

COPROLITES AND MAMMALIAN CARNIVORES
FROM PIPESTONE SPRINGS, MONTANA,
AND THEIR PALEOECOLOGICAL SIGNIFICANCE

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ABSTRACT

Pipestone Springs Main Pocket (PSMP) (Renova Formation, Jefferson County, Montana) has yielded an unusually rich concentration of mostly small-bodied Chadronian (late Eocene) mammals. Coprolites are common at PSMP and indicate which taxa and skeletal elements were consumed, as well as provide insight as to which carnivore species were likely to have deposited their feces at the site. Two distinct coprolite groupings were recognized based on differences in diameter, morphology, and abundance of bone. The sample of larger coprolites ranges in diameter from 16–29 mm and lacks a distinct mode. Some of the larger coprolites contain bone, but if present, it is sparse, poorly preserved, and unidentifiable. The sample of smaller coprolites varies in diameter from 4–15 mm and has a prominent mode at 10–11 mm. Many of the smaller coprolites contain abundant bone that is often highly fragmented. Osteoderms, bone ends, or dental elements identified to taxon in smaller coprolites indicate that marsupials, lizards, lagomorphs, and rodents were prey of smaller PSMP carnivores. Most elements identified as lagomorph or rodent probably represent *Palaeolagus temnodon* and *Ischyromys veterior* based on their high abundance in surface collections. Undigested bone from disaggregated carnivore feces did contribute to the large number of small dentigerous elements recovered from surface collections at PSMP, but it probably was not a major source because only two smaller coprolites had an exposed partial dentary or maxilla. The remains of mammalian carnivores are comparatively rare at PSMP and nine taxa are described, 52% of which represent *Hesperocyon gregarius* and 21% *Brachyrhynchocyon dodgei*. If the percentage of surface collected specimens for each carnivore taxon at PSMP is a reflection of activity at the depositional site, most of the smaller coprolites probably represent *Hes. gregarius*. To test this hypothesis, the ratios between feces diameter and body mass, as well as average lower first molar, (m1), length and body mass in an extant canid were applied to m1s of *Hes. gregarius* and the smaller coprolites from PSMP. Results indicate a mass of 3.3 kg for the smaller PSMP carnivore and 2.9 kg for *Hes. gregarius* from PSMP, both similar to the mass of *Hesperocyon* based on skeletal material. Also, the mode of smaller diameter coprolites is more prominent than the mode of the diameter of feces from an extant canid, which suggests that most of the smaller PSMP coprolites represent the activity of a single species, in this case *Hes. gregarius*. Many larger coprolites at PSMP probably represent *Br. dodgei* based on its high relative abundance, but the lack of a prominent mode for the larger coprolites suggests that one or more other species also contributed to the sample.

KEY WORDS: *Brachyrhynchocyon*, Chadron Formation, *Hesperocyon*, Orella Formation, Renova Formation

TABLE 1. Mammalian faunal list from Pipestone Springs Main Pocket, Climbing Arrow Member, Renova Formation, Jefferson County, Montana. Modified from Tabrum et al. (2001: table 1); sources for selected additions are: *Ischyromys* large species (Homidan and Lofgren 2016), *Pipestoneia douglassi* (Tabrum and Métais 2007), *Hesperopetes* sp., “*Domnina*” *sagittariensis*, and cf. *Oreotalpa florissantensis* (Tabrum unpubl. data).

DIDELPHIMORPHIA	
<i>Didelphidectes pumilus</i>	<i>Adjidaumo minimus</i>
<i>Copedelphys titanelix</i>	<i>Paradjidaumo trilophus</i>
<i>Herpetotherium valens</i>	<i>Aulolithomys bounites</i>
<i>Herpetotherium fugax</i>	<i>Heliscomys</i> sp.
LEPTICTIDA	
<i>Leptictus acutidens</i>	<i>Hyaenodon</i> sp., cf. <i>H. crucians</i>
<i>Leptictus thomsoni</i>	<i>Hyaenodon microdon</i>
LIPOTYPHILA	
<i>Centetodon kuenzii</i>	<i>Hesperocyon gregarius</i>
<i>Micropternodus borealis</i>	<i>Mustelavus priscus</i>
<i>Apternodus mediaevus</i>	<i>Brachyrhynchocyon dodgei</i>
<i>Oligoryctes altitalonidus</i>	<i>Daphoenictis tedfordi</i>
<i>Oligoryctes cameronensis</i>	<i>Parictis montanus</i>
<i>Domnina thompsoni</i>	<i>Dinictis</i> sp.
“ <i>Domnina</i> ” <i>sagittariensis</i>	<i>Palaeogale sectoria</i>
cf. <i>Oreotalpa florissantensis</i>	PERISSODACTYLA
<i>Cryptoryctes kayi</i>	<i>Mesohippus montanensis</i>
LAGOMORPHA	
<i>Megalagus brachyodon</i>	<i>Miohippus grandis</i>
<i>Palaeolagus temnodon</i>	<i>Brontotheriid</i> sp.
RODENTIA	
<i>Ischyromys veterior</i>	<i>Colodon</i> sp., cf. <i>C. kayi</i>
<i>Ischyromys</i> large species	<i>Hyracodon</i> sp.
<i>Pseudocylindrodon neglectus</i>	<i>Rhinocerotid</i> sp.
<i>Cylindrodon fontis</i>	ARTIODACTYLA
<i>Prosciurus vetustus</i>	<i>Stibarus montanus</i>
<i>Douglassciurus jeffersoni</i>	<i>Bathygenys alpha</i>
<i>Hesperopetes</i> sp.	<i>Merycoidodon</i> sp.
<i>Namotomys lloydi</i>	<i>Trigenicus profectus</i>
<i>Montanamus bjorki</i>	<i>Poebrotherium</i> sp.
<i>Zemiodontomys burkei</i>	“ <i>Leptomeryx</i> ” <i>mammifer</i>
	“ <i>Leptomeryx</i> ” <i>speciosus</i>
	<i>Pipestoneia douglassi</i>

INTRODUCTION

History.—Pipestone Springs Main Pocket (PSMP) is the most diverse mammal yielding locality (Table 1) in the Tertiary intermontane basins of southwestern Montana (Fig. 1). Considering that more than thirty holotypes are known from PSMP, the site is arguably the most important locality of Chadronian age currently known (Tabrum et al. 1996, 2001). PSMP also yields coprolites, many of which contain fragmented vertebrate elements (Santana-Grace et al. 2010). The earliest reports of vertebrate fossils from PSMP did not mention coprolites (Douglass 1901; Matthew 1903), but significant collections do exist (Tabrum et al. 2001). Also, although multiple carnivore taxa have been reported from PSMP (Emry and Hunt 1980; Tabrum et al. 2001), only a few specimens from PSMP representing these taxa have been described (Matthew 1903; Clark

and Guensburg 1972; Mellett 1977; Emry and Hunt 1980; Boardman and Hunt 2015). Here, we update these reports and also briefly describe all specimens representing carnivore taxa from PSMP (Tabrum et al. 2001), and thus provide the first systematic review of Creodonta and Carnivora from the site. Also, we describe PSMP coprolites and discuss their paleoecological significance, and where possible, identify the vertebrate elements the coprolites contain, the taxa these represent, and which carnivore taxa may have produced the coprolites.

Localities.—Pipestone Springs Main Pocket (PSMP) consists of two stratigraphically equivalent sites separated by a covered interval about 250 m in breadth (Tabrum et al. 1996). Collections from the two sites are usually curated separately. The east-facing, dip-slope, large northern exposure is equivalent to University of Montana (UMVC)

locality MV5811, Carnegie Museum of Natural History (CM) locality 3575, and Raymond M. Alf Museum of Paleontology (RAM) locality V200301. The smaller, north-facing, southern exposure is equivalent to UMVC locality MV5810, CM locality 3576, and RAM locality V200322. It is important to note that many specimens collected from PSMP and exposures of similar age in the general area have sometimes been lumped together, particularly specimens collected during the early years of exploration of southwest Montana. This is significant because the isolated fossiliferous exposures in the Pipestone Springs area range in age from middle to late Chadronian. Attempts to resolve this problem have been mostly successful (Tabrum and Fields 1980; Garcia 1992; Tabrum et al. 1996, 2001) and our study of PSMP coprolites is based on well-documented fossils housed at the Carnegie Museum of Natural History (CM; $N = 161$), University of Montana (UMVC; $N = 41$), and the Raymond M. Alf Museum of Paleontology (RAM; $N = 156$). Partially visible skeletal elements or teeth are evident on the exterior of some PSMP coprolites, and in about 20 cases, the coprolite was mechanically prepared so that the element and taxon could be identified if possible. Also, our analysis of PSMP carnivores is based on 38 well-documented specimens at the CM, RAM, and UMVC. Nine specimens at the American Museum of Natural History (AMNH) and one at the National Museum of

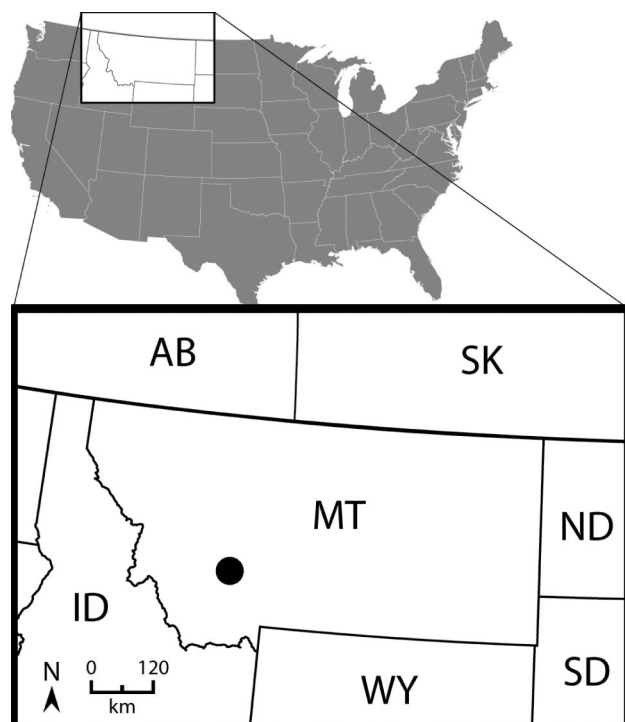


Fig. 1.—Dark circle denotes the location of Pipestone Spring Main Pocket (PSMP) in Jefferson County, Montana (MT); AB: Alberta, SK: Saskatchewan, ID: Idaho, WY: Wyoming, ND: North Dakota, SD: South Dakota.

