Paludicola 12(4):223-246 March 2020

MUSTELIDAE FROM OBSERVATION QUARRY (EARLY BARSTOVIAN) OF NEBRASKA, WITH COMMENTS ON SHEEP CREEK AND LOWER SNAKE CREEK MUSTELIDS

Jon A. Baskin

Department of Biological and Health Sciences, Texas A&M University–Kingsville, Kingsville, TX 78363
jon.baskin@tamuk.edu

ABSTRACT

Seven species of mustelids (Carnivora, Mustelidae) occur in the middle Miocene Observation Quarry, Dawes County, Nebraska. These include *Skopelogale melitodes*, new genus and species. *Leptarctus oregonensis* is also known from the early Barstovian Mascall Formation of Oregon and the Olcott Formation (Lower Snake Creek Fauna) of Nebraska. *Plionictis ogygia*, *Plionictis parviloba*, “*Martes*” *glareae*, and *Sthenictis dolichops* also occur in the Olcott Formation. *Miomustela madisonae* is elsewhere known from the early Barstovian of Montana and the late Hemingfordian and Barstovian of California. The mustelids of Observation Quarry support an early Barstovian (Ba1) age assignment, coeval with the Lower Snake Creek Fauna.

INTRODUCTION

The Observation Quarry Local Fauna (LF) is from the “Sand Canyon Beds”, Dawes County, Nebraska. Ted Galusha of the AMNH, who worked for Childs Frick (Frick, 1937; Galusha, 1975a), collected almost all of the mammals from this locality and described the regional geology (Galusha, 1975b). Korth and Evander (2016) described four new species of small mammals from there. They provided complete locality information and faunal lists and assigned the fauna to the early Barstovian North American Land Mammal Age (NALMA).

Small carnivorans previously reported from Observation Quarry include the procyonids *Arctonasua minima* (Baskin, 1982), *Bassariscus minimus* (Baskin, 2004), and *Probassariscus matthewi*, (Matthew and Cook, 1909; Baskin, 2004), and the mustelid *Miomustela madisonae* (Douglas, 1904; Lofgren et al., 2016; Lofgren and Abersek, 2018). This paper adds the mustelids *Skopelogale* gen. nov., *Leptarctus*, “*Martes*”, *Plionictis*, and *Sthenictis* to Observation Quarry. Additional mustelids that are discussed are *Dinogale*, *Mionictis*, and *Brachypsalis* from the Sheep Creek Formation and/or Lower Snake Creek Fauna of the Olcott Formation.

MATERIALS AND METHODS

The mustelids from the Sheep Creek Fauna, Lower Snake Creek Fauna, and Observation Quarry LF are in the collections of the American Museum of Natural History. Measurements were taken with dial calipers to the nearest 0.1 mm.

Dental Abbreviations—L = length, Le = external length, Li =internal length, W = width; tr = trigonid; tl = talonid; D = depth of mandible between p4 and m1.

Institutional Abbreviations—AMNH FM, Fossil mammal collection of the American Museum of Natural History, New York, New York; AMNH F:AM, Frick Collections of fossil mammals in the AMNH; ANSP, Academy of Natural Sciences, Philadelphia, Pennsylvania; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; LACM (CIT), Natural History Museum of Los Angeles County (former California Institute of Technology collection), Los Angeles, California; MNHN, Muséum national d’Histoire naturelle, Paris, France; PU, Princeton University, Princeton, New Jersey; UCMP, University of California Museum of Paleontology, Berkeley, California; UOMNH, University of Oregon Museum of Natural and Cultural History, Eugene, Oregon.

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821
Family MUSTELIDAE Fischer, 1817
Subfamily LEPTARCTINAE Gazin, 1936
Leptarctus Leidy, 1857

Genotypic Species—*Leptarctus primus* Leidy, 1857.

Holotype—ANSP 11293, left P4.

Horizon—Bijou Hills, Fort Randall Formation, South Dakota, U.S.A.; late Barstovian (Ba2) NALMA.

Leptarctus oregonensis Stock, 1930
(Figures 1A, 2A, B; Tables 1-3)

Holotype—LACM (CIT) 206, partial left maxilla with P4 and M1, right P4, and part of the skull.

Horizon—Mascall Formation, Oregon, early Barstovian (Ba1) NALMA.

Referred Material from the Mascall Formation—UCMP 39102, right P4 (Downs, 1956); UOMNH F-35458, skull lacking the rostrum, with right P4 and M1 and left P3-M1 (Calede et al., 2018). Additional material is listed in Maguire et al. (2018).

Referred Material from the Olcott Formation—AMNH FM 18241, nearly complete skull, Trojan Quarry (Matthew, 1924:fig 37); AMNH F:AM 25261, posterior skull with rostrum broken off, Echo Quarry; AMNH FM 18270, left mandible with p4-m1, Far Surface Quarry (Quarry B on label)(Matthew, 1924:fig 38); AMNH F:AM 25320, mandible with p3-p4, East Sand Quarry; AMNH F:AM 25623, mandibles with right i2-3, c1, p2, m1, m2, left c1, p2, p4-m2, Humbug Quarry; AMNH F:AM 25264, left mandible with p4-m1, Lower Snake Creek.

Referred Material from Observation Quarry—AMNH F:AM 25385, skull with left P2-M1 and right P2-M1; AMNH F:AM 25376, right P4; AMNH F:AM 54484, right M1; AMNH F:AM 25377, isolated talonid of right m1.

Discussion—Matthew (1924) referred a skull (AMNH FM 18241) from the Lower Snake Creek Fauna to *Leptarctus primus* (Leidy, 1857). Stock (1930) noted the similarities of his Mascall specimen to AMNH FM 18241 but distinguished it as *L. oregonensis* mainly because of its smaller size. In his review of North American Tertiary mustelids, Baskin (1998) concluded that AMNH FM 18241 should be assigned to *L. oregonensis*, not *L. primus*. More recently, Calede et al. (2018) noted that their new skull of *L. oregonensis* (UOMNH F-35458) from the Mascall Formation corroborated Baskin (1998). Prybyla et al. (2019: fig. 1) discussed and illustrated AMNH F:AM 25385 from Observation Quarry, but assigned it and AMNH FM 18241 to *L. primus* without discussing their rationale for doing so. In addition, they referred to AMNH FM 18241 as the neotype of *L. primus*. However, a neotype can only be designated if the original type material is non-diagnostic or is lost (Article 75 in Ride et al., 1999). ANSP 11293 is neither. Furthermore, AMNH FM 18241 and the other *Leptarctus* from the Lower Snake Creek Fauna of the Olcott Formation are *L. oregonensis* (Baskin, 1998, 2005; Korth and Baskin, 2009).

Description of AMNH F:AM 25385 from Observation Quarry—The occipital condyles and the left auditory region are missing (Figure 1A). The ventral region of the right bulla extends anteriorly, but not as far forward as in *Leptarctus ancipidens*. The bulla has a keyhole opening just below the midline. Below the opening is a closed notch. The canine alveolus is small and sub-round. The P2 is small, wider posteriorly, with the main cusp anteriorly situated and with a crest on its posterior margin, an internal cingulum, and a postero-internal shelf. There is a short diastema between P2 and P3. P3 is larger, more ovate than P2, the main cusp is slightly anterior of center, with a crest on the posterior margin; anterior, posterior and internal cingula are present; and the tooth is broader posteriorly.

The P4 parastyle is small, low, and situated anterior to the protocone. The protocone is tall, situated just anterior to the midline of the tooth, and connected directly to the postero-externally curving metacone blade. The hypocone is a relatively large cusp, but is lower than the protocone. The anterior, internal, and posterior cingula are low and thin.

M1 has a trapezoidal occlusal outline. The cusps are low; the paracone and taller metacone are connected by a crest; a small metastyle is present on the postero-external margin; and the metastyle is separated from the metacone by a narrow notch. An internal cingulum runs anterior to the very low postero-internal hypocone and a crest extends posteriorly from the protocone to a low cusp on the posterior external margin of the hypocone.

Comparisons—AMNH F:AM 25385 is similar in size and morphology to the skull from the Olcott Formation (Matthew 1924: fig. 37). In AMNH FM 18421, the teeth are worn but are otherwise similar (Figure 2A, B). The P3 has a less well developed internal cingulum and is wider postero-internally. The bullae are absent. AMNH F:AM 25261, the posterior cranium from the Olcott Formation, is smaller than AMNH F:AM 25385 or AMNH FM 18241 and may be from a female or a sub-adult because of its smaller size and some of the sutures are unfused. In it, the parasagittal crests only converge slightly and are less pronounced. The bulla has a keyhole, but doesn't project anteriorly. The skull from the Mascall Formation (Calede et al., 2018) is broken anterior to the P3. The tympanic projections are similar to that of AMNH F:AM 25385; however, unlike the Nebraska crania, the parasagittal crests do not converge.

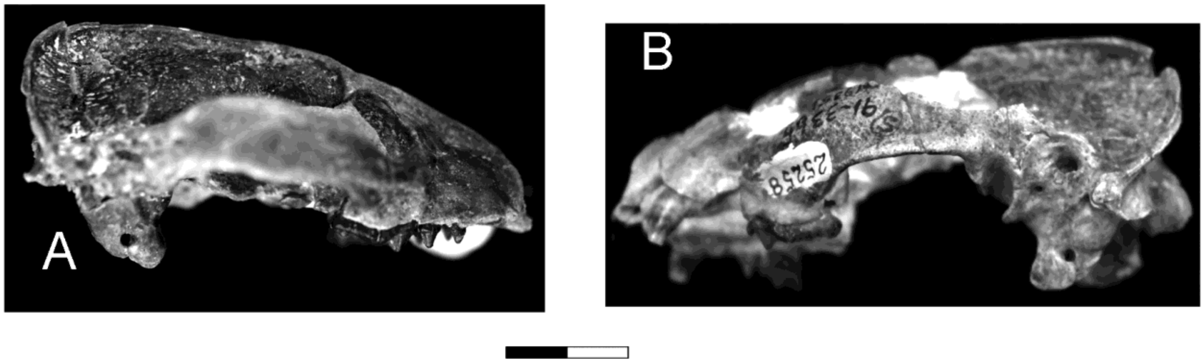

FIGURE 1. A, *Leptarctus oregonensis*, AMNH F:AM 25385 from Observation Quarry; B, *Leptarctus* cf. *oregonensis*, AMNH F:AM 25258 from the Sheep Creek Formation. Scale = 20 mm.

TABLE 1. Measurements of upper dentitions of *Leptarctus*. [1], Observation Quarry; [2], Olcott Formation; [3], Sheep Creek Formation; [4], Mascall Formation, measurements from Calede et al. (2018).

	P2L	P2W	P3L	P3W	P4Le	P4Li	P4W	M1Le	M1Li	M1W	P2-M1
[1]F:AM 25385	3.2	2.2	4.1	3.2	7.1	4.9	5.9	7.8	6.9	7.5	22.6
[1]F:AM 25376					6.1		5.2				
[1]F:AM 54484								7.9	6.6	7.0	
[2]AMNH 18241	3.4	1.9	4.4	3.2	6.9	5.4	5.8	7.6	6.8	7.3	22.7
[3]F:AM 25258	[2.9]		3.7	3.9	8.1	5.5	6.8	7.7	7.0	8.1	23.9
[4]UOMNH 35458			3.9	2.8	7.2		5.1	7.0		6.0	

Leptarctus cf. oregonensis Stock, 1930
(Figures 1B, 2C; Tables 1, 2)

Referred material—AMNH F:AM 25258, skull with left C1, P4-M1 and right C1, P3-P4.

