined for m2 and m3.

Other.—NALMA, North American Land Mammal Age; Cf, Clarkforkian NALMA; Wa, Wasatchian NALMA.

MATERIALS AND METHODS

The right maxilla of *Miacis deuschi*, USNM 392236, was removed from a limestone nodule collected at Houde site 9. This locality lies within the larger University of Michigan locality SC-160 measured at 1,720 m of the Clarks Fork Basin, Wyoming (Bloch, personal commun.), well within the Wa-2 faunal zone as defined by Gingerich (2001). The specimen was prepared using

a 7% acid solution to remove it from the surrounding matrix. Unlike many limestone blocks collected in the Clarks Fork Basin which have been found to contain numerous mammalian and avian skeletons (Houde, 1988; Houde and Olson, 1992; Bloch and Bowen, 2001; Bloch and Boyer, 2001), USNM 392236 was the only specimen retrieved from this particular limestone nodule. Marshall University field crews collected the remainder of the specimens described here from three localities in the Honeycombs region of the southeastern Bighorn Basin, Wyoming; Castle Gardens (UCMP locality V99019, also recorded as USGS D2018); What Lies Beneath (UCMP locality V99566); and Nessa's Niche (UCMP locality V99574). Castle Gardens is an unusually productive Wa-0 site with over 3,000 mammalian specimens collected through a combination of surface collecting and screen washing. The fauna is typical earliest Wasatchian (Wa-0), with *Copecion davis* Gingerich, 1989, *Ectocion parvus* Granger, 1915, *Sifhippus sandrae* Froehlich, 2002 [= *Hyracotherium sandrae* Gingerich, 1989], *Thrytacodon barae* Gingerich, 1989, *Chriacus badgleyi* Gingerich, 1989, and *Diacodexis ilicis* Gingerich, 1989, some of which have been previously described (Strait, 2001). High-resolution carbon isotope stratigraphy has shown that this locality lies within the global carbon isotope excursion that is coincident with the Paleocene–Eocene thermal maximum (Yans et al., 2006). What Lies Beneath is a surface-collected site that is laterally equivalent to Castle Gardens and has also yielded *H. sandrae*. Nessa's Niche is an anthill and although its exact stratigraphic relationship to Castle Gardens has yet to be determined, it has yielded Wa-0 taxa including *H. sandrae*, *T. barae*, *E. parvus*, and *Arfia junnei* Gingerich, 1989.

Fossils described here were compared to late Paleocene and early Eocene miacids from the collections of the American Museum of Natural History, the University of Michigan Museum of Paleontology, and the USGS (now under the auspices of the National Museum of Natural History). In addition, comparisons were made to casts of the early Eocene *Xinyuictis tenius* Zheng et al., 1975 (assigned to *Miacis* by Gingerich, 1983), from Ningjiashan in China, and to published descriptions of the early Sparnacian *Miacis latouri* Quinet, 1968 from Dormaal in Belgium. Dental terminology follows Van Valen (1966) and MacIntryre (1966), and measurements are based on those given by Gingerich (1983).

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821
 Family MIACIDAE Cope, 1880
 Genus MIACIS Cope, 1872

Miacis COPE, 1872, p. 2.

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

Included species.—*Miacis australis* Gustafson, 1986, *M. cognitus* Gustafson, 1986, *M. deutschii*, *M. exiguus* Matthew, 1915, *M. gracilis* Clark, 1939, *M. hargeri* Wortman, 1901, *M. hookwayi* Stock, 1934, *M. latidens* Matthew, 1915, *M. latouri*, *M. medius* Matthew, 1909b, *M. petilus* Gingerich, 1983, *M. rosei* n. sp., *M. sylvestris* Marsh, 1872, *M. washakius* Wortman, 1901, and *M. winkleri*.

Diagnosis.—Carnassials and premolars large or moderate in size, accessory cusps of lower premolars not well-developed; carnassial and tubercular dentition well differentiated, tubercular dentition small; parastyle of P4 small or minute; hypocone present on M1 of some species; M3 of moderate size in some species, absent in others; talonids of molars basined; jaws slender anteriorly or of moderate depth, and symphysis loosely sutured (after Matthew, 1909b). As noted by Gingerich (1983) and Flynn (1998), species attributed to *Miacis* tend to be generalized miacids lacking derived characters diagnostic of other genera, and the genus is in all likelihood a paraphyletic taxon.

Occurrence.—*Miacis* is known from the early through late Eocene of

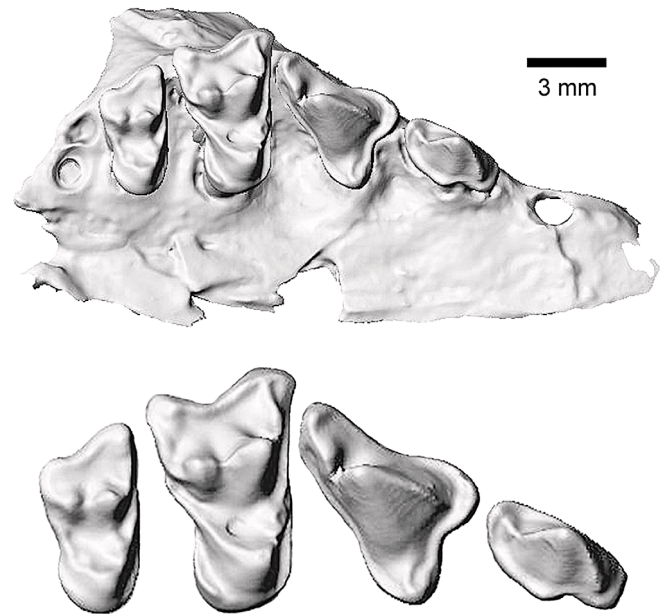


FIGURE 1—*Miacis deutschii* (USNM 392236) in occlusal view. Teeth with maxilla (top) and teeth enlarged (bottom).

North America (base of the early Wasatchian through the Duchesnean NALMA) and Europe. The earliest representatives on these continents are *M. winkleri* from northwestern Wyoming and *M. latouri* from Belgium. Gingerich (1983) suggested that *Xinyuictis tenius* from China be synonymized with *Miacis* but as argued below, we believe *Xinyuictis* Zheng et al., 1975 should be retained as a valid genus.

