MIDDLE EOCENE CARNIVORAMORPHA OF THE UINTA BASIN, UTAH

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ABSTRACT

The middle Eocene of North American was an important time in carnivoramorphan evolution, because it is when the order showed increases in diversity taxonomically and ecomorphologically. We describe new fossils of "miacoids" from the Uinta Formation of northeastern Utah, and assess their phylogenetic and paleobiological significance. A **new species** of *Miocyon* (Matthew, 1909), is described, ***Miocyon vallisrubrae***, which, in several aspects of lower molar morphology, is intermediate between the smaller *Miocyon major* (Matthew, 1909) and the larger *Miocyon scotti* (Wortman and Matthew, 1899). In addition, new well-preserved dental and gnathic specimens of *M. scotti* are described, along with fragmentary cranial and postcranial remains. The taxonomy of *Miocyon* is reviewed in light of the new material, which highlights the divergent specializations of the genus. These include an m1 with a relatively broad talonid and an m2 that is large, broad and relatively flat with little difference in height between the trigonid and talonid. These features suggest a shift from a shearing-dominated diet to a greater reliance on grinding. An ecological analogue for the radiation of this lineage among living carnivorans may be the sympatric African species of jackals. The distribution of similar features in *Miocyon* as well as other "miacoids" suggests an ecomorphologically similar phylogenetic group containing *Miocyon*, *Uintacyon* Leidy, 1872, and *Vassacyon* Matthew, 1909. New specimens from the Uinta Formation are also described of *Tapocyon* Stock, 1934, *Procynodictis* Wortman and Matthew, 1899, a new unnamed miacid, and an unnamed small viverravid. These highlight the adaptive diversity of carnivoramorphans during the Uintan North American Land Mammal Age.

KEY WORDS: Carnivoramorpha, Eocene, North America, Utah

INTRODUCTION

The earliest known members of the order Carnivoramorpha from the Paleocene and Eocene have traditionally been divided into two families: Miacidae and Viverravidae (Cope 1880; Wortman and Matthew 1899). The question of how these two families (collectively referred to in this paper as "miacoids") are phylogenetically related to the extant carnivoran families has been the subject of numerous research projects (Flynn and Galliano 1982; Flynn et al. 1988; Wyss and Flynn 1993; Flynn 1998; Spaulding and Flynn 2009). The most recent analyses suggest that "miacoids" are paraphyletic, and form the base of the carnivoramorphan clade, with viverravids as a nested clade within this basal group (Wesley-Hunt and Flynn 2005). Despite the phylogenetic uncertainty about "miacoids," it is clear that non-"miacoid" taxa attributable to extant families appear by the latest Eocene (Martin 1989). This suggests that the middle Eocene is an important time in the origin and diversification of the extant clades, and yet very little has been known of carnivoramorphan evolution in North America during this interval. In this paper, we describe new fossils of "miacoids" from the middle Eocene Uinta Formation of northeastern Utah, and assess their phylogenetic and paleobiological significance.

The Uintan North American Land Mammal Age (NALMA: Wood et al. 1941; Robinson et al. 2004) was originally based on the mammalian fauna of the Uinta Formation of the Uinta Basin in northeastern Utah (Scott and Osborn 1890; Black and Dawson 1966; Walsh 1996a), and is currently considered to be middle Eocene in age dated to approximately 46.5-40 Ma (Prothero 1998). The stratigraphy and paleoecology of the Uinta Formation have been analyzed recently (Thornton and Rasmussen 2001; Townsend 2004; Townsend et al. 2006; Gunnell et al. 2009), which builds on a long history of paleontological work in the Uinta Basin (Osborn 1895; Riggs 1912; Douglas 1914; Peterson 1919; Stagner 1941; Kay 1934, 1957; Hamblin 1987; Prothero 1996; Rasmussen et al. 1999). In addition to the fauna from the Uinta Formation, the Uintan NALMA is represented by faunas from Wyoming, southern California, southwestern Texas, and Saskatchewan (Walsh 1996a). Carnivoramorphans are a diverse part of all major Uintan faunas (Stock 1934; Dawson 1980; Storer 1984; Gustafson 1986; Walsh 1996b; Spaulding and Flynn 2009).

The first carnivoramorphan species to be described from the Uinta Formation was *Miacis uintensis* Osborn, 1895 (see Scott and Osborn 1887). Later work added several additional species to the carnivoramorphan faunal list and investigated the possible phylogenetic positions of the new taxa (Scott and Osborn 1890; Osborn 1895; Wortman and Matthew 1899; Peterson 1919). Clark's (1939) description of *Miacis gracilis* was the last publication of a new carnivoramorphan from the Uinta Formation, although finds
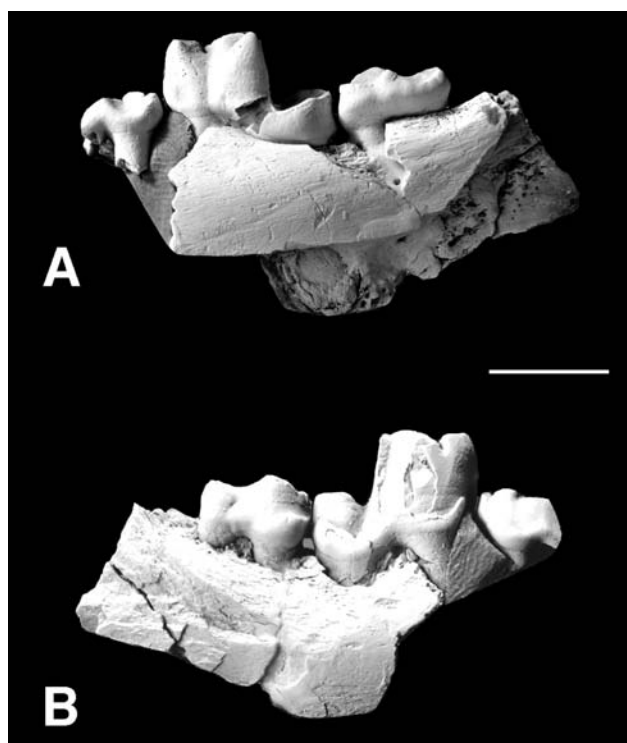
Fig 1.—Holotype of *Miocyon vallisrubrae*. **A,** right dentary (CM 71190) with p4-m2 in lingual view; **B,** buccal view. The p4 fragment is affixed with plasticine. The protoconid apex of m1 is broken off. Specimen coated with ammonium chloride. Scale bar = 1 cm.

in other Uintan age localities have led to major revisions of Uintan taxa (e.g., Stock 1934; Dawson 1980; Gustafson 1986; Bryant 1992; Wesley and Flynn 2003; Spaulding and Flynn 2009). Uintan age carnivoramorphan genera and their distribution are provided in Table 1, while those species found in the Uinta Formation appear in Table 2.