Horizon—Greenside Quarry, lower part of the Sheep Creek Formation (Skinner et al. 1977), Sioux County, Nebraska, U.S.A.; early late Hemingfordian NALMA.

Description and Comparisons—AMNH F:AM 25258 is larger than the Olcott or Observation Quarry crania. Like them, it also has small canines (L = 5.8 mm; W = 4.3 mm). P3 has more pronounced postero-internal and internal cingula (giving it a subtriangular occlusal outline, wider internally) than the early Barstovian specimens. The P4 is relatively large, with a longer metacone blade and a smaller hypocone (Figure 2C), a similarity to the Hemingfordian *L. ancipidens*. The M1 occlusal outline is similar to the early Barstovian specimens (i.e., not transversely elongate as in *L. ancipidens*) but has a stronger parastyle as in *L. ancipidens*. The auditory bulla and small canines are similar to those

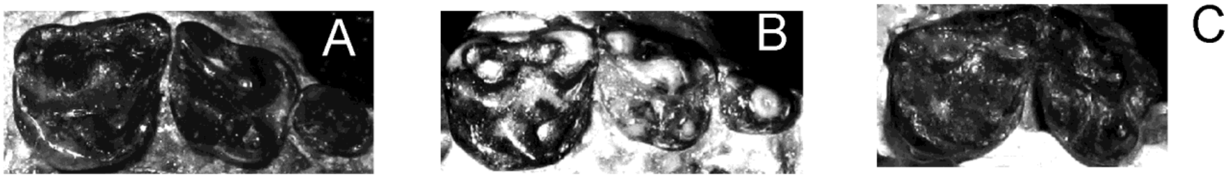

FIGURE 2. *Leptarctus oregonensis*, A, AMNH F:AM 25385, P3-M1 from Observation Quarry; B, AMNH FM 18241, P3-M1 (reversed) from the Olcott Formation; C, *Leptarctus* cf. *oregonensis* , AMNH F:AM 25258, P4-M1 (reversed) from the Sheep Creek Formation.

TABLE 2. Cranial measurements of *Leptarctus* and *Miomustela*. ^{1}, Observation Quarry; ^{2}, Olcott Formation; ^{3}, Sheep Creek Formation; ^{4}, Tesuque Formation. PW = posterior width of parasagittal crest. AW = anterior width of parasagittal crest. L = length of parasagittal crest. CBL = condylar basal length

	Parasagittal crest			CBL
	PW	AW	L	
Leptarctus oregonensis				
^{1}F:AM 25385	26.0	14.4	48.2	(84.0)
^{2}AMNH 18241	25.8	12.6	53.1	83.2
^{2}F:AM 25261	19.8	14.8	43.9	
^{3}F:AM 25258	28.1	16.0	47.0	(93)
Miomustela madisonae				
^{1}49119	12.3	4.6	24.2	
^{1}25332	11.4	4.3	[23.0]	
^{3}25289	11.3		[23.0]	
^{4}27445	14.8	4.2	24.5	

of AMNH F:AM 25385. Lim et al. (2001:fig 2.1, mislabeled fig. 2.2) and Lim and Martin (2002:fig. 2B top) illustrated a lateral view of the tympanic bulla of AMNH F:AM 25258, which they identified as belonging to *L. primus*.

Comment—Korth and Baskin (2009) referred AMNH F:AM 25258 to *Leptarctus* cf. *oregonensis* but did not describe it.

MUSTELIDAE SUBFAMILY INCERTAE SEDIS

Comments—Molecular phylogenies of musteloid carnivorans purport to constrain divergence times of genera, subfamilies, and families of extant members of this group. Sato et al. (2012) placed the most recent common ancestor (MRCA) of the extant subfamilies of Mustelidae at 16 Ma. Law et al. (2017) further refined the divergence dates and determined that the MRCA of each of the extant subfamilies occurred between 17.8-11.6 Ma, with all mustelids (other than *Taxidea taxus*, the American badger, which diverged first) diverging after 15.5 Ma. Studies based on DNA supports a sister group relationship between Ictonychinae (including the galictins) and Lutrinae (Sato et al., 2012) or Ictonychinae and Lutrinae plus Mustelinae (Law et al., 2017). The MRCA of the three occurs at 10-12 Ma (Law et al., 2017).

The Hemingfordian-Barstovian NALMA boundary is approximately 16 Ma (Tedford et al., 2004). If the molecular phylogeny and clock are correct, it would mean that most, if not all, late Hemingfordian and early Barstovian mustelids from North America, other than the extinct oligobunines and leptarctines, should not be assigned to a modern subfamily and should be regarded as stem neomustelids.

TABLE 3. Measurements of lower dentitions of *Leptarctus* from the Olcott Formation, *Skopelogale* from Observation Quarry, and *Miomustela*. F:AM 100010 is a cast of CM 848, the holotype of *Miomustela madisonae*; F:AM 104860 is from Observation Quarry. Measurements in parenthesis are alveolar lengths.

	p2L	p2W	p3L	p3W	p4L	p4W	m1L	m1Ltr	m1Wtr	m1Wtl	m2L	m2W	p2-m1	p2-m2	D
Leptarctus oregonensis															
AMNH 18270	3.2		4.3		5.3	3.3	9.6	5.2	3.8	4.1			22.5	26.8	8.3
F:AM 25320	(3.9)		5.0		6.7		(10.2)		4.7				26.9		
F:AM 25223	2.9	2.2	4.2		5.1	3.4	8.7	5.1	4.4	4.3	3.5	3.3	20.5	24.9	9.4
F:AM 25234	2.9		3.8		5.3	3.4	8.5	4.7	4.5	4.6	4.3		22.5	26.7	10.1
Skopelogale melitodes															
F:AM 49101	(2.3)		3.8	2.0	4.5	2.5	7.4	4.5	3.8	3.7	(2.9)		(19.0)	(20.6)	6.9
Miomustela															
F:AM 100010			2.3	1.1	3.3	1.45	4.9		2.2	1.6					4.5
F:AM 104680	(1.5)		1.85	1.0	2.6	1.3	4.1		1.85	1.3					3.4

Skopelogale melitodes gen. et sp. nov.
(Figure 3; Table 3)

Holotype—AMNH F:AM 49101, right mandible with p3-m1.

Horizon—Observation Quarry, ‘Sand Canyon Beds’, Dawes County, Nebraska.

Diagnosis—A small mustelid with p1 absent; p3 and p4 short and tall; p4 lacking a posterior accessory cusp; and m1 with metaconid large, entoconid absent, talonid short and wide, and talonid basin deep and circular.

Etymology—The genus name is derived from the Greek ‘skopelos’ (=observation point) and ‘gale’ (=weasel), which refers to the mustelid from Observation Quarry. The specific epithet melitodes is Greek (=of honey) in honor Jim Honey and also for his proclivity for late night dining on honey sandwiches on our many field trips together.

Description—The dentary is short and moderately deep (depth below m1 is 0.93 of the m1 length), with a slightly curved ventral margin. There is no p1. The p2 alveoli are offset in the jaw; the smaller anterior root is set interior to the midline. The p3 and p4 are somewhat wider posteriorly. The p3 is shorter than but nearly as tall as the p4; the main cuspid is anterior to the midline of the tooth; and there is a small anterior accessory cuspid and a short heel. The p4 main cuspid is centrally located and is taller than the protoconid of m1; the anterior accessory cuspid is moderately well developed; and there is no posterior accessory cuspid on the posterior cingulum.

The m1 trigonid is longer than the talonid, accounting for about 60% of the tooth length. The cuspids of the trigonid are separate from each other. The protoconid is the most prominent cusp. The paraconid and metaconid are subequal in height; both are slightly shorter than the protoconid. The antero-medially situated paraconid is only slightly elongated. The paraconid and metaconid are separated by a wide V-shaped valley; the paraconid and protoconid, by a very short and narrow notch. The metaconid is situated posterior to the protoconid. There is a wear facet on the back side of the protoconid. The talonid basin is deep and circular. The internal margin of the talonid is much lower than the posterior or external margin. The rounded hypoconid is the only noticeable cusp of the talonid. The hypoconid is connected to the postero-internal margin of the protoconid by a low crest. The cristid obliqua extends from the hypoconid with decreasing height to connect to the posterior side of the protoconid. No accessory roots are visible.

The m2 is single rooted. The relatively large alveolus extends posteriorly.

Discussion and Comparisons—AMNH F:AM 49101 attracted my attention while studying the basssariscines from Observation Quarry (Baskin, 2004). Although it was cataloged as *Bassariscus*, the single rooted m2 clearly indicated it was not a procyonid. In addition, the Lower Snake Creek and Observation Quarry bassariscines possess a single rooted p1, p4 with a small posterior accessory cusp, m1 with metaconid taller than paraconid and lower than protoconid and a narrower talonid, and a double rooted m2. The small size, large m1 metaconid, and absence of a p1 initially suggested that AMNH F:AM 49101 might be a mephitine. Mephitine synapomorphies for the lower dentition and mandible include chin on the mandible, p1 absent, and m1 with accessory roots, a ridge on the posterior face of the protoconid, and hypoconid dominant over entoconid (Wang et al., 2005). Of these, only p1 absent (which