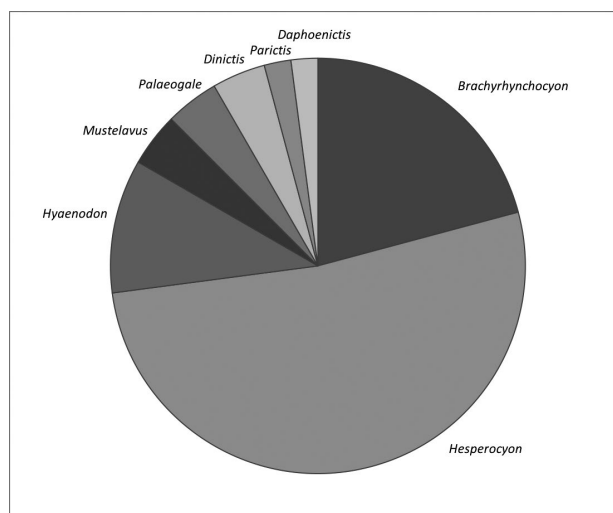


Fig. 2.—Relative abundance of the eight mammalian carnivore genera recovered from PSMP.

Natural History (USNM) were also included even though there is some uncertainty about the exact provenance of some of these specimens (Tabrum et al. 1996).

Measurements.—Dimensions of mammalian teeth and the diameter of coprolites were recorded in mm using a Carrera Precision digital caliper. Teeth were measured following Wang (1994: fig. 6). A high resolution Canon camera system was employed to photograph PSMP coprolites and mammalian elements.

Biostratigraphic and Geologic Setting.—The PSMP assemblage was recovered from a thick tuffaceous mudstone within a sequence of mostly fine grained strata that represent the Climbing Arrow Member of the Renova Formation of Kuenzi and Fields (1971), within sequence two of the Cenozoic sequence stratigraphy of southwest Montana developed by Hanneman and Wideman (1991). Strata that yield the PSMP assemblage are of both reversed and normal polarity (Prothero 1984), which probably correlates with Chrons C15r–C16r, or about 35.0–35.5 Ma (Tabrum et al. 1996). The PSMP assemblage is recognized as one of the principal middle Chadronian faunas of North America (Emry et al. 1987; Tabrum et al. 1996; Prothero and Emry 2004).

The bone producing mudstone is uniformly fine grained and contains a high percentage of reworked volcanic ash. Its exposed thickness varies from 50 cm to about 4 m and sedimentary structures are not evident, nor is there any indication of paleosol development or bioturbation. Numerous isolated vertebrate elements and coprolites are seemingly randomly distributed throughout the unit, both laterally and vertically, and no particular exposure exhibits a measurably greater concentration than any other. Ninety-eight percent of vertebrate elements are from small to *Meshippus*-sized (<34 kg) mammals (Santana Grace et

TABLE 2. Measurements in mm of the upper dentition of <i>Hyaenodon microdon</i> from PSMP.			
Tooth Site		RAM 17601	AMNH 9623
P3	L	—	5.4
	W	—	2.8
P4	L	5.6	5.8
	W	4.2	3.8
M1	L	5.8	—
	W	3.4	—

al. 2010) (Table 1). Although the bones of small animals can easily be concentrated by fluvial processes (Dotson 1973; Korth 1979), the random dispersal of PSMP specimens throughout the horizontal and vertical extent of this sedimentary unit indicates that the fossils were not hydrodynamically sorted.

The depositional setting of the fossiliferous tuffaceous mudstone at PSMP is uncertain. It may represent either one, or a series of ash-rich mud flows that entrained and transported exposed vertebrate elements. Similar thick bedded, internally massive volcanoclastic mudstones were described by Runkel (1990) from Eocene strata in the Big Bend region of Texas, which were interpreted as clast deficient mudflows. Another possibility is that the fossiliferous mudstone at PSMP represents a series of floodplain deposits in a fluvial system that was periodically inundated with volcanic ash, which entombed specimens lying on the floodplain. In either case, the end result was a thick, essentially featureless unit that contains thousands of vertically and horizontally dispersed, mostly isolated vertebrate elements and coprolites. Recently collected examples of articulated material, such as two partial skeletons of *Ischyromys* and a few nearly complete tortoise shells are housed at the RAM, but await description.

Institutional Abbreviations.—AMNH, American Museum of Natural History, New York; ANS, The Academy of Natural Sciences of Drexel University, Pennsylvania; BM (NH), Natural History Museum, London, United Kingdom; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; NMC, National Museum of Canada, Ottawa, Ontario, Canada; PU, Princeton University, Princeton, New Jersey (collections now at YPM); RAM, Raymond Alf Museum of Paleontology, The Webb Schools, Claremont, California; UMVC, University of Montana Vertebrate Collection, Missoula, Montana; USNM, Department of Paleobiology, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut.

PIPESTONE SPRINGS CREODONTA
AND CARNIVORA

Mammalian carnivores were first described from PSMP by Douglass (1901). Soon thereafter, Matthew (1903) named *Bunaelurus infelix*, *Pseudopterodon minutus*, and *Cynodictus paterculus*, based on nine AMNH specimens collected in 1902, taxa now included in *Palaeogale sectoria*, *Hy. microdon*, and *Hesperocyon gregarius*, respectively (Mellett 1977; de Bonis 1981; Wang 1994). Only a few other carnivore specimens from PSMP have been described since the early 1900s (Clark and Beerbower in Clark et al. 1967; Clark and Guensburg 1972; Mellett 1977; Emry and Hunt 1980; de Bonis 1981; Hunt 1996; Boardman and Hunt 2015). The forty-eight carnivore specimens described here are referred to nine taxa, single specimens of *Parictis montanus* and *Daphoenictis tedfordi*, two specimens each of *Mustelavus priscus*, *Hy. microdon*, *Pal. sectoria*, and *Dinictis* sp., three specimens of *Hyaenodon crucians*, ten specimens of *Br. dodgei*, and twenty-five specimens of *Hes. gregarius*. Carnivore taxa are relatively rare at PSMP, and of the known sample, *Hes. gregarius* and *Br. dodgei* comprise 52% and 21% of specimens recovered, respectively (Fig. 2). The classification scheme followed here is that of Janis et al. (1998).

SYSTEMATIC PALEONTOLOGY

Order Creodonta Cope, 1875
Family Hyaenodontidae Leidy, 1869
Hyaenodon Laizer and de Parieu, 1838

Hyaenodon microdon Mellett, 1977
(Fig. 3)

Holotype.—AMNH 9623, partial maxilla with P3–4, and broken M1, from Pipestone Springs, Climbing Arrow Member, Renova Formation, Jefferson County, Montana (Matthew 1903: fig. 6; Mellett 1977: figs. 33a–b).



Fig. 3.—*Hyaenodon microdon* from PSMP, occlusal view of RAM 17601, left maxilla fragment with P4–M1.

TABLE 3. Measurements in mm of the lower dentition of *Hesperocyon gregarius* from PSMP compared to measurements of *H. gregarius* provided by Wang (1994: appendix III).

Specimen	m1		m2		m3	
	L	W	L	W	L	W
CM 73140	—	—	4.4	2.8	—	—
CM 8795	—	—	5.4	3.5	—	—
CM 8796	—	—	5.1	3.3	—	—
CM 9803	8.5	4.0	—	—	—	—
CM 70506	9.3	4.3	—	—	—	—
CM 2096	—	—	5.1	2.9	—	—
CM 70676	8.9	4.2	—	—	—	—
AMNH 9614	7.7	3.9	5.2	3.5	—	—
AMNH 9617	8.7	3.9	—	—	—	—
AMNH 9619	—	—	5.6	3.3	—	—
AMNH 9618	9.3	4.0	5.1	3.1	—	—
AMNH 9616*	9.2	4.2	5.5	3.3	3.3	2.3
Wang 1994	7.7-11.3	3.3-5.7	3.1-6.2	1.9-4.4	1.6-3.2	1.5-2.8

*Holotype of *Cynodictis paterculus*

Referred Specimen from PSMP.—RAM 17601, left maxilla fragment with P4–M1 (Fig. 3).

Discussion.—The holotype of *Hy. microdon* and RAM 17601 are the only known specimens of this species from PSMP. AMNH 9623 was originally referred to *?Pseudopterodon minutus* by Matthew (1903), because he thought it might represent the upper den-

tion of *Hyaenodon minutus*, a species described by Douglass (1901) from Pipestone Springs two years earlier. *Hyaenodon minutus* is now considered to be a junior synonym of *Hy. crucians* and AMNH 9623 the holotype of *Hy. microdon* (Mellett 1977).

RAM 17601 represents *Hy. microdon*, because the size and morphology of the P4 is very similar to that of the holotype (Table 2). Although some uncertainty remains concerning its provenance, the holotype (AMNH 9623) is thought to have been collected at PSMP (Tabrum et al. 1996). RAM 17601 confirms the presence of *Hy. microdon* at PSMP.

Hyaenodon crucians Leidy, 1853
(Fig. 4)

Holotype.—ANS 11046, skull and ANS 11047, jaws, White River Beds (Leidy 1853: figured in Leidy 1869: pl. II, figs. 1–3; Mellett 1977: fig. 25).

Referred Specimens from PSMP.—CM 737, partial right m1 (Mellett 1977: fig. 23D); UMVC 18179, right m1 fragment (Fig. 4); and AMNH 9624, a P2 or P3.



Fig. 4.—*Hyaenodon crucians* from PSMP, lingual view of UMVC 18179, right m1 fragment.

TABLE 4. Measurements in mm of the upper dentition of *Hesperocyon gregarius* from PSMP compared to measurements of *H. gregarius* provided by Wang (1994: appendix III).

Tooth Site		CM 72587	CM 72588	CM 87507	Wang 1994
P3	L	5.7	—	—	—
	W	2.6	—	—	—
P4	L	9.3	8.4	—	7.6–10.7
	W	5.4	4.9	—	4.3–6.7
M1	L	6.6	6.1	—	5.2–7.9
	W	7.6	7.3	—	6.3–9.7
M2	L	3.4	3.3	3.3	2.6–5.0
	W	3.6	4.4	4.6	3.6–6.5

Discussion.—At least one additional species of *Hyaenodon* is represented at PSMP based on CM 737, UMVC 18179, and AMNH 9624. CM 737, a partial m1 described by Douglass (1901) as the holotype of *H. minutus*, is now included in *Hy. crucians* (Mellett 1977). UMVC 18179 is a partial m1 (Fig. 4) collected in the 1980s. AMNH 9624, a P2 or P3, was described as ?*Hyaenodont* indeterminate by Matthew (1903) but not referred to by specimen number. UMVC 18179 is 10.2 mm in length. The length of CM 737 is estimated to be about 9.5 mm, and the P2 or P3 of AMNH 9624 is 9.6 mm in length and 5.3 mm in width. These dimensions far exceed those of *Hy. microdon* (Table 2) (m1 length of *Hy. microdon* is approximately 4.9 mm, estimated from fig. 23 in Mellett 1977).