This paper describes new carnivoramorphan material from the Uinta Formation collected in recent years (Friscia 1997; Rasmussen et al. 1999). The Uinta Formation consists of three members, Uinta A, B, and C (Walsh 1996b; Townsend et al. 2006). The new carnivoramorphan fossils come from localities in Uinta B and C. All but the uppermost part of Uinta B contains early Uintan mammals, while Uinta C is late Uintan in age (Townsend et al. 2006). The recent finds include a new species of the large and poorly known genus *Miocyon* Matthew, 1909, along with additional specimens of *Miocyon scotti* (Wortman and Matthew, 1899). Two new small carnivoramorphans are also presented, as well as new specimens of established taxa that expand our understanding of particular groups. This new material will be discussed in the context of early carnivoramorphan phylogeny and adaptation.

Institutional Abbreviations.—AMNH, American Museum of Natural History, New York, NY; **CM**, Carnegie Museum of Natural History, Pittsburgh, PA; **SD-MNH,**. San Diego Museum of Natural History; **SMNH**, Saskatchewan Museum of Natural History, Regina, Saskatchewan; **TMM**, Texas Memorial Museum, Austin, TX; **USNM**, United States Natural History Museum, Washington, DC; **UW**, University of Wyoming, Laramie, WY; **WU**, Washington University, St. Louis, MO; **YPM-PU**, Princeton University Collections at Yale Peabody Museum, New Haven, CT.

Dental Abbreviations.—c, lower canine; **C,** upper canine; **m,** lower molar; **M,** upper molar; **p,** lower premolar; **P,** upper premolar.

SYSTEMATIC PALEONTOLOGY

Order Carnivoramorpha Wyss and Flynn, 1993
Family Miacidae Cope, 1880

Genus *Miocyon* Matthew, 1909

Uintacyon (Miocyon) Matthew, 1909:346.

Type species.—*Prodaphaenus scotti* Wortman and Matthew, 1899.

Included species.—*Miocyon major* (Matthew, 1909); *Miocyon magnus* Bryant, 1992; *Miocyon vallisrubrae,* new species.

Emended Diagnosis.—(Following Bryant 1992) Larger "miacoids" with relatively short, deep, and broad dentaries. Differs from other large "miacoids" (e.g., *Tapocyon* Stock, 1934, and *Didymictis* Cope, 1875) in having m1 with enlarged talonid basin relative to trigonid area, equidistant trigonid cusps on m1 and m2; unreduced m2 with square occlusal view; trigonid of m2 only slightly taller than talonid; crenulated rim on edge of m2, with no definite hypoconid, entoconid, or hypoconulid; large disto-buccal cingulum on m2. Differs from *Vassacyon* Matthew, 1909, in lacking hypocone on upper molars, and displaying smaller metaconule on M1. Differs from *Uintacyon* Leidy, 1872, in its unreduced and less trenchant talonid on m1 and m2.

Discussion.—In addition to the above formally named species of *Miocyon*, there is a single m2, UW 12566, from the Wiggins Formation of Wyoming that was tentatively placed in *Prodaphaenus scotti* Wortman and Matthew, 1899, by Eaton (1985) and retained in *Miocyon scotti* by Bryant (1992), who considered *Prodaphaenus* Matthew, 1899, to be a junior synonym of *Miacis* Cope, 1872. The type species of *Prodaphaenus* Matthew, 1899, not Wortman and Matthew, 1899, was inadvertently established in a list of names as *Miacis uintensis* Osborn, 1895, a species not congeneric with *Prodaphaenus scotti* Wortman and Matthew, 1899, and currently placed in *Miacis* Cope, 1872 (type species *Miacis parvivorus* Cope, 1872; Stock 1934). *Prodaphaenus* Matthew, 1899, is therefore a junior subjective synonym of *Miacis* Cope, 1872. Designation of

Table 1. Distribution and localities of carnivoramorphan genera across Uintan localities.

Genus	Uinta Basin, Utah	Badwater, Wyoming	Tepee Trail, Wyoming	San Diego, California	Trans-Pecos, Texas	Swift Current Creek, Saskatchewan	Hough Draw, Montana
Miacis	*			*			
Miocyon	*		*	*	*	*	
Tapocyon	*	*		*			*
Procynodictis	*	*	*	*	*		
Protictoides			*				
Viverravus	?					*	

Prodaphaenus scotti as the type species of *Prodaphaenus* Matthew, 1899, by Wortman and Matthew (1899) is invalid. A new genus-group name, *Miocyon* Matthew, 1909, was proposed at the level of subgenus, *Uintacyon (Miocyon)*, with *Prodaphaenus scotti* Wortman and Matthew, 1899, subsequently designated as type species by Bryant (1992). Nomenclatural clarification of this contorted synonymy is given by Matthew (1909) and Bryant (1992).

The Wyoming specimen is nearly 20% larger in linear dimensions than *M. scotti* (Table 3) from the Uinta Formation and should be removed from this species. An m2 from Saskatchewan (SMNH P1578.1) was also assigned to *M. scotti* (Storer 1984), but it is nearly identical in size to the Wyoming specimen and is best considered conspecific with it. The Wyoming and Saskatchewan fossils represent the largest species of *Miocyon*, but neither specimen is complete enough to serve as a holotype for a new species. (The classification of the Uinta Formation specimens below is a revision of Friscia 1997.)

Miocyon vallisrubrae, new species
(Figs. 1, 2C–F, 3C)

Synonymy.—*Uintacyon scotti:* Gustafson, 1986:46, not Wortman and Matthew, 1899 [Misidentification].

Holotype.—CM 71190, fragmentary right dentary with crowns of m1-m2, and a posterior fragment of p4 (Figs. 1, 2).

Type Locality.—WU-18 ("Gnat-Out-Of-Hell"), Uinta B Member, located in Uintah County, Utah (Thornton and Rasmussen 2001; Townsend et al. 2006; Gunnell et al. 2009). This locality is early Uintan in age, falling in chron 20R dated to 44-46 Ma (Prothero and Swisher 1992).

Referred Specimens.—TMM 40165-4, skeleton and skull referred to *Uintacyon scotti* by Gustafson (1986), from locality T 14 in the Chisos Formation, Brewster County, Texas.

Age and Geographic Distribution.—Early Uintan NA-LMA (middle Eocene) of Utah and Texas.

Measurements.—Table 3.

Etymology.—Latin for "from the red valley". Named for Red Wash, a major drainage in the eastern Uinta Basin, and also for the Red Wash petroleum installation, the employees of which have helped logistically with the Washington University field projects.