Discussion.—Only three species of *Miacis* are currently recognized from the faunal zones Wa-0 to Wa-3 of the early Wasatchian NALMA: *M. winkleri*, *M. deutschii*, and *M. exiguus*. *Miacis winkleri* and *M. deutschii* were differentiated by Gingerich (1983) on the basis of stratigraphic position (*M. winkleri* was found at Wa-1 localities, *M. deutschii* at Wa-2 localities), size (*M. winkleri* being smaller), and in *M. winkleri* having relatively higher trigonids and less-basined talonids on lower molars. *M. deutschii* was distinguished from *M. exiguus* in that the larger *M. exiguus* first appeared in the Clarks Fork Basin at Wa-3 localities with lower and broader-crowned lower molars (Gingerich, 1983). Gingerich (1983) went on to suggest that while *M. winkleri* (subsequently identified from localities of Wa-0 age; Gingerich, 1989) was likely an immigrant to the Clarks Fork Basin, *M. winkleri*, *M. deutschii*, and *M. exiguus* probably formed a single anagenetic lineage that had evolved in situ.

MIACIS DEUTSCHII (Gingerich, 1983)

Figure 1

Miacis deutschii GINGERICH, 1983, pp. 207–209, fig. 5.

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 m1 and m2. Differs from the latter principally in being smaller (about 10 percent smaller in linear dimensions), and also in having slightly narrower lower molars, and relatively broader upper molars” (Gingerich, 1983:207).

Description.—Maxilla complete except for frontal process and posterior portion of nasal process. Palatine, including sphenopalatine foramen, largely intact and in articulation with maxilla although held more in place by matrix than by any strong sutural contact between the two bones. Well-defined articular surfaces for contact between maxilla and premaxilla and maxilla and zygomatic. Also present is a smaller, incomplete articular surface where maxilla overlapped nasal bone. Large infraorbital foramen (2.4 mm wide) opens onto lateral surface of maxilla dorsal to posterior root of P3 and incisivo-maxillary canal just medial to infraorbital foramen passes through wall of maxilla. Maxilla includes P3–M2, a large alveolus for canine, single alveolus

TABLE 1.—Tooth measurements (mm) for North American early Eocene *Miacis* and comparison to European *Miacis latouri* and Asian *Xinyuictis tenius*. *Miacis rosei* n. sp. and *M. deuschi*¹ are described in this study, measurements for *M. exiguus* and *M. deuschi*² from Gingerich (1983), *M. latouri* from Quinet (1968), and *X. tenius* from Zheng et al. (1975). Definitions of measurements are given in abbreviations, sample sizes are given in parentheses.

	<i>M. rosei</i>	<i>M. winkleri</i>	<i>M. deuschi</i> ¹	<i>M. deuschi</i> ²	<i>M. exiguus</i>	<i>M. latouri</i>	<i>X. tenius</i>
P3L			4.0				
P3W			2.1				
P4L			5.0		6.0		5.1
P4LnL			5.9				5.8
P4W			3.9		4.7		3.6
M1L	3.0		4.5	4.3	4.8–5.2 (3)	3.8	
M1Wa	4.4		6.2	6.6	6.7–8.1 (3)	4.9	
M1Wp	4.1		6.1				4.6
M2L			2.9		3.4–3.7 (3)		
M2Wa			4.9		5.6–6.7 (2)		
M2Wp			4.3				
m1L		4.3–4.6 (4)		4.7–5.1 (6)	5.2–5.8 (11)		4.5
m1W		2.9–3.1 (4)		3.0–3.6 (6)	3.5–4.0 (11)		3.1
m2L		3.4–3.9 (3)		3.4–4.0 (4)	4.0–4.3 (7)		3.5
m2W		2.2–2.6 (4)		2.6–3.1 (4)	2.8–3.3 (7)		2.3
m3L	1.9	2.7–3.1 (3)		—	3.3 (1)		
m3W	1.4	1.7–2.1 (3)		—	2.5 (1)		

for P1, and two alveoli each for double-rooted P2 and M3. Teeth show relatively little wear and, in combination with the lack of sutural fusion, indicate the specimen was from a skeletally immature individual. Measurements for teeth given in Table 1.

P3 with strong ridges extending anteriorly and posteriorly from principal cusp. Anterior cingular cusp little more than a small bump on anterior margin of tooth. Small posterior accessory cusp and slightly better developed posterior cingular cusp present. Cingula extend from posterior cingular cusp anteriorly on both labial and lingual sides of tooth but lingual cingulum more extensive, continuing along entire margin of tooth to anterior cingulid cusp.

P4 preparacrista a distinct ridge beveled on lingual surface as it extends from apex of posteriorly inclined paracone to parastylar shelf. Parastyle small and more of a crest than a well-differentiated cusp. Well-defined cingulum extends labially to lateral side of paracone and a slightly narrower cingulum extends lingually to protocone. Embayment of anterior margin of tooth is not particularly marked. Protocone is better developed and more conical than parastyle, and positioned anterolingual to paracone but posterior to parastyle and parastylar lobe. A narrow ridge extends from apex of protocone to base of paracone and a narrow cingulum extends posteriorly from this cusp to base of well-defined metacone. Postparacrista nearly vertical and extends from apex of paracone posteriorly to deep carnassial notch. Carnassial notch relatively wide between postparacrista and metacone but narrows quickly and ends as a small keyhole. Metastylar blade between metacone and metastyle short and oriented more transversely than anteroposteriorly. A faint cingulum on labial margin of tooth extends from metastyle to a point opposite carnassial notch.

Paracone largest cusp of M1; oriented a little anterolabially and twinned at its base with a posterolabially oriented metacone about half its height. A thick, transversely oriented, bladelike paracrista extends labially from paracone to parastylar shelf. No stylocone present and worn parastyle extends only a little beyond margin of paracingulum. Metacrista steep and worn, and much less well defined than preparacrista. Ectoflexus anterior to twinned base of para- and metacones. Posterior to ectoflexus, metastylar shelf expands nearly as far labially as parastylar shelf. Small metastyle present. A raised ridge extends along labial margin of crown from parastyle to metastyle, creating a slight basin on stylar shelf between this ridge, the paracrista anteriorly, and para- and metacones lingually. Protocone subequal in height with metacone but differs from that cusp in being vertically oriented. Large and worn paraconule separated from protocone and preprotocrista by a well-defined carnassial notch (no postparaconule crista or wing is present) and paracingulum shows wear along its anterior margin. Small cusplules occur along postprotocrista but no metaconule or carnassial notch can be discerned resulting in a postprotocrista that is continuous with the metacingulum, the latter terminating at base of metacone. Trigone basined but posterior margin is noticeably lower than anterior margin, creating an overall slope to the surface. A round pit at base of protocone indicates point of contact between trigone and hypoconid during maximum occlusion. The pre- and postcingula of comparable width, but postcingula extends a little further lingually than precingulum. A slight swelling on lingual side of protocone can be traced from pre- to postcingulum. Precingulum extends further labially than does postcingulum, the latter terminating at midpoint of postprotocrista/metacingulum. Postcingulum and postprotocrista/metacingulum are well separated from one another.

M2 generally similar to M1 but differs from it in the following ways. Para- and metacone of M2 relatively smaller and paracrista extends labially to less well-defined parastyle rather than posterior to parastyle. Metastylar shelf of

M2 does not project nearly as far labially as parastylar shelf. A small crista extends from paraconule to base of paracone, a structure not found on M1.