Three large species of *Hyaenodon* (*Hy. horridus*, *Hy. montanus*, and *Hy. crucians*) were listed as occurring at Pipestone Springs by Mellett (1977: fig. 3) and Gunnell (1998), but Tabrum et al. (1996:285) were unable to document the presence of either *Hy. horridus* or *Hy. montanus* at the PSMP localities and believed that the pertinent specimens were actually collected from other sites. The lengths of UMVC 18179 (10.2 mm) and CM 737 (9.5 mm) indicate that they could represent the m1 of either *Hy. montanus* or *Hy. crucians*: m1 length ranges from 9.5–10.5 mm in *H. montanus* and 7.5–10.4 mm in *Hy. crucians* (Mellett 1977: tables 4 and 12). The m1 length of *Hy. horridus* (Mellett 1977: table 8) is significantly larger. However, lengths and widths of the P2 or P3 of *Hy. montanus* (Mellett 1977: table 3) far exceed those of AMNH 9624 (P2 or P3, length 9.7, width 5.2). Only the dimensions of the P2 or P3 of *Hy. crucians* (P2, length 10.2–13.5 mm, width 4.3–6.5 mm; P3 length 10.0–15.0 mm, width 4.7–7.3 mm; Mellett 1977: table 11) are similar to those of AMNH 9624. Thus, the larger hyaenodont at PSMP, represented by AMNH 9624, CM 737, and UMVC 18179, compares most closely with *Hy. crucians*.

Order Carnivora Bowdich, 1821
Family Canidae Fischer de Waldheim, 1817
Hesperocyon Scott, 1890

Hesperocyon gregarius Cope, 1873
(Fig. 5)

Lectotype.—AMNH 5297a, fragment of left ramus with p2–m1 and alveolus of p1, White River Formation of northeastern Colorado (Wang 1994: figs. 11D–E).

Referred Specimens from PSMP.—CM 72587, left maxilla with P3–M2 (Fig. 5); CM 72588, right maxilla with P4–M2; CM 73140, right m2; CM 70677, right dentary with alveolus of p1, roots of p2–4, and broken m1; CM 8795, left dentary with m2 and alveolus of m1; CM 8796, left dentary with m2 and alveolus of m3; CM 9803, right dentary with p1–m1; CM 9804, right dentary with p4 and alveoli of p1–2; CM 70506, left dentary with p4–m1; CM 2096, right dentary with m2; CM 70193, right dentary with damaged p4–m1 and m2 fragment; CM 70679, left m2 trigonid and p2 fragment; CM 70678, left maxilla with fragmentary P3–P4; CM 87506, right p3; CM 87507, right

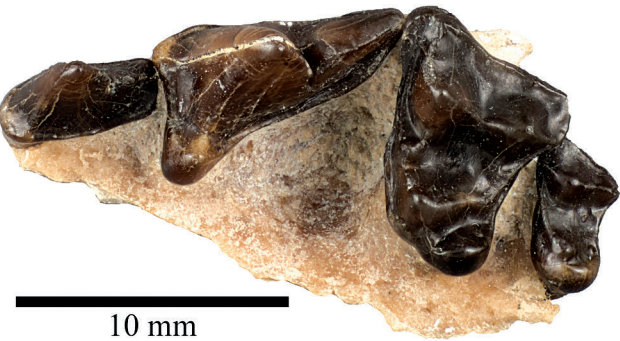


Fig. 5.—*Hesperocyon gregarius* from PSMP, occlusal view of CM 72587, left maxilla with P3–M2.

TABLE 5. Measurements in mm of the lower dentition of *Mustelavus priscus* from PSMP compared to the holotype (YPM 13755).

Tooth Site		UM 6713	UM 6714	CM 87540	YPM 13755
p1	L	—	2.3	—	—
	W	—	1.1	—	—
p2	L	3.3	3.2	—	3.5
	W	1.5	1.6	—	1.6
p3	L	3.5	3.8	3.8	3.5
	W	1.7	1.6	1.8	1.8
p4	L	4.2	3.9	—	4.0
	W	2.0	1.9	—	2.2
m1	L	5.7	5.6	—	5.5
	W	3.2	2.8	—	3.0

maxilla with M1–2; CM 70676, right dentary with m1 and alveoli of p1–4 and m2–m3; UM 9232, left p4; UMVC 8107, left dentary with p2; RAM 17600, right p3; AMNH 9614, right dentary with m2 and broken m1; AMNH 9617, left dentary with broken p4–m1; AMNH 9618, left dentary with p3–m2, broken p2, and alveolus of m3; AMNH 9619,

left dentary fragments with c, p2?, and m2; AMNH 9622, right p4; and AMNH 9616, right dentary with m1–3 and broken p3–4 (holotype of *Cynodictus paterculus*).

Discussion.—*Cynodictus paterculus* was based on AMNH 9616 (holotype) and two other dentaries (AMNH 9618 and 9619) collected during the 1902 AMNH expedition to southwestern Montana (Matthew 1903). Three other specimens collected on the expedition were also identified as *C. paterculus* (AMNH 9614, 9617, 9622), but were not described. Matthew (1903) did not figure any of these six specimens. *Cynodictus paterculus* is now considered to be a junior synonym of *Hes. gregarius* (Wang 1994). *Hesperocyon gregarius* is often recovered in Chadronian, Orellan, and Whitneyan strata throughout North America (Wang 1994) and is the most common mammalian carnivore recovered at PSMP (25 specimens).

The six AMNH specimens of *Hes. gregarius* from PSMP were compared directly to the holotype of *Hesperocyon gregarius* (AMNH 5297a) and are very similar to the holotype in size and morphology. Also, specimens of *Hes. gregarius* from PSMP compare favorably in size to the large sample of *Hes. gregarius* measured by Wang (1994) (Tables 3 and 4).

Family Mustelidae Fischer de Waldheim, 1817
Mustelavus Clark, in Scott and Jepsen, 1936

Mustelavus priscus Clark, in Scott and Jepsen, 1936
(Fig. 6)

Holotype.—YPM 13755, somewhat crushed skull with lower jaws in occlusion from the Peanut Peak Member of the Chadron Formation, South Dakota (Scott and Jepsen 1936; Clark 1937: pl. XIV, fig. 2, 2a).

Referred Specimens from PSMP.—UMVC 6713, right



Fig. 6.—*Mustelavus priscus* from PSMP. A, labial, B, lingual, and C, occlusal views of UMVC 6714, left dentary with p1–m1.

TABLE 6. Measurements in mm of the lengths of the m1–m2 of *Parictis montanus* and *Parictis gilpini* from Baskin and Tedford (1996: table 1).

Specimen	m1	m2
<i>Parictis montanus</i>	—	
CM 9571	7.6	4.0
<i>Parictis gilpini</i>		
FMNH 22405	8.1	4.5
FMNH 729	8.5	4.7
AMNH 50421	8.0	4.0
UNSM 19930	8.3	4.5
AMNH 76196	8.4	5.2

dentary fragment with p3–m1 and a broken p2; UMVC 6714, left dentary with p1–m1 (Fig. 6); and CM 87540, left dentary fragment with p3 (questionable referral).

Discussion.—The m1 of the holotype of *M. priscus* (YPM 13755) is notable for having a large and elevated protoconid positioned slightly anterior to the metaconid, with a paraconid subequal in size to the metaconid (Scott and Jepsen 1936; Clark 1937). The m1 of both UMVC 6713 and UMVC 6714 exhibits the trigonid morphology of YPM 13755 and both of these PSMP dentitions are similar in size to the holotype (Table 5). The p3 of CM 87540 is more similar in size and morphology to the p3 of *M. priscus* (Table 5) than to any other carnivore known from PSMP and may also represent this species.

Family Ursidae Fischer de Waldheim, 1817
Parictis Scott, 1893

Parictis montanus Clark and Guensburg, 1972

Holotype.—CM 9571, right maxilla with P4–M2, right dentary with canine root, p1–3, broken p4, m1–2 and alveolus of m3 and left dentary with root of p3, p4–m2 and alveolus of m3, from Pipestone Springs, Renova Formation, Montana (Clark and Guensburg 1972: figs. 7, 8, 9a–b).

Discussion.—CM 9571 was listed as a new and undescribed species of *Parictis* from Montana by Clark and Beerbower (in Clark et al. 1967: fig. 10, 1 and 5–6, fig. 11, 3–4). Shortly thereafter, CM 9571 was designated as the holotype of *P. montanus* (Clark and Guensburg 1972). CM 9571 remains the only known specimen of this species from PSMP. *Parictis montanus* is distinguished from other species of *Parictis* based mainly on size: *Par. parvus* and *Par. primaevus* are smaller, while *Par. major* and *Par. dakotensis* are larger (Baskin and Tedford 1996: table 1). *Parictis montanus* and *Par. gilpini* are similar in size (Table 6) and are distinguished primarily on differences in

the upper dentition as a larger P4 protocone and broader M1 are present in *Par. montanus* compared to *Par. gilpini* (Clark and Guensburg 1972).

Family Amphicyonidae Haeckel, 1866
Brachyrhynchocyon Loomis, in Scott and Jepsen, 1936

Brachyrhynchocyon dodgei Scott, 1898
(Fig. 7)

Holotype.—PU 11422, right dentary with p2–m2 from the *Titanotherium* beds of the Hat Creek Basin, Nebraska (Scott 1898: pl. XIX, figs. 6–7).

Referred Specimens from PSMP.—UMVC 400, premolar; RAM 17597, lingual half of left P4; RAM 17598, left p3; RAM 17599, left dentary with m1 and damaged m2



Fig. 7.—*Brachyrhynchocyon dodgei* from PSMP. **A**, labial, **B**, lingual, and **C**, occlusal views of RAM 17599, left dentary with m1 and damaged m2.

TABLE 7. Measurements in mm of the lower dentition of *Brachyrhynchocyon dodgei* from PSMP compared to measurements of *Br. dodgei* from Chadronian localities in North America (Hunt 1996: table 4; includes some Pipestone Springs specimens).

Tooth Site		RAM 17699	CM 9825	CM 9057	CM 9573	CM 73179	Hunt 1996
p2	L	—	7.2	7.2	—	—	—
	W	—	4.0	4.1	—	—	—
p3	L	—	8.5	—	7.7	—	—
	W	—	4.8	—	4.8	—	—
p4	L	—	11.9	11.2	11.4	—	10.0–12.7
	W	—	5.6	5.2	5.8	—	5.0–6.3
m1	L	15.4	14.7	—	—	14.3	13.4–17.0
	W	8.2	7.8	—	—	7.4	6.1–7.7
m2	L	—	9.3	—	—	—	7.0–9.8
	W	—	6.6	—	—	—	5.1–6.5

(Fig. 7); CM 9057, left dentary with p3–m1 and alveoli for p1 and m2–3; CM 9573, right dentary with p3, broken p4 and alveoli for p1 and m1–3; CM 9825, left dentary with p2–m2, and alveoli for p1 and m3; CM 21421, right dentary with broken p1–3; CM 73139, left dentary with m1; CM 9256, anterior part of skull with left I1–P3 and right I1–C, P2–M1 (figured by Clark et al. 1967: fig. 15).