Diagnosis.—Intermediate in size between the smaller *M. major* and larger *M. scotti*; much smaller than *M. magnus*. Differs from *M. major* in having posterior cuspule on p4; less oblique orientation of cristid obliqua on m1; more widely spaced paraconid and metaconid on m1, with consequently shallower notch between cusps; lower cusp relief on trigonid of m2, with shallower notches between trigonid cusps; less defined and less obliquely-oriented cristid obliqua on m2; presence of crenulations on paracristid, posterior edge of talonid, and mesiobuccal cingulum of m2. Differs from *M. scotti* in smaller posterior accessory cusp on p4; less oblique orientation of cristid obliqua on m1; lack of crenulations on posterior edge of talonid of m1; retention of defined cristid obliqua on m2; more lingual position of paraconid and metaconid; smaller mesiobuccal cingular shelf on m2. Differs from *M. magnus* in its more trenchant talonid on m2 and its smaller size.

Description of Referred Specimen.—The posterior part of p4 shows a posterior accessory cusp, and slight cingula on the buccal and lingual sides, which form a cuspule where they join posterior to the accessory cusp (Fig. 1).

The cusps of the trigonid of m1 are equidistant from

Table 2. List of species of Carnivormorpha from the Uinta Formation, Uinta Basin, Utah.

Miacis vulpinus (Scott and Osborn, 1887)
Miacis gracilis Clark, 1939
Miacis uintensis Osborn, 1895
Miacis species indeterminate
Miocyon scotti (Wortman and Matthew, 1899)
Miocyon vallisrubrae, new species
Procynodictis vulpiceps Wortman and Matthew, 1899
Tapocyon robustus (Peterson, 1917)
Viverravidae, species indeterminate

TABLE 3. Comparative characters of described specimens of *Miocyon* and *Tapocyon* (measurements in mm).

SPEC. NUM.	SPECIES	AGE	m1 Length	m1 Width	m2 Length	m2 Width
AMNH 12159	*M. major*	Bridgerian	10.6	7.5	7.2	6.0
TMM 40165.4	*M. vallisrubrae*	Uintan	11.1	--	--	--
CM 71190	*M. vallisrubrae*	Uintan	12.2	6.7	8.5	7.0
CM 71191	*M. scotti*	Uintan	15.1	9.0	--	--
CM 71196	*M. scotti*	Uintan	14.2	8.3	--	--
CM 71194[a]	*M. scotti*	Uintan	--	--	10.4	9.0
UW 12566	*Miocyon sp.*	Uintan	--	--	12.4	9.4
SMNH P1578.1	*Miocyon sp.*	Duchesnean	--	--	11.9	9.7
SMNH P1900.1	*M. magnus*	Duchesnean	--	--	20.0	13.8
CM 71198	*T. robustus*	Uintan	11.8	7.5	5.9	4.2
CM 3023	*T. robustus*	Uintan	12.5	8.0	6.6	4.5

[a] Measurements for CM 71194 were taken on the right dentary.

each other. The protoconid is broken on the holotype, but would have been taller than either the paraconid or metaconid. The paraconid is slightly taller than the metaconid. The metacristid and paracristid are notched. There is a mesiobuccal cingulum on m1. The talonid of m1 is trenchant with the lingual edge ending in a cingulum. The talonid basin is shallow, and the cristid obliqua is oriented nearly straight mesiodistally, not obliquely (Fig. 2C).

The m2 of *M. vallisrubrae* (Fig. 2C) is distinguished by its low trigonid relative to *M. major*, although it is not as low as in *M. scotti* or *M. magnus*. All of the trigonid cusps are well defined but low. There are crenulations on the para- and metacristids as well as on the crest connecting the paraconid and metaconid. There is a projecting mesiobuccal cingular shelf, with crenulations. The talonid is only slightly lower than the trigonid. No cusps are identifiable along the talonid rim, but it is crenulated. The cristid obliqua is not well defined. The distobuccal cingulum is notched. The talonid is fairly broad but only slightly concave lingual to the cristid obliqua.

Discussion.—Gustafson (1986) originally attributed a specimen from Trans-Pecos, Texas, as *M. scotti* (TMM 40165-4). Comparison of that specimen with the new material from the Uinta Formation reveals that it more closely resembles *M. vallisrubrae* than *M. scotti*. The Texas specimen is more similar in size to *M. vallisrubrae* than the larger *M. scotti* (see Table 3), and the m1 has a less oblique orientation of the cristid obliqua and its talonid is less crenulated than *M. scotti*; therefore, we here tentatively attribute it to *M. vallisrubrae*.

Bryant (1992) listed several possible shared specializations found on the m2 of all species of *Miocyon*. The specializations shared by *M. vallisrubrae* are a low trigonid with angular cusps, shallow talonid, and a crenulated talonid rim.

Miocyon vallisrubrae is found alongside *M. scotti* at WU-18. A major difference between the two is size, which raises the question of whether they may be different sexes of the same species. Sexual dimorphism has been found in other genera of "miacoids" (e.g., *Uintacyon*, Gingerich 1983), but in these cases the sexual dimorphism is usually displayed in the anterior dentition, especially the canine. Without more complete specimens of the Uintan species, sexual dimorphism cannot be definitively excluded. However, in the specimens at hand the post-canine teeth are dissimilar enough in morphology to warrant a new specific designation (see paleoecological discussion below).

Miocyon scotti (Wortman and Matthew, 1899)
(Figs. 3A–B, 4C)

Referred Specimens.—CM 71191, right dentary with alveoli and roots for c-m2, and crowns for p2, p3, and m1, associated maxilla with P4 and roots for P3 and a fragment of the frontal, from Locality WU-18; CM 71196, left dentary with m1, from Locality WU-18; CM 71194, right dentary with alveoli and roots for p1-m3 and crowns for p3-p4 and m2, left dentary with alveoli and roots for p3-m2, and crowns for m2, from Locality WU-110; CM 71192, edentulous right dentary with alveoli for m1-m3, with associated distal left humerus, from Locality WU-8; CM 71195, fragmentary right dentary with associated m1, from WU-115; CM 71193, right M1, from Locality WU-101. All localities are located in Uinta B rocks and are of early Uintan age.

