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Middle Miocene carnivorans from the Monarch Mill Formation, Nevada

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The lowest part of the Monarch Mill Formation in the Middlegate basin, west-central Nevada, has yielded a middle Miocene (Barstovian Land Mammal Age) vertebrate assemblage, the Eastgate local fauna. Paleobotanical evidence from nearby, nearly contemporaneous fossil leaf assemblages indicates that the Middle Miocene vegetation in the area was mixed coniferous and hardwood forest and chaparral-sclerophyllous shrubland, and suggests that the area had been uplifted to 2700–2800 m paleoaltitude before dropping later to near its present elevation of 1600 m. Thus, the local fauna provides a rare glimpse at a medium- to high-altitude vertebrate community in the intermountain western interior of North America. The local fauna includes the remains of fish, amphibians, reptiles, birds, and 25 families of mammals. Carnivorans, the focus of this study, include six taxa (three of which are new) belonging to four families. Canidae are represented by the borophagine *Tomarctus brevirostris* and the canine *Leptocyon* sp. indet. The earliest record and second North American occurrence of the simocyonine ailurid *Actiocyon* is represented by *A. parverratis* sp. nov. Two new mustelids, *Brevimalictis chikasha* gen. et sp. nov. and *Negodiaetictis rugatrulleum* gen. et sp. nov., may represent Galictinae but are of uncertain subfamilial and tribal affinity. The fourth family is represented by the felid *Pseudaelurus* sp. indet. *Tomarctus brevirostris* is limited biochronologically to the Barstovian land mammal age and thus is consistent with the age indicated by other members of the Eastgate local fauna as well as by indirect tephrochronological dates previously associated with the Monarch Mill Formation. *Actiocyon parverratis* sp. nov. extends the temporal range of the genus *Actiocyon* from late Clarendonian back to the Barstovian. The Eastgate local fauna improves our understanding of mammalian successions and evolution, during and subsequent to the Mid-Miocene Climatic Optimum (~14–17 Ma).

Key words: Mammalia, Mustelidae, Canidae, Ailuridae, Felidae, Miocene, Barstovian, Nevada.

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Introduction

The Middlegate Basin is a small depositional basin within the Great Basin subregion of the Basin and Range physiographic province. The Middlegate Basin occurs in west-central Nevada, between the southern end of the Clan Alpine Mountains to the west and a spur of the Desatoya Mountains to the east. In this small basin, one igneous and two sedimentary rock units were identified and described by Axelrod (1956, 1985). From stratigraphically lowest to highest, these are the Clan Alpine volcanics, the Middlegate Formation, and the Monarch Mill Formation. Assemblages of fossil vertebrates of Miocene age have been recovered from this basin west of the town of Eastgate, Churchill County, Nevada (Fig. 1). The vertebrate fossils come from different levels of the Monarch Mill Formation (Smith 2002). The most diverse of these vertebrate faunal assemblages is termed the Eastgate Local Fauna (LF) and includes fossil remains of fish, amphibians, reptiles, birds, and mammals. An unpublished study of the Eastgate LF (Smith 2002) identified about 60 species of mammals in seven orders: Lipotyphla, Chiroptera, Lagomorpha, Rodentia, Carnivora, Artiodactyla, and Perissodactyla. Herein we provide a brief overview of the geological setting of the Middlegate Basin, for which detailed study is needed, and a short background and history of the fossil vertebrates from the basin. The main focus of this study, however, is the Carnivora of the Eastgate LF, with emphasis on their paleobiogeography.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; LACM/CIT, Natural History Museum of Los Angeles County, California Institute of Technology collection, Los Angeles, California, USA;

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OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma, USA; UCMP, University of California Museum of Paleontology, Berkeley, California, USA. OMNH and UCMP numbers preceded by a "V" refer to fossil vertebrate localities; UCMP numbers preceded by a "PA" refer to fossil plant localities.

Other abbreviations.—AP, greatest anteroposterior length of tooth; CLAMP, Climate-Leaf Analysis Multivariate Program; LF, local fauna; T, greatest transverse width of tooth; TA, greatest transverse width of anterior half of tooth; TP, greatest transverse width of posterior half of tooth; TRL, greatest length of trigonid part of tooth; TRW, greatest width of trigonid part of tooth; TAL, greatest length of talonid part of tooth; TAW, greatest width of talonid part of tooth. We follow standard convention in abbreviating tooth families as I, C, P, and M, with upper and lower case letters referring to upper and lower teeth, respectively.

Geological and paleontological setting

Historical overview.—In the middle 1950s, Daniel Axelrod began to collect fossil plants from the Middlegate Basin, in the course of which he discovered scanty mammalian bone fragments at three separate localities. The fossil plants were recovered from the Middlegate Formation, while the fossil vertebrates came from the overlying Monarch Mill Formation (Axelrod 1956). The first fossil mammal locality discovered was about 30 m stratigraphically above and east of Axelrod's principal plant locality (UCMP PA 5101). Axelrod (1956: 204) listed a tooth, jaw, and cervical vertebrae of a rhinoceros (*Aphelops*?) from this locality. The rhinoceros was collected by Laura Mills, who sent the material to Richard W. Wilson, then at South Dakota School of Mines and Technology. He identified the remains as *Aphelops* and returned the specimens to Ms. Mills. William J. Pelletier discovered a second fossil mammal locality south of U.S. Highway 50, southeast of the town of Middlegate, Nevada (Axelrod 1956: 204). Axelrod (1956, 1985) did not provide information regarding Ms. Mills or Mr. Pelletier. These fossils were identified by Donald E. Savage (UCMP) as belonging to a gomphotheriid (Proboscidea) and a camel. There is no UCMP locality number for these specimens and they were apparently not preserved in a collection.

A third fossil mammal locality (UCMP V5200) was discovered farther south and east of the second locality. This locality occurs in the basal-most part of the upper member of the Monarch Mill Formation. Axelrod (1956) referred to the faunal assemblage from UCMP V5200 as the Monarch Mill fauna. Richard Tedford (then at UCMP) identified the mammal material recovered from this locality as machairodont (Felidae), *Teleoceras* (Rhinocerotidae), cf. *Paracamelus* and cf. *Pliauchenia* or *Procamelus* (Camelidae), and Gomphotheriidae, which suggested a late Miocene age (Hemphillian Land Mammal Age) for the Monarch Mill fauna (Axelrod 1956).

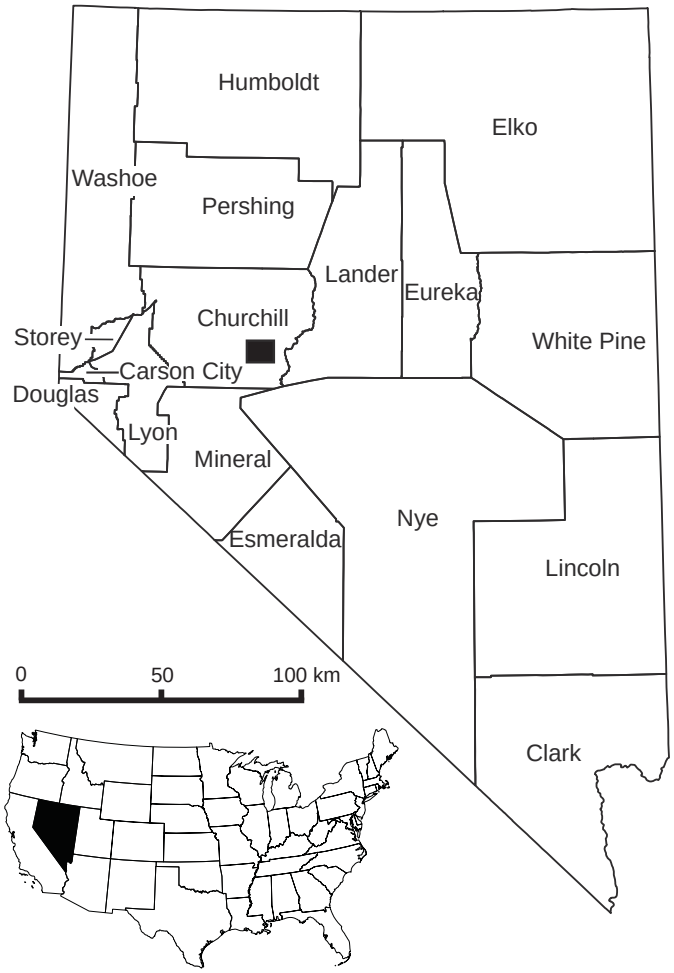


Fig. 1. Map of the United States with the state of Nevada indicated in black, and enlarged map of Nevada, with Eastgate study area indicated as black rectangle.

Based on locality information at UCMP, a fourth fossil mammal locality in the Middlegate Basin was discovered in 1967. This locality was reported later by Axelrod (1985) in his description of a nearby fossil plant locality that yielded the Eastgate flora. This fourth mammal locality is located about 0.8 km southwest of the site from which the Eastgate flora was collected, and it yielded the first specimens of the Eastgate LF (see Fig. 1), which were referred to the Barstovian land mammal age (Nevaxel locality of Savage and Russell 1983: 252). Subsequent prospecting for vertebrate fossils near this locality by UCMP and OMNH field parties revealed additional localities and fossils in the vicinity (Smith 2002). These Barstovian localities yielded the carnivore fossils of the Eastgate LF described in the present report.

Geologic setting of the Middlegate Basin.—The Clan Alpine Mountains run along a north-south axis, with their south end near the low pass and town known as Middlegate, Nevada. Eastgate Wash drains the Middlegate Basin and

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exits through the Middlegate Pass. Axelrod (1956) first described the eastward-dipping exposures in the middle and western parts of the Middlegate Basin and made a preliminary geologic map of them. He designated as the Middlegate Formation those rocks cropping out from the southeastern side of the Clan Alpine Mountains east toward the town of Eastgate. Axelrod (1956) reported a maximum thickness of 396 m for the Middlegate Formation.

Axelrod (1956) examined the geology of the area, in part, to determine the stratigraphic context of the Middlegate flora within the Middlegate Formation. The Middlegate Formation consists mainly of sedimentary rocks that rest unconformably on the Clan Alpine volcanics. For purposes of mapping, Axelrod (1956) divided the Middlegate Formation into three informal units (lower, middle, and upper members), as follows: the lower member ranges from ~1–91 m thick and consists of sedimentary breccia, conglomerate, and sandstone (derived from the underlying volcanics); the middle member reaches a maximum thickness of 122 m and consists of a siliceous shale with alternating soft tuffaceous claystone; and the upper member includes sandstone and rhyolitic tuff, interbedded with claystone and thin shale presumed to be of lacustrine origin. Axelrod (1956) placed the Middlegate flora within the middle member of the Middlegate Formation.

Axelrod (1956) named the Monarch Mill Formation after a nearby stamp mill in the Middlegate Basin. His original description was based on exposures in the middle and western parts of the Middlegate Basin. The Monarch Mill Formation unconformably overlies the Middlegate Formation (Stewart et al. 1999). Axelrod (1956) mapped six sedimentary rock units for the Monarch Mill Formation (see Fig. 2). Stewart et al. (1999) indicated that the Monarch Mill Formation is about 700 m thick in the central part of the Middlegate Basin, thinning at the margins.

Later, Axelrod (1985) traced the Monarch Mill Formation into the eastern and southeastern parts of the Middlegate Basin, where he reported coarser clastic sediments than those from the middle and western parts of the Middlegate Basin. He placed the base of the Monarch Mill Formation at the bottom of a widespread sedimentary breccia that grades basinward into a conglomerate 4–7 m thick, containing cobble- to small boulder-size particles.

Excluding the brecciated basal unit, Axelrod (1985) provided additional characteristics for the Monarch Mill Formation. He noted: (i) a conglomerate scattered throughout the east and southeast region of the Middlegate Basin and composed of coarse, pebbly sandstone that is poorly indurated and poorly bedded; (ii) mudstone, shale, fine-grained tuff; and (iii) slopes that are covered with rubble and vegetation. Axelrod (1985) placed the Barstovian mammalian locality mentioned above (Nevaxel site) in the basal breccia/conglomerate of the Monarch Mill Formation.

Additional studies of the geology in the Middlegate Basin area were conducted by Barrows (1971), who examined the geology of the Desatoya Mountains, and Noble (1972), who described the Middlegate area as representing a boundary for

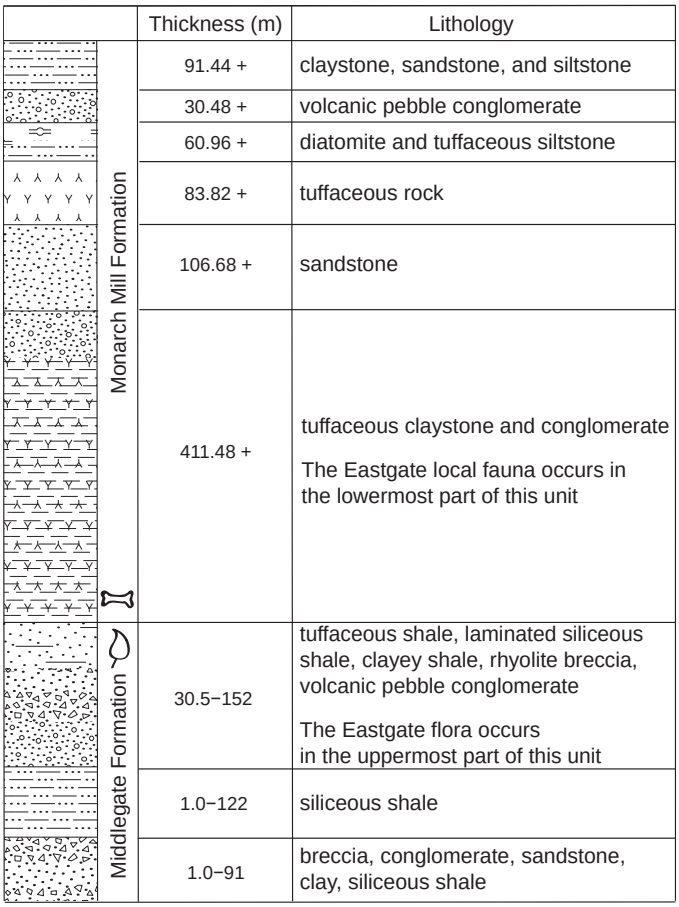


Fig. 2. Basic stratigraphic column of the Monarch Mill and Middlegate formations showing the dominant lithologies (modified from Axelrod 1956). The general stratigraphic positions of the Eastgate local fauna and flora are indicated with the appropriate symbols. The specific units dated by Stewart et al (1999) and Swisher (1992) are not shown because of the paucity of available data.