Discussion.—Four CM specimens of *Br. dodgei* from Pipestone Springs were initially described and referred to *Daphoenocyon dodgei* with CM 9256 designated as a “paratype” by Clark and Beerbower in Clark et al. (1967). *Daphoenocyon* is now considered a junior synonym of *Brachyrhynchocyon*, and the latter can be distinguished from other Chadronian amphicyonids by its short robust premolars and thick massive mandible (Hunt 1996).

Brachyrhynchocyon dodgei is the second most common species of mammalian carnivore at PSMP. Most of its

dentition is represented in CM specimens recovered at PSMP. Comparison of the size of the lower dentition of *Br. dodgei* from PSMP to specimens of the species known from several Chadronian sites in North America (Table 7) indicates that they represent the same species. The holotype and only known specimen of *Brachyrhynchocyon montanus* (CM 8851) was initially reported from PSMP (Hunt 1996), but restudy of available locality data indicates that CM 8851 was collected from outcrops of the Dunbar Creek Member (Oligocene) of the Renova Formation a few km north of PSMP. *Brachyrhynchocyon montanus* is distinguished from *Br. dodgei* based on its smaller size (Hunt 1996: table 4).

Daphoenictis Hunt, 1974

Daphoenictis tedfordi Hunt, 1974

Holotype.—NMC 9205, left dentary with p2–m2 and alveoli of canine, p1, and m3 from Locality 133, Cypress Hills Formation, Cypress Hills, Saskatchewan, Canada (Russell 1972: figs. 13A–B).

Referred Specimen from PSMP.—USNM 215031, right m1 (Emry and Hunt 1980: fig. 2).

Discussion.—The only confirmed specimen of *Daphoenictis* from the Renova Formation of Montana, USNM 215031, was collected by C.L. Gazin at the “Main Locality” at Pipestone Springs in 1948 and was later discovered in a tray of unidentified USNM specimens (Emry and Hunt 1980). USNM 215031 was originally referred to *Daphoenictis* sp. because its small size and dental features



Fig. 8.—*Dinictis* sp. from PSMP, occlusal view of CM 8790, left dentary with m2 and base of posterior half of m1.

TABLE 8. Measurements in mm of the lower dentition of <i>Palaeogale sectoria</i> from PSMP. Measurements of AMNH 9620 (holotype of <i>Bunaelurus infelix</i>) from Matthew (1903).			
Tooth Site		ANMH 9620	CM 73141
p4	L	4.1	3.6
	W	1.9	1.5
m1	L	5.9	4.6
	W	2.3	1.9
m2	L	—	1.6
	W	—	1.2

suggested it might be a primitive variant of *D. tedfordi* (Emry and Hunt 1980). Currently, *Daphoenictis* is represented by the single species, *D. tedfordi*, which is known from twelve specimens of Chadronian age from Saskatchewan, Nebraska, Wyoming, Colorado, and Montana (Boardman and Hunt 2015), the Montana occurrence in reference to USNM 215031. We follow Boardman and Hunt (2015) and refer USNM 215031 to *D. tedfordi*.

Family Nimravidae Cope, 1880

Dinictis sp.
(Fig. 8)

Referred Specimens from PSMP.—CM 8790, left dentary with m2 and base of posterior half of broken m1 (Fig. 8); and CM 8791, left dentary with m2.

Discussion.—*Hoplophoneus* and *Dinictis* are the only known North American Chadronian nimravid genera (Martin 1998: fig. 12.5). The dental formula of *Hoplophoneus* differs from that of *Dinictis* in the absence of m2 (Martin 1998). Both CM 8790 and CM 8791 have an m2 and appear to represent *Dinictis*, although the specimens are far too fragmentary for species identification. The length of the m2 of CM 8790 is 4.4 mm, while that of CM 8791 is 3.9 mm. Measurements of m2s (by D.L. Lofgren) in three mandibles of *Dinictis* (AMNH 53663A, 38983, and 38805) from the Chadron Formation near Scenic, South Dakota, indicate that the length of the m2 of *Dinictis* was approximately 4.3 to 4.4 mm.

Family incertae sedis
Palaeogale von Meyer 1846

Palaeogale sectoria Gervais, 1848–1852
(Fig. 9)

Holotype.—BM(NH) 27816, left dentary with p1–4, m1 from Antoingt, France (de Bonis 1981: fig. 6).

Referred Specimens from PSMP.—AMNH 9620, a dentary fragment with p4–m1; and CM 73141, a left dentary with p4–m2 (Fig. 9).

Discussion.—AMNH 9620 was originally described as the holotype of *Bu. infelix* by Matthew (1903) who distinguished it from *Bu. lagophagus* based on differences in the p4. Simpson (1946) synonymized *Bunaelurus* with *Palaeogale* and consequently AMNH 9620 became *Pal. infelix*, a species tentatively considered to be distinct from *Pal. lagophagus* (Baskin and Tedford 1996), both now considered junior synonyms of *Pal. sectoria* (de Bonis 1981). A second specimen of *Pal. sectoria* (CM 73141)



Fig. 9.—*Palaeogale sectoria* from PSMP. A, labial, B, lingual, and C, occlusal views of CM 73141, left dentary with p4–m2.



Fig. 10.—Examples of the shape of PSMP coprolites that also illustrate the two size groups shown in Figure 11. **A**, RAM 18171 (diameter 24.5 mm), **B**, RAM 17364 (diameter 10.6 mm).

from PSMP was found in 1993. CM 73141 has the distinctive *Palaeogale* m1, in which the metaconid is absent and a large protoconid and a smaller, trenchant paraconid form the carnassial blade (Fig. 8). The p4 and m1 of CM 73141 are smaller than the p4 and m1 of AMNH 9620 (Table 8), but both specimens appear to represent *Pal. sectoria*.

PIPESTONE SPRINGS COPROLITES

Coprolites recovered from PSMP are light grey in color and circular in cross section and the most complete specimens have an elongate-cylindrical shape (Fig. 10). About 80% of PSMP coprolites have fragmentary bone on the surface and/or in cross section, a feature, which in combination with their shape, indicates that they represent fossilized feces deposited by carnivorous mammals. Owl pellets and mammalian carnivore feces are similar in shape, but PSMP coprolites lack the high concentration of well-preserved bone, sometimes including skulls and partial skeletons of small mammals, seen in owl pellets from Tertiary strata (Gawne 1975; Lucas et al. 2012). The amount of bone in any single PSMP coprolite is less than 10% of the total volume of the coprolite, while it is typically 40–50% in modern owl pellets (Andrews 1990). Finally, bone breakage is great in PSMP coprolites, a very common condition

observed in the feces of modern mammalian carnivores (Andrews and Evans 1983), but uncommon in modern owl pellets (Dodson and Wexlar 1979; Terry 2007).

Of the other late Eocene predators that might have deposited coprolites at PSMP, the remains of fish and crocodilians have not been found. Plastron and carapace fragments and nearly complete tortoise shells have been collected at PSMP. Extant tortoises are almost strictly herbivorous, but they have been observed eating isolated vertebrate bones (even those of another tortoise), road kill carrion (great horned owl and armadillo), and mammalian scat (fox and raccoon) (Ernst and Lovich 2009). Also, the large anguid lizard, *Helodermoides*, is known from PSMP (Douglass 1903; Gilmore 1928; Sullivan 1979) and had a skull length of about 48 mm (Gilmore 1928). Extant anguids catch and swallow their prey and their diet is largely arthropods, but they do eat nestling rodents and other small vertebrates (Behler and King 1979). Bone in the smaller PSMP coprolites is usually highly fragmented, which indicates significant mastication of elements as they were consumed. Thus, some of the coprolites at PSMP could represent tortoise or *Helodermoides* feces, but that possibility seems unlikely, particularly for tortoises.

Of the 358 coprolites analyzed from PSMP, 316 had measureable diameters. These ranged from 4 to 29 mm,

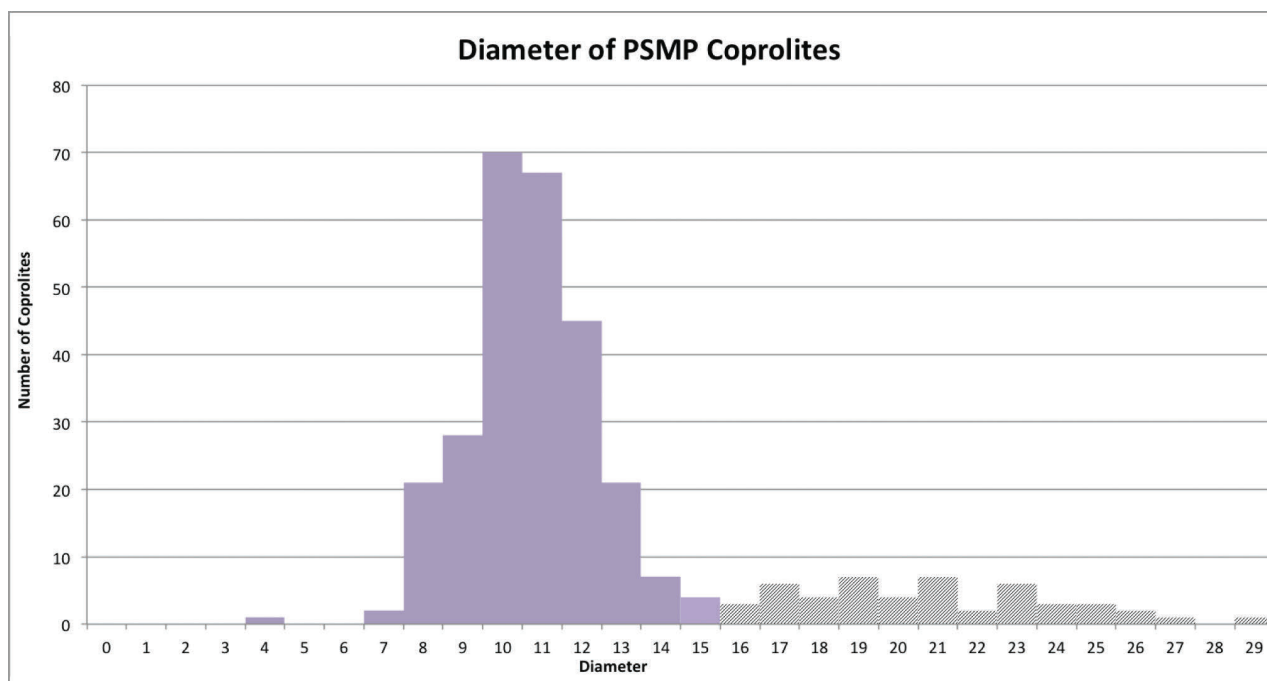


Fig. 11.—Histogram of diameters of measurable PSMP coprolites; hatched is larger diameter group and shaded is smaller diameter group.

with two distinct size clusters evident (Fig. 11). There are 269 smaller sized specimens (Fig. 10B) that range in diameter from 4–15 mm and exhibit a prominent mode at 10–11 mm. In contrast, the 47 specimens that comprise the group of larger diameter coprolites (Fig. 10A) have a range of 16–29 mm, but lack a distinct mode.