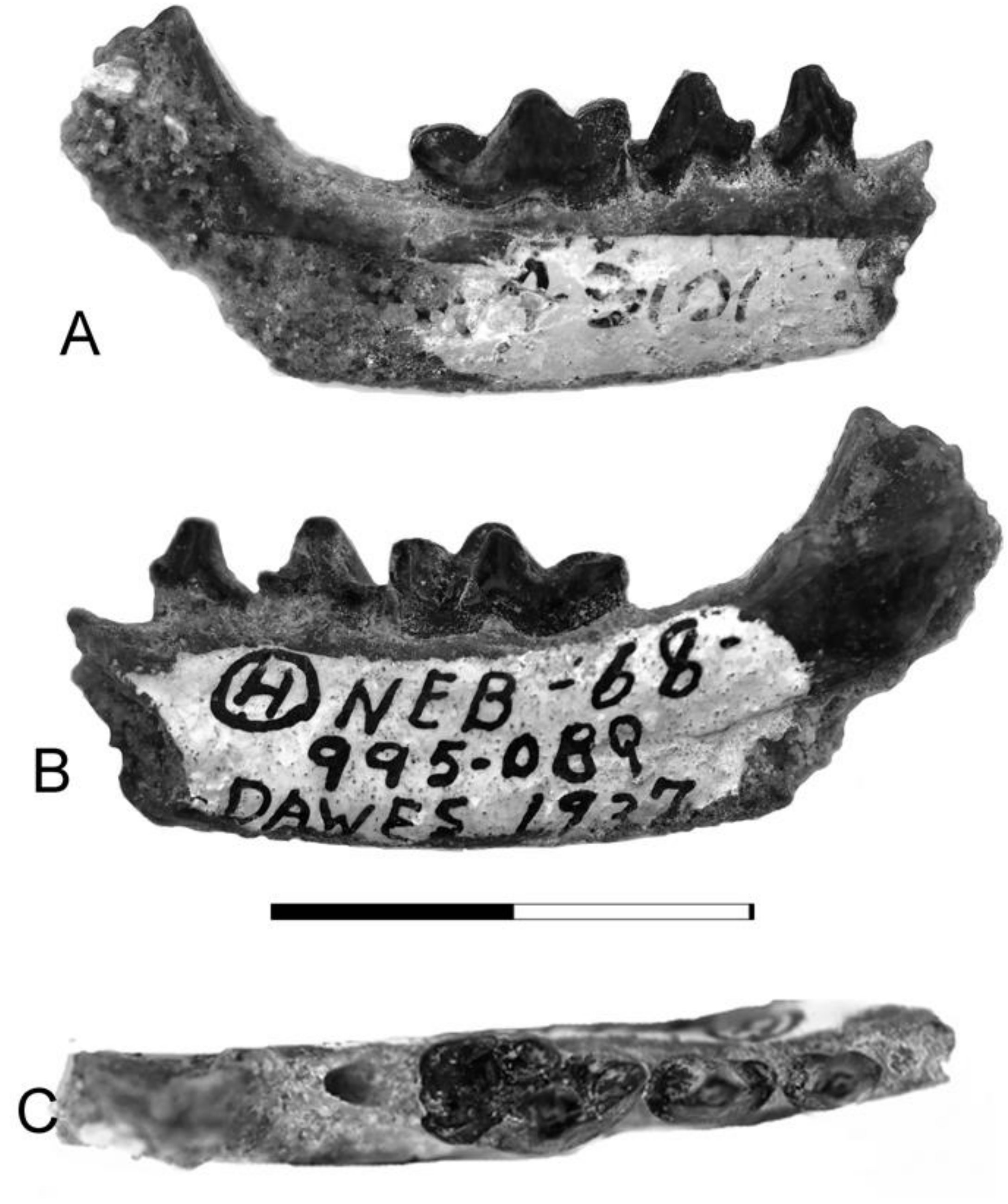

FIGURE 3. *Skopelogale melitodes*, AMNH F:AM 49101. A, lateral; B, medial; C, dorsal views. Scale = 2 cm.

can be found in other mustelids such as the leptarctines) and having hypoconid the tallest feature of the talonid are clearly present in AMNH F:AM 49101. A wear facet on the posterior side of the protoconid obscures whether a ridge was present.

Compared to the late Clarendonian *Martinogale faulli* (Wang et al., 2005), the oldest mephitine described from the New World, AMNH F:AM 49101 is much larger and has m1 with more inflated cusps, a taller more posteriorly situated metaconid, a lower hypoconid that is not widely separated from the protoconid, and a broader, less elongate talonid. It differs from Pleistocene and Recent New World mephitines in the absence of the m1 entoconid and in having the m1 with a shorter, wider, and deeper talonid basin that is enclosed lingually by a low wall and in having a less bladelike more inflated paraconid. The premolars are not greatly widened posteriorly.

Proputorius sansaniensis (Filhol, 1890), from the Middle Miocene (MN6, about 14-15 Ma) of France (Ginsburg, 1961; Peigné, 2012), has been considered an early mephitine (e.g., Petter, 1967, Ginsburg, 1999). However, Geraads and Spassov (2016) stated that it had no unambiguous mephitid synapomorphies such as accessory roots on the m1. Although Baskin (1998) noted the presence of an extra root on *P. sansanensis*, one is present on only a single specimen (MNHN Sa 930) and it is extremely small. *Proputorius sansaniensis* is larger than AMNH F:AM 49101 but has similar tooth length proportions. It has a reduced, two-rooted p2 and a basined talonid on m1. It differs in having the main cusp of the p4 lower than the protoconid of m1; the m1 with a more open trigonid, a notch between the protoconid and hypoconid, metaconid reduced and set more posteriorly, and a more elongate talonid.

The oligobunine *Brachypsalis* is much larger (ml L =12.8 to 16.5 mm), a p1 is present, p3 and p4 are broader, p4 has a posterior accessory cusp, m1 metaconid is smaller, and m2 is relatively large.

Miomustela madisonae (Douglas, 1904; Hall, 1930) from Observation Quarry (Lofgren et al., 2016) also has p1 absent. It is much smaller than AMNH F:AM 49101, and has m1 paraconid more blade-like, metaconid and paraconid similar in height, but much lower than the protoconid, and talonid narrower and not as deeply basined.

The late Hemingfordian to early Clarendonian *Plionictis* (Matthew, 1924) has p1 variably present and has m1 with a smaller metaconid and a narrower, trenchant talonid (Baskin, 1998). *Plionictis ogygia* (Matthew, 1901) has premolars relatively shorter and m1 similar in length but narrower than in AMNH F:AM 49101. *Plionictis parviloba* (Matthew, 1924) is much larger.

The late Hemingfordian to early Clarendonian *Sthenictis* (Peterson, 1910) differs from *Skopelogale* in its much larger size and in having a p1 and having m1 with a reduced metaconid and a trenchant talonid. *Sthenictis bellus* and *S. dolichops* are known from the Sheep Creek and Olcott Formations, respectively (Matthew, 1924, Skinner et al., 1977). *Sthenictis bellus*, the smallest species in the genus, is much larger than AMNH F:AM 41901.

The “*Martes*”-like *Dinogale siouxensis* (Cook and Macdonald, 1962) from Stonehouse Draw, Lower Sheep Creek Formation is larger (Tables 4, 5) than AMNH F:AM 49101. It possesses a p1, p4 with a posterior accessory cusp, m1 with a slightly basined talonid, and diatemata between p1-p2, p2-p3, and p3-p4. The m1 metaconid is a small cuspid, closely appressed to the protoconid, set slightly posterior to the protoconid. “*Martes*” *glareae* from the Olcott Formation differs from AMNH F:AM 49101 in having a small p1, slender premolars, p4 with a posterior accessory cuspid, and m1 narrower and more blade-like, with trigonid more open, a small metaconid, and talonid elongate and shallowly basined.

The late Hemingfordian to Clarendonian *Mionictis* (Matthew, 1924) also lacks p1 and has a tall p4. *Mionictis* is much larger than AMNH F:AM 49101 and has the m1 metaconid less tall than the protoconid and continuous with the internal rim of the talonid. The type species, *M. incertus* (AMNH FM 18263) and the smaller *M. elegans* (AMNH FM 18267) are both from the Olcott Formation (Matthew 1924); the smallest species *Mionictis letifer* (AMNH FM 81006) is from the Sheep Creek Formation (Cook and Macdonald, 1962). All three have an elongate, shallowly basined, and not widened talonid. The Clarendonian *Mionictis*? *pristinus* (Matthew and Gidley1904) is significantly larger than these three species (Valenciano et al., 2019:figs. 6, 9) and has the m1 talonid broader and more deeply basined, similar in morphology to that of AMNH F:AM 49101.

The p1 is also absent in *Leptarctus*. Leptarctines, including the European *Trocharion* (Major, 1903; Robles et al., 2010), differ from AMNH F:AM 49101 in having m1 with an entoconid, the trigonid separated from the talonid by valleys, and the m2 double-rooted. *Leptarctus oregonensis* from the Olcott Formation further differs in the following characters of the p4 and m1. The p4 has a prominent postero-external accessory cusp, a postero-internal cingulid, and the main cusp as tall as m1 protoconid. The m1 has a large metaconid as tall as the paraconid, but not as tall as the protoconid, a metaconid separated from the entoconid by a deep valley, a hypoconid separated from the protoconid by a V-shaped valley, and a basined talonid the same width as the trigonid.

Galictines and lutrines also lack a p1. Galictines have a deep jaw, crowded premolars, and m1 with an open bladelike trigonid, a lingually expanded and basined talonid with a posterolingual cingulum extending from the base of the reduced metaconid to the hypoconid, and hypoconid separated from the protoconid by a small notch (Baskin, 1998). Although differing in many respects, the m1 talonid basin of AMNH F:AM 49101 is most similar to that of the galictine *Cernictis*, especially *C. hesperus* (Hall, 1935).

Skopelogale adds a fourth new genus known only from lower jaws of recently described Hemingfordian and Barstovian mustelids. Smith et al. (2016) named two new genera as possible galictines from the lowest part of the Barstovian Monarch Mills Formation of Nevada. *Brevimalictis chikasha* (Smith et al., 2016) is smaller than *S. melitodes*, with a shallower jaw and m1 with a much smaller metaconid and a shallower talonid. *Negodiaetictis rugatrulleum* (Smith et al., 2016) has m1 with a large metaconid, but differs in its larger size, more curved ventral margin, crenulated enamel on the teeth, and m1 with a more blade-like paraconid-metaconid, a notch between the protoconid and hypoconid and between the hypoconid and hypoconulid, and a more elongate talonid. *Wataytabutsigwii* (McLaughlin et al., 2016) from the late Hemingfordian of Oregon is represented by a fragmentary jaw and teeth. It is much larger and m1 possesses a highly trenchant talonid. *Legionarictis* (Tseng et al., 2009b), from the Barstovian Temblor Formation of California, is only known from a cranium, so no direct comparison can be made.

Miomustela Hall, 1930
Miomustela madisonae (Douglas, 1904)
(Figure 4; Tables 2, 3)

Holotype—CM 848 (cast AMNH FM 100010), left mandible with c, p3-m1.

Horizon—“Madison Valley beds”, early Barstovian NALMA of Montana (Tedford et al., 2004).

Discussion—*Miomustela madisonae* was originally described as *Mustela*? *minor* (Douglas, 1904), then renamed *M.? madisonae* (Douglas, 1929). Hall (1930) established the genus *Miomustela* for this species. Jasinski (2015) noted its presence in the early Barstovian of New Mexico. Lofgren et al. (2016) and Lofgren and Abersek (2018) described this species from the Barstow Formation of California and from Observation Quarry

Referred Material from Observation Quarry—AMNH F:AM 49119, posterior cranium with right P2-M1, left P3 and broken M1; AMNH F:AM 104677, skull with right P2-M1 and left C, P2, P4, M1; AMNH F:AM 25332, posterior cranium; AMNH F:AM104680, right dentary with p3-m1.

Other Referred Material—AMNH F:AM 25289, posterior cranium, Greenside Quarry, Sheep Creek Formation, Nebraska; AMNH F:AM 27445, cranium with left C, P3-M1, right P3-M1; Skull Ridge Member, Tesuque Formation, early Barstovian, New Mexico.

Descriptions—Lofgren et al. (2016) described AMNH F:AM 104677 and 104680. Additional comments on these two are added below. In AMNH F:AM 49119**,** the parasagittal crests converge markedly anteriorly; the bulla is antero-posteriorly elongate; the post carotid foramen is medial; the carotid artery is enclosed in a tube on the medial side of the bulla. The P4 lacks a carnassial notch; the parastyle is very small; the metacone blade is much lower than the protocone; and the knob-like protocone is set on the anterior internal margin of the paracone. The M1 is narrower internally, with an internal cingulum; the parastyle is a prominent cusp; the paracone and metacone are close together; and the hypocone is situated postero-internally.

In AMNH F:AM 104677, the secondary palate extends well behind M1. The short C has a posterobasal cingulum. There is no alveolus for a P1. The P2 is small, double rooted, unicusped, with a posterior shelf; the elongate, posterior half of tooth is angled externally. The P3 has well-developed anterior and posterior cingula, a narrow internal cingulum, a rounded anterior margin, and a slight swelling on the posterior margin of the main cusp.