Middle Miocene volcanism. Stewart et al. (1999: 12) characterized the Miocene sedimentary rocks in the Middlegate Basin (both Middlegate and Monarch Mill formations) as "lacustrine, deltaic, fluvial, and landslide deposits." They further noted that "the Monarch Mill Formation is primarily a fluvial unit, although lacustrine strata are probably also present … Ash-layers in both the Middlegate Formation and the Monarch Mill Formation indicate air-fall from distant sources, mostly from the Snake River Plain."

Further detailed description, study, and mapping of the Monarch Mill Formation is warranted, but is beyond the scope of the present study. In particular, re-examination of the lithologies and mapping of the eastern and southern region of the Monarch Mill Formation could help to precisely place the 18 new fossil localities now yielding the Eastgate LF (Smith 2002) stratigraphically within the formation. The 18 Eastgate localities occur within a limited area (1.61 km^2), but are separated by topographic features that hamper direct stratigraphic correlation among the fossil localities.

Axelrod (1956) suggested that the basal unit of the Monarch Mill Formation directly overlies a thin, siliceous

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shale, cream to white in color. This cream-to-white siliceous shale is sporadically exposed throughout the eastern and southern region of the Middlegate Basin. In this study, we made reference to the placement of new vertebrate-bearing sites with respect to sporadic outcrop of this horizon. On this basis, we provisionally regard all 18 localities yielding the Eastgate LF as lying within the basal part of the Monarch Mill Formation. The vertebrate localities currently occur at about 1600–1700 m elevation.

Age of the Middlegate and Monarch Mill formations.—Swisher (1992: table 5.3.2) provided $^{40}Ar/^{39}Ar$ ages of about 15.5 Ma on biotite, 15.95 Ma on plagioclase, and 15.86 Ma on anorthosite from the Middlegate Tuff (sample no. 86CS-MG1), although he did not indicate where the tuff was sampled stratigraphically or geographically. Because the Middlegate Formation unconformably underlies the Monarch Mill Formation, these dates provide a maximum possible age for localities yielding the Eastgate LF. Stewart et al. (1999) identified 10 units (many of which are probably laterally equivalent) in the Monarch Mill Formation and sampled the chemical composition of volcanic glass shards in the tephra layers of each unit. Based on their tephrochronology, an overall age range of 14.7 Ma to 9.8 Ma was indicated for the Monarch Mill Formation. Stewart et al. (1999) noted, however, that some of the correlations on which the age range is based are problematic. For example, their sample 1-37-26J closely matches a sample from the nearby Virgin Valley, with an extrapolation age of 15.41–15.54 Ma, which is inconsistent with the high stratigraphic position of this sample within the section. Therefore, they estimated an age of about 10 Ma for this sample. To date, no radiometric date has been obtained for the tephras associated with the Eastgate LF.

Vertebrate paleontology of the Middlegate Basin.—As noted above, Axelrod (1985) reported fossil vertebrates of Miocene age from four localities in the Middlegate Basin, ranging in age from Barstovian to Hemphillian. Of these, the only one relevant in the present context is the locality about 0.8 km south of fossil plant locality UCMP PA 533, near Eastgate. This fossil mammal locality, UCMP V70138 (the Nevaxel site of Savage and Russell 1983), is the first of the 18 localities to yield what we term the Eastgate LF. Axelrod (1985) provided a preliminary list of taxa for the Nevaxel locality, as identified by Donald E. Savage (Table 1).

Additional localities yielding fossils referred to the Eastgate LF were collected in the late 1960s to 1980s by UCMP field parties (D.E. Savage, personal communication 1995). For the most part, these fossils were collected from the surface of the rock exposures in the eastern and southern region of the Middlegate Basin. In 1995, one of us (KSS), with the help of D.E. Savage, renewed fieldwork near Eastgate, including surface collecting and screenwashing of rock matrix from several additional localities. The renewed work (1995, 2005) proved fruitful, with the recovery of another order (Chiroptera) and five families (Felidae, Ochotonidae, Eomyidae, Geomyidae, and Dipodidae) of mammals not previously reported for the Eastgate LF (Smith 2002). Smith et al. (2006) described one of the eomyid rodents, *Apeomyoides savagei*, from the Eastgate LF. Although the localities yielding the Eastgate LF need to be placed in a more precise stratigraphic context, we tentatively believe they originate from relatively low in the Monarch Mill Formation. The radiometric date of 15.5 Ma for the upper part of the underlying Middlegate Formation (Swisher 1992) and the tephrochronology of the Monarch Mill Formation (Stewart et al. 1999) constrain the age of the Eastgate LF to 10–15 Ma, as noted above. Smith (2002) and Smith et al. (2006) tentatively assigned the Eastgate LF to the early Barstovian North American Land Mammal Age. Refinement or re-evaluation of this working hypothesis awaits formal description of the remaining members of the fauna. The present paper is a contribution toward that goal.

Paleobotany and paleoenvironment of the Middlegate Basin.—Axelrod (1956) described the Eastgate and Middlegate paleofloras based on leaf assemblages from the Middle Miocene of the Middlegate Basin, western Nevada. These leaf assemblages were collected from the Middlegate Formation and thus are somewhat older (~15.5–16 Ma as indicated above) than the Eastgate LF from the overlying Monarch Mill Formation. As summarized by Graham (1999), the Middlegate flora suggests a chaparral-shrubland that was dominated by sclerophyllous shrubs and trees including *Arbutus prexalapensis*, *Cedrela trainii*, *Cercocarpus antiquus*, *C. pacifica*, *Lithocarpus nevadensis*, *Quercus hannibali*, *Q. shrevoides*, and *Q. simulata*. This assemblage was interpreted as reflecting the vegetation of relatively dry south-facing slopes. The younger Eastgate flora, by contrast, indicates mixed coniferous and hard-

Table 1. List of mammals identified by Donald E. Savage from the "Nevaxel locality" (UCMP V70138), constituting the original Eastgate LF (from Axelrod 1985; taxonomy updated), Eastgate, Churchill County, Nevada, USA; Monarch Mill Formation, Barstovian (Miocene).

Order	Family	Genus
Lipotyphla	Soricidae	*Pseudotrimylus* sp. *Plesiosorex* sp.
	Talpidae	*Mystipterus* sp.
Lagomorpha	Leporidae	*Hypolagus* sp.
Rodentia	Sciuridae	Gen. et sp. indet.
	Castoridae	*Monosaulax* sp.
	Aplodontidae	*Liodontia* sp.
	Cricetidae	*Copemys* sp.
	Heteromyidae	Gen. et sp. indet.
Carnivora	Canidae	*Tomarctus* sp.
Perissodactyla	Equidae	*Hypohippus* sp.
	Rhinocerotidae	*Teleoceras* sp. *Aphelops* sp.
Artiodactyla	Merycoidodontidae	Gen. et sp. indet.
	Camelidae	Gen. et sp. indet.
	Palaeomerycidae	*Aletomeryx* sp.
	Antilocapridae	Gen. et sp. indet.

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wood forest, probably from relatively mesic north-facing canyons. It includes *Abies concoloroides*, *Larix cassiana*, *L. nevadensis*, *Amelanchier grayi*, and *Aesculus preglabra*.

Wolfe et al. (1997) used statistical methods (CLAMP, Climate-Leaf Analysis Multivariate Program) on leaf physiognomy to determine the paleoaltitude and other environmental parameters for the Eastgate and Middlegate floras. Their results suggest that these two paleofloras dating to 15.5–16 Ma grew at relatively high altitude, about 2700–2800 m above sea level, whereas later paleofloras in the region (ranging from 12–14 Ma) yield estimates near present-day altitudes. Today the Middlegate flora locality is at 1600 m altitude. Wolfe et al. (1997) interpreted the difference to indicate subsidence of this part of the Great Basin since the early Middle Miocene. They also used CLAMP to calculate mean annual temperature of the paleoenvironment based on the Eastgate and Middlegate floras at 10.2°C and 10.3°C, respectively. The paleofloras and the slightly younger Eastgate LF existed during the Mid-Miocene Climatic Optimum, when extensive ice probably occurred in the Antarctic but prior to the buildup of ice sheets in the Northern Hemisphere (Flower and Kennett 1994; Zachos et al. 2008). Although the Eastgate and Middlegate fossil leaf assemblages occur lower in the local stratigraphic section than the localities yielding the Eastgate LF, they provide an approximate paleoenvironmental setting for the carnivores described herein.

Systematic paleontology

Order Carnivora Bowdich, 1821

Family Canidae Fischer von Waldheim, 1817

Subfamily Borophaginae Simpson, 1945

Genus *Tomarctus* Cope, 1873

Type species: *Tomarctus brevirostris* Cope, 1873; see below.

Tomarctus brevirostris Cope, 1873

Fig. 3A.

Type material: AMNH 8302, dentary with m1.

Type locality: Court House Butte, Weld County, Colorado, USA.

Type horizon: Pawnee Creek Formation, probably early Barstovian (Miocene).

Material.—OMNH 54975, left edentulous dentary fragment; UCMP 141836, left dentary fragment with partial m1 and m2; UCMP 141908, left dentary fragment with p2, p4, partial m1, and m2; UCMP 141920, right dentary fragment with partial m1; and UCMP 141916, left m2. All specimens are from UCMP V70147 (OMNH V972), Eastgate, Churchill County, Nevada, USA; Monarch Mill Formation, Barstovian (Miocene).

Measurements.—See Table 2.

Description.—Among specimens from Eastgate, UCMP 141908 (mandible; Fig. 3A) is the most diagnostic of *Tomarctus brevirostris*. The premolars are robust and bear accessory cuspules; p2 and p4 both have anterior cingular cusps, posterior accessory cusps, and posterior cingular cusps. The m1 is broken anteriorly, missing the trigonid, but the talonid is broad. The m2 is complete with the metaconid equal in height to the protoconid. In addition to these characters, the length and width of the p2, p4, and m2 (Table 2) are consistent with those of *T. brevirostris*.

Table 2. Measurements (in mm) of *Tomarctus brevirostris* teeth from Eastgate, Nevada, USA; lower Monarch Mill Formation, Barstovian (Miocene).

Specimen	Tooth	Anteroposterior length (AP)	Greatest transverse width (T)
UCMP 141908	p2	8.3	4.7
	p4	11.5	7.1
	m1	–	6.2
	m2	10.0	6.3
UCMP 141916	m2	13.3	8.6

Remarks.—No cranial elements, upper teeth, or postcranial elements are known from Eastgate or the surrounding region. The premolars with accessory cusps allow us to assign the Eastgate specimens to Aelurodontina, and putatively primitive characters of the molars indicate referral to *Tomarctus* not *Aelurodon* (Wang et al. 1999): the m1 talonid is broad; the m2 metaconid is equal in height to the protoconid, and the metaconid is larger than in *Aelurodon*. The premolars are not as robust as they are in *Aelurodon*. In addition to these characters, the length and width of the cheek teeth are smaller than those for any species of *Aelurodon* listed by Wang et al. (1999).

Two species of *Tomarctus* (*T. hippophaga* [Matthew and Cook, 1909] and *T. brevirostris* Cope, 1873) were recognized by Wang et al. (1999). The species are mainly distinguished by characters that are not preserved in the Eastgate specimens, though *Tomarctus hippophaga* is smaller than *T. brevirostris*. The size of the specimens from Eastgate indicates referral to the larger species, *T. brevirostris*. This is the first reported occurrence of *T. brevirostris* for the Barstovian of Nevada.

Stratigraphic and geographic range.—Early Barstovian of California, Colorado, Nebraska, Nevada, and New Mexico, USA; late Barstovian of Colorado and Texas, USA (Wang et al. 1999).

Subfamily Caninae Fischer von Waldheim, 1817

Genus *Leptocyon* Matthew, 1918

Type species: *Leptocyon vafer* Leidy, 1858; "Loup Fork beds", Niobrara River, Nebraska, USA; probably Valentine Formation, Barstovian (Miocene).

Stratigraphic and geographic range.—Orellan to late Clarendonian (Early Oligocene to late Miocene) of North America: Saskatchewan, Canada; and Arizona, California, Colorado, Florida, Nebraska, Nevada, New Mexico, and Texas, USA (Tedford et al. 2009).