Well-preserved coprolites in the smaller diameter group have tapered ends or one blunt and one tapered end (Fig. 12), with segmenting distinguishable in a few specimens (Fig. 12E). Fragmentary or complete vertebrate elements are visible on the surface of 85% of the smaller coprolites (Fig. 12). In cross sectional view of broken smaller coprolites, abundant bone is often present and is usually highly fragmented. On the surface of a few smaller coprolites, individual mammalian elements can be identified, such as an astragalus (Fig. 13A) and limb ends (Figs. 13B–C). Lizard osteoderms (Fig. 14A) are also preserved. Only in a single coprolite were elements in articulation observed (Fig. 13D). Mammalian taxa could be identified based on dental elements in about ten specimens or 4% of the smaller sized coprolites, such as an isolated tooth of *I. veterior* (Fig. 14B) and multiple teeth or a mandible with deciduous teeth of *Palaeolagus temnodon* (Figs. 14C–D). RAM 18168 had an upper molar of a marsupial partially exposed on its surface (Fig. 15A). Mechanical preparation revealed that this was an M4, part of a maxillary fragment with M2–4 of *Herpetotherium valens* (Fig. 15B). Further preparation of RAM 18168 revealed the presence of an edentulous dentary, perhaps representing the same individual as the maxillary fragment (Fig. 15C). Also, a partial

humerus embedded in a PSMP coprolite was listed in the hypodigm of the fossorial mammal *Cryptoryctes kayi* (Reed 1954).

The most complete specimens in the large diameter grouping of PSMP coprolites have blunt ends and no evident segmentation (Fig. 16). About 50% of the larger diameter coprolites have visible bone on their surface, but this bone consists of small and poorly preserved fragments that rarely number more than two in a single specimen. In broken larger diameter coprolites, bone is uncommon in cross section, and consists only of small fragments that are poorly preserved if present.

PSMP coprolites in the smaller and larger diameter groups represent two contrasting morphotypes. They differ in size, tapering of ends, segmentation, abundance of bone, preservation of bone, and percentage of specimens with visible surface bone (Figs. 12, 16). Although both the smaller and larger coprolites can have visible bone on their surface and in cross section, the amount of bone per unit of volume and preservation of bone is much greater in the smaller coprolites. The presence of two distinct morphotypes indicates that PSMP coprolites represent the fossilized feces of at least two species of carnivores. The smaller species consumed marsupials, rabbits, rodents, *Cryptoryctes*, and lizards, while the diet of the larger species remains unknown.

Preservation of bone in the two size classes of coprolites at PSMP provides insight into the diet and degree of digestive capacity of the carnivores that produced these fossilized feces. Bone ingested and deposited by the carnivore



Fig. 12.—Coprolites that represent the smaller size group of Figure 10B. **A**, RAM 17564; **B**, RAM 17536; **C**, RAM 17523; **D**, RAM 17557; **E**, RAM 17392; **F**, RAM 17369; **G**, RAM 17440.

with the larger diameter feces was much less abundant per coprolite and was not identifiable because of poor preservation. The low volume of bone in the larger feces could be related to the amount of bone ingested, size and condition of bone when ingested, level of stomach acidity, and other factors. However, it is evident that multiple carnivores did ingest bone and that the larger ones were probably able to digest it to a greater degree.

IDENTIFICATION OF MAMMALIAN PREDATORS AT PSMP

Nine carnivorous mammalian taxa have been recovered from PSMP and the feces of two or more of them are the most likely source for the hundreds of coprolites recovered from the site. Identification of the predator species that deposited coprolites at any fossil site is primarily based on size, in that the diameter of a coprolite is usually proportional to the size of the animal that deposited it (Hunt et

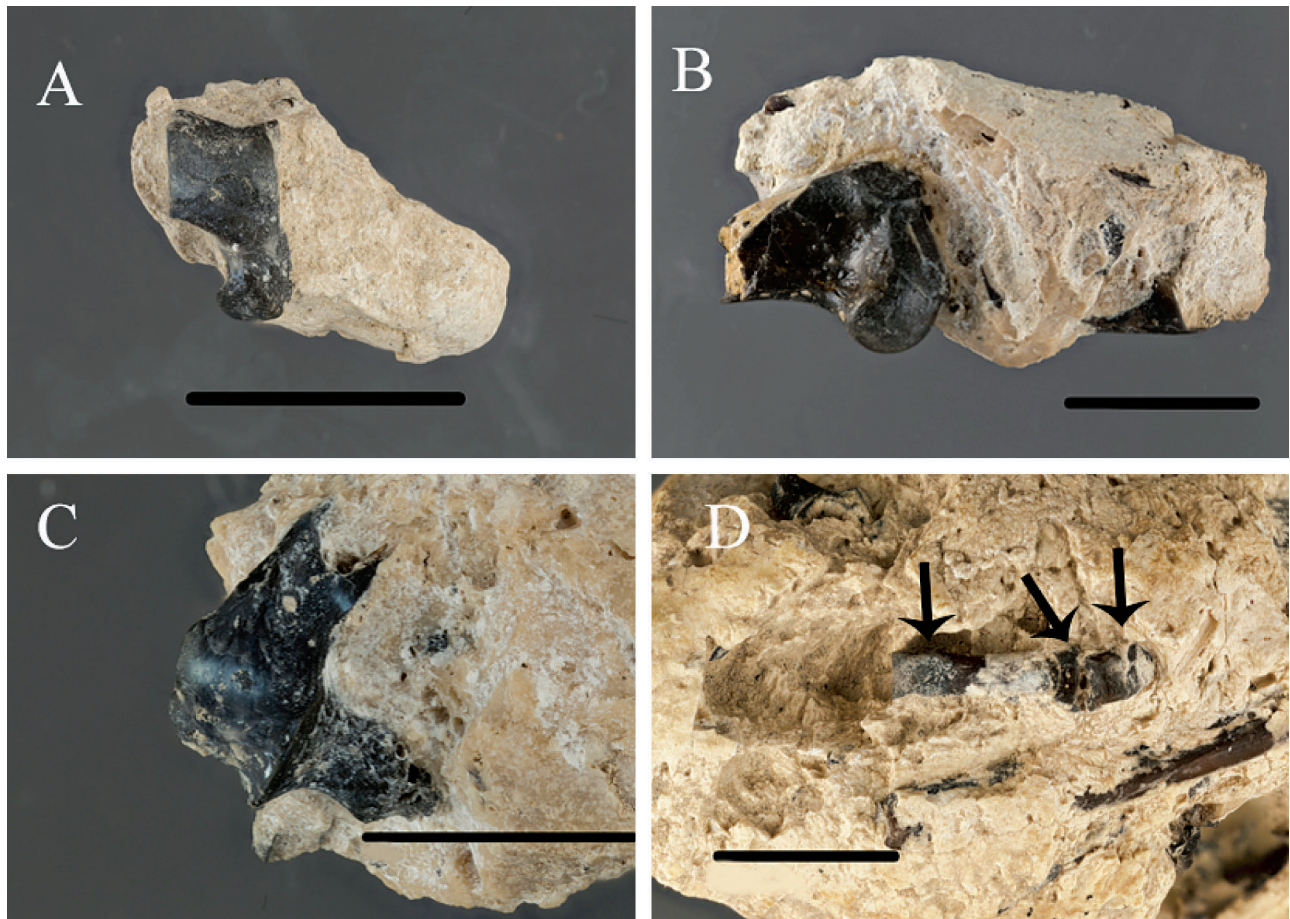


Fig. 13.—Smaller sized coprolites containing identifiable mammal bone. **A**, CM 90787, rodent astragalus (probably *Ischyromys*); **B**, CM 90788, proximal humerus; **C**, RAM 17409, distal humerus; **D**, CM 90789, articulated phalanx (left and middle arrows delineate distal and proximal ends of medial phalanx, respectively, right arrow delineates distal end of proximal phalanx). Scale bar for A–B is 10 mm and 5 mm for C–D.

al. 1994). Thus, a likely fecal producer is identified whose skeletal elements are the appropriate size and are present at the coprolite yielding locality or found in strata of similar age nearby. For example, two Pleistocene coprolites (26.8 mm and 22.4 mm in diameter) from the Sopas Formation of Uruguay were thought to have been produced by a large felid because they resemble recent felid feces, with *Felis concolor* and *Panthera onca* as the most likely choices based on the felids known from the formation (Verde and Ubilla 2002).

The most comprehensive studies of Tertiary mammalian coprolites from North America are from White River Group strata in Nebraska and Wyoming. LaGarry (2004) collected 1,250 specimens from two sites at about the same stratigraphic level within the Orellan Member of the Brule Formation in Nebraska (Orellan). Within this large sample, the diameter of 286 coprolites could be measured and these specimens ranged from 6 mm to 37 mm in diameter, with a single mode at 20 mm (LaGarry 2004: fig. 7A). The 31 mm range and mode of 20 mm indicated that one or more species of carnivores of approximate coyote-size

were represented by the coprolites, with the main producer most likely to have been the amphicyonid *Daphoenus vetus*, based on the body size and dentition of members of the Orellan carnivore guild (LaGarry 2004). A less specific example was provided by Edwards and Yatkola (1974: fig. 1), who argued that at least two unidentified predators were present based on the diameters of 106 coprolites from White River Group strata in Nebraska and Wyoming, because the 21 mm range of their sample exceeded the range in diameter of modern wolf feces (12.5 mm in Mech 1970).