Emended Diagnosis.—Intermediate in size between *M. vallisrubrae* and *M. magnus*; much larger than *M. major* (Table 3). Differs from *M. major* in having small secondary accessory cusp on p4; more widely spaced paraconid
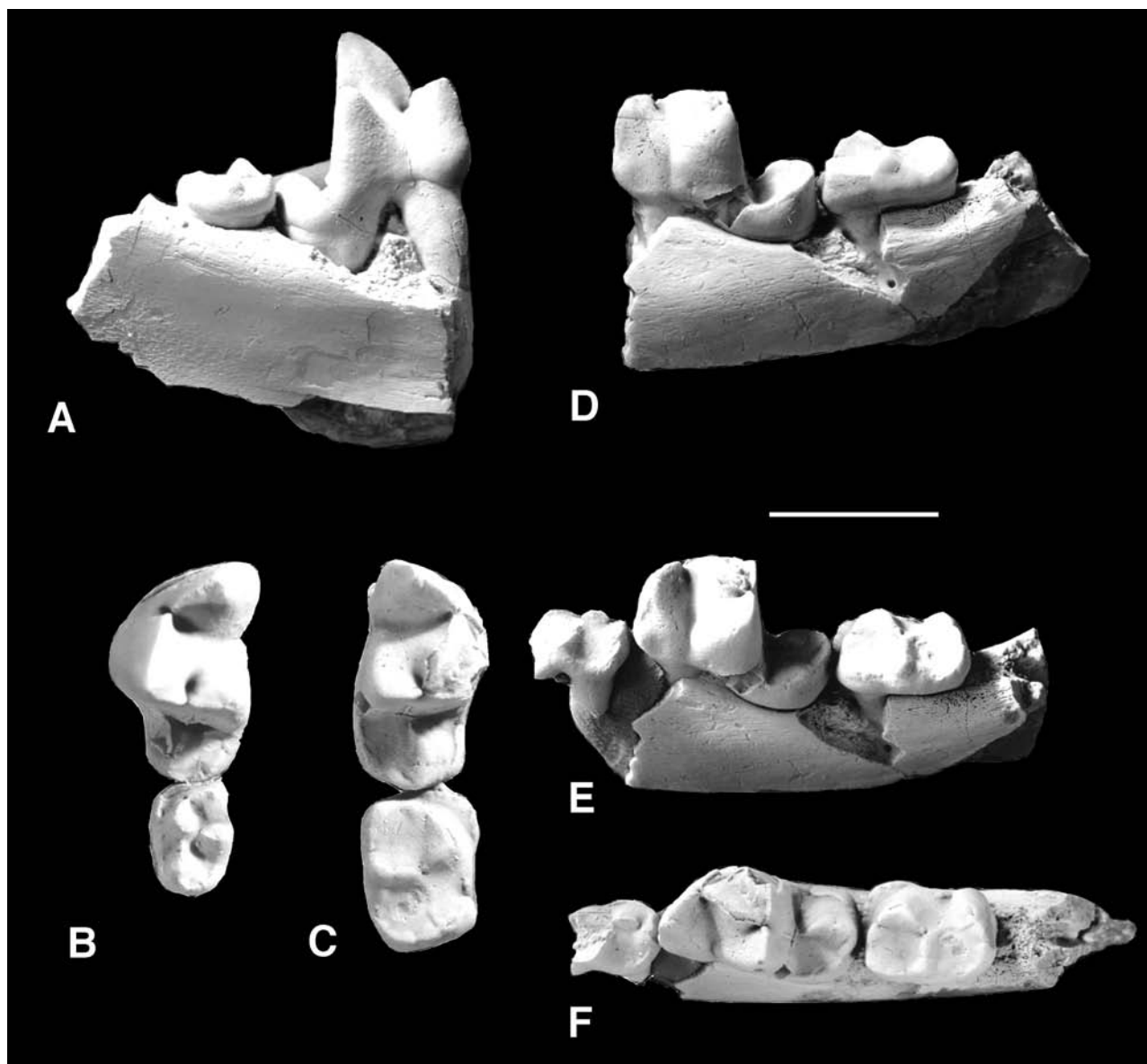
Fig. 2.—Comparative views of the dentary and m1-2 of *Tapocyon robustus* and *Miocyon vallisrubrae*. **A**, left dentary with m1-2 of *T. robustus* (CM 71198) in lingual view; **B**, teeth of same in occlusal view; **C**, m1-2 (holotype, CM 71190) of *M. vallisrubrae* in occlusal view; **D**, dentary and m1-2 of same specimen in lingual view; **E**, same in oblique lingual view and with p4 affixed; and **F,** same in occlusal view. Notice the relatively enlarged grinding surfaces in *Miocyon* compared to *Tapocyon*. Scale bar = 1 cm.

and metaconid on m1, with consequently shallower notch between them; lower cusp relief on trigonid of m2, with shallower notches between cusps; presence of crenulations on paracristid, posterior edge of talonid, and mesiobuccal cingulum of m2; larger mesiobuccal cingulum on m2; non-trenchant talonid on m2, with weak cristid obliqua, and enlarged distobuccal cingulum. Differs from *M. vallisrubrae* in having larger posterior accessory cusp on p4, and a crenulated distal cingulum on p4; more oblique orientation of cristid obliqua on m1; having crenulations on distal edge of talonid of m1; lacking a definite cristid obliqua on

m2, paraconid and metaconid of m2 more buccally located on tooth; large, inflated, lobate mesiobuccal and distobuccal cingula on m2. Differs from *M. magnus* in lacking trenchant talonid on m2.

Description.—The lower canine of CM 71191 is buccolingually compressed. It is large (10.0 mm in bucco-lingual cross section) and procumbent; its root extends back into the mandible to under p2.

The crown of p1 is missing from all specimens. Its alveolus is present on CM 71194, which indicates that
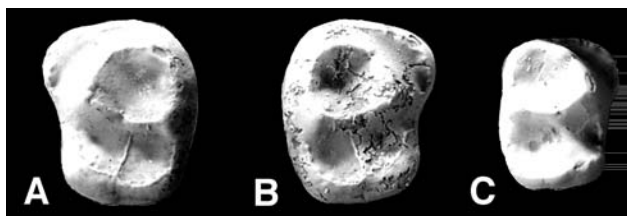
Fig. 3.—Lower second molars of *Miocyon*. **A, B**, left and right m2 of *M. scotti* (CM 71194) in occlusal view; **C**, right m2 of *M. vallisrubrae* in occlusal view. Tooth dimensions given in Table 3.

the tooth is small and single rooted. There is a diastema between p1 and the canine (3.4 mm) and also between p1 and p2 (1.9 mm). The p2 of CM 71191 has two roots and a tall protoconid (length = 5.5 mm, width = 3.4 mm). The posterior accessory cusp is small and is separated from the protoconid, making a wide talonid basin. A small cingulum is present on the lingual side of the protoconid. The alveolus for CM 71194 also shows two roots. There is a diastema (1.5 mm) between p2 and p3.

The p3 has two roots (length = 5.8 mm, width = 4.0 mm). The p3 of CM 71194 is nearly complete and a small talonid basin with a posterior accessory cusp is present, as is an even smaller anterior accessory cusp. The p3 of CM 71191 is similar, although it lacks the anterior accessory cusp.

The crown of p4 is broken in all specimens, but CM 71194 shows the most complete morphology. The p4 is large compared to the other premolars (length = 10.2 mm, width = 5.6 mm). No anterior accessory cusp is present. There is a small cingulum present on the mesiobuccal and distal borders. The first posterior accessory cusp is large and situated buccally. There is a small second posterior cusp, and many small cuspules along the distolingual border.