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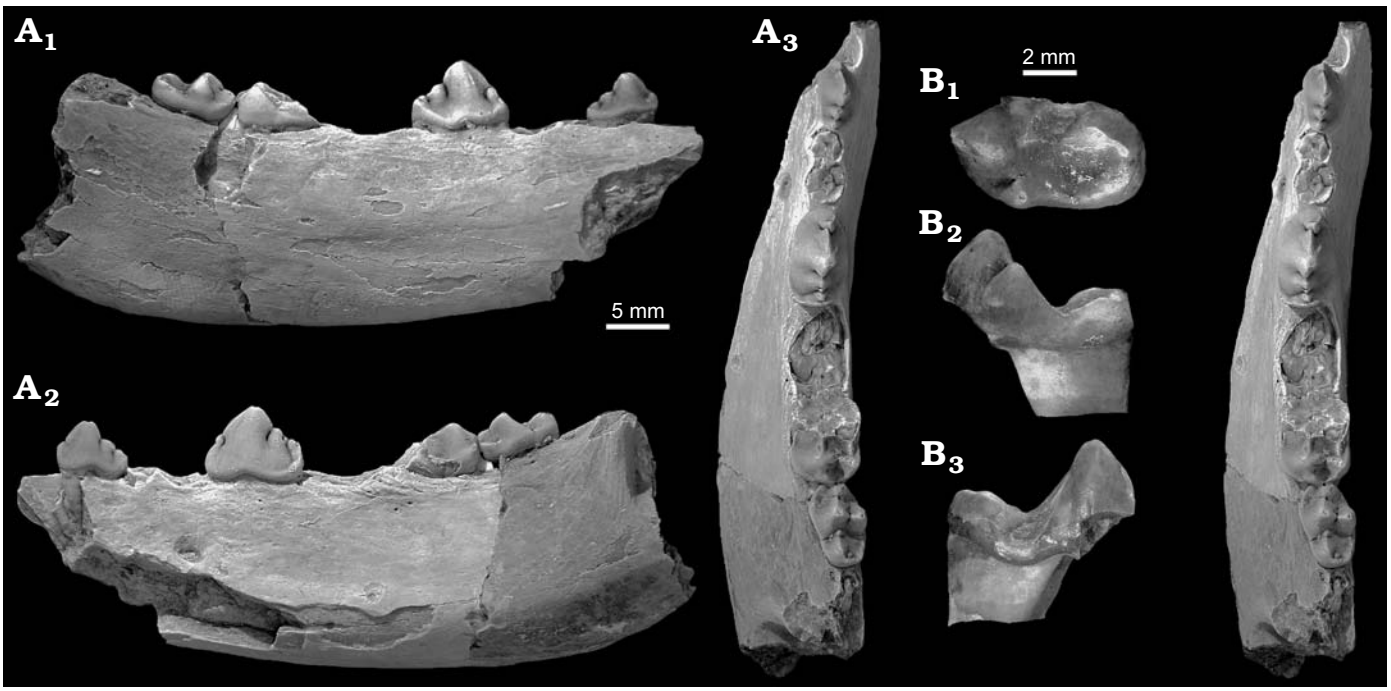


Fig. 3. Canidae of the Eastgate LF, basal-most unit of the Monarch Mill Formation, Barstovian (Miocene), Churchill County, Nevada, USA. **A**. *Tomarctus brevirostris*, Cope, 1873, UCMP 141908, left dentary with p2, p4, partial m1, and m2 in lingual (A_1), labial (A_2), and occlusal (A_3, stereopair) views. **B**. *Leptocyon* sp., UCMP 141482, right m1 in occlusal (B_1), lingual (B_2), and labial (B_3) views.

Leptocyon sp.

Fig. 3B.

Material (Fig. 3B).—UCMP 141482, partial right m1 from UCMP V70138 (OMNH V967), Eastgate, Churchill County, Nevada, USA; Monarch Mill Formation, Barstovian (Miocene).

Measurements (in mm).—m1: AP, indeterminate (broken); T, 4.66.

Description.—UCMP 141482 is missing the paraconid and anterior root. The occlusal surface is slightly worn. The protoconid is much higher and more prominent than the metaconid. There is a deep notch between the protoconid and metaconid. A protostylid is present on the posterolabial base of the protoconid. The entoconid is much smaller than the hypoconid. The hypoconid is situated laterally on the talonid. The cristid obliqua is weak and does not reach the metaconid; thus, the talonid basin is open labially. The surface of the trenchlike talonid basin is rugose. The labial cingulum is moderately developed. A small hypoconulid is present.

Comparisons.—This small, isolated partial m1 is identified as *Leptocyon* sp. based on its size and presence of an open talonid and a reduced entoconid. These characters are among those listed by Munthe (1998) for this genus. Tedford et al. (2009) recognized the several species of the genus *Leptocyon* as paraphyletic; of the morphological characters these authors used to diagnose the genus, few can be observed in UCMP 141482. Unfortunately, no additional comment or further identification is possible.

Family Ailuridae Gray, 1843b
Subfamily Simocyoninae Dawkins, 1868
Genus *Actiocyon* Stock, 1947

Type species: *Actiocyon leardi* Stock, 1947; Cuyama beds, Apache Canyon, Ventura County, California, USA; Caliente Formation; Clarendonian (Miocene).

Actiocyon parverratis sp. nov.

Figs. 4, 5.

Etymology: From Latin *parvus*, small; and *erratis*, wanderer—a small wanderer.

Type material: Holotype: UCMP 141928, associated right and left dentaries, each with p2–m2 (Fig. 4). Paratypes: UCMP 141911, left maxilla fragment with P4 from UCMP V70147 (OMNH V972) (Fig. 5) and OMNH 54988, right partial dentary with p3–m1 from UCMP V70138 (OMNH V967), both Eastgate, Churchill County, Nevada, USA, Monarch Mill Formation, Barstovian (Miocene).

Type locality: UCMP V74103 (OMNH V973), Eastgate, Churchill County, Nevada, USA.

Type horizon: Basal-most unit of the Monarch Mill Formation (Axelrod 1985), Barstovian (Miocene).

Diagnosis.—*Actiocyon parverratis* sp. nov. differs from *Simocyon* Wagner, 1858 in its much smaller size, in having p2 and p3 present and/or unreduced, in lacking a protocone and variably lacking a small parastyle on P4, in having m2 with joined trigonid crests forming a small subcircular structure, and in having m2 trigonid narrower than talonid. *Actiocyon parverratis* sp. nov. differs from *Alopecocyon* Viret, 1951 in characters of the m2, which has protoconid larger (instead of smaller) than metaconid, joined trigonid

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Fig. 4. Ailurid carnivoran *Actiocyon parverratis* sp. nov. from the Eastgate LF, basal-most unit of the Monarch Mill Formation, Barstovian (Miocene), Churchill County, Nevada, USA. UCMP 141928, holotype left (**A**) and right (**B**) dentaries in occlusal (A_1, B_1, stereopairs), lingual (A_2, B_2), and labial (A_3, B_3) views.

crests forming a subcircular instead of a semicircular structure (fide Beaumont 1964), talonid longer and wider than trigonid, and prominent cusps forming a median talonid ridge. *Actiocyon parverratis* sp. nov. differs from *Actiocyon leardi* Stock, 1947 in having the maxilla with relatively larger and lower-positioned infraorbital foramen, P4 with less well-developed and undivided small hypocone on internal cingulum, and smaller overall size.

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Measurements (in mm).—P4: AP, 8.3; T, 5.1. For measurements of lower jaws and teeth see Table 3.

Description.—*Cranium* (Fig. 5): The cranial fragment UCMP 141911 includes a small portion of the left maxilla with the proximalmost base of the zygomatic arch (broken at the articulation with the jugal), a very short section of the anteroventral margin of the orbit, a moderately large infraorbital foramen above the anterior root of the P4 (Fig. 5A), and a very small portion of the palate adjacent to the P4 (Fig. 5B). The palate shows a deep hollow posterolingual to the P4 that would have accommodated the protoconid of the lower carnassial during occlusion. The maxillary fragment also shows some of the alveoli for adjacent teeth. It preserves half of the posterior alveolus of the P3. There are two alveoli preserved for the M1: an anterolabial alveolus filled with a root that had a triangular occlusal outline, and an incomplete posterior alveolus showing an anterior bifurcation and longitudinal groove. There is also a rugose, pitted area in the palate into which the base of the M1 nested; although the bone is broken, the pitted area extends lingually indicating that there would have been an additional (third) lingual alveolus for this molar.

Upper teeth (Fig. 5): The P4 is in excellent condition with only minor wear along the blade. Three roots are present, two side-by-side anterior roots and one massive, anteroposteriorly elongated posterior root. The crown has a subtriangular outline in occlusal view, is relatively short, and is widest anteriorly. The paracone is the most prominent cusp; from its apex a low but sharp ridge extends anteriorly to the anterior cingulum. The blade of the paracone (postparacrista) joins the blade of the metastyle (metacone; premetacrista), forming an oblique blade. These blades join on the occlusal surface at a deep, narrow carnassial notch. The metastylar blade is relatively short; it is highest near the carnassial notch and low at its posterolabial end. The lingual surface of the carnassial blade shows slightly crenulated enamel where it is unworn, whereas the labial enamel is smooth. A strong anterior cingulum is present but a parastyle is absent. The anterior cingulum is continuous with a broad protoconal shelf lacking a protocone. In occlusal view there is a shallow indentation in the cingulum between the anterior parastylar shelf and the protoconal shelf. The protoconal shelf does not extend quite as far forward as the parastylar shelf. A low but distinct swelling of the wide internal cingulum indicates an incipient hypocone. The internal cingulum narrows just posterior to the hypoconal swelling and widens again posteriorly. The labial cingulum is discontinuous with the anterior cingulum, but narrow sections are present from the midpoint of the tooth posteriorly.

Table 3. Measurements (in mm) of *Actiocyon parverratis* sp. nov., dentaries and teeth from Eastgate, Nevada, USA; lower Monarch Mill Formation, Barstovian (Miocene). Abbreviations: AP, anteroposterior length; HD, height of dentary from bottom of horizontal ramus to top of coronoid process; HR, depth of horizontal ramus below m1 protoconid; T, greatest transverse width; TA, anterior width (trigonid width of lower molars); TP, posterior width (talonid width of lower molars).

Element	Measurement	OMNH 54988	UCMP141928	
			left mandible	right mandible
Dentary	HR	9.5	9.1	9.1
	Alveolar length c1–m2	–	40.3	–
	HD	–	25.3	–
p2	AP	–	4.6	4.6
	T	–	2.4	2.2
p3	AP	5.8	5.1	5.2
	T	3.1	2.6	2.6
p4	AP	7.3	6.4	6.2
	T	3.8	3.3	3.7
m1	AP	10.7	10.4	10.3
	TA	5.1	4.6	4.3
	TP	4.9	4.7	4.7
m2	AP	–	7.0	7.2
	TA	–	3.4	3.2
	TP	–	3.6	3.6

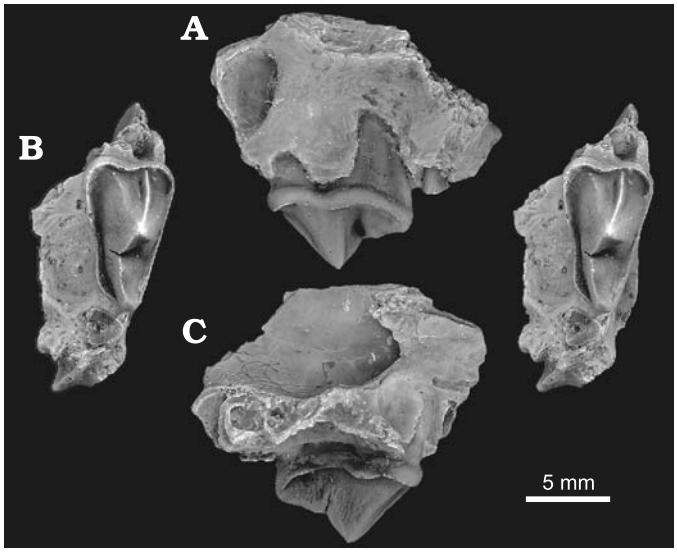


Fig. 5. Ailurid carnivoran *Actiocyon parverratis* sp. nov. from the Eastgate LF, basal-most unit of the Monarch Mill Formation, Barstovian (Miocene), Churchill County, Nevada, USA. UCMP 141911, paratype left maxilla fragment with P4 in labial (**A**), occlusal (**B**, stereopair), and lingual (**C**) views.

Dentary (Fig. 4): The dentary is moderately robust with dentary depth beneath the protoconid of m1 exceeding the height of m1 (Fig. 4A). Both dentaries are broken anteriorly and in the more complete left dentary (Fig. 4A) only parts of the roots of two lower incisors can be distinguished among the fragmented bone. The mandibular symphysis is long and low and extends posteriorly to the level of the middle of p2. The broken root of a robust canine is present in its alveolus in the left dentary. Both dentaries show an alveolus for a single-rooted p1. The left dentary preserves most of the ascending ramus. The condyloid process is hemicylindrical, horizontally oriented, transversely widened (broken laterally), and situated slightly above the level of the tips of the main cusps on the lower teeth. The angular process is broken off at its tip. The coronoid process is tall, canted only slightly

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outward from the plane of the horizontal ramus, laterally has a large and deep masseteric fossa, and is subparallel-sided in lateral profile in its upper half, with a rounded dorsal edge. The dentary possesses at least one mental foramen ventral to the incisors and three or four lateral mental foramina in a series positioned at the same level at mid-depth of the horizontal ramus; in the left dentary the first is small and situated ventral to the small diastema between c1 and p1 alveoli (absent in the right dentary of the holotype), the second is large and situated below the small diastema between p1 and anterior root of p2 alveoli (below the p1 in the right dentary of the holotype), the third is large and situated below the p3 in all three available dentaries, and the fourth is small and situated below the anterior root of p4 (possibly absent in the right dentary of the holotype). The mandibular foramen is positioned about level with the middle depth of the horizontal ramus and below the middle of the coronoid process. There is a prominent tubercle for insertion of the temporalis muscle at the anterolingual base of the coronoid process. A long, prominent, teardrop-shaped insertion scar for the internal pterygoid muscle internus occurs on the lingual side of the angular process. Low on the lateral side of the ascending ramus below the masseteric fossa is a long, low horizontal ridge that probably separates the insertion scar for the deep portion of the masseter muscle from that for the superficial masseter part of the masseter muscle. A possible tooth puncture mark appears on the right dentary below the front of the p2 of the holotype specimen.