Other examples of predator identification based on Tertiary coprolites from North America are difficult to evaluate because they do not include coprolite diameter or just provide an approximate range of coprolite diameters from multiple sites. For example, Parris and Holman (1978) reported 100 coprolites (55 with bone) from the Scenic Member of the Brule Formation (Orellan) of South Dakota and postulated that they recorded the activity of mustelids, canids, felids, hyaenodontids, and/or tayassuids, but coprolite diameters were not provided. Also, without any other

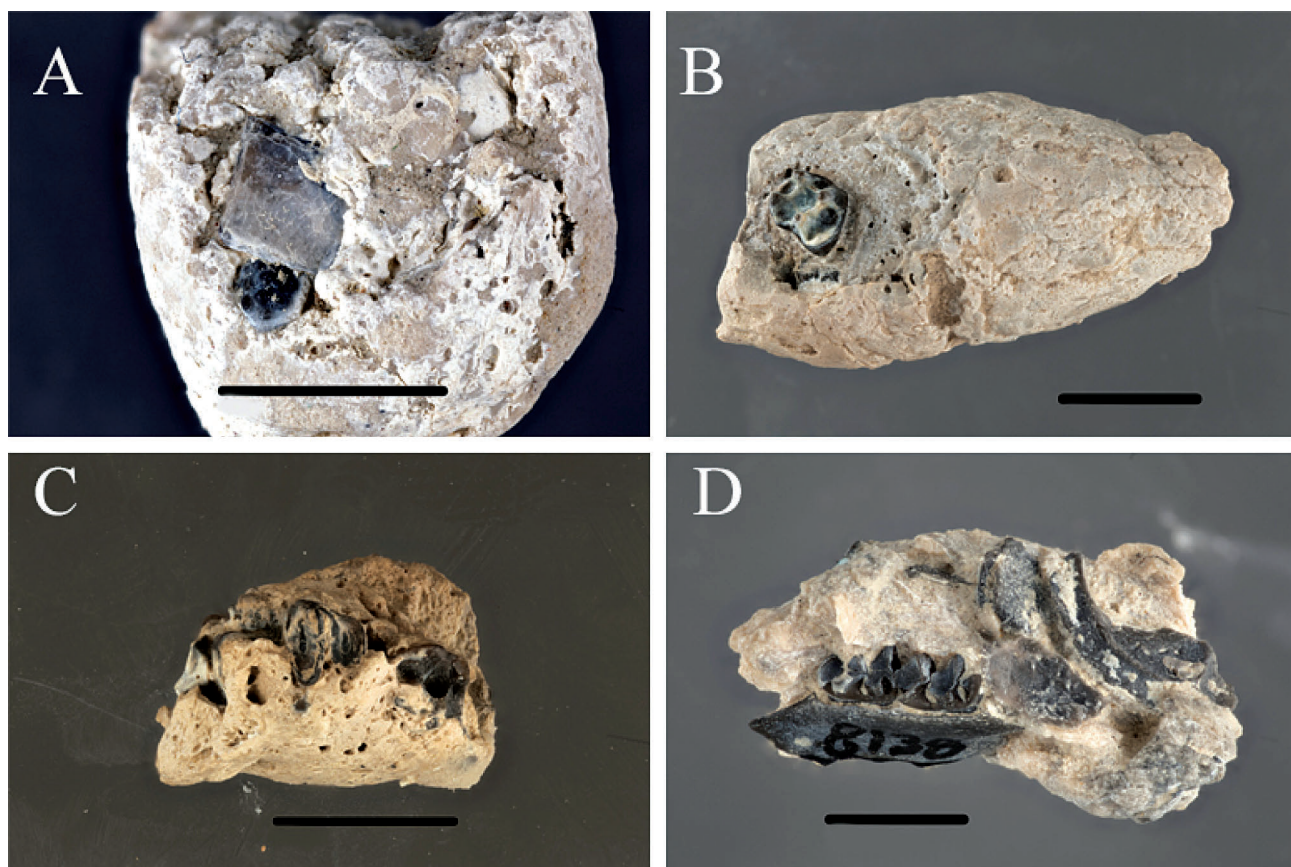


Fig. 14.—Smaller sized coprolites containing vertebrate elements identifiable to taxon. **A**, RAM 18170, lizard osteoderms; **B**, CM 90785, left DP4 of *Ischyromys veterior*; **C**, CM 90786, left p4-m1 of *Palaeolagus temnodon*; **D**, UMCV 8138, partial dentary of juvenile *Palaeolagus temnodon*. Scale bar is 5 mm for each image.

specific data except that the coprolites from late Miocene (Hemphillian) Ordinance, Arlington 4, and MacKay Reservoir sites in Oregon had a diameter range of 3 to 33 mm, *Pliotaxidea* was identified as the probable source for small coprolites from the Ordinance and Arlington 4 localities and an unidentified large carnivore the source for larger coprolites recovered from the McKay Reservoir locality (Martin 1981).

Three hundred sixteen of the 358 coprolites from PSMP had measurable diameters, a high proportion (88%) compared to the large Orellan sample from the Brule Formation in Nebraska, in which 286 coprolites had measurable diameters out of a total of 1,250 specimens (23%) (LaGarry 2004). Diameters of the Chadronian PSMP coprolites differ significantly from the samples measured by Edwards and Yatkola (1974: fig. 1) and LaGarry (2004: fig. 7A) from Chadronian and Orellan White River Group strata of the Great Plains. The PSMP sample has a prominent mode at 10–11 mm and a range of 4–29 mm (Fig. 11). The histogram provided by Edwards and Yatkola (1974: fig. 1) has a less distinct mode at 18–20 mm and all specimens exceed 14 mm in diameter. The sample of LaGarry (2004: fig. 7A)

has a mode of 20 mm with few specimens having a diameter that matches the 10–11 mm mode of PSMP coprolites (Fig. 11). Also, bone in larger PSMP coprolites is sparse, poorly preserved, and unidentifiable. In contrast, bone in larger White River Group coprolites was often abundant and many elements were readily identifiable (Parris and Holman 1978; LaGarry 2004). Thus, the Chadronian coprolite assemblage from PSMP differs in significant ways from Chadronian and Orellan assemblages from Nebraska, South Dakota, and Wyoming, and it is likely that the carnivores responsible for the PSMP coprolites would differ as well.

The range in diameter is 12 mm for the smaller PSMP coprolite morphotype and 14 mm for the larger coprolite morphotype (Fig. 11). These are similar to the 10–12 mm range in diameter to the feces of modern fox (10–12 mm), coyote (18–19 mm) (Green and Flinders 1982; Danner and Dodd 1982), spotted hyena (15 mm) (Edwards and Yatkola 1974), and wolf (12.5 mm) (Mech 1970), but is smaller than the 25 mm diameter range for extant wolves reported by Weaver and Fritts (1979). If the range in diameter of a sample of fossil coprolites is comparable to the range

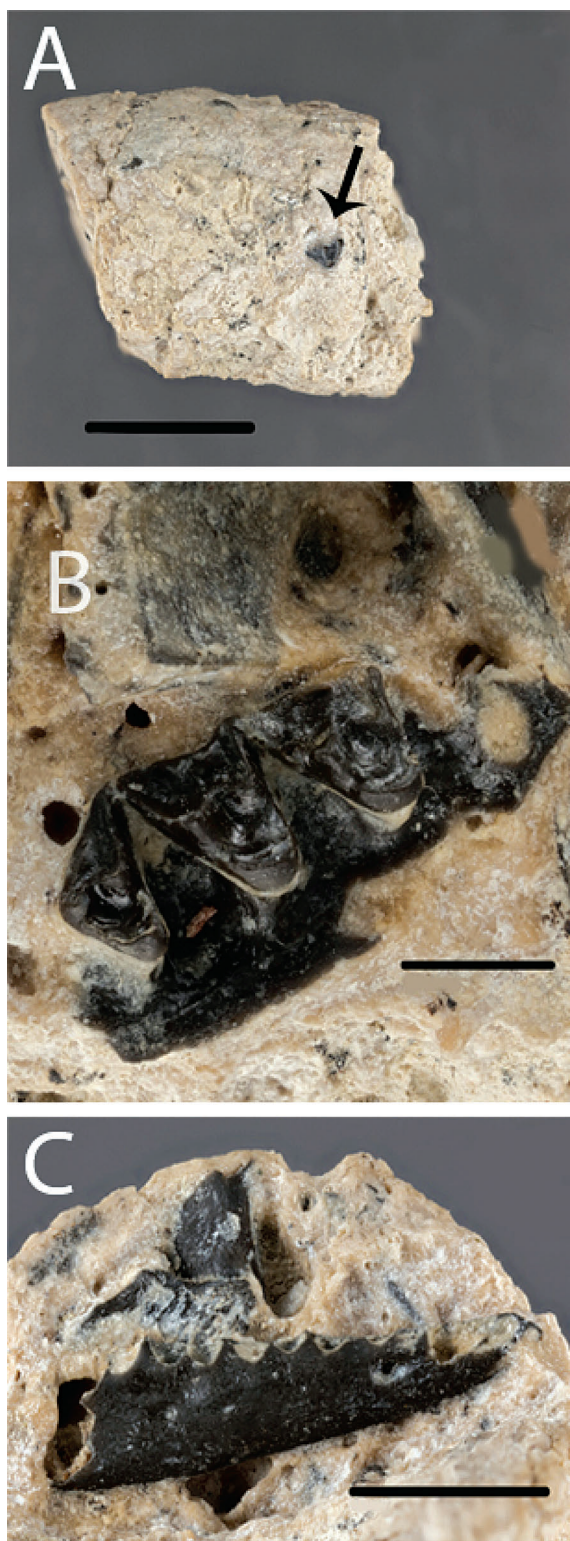


Fig. 15.—RAM 18168, a smaller sized coprolite with multiple mammalian elements. **A**, before preparation only an upper molar (arrow) is partially exposed; **B**, preparation reveals a partial maxilla with M2–4 of *Herpetotherium valens*; **C**, preparation also revealed an edentulous dentary fragment. Scale bar for A is 10 mm and 5 mm for B–C.

of the diameter of the feces of extant carnivorous species, the fossil sample could represent the activity of a single species. Because the smaller coprolite morphotype from PSMP has a prominent diameter mode and a range in diameter comparable to feces of modern carnivores, it is plausible that it mostly represents the activity of a single species. The larger coprolite morphotype also has a range in diameter comparable to feces of modern carnivores, but the larger coprolite sample lacks a mode and thus appears to represent the activity of multiple species.

To identify a likely producer for the majority of specimens for each coprolite morphotype, the modes of their respective diameters are compared to the size and relative abundance of each carnivore species recovered at PSMP. With the average length of the m1 employed as a proxy for relative size of each carnivore species from PSMP, smaller species can be identified as *M. priscus* (m1 length 5.65 mm, Table 5), *Pal. sectoria* (5.25 mm, Table 8), *Par. montanus* (7.6 mm, Table 6), *Hy. crucians* (9.8 mm), *Hyaenodon microdon* (approximately 4.9 mm), and *Hes. gregarius* (8.8 mm, Table 3). Within this group of smaller carnivores, the relative abundance of *Hes. gregarius* far exceeds that of any of the other species as its dentigerous elements constitute 71% of the small species cohort (25 of 35 specimens). Thus, *Hes. gregarius* is most likely to have been the primary small predator at PSMP, and its feces probably represent the majority of specimens of the small coprolite morphotype at PSMP.