The first lower molar of CM 71191 has two roots and the trigonid is long mesiodistally with the distance between paraconid and metaconid equal to the length of both the paracristid and the metacristid. The paraconid is situated more buccally than the metaconid, giving the equilateral triangle of the trigonid cusps an orientation oblique to the tooth row. On all specimens the protoconid is broken but was probably only slightly taller than the paraconid. Trigonid height is 9.0 mm, from the labial edge below the protoconid to the height of the paraconid.

The talonid basin of m1 is narrow bucco-lingually, especially at the mesial end. This compression is due to the orientation of the cristid obliqua, which runs from the hypoconid area (see below) in the direction of the metaconid. This morphology of the cristid obliqua gives the talonid basin an ovate appearance with the long axis running mesiolingually to distobuccally. There is no definite hypoconid but the highest point of the edge of the talonid basin is at the distobuccal corner. There are several small cuspules along the distal and lingual edge of the talonid; consequently, a definitive entoconid or hypoconulid cannot be identified. The buccal edge of the talonid basin slopes to the base of the tooth where there is a small cingulum. There is also a cingulum at the base of the mesial end of the tooth.

The left m1 of CM 71196 shows a very similar morphology to the right m1 of CM 71191, and because they were found at the same locality within a meter of each other, they may represent the same individual. The m1 of CM 71195 is broken between the trigonid and talonid but also shows a similar morphology to the two preceding specimens.

The m2 of CM 71194 is low crowned and the trigonid is only slightly higher than the talonid. In occlusal view the tooth is somewhat rectangular in outline (Figs. 3A-B). There is a large cingulum present on the mesiobuccal corner of the tooth forming a broad shelf (Figs. 3A–B). The trigonid is low and the cristids joining the cusps are rounded in occlusal outline. The protoconid is the largest cusp, and both the paraconid and metaconid are small and barely distinguishable. The talonid basin is shallow, broad, and divided by a weak cristid obliqua. The buccal half of the talonid basin is formed by a wide and shallow distobuccal cingulum, making the talonid completely non-trenchant. No cusps are identifiable along the entire perimeter of the talonid basin. The entire edge of the tooth is rounded giving it a bulbous appearance. The crown of m3 is missing from all specimens but had one root at the very edge of the ascending ramus.

The dentaries of all five specimens are deep dorsoventrally. Below m1, the dentary is more than twice as deep as the trigonid height (dentary depth of CM 71191 is 18.2 mm; dentary length, from distal side of m1 to mesial edge of canine is 43.4 mm). The depth does not change between ml and p2. The dentary is very robust below m1, especially bucco-lingually (10.1 mm). The dentary is widest below m1, and narrowest below p3. It is wide again anterior to p3 due to the deeply-rooted, procumbent canine. The oblique orientation of the canine gives the dentary a slightly sigmoid shape in occlusal view. The mandibular symphysis is highly rugose and extends posteriorly to below p3 (CM 71191).

The P3 of CM 71191 is missing but judging from the alveoli and roots it had two roots. P4 (length = 12.9 mm, width = 9.9 mm) is similar to the holotype of *M. scotti* (YPM-PU 11238). The incomplete tooth has a broken protocone and metastyle. The base of the broken protocone indicates that it was not large. A cingulum is present lingually and buccally, but not along the mesial edge. The protocone lies only slightly distal to the paracone. There is no parastyle. The mesial edge of the tooth is notched in occlusal view between the paracone and protocone.

The M1 of CM 71193 (Fig. 4C) is similar to that of the fragmentary holotype of *M. scotti* (YPM-PU 11238). It is the same size (length = 11.1 mm, width = 13.2 mm), bears a small metastylar wing, and has a procingulum. The paracone is much larger than the metacone and more lingually placed than it. The labial ridge is worn, so it does not show the crenulations that the holotype does, but there are crenulations present on the metacrista. A small protoconule is present, as in the holotype.
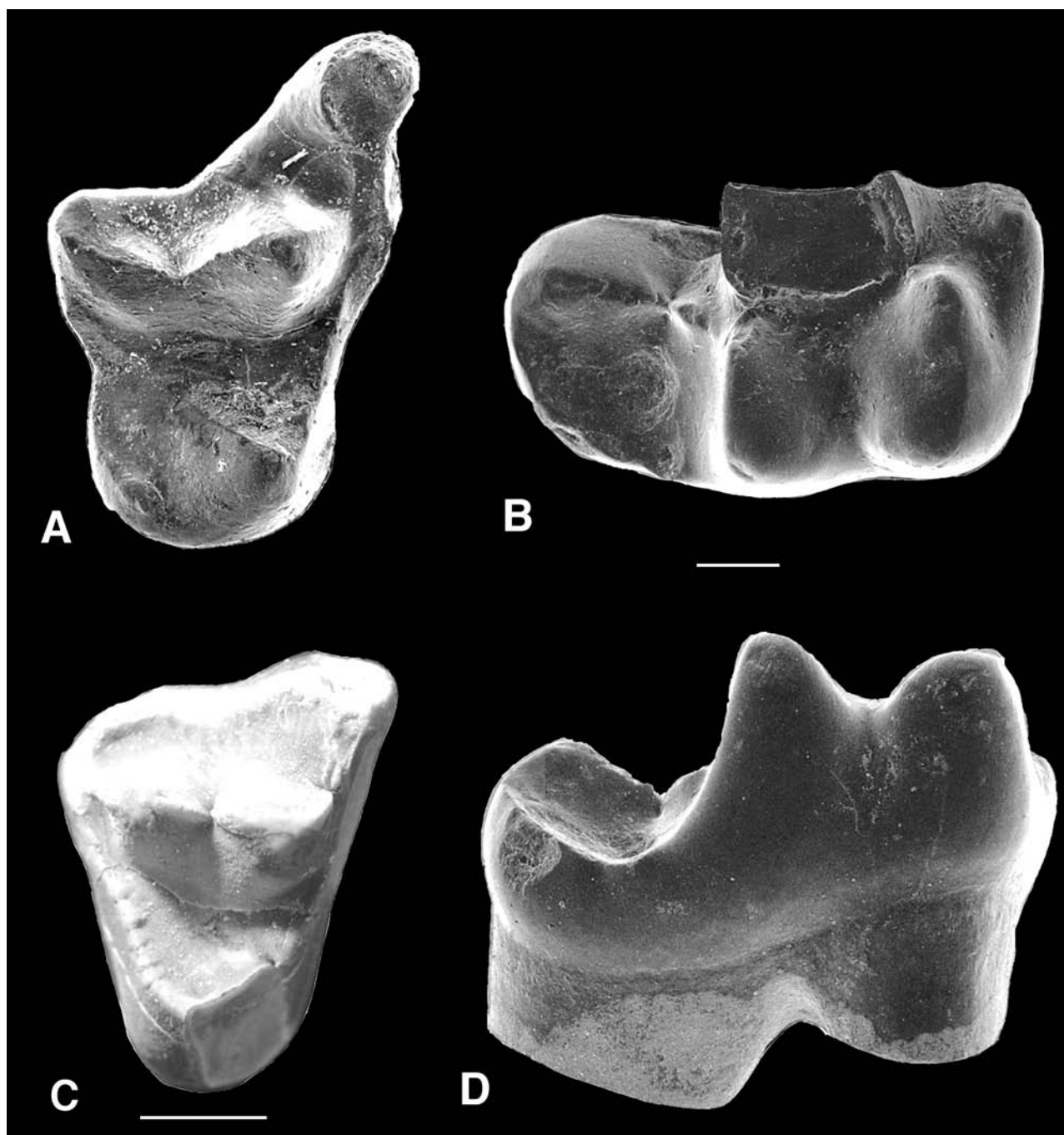
Fig. 4.—**A**, Scanning electron micrograph (SEM) of upper molar (CM 71188) of small viverravid from WU-2 in occlusal view. **B, D,** SEM of occlusal and buccal view of lower first molar of small viverravid (CM 71189) from WU-18; scale bar for A, B, and D = 500 microns; SEM by M. Veith, Washington University. **C,** Occlusal view of upper first molar of *Miocyon scotti* (CM 71193); scale bar = 4 mm.