Lower teeth (Fig. 4): The p1 is lost from available specimens but a single alveolus between the lower canine and p2 indicates it was a small, single-rooted tooth (Fig. 4). The p2 and p3 are respectively larger in size, with two roots and a single main cusp (protoconid) each (no posterior accessory cusps are present).

The p4 has a posterior accessory cusp that is strong and separated from the protoconid by a narrow notch. The notch bears a small, narrow, carnassial-like slit. The principal cusp of the p4 is lower than the protoconid of the m1.

The m1 (lower carnassial) shows a moderately open trigonid, with the protoconid-paraconid blade (paracristid) oblique to the long axis of the lower toothrow and bearing a carnassial notch with a deeply incised, narrow slit beneath the notch. The protoconid of the m1 is the tallest cusp on the tooth, followed by the metaconid and paraconid, respectively. In the transverse plane, the metaconid of the m1 occurs lateral but slightly posterior to the protoconid. The protoconid-metaconid ridge (protocristid) also has a deeply incised narrow slit beneath the notch between these two cusps. The talonid of the m1 is slightly narrower than the trigonid; it bears a prominent hypoconid, a small hypoconulid adjacent to the hypoconid, and no entoconid. The m1 hypoconid is separated from the protoconid by a small notch, is slightly lingually to the protoconid, and has a broad, flat base that fills the labial part of the talonid basin. Lingual to this, the talonid basin is open. Posterolingually the talonid basin has a continuous rim. On the m1 there is a short, weak anterolabial cingulid beneath the carnassial notch (longer and stronger in OMNH 54988), and another short, weak labial cingulid below the notch between the protoconid and hypoconid (stronger in OMNH 54988) showing a distinct small wear facet. In OMNH 54988, the enamel is weakly crenulated, whereas the enamel is smooth on both m1s of the holotype.

The m2 is relatively long, its length exceeding half the length of the m1, and its occlusal outline is an elongate oval. The m2 is positioned higher in the dentary than the talonid of m1, rising posteriorly. The m2 talonid is slightly wider and distinctly longer than its trigonid. An anterolabial cingulid is present. The trigonid bears small but distinct protoconid and metaconid cusps, with a very low paraconid. The paraconid is connected by low crests to the metaconid and protoconid; together the crests form a continuous subcircular rim enclosing the trigonid basin. The protoconid-metaconid ridge (protocristid) has a median small notch and corresponding slit. The talonid basin is largely filled with a longitudinal ridge that bears two swellings, possibly representing the lingually-shifted hypoconid and hypoconulid (?) and contacting the posteromedial margin of the talonid cingulid. Lingual to this median longitudinal ridge is a small, shallow, rugose talonid basin. The talonid is rimmed by a nearly continuous cingulid.

Remarks.—Except for its larger size and other differences mentioned above, the second specimen (OMNH 54988) agrees with the holotype in anatomical details. Referral of this species to the genus *Actiocyon* is based on the similarity of the available P4 (UCMP 141911) to that of the type and only known specimen of *Actiocyon leardi*, LACM/CIT 2747, and to other teeth of the related Holarctic *Simocyon* and Eurasian *Alopecocyon*. Confirmation of this assignment awaits the discovery of associated lower jaws and teeth of *A. leardi*.

Simocyonines are relatively widespread but rare in Eurasia, and fossils of members of this group are extremely rare in North America. In North America, a single species (and specimen) of *Actiocyon*, *A. leardi* is known from a single locality in California. Similarly, the simocyonine *Simocyon* is known in North America by a single species *S. marshi* (Thorpe, 1921) and a single specimen from Oregon, plus referred specimens from Idaho and Nevada (Baskin 1998; Tedrow et al. 1999). Webb (1969b), Baskin (1998), and Salesa et al. (2011) noted the strong resemblance of *Actiocyon* to the related Eurasian genus *Alopecocyon*. Viret (1951) noted the resemblance between Eurasian *Alopecocyon* and *Simocyon*. *Simocyon* includes large-bodied ailurids, whereas *Actiocyon* and *Alopecocyon* include small-bodied forms. *Actiocyon parverratis* sp. nov. shares with these taxa a very long m2 and a tall, nearly parallel-sided coronoid process of the dentary; it differs from *Simocyon* in its much smaller size (*Simocyon* species range in m1 length from 21.0–25.5 mm; measurements from Peigné et al. 2005; Thorpe 1921; Wang 1997) and in having p2 and p3 present and/or unreduced. Differences between *Actiocyon* and *Alopecocyon*, if any, need to be studied in detail with reference to numerous and scattered Eurasian specimens.

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The only elements represented in specimens of both *Actiocyon parverratis* sp. nov. and *A. leardi* are the P4 and adjacent parts of the maxilla. The infraorbital foramen in *A. parverratis* sp. nov. is lower and appears to be relatively larger than that in *Actiocyon leardi* (in which this area is poorly preserved). The infraorbital foramen, anterior base of the zygomatic arch, and observable palatal characters are generally similar to the conditions seen in *Alopecocyon gaillardi* (Wegner, 1913) (see Viret 1933: pl. 2: 1, 1a, 2, 2a). The small, relatively robust P4 bearing an expanded protoconal shelf but lacking a protocone resembles the condition seen in the simocyonines *Simocyon* and *Alopecocyon*, as described by Beaumont (1964); and in particular for *Actiocyon leardi*, in which there is "no anterointernal cusp [protocone], its place being taken by a very well developed cingulum that continues along the inner side of the tooth as a shelf with bordering crenulate edge but is more moderately developed from about the middle of the crown to the rear of the tooth" (Stock 1947: 85). *Actiocyon parverratis* sp. nov. differs from *Simocyon* and resembles *A. leardi* and published drawings of at least the Eurasian species *Alopecocyon gaillardi* and *A. leptorhynchus* (Filhol, 1883) (see Viret 1933; Thenius 1949b) in lacking a protocone and tending to have a small or no parastyle. Other characters of the P4 also generally compare favorably with those of *A. leardi*. The lack of a parastyle resembles the condition in *A. leardi* as illustrated by Stock (1947), although Beaumont (1964) indicated that the parastyle is highly variable in Eurasian *Alopecocyon* and *Simocyon*. The well-marked internal cingulum is apparently shared with *Simocyon* and *Alopecocyon*. The tiny incipient hypocone occurring as a rise in the internal cingulum in the Eastgate specimen differs from the condition in *A. leardi*, wherein the edge of the internal cingulum is crenulated along its widened front half and "divided by a notch into two parts" (Stock 1947: 87). The metastylar blade of the Eastgate P4—being tallest near the carnassial notch and low at its posterolabial end—is opposite the normal situation in carnivoran P4s, in which the metastyle is highest at the posterolabial end of the blade. We observed this somewhat unusual condition of the Eastgate specimen also in published illustrations of some species of *Simocyon* such as *S. zdanskyi* Kretzoi in Kadić and Kretzoi, 1927, and *S. batalleri* Viret, 1929 (e.g., see illustrations in Spassov and Geraads [2011: figs. 1a, 2a–c] and in Peigné et al. [2005: fig. 3]). However, in other *Simocyon* species such as *S. primigenius* (Roth and Wagner, 1854) there are prominences on the metastylar blade of about equal height near the carnassial notch and at the posterolabial end, separated by a slightly lower intermediate section (e.g., see the illustration in Spassov and Geraads 2011: fig. 1b). In *Alopecocyon*, the metastylar blade appears similarly variable; *Actiocyon leardi* has both anterior and posterior ends about equal in height (Stock 1947: pl. 19: 1a), while *Alopecocyon gaillardi* and *A. goeriachensis* (Toula, 1884) have the anterior end higher than the posterior (Viret 1933: pl. 2: 1, 2; Toula 1884: pl. 8: 8a).

Unfortunately, no dentaries or lower teeth are known for *Actiocyon leardi* and the P4 is the only upper tooth known in *A. parverratis* sp. nov., restricting size comparisons between these taxa to the P4s. The P4 of *A. parverratis* sp. nov. is smaller than the same tooth in *A. leardi* (AP, 8.3 mm; T, 5.1 mm compared to AP, 11.6 mm; T, 8.0 mm; latter measurements from Stock 1947). Thus, the P4 of *A. parverratis* sp. nov. is 28% shorter in anteroposterior length and 36% narrower in transverse width than the same tooth in the larger *A. leardi*. However, in *A. parverratis* sp. nov. there is a size difference between the two available specimens, the holotype mandible UCMP 141928 and the second partial dentary OMNH 54988 (Table 3). In the depth of the dentary and in various dimensions of the lower teeth that can be observed in both specimens, the two specimens of *A. parverratis* sp. nov. differ by 2.6% to 16.1% of the dimensions of the larger specimen. Depending in part on contemporaneity of the two Eastgate localities from which the two specimens originated (V74103 and V70138, which are only separated by about 12 m stratigraphically), this size difference within the hypodigm specimens might represent simple intraspecific variation, sexual dimorphism, or change through time. We cannot speculate about the significance of this size difference without additional data.

The m2 of *Actiocyon parverratis* sp. nov. is generally similar in its great length and presence of a median talonid ridge to the m2 of North American *Simocyon* cf. *S. marshi* (Tedrow et al. 1999) and Eurasian *Simocyon primigenius* and possibly to some *Alopecocyon* species as described by Beaumont (1964: 834–835, pl. 1: 3, 4). However, it differs from m2 proportions in other related species. For example, the m2 of *A. parverratis* sp. nov. differs from those of *Alopecocyon getti* (see Mein 1958: fig. 41) and *Alopecocyon goeriachensis* (see Viret 1951: pl. 1: 9a, b), in having a much longer and wider talonid, a larger protoconid, a prominent median talonid ridge, and a larger hypoconulid.

The lower teeth of *Actiocyon parverratis* sp. nov. generally resemble those of some Eurasian *Alopecocyon* species (e.g., *A. leptorhynchus*, Thenius 1949b: figs. 9, 10; Beaumont 1964), but differ from others (e.g., *A. getti*; Mein 1958: fig. 41). Published drawings of these Eurasian taxa are generally insufficient for detailed comparisons. Like other authors before us, we note the great similarity between and possible synonymy of North American *Actiocyon* and Eurasian *Alopecocyon*. However, a revision of these genera is beyond the scope of the present paper.

Stratigraphic and geographic range.—Western Nevada, USA; Monarch Mill Formation, Barstovian (Miocene).

Family Mustelidae Fischer von Waldheim, 1817

Subfamily incertae sedis

Genus *Brevimalictis* nov.

Etymology: From Latin *brevis*, short; *mala*, jaw bone; and *ictis*—indicating a short-jawed mustelid that is most similar to the galictin group.

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Type species: *Brevimalictis chikasha* gen. et sp. nov., monotypic; see below.

Diagnosis.—The same as for the type and only species.

Brevimalictis chikasha sp. nov.

Fig. 6.

Etymology: Named in honor of the unconquerable Chickasaw (Chikasha is the traditional spelling) people, who are known for their highly progressive, education-focused values, and preservation of their native culture.

Holotype: UCMP 113319, left dentary with p3–m1.

Type locality: UCMP V70140 (OMNH V968), also known as Nevaxel V, near the town of Eastgate, Nevada, USA.

Type horizon: Basal-most unit of the Monarch Mill Formation (Axelrod 1985), Barstovian (Miocene).

Diagnosis.—A small mustelid about the size of an extant female or small male long-tailed weasel, *Mustela frenata* Lichtenstein, 1831. *Brevimalictis* gen. nov. differs from Mustelinae in having the m1 talonid basined, not semitrenchant. It differs from Lutrini in having m1 with a long rather than shortened trigonid and with a reduced rather than strong metaconid. *Brevimalictis* gen. nov. differs from the Galictinae in having a shallow rather than deep jaw.

Measurements (in mm).—p3: AP, 2.6; T, 1.5; p4: AP, 3.3; T, 1.7; m1: AP, 6.0; AP of trigonid, 4.0; AP of talonid, 2.0; TA, 2.5; TP, 2.2; p2–m2 alveolar length, 14.3; c–m2 alveolar length, 16.1; dentary depth beneath m1 protoconid, 4.0; and dentary total length (from below incisor alveoli to damaged mandibular condyle), 25.7.