Material examined.—USNM 392236 (Fig. 1), right maxilla with P3–M2.

Occurrence.—USNM 392236 was collected from Houde site 9. This locality occurs within UM locality SC-160 measured at 1,720 m stratigraphically in the Clarks Fork Basin, Wyoming. Gingerich (1983) initially cited the stratigraphic range for this species as between 1,720 and 1,760 m (within the Wa-2 faunal zone) but *M. deuschi* has also been found in Wa-3 sediments of the northern Bighorn Basin (Clyde, 2001).

Discussion.—The upper dentition of *M. deuschi* is known from the specimen described here and a single M1 (UM 80452) described by Gingerich (1983); no maxillary teeth are known for the slightly older and smaller *M. winkleri*. The M1 of USNM 392236 is generally similar to that of UM 80452, differing most notably in that para- and metastylar lobes are relatively less labially projecting than in UM 80452. The new specimen also differs from UM 80452 in that the pre- and postcingula do not extend as far lingually; the cingula of UM 80452 more nearly form a complete cingulum about the margin of the protocone. USNM 392236 differs from the type specimen of *M. exiguus*, AMNH 15176, in that it is considerably smaller (Table 1), the lingual cingulum of P3 is better developed (the cingulum does not extend anteriorly beyond the principal cusp in *M. exiguus*), the metastylar blade of P4 is relatively shorter, and the pre- and postcingula of M1 are not as well-developed (in *M. exiguus* they form a wide and continuous shelf about the protocone). A well-developed and nearly continuous lingual cingulum is also present on M1 of the smaller miacid from Dormaal, *M. latouri*, which otherwise looks quite similar to *M. deuschi*. Differences between *M. deuschi* and *Uintacyon* are discussed below.

The Asian *Xinyuictis tenius* is known from a single specimen, IVPP 4785, which includes P4, M1, p2, m1, and m2, and comparisons here are made to USNM 392236 and to lower molars of *M. winkleri* and *M. deuschi* (Table 1). The P4 of *X. tenius* differs from that of *M. deuschi* in that the parastylar shelf and protocone are notably narrower. M1 of *X. tenius*, which is missing the parastyle and part of the parastylar lobe, differs from that of *M. deuschi* in having an anteroposteriorly narrower protocone with steeper-sided (i.e., less inflated) walls, and narrower pre- and postcingula, and a well-developed cusp on the labial ridge of the tooth at the ectoflexus. The m1 and m2 of *X. tenius* differ from *M. winkleri* and *M. deuschi* in having much more open trigonids (owing to the relatively greater distance between para- and metaconids), and paraconids that are vertically inclined and subequal in overall size to the metaconid rather than anteriorly inclined, lower and significantly smaller than the metaconid as is found in

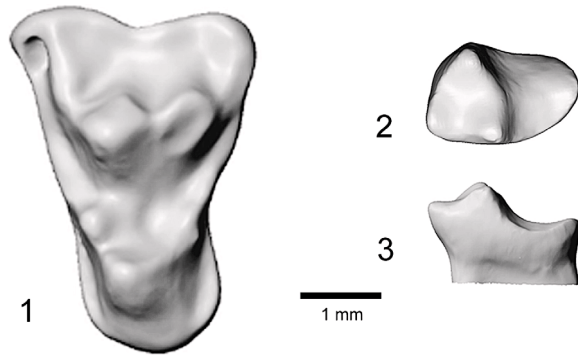


FIGURE 2—*Miacis rosei* n. sp. 1, LM1 (UCMP 216045) in occlusal view (1) and Rm3 (UCMP 216047) in occlusal (2) and lingual (3) views.

the early Wasatchian taxa. These differences in morphology between the North American taxa and the Asian specimen suggest that the genus *Xinyuictis* should be retained for the Asian species. Furthermore, “*M.*” *lushiensis* (Chow, 1975) from China and “*M.*” *thailandicus* Ducrocq et al., 1992 from Thailand, which share a morphology in which the paraconid of the lower molars is much larger than the metaconid, are more likely to be derived from *Xinyuictis* than have any phylogenetic relationship with North American taxa currently attributed to *Miacis*.

MIACIS ROSEI new species

Figure 2

Diagnosis.—Smallest known miacid; M1 pre- and postcingula less well-developed than in *M. deuschi*, small metaconule cuspule present and postprotocrista well separated from postcingulum of the protocone unlike all species of *Uintacyon*; m3 talonid lacks basining found in *M. winkleri*.

Description.—Dental dimensions about two-thirds those of the smallest described North American species *M. winkleri* and *M. deuschi* (Table 1). M1 (UCMP 216045) with considerable wear on paracone, metacone, paracristae, metacristae and paracingulum. Paracone tallest cusp, metacone slightly taller or subequal in height to protocone; ectoflexus just anterior of where bases of para- and metacones meet. Paracrista extends to labial margin of tooth posterior to well-developed parastyle; well-developed metastylar shelf extends labially as far, if not farther than, parastylar shelf. Paraconule well-developed and separated from preprotocrista by carnassial notch; labial to paraconule are worn remnants of two small cuspules. No distinct metaconule present but several small cuspules along the continuous postmetacrista/metacingulum give trigone a slightly concave shape. Paracingulum wide, extends to parastyle anterior to paracrista, and forms a distinct depression in wall of parastyle; metacingulum extends only as far labially as base of the metacone. Postcingulum of protocone better developed than precingulum but neither extend very far lingually; no continuous cingulum present. Labialmost extensions of pre- and postcingula meet the tooth wall well above para- and metacingula, respectively, creating a clear separation between precingulum and paracingulum anteriorly, and postcingulum and metacingulum posteriorly.

M3 (UCMP 216047) double-rooted and with considerable wear. Proto- and metaconids vertically oriented and subequal in height, paraconid smaller and angled anteriorly. Talonid markedly lower than trigonid. No distinct talonid cusps present but tooth narrows posteriorly forming a slightly raised surface at what was likely the hypoconulid. No evidence of talonid basining.

Etymology.—Named for Kenneth D. Rose in recognition of his contributions to our understanding of early Tertiary mammal evolution and biostratigraphy, his extensive fieldwork in the Bighorn Basin, particularly the southern basin, of Wyoming, and his mentoring of current and former students.

Type.—Holotype UCMP 216045, left M1.

Material examined.—UCMP 216047, right m3.

Occurrence.—The holotype was collected from the UCMP locality V99574, Nessa's Niche, NE¼, Section 23, Township 46 North, Range 90 West, and the lower molar from UCMP locality V99019, Castle Gardens (USGS locality D2018), in the SW¼, Section 18, Township 46 North, Range 89 West, Washakie County, Wyoming.