The P4 possesses a small parastyle and a long, low metacone blade. The protocone is a low knob separated from the paracone and situated at a level about midway between the apex of the paracone and parastyle. A weak cingulum runs around the parastyle to the protocone. The carnassial notch is absent.

The M1 occlusal surface is concave posteriorly, transversely elongate, and slightly wider across the paracone and metacone than across the protocone and hypocone. The parastyle is large. The protocone, paracone, metacone, and hypocone are relatively tall and all are situated at or close to the tooth margin. The hypocone is postero-internal to the protocone.

AMNH F:AM 25332 has weak parasagittal crests. The bulla is elongate. The mastoid process is small but distinct and closely appressed to the posterior bulla, the tip extends back slightly; the mastoid is small (similar to *Mustela*). The external auditory meatus opens laterally and is completely surrounded by a rim formed by a very short auditory tube (tube is slightly longer in AMNH F:AM 25389, a posterior cranium from the late Heminfordian Greenside Quarry, Sheep Creek Formation); the bulla extends posteriorly into the paroccipital process which forms a shallow recess. The inferior petrosal sinus extends from the posterior lacerate foramen to the level of the posterior carotid foramen. A tentorium is present.

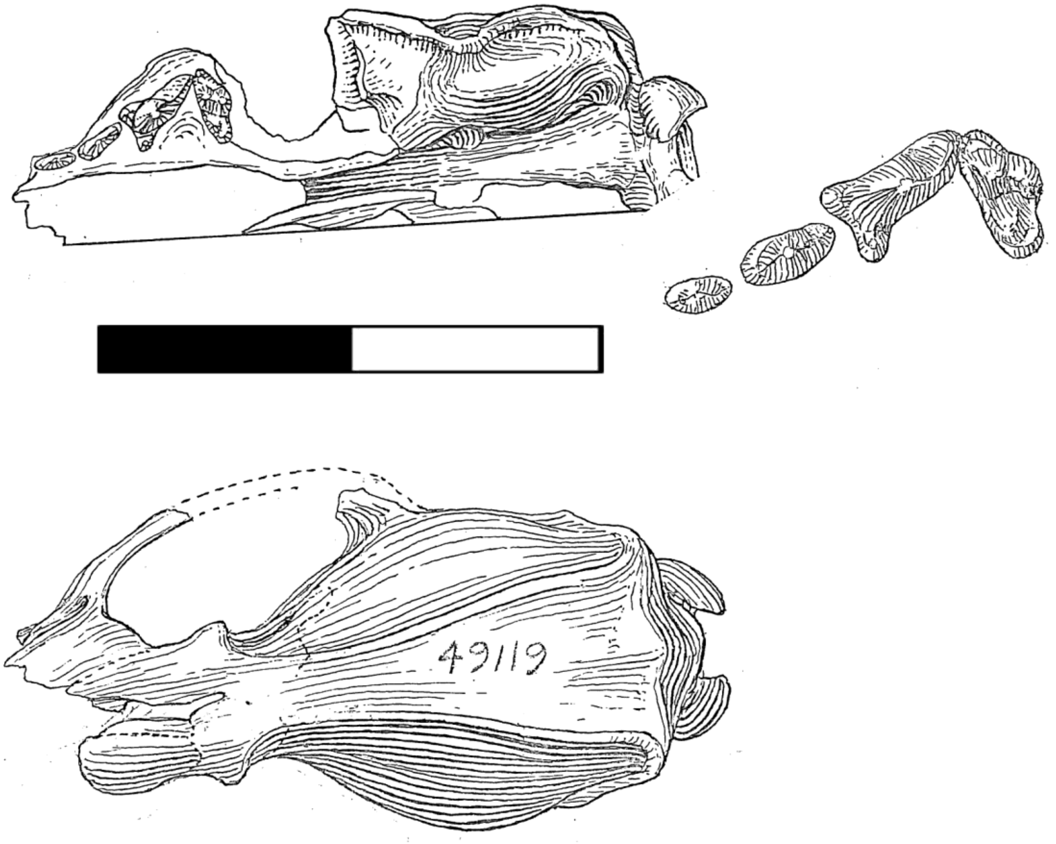

FIGURE 4. *Miomustela madisonae,* AMNH F:AM 49119. Scale =2 cm for dorsal and ventral views of skull; = 1 cm for left P2-M1.

AMNH F:AM 104680 has premolars with slightly widened posterior cingulids. There is no alveolus for a p1. The p2 is set at an angle with the alveolus for the posterior root on the internal margin of the ramus and that of the anterior root on the external margin. The p3 is narrower anteriorly, broader posteriorly, has an anteriorly situated main cuspid and anterior and posterior cingulids; the posterior cingulid is wider internally. There is a short diastema between p3 and p4. The p4 is wider posteriorly with a well-developed anterior cingulid and a postero-internal cingulids. The main cuspid is situated just anterior to the midline, with a small posterior accessory cuspid on its postero-external margin. The p4 anterior cingular cusp is a small, low, anterior projection of the cingulid; the posterior accessory cusp, prominent, closely attached to protoconid, internal to midline; and the posterior cingulid is broad, convex posteriorly, and does not form a distinct cusp. The m1 trigonid is open, with a deep wide V shaped notch separating the protoconid and paraconid. The paraconid and metaconid are subequal in height, and both are lower than the protoconid. The metaconid is positioned posterior to the apex of the protoconid. The talonid is short, low, narrow, and basined; the external margin is indented toward the internal side. The hypoconid is trenchant and the internal cingulum is low and connects to the posterior margin of the hypoconid. The m2 is single rooted. The anterior margin of the coronoid process is at a nearly 90 degree angle with the mandibular tooth row.

Comparisons—The Observation Quarry mandible is smaller and slenderer than the type of *Miomustela madisonae*. The p3 and p4 are narrower anteriorly with a better developed anterior cingular cusp especially on p4. The p4 posterior accessory cusp is much smaller and the posterointernal cingulum more prominent. The m1 talonid is rimmed internally by a low cingulum, but the trigonid being open internally in CM 848 may be as a result of wear. The m2 is single rather than double rooted.

The mephitine *Martinogale faulli* (Wang et al., 2005) is smaller; p4 has a posterior accessory cusp; m1 metaconid is more posterior and more closely appressed to the protoconid, talonid is less elongate and has a much more poorly developed internal rim; P4 has a stronger parastyle, protocone is taller and larger, more separated from and anterior to the paracone; M1 has a much stronger parastyle, less well developed metastyle exterior to the metacone, a more widely separated protocone and paracone and a more posterointernal hypocone. The bulla is more elongate and has a much more poorly developed auditory tube. Both have a condyloid foramen.

Discussion—Hall (1930) inferred a relationship between his new genera *Miomustela* and *Martinogale* based on small size, p1 absent, m1 with an open trigonid, relatively large metaconid, and basined talonid. He (1930) considered *Martinogale* near the ancestry of *Mustela*. *Martinogale* has since been allied to *Spilogale*, the spotted skunk (see references in Wang et al., 2005), although Geraards and Spassov (2016) disputed this relationship. Baskin (1998) assigned *Miomustela* to subfamily incertae sedis within the neomustelids. He remarked that although a mastoid sinus also occurs in mephitines, dental differences preclude mephitine affinities.

Schultzogale inexpectata (Lim and Martin, 2000) from the early Hemingfordian Runningwater Formation of Nebraska has been considered a leptarctine. Although accepting *Schultzogale* as a leptarctine, in large part because of the parasagittal crests, Wang et al. (2004) noted differences between *S. inexpectata* and leptarctines, such as the triangular shape of the M1 in the former. *Schultzogale* is a junior subjective synonym of *Miomustela*. *Miomustela inexpectata* (Lim and Martin, 2000) has parasagittal crests and a mastoid sinus (Baskin, 1998), as does *Miomustela* from Observation Quarry (AMNH F:AM 49119, 25332). The parasagittal crests in the illustration of *M. inexpectata* (Lim and Martin, 2000:fig. 2a) do not converge anteriorly as markedly as in AMNH F:AM 49119.

“*MARTES*”

Comment—Because early or middle Miocene taxa referred to *Martes* are not closely related to the direct ancestry of extant *Martes* (Anderson, 1994; Sato et al., 2003), Samuels and Cavin (2013) referred these taxa to “*Martes*.” The most recent common ancestor of extant martens, fishers, and the wolverine is late Miocene in age (Wang et al., 2012; Law et al., 2017).

“*Martes*” *glareae* (Sinclair, 1915)
(Figure 5; Tables 4, 5)

Holotype—PU 12071 (AMNH FM cast 143788), left mandible with p3-m1.

Horizon—Princeton Quarry 1000C, Olcott Formation, Sioux County, Nebraska; early Barstovian NALMA.

Comment—Sinclair (1915) differentiated his *Martes glareae* from Matthew’s (1901) *Mustela ogygia* on the presence in the former of a p1, p4 with a posterior accessory cusp, and a longer heel on the m1. Matthew (1924) named *Plionictis* for *P. ogygia*, *P.glareae*, and *P. parviloba*. He (1924) considered the differences between *P. glareae* and *P. ogygia* were of little or no significance, especially given the worn state of the holotype of *P. ogygia*, but did not synonymize the two. Webb (1969) made *Plionictis* a subgenus of *Martes* and synonymized the two species as *M.* (*P.*) *ogygia*. Baskin (1998) distinguished the two genera and retained Sinclair’s species in *Martes* because of the basined m1 talonid.

Description of PU 12071—The cast has a small alveolus antero-internal to the anterior alveolus of the p2. The p2 is double rooted. The p3 and slightly longer p4 are slender, secant teeth. The p4 has a small accessory cuspid on the postero-external margin of the main cuspid. The m1 metaconid is a small cusp set on postero-internal margin of the protoconid and is equal in height to the paraconid; the talonid is basined, rounded posteriorly (u shaped) and wider internally and narrower externally than the trigonid

Referred Material from Observation Quarry—AMNH F:AM 54469, left P4-M1; 25381, left M1; 25380, left m1.

Referred Material from the Olcott Formation—AMNH F:AM 21450 right mandible with p4-m1, Kilpatrick Pasture; AMNH F:AM 24887 left ramus with p2, p4-m1.

Description and Comparisons of Material from Observation Quarry—The P4 protocone is a very low knob attached to the antero-internal corner of the paracone; it does not extend very far beyond the antero-external margin of the tooth. The protocone is much smaller than that of *Plionictis* (AMNH F:AM 25334) from Observation Quarry. There is a moderately well developed, but thin, cingulum internal to the metacone blade. The paracone occupies much more of the blade than in *Plionictis* (i.e., a very short metacone).

M1 of AMNH F:AM 54469 is only slightly restricted medially (mid-length =3.0 mm) and is expanded postero-internally. *Plionictis* only has a slight expansion, and is almost parallel sided anterior and posterior. There is no metaconule, the internal cingulum is expanded anteriorly in front of the protocone. The paracone and metacone are in contact.

M1 of AMNH F:AM 25381 is noticeably dumbbell shaped (mid-length =4.1 mm), with a prominent parastyle. The protocone is relatively small and close to the anterior margin. The internal cingulum extends noticeably anterior to the protocone but does not extend externally onto the anterior margin. The metaconule is close to the posterior margin

The m1 is smaller than, but similar to, that of AMNH F:AM 24887 from the Olcott Formation. It is much smaller than that of *Dinogale siouxensis* (AMNH FM 81009). AMNH F:AM 25380 has a wide

TABLE 4. Measurements of upper dentitions of [1], “*Martes*” and [2] *Plionictis*. [a] = width across protocone-paracone; [b] = width across metacone; [c] = external length; [d] = internal length.