Description.—Dentary: The holotype and only known specimen UCMP 113319 is a short, slender left dentary with broken coronoid and condyloid processes but intact angular process. The dentary contains p3–m1 and empty alveoli for c, p2, and m2. The mandibular condyle is transversely oriented. In lateral view, the ventral margin of the horizontal ramus is nearly straight in the region beneath the p3 to m1. The angular process projects ventrally at about 45 degrees and slightly laterally from the long axis of the mandible, and has a troughlike medial surface. Laterally the dentary bears a deep, concave masseteric fossa with a rounded anterior margin that terminates below the m2 alveolus, and has prominent superior and inferior ridges. Anteriorly the dentary has at least four mental foramina. The anteriormost mental foramen occurs below the lower incisors. The second (and largest) occurs below the posterior alveolus of p2, the third occurs below the posteriormost part of the p3, and the fourth occurs below the posterior root of p3 and anterior root of p4. On the lingual aspect of the ramus the bone is weathered but the pterygoideus muscle scar can be discerned at the medial base of the coronoid process just posteromedial to the m2 alveolus. The mandibular foramen is located about halfway between the condyle and m2 alveolus and ventral to the pterygoideus scar. The mandibular symphysis extends posteriad to a level beneath the p3. Incisive alveoli are poorly preserved such that the number of lower incisors cannot be determined with certainty, but at least two appear to have been present. Two alveoli are present for the missing p2, posterior to the single canine root. The posterior of the two alveoli for the p2 is larger than the anterior one; the two are aligned obliquely relative to the long axis of the toothrow and horizontal ramus. The p2 alveoli indicate a relatively large tooth set at an oblique angle to the other premolars. The p3, p4, and m1 each have two roots. Posteriorly a single alveolus is present for the missing m2 on the rising anterior base of the coronoid process.

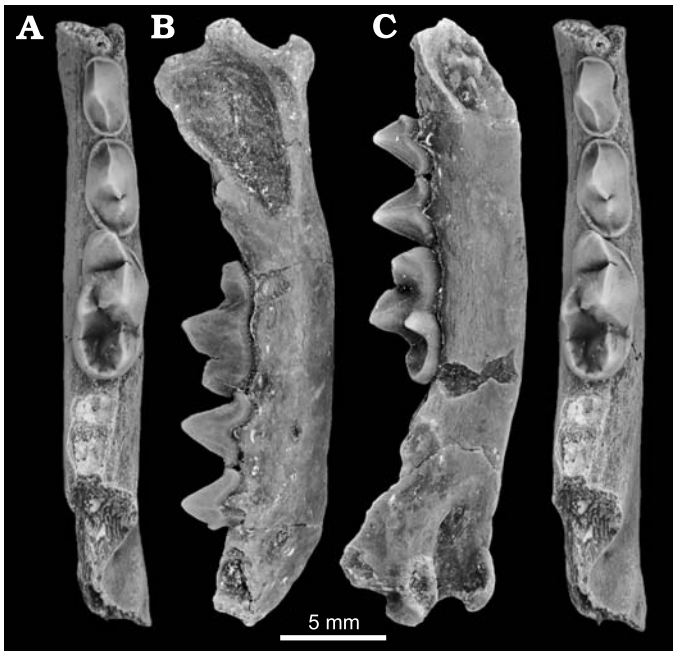


Fig. 6. Mustelid carnivoran *Brevimalictis chikasha* gen. et sp. nov. from the Eastgate LF, basal-most unit of the Monarch Mill Formation, Barstovian (Miocene), Churchill County, Nevada, USA. UCMP 113319, holotype right dentary with p3–m1 in occlusal (**A**, stereopair), labial (**B**), and lingual (**C**) views.

Lower premolars: The premolars increase in size from front to back and have a single high cusp each. Crowding of the lower premolars and absence of p1 indicates that the species had a short muzzle as in many other mustelids. The p3 and p4 lack posterior accessory cusps; each premolar has an anterior and posterior ridge extending from the apex of the main cusp down to the anterior and posterior cingulid, respectively, where a tiny cingular cuspule is formed at each end of these premolars. Cingulids are absent medially and laterally on each premolar.

Lower molars: The m1 trigonid is transversely narrow (but wider than the talonid), elongate and open lingually. The paraconid is more worn (or the cutting edge is damaged) than the other cusps; this cusp is relatively high but lower than and anterior to the protoconid. The protoconid is the highest cusp and forms a carnassial blade (paracristid) with the paraconid; the carnassial blade is slightly oblique but nearly in line with the long axis of the toothrow. The metaconid is small, distinct, and much shorter than the paraconid. The metaconid is placed lingual and slightly

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posterior to the protoconid, to which it is connected by a short, rounded ridge (protocristid) lacking a sharp notch—the ridge circumscribes the margin of the talonid to join the hypoconid. The m1 talonid is lower than the trigonid and is basined. The hypoconid is situated on the labial margin of the talonid and shows a shearing facet on its external (labial) slope. A small, vertical, ridgelike accessory cuspule (protostylid) occurs at the posterior base of the protoconid, and a distinct notch is formed between the protostylid and the hypoconid. There is a flattened swelling extending basinward from the lingual base of the hypoconid, filling part of the talonid basin. The entoconid and hypoconulid are absent, and there is a very low rim on the lingual aspect of the basin. The talonid is shallowly basined, with a continuous cingular rim extending from the hypoconid to the posterior base of the metaconid. The lingual rim of the talonid is much lower than the labial rim with hypoconid. Cingulids are absent on the m1 except for a slight swelling beneath the anterior end of the paraconid.

Although the m2 is absent, the dentary has a single alveolus indicating a single root for this tooth locus. The alveolus is tilted forward as in many mustelids. Based on the size of the alveolus, the m2 was small in this specimen, which is typical for mustelids (Baskin 1998).

Remarks.—*Brevimalictis chikasha* gen. et sp. nov. (UCMP 113319) is smaller than most known Neogene North American Mustelidae. Its m1 AP of 6.0 mm is roughly similar to that of several genera of Miocene mustelids (*Promartes* Riggs, 1942: AP 8.3–10.4 mm; *Miomustela* Hall, 1930: AP 5.1 mm; *Pliogale* Hall, 1930: AP 5.7–8.4 mm; *Pliotaxidea* Hall, 1944: AP 8.2–10.9 mm; and *Plionictis* Matthew, 1924: AP 7.6–9.5 mm; *Martes* Pinel, 1792: AP 7.0–13.0 mm; measurements from Baskin 1998). The taxidiine badger *Chamitataxus* Owen, 2006 is also relatively small but is known only by a cranium and upper teeth (Owen 2006), which are not yet known for *Brevimalictis* gen. nov. *Brevimalictis* gen. nov. differs in various qualitative features of its dental morphology from all of these genera. In particular it differs from members of the mustelid taxa Oligobuninae (e.g., *Promartes*), Taxidiinae (e.g., *Pliotaxidea*), and ischyrictine Mustelinae (e.g., *Plionictis*) in various dental characters of those taxa provided by Baskin (1998). *Brevimalictis* gen. nov. differs from the Oligobuninae in that the m1 is relatively long and its talonid is not labially indented, and the lower jaw length is reduced. It differs from Taxidiinae in that the p4 lacks a posterolateral accessory cusp, the m1 lacks an entoconid and accessory cusp lateral to the hypoconid, the m1 paraconid and metaconid differ in size and are not approximated, and the m2 has a single small root. *Brevimalictis* gen. nov. differs from Ischyrictini in having a basined rather than semitrenchant or trenchant talonid on m1. *Brevimalictis* gen. nov. differs from members of the family Mephitidae (formerly considered a subfamily of Mustelidae) in lacking accessory roots on m1.

Brevimalictis gen. nov. differs from *Miomustela* (see Hall 1930: pl. 8) in having its largest lateral mental foramen farther anterior (below the posterior root of p2 instead of below the posterior root of p3), crowded lower premolars, p4 without a posterior accessory cusp, and m1 with a protostylid and hypoconid. As for *Pliogale* Hall, 1930, the m1 of *Brevimalictis* gen. nov. differs in lacking an entoconid and a cuspidate rim on the talonid, a narrow notch separates a protostylid from the hypoconid; and m2 has a single root, which is fused-double in *Pliogale*. In *Pliotaxidea*, the m1 is much longer (AP) and has a relatively wider talonid (TAW) than the m1 of *Brevimalictis* gen. nov. *Brevimalictis* gen. nov. differs from *Plionictis* (Matthew 1901, 1924) in having lower premolars that lack weak posterior accessory cusps, m1 metaconid is smaller and not as well separated from the protoconid, m1 protostylid is present, m1 hypoconid is separated from the protostylid by a notch, and m1 metaconid and hypoconulid are absent. Tseng et al. (2009) described a new genus of mustelid, *Legionarictis*, from the Temblor Formation in California, but the mandible and lower teeth for this taxon are not known so no direct comparison can be made. Based on the length of the P4 (AP 11.5 mm) of *Legionarictis*, it is a mustelid that is much larger than *Brevimalictis chikasha* gen. et sp. nov.

Brevimalictis gen. nov. agrees in some features with those used by Baskin (1998) to characterize the Ischyrictini, the Galictini and the Lutrini, but also shows differences from each of these tribes. The characters of *Brevimalictis* gen. nov. agree most closely with those of the Galictini as diagnosed by Baskin (2011), in that it has crowded premolars, p1 absent, m1 with an open bladelike trigonid, m1 with a lingually expanded and basined talonid, m1 talonid with a posterolingual cingulum extending from the base of a reduced metaconid to the hypoconid, m1 hypoconid separated from the protoconid by a small notch, and in its small size; it differs from galictins in having a shallow rather than deep jaw.

Brevimalictis gen. nov. shares some characters in common with Lutrini (Baskin 1998), specifically in having m1 with an accessory cuspule on the posterior margin of the protoconid and having the metaconid connecting to a broad, basined talonid; it differs from lutrins in having m1 with an elongated trigonid and reduced metaconid. *Brevimalictis chikasha* gen. et sp. nov. further differs from the lutrin *Mionictis* Matthew, 1924 in being much smaller than known species of that genus (*Mionictis* species range in m1 length 10.6–16.4 mm; measurements from Baskin 1998). It differs from *Limnonyx* Crusafont-Pairó, 1950 in having m1 trigonid wider than talonid, and in having depth of dentary less than length of m1 (*Limnonyx* has an m1 length of 12.1 mm; measurement from Baskin 1998). *Brevimalictis* differs from *Satherium* Gazin, 1934 in having p4 without a posterior accessory cusp, m1 with a more anteroposteriorly directed carnassial blade, no metastylid, and much smaller size (*Satherium* range in m1 length 16.5–18.3 mm; measurements from Baskin 1998). It differs from *Enhydritherium* Berta and Morgan, 1985 in having m1 narrow and without inflated cusps, metaconid smaller than protoconid, protostylid (accessory cuspule) present, and much smaller size

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(*Enhydritherium* range in m1 length 15.8–17.0 mm; measurements from Baskin 1998).

Brevimalictis gen. nov. differs from Baskin's (1998) characterization of Mustelinae, including the Ischyrictini, in having the m1 talonid basined, not semitrenchant to trenchant; it agrees with Mustelinae in having the m1 metaconid reduced and m2 single rooted.

Brevimalictis gen. nov. differs from *Negodiaetictis rugatrulleum* gen. et sp. nov. from Eastgate (described below) in having a p4 without posterior accessory cusp, m1 with simple basined talonid that is narrower than the trigonid, in lacking crenulated enamel on the teeth, and in much smaller size.

Stratigraphic and geographic range.—Western Nevada, USA; Monarch Mill Formation, Barstovian (Miocene).

Subfamily incertae sedis

Genus *Negodiaetictis* nov.

Type species: *Negodiaetictis rugatrulleum* gen. et sp. nov., monotypic; see below.

Etymology: From Latin *nego*, decline; *diaeta*, prescribed regimen of food; and *ictis*—indicating a mustelid that ate whatever it wanted to consume.

Diagnosis.—The same as for the type and only species.

Negodiaetictis rugatrulleum sp. nov.

Fig. 7.

Etymology: From Latin *ruga*, wrinkled; *trulleum*, basin—in reference to the talonid basin of the m1.

Holotype: OMNH 54974, right partial dentary with p3–m1 and alveoli for c and p2.

Type locality: OMNH V972 (UCMP V70147), Eastgate, Churchill County, Nevada, USA.

Type horizon: Basal-most unit of the Monarch Mill Formation (Axelrod 1985), Barstovian (Miocene).

Material.—OMNH 54888, right m2 from type locality.

Diagnosis.—Unique among mustelids in having crenulated enamel on all known lower teeth (p3–m1), especially pronounced on the talonid basin of m1.

Measurements (in mm).—p3: AP, 5.6; T, 3.3; p4: AP, 5.8; T, 4.0; m1: AP, 9.4; TRL, 5.8; TAL, 4.1; TRW, 4.5; TAW, 4.5; m2: AP, 4.1; T, 3.5; p2–4: alveolar length, 15.9; p2–m1: alveolar length, 23.6; p3–4: length, 12.3; p3–m1: length, 20.7. Depth of dentary bone beneath protoconid of m1 9.0.

Description.—*Dentary*: This element is short and moderately deep (slightly less deep than the length of m1), with a curved ventral margin. The preserved part shows two small mental foramina, one below the p2 and one below the posterior root of p3. The posterior edge of the mandibular symphysis is preserved and reaches a level below the middle of the p3.