Discussion.—Besides being notably smaller than *M. winkleri*, *M. deuschi*, and *M. latouri*, *M. rosei* differs little from these other early Eocene taxa. M1 of *M. rosei* is generally similar to that of

M. deuschi (particularly UM 80452) and *M. latouri*, differing primarily in the extent to which the pre and postcingula of the protocone are developed; these cingula are relatively wider and extend a little further labially as well as lingually in *M. deuschi* and *M. latouri*. *M. rosei* differs from *X. tenuis* in much the same ways that *M. deuschi* differs from the Asian taxon, that is in having a more inflated protocone and lacking the distinct cuspule along the labial margin of the tooth at the ectoflexus. The m3 has not been described for *M. latouri*, *X. tenuis*, or *M. deuschi* but several specimens are known for *M. winkleri*. The m3 of *M. rosei* is similar to that of *M. winkleri* in being double-rooted and low-crowned but the talonid of the latter, unlike *M. rosei*, shows some basining as in other *Miacis*.

Genus UINTACYON Leidy, 1872

Uintacyon LEIDY, 1872, pl. XXVII, figs. 6–10.

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

Included species.—*Uintacyon asodes* Gazin, 1952, *U. bathygnathous* Scott, 1887, *U. gingerichi* n. sp., *U. jugulans* Matthew, 1909b, *U. massetericus* Cope, 1882, *U. rudis*, and *U. vorax* Leidy, 1872.

Diagnosis.—Premolars reduced without accessory cusps, p2–3 of equal size; carnassials reduced and post carnassial teeth enlarged; upper molars with distinct parastyle crest extended antero-externally, strong paraconule, weak metaconule, and lacking hypopones; talonids trenchant on all molars; M3 small; m3 single-rooted and small; lower jaw short, robust anteriorly, and with heavy symphysis (after Matthew, 1909b).

Occurrence.—*Uintacyon* is known from the latest Paleocene to the middle Eocene (middle Clarkforkian to Uintan NALMA) of North America. It has not, however, previously been recorded from a Wa-0 locality (Gingerich and Clyde, 2001).

Discussion.—The only species of *Uintacyon* currently recognized from the earliest part of the early Eocene is *U. rudis*, the next species, *U. massetericus*, appearing in the middle Wasatchian. The slightly basined talonids of *U. rudis* have distinguished it from all other members of the genus where the trenchant talonids possess no basining at all (Rose, 1981) and it has been distinguished from *M. winkleri* (and *M. deuschi*) in having lower m1 paraconids and metaconids subequal in height rather than the paraconid being notably lower than metaconid as in early *Miacis* (Heinrich, 1997). Further elaboration of morphologic differences between *Miacis* and *Uintacyon* are considered following description of a new species.

UINTACYON GINGERICHI new species

Figure 3

Miacis deuschi (Gingerich, 1983); STRAIT, 2001, p. 135.

Diagnosis.—Size comparable to *Miacis deuschi*. Differs from *M. deuschi* and *M. winkleri* in m1 paraconid more nearly vertical rather than anteriorly inclined, para- and metaconids subequal in height rather than metaconid distinctly higher, and talonid basin wider. Differs from *M. deuschi* and *M. exiguus* in P4 parastyle reduced; M1 pre- and postcingula less well-developed, metacingulum narrower and less labially expanded, metaconule absent. Differs from *Uintacyon rudis* in being smaller; trigonid with sharper cusps; paraconid relatively less robust.

Description.—UCMP 216044 includes left maxillary fragment with premaxillary contact, canine, first and third premolars and alveoli for P2 (Fig. 3.1). Measurements of all teeth given in Table 2.

Canine robust, base nearly as wide as anteroposteriorly long; tip of tooth is missing. P1 single-rooted with well-developed principal cusp but no accessory cusps. P3 with very small anterior accessory cusp lingually offset from principal cusp, well-developed posterior cingulid cusp at the posterior margin of the tooth. A slight cingulum extends from anterior accessory cusp labially around anterior margin of the tooth; a more prominent internal cingulum extends from the posterior accessory cusp to the base of the principal cusp.

Two P4s are known; UCMP 216044 is missing the protocone, UCMP 212555 is complete and includes a small piece of maxilla (Fig. 3.2). Paracone