	P4L	P4W[a]	P4W[b]	M1L[c]	M1L[d]	M1W
[1]F:AM 54469	7.2	4.1	2.9	3.1	4.6	7.3
[1]F:AM 25381				4.5	5.4	8.7
[2]AMNH 9042	7.5	5.0	3.1	3.4	3.4	7.5
[2]F:AM 25334	7.4	4.5	2.8		5.3	8.1
[2]F:AM 25314	8.5	5.6	3.3	3.7	4.3	8.1
[2]F:AM 25485	8.2	5.5	3.4	3.5	4.1	7.6

open elongate trigonid and an elongate, shallowly basined talonid that is slightly narrower than the trigonid. The metaconid is a small cusp on the posterointernal flank of the protoconid, equal in height to the paraconid. The paraconid is very elongate, its apex is along the midline of the tooth. The talonid rim is low and connects with the posterior margin of the metaconid. The hypocone is a very small low cusp. The metaconid is a larger more posteriorly set cusp than *Dinogale*.

The m1 of the type of “*M.*” *glareae* has a similar trigonid morphology to AMNH F:AM 25380. The talonid has a more prominent, subtrenchant, postero-external heel (this area is worn in 25380) and a less well developed internal talonid rim than AMNH F:AM 25380, but the two have a basined talonid.

Description of Material from the Olcott Formation—AMNH F:AM 21450 has p4 with a small posterior accessory cusp. The m1 metaconid is small and the talonid is basined. AMNH F:AM 24887 has a double rooted p1. The m1 has a prominent metaconid and a deeply basined talonid.

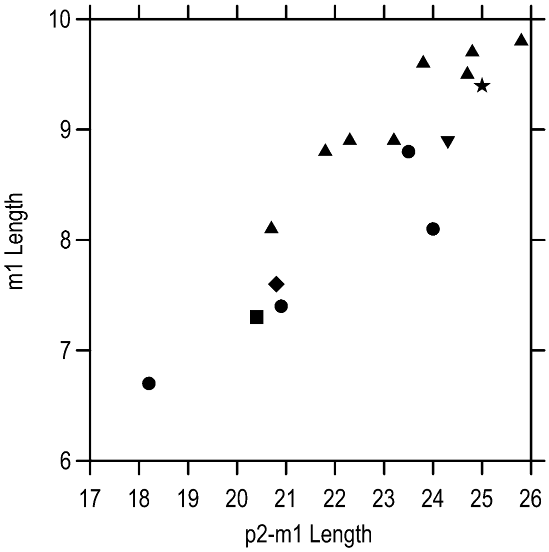

FIGURE 5. Bivariate plot of m1 length versus p2-m1 length for “*Martes*” and *Plionictis*. Measurements are in mm. Diamond = type of “*Martes glarae*, PU 12701; Inverted triangle = AMNH F:AM 24887, “*Martes glarae* from the Olcott Formation; Square = AMNH FM 9042, type of *Plionictis ogygia*; Star = neotype of *P. parvibola*, AMNH FM 17208; Circles = *Plionictis* from Observation Quarry; Triangles = *Plionictis* from the Olcott Formation.

TABLE 5. Measurements of lower jaws of "*Martes*", *Dinogale*, and *Plionictis*. [1] holotype of *Martes. glarea* , [2] "*M.*" *glareae* from Observation Quarry, [3] "*M.*" *glareae* from the Olcott Formation, [4] holotype of *Plionictis ogygia*, [5] *P. ogygia* from Observation Quarry, [6] *P. ogygia* from the Olcott Formation, [7] holotype of *P. parviloba*, [8]*P. parviloba* from Observation Quarry, [9]*P. parviloba* from the Olcott Formation, [10]*P. oaxacaensis* (measurements from Ferrusquía-Villafranca, 1990).

	p2L	p2w	p3L	p3W	p4L	p4W	m1L	m1W	m2L	m2w	p2m1	p2m2	Depth
"Martes"													
[1]PU 12071	(4.0)		4.4	1.9	5.5	2.0	7.5	3.0			20.8	[23.2]	
[2]F:AM 25380							8.5	3.3					
[3]F:AM 21450					7.7	2.9	9.4	4.2					8.6
[3]F:AM 24887	4.2	1.8	(4.6)		6.2	3.3	8.9	4.2			24.3	26.4	7.6
Dinogale siouxensis													
AMNH 81009	4.7	2.3	5.5	2.6	7.7	3.1	10.7	4.4			30.4	34.5	11.3
Plionictis													
[4]AMNH 9042	3.5	1.8	4.9	2.1	5.2	2.4	7.3	3.3	2.9	1.6	20.4	22.2	8.7
[5]F:AM 25333	3.2	1.5	4.0	1.7	4.6	2.1	6.7	2.7			18.2	[20.0]	6.6
[5]F:AM 25335	3.6	1.8	4.3	2.3	5.4	2.6	7.5	3.1			20.9		
[6]F:AM 25312	3.4	2.1			5.9	2.5	8.1	3.7			20.7	23.1	6.8
[7]AMNH 17208	3.8	1.2	4.4	1.6	5.7	1.9	9.4	3.8			25.0	27.7	10.2
[8]F:AM 25342	3.7	1.9	5.1	2.3	6.3	2.7	8.8	4.1	3.4	3.0	23.5	26.6	9.5
[8]F:AM 25343	4.1	2.2	4.6	2.5	6.1	3.0	[8.1]				[24]	[27.9]	9.4
[9]F:AM 25313	3.8	1.9	4.7	2.1	6.1	2.8	8.8	3.7			21.8	24.4	7.4
[9]F:AM 25317	3.7	2.3	4.1	2.4	6.6	2.7	9.5	3.7			24.7	27.3	9.5
[9]F:AM 25318	4.0	2.3	4.2	3.2	5.4	3.2	9.7				24.8	26.3	
[9]F:AM 25319	4.2	2.2			7.4	3.0	9.8	3.6			25.8	28.5	10.2
[9]F:AM 25321	3.8	1.7	3.9	2.3	5.3	2.6	8.9	3.4			22.3	24.8	8.4
[9]F:AM 49132	3.9	2.4	(4.8)		(6.2)		(9.6)				23.8	27.1	8.3
[9]F:AM 49133	3.9	2.2	4.6	2.4	6.3	2.3	8.9	3.4			23.2	25.4	
[10] IGM 3977	(3.9)		4.0	2.1	(4.0)	2.5	7.1	3.8	3.0				7.2

Plionictis Matthew, 1924

Type species—*Mustela ogygia* (Matthew, 1901)
Included species—*Plionictis ogygia, Plionictis parviloba, Plionictis oaxacaensis*.

Discussion—Matthew (1901) named *Mustela ogygia* from a skull with lower jaw found in northeastern Colorado. Later he (1924) made it the name bearer for his new genus *Plionictis*. The larger *P. parviloba* (Matthew, 1924) has a more complex nomenclatural history. Cope (1873) named a small carnivore from the "Loup Fork Beds" of eastern Colorado *Aelurodon mustelinus* from a jaw with p4, m1, and a single-rooted m2. At the time, Cope considered that *Aelurodon* was a felid, then later a canid. Cope (1874:520) repeated the description, but referred to the species as *Martes mustelinus*, because he now recognized it was a mustelid. He (1877:306), without comment, then identified the species as "*Mustela parviloba*, Cope (*Martes mustelinus*, Cope)", apparently because the specific epithet was preoccupied by *Plesiogale mustelina* (Pomel, 1854), which Filhol (1879) assigned to *Mustela mustelina*. This is supported by Coues (1877:16) who included "*Mustela parviloba*, Cope (change of name on reference of the species to *Mustela*)" in his synonymy of *Mustela mustelina*. Matthew (1924) stated that the specimen came from the Pawnee Creek beds of Colorado and referred it to *Plionictis*. The type specimen was reported lost (Galbreath, 1953:101). Matthew (1924: p 135) illustrated a lower jaw (AMNH FM 17208) from the Olcott Formation (Skinner et al., 1977) which should be considered the neotype of *Plionictis parviloba*. It is currently noted as the type on its AMNH specimen card.

Plionictis oaxacaensis from the Nejapa Fauna, Early Barstovian of Oaxaca State, Mexico (Ferrusquía-Villafranca, 1990) has a p1. The m1 is similar in size to *P. ogygia*, but differs in having sharper, transversely narrower cheek teeth, especially the carnassials, and a relatively large m2.

There are a smaller and a larger (or possibly just one variable) species of *Plionictis* in the Sheep Creek, Lower Snake Creek, and Observation Quarry Faunas. There are no significant differences other than size (Figs. 5, 6) to distinguish among *Plionictis* from these units. *Plionictis* differs from "*Martes*" in having a trenchant versus basined talonid on m1 (Baskin, 1998). Matthew (1924) characterized *Plionictis* as having p1 absent and a larger m1 metaconid than *Martes.* The m1 metaconid tends to be more reduced in the Sheep Creek specimens, although some Olcott Formation specimens also have a very small metaconid. The p1 is absent in the type of *P. ogygia* (AMNH FM 9042) and present in the type of *P. parviloba* (AMNH FM 17208). The p1 is variably present in *Plionictis* from the Barstow Formation (Lofgren et al., 2016). Seven of nine mandibles from the Olcott Formation have an alveolus for p1. The p1 can be variably present in extant mustelids (e.g., Hancox, 1988).

Plionictis ogygla (Matthew, 1901)

(Figures 5, 6A; Tables 4, 5)

Mustela ogygia Matthew, 1901
Plionictis ogygia Matthew, 1924

Type Specimen—AMNH FM 9042, skull and lower jaws

Horizon—"Pawnee Creek beds" (Galbreath, 1953; =upper Ogallala Group, Tedford, 2004), Cedar Creek, Logan County, Colorado; middle Barstovian NALMA.

Referred Material from Observation Quarry—AMNH F:AM 25334, left maxilla fragment with P4; 54470, right M1; AMNH F:AM 25333, right mandible with p2-m1; AMNH F:AM 25335, left ramus with p2, p3, broken p4, m1.

Referred Material from the Olcott Formation—AMNH F:AM 25312, left ramus with p2, p4-m1.

Description and Comparisons—AMNH F:AM 25334—The P4 protocone is a knob at the end of a short isthmus that is well separated from the paracone and anterior to the antero-external margin of the paracone. The paracone is relatively short. There is a very weak cingulum on the internal margin of the metacone blade. The metacone is elongate takes up most of blade. The protocone is situated more anteriorly than in the holotype (AMNH FM 9042). It is similar to the P4 in AMNH F:AM 25314 or 25485, skulls from the Olcott Formation identified as *Plionictis* cf. *parviloba*.