The frontal of CM 71191 has sharp supraorbital ridges, meeting at a well-defined sagittal crest. On the interior surface there are depressions for large olfactory bulbs, and paired diploic foramina posterior to these depressions on either side of the sagittal suture. There are sutures posterior to the supraorbital ridges for contact with the parietals.

The distal humerus of CM 71192 is broad mediolaterally (bicondylar width = 43.5 mm). The medial epicondyle is large and wide (width from trochlear lip = 15.8 mm). The surface for the attachment of the digital flexors is irregular.

There is a large, complete, and oval entepicondylar foramen (length of long axis = 12.4 mm). The medial trochlear lip is well defined and is the most prominent part of the articular surface. The rest of the articular surface is flat with little distinction between the trochlear and capitular surfaces. The lateral ridge, although broken, is apparently thick. Proximally, there is the beginning of a large deltoid ridge. The olecranon fossa is broad mediolaterally (13.6 mm). The lateral epicondyle is small and slightly roughened, suggesting minimal muscle attachment.

Discussion.—These new Uintan specimens of *M. scotti* make it the best known species of the genus judged by the number of known individuals. *M. scotti* has the most derived m2 among species of *Miocyon* in the morphology of the talonid basin, which serves as a broad, shallow grinding surface, in contrast to the reduced or more trenchant basins of most early Tertiary "miacoids". The cristid obliqua is reduced to a small ridge of enamel crossing a new, expanded, shallow basin composed of the talonid basin and a greatly enlarged distobuccal cingulum.

Tapocyon Stock, 1934

Tapocyon robustus (Peterson, 1919)
(Figs. 2A–B)

Referred Specimen.—CM 71198, left m1-2, from Locality WU-48. This locality is located in Uinta C rock, and is late Uintan in age.

Description.—There is a small cingulum on the mesial edge of m1. The protoconid of m1 is much larger than either the para- or metaconid, and the paraconid is slightly larger than the metaconid. The para- and metacristid are both deeply notched and the paracristid is longer than the metacristid. The metaconid and protoconid are at the same distance mesiodistally on the tooth. The paraconid is situated far mesially and is slightly buccal to the metaconid. The talonid is relatively small compared to the trigonid, and the talonid basin is neither deep nor broad. A hypoconid is present and the lingual edge of the talonid is crenulated. The cristid obliqua reaches the trigonid just lingual to the protoconid.

The m2 bears a pronounced cingulum labially. The trigonid cusps are distinct; only a weak paracristid is present. The talonid is nearly as wide as the trigonid, with the cristid obliqua meeting the trigonid just lingual to the protoconid. A small hypoconid and entoconid are present.

Discussion.—In most measurements this specimen is slightly smaller than the holotype of *T. robustus* (Table 3), but not significantly so and it is nearly identical in morphology. The buccal cingula are more pronounced in the new specimen. The specimen is larger than *Tapocyon dawsonae* Wesley and Flynn, 2003, and differs from it morphologically in the ways outlined by those authors. *Tapocyon* is the

only large Uintan carnivoramorphan to display an m1 with such a high trigonid and a relatively small talonid. Dawson (1980) suggested that *Tapocyon* may have had dietary specializations similar to those of modern hypercarnivorous felids.

Procynodictis Wortman and Matthew, 1899

Procynodictis vulpiceps Wortman and Matthew, 1899

Referred Specimen.—CM 71197, left mandible with a complete crown of p4, partial crowns of p3 and m1, and alveoli for p3-m3, and right mandible with alveoli for p3-m3, with complete crowns of m2-m3, and a partial crown of m1. The specimen also includes a poorly preserved upper dentition and skull, but these are still encased in matrix, from Locality WU-80. This locality is located in Uinta B rock and is early Uintan in age.

Measurements.—Left p4 length = 8.0 mm, width = 4.5; m2 length = 4.0, width = .4; m3 length = 2.2, width = 2.0.

Description.—CM 71197 bears a p4 with rounded cusps. The anterior accessory cusp is not preserved, but both posterior accessory cusps are present, and are situated very close to the protoconid. The talonid of m1 is preserved on both specimens and has a buccal cingulum, but no buccal shelf. Neither a hypoconid nor entoconid is distinguishable.

The m2 is small, with a much smaller talonid than trigonid. The trigonid cusps are distinct and not joined by cristids. The protoconid is the largest cusp, and the paraconid is reduced relative to the other cusps. No entoconid or hypoconid are distinguishable from the raised talonid edge. The talonid basin is shallow, and the cristid obliqua is obliquely oriented and reaches the talonid just below the metaconid.

The m3 is very small and oval in outline. It bears two small indeterminate cusps and a ridge extending from the mesial cusp to the buccal edge of the tooth.

Discussion.—The holotype of *P. vulpiceps* (AMNH 2514) and other referred specimens (AMNH 2506, 1895; CM 37480) are much more complete and better preserved than this specimen. The new specimen bears the characteristic rounded cusps on p4 of this species and has a similar jaw depth. It is similar in size to the holotype, although the m2 bears a more narrow cingulum than that of the holotype (Wortman and Matthew 1899: fig. 7). CM 71197 is larger than both *Miacis uintensis* and *Miacis gracilis*. Wang and Tedford (1994) synonymized *P. vulpiceps* with *M. gracilis*. We consider the two to be distinct species, although possibly not distinct genera. *P. vulpiceps* is twice as large as *M. gracilis* (as measured by p4 area), lacks a second posterior accessory cusp on p3, has a smaller anterior accessory cusp on p4, a larger paraconid on m1 with a more deeply notched paracristid, and a larger protoconid on m2. *P. vulpiceps*

is closer to *M. uintensis* in morphology than it is to *M. gracilis*, but it is slightly larger; closer examination of these two species with the original specimens may reveal that they are synonymous.