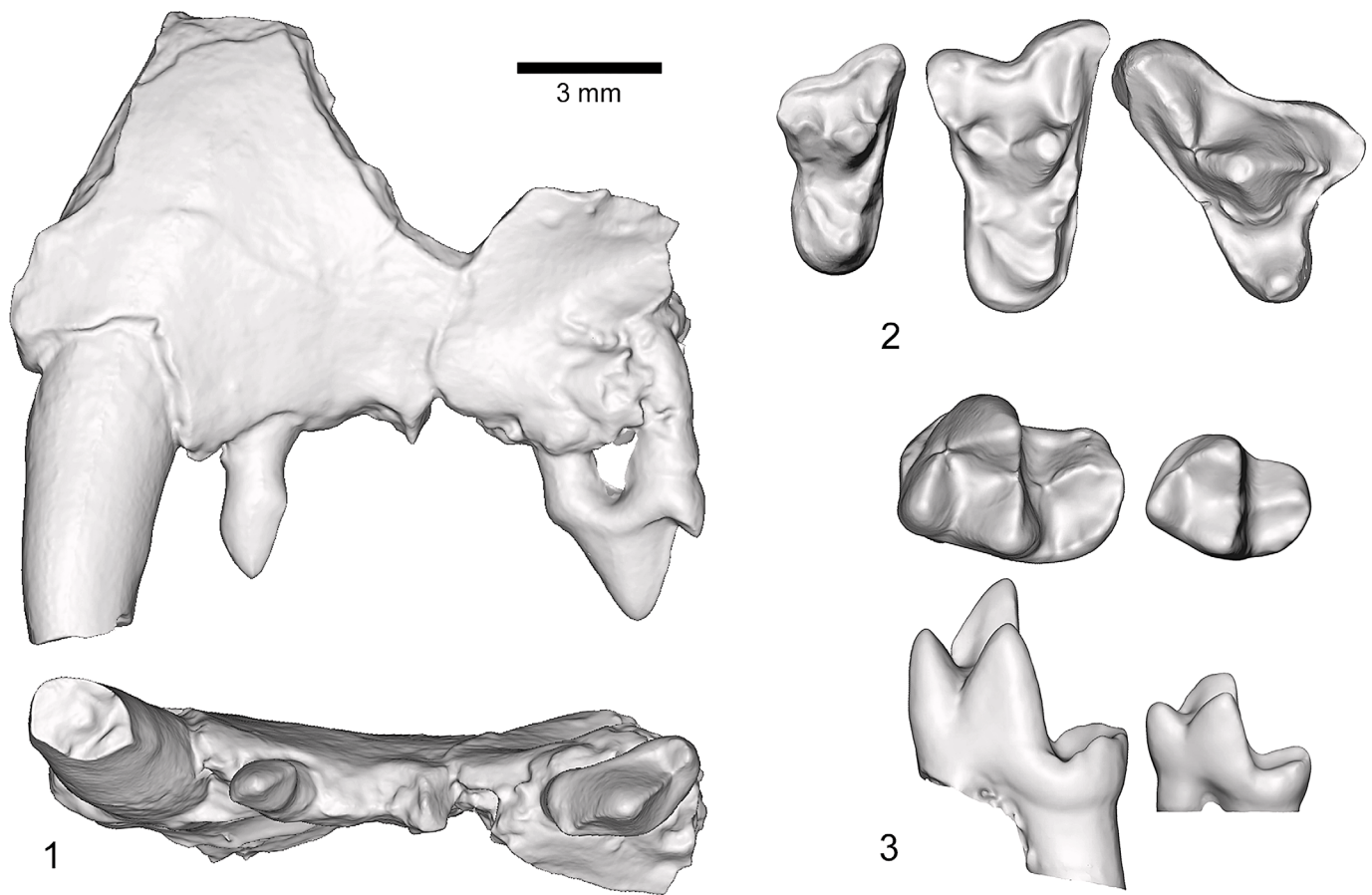


FIGURE 3—*Uintacyon gingerichi* n. sp. 1, LC1, P1, P3, and maxilla (UCMP 216044) in lateral (*top*) and occlusal (*bottom*) views. 2, RP4 (UCMP 212555), M1 (UCMP 216043), and M2 (UCMP 216044) in occlusal view. 3, Rm1 (UCMP 212540) and Rm2 (UCMP 212722) in occlusal (*top*) and lingual (*bottom*) views.

of P4 posteriorly inclined, preparacrista straight with beveled lingual margin along most of its length. Parastylar lobe labiolingually compressed; lingual side less steeply sloped than in other miacids. No parastyle present but a low ridge exists on labial margin of parastylar lobe unlike all known *Uintacyon*. Protocone well-developed and relatively far anterolingually of base of paracone but posterior to parastylar lobe, and cingula (better developed in UCMP 212555 than 216044) extend along length of labial and lingual margins to base of metastyle. Carnassial notch narrow and deep ending in a small

keyhole. Metastylar blade of moderate length and oriented more transversely than anteroposteriorly. Paracone and postparacrista of UCMP 212555 show relatively heavy wear but greatest wear is along anterolingual margin of metastylar blade and internal cingulum, where tooth contacted paracristid of m1.

Enough of the maxilla of UCMP 216043 is present anterior to M1 to distinguish a recess for m1 protoconid during maximum occlusion. As in all *Uintacyon*, M1 much wider transversely than long anteroposteriorly (Fig. 3.2). Paracone most prominent cusp and twinned to a smaller, posteriorly oriented metacone. A low, heavily worn, bladelike preparacrista extends across wide

TABLE 2—Tooth measurements (mm) for early Eocene *Uintacyon* and *Vassacyon*. *Uintacyon gingerichi* n. sp. and *V. boweni* n. sp. described in this study are compared to measurements for *U. rudis* and *V. promicrodon*¹ from Gingerich (1983) and *V. promicrodon*² from the USGS collections. Definitions for measurements given in abbreviations, parentheses denote sample size.

	<i>U. gingerichi</i>	<i>U. rudis</i>	<i>V. boweni</i>	<i>V. promicrodon</i> ¹	<i>V. promicrodon</i> ²
CL	2.7				
CW	2.3				
P1L	1.4				
P1W	1.1				
P3L	3.3	4.6			
P3W	1.8	2.3			
P4L	5.1–5.3 (2)	6.8–7.3 (5)		9.4	9.0–9.6 (2)
P4LnL	6.0				9.8–10.9 (2)
P4W	3.9	4.8–5.5 (4)		6.7	6.5–6.8 (2)
M1L	3.9–4.0 (2)	4.6–5.6 (8)		6.2–6.6 (3)	6.9–7.5 (2)
M1Wa	6.0	7.5–8.2 (7)		9.3–9.7 (3)	9.4–10.5 (2)
M1Wp	5.5				8.9–10.0 (2)
M2L	2.6	3.0–3.4 (4)	3.8–4.0 (2)	4.1–5.0 (2)	4.8–5.0 (5)
M2Wa	4.6	5.5–6.5 (4)	6.7–7.3 (2)	7.2–7.3 (2)	8.0–8.3 (5)
M2Wp	4.0		5.8–6.5 (2)		7.2–7.7 (5)
m1L	4.8	5.4–6.3 (21)		7.8–8.1 (4)	8.4–9.3 (8)
m1W	3.3	3.5–4.5 (23)		5.2–5.6 (4)	5.5–6.6 (8)
m2L	3.2–3.4 (2)	3.6–5.3 (23)		5.5–6.4 (4)	5.5–6.2 (16)
m2W	2.4 (2)	2.7–3.8 (23)		4.1–4.8 (5)	3.8–4.3 (16)

parastylar shelf to crescent-shaped parastyle; preparacrista with considerable wear. No stylocone can be discerned posterior to parastyle. Ectoflexus deepest just anterior to where bases of para- and metacones meet, and a low ridge extends along labial margin of crown from parastyle to a point just posterior to ectoflexus. Metastylar shelf with several small cusps along its length, extends to posterolabial corner of shelf; metastylar shelf projects only a little less labially than parastylar shelf and postmetacrista. Well-defined carnassial notch between prominent paraconule and preprotocrista; both paraconule and preprotocrista show some wear but much less than paracingulum anterolabial to paraconule. No metaconule is apparent; rather a small notch exists between heavily worn postprotocrista and short, narrow metacingulum that terminates at metacone. Notch meets postcingulum of protocone giving trigone a steeply sloped appearance (from anterior to posterior) with no internal basining, a morphology typical of *Uintacyon* and differentiating it from all other miacids. Neither pre- nor postcingulum is very wide but postcingulum extends further lingually about protocone. M2 (UCMP 216044) generally similar to M1 except that parastyle is less well-developed, metastylar shelf considerably smaller (the width of the tooth at the ectoflexus is slightly greater than the metastylar width), and pre- and postcingula of protocone very reduced (Fig. 3.2). Wear patterns on M2 similar to M1 with greatest wear on postprotocrista.