Lower premolars: The p1 is absent, the anterior alveolus for p2 being directly adjacent to that for c. The existing premolars, p2–4, are crowded together between c and m1, indicating a shortened rostrum. The p2 is represented only by two empty alveoli set at an oblique angle to the axis of the lower toothrow (Fig. 7A). The anterior alveolus, placed against the posterior border of the c alveolus, is the smaller of the two sockets that held p2. Similarly, p3 is also two-rooted, with the anterior root smaller than the posterior, and the two roots and crown oriented at an angle oblique to the axis of the dentary. The crown of p3 is of robust construction, is wider posteriorly than anteriorly, bears one main cusp, and is covered with crenulated enamel. No posterior accessory cusp is present. The anterior and posterior cingulids are strong but lack cingular cusps, though the posterior cingulid bears a continuous series of tiny cuspules. The labial and lingual cingulids are weak. The crown and roots of p4 are aligned with the axis of the lower toothrow and dentary. Two roots are present, of which the posterior is larger. The crown is wider posteriorly than anteriorly, is covered with crenulated enamel, and bears a strong, posterolabially placed accessory cusp in addition to the main cusp. The labial and lingual cingulids are weak; the anterior and posterior cingulids are strong but lack cingular cusps. The posterior cingulid bears a series of very small cingular cuspules.

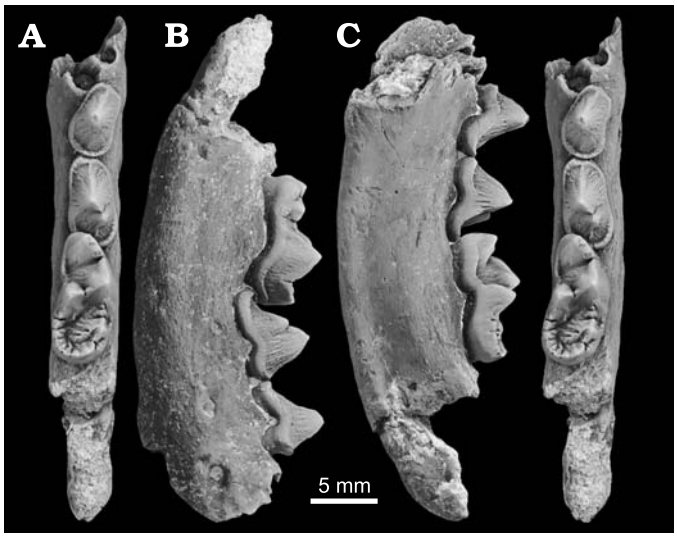


Fig. 7. Mustelid carnivoran *Negodiaetictis rugatrulleum* gen. et sp. nov. from the Eastgate LF, basal-most unit of the Monarch Mill Formation, Barstovian (Miocene), Churchill County, Nevada, USA. OMNH 54974, holotype right dentary (posteroinferior margin cropped from images) with p3–m1 and alveoli for c and p2 in occlusal (**A**, stereopair), labial (**B**), and lingual (**C**) views.

Lower molars: The m1 has a relatively low, open trigonid with an oblique protoconid-paraconid (paracristid) carnassial blade and a relatively high talonid, and is covered with crenulated enamel. A very short but distinct lingual cingulid is present below the anterior portion of the trigonid valley. Labially, a thin cingulid extends posteriorly from a point below the paraconid, becoming weak below the protoconid, then becoming disjunct posteriorly, with short, strong, crenulated segments labial to the notch between the protoconid and hypoconid and the notch between the hypoconid and hypoconulid. No accessory roots are present, only large anterior and posterior roots. The metaconid is well developed,

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taller than the paraconid, and positioned slightly posterior to the protoconid. The protoconid and metaconid are joined by a V-shaped crest (protocristid) with a median notch like that in the carnassial blade. The talonid is slightly shorter and slightly wider than the trigonid, and is expanded lingually. The talonid is basined but the basin is partly filled by an internal, crenulated low mound that extends basinward from the hypoconid. The hypoconid is moderately large and is separated from the posterior margin of the protoconid by notches and two low, small accessory cuspules, which might represent a modified protostylid. The hypoconid is connected through a basin-ringing posterior and lingual rim composed of a continuous series of small cuspules separated from one another by notches to a point just posterior to the postmetacristid. Here the talonid rim is separated by a tiny notch from the ridge running down the posterior face of the metaconid. There is no distinct entoconid.

The m2 is lacking from the type specimen and is represented only by the partial anterior rim of an alveolus that is filled with rock matrix. Due to the condition of the specimen (Fig. 7) it cannot be determined whether a second root or additional lower molar was present. However, an isolated m2 (OMNH 54888) was found. We believe that it may belong to the holotype jaw because: (i) the two specimens were discovered in the same quarry in the same field season; (ii) the two are identical in preservation and color; (iii) the m2 (OMNH 54888) has a small anterior interdental contact facet matching the size and shape of the facet on the posterior face of m1 on the holotype (OMNH 54974); (iv) the slight degree of occlusal wear is consistent between the specimens; and (v) OMNH 54888 has crenulated enamel, as would be predicted for m2 of this species.

The isolated m2 is single-rooted with the strongly tapering root slanting posteriorly from the crown. The occlusal surface of the crown would have been tilted forward slightly from the horizontal and relative to the occlusal surface of m1. The crown is small with an ovate outline in occlusal view, and is slightly longer than broad. The paraconid is absent. The low protoconid and metaconid join to form a transverse crest (protocristid) just behind the middle of the crown, dividing the crown into anterior (trigonid) and posterior (talonid) portion, of which the former is larger. Both the anterior and posterior basins have heavily crenulated enamel like that of the m1.

Remarks.—*Negodiaetictis rugatrulleum* gen. et sp. nov. resembles various taxa of Mustelidae, especially some Galictini and Lutrini. Definitions of these and other mustelid subclades vary among authors but continue to be refined, and placement of mustelid genera into infrafamilial groupings is unavoidably inconsistent due largely to the incompleteness of the group's fossil record. The family requires revision, beyond the scope of the present article, which compounds the problem of making comparisons with additional poorly represented but presumably distinct and related taxa. *Negodiaetictis rugatrulleum* gen. et sp. nov. most closely fits Baskin's (2011: 2) diagnosis of Galictini; it shares with galictins small size, a relatively deep jaw (dentary depth is 95% of m1 length), crowded premolars, p1 absent, m1 with an open bladelike trigonid, m1 with 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. Based on specimens in hand, *Negodiaetictis* differs from Baskin's (2011) diagnosis of Galictini in only a few features, including unreduced metaconid, presence of a small cuspule in the notch separating the protoconid from the hypoconid, and heavier degree of enamel crenulation.

Based on our own comparisons and on what we have gleaned from the literature, *Negodiaetictis* gen. nov. differs from *Brevimalictis* gen. nov., *Cernictis* Hall, 1935, *Eira* Smith, 1842, *Enhydrictis* Stefani, 1891, *Galictis* Bell, 1826, *Grisonella* Thomas, 1912, *Lartetictis* Ginsburg and Morales, 1996, *Limnonyx*, *Lutravus* Furlong, 1932, *Mionictis*, *Pannonictis* Kormos, 1931, *Sminthosinis* Bjork, 1970, *Trigonictis* Hibbard, 1941, and *Trochictis* Meyer, 1842, in having crenulated enamel on lower cheek teeth, rugose enamel on the m1 talonid (especially on the hypoconid, hypoconulid, and talonid basin), and m1 talonid rim consisting of a beaded series of cuspules separated from one another and from the protoconid, metaconid, hypoconid, and hypoconulid by small notches. *Negodiaetictis* gen. nov. further differs from *Enhydrictis* (a Eurasian genus) in having p2 large and two-rooted, having p4 with a posterior accessory cusp, having m1 lacking a distinct entoconid, and having the m1 metaconid posterior crest separated by small notch from the adjacent internal rim of the talonid (fide Pilgrim 1932; Baskin 2011). It further differs from *Pannonictis* in having p4 with a posterior accessory cusp (Baskin 2011).

Negodiaetictis gen. nov. is comparable to certain Eurasian taxa in some respects. One example is the Eurasian genus *Trochictis*, which is often placed in Melinae, but variously in Gulolinae (e.g., by Ginsburg 1999), and said to be referable possibly to Galictinae by Baskin 2011. The species *Trochictis depereti* Major, 1903 shows some similarities to *Negodiaetictis* gen. nov., such as an m1 talonid with a large basinward-sloping expansion of the hypoconid and rimmed with a posterior cingulid having a series of small cuspules (Thenius 1949a: fig. 3). Pilgrim (1932: 854) also noted "crenulation of the entoconid" of m1 in Eurasian *Trochictis*? *pusilla* Major, 1903 and *T. taxodon* Gervais, 1852. However, *N. rugatrulleum* gen. et sp. nov. differs in general from *Trochictis* as noted above, and further differs in lacking p1, having crowded p2—p4, having the m1 protoconid taller than the metaconid, having the m1 talonid base higher than the trigonid base, and having the m1 lacking a distinct entoconid. Helbing (1927) noted a resemblance between Eurasian *Trochictis* and North American *Mionictis*. In addition to the differences noted above, *Negodiaetictis rugatrulleum* gen. et sp. nov. further differs from *Mionictis* in having the p4 with a prominent posterior accessory cusp. For further discussion of species sometimes referred to *Mionictis*, see below.

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Relative to extinct North American members of the Galictini, *Negodiaetictis rugatrulleum* gen. et sp. nov. differs from *Cernictis* (see also Baskin 2011) in having m1 with a relatively longer talonid (more than half the length of the trigonid), anterior end of labial cingulid not extending upward on the anterior border of paraconid, hypoconid not trenchant, talonid basin partly filled by basal expansion of the hypoconid, posterior face of the metaconid bearing a ridge and separated from a high lingual margin of talonid by a metastylid, posterior talonid cingulid of m1 composed of a series of connected small cuspules, tooth enamel crenulated, and smaller size (*Cernictis* has an m1 length that ranges from 10.6–11.5 mm; measurements from Baskin 2011). Some specimens of *Trigonictis* show the m1 talonid rim with a series of beaded cuspules (e.g., Ray et al. 1981: fig. 3, but less pronounced than in *N. rugatrulleum* gen. et sp. nov.), but otherwise *Negodiaetictis* gen. nov. differs from *Trigonictis* in having a strong posterolabial accessory cusp on p4, carnassial paraconid-protoconid blade (paracristid) shorter and more obliquely oriented, with the trigonid less open; m1 talonid longer relative to length of trigonid, m1 talonid basin partly filled by expanded base of hypoconid, tooth enamel crenulated, and smaller size. *Negodiaetictis* gen. nov. further differs from *Brevimalictis chikasha* gen. et sp. nov. in much larger size, p4 with posterior accessory cusp, metaconid nearly equal height to protoconid, and m1 talonid with rugose rim, basin, and cusps. *Negodiaetictis* gen. nov. differs from *Sminthosinis* in having p4 with strong posterolabial accessory cusp, m1 metaconid positioned slightly posterior relative to the protoconid, m1 posterior cingulid composed of series of small connected cuspules, and strongly crenulated enamel on all known teeth, especially m1 talonid. *Negodiaetictis* gen. nov. differs from *Lutravus* in having p4 with a strong posterolabial accessory cusp, m1 with a large metaconid separated from the internal cingulid of the talonid by a metastylid, hypoconid separated from the protoconid by a small accessory cuspule rather than a narrow notch, posterior cingulid composed of a series of connected small cuspules, crenulated enamel on all teeth, especially pronounced on m1 talonid basin and on hypoconid. *Negodiaetictis* gen. nov. differs from the extant galictin genera *Eira* and *Galictis* in having a two-rooted p2, and having the p4 with a posterior accessory cusp, and from *Grisonella* in having the m1 with a stronger metaconid.

Regarding Baskin's (1998) characteristics for Lutrini, *Negodiaetictis rugatrulleum* gen. et sp. nov. differs in lacking a p1 (although p1 is only primitively present in members of the tribe and many have short muzzles and crowded premolars) and in having m1 with a relatively short trigonid and long, narrow talonid and crenulated enamel on the teeth. However, allowing for notches associated with the rugose enamel and beaded rim of the m1 talonid, *Negodiaetictis rugatrulleum* gen. et sp. nov. resembles lutrins in having m1 with an accessory cuspule (protostylid?) on the posterior margin of the protoconid (partly separated by a small notch) and a strong metaconid connecting to a broad, basined talonid (with the connection interrupted by small notches). The Eastgate taxon differs from the Eurasian lutrin *Limnonyx* (as illustrated by Willemsen 1992: pl. 5: 5, 23) in having m1 with much larger, especially longer, talonid relative to trigonid, talonid basin largely filled by basinward expansion of hypoconid, and smaller size than the two known species (Willemsen 1992). It differs from the Eurasian genus *Cyrnaonyx* Helbing, 1935 in having the m1 talonid about the same width as the trigonid, not lingually expanded, and without a strongly developed external talonid cingulum (Willemsen 1992). *Negodiaetictis* gen. nov. differs from North American *Satherium* species in having dentary depth below m1 less than m1 length, m1 relatively narrower for its length, with slightly more open trigonid; m1 talonid posterior cingulid composed of a series of small connected cuspules, m1 talonid basin partly filled by basinward expansion of base of hypoconid, strongly crenulated enamel, and much smaller size (Gazin 1934). *Negodiaetictis* gen. nov. differs from *Lutra* Brisson, 1762 in having the m1 with a relatively more open trigonid, the talonid narrower than the trigonid and longer relative to the trigonid length, and lacking an anteroposteriorly elongate hypoconid. It differs from *Lontra* Gray, 1843a in having a relatively more open m1 trigonid and narrower talonid lacking an expanded labial cingulum. It differs from *Aonyx* Lesson, 1827 in having the m1 talonid the same width as the trigonid, entoconid absent, and the external cingulum of the talonid weakly developed. It differs from *Pteroneura* in having the m1 with a more open trigonid, a relatively longer talonid, and the talonid about the same width as the trigonid. *Negodiaetictis* gen. nov. differs from European *Paralutra* Roman and Viret, 1934 in having a relatively much longer m1 talonid. It differs from *Enhydritherium* in having a shallower dentary beneath m1, a much more open m1 trigonid, m1 taller and much narrower relative to its length, m1 talonid shorter than trigonid, talonid basin partly filled by basal expansion of hypoconid, crenulated enamel, and smaller size (Berta and Morgan 1985).