The M1 is worn and the parastyle is broken. It is longest internally, slightly narrower medially. The paracone and metacone are small; the talon basined; and the small metaconule is present on the postprotocrista. Crests connect the paracone with the preprotocrista and the metacone with the metaconule. The internal cingulum is expanded posteriorly and extends anterior and external to the protocone .The M1s from the Olcott Formation have the protocone close to the anterior margin and are noticeably longer internally than badly worn type. The M1 of AMNH FM 9042 does not lengthen significantly internally. The M1s in the Olcott skulls are noticeably longer internally

AMNH F:AM 25333—The p1 is absent. The p2 is a slender, secant tooth; the main cuspid is anteriorly situated. The p3 is also slender and sectorial; the main cuspid is anterior to the midline; an anterior cingulum and posterior heel are present. The p4 is likewise slender and secant, with an anterior cingulum and posterior heel; a posterior crest on the main cuspid runs to the postero-external margin, and there is a slight swelling on this crest, perhaps an incipient posterior accessory cuspid. The m1 is elongate and secant, with the paraconid extending antero-internally forming an open trigonid. The protoconid is the tallest cuspid. The metaconid is a prominent cuspid that is slightly lower in height than the paraconid, but much lower than the protoconid and is situated somewhat posterior of the protoconid. The metaconid and protoconid are joined at their bases. The talonid is relatively elongate. The hypoconid is low, but semi-trenchant. Basically the

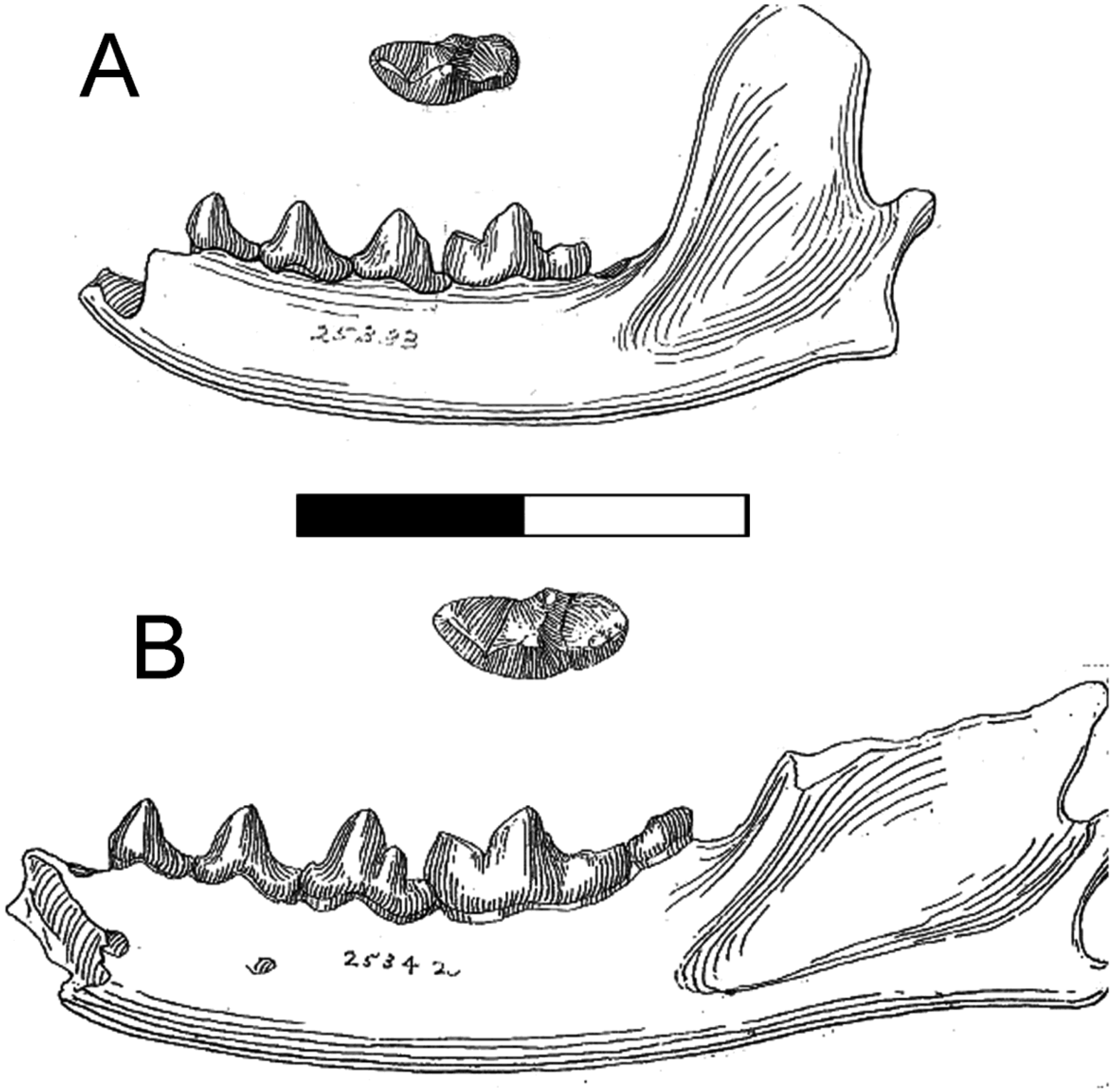

FIGURE 6 A, *Plionictis ogygia* (AMNH F:AM 25333), B, *P. parviloba* (AMNH F:AM 25342), from Observation Quarry. Scale = 2 cm.

talonid is open internally, but there is a slender, very, low internal cingulum extending from the posterior margin of the metaconid to the posterointernal corner. The talonid is narrower (2.4 mm) than the trigonid (2.7 mm). The m2 is represented by a small, round alveolus. The condyloid process is tilted internally.

AMNH F:AM 25333 is much smaller than the neotype of *P. parvibola* (AMNH FM 17208) and the p4 is not as tall. It is a little smaller than the type of *P. ogygia* but differs in having a shallower mandible and the main cusp of p3 and p4. On the type of *P. ogygia* the posterior portion of m1 rises with the ascending condyloid process. The m1 is horizontal on AMNH F:AM 25333; the coronoid process is not as tall. AMNH F:AM 25333 is similar in size to *"M." glareae*; the p3 and p4 are narrower posteriorly; m1 metaconid is somewhat larger; the talonid is trenchant, but with a very low internal rim.

AMNH F:AM 25335—The mandible has cheek teeth similar to those of AMNH F:AM 25333. The p3 has broader anterior and posterior cingulids. In p4, the main cusp is broken; there is a prominent posterior accessory cuspid and well developed anterior and posterior cingulids. The m1 metaconid is a little lower than the paraconid (as in AMNH F:AM 25333 and 25342), and the talonid is trenchant. Compared to *"M." glareae*, AMNH F:AM 25335 has p3 more convex externally, more concave internally (vs straight sides in *"M." glareae*). The p4 has a stronger posterior accessory cusp. The m1 talonid is narrower (it is constricted externally and the hypoconid is set more laterally) .

AMNH F:AM 25312—This mandible from the Olcott Formation has a p1 alveolus. The m1 metaconid is relatively small.

Plionictis parviloba (Cope, 1873)
(Figures 5, 6B; Tables 4, 5)

Type Specimen—unnumbered and un-illustrated, a jaw with p4, m1, and a single rooted m2.

Type Locality—Loup Fork Beds (=Pawnee Creek beds) of eastern Colorado, USA.

Neotype Specimen—AMNH FM 17208, right ramus with p2-m1; Olcott Formation (site unknown; Skinner et al., 1977).

Referred Material from the Olcott Formation—AMNH F:AM 25313, left ramus with c, p2-m1, Boulder Quarry; AMNH F:AM 25317, right ramus with p2-m1, Humbug Quarry; AMNH F:AM 25318, left ramus with c, p2-p4, damaged m1, Humbug Quarry; AMNH F:AM 25319, left ramus with c, p2, p4-m1, Humbug Quarry; AMNH F:AM 25321, right ramus c, p2-m1, Trojan Quarry; AMNH F:AM 49132 right ramus with C, p2, Humbug Quarry; AMNH F:AM: 49133, right ramus with p2-p4, damaged m1, Humbug Quarry; AMNH F:AM 25314, skull with left P4-M1, right P2-M1, Echo Quarry; and AMNH F:AM 25485, skull with left P3-M1, right P2-M1.

Referred Material from Observation Quarry—AMNH F:AM 25342, left mandible with p2-m2; 25343, left mandible with p2-p4.

Description of *Plionictis parviloba* from Observation Quarry—AMNH F:AM 25342—The p1 alveolus is not reduced (L = 1.5 mm) The p2-p4 are slender secant teeth similar in morphology to the smaller AMNH F:AM 25333. The p4 has a small but better developed posterior accessory cuspid and a well-developed posterior cingulum. The m1 the metaconid is more separated from the protoconid than in AMNH F:AM 25333, and the talonid is more worn; but otherwise they are similar. The m2 is suboval with a protoconid about midway on the external margin, and a smaller but somewhat taller metaconid slightly posterior on the internal margin.

AMNH F:AM 25342 compares well in overall size and m1 morphology with the neotype of *P. parviloba*. The premolars of the neotype are more slender and secant, but there appears to be abnormal loss of the enamel, especially on p2 and p3. The p4 of AMNH F:AM 25342 has a noticeable posterior accessory cuspid.

AMNH F:AM 25343—The p4 has a tall main cusp, no posterior accessory cusp, and a short heel. The ventral margin of the mandible indents under the deep masseteric fossa.

Sthenictis Peterson, 1910
(Figures 7-9; Table 6)

Genotypic Species—*Sthenictis robustus* (Cope, 1890)

Included Species—*Sthenictis robustus*, *Sthenictis dolichops*, *Sthenictis bellus*, *Sthenictis lacota*, *Sthenictis neimengguensis*.

Remark—Baskin (2005) and Tseng et al. (2009a) commented on the species of *Sthenictis*. Baskin (2005) summarized the convoluted nomenclatural histories of *S. robustus* and *S. lacota*.

Sthenictis robustus (Cope, 1890)

Stenogale robusta Cope, 1890
Potamotherium robustum Matthew and Gidley, 1904
Brachygale robusta Peterson, 1910
Sthenictis robustus errata sheet inserted in Peterson, 1910
Sthenictis robustus Cope and Matthew, 1915

Holotype—AMNH FM 8541, left mandible with p3, c1 root, damaged p2, p4, and m1, and alveoli for i1-3, p1, m2.

Horizon—Valentine Formation near Fort Niobrara, Nebraska; late Barstovian NALMA

Description and Discussion—*Sthenictis robustus* (Cope, 1890) is known only from the holotype. It is the smallest species of the genus. Although all the teeth are broken, the m1 has the small metaconid and semi-trenchant, elongate talonid that characterize of this genus (Baskin 1998). As best can be determined, this specimen has hitherto not been illustrated (Figure 8).

Sthenictis dolichops Matthew, 1924

Sthenictis bellus Matthew, 1932

Holotype—AMNH FM 18264, left mandible with p2-m1, and alveoli for c, p1, m2.

Horizon—Trojan Quarry, Olcott Formation, Sioux County, Nebraska.