Miacis Cope, 1872

Miacis species indeterminate

Referred specimen.—CM 71199, right mandible with p4-m1, from Locality WU-18. This locality is early Uintan in age.

Description.—The p4 has a small anterior accessory cusp, and the first posterior accessory cusp is large and separated from the protoconid. Posterior to the first posterior accessory cusp, the tooth is broken. The protoconid is high and pointed.

The trigonid of m1 is compressed mesiodistally. The metaconid is in line bucco-lingually with the protoconid. The talonid basin is wide bucco-lingually, mainly due to a less oblique orientation of the cristid obliqua, which meets the trigonid just lingual to the protoconid. The jaw of the new specimen is gracile and slender.

Discussion.—This specimen is 20% smaller in linear dimensions (p4 length = 6.1 mm, width = 2.4 mm; ml length = 7.4 mm, width = 3.8 mm) than the holotype of *M. gracilis* (CM 11900, p4 length = 6.8 mm, width = 2.6 mm; ml length = 8.3, width = 4.3). The trigonid is more closed in CM 71199; i.e., the metaconid is lingual to the protoconid, whereas in *M. gracilis* it is posterior to the protoconid. The talonid basin is wider and deeper in the new specimen than in *M. gracilis*, and this combined with the closed trigonid makes the trigonid and talonid more equal in size than in *M. gracilis*. The new specimen also differs from *M. gracilis* in having a shallower jaw (height below m1 is 7.6 in the new specimen and 11.4 mm in *M. gracilis*). The new specimen is much smaller than the corresponding dental elements of either *M. uintensis* or *Procynodictis vulpiceps*, the other small carnivoramorphans from the Uinta Basin. *Miacis hookwayi* Stock, 1934, of the California Uintan is a smaller animal and has a relatively wider talonid on m1.

In comparison to Bridgerian members of the genus *Miacis*, the new Uintan specimen shows the greatest similarity to teeth of *Miacis hargeri* Wortman, 1901. It is similar in size and the arrangement of cusps on the trigonid of m1, but *M. hargeri* lacks the wide talonid basin of m1 and the large posterior accessory cusp of p4 of CM 71199. The new specimen is larger than the other Bridgerian members of *Miacis*, all of which lack the large posterior accessory cusp on p4. CM 71199 is too fragmentary to formally erect a new species (a revision of the entire genus *Miacis* is needed). The specimen demonstrates the presence of a new small miacoid species in the Uintan fauna.
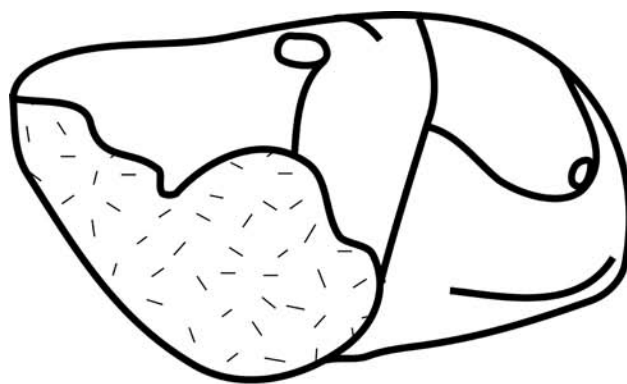
Miocyon vallisrubrae
talon./trigon. = 0.67
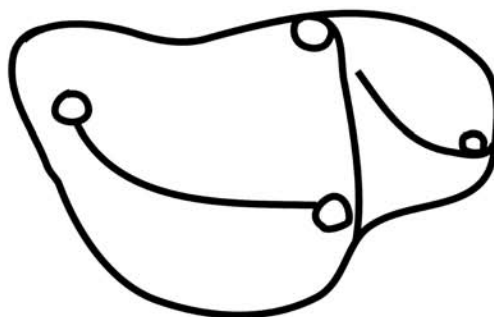
Tapocyon robustus
talon./trigon. = 0.36
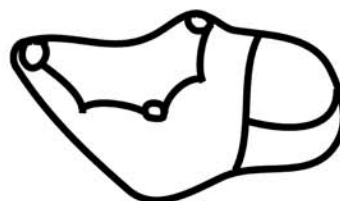
Miacis gracilis
talon./trigon. = 0.45

Fig. 5.—Occlusal outlines (drawn with camera lucida) of some Uintan age carnivoranmorphans. Mesial is to the left; lingual is to the top. Ratios were taken of talonid to trigonid occlusal area. Areas were measured as triangles with height at widest bucco-lingual distance, and base as mesiodistal length along buccal edge (for talonid) or lingual edge (for trigonid). All teeth are drawn to the same scale.

Family Viverravidae

Genus and species indeterminate
(Figs. 4A–B, 4D)

Referred Specimens.—CM 71188, right M1, from Locality WU-2; CM 71189, left m1 from Locality WU-18. Both localities are early Uintan in age.

Discussion.—Two isolated teeth in the Uinta Formation document a tiny viverravid, comparable in size to much older viverravids of the Paleocene and earliest Eocene. This is the first record of a viverravid from the Uinta Formation, and it is the smallest carnivoramorphan in the formation. *Viverravus* Marsh, 1872, is known from Uintan age deposits in Saskatchewan (Storer 1984). Among living carnivorans, the Uintan viverravid is nearly as small as *Mustela nivalis* Linnaeus, 1766, the least weasel, which is among the world's smallest extant carnivorans.

An upper M1, CM 71188 (Fig. 4A), is identified as a viverravid by its large metastylar wing. The metacone is larger than the paracone and the two are joined by a trenchant crest. The one distinctive trait is the presence of a pericone on the mesiolingual border of the tooth, which is different from most viverravids.

A lower m1, CM 71189 (Figs. 4B, 4D), is a damaged tooth with the protoconid missing, which would have been the tallest cusp on the trigonid. The talonid is trenchant, with the cristid obliqua mesiolingually oriented with minimal basin development.

The two specimens are comparable enough in size and morphology to be congeneric. Both specimens come from unusual localities, in that the sites are among the few yielding a diversity of small mammals (Thornton and Rasmussen 2001). Although the record of a small viverravid is a notable addition to the Uinta Formation fauna, the present specimens are insufficient for a more detailed treatment.