Negodiaetictis rugatrulleum gen. et sp. nov. resembles the lutrin *Mionictis* in most characters at the generic level such as having premolars that are robust and crowded, with sharp posterior crests but no cingular cusps; and a stout m1 with open trigonid, with the trigonid low but somewhat larger than the talonid, a semibasined talonid that is broadly expanded internally, a well-developed metaconid situated posterior to the protoconid and bearing a strong, sloping posterior crest extending downward and backward, the hypoconid prominent with a flat, gently sloping internal surface, and the hypoconid separated from the protoconid by a notch and a small accessory cusp posterior to the protoconid (Matthew 1924; Baskin 1998). However, the Eastgate taxon differs from all named species of *Mionictis* (as listed and characterized by Baskin 1998) in having a strong posterolabial accessory cusp on p4, crenulated enamel on all known lower teeth, especially the talonid basin of the carnassial, and in having the posterior cingulum of the p3, p4, and

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talonid of m1 broad and composed of a series of closely connected, small cuspules. *Negodiaetictis rugatrulleum* gen. et sp. nov. differs from *M. incertus* Matthew, 1924, the type species for the genus, in having the m1 with a high talonid, with a posterior ridge of the metaconid that is not continuous with the internal cingulid or posterior cingulid (the metaconid of *Negodiaetictis* gen. nov. is instead separated by a notch that is partly filled with a cuspule, which in turn is separated by another small notch from the posterior cingulid), with the posterior cingulid formed by a series of small cuspules, and with the hypoconid internal surface and talonid basin much crenulated. It further differs from *M. incertus* in having the other surfaces of the known teeth moderately crenulated, p4 with a large posterior accessory cusp, and in smaller size. *Negodiaetictis* gen. nov. differs from *M. elegans* Matthew, 1924 in having premolars less compressed and in smaller size. *Negodiaetictis rugatrulleum* gen. et sp. nov. is about the same size as, and most closely resembles *M. letifer* Cook and Macdonald, 1962 in premolar alveoli and crowding, and in p4 morphology, but differs from that species in having the posterior ridge of the metaconid separated by a notch containing a small cuspule from the rest of the lingual talonid cingulid, most of the talonid cingulid composed of a series of closely-connected small cuspules, posterobasal cuspule of protoconid smaller, and enamel crenulation on all known teeth. *Negodiaetictis rugatrulleum* gen. et sp. nov. differs from *Mionictis pristinus* (originally placed in *Lutra* by Matthew and Gidley [1904], later in *Brachypsalis* [Cope, 1890] by Webb [1969a], and most recently referred to *Mionictis* by Baskin [1998]) in having p4 with a large posterolabial accessory cusp, m1 without a hypoconulid but with talonid cingulid composed of a series of connected small cuspules, crenulated enamel, and much smaller size. Baskin (1998) tentatively assigned the taxon previously known as *Brachypsalis angustidens* Hall, 1930 to *Mionictis*? *angustidens*; the uncertainty is due in part to the type specimen being heavily worn, especially the carnassial. The Eastgate species differs from *M.*? *angustidens* in having p4 with a much stronger posterolabial accessory cusp, p4 broader posteriorly than anteriorly, crenulated enamel, and smaller size.

Negodiaetictis rugatrulleum differs from Eurasian *Lartetictis dubia* (Blainville, 1842) (as illustrated under the name *Mionictis dubia* by Thenius 1949a: figs. 1, 2) in having p4 with a large posterolabial accessory cusp, m1 with an accessory cusp posterior to the protoconid, posterior cingulid of talonid with series of small cuspules, and crenulated enamel on all known tooth surfaces, especially in the m1 talonid basin.

Virtually all previous North American specimens of *Mionictis* spp. are from the early Barstovian to late Hemphillian of the Great Plains, with one possible early Hemphillian occurrence (of *M.*? *angustidens*; Baskin 1998) from Kern River, California. *Negodiaetictis rugatrulleum* gen. et sp. nov. closely resembles the late Hemingfordian *M. letifer* of the middle Sheep Creek beds, northwestern Nebraska; and early Barstovian to late Clarendonian *M. pristinus* from Little White River (type locality) and several other localities, Nebraska (Baskin 1998).

Negodiaetictis rugatrulleum gen. et sp. nov. differs from the non-aquatic lutrine *Teruelictis riparius* Salesa, Antón, Siliceo, Pesquero, Morales, and Alcalá, 2013 from the late Miocene of Spain in lacking a p2 and in having an m1 with crenulations and a protoconid that is noticeably higher than the paraconid, and an m1 with a tall, large talonid basin (Salesa et al. 2013). However, these taxa are similar in having a large metaconid that is nearly as high as the protoconid. Both taxa have a metaconid that is adjacent to the protoconid. The configuration of the metaconid, protoconid, and distal cristids arising from these cusps in *Teruelictis riparius* forms an M-pattern on the occlusal surface of the distal wall of the trigonid, which is not seen in *N. rugatrulleum* gen. et sp. nov.

Mustelids are well known for their opportunistic feeding habits. The crenulated enamel on the teeth of *Negodiaetictis rugatrulleum* gen. et sp. nov. is unique among Mustelidae. The presence of crenulations may indicate a diet of plant material such as seeds (see Discussion). Whether *Negodiaetictis rugatrulleum* is a galictin or lutrin (or lutrine) or a member of some other clade of mustelids, it apparently had a unique dietary specialization, possibly including plant matter.

Stratigraphic and geographic range.—Western Nevada, USA; Monarch Mill Formation, Barstovian (Miocene).

Family Felidae Fischer von Waldheim, 1817

Subfamily Felinae Fischer von Waldheim, 1817

Genus *Pseudaelurus* Gervais, 1850

Type species: *Pseudaelurus quadridentatus* (Blainville), 1843; Sansan, Gers, France; Sansan freshwater lake deposits, mammal zone MN6, Astaracian, (Miocene).

Stratigraphic and geographic range.— Europe, Early to Middle Miocene (European Neogene Mammal Faunal zones MN3–MN9; Dam 2003); Asia, Early to Middle Miocene (East Asian Land Mammal ages: Xiejian to Shanwangian; Wang et al. 2013); Africa, Early Miocene; North America, late Hemingfordian to late Barstovian (Early to Middle Miocene; Rothwell 2003).

Pseudaelurus sp.

Fig. 8.

Material.—UCMP 141531, partial left dentary with anterior root of p3 and partial p4, from UCMP V70138 (OMNH V967), Eastgate, Churchill County, Nevada, USA; Monarch Mill Formation, Barstovian (Miocene).

Measurements.—See Table 4.

Description.—*Dentary*: UCMP 141531 is a dentary fragment with a fragment of the p3 (anterior cingular cusp and anterior root only), p4 (lacking main cusp) and root-filled alveoli for the m1. The dentary fragment is short and stout and is fractured in two places: anterior to the anterior root of p3

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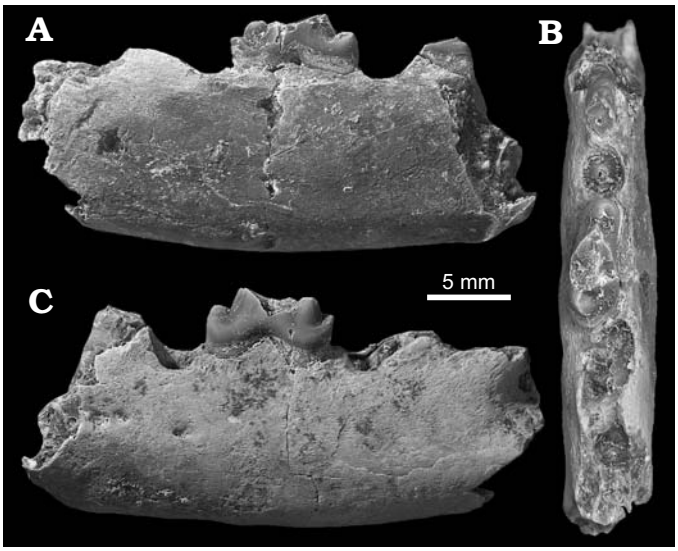


Fig. 8. Felid carnivoran *Pseudaelurus* sp. from the Eastgate LF, basal-most unit of the Monarch Mill Formation, Barstovian (Miocene), Churchill County, Nevada, USA. UCMP 141531, partial left dentary with anterior root of p3 and partial p4, in lingual (**A**), occlusal (**B**), and labial (**C**) views.

and posterior to the posterior root of m1. The anterior part of the masseteric fossa is preserved and terminates below the posterior root of the m1. On the lateral aspect of the dentary are two mental foramina, one below the anterior root of p3 and the second below the posterior root of the p3.

Lower teeth: The p4 has distinct anterior and posterior cingular cusps, and a distinct posterior accessory cusp. The principal cusp of p4 is broken off near its base, level with the apex of the accessory cusp.

Remarks.—Rothwell (2003) recognized five species of *Pseudaelurus* (*P. validus* Rothwell, 2001, *P. skinneri* Rothwell, 2003, *P. intrepidus* Leidy, 1858, *P. marshi* Thorpe, 1922, and *P. stouti* [Schultz and Martin, 1972]) from the Barstovian of North America. Although Rothwell (2003) did not synonymize *P. aeluroides* Macdonald, 1954 with *P. marshi*, he suggested that the two species are likely synonymous because of similar size and characteristics described by Macdonald (1954). Rothwell (2003: 12) provided a generic diagnosis for *Pseudaelurus*, but none of the diagnostic derived characters is preserved in the Eastgate fossil. Similarly, in the diagnoses for individual species within the genus, relevant diagnostic characters are not preserved in the Eastgate fossil, with one exception. One species, *P. skinneri*, lacks prominent anterior cingular cusps on p3 and p4 whereas most species of *Pseudaelurus* possess these cusps. The Eastgate specimen possesses anterior cingular cusps (although not particularly prominent ones) on p3 and p4, and thus probably does not represent *P. skinneri*. In Rothwell's (2003) phylogenetic analysis of *Pseudaelurus* species, 23 characters were examined. Of these, 13 are based on the dentition, but none of these characters are well preserved in the Eastgate felid. Rothwell's (2003) only phylogenetic character pertaining to the p3 and p4 is his character 4, in which p3 and p4 heights are similar in *P. stouti*, while p3 is considerably smaller than p4 in all other North American *Pseudaelurus* species. The p3 in the Eastgate dentary is mostly missing; thus, the relative heights of p3 and p4 cannot be compared. The relative sizes, as reflected in length of the c–p3 and length of m1, were used as well by Rothwell (2003) in part to differentiate among the species of *Pseudaelurus* (see Table 4). Unfortunately, these characteristics also are missing in UCMP 141531 from Eastgate, so that no measurements can be directly compared with any of the species. However, the Eastgate specimen is relatively small, suggesting that it might represent one of the smaller species of *Pseudaelurus*.

Table 4. Measurements (in mm) of p4 and m1 of *Pseudaelurus* spp. from the Barstovian (Miocene) of North America (from Rothwell 2003, except *P. aeluroides* from MacDonald 1954 and UCMP 41531 from Smith 2002).

Taxon	Tooth	Anteroposterior length (AP)	Greatest transverse width (T)
Pseudaelurus aeluroides	p4	11.4	5.4
	m1	15.6	6.7
Pseudaelurus intrepidus	p4	12.0	6.0
	m1	15.0–20.0	–
Pseudaelurus marshi	p4	13.3	–
	m1	14.0–19.0	–
Pseudaelurus stouti	p4	6.6–7.3	3.3
	m1	8.8–10.0	4.4
Pseudaelurus validus	p4	11.3	5.0
	m1	15.0	6.3
Pseudaelurus sp. (UCMP 41531)	p4	7.3	3.0

Discussion and concluding remarks

To date, 21 vertebrate fossil localities have been identified from the Monarch Mill Formation, Churchill County, Nevada. Three of the localities are Hemphillian in age (Axelrod 1985). The other localities are tentatively considered to be early Barstovian in age (Smith 2002), and collectively have yielded the Eastgate LF. There are no known localities of Clarendonian age in the Monarch Mill Formation. Fossil vertebrates were collected from the Monarch Mill Formation near the town of Eastgate for more than 40 years by researchers at the UCMP and two field seasons by OMNH researchers. Most of the fossils obtained by UCMP were recovered by surface collecting, whereas OMNH quarried rock matrix for screenwashing to recover small vertebrates. In the process, these efforts yielded the carnivores described in the present report.

Although an early Barstovian age for the Eastgate LF has been suggested (Smith 2002), neither absolute nor relative age is well established for this fauna. No radiometric dates have been obtained directly from the Monarch Mill Formation. However, Swisher's (1992) date of 15.96 Ma from

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the uppermost part of the Middlegate Formation, mentioned above, provides a maximum possible age for the Eastgate LF at the base of the overlying Monarch Mill Formation. Because the Monarch Mill Formation unconformably overlies the Middlegate Formation, there is a temporal gap of unknown duration between the two units. Using tephrochronology, Stewart et al. (1999) provided an indirect age range of 9.8–14.7 Ma for eight tephras within the Monarch Mill Formation. This temporal range is consistent with a Barstovian correlation, based on mammalian biochronology (Tedford et al. 2004), for the Eastgate LF. A single locality (UCMP V5200) in the upper member of the Monarch Mill Formation has yielded a mammalian assemblage of Hemphillian aspect (Axelrod 1985). However, Stewart et al. (1999) noted a number of uncertainties in their stratigraphic correlations. Detailed stratigraphic and chronological data for the Monarch Mill Formation are needed.