Following the same line of reasoning, larger PSMP carnivore species are *Dinictis* sp. (average m1 length 18.0 mm; based on measurements of AMNH 53663A, 38983, and 38805 from South Dakota), *Br. dodgei* (14.8 mm, Table 7), and *Daphoenictis tedfordi* (14.2 mm). Within this larger sized group, dentigerous remains of *Br. dodgei* constitute 77% of the large species cohort (10 of 13 specimens). Thus, *Br. dodgei* probably produced a significant portion of the large coprolites at PSMP, but the lack of a prominent mode suggests that more than one larger species deposited feces at PSMP. It is worth noting that teeth of *Hesperocyon* are present in some larger coprolites at other Chadronian and Orellan localities (Parris and Holman 1978; LaGarry 2004), but have not been found in PSMP coprolites. The absence of *Hesperocyon* in larger coprolites from PSMP is difficult to assess because of the extremely sparse representation of bone. Thus, prey taxa of the larger carnivore at PSMP could have been nearly any species of small to medium size, including *Hesperocyon*.

To help access the likelihood that the canid *Hesperocyon* might have been the producer of the small PSMP coprolites, as well as to provide an example of the relationship of the diameter of a carnivore's feces to its body mass, feces were collected and measured over a three month period from a six-year old Jack Russell Terrier with a body mass of 5.0 kg and m1 length of 15.0 mm. The quantitative relationship between feces diameter and body mass, as well as m1 length and body mass in an extant canid, can then be applied to *Hes. gregarius* to determine its hypothetical

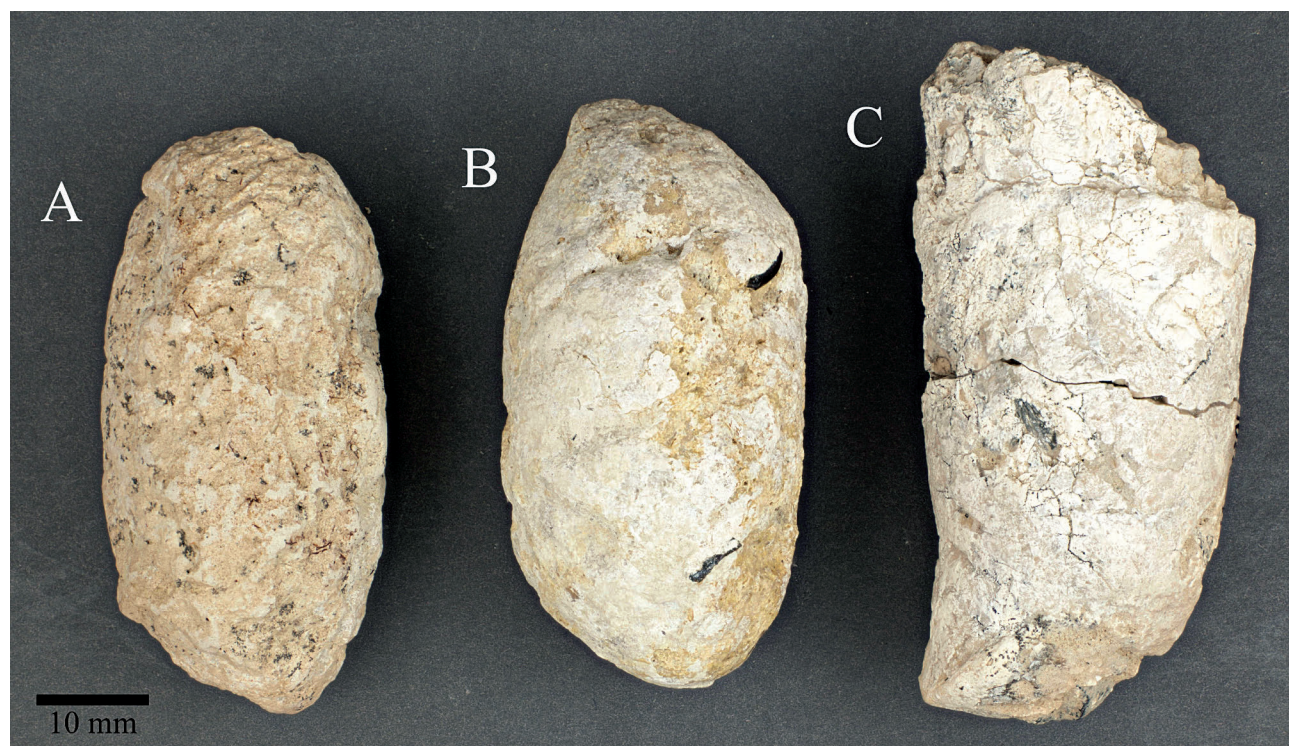


Fig. 16.—Coprolites that represent the larger size group of Figure 10A. **A**, RAM 17504; **B**, RAM 17540 (tooth fragment in upper right quadrant); **C**, RAM 17517.

body mass based on m1 length and the diameter of the smaller coprolites from PSMP. The estimated body mass for *Hesperocyon* from Chadronian and Orellan White River Group strata is about 3.0 kg (LaGarry 2004: table 5). Most Jack Russell Terrier (JRT) bowel movements resulted in multiple segments being deposited in a single pile and the maximum diameter of each segment was recorded. If a second bowel movement followed shortly after the first, segments of the second were often significantly narrower in diameter than those in the first. This highlights the fact that larger animals can produce small diameter coprolites (Hunt et al. 1994) and the mode of a coprolite sample will usually be the most accurate reflection of the size of the carnivore. Feces deposited by the JRT as one long segment ranged from 65 to 90 mm in length and had significant differences in diameter at the anterior and posterior ends. The maximum diameter of a JRT feces was always at or adjacent to the anterior end. Examples of these differences in diameters of four long JRT fecal segments are: (1) length 72 mm, diameters 16.4 (anterior end) and 11.3 mm (posterior end); (2) length 65 mm, diameters 13.5 and 10.8 mm; (3) length 90 mm, diameters 20.5 and 16.6 mm; (4) length 80 mm, diameters 17.8 and 11.7 mm.

The JRT feces exhibited a bell curve distribution and varied from 8–21 mm in diameter, with a range of 14 mm and a mode of 16 mm (Fig. 17). Coprolites of the smaller morphotype at PSMP have a mode of 10–11 mm and a

range of 12 mm. Both the mode and bell curve distribution of the JRT feces are prominent and are reflective of what can be measured for a single canid individual. Surprisingly, the mode of the smaller PSMP coprolites is more prominent and the range less broad compared to the JRT, an observation that provides further support that the smaller coprolite morphotype at PSMP could largely represent a single species of carnivore.

The JRT has a mass of 5 kg and a feces diameter mode of 16 mm, while the smaller PSMP coprolites have a diameter mode of 10–11 mm. If the ratio between mass and feces diameter mode of the JRT is applied to the hypothetical small carnivore at PSMP and the mode of the smaller coprolites, the mass of the small carnivore would be about 3.3 kg (mass in kg = 5 kg multiplied by 10.5 mm/16 mm). Using the same relationship between average m1 length and mass (m1 length of the JRT is 15 mm, *Hes. gregarius* from PSMP is 8.8 mm), the mass of *Hesperocyon* would be about 2.9 kg (mass in kg = 5 kg multiplied by 8.8 mm/15 mm). Both calculations are similar to the 3 kg body mass of *Hesperocyon* estimated by LaGarry (2004: table 5) based on skeletal remains from the White River Group, and again provide further support for *Hes. gregarius* as the main producer of the smaller coprolites at PSMP.

Using the same ratio between m1 length and mass of the JRT (15 mm, 5 kg) and the estimated m1 length for each of the other smaller PSMP carnivores, results in these

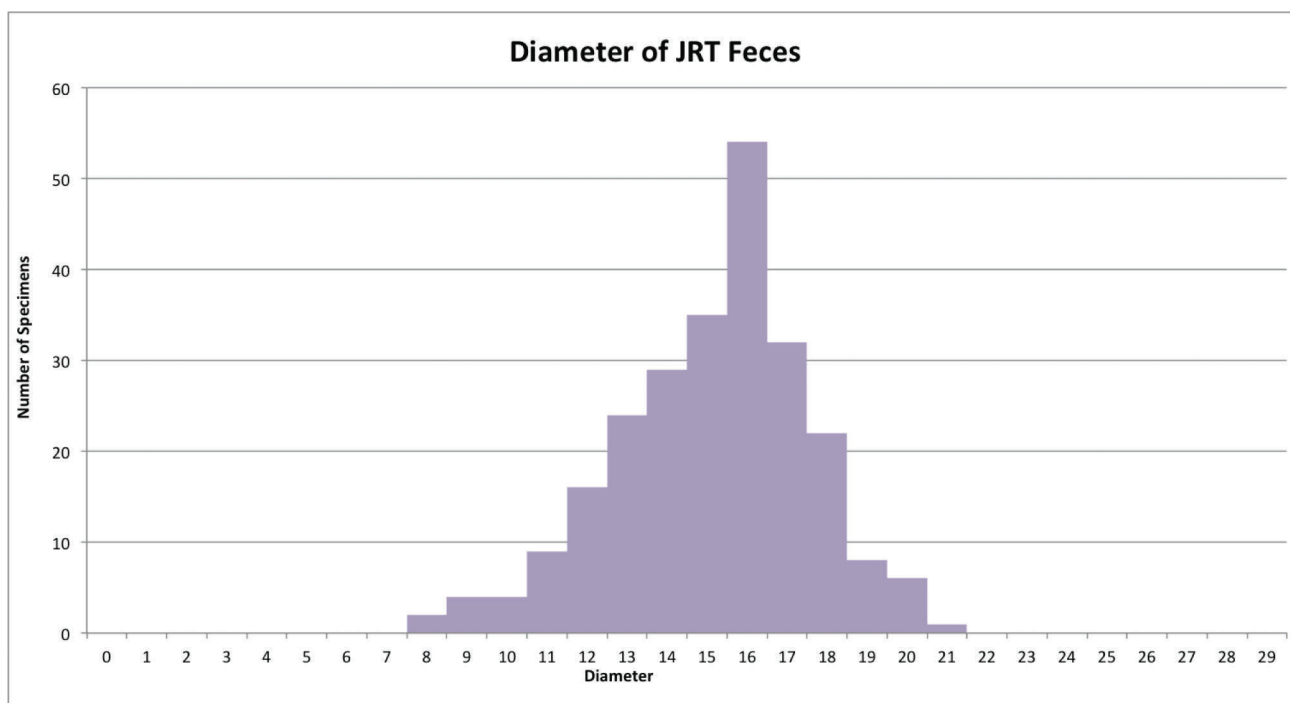


Fig. 17.—Histogram of the diameters of feces for a 5.0 kg Jack Russell Terrier.

approximate body masses: 1) *Palaeogale sectoria* (ml length 5.25 mm), 1.7 kg (mass in kg = 5 kg multiplied by 5.25 mm/15 mm); 2) *Mustelavus priscus* (5.65 mm), 1.9 kg; 3) *Parictis montanus* (7.6 mm), 2.5 kg; 4) *Hyaenodon crucians* (9.8 mm), 3.3 kg; 5) *Hyaenodon microdon* (approximately 4.9 mm), 1.6 kg. The ratio between mass and feces diameter mode of the JRT applied to the hypothetical small carnivore at PSMP and the mode of the smaller coprolites, resulted in a 3.3 kg body mass estimate for the PSMP carnivore. The estimated body mass of *Hy. crucians* (3.3 kg) is congruent to the estimated the body mass of the PSMP carnivore, while all the other small carnivores, except *Hes. gregarius* (2.9 kg), had much smaller estimated body masses (1.6 to 2.5 kg). Thus, although only three specimens of *Hy. crucians* have been recovered from PSMP, it appears that *Hy. crucians* was a more likely contributor of feces to the smaller coprolite sample at PSMP than any other smaller carnivore known from the site.