UCMP 212540, a right m1, is complete except for the anterior root (Fig. 3.3). Trigonid is high and open and cusps show little evidence of wear. Anterolabial cingulum well-developed. Protoconid substantially taller than para- and metaconids (subequal in height); metaconid significantly more robust than paraconid. Paraconid with slight anterior orientation, metaconid vertical, protoconid oriented a little posteriorly. Talonid anteroposteriorly long and wider posteriorly; cristid obliqua meets trigonid lingual to carnassial notch between proto- and metaconids. Several small cusps occur along margin of talonid in addition to a well-developed entoconid, worn hypoconid, and very small hypoconulid. Entoconid and reasonably well-developed cusp just anterior to it, create a raised entocristid along lingual margin of talonid; has the effect of producing a basined talonid that is only found in *U. rudis* among described *Uintacyon* species. Heavily worn hypoconid and adjacent basin wall indicate a point of contact with lingual surface of paracone and metacone of M1.

Two m2s are known for *U. gingerichi*, one is complete (UCMP 212722), the other (UCMP 216138) is missing the tip of the protoconid. Protoconid is largest and tallest cusp of trigonid; well-developed cingulid present anterolabial to cusp. Paraconid much smaller than metaconid and with distinct anterior inclination unlike vertical orientation of meta- and protoconids. Related to this, paralophid behind apex of paraconid and carnassial notch is horizontal whereas metalophid from metaconid to notch is sloped creating a distinct V with the protoconid. Talonid much lower and narrower than trigonid; cristid obliqua meets talonid directly beneath carnassial notch that separates proto- and metaconids. Hypoconulid poorly developed and talonid only slightly basined.

Etymology.—Named for Dr. Philip D. Gingerich in recognition of his contribution to early Tertiary mammal paleontology and stratigraphy in the Clarks Fork and Bighorn basins, his work on early miacids from this region, and his efforts at resolving land mammal faunal zones across the Paleocene–Eocene boundary, including Wa-0, from which the new species was collected.

Type.—Holotype UCMP 216043 and 216044, specimens from the same individual collected in 2003 and 2004, respectively. UCMP 216043, right maxillary fragment with M1; UCMP 216044; left maxillary fragment with canine, P1, alveoli for P2, and P3, incomplete left P4, right M2, and several cranial fragments.

Material examined.—UCMP 212555, right P4; UCMP 216046, left labial half of M1; UCMP 212540, right m1; UCMP 212554, left m1 trigonid; UCMP 212722, right m2; and UCMP 216138, left m2. Although collected in consecutive field seasons, there is little doubt that specimens 212540 and 212554 are from the same individual.

Occurrence.—The holotype specimens come from UCMP locality V99566, What Lies Beneath, NE¼, Section 19, Township 46 North, Range 89 West, Washakie County, Wyoming. UCMP 212540, 212554, 212555, 212722, and 216138 were collected from the Castle Gardens locality UCMP V99019 (USGS locality D2018), SW¼, Section 18, Township 46 North, Range 89 West, Washakie County, Wyoming. UCMP 216046 is from UCMP locality V99574, Nessa's Niche, NE¼, Section 23, Township 46 North, Range 90 West.

Discussion.—Several characteristics clearly identify the new species as a member of *Uintacyon*, including the transversely elongate shape of the first and second upper molars, its distinctly sloped trigone lacking internal basining, and elimination of the parastyle on P4. Among known species of the genus, *U. gingerichi* is most similar to *U. rudis*, sharing with that taxon distinct basining of the lower molars, whereas all other described species of the genus are characterized by trenchant talonids. *Uintacyon*

gingerichi differs from *U. rudis* primarily on the basis of its smaller size (Table 2), but the m1 trigonid cusps of *U. gingerichi* are also relatively sharper than those of *U. rudis* and the paraconid is not quite as vertically oriented, and in both respects is somewhat of an intermediate between the morphology found in early *Miacis* and *U. rudis*. These differences suggest that although *U. rudis* is known from stratigraphically older sediments (first appearance in the middle Clarkforkian), *U. gingerichi* may be the more basal member of the genus. An alternative possibility discussed further below, is that *U. gingerichi* is an evolutionary dwarfed version of *U. rudis*.

There are a number of characters that clearly distinguish *U. gingerichi* from the earliest Eocene *M. winkleri* and *M. deutschi*. Among the more prominent are the absence of the parastyle, more anterolingually positioned protocone, and a relatively longer metastylar blade on P4; distinctly narrower cingula (paracingulum, metacingulum, and pre- and postcingula of the protocone) and a low metacingulum that meets the postcingula rather than being well separated from it on M1; and a higher, more vertical paraconid and wider talonid basin on m1. Associated with some of these characters are other differences that can be generalized to the generic level, such as the more rectangular appearance and narrower, more steeply sided upper molars of *Uintacyon* compared to *Miacis*. One other interesting difference between *U. gingerichi* and *M. deutschi* relates to the wear patterns found on the P4 and anterior margin of M1. UCMP 216043 and 212555 are more heavily worn than the same teeth on USNM 392236 (UM 80452 is a virtually unworn M1), but the greatest amount of wear appears to be more labial in *U. gingerichi*, occurring on the posterior metastylar blade of P4 and parastyle, preparacrista, and nearly obliterating the labial aspect of the paracingulum of M1 whereas in *M. deutschi* wear is greatest on the carnassial notch of P4 and the paraconule, adjacent cuspule, and lingual aspect of the paracingulum of M1. This relatively more restricted wear pattern appears to be true of *M. exiguus* as well, based on analysis of specimens from the UM and USGS collections. Comparison of UCMP 216043 and UM 69127, an upper maxilla with M1–2 attributed to *M. exiguus* by Gingerich (1983), also shows that anterior to the parastyle and labial paracingulum, the maxilla is more deeply recessed in *Uintacyon*, allowing increased accommodation of the protoconid of m1. These differences suggest that in the earliest *Uintacyon* there was an emphasis on increased surface area for shearing during mastication, with the longer metastylar blade, reduced parastyle, and narrower paracingulum all contributing to an enhanced slicing mechanism. In early *Miacis*, however, shear was more specific to the carnassial notches and there appears to have been a greater emphasis on crushing and grinding as indicated by the wider cingula at the margins of M1.

Genus VASSACYON Matthew, 1909a

Uintacyon (in part), WORTMAN AND MATTHEW, 1899, p. 110.

Prodaphenous (in part), WORTMAN, 1901, p. 449.

Vassacyon MATTHEW, 1909b, p. 93.

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

Included species.—*Vassacyon boweni* n. sp.

Diagnosis.—Premolars reduced and spaced, increase in size posteriorly; upper molars with short parastyle, well-developed hypocone and proportioned as in *Uintacyon*; m1 with large, broadly basined talonid, m2 with low trenchant talonid (after Matthew, 1909b, 1915).

Occurrence.—*Vassacyon* has been identified from the Wasatchian faunal biochrons Wa-2 through Wa-5 of the Clarks Fork and Bighorn basins (Gingerich and Clyde, 2001) and although catalogued as *V. promicrodon*, it is possible that some of the oldest specimens may not belong to that species. Specimens attributed to *Vassacyon* sp. have been recorded from later Wasatchian (Lost Cabinian) and early Bridgerian localities in the Wind River Formation of central Wyoming (Stucky, 1984). The new species extends the range of the genus to the base of the Wasatchian.