PHYLOGENETIC DISCUSSION OF *MIOCYON*

A "miacoid" clade consisting of *Vassacyon*, *Uintacyon*, *Prodaphaenus scotti* (now *Miocyon*), and *Tapocyon* was identified by Flynn (1998). This clade was based mainly on characters of the dentary, including depth at the symphyseal region, and also on the shortened facial region. Heinrich (1997) also concluded that *Uintacyon* and *Vassacyon* belonged together in a clade relative to other "miacoids" that he analyzed, which did not include *Miocyon* or *Tapocyon*; this was based on the shared presence of subequal height of the metaconid and paraconid on m1 and m2, and complete lack of a parastyle on P4. The specific characters defining this clade generally reflect a trend to broad, low molar crowns with reduced trigonids, expanded talonids, and a consequent increase in relative grinding area. Flynn (1998) interpreted *Vassacyon* as the sister group to the other genera (*Tapocyon*, *Uintacyon*, and *Miocyon*; his clade 12). His most distinctive character uniting the last three

taxa is a broad parastyle on M1 that projects buccally. A reanalysis of figures from the literature (Matthew 1909; Dawson 1980; Gingerich 1983; Flynn 1998; Wesley and Flynn 2003) as well as museum specimens, casts, and the new fossils described in this paper shows that the parastyle in *Miocyon*, *Uintacyon*, as well as *Vassacyon* is broad, but does not project as far buccally as it does in *Tapocyon*. In this character *Tapocyon* is more similar to other miacids such as *Procynodictis* and *Miacis*; so the condition of *Tapocyon* can be interpreted as a primitive character for this clade. *Tapocyon* has since been placed as a sister taxa to the extant Carnivora (Wesley-Hunt and Flynn 2005), although the study does not include the other genera of this group. If *Tapocyon* is indeed a sister taxa to a clade including *Miocyon*, *Uintacyon*, and *Vassacyon*, this entire clade may be a sister group to all extant Carnivora.

Vassacyon is intermediate between *Uintacyon* and *Miocyon* in the trend from high, narrow lower molar crowns to lower, broad molars seen throughout this clade. The ultimate expression of this evolutionary trend is seen in the genus *Miocyon*, especially *M. scotti*. This species has lost the traditionally defined talonid basin on m2 (i.e., defined by the posterior molar cusps), becoming completely non-trenchant with accompanying loss of a cristid obliqua and a greatly enlarged distobuccal cingulum. *M. magnus* is closest to *M. scotti* in this respect, although it is still somewhat trenchant. Among the remaining members of *Miocyon*, the most primitive, judging from this assemblage of dental traits, is the Bridgerian *M. major*. *M. vallisrubrae* and the indeterminate species from Wyoming and Saskatchewan differ from it in having an enlarged talonid basin on m1 and m2, and subequal trigonid heights.

An interesting outcome of this study of the group containing *Miocyon*, *Uintacyon*, and *Vassacyon* is that, the most primitive forms morphologically are also the earliest geologically. *Uintacyon* is the earliest member of the lineage to appear in North America and may have been an immigrant from Asia during Clarkforkian times (Gingerich 1983). *Vassacyon* appears later in the Wasatchian of Wyoming (Flynn 1998). *M. major* is a Bridgerian species (Flynn 1998), and the remaining species of *Miocyon* are either Uintan or Duchesnean. *Tapocyon* is a late occuring genus that may have evolved in a parallel to *Uintacyon*, *Vassacyon*, and *Miocyon*. The morphology and chronology suggest that these last three genera may represent an approximate lineage, with minor species level radiations within each genus.

DISCUSSION OF DENTAL ADAPTATIONS AND
ECOLOGY OF *MIOCYON*

Miocyon presents a suite of characters suggesting a unique dietary adaptation unknown in other early Tertiary carnivoramorphans. Previously these "miacoids," including earlier members of the "Miacoidea" and Vivierravidae, all display a fairly basic carnivoran dental pattern in retain-

ing large shearing surfaces on high-crowned cheek teeth to process their food. In contrast, the large m1 with a broad, but shortened, trigonid, and the extremely low crowned m2, found in *Miocyon*, are consistent with a larger grinding emphasis in mastication. This can be easily discerned by a comparison of talonid/trigonid area ratios in *Miocyon* and other typical Uintan age carnivoramorphans. The talonid basin is where most grinding occurs in tooth occlusion, whereas the surfaces of the trigonid are used mainly for shearing (Kay and Hiiemae 1974). Fig. 5 illustrates occlusal outlines of m1 in *Miacis gracilis*, *T. robustus*, and *Miocyon vallisrubrae*. *M. gracilis* displays a typical early carnivoramorphan pattern in which the talonid is proportionally much smaller than the trigonid in occlusal area. This condition characterizes all small-bodied carnivoramorphans from the Uintan age and earlier. *T. robustus* is a much larger carnivoramorphan, but the occlusal area ratio of talonid to trigonid is similar to that of *M. gracilis*, with the talonid being much smaller than the trigonid. *M. vallisrubrae* is not much larger than *T. robustus*, but the talonid is nearly equal in occlusal area to the trigonid. These tooth characters in combination with the robust jaw morphology may characterize a more omnivorous diet than seen in other early carnivoramorphans. The broad, flat occlusal surfaces suggest that hard object grinding may have been a significant component of the diet.

The assemblage of distinctive characters found in *Miocyon* can be seen developed to a lesser extent in other related "miacoids." *Uintacyon* and *Vassacyon* show an unreduced m2 and an unreduced talonid relative to trigonid on m1 compared to other contemporaneous carnivoramorphans. *Vassacyon* also shows the unique trait of possessing a hypocone on the upper molars, which is also an adaptation to a more generalized diet by providing a new crushing surface against the enlarged talonid basin for grinding mastication.

A modern equivalent of *Miocyon* may be the comparably-sized modern jackal species (various species of *Canis* Linnaeus, 1758) of the savanna of eastern Africa. Jackals are dietary opportunists, eating meat when they can get it, but scavenging or eating insects or vegetable matter when meat is scarce (Kingdon 1997). The presence of two species of *Miocyon* at one locality (WU-18) also finds an analogy in modern jackals. Three species of jackals are found sympatrically in eastern Africa and various modes of character displacement have been proposed to account for their overlapping ranges (Van Valkenburgh and Wayne 1994). Studies of character displacement in the fossil record have met with limited success (Gingerich 1996; Werdelin 1996). The sample size of *Miocyon* is too small to currently evaluate the process in this case, but we hypothesize that this may be a relevant test when more specimens in a stratigraphic framework become available.

CONCLUSIONS

The Uintan NALMA was an important time in carnivoramorphan evolution. It sits near the base of the carnivoran radiation that gave rise to the modern families. The causes for this radiation are only beginning to be understood. An invasion of new ecological niches was a definite contributor to the diversity, and *Miocyon* and its close relatives are an example of a unique adaptive trend. This group may document the first movement of carnivoramorphans from a narrow fauna-eating niche, to a more generalized or omnivorous diet. Only by looking at these and other "miacoid" lineages in both a phylogenetic and paleoecological context will we begin to tease out the origins of modern carnivoran groups.

ACKNOWLEDGMENTS

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