Referred Material from the Olcott Formation—AMNH F:AM 25322, right ramus with C, p2-m1, Humbug Quarry; 25328, with p2-m1, Echo

TABLE 6 Measurements on mandibles and lower teeth of *Sthenictis*. [1], holotype of *S. robustus*; [2], holotype of *S. lacota*; [3], holotype of *S. dolichops*; [4], holotype of *S. bellus*; [5], *S. dolichops*, from Observation Quarry; [6], *S. dolichops*, from Olcott Formation.

	p2L	p2W	p3L	p3W	p4L	p4W	m1L	m1W	p2m1	p2m2	p3m1	D
AMNH 8541[1]	4.9	2.6	6.5	3.2	6.8	[3.6]	11.4	[4.8]	32.1	35.0	25.8	12.6
AMNH 10810[2]	8.1	4.8	9.4	4.8	13.8	6.7	18.3	6.8	46.5	52.7	38.1	19.0
AMNH 18264[3]	6.6	3.6	8.0	4.2	10.2	5.4	15.9	6.5	42.9	50.5	34.2	19.3
AMNH 20501[4]	5.4	2.9	7.2	3.2	8.0	3.9	13.5	5.7	34.1	38.6	27.8	13.0
F:AM 25347[5]	(6.9)		7.9	3.4	9.8	4.2	15.1	6.25	38.4		32.8	18.3
F:AM 25341[5]							14.9	6.2				
F:AM 25282[5]							12.6	5.5				
F:AM 25322[6]	6.3	2.8	7.3	3.0	8.8	3.9	12.8	5.2	35.8	40.3	28.7	14.2
F:AM 25324[6]					9.3	4.0	13.3	5.6				
F:AM 25325[6]					9.8	4.1	13.2	5.8	36.9		29.7	
F:AM 25328[6]	7.8	4.0	9.33	3.7	11.0	4.4	15.8	6.7	44.9	50.0	35.8	18.5
F:AM 25329[6]	7.5	3.8	[8.4]		10.3	5.4	15.8	6.8	42.1	47.4	33.3	17.7

Quarry; 25329, left mandible with C, p2, p4-m1, East Jenkins Quarry; 25324, right ramus with p4-m1, Quarry 3; 25325, right mandible with p4-m1, Echo Quarry.

Referred Material from Observation Quarry—AMNH F:AM 25347, left mandible with c, p3-m1; 25341, left m1; 25382, left m1; and 54479, right M1.

Referred Material from the Sheep Creek Formation—AMNH FM 20501 (holotype of *Sthenictis bellus*), right mandible with p2-ml.

Description of AMNH F:AM 25347—The specimen has a large canine (8.7 x 6.7) that projects 17 mm above the ramus. The p1 is small and single-rooted. The posterior root of the p2 is more elongate than the anterior root. The narrow p3 has a single main cuspid, with a short posterior heel, and a blunt anterior end. The p4 main cuspid is centrally located, with a small posterior accessory cuspid and has a posterior cingulum. The m1 has an open trigonid. The paraconid is separated from protoconid by a narrow slit. The small metaconid is on the postero-internal margin of the protoconid and is equal in height to paraconid. The talonid is rounded posteriorly; a low, rounded hypoconid occupies much of the external half of the low but trenchant talonid which lacks a basin; the internal half is a flat shelf that is open internally but has a very low rim. AMNH F:AM 25341 and 25282 have a reduced metaconid and a trenchant hypoconid; AMNH F:AM 25382 is very worn.

The M1 is not constricted medially (as in e.g. *Martes*), has the anterior margin relatively straight, and is expanded postero-internally. The paracone and metacone are connected by a crest; the protocone is close to the anterior margin; the metaconule is internal to the metacone on the posterior margin. Dimensions are as follows: Le = 5.8 mm, Li = 8.0 mm, W =10.7 mm.

Comparisons and Discussion—The Observation Quarry mandible (Fig. 9) is similar to the type of *S. dolichops* (AMNH FM 18264), but has a shorter tooth-row length; the premolars are narrower and have smaller less inflated main cusps, and are narrower especially posteriorly. The m1 of AMNH FM 18264 has a higher internal rim of the talonid, enclosing the internal margin but is otherwise similar. The longer premolars of AMNH F:AM 25347 more closely resemble those of AMNH F:AM 25238 from Jenkins Quarry, Olcott Formation which also has a very similar m1 talonid. AMNH F:AM 25238 has diastemata between p2-p3 and p3-p4. The smaller AMNH F:AM 25325 from Echo Quarry is worn and damaged, but the talonid is a close match to AMNH F:AM 25347; the hypoconid is large and round, there is a posterior hypoconulid. The largest species, *S. lacota* (AMNH FM 10810), is known from a right mandible with p2, p3, broken p4 and m1, and alveoli for p1and m2 (Matthew and Gidley, 1904: fig. 6) from the “Loup Fork” (Clarendonian) of Little White River, South Dakota. In addition to its large size (Table 6), it has more closely spaced premolars than the Observation Quarry mandible (AMNH F:AM 25347).

The type and only specimen of *Sthenictis bellus* (AMNH FM 20501) is from the late Hemingfordian Sheep Creek Formation (Matthew, 1932). Other than smaller size and more slender premolars compared to *S. dolichops*, Matthew (1932) noted that *S. bellus* appeared to have m2 with two roots in a single alveolus (the alveolus is wider anteriorly and narrower posteriorly) versus a larger alveolus for a single root in *S. dolichops*. It cannot be determined if a p1 was present. Three specimens from the Olcott

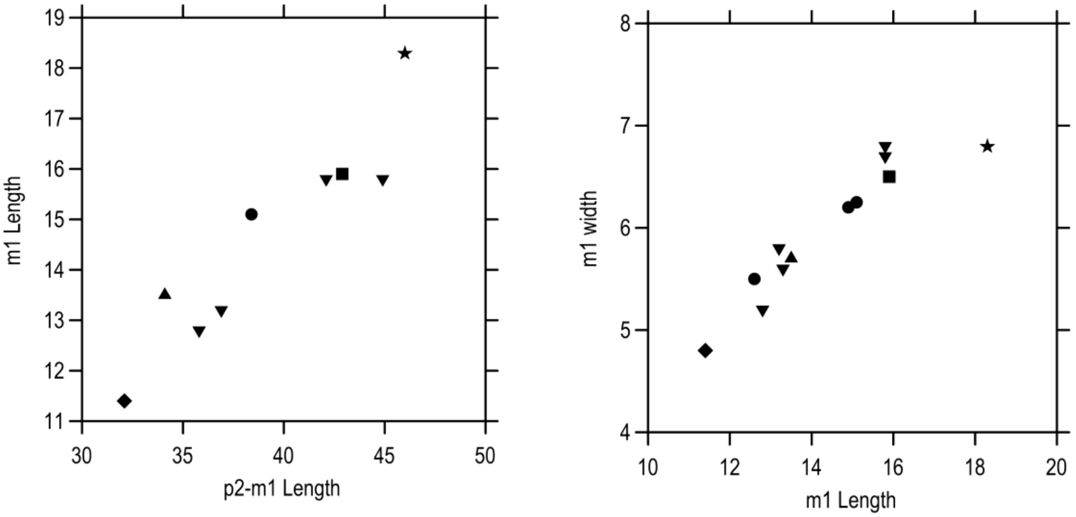

FIGURE 7. Bivariate plots of m1 length versus p2-m1 length (left) and m1 width versus m1 length (right). Measurements are in mm. Circle = *Sthenictis* from Observation Quary, AMNH F:AM 10810; Inverted triangles = *Sthenictis* fro m the Olcott Formation; Diamond = holotype of *S. robustus*, AMNH FM 8541; Triangle = holotype of *S. bellus*, AMNH FM 20501; Square = holotype of *S.dolichops*, AMNH FM 18264; Star = holotype of ?*S. lacota*, AMNH FM 10810.

Formation and an isolated m1 from Observation Quarry are similar in size to *S. bellus* (Table 6). Both species may be present in the Olcott Formation and Observation Quarry (Table 6), or *S. dolichops* may be the senior synonym. Species of Recent martens display size variation similar to that in the three Nebraska samples (Anderson, 1970). This supports synonymizing *S. bellus* with *S. dolichops*.

Subfamily Oligobuninae Baskin, 1998
Brachypsalis Cope, 1890

Discussion—*Brachypsalis matutinus* (Matthew, 1924) is known from the Sheep Creek Formation; *B. modicus* (Matthew, 1918) and *B. obliquidens* (Sinclair, 1915), from the Olcott Formation (Skinner et al., 1977). According to Korth and Evander (2016: table 1), Prothero et al. (2008) reported *B. obliquidens* from Observation Quarry. However, this is an error since Prothero et al. (2008: fig. 5) compared a specimen from California with *B. obliquidens* (AMNH FM 25305) from the Olcott Formation. *Brachypsalis* is not known from the “Sand Canyon Beds” of Observation Quarry. *Brachypsalis* sp. (AMNH FM 25456, right and left maxillae and mandibles with P1-M2 and p1-m2) is from the Hemingfordian Box Butte Formation, Sand Canyon region, Dawes County, Nebraska (Galusha, 1975b).

CONCLUSIONS

Subdivision and radioisotope ages of the Hemingfordian and Barstovian NALMAs follow Tedford et al. (2004:fig. 6.3). In the original definition of the NALMAs, Wood et al. (1941) assigned the Lower Sheep Creek Fauna to the Hemingfordian NALMA. They considered the Snake Creek Faunas too poorly understood to assign to a NALMA. By the early 1940’s the Lower Snake Creek was recognized as Barstovian, at that time considered upper Miocene (e.g. Gregory, 1942; Stirton, 1944). Evernden et al. (1964) placed the Upper Sheep Creek and Lower Snake Creek Faunas in the Hemingfordian. Skinner et al. (1977) described the lithostratigraphic and biostratigraphic succession of the Sheep Creek and Snake Creek units in northwestern Nebraska. They named the Olcott Formation, assigned the Lower Snake Creek Fauna to this stratigraphic unit, and placed the Hemingfordian-Barstovian boundary between the Sheep Creek and Olcott Formations. Woodburne (1969:284) considered the early Barstovian Observation Quarry “as post Sheep Creek and pre Lower Snake Creek.” Tedford (in Tedford et al., 1987:168) posited that the early Barstovian Observation Quarry LF “may fill the gap between the faunas of the Sheep Creek and Olcott Formations.”

TABLE 7. Carnivorans in the AMNH collections from the late Hemingfordian Sheep Creek Formation and the early Barstovian Lower Snake Creek (Olcott Formation) and Observation Quarry. Data for Amphicyonidae are from Hunt (1998); Canidae from Wang et al. (1999) and Tedford et al. (2009); and Felidae from Rothwell, 2003).