Another proposed method to identify a specific type of predator is based on the degree of bone alteration found in their coprolites. When carnivores consume prey, the amount of bone breakage and the presence of tooth marks, as well as the frequency of elements that remain in articulation are all factors that may vary between different carnivore families and could be useful in helping to recognize the taxon most likely to have produced a particular coprolite (Andrews and Evans 1983; Andrews 1990). Because of the rarity of bone in the larger PSMP coprolites, these factors can only be assessed for the smaller coprolites at PSMP, and they exhibit a high degree of bone breakage

with only one coprolite exhibiting elements in articulation (Fig. 13D). The families of carnivorous mammals known from PSMP are canids, mustelids, nimravids, hyaenodontids, amphicyonids, ursids, and a taxon of unknown family affinity (*Pal. sectoria*). Andrew and Evans (1983) determined a pattern of bone alteration for scats of three families of mammalian carnivores, Viverridae, Canidae, and Mustelidae, and canids and mustelids are both known from PSMP. Bone damage in the scat of extant canids is greater than in mustelids, and articulation of elements is minimal or absent in canids but is often present in mustelid scat (Andrews and Evans 1983). Bone is usually highly fragmented and articulation is minimal in the smaller PSMP coprolites. Thus, the bone alteration pattern for the smaller coprolites is more similar to those of extant canids than to those of mustelids. Although the bone alteration patterns for the feces of extinct families of carnivorous mammals that occur at PSMP (nimravids, hyaenodontids, amphicyonids) are not known, the bone alteration pattern observed in smaller for PSMP coprolites does support the hypothesis that *Hes. gregarius* was the primary producer of these coprolites.

COPROLITES AND SURFACE COLLECTED SAMPLES

In contrast to the difficulty in confidently identifying the predators that deposited coprolites at a particular locality, identification of the prey taxa can be relatively simple as their elements comprise part of the coprolite. For example,

bone in coprolites from the White River Group can range in completeness from an isolated phalanx to associated vertebrae, and the taxa identified can vary from horses, camels, and oreodonts, to rodents and lipotyphlans (LaGarry 2004) or a new species of snake (*Coprophis dakotaensis*) (Parris and Holman 1978). In comparison, the number of prey taxa identified in coprolites from PSMP is relatively small, partly because no taxa could be identified in the larger coprolites, and only a fraction of the smaller coprolites had identifiable elements exposed at the surface. Taxa identified in the smaller sized coprolites include lizards (Fig. 14A), *I. veterior* (Fig. 14B), *Palaeolagus temnodon* (Figs. 14C–D), and *Her. valens* (Fig. 15); and the fossorial mammal *C. kayi* (Reed 1954). Of the ten coprolites that have mammalian remains identifiable to taxon, in eight of these, the taxon is either *Ischyromys* or *Palaeolagus*. At PSMP, dentigerous elements of *Ischyromys* and *Palaeolagus* constitute about 50% of identifiable surface collected samples (Santana-Grace et al. 2010) (Fig. 18) and lizard osteoderms are common. Based on admittedly limited data, the proportions of the most common mammal genera in the coprolite fauna at PSMP appear to reflect that seen in surface collected samples. A similar example was presented by Martin (1981), where late Miocene coprolites from the Ordinance, Arlington 4, and MacKay Reservoir sites in Oregon were dominated by juvenile and young adult animals, similar to the samples recovered from surface collecting.

DISCUSSION AND SUMMARY

The PSMP assemblage is a principal North American middle Chadronian mammalian fauna (Tabrum et al. 1996; Emry and Prothero 2004) and its diversity (Table 1) is one few other Tertiary sites can match. Coprolites are also commonly recovered from PSMP and serve as important data for paleoecology as they reflect the activity of the carnivores that frequented or lived adjacent to the depositional site and provide the basis for identification of the predators that produced them. Identification is based upon the correlation between coprolite diameter and the relative abundance and size of the mammalian carnivore taxa. Based on coprolites and dental elements of carnivores recovered from PSMP, plausible candidates can be proposed for the carnivore taxa that deposited feces at this Tertiary coprolite-bearing site. However, fundamental limitations do exist because the presence of the remains of a specific predator at a coprolite yielding site does not necessarily indicate that the species deposited coprolites at the locality (Andrews 1990). Also, a predator may have frequently left their feces at the depositional site, but left little, if any, skeletal remains.

The range in diameters of PSMP coprolites is too broad to represent one species (Fig. 11). Also, there are two distinct size groups that have multiple differences in morphology and bone preservation and each group has a range in diameter comparable to feces of certain modern carni-

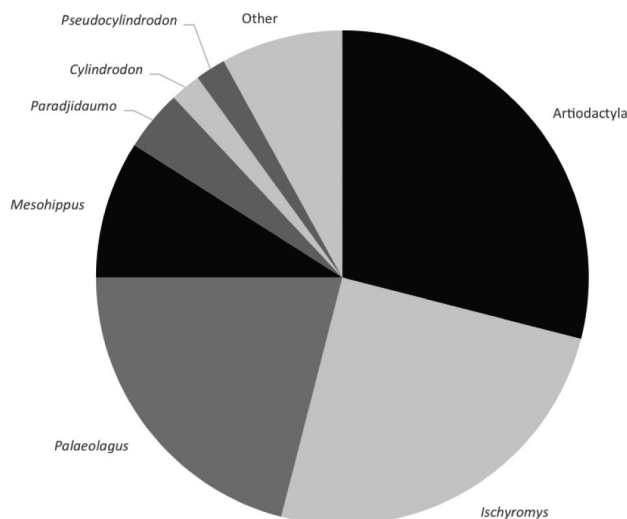


Fig. 18.—Percentage of the total PSMP assemblage for Artiodactyla, Mesohippus, Palaeolagus, and the most abundant rodent genera (*Ischyromys*, *Paradjidaumo*, *Cylindrodon*, and *Pseudocylindrodon*) based on dentigerous elements from surface collections.

vores. Thus, there is little doubt that more than one species must be represented by the PSMP coprolite sample.

The larger grouping of PSMP coprolites lacks a mode, which suggests that more than one larger species deposited feces at PSMP. Based on relative abundance of the three larger carnivores known from PSMP (*Dinictis* sp., *Daphoenictis tedfordi*, and *Br. dodgei*) (Fig. 2), *Br. dodgei* is most likely to have produced the majority of the larger coprolites at PSMP because its specimens represent 77% of this size cohort. This hypothesis for carnivore identification for the larger coprolites is based solely on the relationship between coprolite diameter and relative abundance of *Br. dodgei*.

In contrast, multiple lines of evidence support the identification of *Hes. gregarius* as the carnivore that deposited the smaller PSMP coprolites. These are: (1) strong correlation between the prominent mode for this coprolite size group (Fig. 11) and the high relative abundance of *Hes. gregarius* (71% of smaller sized carnivore cohort and 52% of entire PSMP carnivore assemblage) (Fig. 9); (2) the ratio between feces diameter and body mass, as well as average m1 length and body mass in an extant canid (JRT), when applied to m1s of *Hes. gregarius* and the smaller coprolites at PSMP, results in a hypothetical body mass of 3.3 kg for the small PSMP carnivore or 2.9 kg for *Hes. gregarius* from PSMP, both similar to the 3 kg estimated body mass of *Hesperocyon* based on skeletal remains from White River Group strata (LaGarry 2004); (3) the mode of the smaller PSMP coprolites is more prominent and the range less broad compared to the JRT feces (compare Figs. 11 and 17), and this would be unlikely if multiple small carnivores had contributed to the sample of smaller coprolites; (4) bone is usually highly fragmented and

articulationis minimal in smaller PSMP coprolites, a bone alteration pattern more similar to that of extant canids than mustelids. In total, these data provide strong support that the smaller coprolites at PSMP were deposited mostly by a single species of carnivore, in this case, the canid *Hes. gregarius*.

The primary source of the PSMP vertebrate assemblage has been attributed to mammalian carnivores that only ingested part of the skeleton of their prey (Santana Grace et al. 2010). This is particularly evident with elements such as mandibles of *Mesohippus* and of similar sized artiodactyls that are too large and intact to have traversed the digestive system of the carnivores known from PSMP. Also, the abundance of relatively intact dental remains of very small mammals in surface collections from PSMP suggests an avian origin (probably owl regurgitate) for part of the smaller bodied component of the PSMP assemblage (Santana Grace et al. 2010). However, coprolites from PSMP indicate that smaller bone material could pass through the digestive system of mammalian carnivores and remain identifiable, and well-preserved dentigerous elements, such as a partial maxilla of *Her. valens* (Fig. 15B) and juvenile mandible of *Palaeolagus temnodon* (Fig. 14D), have been found in two of the smaller coprolites at PSMP. Thus, fragile mammalian dental elements did remain relatively intact even after ingestion and deposition as feces at PSMP, and disaggregated carnivore feces must have been a source of some of the small well-preserved dentigerous elements found at PSMP. However, only two cases of tooth-bearing elements were observed in the 269 smaller coprolites, a rarity that indicates that disaggregated carnivore feces was not a major source of the large number of very small elements recovered from PSMP. Nevertheless, PSMP coprolites do provide important insight into which carnivore taxa were active in the depositional area, the species they consumed, and the skeletal elements that passed through their digestive systems, as *Hes. gregarius* appears to consume *C. kayi*, *Pal. temnodon*, *I. veterior*, *Her. valens*, and at least one species of lizard.

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