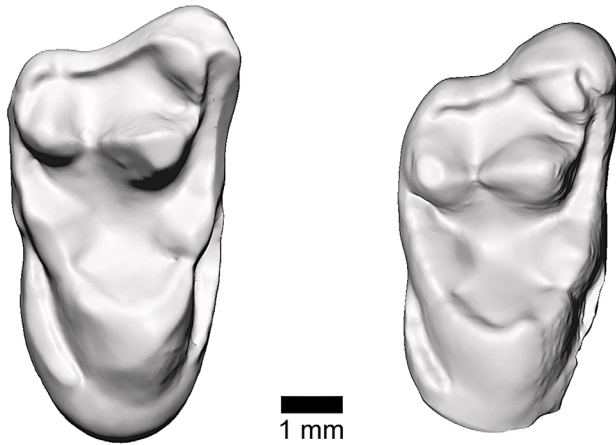


FIGURE 4—*Vassacyon bowni* n. sp. RM2s (UCMP 216164 on left, and UCMP 212163 on right) in occlusal view.

Discussion.—*Vassacyon* is by far the largest of the early Eocene miacids and until now has been represented by a single, morphologically variable species, *V. promicrodon*. While Matthew (1909a, 1915) suggested that *V. promicrodon* displayed a morphology intermediate between *Miacis* and *Vulpavus*, Gingerich (1983) considered *Vassacyon* to be derived from *Uintacyon*. A phylogenetic analysis of early miacids supported this latter contention, identifying synapomorphies shared by *U. rudis* and *V. promicrodon* that included subequal heights of the para- and metaconids on m1 and m2, and complete loss of the parastyle on P4 (Heinrich, 1997).

VASSACYON BOWNI new species
Figure 4

Diagnosis.—Smaller than *Vassacyon promicrodon*, larger than all other Clarkforkian and early Wasatchian miacids; M2 lacks hypocone and more transversely elongate than *V. promicrodon*; M2 metaconule well-developed, unlike *Miacis* and *Uintacyon*.

Description.—UCMP 216164 and 216163 are nearly complete (tooth roots are missing for both teeth); the former shows moderate wear particularly along para- and metacingula and postcingulum, the latter is largely unworn. Measurements given in Table 2.

Paracone considerably larger than metacone. Short paracrista separated from paracone by deep, wide notch; paracrista meets labial side of tooth posterior to small parastyle. Parastylar lobe larger and more labially projecting than metastylar lobe, as is typical for M2 of miacids, with width of the tooth at ectoflexus being slightly greater than width incorporating the metastylar lobe. A raised ridge extends along labial margin of tooth from paracrista to metastylar lobe. Paraconule well-developed and a wide paracingulum extends from paraconule to parastyle. Metaconule not as well-developed as paraconule but more prominent than in most miacids and helps create a deeply basined trigone; metacingulum extends only as far labially as base of metacone. Presence of metaconule results in a postcingulum that is well separated from metacingulum. Pre- and postcingula well-developed but limited to anterior and posterior margins of protocone respectively and do not approach one another on lingual side of tooth. There is no indication of a hypocone on the postcingulum of either tooth.

Etymology.—Named for Thomas M. Bown in recognition of his many important contributions to our understanding of the geology, paleontology, and biostratigraphy of the Bighorn Basin, and for introducing the Honeycombs region of the southern Bighorn Basin to SGS.

Type.—Holotype UCMP 216164, right M2.

Material examined.—UCMP 216163, right M2.

Occurrence.—Both specimens were collected from UCMP locality V99019, Castle Gardens (USGS locality D2018) in the SW¼, Section 18, Township 46 North, Range 89 West, Washakie County, Wyoming.

Discussion.—The M2 of the new species of *Vassacyon* shares with *V. promicrodon* (and differs from early Eocene *Uintacyon* and *Miacis*) a short paracrista, reduced parastyle, a well-developed metaconule (albeit smaller than the paraconule), and a deeply basined trigone. It differs from *V. promicrodon* in being found

in stratigraphically older sediments, lacking the characteristic hypocone, and in being generally smaller although some overlap in size may occur (Table 2). Comparisons of length to width measurements for the two species of *Vassacyon* also indicates the somewhat more transversely elongated nature of the upper molar in the new species. In all of the early miacid lineages, stratigraphically older species tend to possess this greater transverse elongation of the upper molars, suggesting a more squared tooth crown is convergently acquired.

In his analysis of the phylogenetic relationships of early Eocene miacids, Heinrich (1997) found several characters of the lower molars and P4 that united *Vassacyon* and *Uintacyon* as sister taxa. While none of these characters can be assessed in the new species, reconsideration of several characters not included in that analysis but which seem important in light of the new *Uintacyon* and *Miacis* material are mentioned here. The presence of small cuspsules rather than a well-defined metaconule (as in *M. rosei*), appears to be intermediate in form between the moderately well-developed metaconule and basined trigone of *V. bowni* and the morphology found in *U. gingerichi* n. sp. where not only is no metaconule present but the trigone is sloped from anterior to posterior such that the metacingulum and postcingulum nearly meet. The upper molars of *U. gingerichi* and *V. bowni* also indicate functional differences in mastication with an emphasis on shearing in *Uintacyon* and more crushing and grinding in *Vassacyon*, a trend further developed in *V. promicrodon* with the appearance of the hypocone. Together these two characteristics argue against a close phylogenetic relationship between *Uintacyon* and *Vassacyon*.

DIVERSIFICATION OF BASAL MIACIDAE

Identification of three new species, *Miacis rosei*, *Uintacyon gingerichi*, and *Vassacyon bowni*, from Wa-0 localities at the base of the Wasatchian NALMA, and reconsideration of the early Eocene Asian miacid *Xinyuictis tenius*, suggests that the family Miacidae had diversified to a greater extent by the Paleocene–Eocene boundary than previously recognized. At least four separate lineages, *Uintacyon*, *Miacis*, *Vassacyon*, and *Xinyuictis*, now appear to have evolved from a common ancestor during the Paleocene, and a fifth enigmatic lineage, *Oödetes*, may yet prove to have representation in the Paleocene. Given that only one species, *Uintacyon rudis*, is currently known from the Paleocene, the argument that as many as five genera existed in the Paleocene suggests much of the early evolution of the family Miacidae has yet to be documented.