	Sheep Creek	Olcott Fm.	Observation Q
Procyonidae			
Probassariscus matthewi			x
Bassariscus antiquus		x	
Bassariscus minimus		x	x
Arctonasua minima			x
Mustelidae			
Leptarctus oregonensis		x	x
Leptarctus cf. *oregonensis*	x		
Skopelogale melitodes			x
Miomustela madisonae			x
Plionictis sp.	x		
Plionictis ogygia		x	x
Plionictis parviloba		x	x
Sthenictis bellus	x		
Sthenictis dolichops		x	x
Dinogale siouxensis	x		
“Martes” glareae		x	x
Mionictis letifer	x		
Mionictis incertus		x	
Mionictis elegans		x	
Brachypsalis matutinus	x		
Brachypsalis obliquidens		x	
Brachypsalis modicus		x	
Amphicyonidae			
Pliocyon medius	x	x	x
Cynelos idoneus	x		
Cynelos sinapius		x	
Amphicyon frendens	x		
Amphicyon ingens		x	
Canidae			
Cynarctoides acridens	x	x	x
Paracynarctus sinclairi		x	x
Tomarctus hippophaga		x	x
Tomarctus brevirostris		x	
Euoplocyon brachygnathus		x	
Psalidocyon maranae		x	
Microtomarctus conferta,		x	
Protomarctus optatus	x		
Leptocyon leidyi	x	x	x
Felidae			
Pseudaelurus stouti		x	x
Pseudaelurus marshi		x	x
Pseudaelurus aeluroides		x	
Pseudaelurus validus	x	x	
Pseudaelurus intrepidus		x	
Pseudaelurus skinneri	x		

TABLE 8. Sørensen-Dice similarity coefficients (SDSC) for the carnivoran taxa (Table 7) from the Olcott Formation (OLC), Observation Quarry (OBQ), and the Sheep Creek Formation (SHC). ***a*** = Number of species in sample A and sample B (joint occurrences); ***b*** = Number of species in sample B but not in sample A; ***c*** = Number of species in sample A but not in sample B; SDSC = 2***a*** / (2***a*** + ***b*** + ***c***)

	OLC-OBQ	OLC-SHC	OBQ-SHC
a	13	4	3
b	14	23	14
c	4	10	11
SDSC	0.59	0.20	0.19

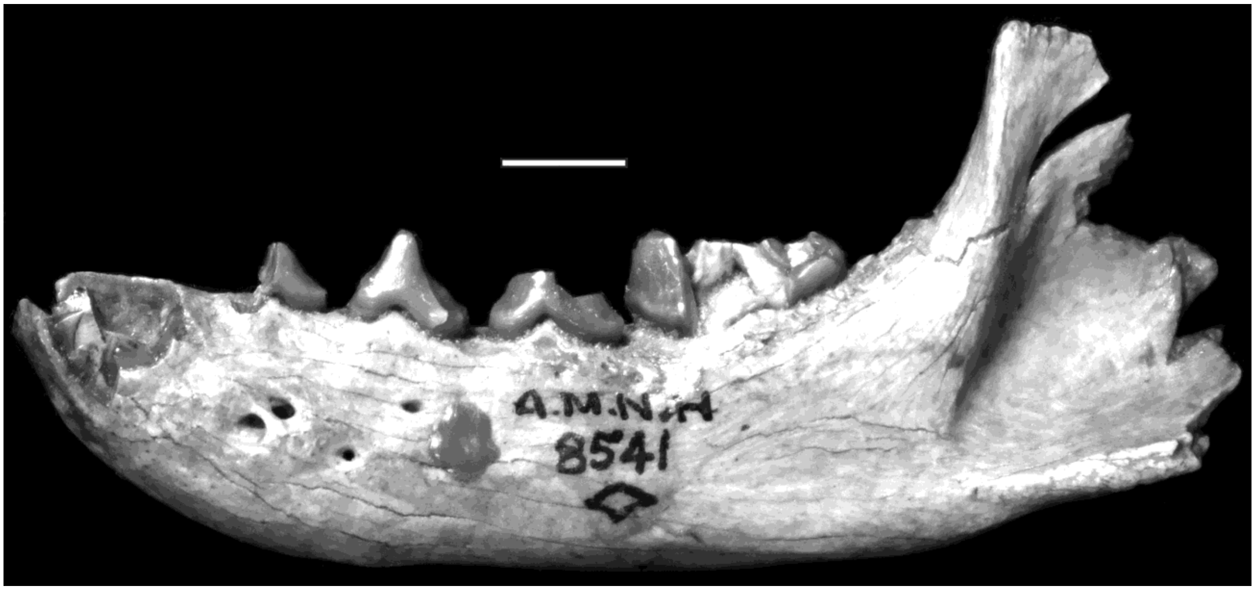

FIGURE 8. Holotype of *Sthenictis robustus*, AMNH FM 8541. Scale = 1 cm.

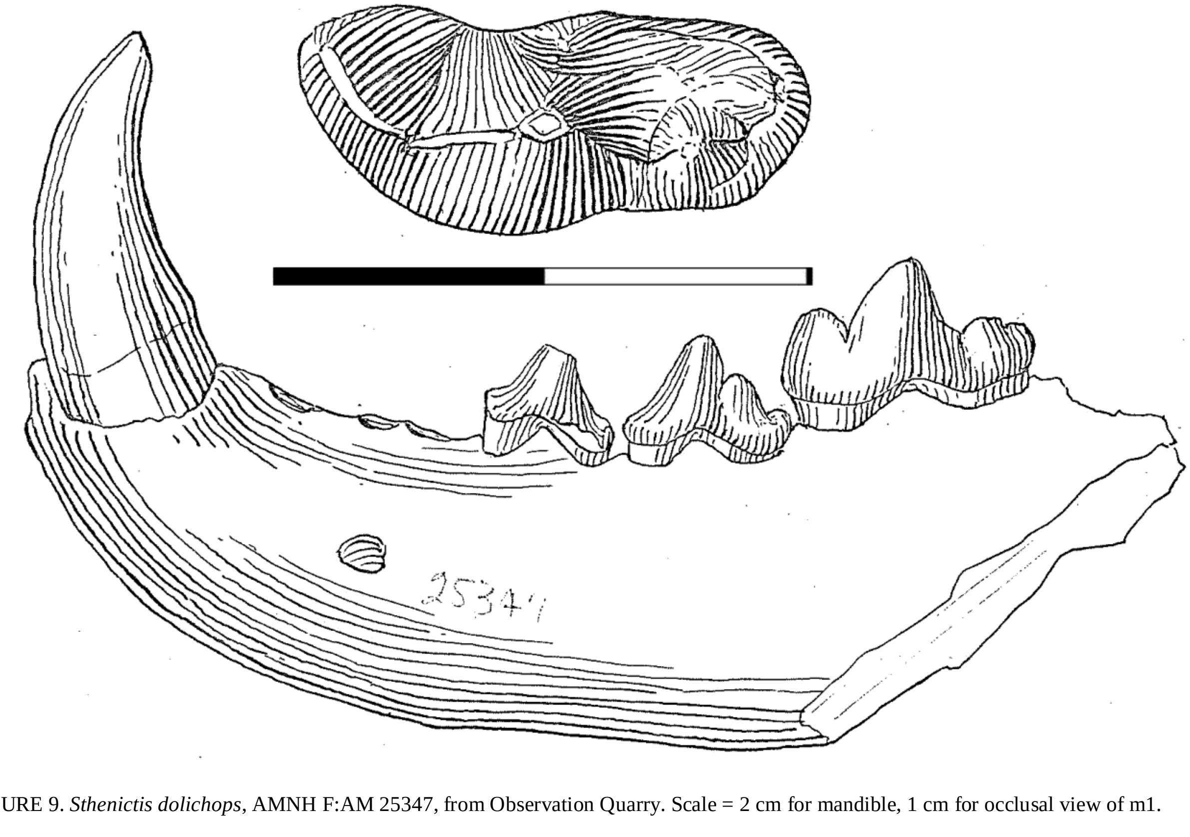

FIGURE 9. *Sthenictis dolichops*, AMNH F:AM 25347, from Observation Quarry. Scale = 2 cm for mandible, 1 cm for occlusal view of m1.

The Lower Snake Creek Fauna is correlative with the Green Hills Fauna of the Barstow Formation in California (Woodburne et al., 1990). Because the Green Hills Fauna underlies the type Barstovian Fauna, Evander (1986) assigned the Lower Snake Creek Fauna to the latest Hemingfordian, which he stated posed a problem for placing Observation Quarry in the early Barstovian. Korth and Evander (2016) determined that the small mammals supported the early Barstovian age assignment for Observation Quarry. Lander (2015) placed the boundary at the base of the Upper Sheep Creek LF. This paper follows Tedford et al. (1987) and Woodburne et al. (1990) in placing the Hemingfordian-Barstovian boundary in western Nebraska between the Sheep Creek and Olcott Formations, at ~16 Ma.

Tedford (in Tedford et al, 1987, 2004) emphasized the first appearance of both immigrant and autochthonous taxa to define the start and subdivisions of NALMAs. Observation Quarry has the following taxa (Korth and Evander, 2016) that signal the start of the Barstovian: *Copemys*, *Probassariscus*, "*Martes*", *Umbogaulus*, *Monosaulax*, and *Dyseohyus*. The Lower Snake Creek Fauna records *Probassariscus*, "*Martes*", *Monosaulax*, and *Pterogaulus*. Tedford et al. (1987) emphasized the correlation of the Lower Snake Creek Fauna with the Green Hills Fauna for including both in the Barstovian NALMA. In California, *Miomustela madisonae* is known from the late Hemingfordian and Barstovian (Lofgren and Abersek, 2018); and *Probasssariscus antiquus* from the Green Hills Fauna (Pagnac, 2009).

Sheep Creek, Lower Snake Creek (Olcott Formation), and Observation Quarry contain 14, 27, and 17 carnivoran taxa respectively (Table 7). Sørensen-Dice similarity coefficients for the three localities (Table 8) show that Barstovian Lower Snake Creek and Observation Quarry are three times more similar to each other than either of these two is with the Hemingfordian Sheep Creek. Procyonids and "*Martes*" occur only in the two Barstovian localities. *Leptarctus oregonensis* from the Barstovian has a more derived dentition than *L.* cf. *oregonensis* from Sheep Creek. The type of *Leptarctus primus*, which has a more derived P4 than *L. oregonensis* (Baskin, 1998), is from the late Barstovian (Ba2) (Pagnac, 2012).

Pseudaelurus skinneri from Sheep Creek is the plesiomorphic sister taxon to the Barstovian *P. stouti*, *P. marshi*, and *P. intrepidus* (Rothwell, 2003). Among the canids, *Pseudaelurus marshi*, *Paracynarctus sinclairi*, and *Tomarctus hippophaga* are restricted to the early Barstovian; *Pseudaelurus stouti*, the Barstovian. *Cynarctoides acridens* and *Leptocyon leidyi* also occur in the Sheep Creek Formation. Observation Quarry is therefore correlative with the Lower Snake Creek Fauna and both are early Barstovian (Ba1) in age.

ACKNOWLEDGMENTS

Access to the AMNH collections was granted by Drs. Richard Tedford and Jin Meng, and assistance was provided by Judith Galkin. I was first urged to describe the small carnivorans from the Olcott Formation by Robert Evander. At the time I was working on the North American mustelids and procyonids in the AMNH for the chapters I was writing for Christine Janis' book. (Janis et al., 1998). Richard Tedford encouraged my research and was an in depth resource for information about the systematics and biostratigraphy of these carnivorans. The late Ray Gooris of the AMNH prepared figures 4, 6, and 9. Alberto Valenciano and Lawrence Flynn provided comments that improved the manuscript.

Dedication—While a graduate student at the University of Arizona, my interest in small carnivorans was sparked on one of our many vertebrate paleontology excursions led by Dr. Everett Lindsay to Jim Honey's field area in the Milk Creek Formation in the Walnut Grove Basin, near Prescott, Arizona (Honey, 1977; Honey and Izett, 1988; Honey and Taylor, 1978). While taking a break from excavating camel and rodent jaws from the main quarry, I found a palate and lower jaw of a *Bassariscus* that led to my interest in the procyonids from Observation Quarry (Baskin, 2004) which, in turn, led to the present paper. On one of the last times we were together, I spent two weeks with him at the AMNH, Jim on the camel floor and me on the other mammals (including carnivores) floor, working on our chapters for the Tertiary Mammals book (Janis et al., 1998). Among other localities, Jim was studying the camelids from the Olcott Formation (Honey et al., 1998; Honey, 2004), the source of the mustelids described in this paper. Our mutual interests later led to us being co-authors on a paper with Bob Martin, one of our long-time colleagues (Martin et al., 2002). I am honored to be involved in producing this volume in his memory.

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