The newly described upper dentitions of *Miacis deuschi* and *Uintacyon gingerichi* also provide some additional evidence into functional differences that likely relate to the evolutionary divergence of *Miacis* and *Uintacyon*. Unlike the short metastylar blade of P4 and the smaller, more concentrated wear facets along the paraconule and adjacent aspect of the paracingulum of M1 in *M. deuschi*, *U. gingerichi* exhibits an elongated metastylar blade with a relatively longer wear surface along the margin of this blade and the labial aspect of the paracingulum, the latter being all but obliterated by wear in UCMP 216043. These differences suggest that, compared to *Miacis*, the more transversely elongated upper molars of early *Uintacyon* provided for an increased shearing surface between P4 and M1 in the upper dentition and the trigonid of m1 in the lower dentition. Whether increased shearing capabilities are plesiomorphic for Miacidae or a derived character of early *Uintacyon* will have to await future phylogenetic analyses, but it seems likely that in this respect *Miacis deuschi* is closer to the primitive morphology.

EVIDENCE FOR MIACID DWARFING DURING THE WA-0
FAUNAL ZONE

One of the interesting characteristics of the mammalian fauna from Wa-0 localities is their smaller body size (body mass estimates based on tooth size) when compared to their closest Clarkforkian and Wasatchian relatives (Gingerich, 1989; Strait, 2004).

Gingerich (1989, 2003), for example, demonstrated estimated body masses for the condylarths *Ectocion parvus* and *Copacion davisii*, and the perrisodactyl *Hyracotherium sandrae* on the order of 50–60% that of the larger *E. osbornianus* (Cope, 1882), *C. brachypternus* (Cope, 1882) and *H. grangeri* (Kitts, 1956) species, with no discernible differences in tooth morphology other than size. There are several possible reasons for this finding including ecological replacement of the larger by smaller species, but Gingerich (see also Strait, 2004) has suggested that the smaller species may represent an example of evolutionary dwarfing, a term he uses “. . . to indicate that the observed case is unusual, that it involves small size, and to suggest inherited adaptive change (as opposed to temporary ecological stunting)” (2003: 468). The inherited adaptive change he is referring to is a reduction in body size as a response to the well documented period of climactic warming and elevated pCO₂ levels associated with the earliest Eocene (Bowen et al., 2001; and references cited therein), and Gingerich (2003) suggests that both are involved. An additional piece of circumstantial evidence to support the contention that climactic change selected for smaller body size in the earliest Eocene is that no mammalian species from Wa-0 are known to be larger than their closest relatives from stratigraphically older and younger deposits (Gingerich, 2003).

While wider geographic and temporal sampling will be needed to assess whether or not the new Wa-0 miacids are immigrants from nearby basins, three criteria, if met, would argue persuasively in favor of the dwarfism hypothesis. These include: 1) that the two species of interest should be sister taxa with few, if any, morphological differences other than size; 2) that only the smaller species should be found in Wa-0 sediments; and 3) that the larger sister taxon should stratigraphically bracket, i.e., occur in both earlier (Cf-3) and later (Wa-1) sediments than the smaller species. How well do *M. rosei*, *U. gingerichi*, and *V. bowni* meet these criteria?

A meaningful phylogenetic analysis incorporating the new taxa, and in particular *M. rosei* and *V. bowni*, will have to await the finding of more complete material. Sister taxa of these two species, however, are relatively easy to decipher; there is only one other identified species of *Vassacyon*, *V. promicrodon*, and of the early Eocene *Miacis* species the smaller size of *M. winkleri*, in the absence of any characters that indicate a closer relationship with *M. deutschii*, suggests that *M. winkleri* is the sister taxon of *M. rosei*. Morphologically, *V. bowni* differs from *V. promicrodon* in lacking a hypocone on M2, and *M. rosei* differs from *M. winkleri* in lacking talonid basins on m3 (it differs from *M. deutschii* in having less well developed pre- and postcingula on M1, no M1 is known for *M. winkleri*). The morphological differences among the *Miacis* species are not particularly diagnostic, m3 being one of the most variable teeth in the dentition of miacids and the degree of cingula development being unknown for *M. winkleri*. *M. winkleri* does not stratigraphically bracket *M. rosei*, and no *Miacis* specimens have been identified in the Clarkforkian, but the criterion that most persuasively argues against *M. rosei* being a dwarfed species of *M. winkleri*, is that both *M. rosei* and *M. winkleri* are known from Wa-0 localities. Like *Miacis*, *Vassacyon* is unknown from the Clarkforkian, and so *V. promicrodon* clearly does not stratigraphically bracket *V. bowni* (the earliest deposits with identified *V. promicrodon* are from faunal zone Wa-2, Gingerich and Clyde, 2001), but it is the presence of a hypocone only in the larger species, a derived character for Miacidae, that more strongly supports an interpretation of an anagenetic relationship between *V. bowni* and *V. promicrodon* rather than a case of dwarfism. In neither the *Miacis* nor the *Vassacyon* examples, then, can evolutionary dwarfism be completely ruled out to account for the presence of small Wa-0 species, but neither is there good support for such a hypothesis.

If any of the three new Wa-0 species is an example of evolutionary dwarfism it is *U. gingerichi*. *U. gingerichi* has a potential

sister taxon, *U. rudis*, found in both underlying Clarkforkian (Cf-3) and overlying Wasatchian (Wa-1) sediments but not in the Wa-0 faunal zone. The morphological differences that distinguish these taxa, namely the somewhat smaller and more anteriorly inclined paraconid of the lower molars, could conceivably be associated with individual variation. Calculations of body mass using regressions from m1 length on mass for 72 species of extant carnivores (Van Valkenburgh, 1990) give estimates for *U. rudis* ranging from 0.80 to 1.27 kg and an estimate for *U. gingerichi* (UCMP 212540) of 0.57 kg (m1 lengths from Table 2). Based on these estimates *U. gingerichi* is on the order of 50–60% of the body mass of *U. rudis*, percentages very similar to those found by Gingerich (2003) for the examples of evolutionary dwarfism cited earlier. Whether or not *U. gingerichi* is indeed an example of evolutionary dwarfism is difficult to know with any degree of certainty, but at present the available information is consistent with this interpretation.

CONCLUSIONS

The finding of three new taxa from the Wa-0 faunal zone at the base of the Wasatchian Land Mammal Age; *Miacis rosei*, *Uintacyon gingerichi* and *Vassacyon bowni*, increases substantially the number of miacid taxa known from the earliest Eocene. While *Uintacyon* and *Miacis* have previously been documented from late Clarkforkian and earliest Eocene sediments, respectively, *Vassacyon* was previously unknown from deposits earlier than the Wa-2 faunal zone, suggesting that much of the early miacid diversification in North America probably took place in the Paleocene. All three taxa are markedly smaller than other members of their respective genera, an observation consistent with what has been found for mammalian species recovered from Wa-0 sediments more generally. There is also reasonable evidence to suggest that at least one species, *U. gingerichi*, may be an example of evolutionary dwarfism postulated to have occurred among mammalian taxa as a response to climactic warming in the earliest Eocene.

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