Woodburne and Swisher (1995) placed the Hemingfordian–Barstovian boundary at about 15.9 Ma. Tedford et al. (1987, 2004) divided the Barstovian into early and late intervals, informally designated as Ba1 and Ba2. Chronologically, the early Barstovian extends from the Hemingfordian–Barstovian boundary (ca. 14.7–16 Ma) and the late Barstovian ends at the Barstovian–Clarendonian boundary, at about 12.5 Ma (Woodburne 2004). Tedford et al. (2004) and Woodburne (2004) defined the onset of Barstovian time on the first North American occurrences of the hemicyonine ursid *Plithocyon* and on the "Proboscidean Datum", the first occurrence of *Zygolophodon*. Unfortunately, neither proboscideans nor *Plithocyon* are known from Eastgate. In their revision of the canid subfamily Borophaginae, Wang et al. (1999: fig. 141) refined the temporal range of *Tomarctus brevirostris*, known in the Eastgate fauna, to an interval from early Barstovian to early late Barstovian (Ba1 to early Ba2). The simocyonine ailurid *Actiocyon* was previously known from a single species, *A. leardi*, having a first and only appearance in the late Clarendonian (Cl3; Tedford et al. 2004). As part of the Eastgate fauna, we recognize the new species *Actiocyon parverratis* sp. nov. Assuming the age estimate of the Eastgate LF is correct, this record extends the temporal range for the genus *Actiocyon* in North America back to the Barstovian, and constitutes the earliest record of a simocyonine ailurid to reach North America from Eurasia.

The ailurid Simocyoninae are relatively widespread but rare in Eurasia; however, in North America this group is not widespread and where present it is extremely rare. Kundrát (2011) recognized two subfamilies of the extinct taxa of Ailuridae for Europe, Asia, and North America: (i) Simocyoninae (including *Simocyon primigenius*, *S. diaphorus* [Kaup, 1832], and *S. batalleri*, *Alopecocyon* spp., and *Actiocyon leardi* and *A. parverratis* sp. nov.) and (ii) Ailurinae (including *Ailurus fulgens* Cuvier, 1825, *Parailurus anglicus* [Dawkins, 1888], *P. baikalicus* Sotnikova, 2008, and *Pristinailurus bristoli* Wallace and Wang, 2004). He listed a single taxon as problematic (*Amphictis ambiguous* Pomel, 1853) and two taxa as incertae sedis (*Magerictis imperialensis* Ginsburg Morales, Soria, and Herraez, 1997, *Protursus simpsoni* Crusafont and Kurtén, 1976).

Magerictis imperialis, from the Middle Miocene (16–17 Ma) of Spain (Salesa et al. 2006), is the oldest known fossil ailurid of the group Ailurinae, whereas Ailurinae are not known from North America until the Late Miocene (early Blancan). Tedford and Gustafson (1977) reported the geologically oldest North American ailurine, *Parailurus* Schlosser, 1899, from the early Blancan Taunton LF in Washington State. The second specimen and taxon of ailurine from North America, *Pristinailurus* Wallace and Wang, 2004, was reported from the Late Miocene–Early Pliocene Gray Fossil Site in Tennessee, USA, by Wallace and Wang (2004). During the Late Miocene (early Blancan) of North American, *Parailurus* (Ailuridae, Ailurinae) was widespread in Europe and North America (Tedford and Gustafson 1977; Wallace and Wang 2004; Sotnikova 2008), whereas the much rarer Simocyoninae are represented in four western states (California, Idaho, Nevada, and Oregon). As was previously established (Qiu 2003; Tedford et al. 2004; Woodburne 2004; Wallace and Wang 2004; Wallace 2011; this paper), the Simocyoninae inhabited North America well before Ailurinae arrived on the continent.

Simocyon species are large-bodied ailurids; *Actiocyon* and *Alopecocyon* include small-bodied forms. Differences between *Actiocyon* and *Alopecocyon*, if any, need to be studied in detail with reference to numerous and scattered Eurasian specimens. Although there appears to be great similarity between the North American *Actiocyon* and Eurasian *Alopecocyon*, their taxonomic relationship remains unclear at this time.

The mustelids underwent numerous dispersal events and are important in defining the biostratigraphy of the Miocene (Baskin 1998). The Mustelidae are represented at Eastgate by two new genera and species. *Brevimalictis chikasha* gen. et sp. nov. is a small possible galictine or lutrine with a shortened rostrum. The second new mustelid at Eastgate, *Negodiaetictis rugatrulleum* gen. et sp. nov., is also a possible galictine or lutrine. It has crenulated lower teeth that distinguish it from other short-faced, crowded-tooth mustelids. Complexity in the crown surfaces of molar teeth in carnivorans and rodents is considered to be related to the proportion of plant material in the diet (Evans et al. 2007). The crenulated enamel in cheek teeth of *Negodiaetictis rugatrulleum* gen. et sp. nov. is almost unique among Mustelidae (developed to a much lesser extent in the European badger, *Meles meles*). Crenulated enamel may be indicative of feeding on tough plant material such as fibrous seeds, as has been suggested for primates (Kinzey 1992; Lucas and Luke 1984; Lucas and Teaford 1994; Vogel et al. 2008). Several kinds of extant mustelids, including *Galictis*, *Martes*, *Meles*, *Mellivora*, *Melogale*, *Taxidea*, and some species of *Lontra* and *Mustela* occasionally eat fruits, nuts, and seeds as well as eggs, arthropods, and small vertebrates. For example, North American river otters (*Lontra canadensis*) have been known to eat macroalgae, tubers and roots, and leaves of

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aquatic plants as well as aquatic vertebrates and invertebrates. European and Asian badgers (*Meles*) sometimes eat leaves, stems and bark, grains, nuts, tubers, fruits, and fungi. North American badgers (*Taxidea taxus*) will eat corn and sunflower seeds (Animal Diversity Web http://animaldiversity.ummz.umich.edu/accounts/Mustelidae/#food_habits). Whether *Negodiaetictis rugatrulleum* gen. et sp. nov. is a galictine or a member of some other clade of mustelids, it apparently had a unique dietary specialization, possibly including plant matter.

A single fragmentary lower jaw with a partial p4 is the only fossil of a felid known from Eastgate. The fossil cat, *Pseudaelurus* sp., is small relative to most named species of the genus *Pseudaelurus*; the Eastgate specimen may represent a new species, but this cannot be determined with the specimen at hand. Rothwell (2003) suggested that *P. stouti* is the only small felid known from the Barstovian of North America and that it may be endemic to the New World. Glass and Martin (1978) suggested that *P. stouti* may have affinities with small South American felids.

A noteworthy aspect of the carnivoran composition at Eastgate is the relatively great diversity, with four families and six species represented. The uniqueness of the Eastgate carnivores is difficult to assess. Half of the six known taxa are new. We hypothesize that the uniqueness may be related to high paleoaltitude, as indicated by paleobotanical evidence (Wolfe et al. 1997; see also *Paleobotany and paleoenvironment of the Middlegate Basin* in Geological and paleontological setting section). We are fortunate that the fossil flora provides a relatively detailed environmental setting for the Eastgate carnivores. Because such evidence is lacking for other Barstovian faunas in the intermontane region, the magnitude of altitudinal zonation in mammalian faunas during this time interval cannot be directly addressed.

More generally, carnivore diversity in the Eastgate LF presumably reflects complex interactions of biogeographic, environmental, and paleoecological factors, the relative importance of which remains to be studied. The Eastgate LF improves our understanding of mammalian succession and evolution during the Mid-Miocene Climatic Optimum. While terrestrial ecosystems such as grasslands were expanding globally during the Neogene, the Eastgate LF provides a rare glimpse into a relatively high-elevation, temperate forest ecosystem in the Great Basin during the Barstovian.

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References

Axelrod, D.I. 1956. Mio-Pliocene floras from west-central Nevada. *University of California Publications in the Geological Sciences* 33: 1–321.

Axelrod, D.I. 1985. Miocene floras from the Middlegate Basin west-central Nevada. *University of California Publications in the Geological Sciences* 129: 1–279.

Barrows, K.J. 1971. *Geology of the Southern Desatoya Mountains, Churchill and Lander Counties, Nevada*. 349 pp. Ph.D. Dissertation, University of California, Los Angeles.

Baskin, J.A. 1998. Mustelidae. *In*: C.M. Janis, K.M. Scott, and L.L. Jacobs (eds.), *Evolution of Tertiary Mammals of North America: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals. Vol. 1*, 152–173. Cambridge University Press, Cambridge.

Baskin, J.A. 2011. A new species of *Cernictis* (Mammalia, Carnivora, Mustelidae) from the late Miocene Bidahochi Formation of Arizona, USA. *Palaeontologia Electronica* 14 (3): 26A.

Beaumont, G. de 1964. Essai sur la position taxonomique des genres *Alopecocyon* Viret et *Simocyon* Wagner (Carnivora). *Eclogae Geologicae Helvetiae* 57: 829–836.

Bell, T. 1826. [Untitled entry for Zoological Club, January 10, 1826]. *Zoological Journal* 2: 551–552.

Berta, A. and Morgan, G.S. 1985. A new sea otter (Carnivora: Mustelidae) from the late Miocene and early Pliocene (Hemphillian) of North America. *Journal of Paleontology* 59: 809–819.

Bjork, P.R. 1970. The Carnivora of the Hagerman local fauna (late Pliocene) of southwestern Idaho. *Transactions of the American Philosophical Society* 60 (7): 1–54.

Blainville, H.M.D. de 1839–1864. *Ostéographie ou description icono-*

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graphique comparée du squelette et du système dentaire des mammifères récents et fossiles. Atlas of 323 lithographic plates. Librairie J.-B. Baillière et Fils, Paris.

Bowdich, T.E. 1821. *An Analysis of the Natural Classifications of Mammalia for the Use of Students and Travelers*. 115 + [31] pp. J. Smith, Paris.

Brisson, M.J. 1762. *Le regnum animale in classes IX. distributum, sive synopsis methodica sistens generalem animalium distributionem in classes IX, & duarum primarum classium, quadrupedum scilicet & cetaceorum, particularem divisionem in ordines, sectiones, genera & species. Cum brevi cujusque speciei description, citationibus auctorum de iis tractantium, nominibus eis ab ipsis & nationibus impositis, nomimibusque vulgaribus. Ed. 2*. 296 pp. Lugduni Batavorum: Apud Theodorum Haak, Leiden.

Cook, H.J. and Macdonald, J.R. 1962. New Carnivora from the Miocene and Pliocene of western Nebraska. *Journal of Paleontology* 36: 560–567.

Cope, E.D. 1873. On the extinct Vertebrata of the Eocene of Wyoming, observed by the expedition of 1872, with note on the geology. *In*: F.V. Hayden (ed.), *Sixth Annual Report, United States Geological Survey of the Territories,* 545–649. U. S. Government Printing Office, Washington, D.C.

Cope, E.D. 1890. On two new species of Mustelidae from the Loup Fork Miocene of Nebraska. *American Naturalist* 24: 950–952.

Crusafont, M. and Kurtén, B. 1976. Bears and bear-dogs from the Vallesian of the Vallés-Penedés Basin, Spain. *Acta Zoologica Fennica* 144: 1–29.

Crusafont-Pairó, M. 1950. *Limnonyx* un nuevo lútrido del Mioceno español. *Instituto Geologia y Minas de España, Notas et Comuns* 20: 129–142.

Cuvier, F.G. 1825. Panda. *In*: É. Geoffroy Saint-Hilaire and F. G. Cuvier (eds.), *Histoire Naturelle des Mammifères, avec des figures originales, coloriées, dessinées d'après des animaux vivans: publié sous l'autorité de l'administration du Muséum d'Histoire naturelle, part 3*, 3 unnumbered pp. A. Belin, Paris.

Dam, J.A. van 2003. European Neogene mammal chronology: past, present and future. *In*: J.W.F. Reumer and W.Wessels (eds.), Distribution and Migration of Tertiary Mammals in Eurasia. A Volume in Honour of Hans de Bruijn. *Deinsea* 10: 85–95.

Dawkins, W.B. 1868. Fossil animals and geology of Attica, by Albert Gaudry. *Quarterly Journal of the Geological Society of London* 24 (2): 1–7.

Dawkins, W.B. 1888. On *Ailurus anglicus*, a new carnivore from the Red Crag. *Quarterly Journal of the Geological Society of London* 44: 228–231.

Evans, A.R., Wilson, G.P., Fortelius, M., and Jernvall, J. 2007. High-level similarity of dentitions in carnivorans and rodents. *Nature* 445: 78–81.

Filhol, H. 1883. Notes sur quelques mammifères fossiles de l'époque miocène II. Observations relatives à divers carnassiers fossiles provenant de La Grive-St.-Alban (Isère). *Archives du Muséum d'Histoire Naturelle de Lyon* 3: 56–69.

Fischer von Waldheim, G. 1817. Adversaria zoologica. *Mémoires de la Société Impériale des Naturalistes de Moscou* 5: 368–428.

Flower, B.P. and Kennett, J.P. 1994. The middle Miocene climatic transition: East Antarctic ice sheet development, deep ocean circulation and global carbon cycling. *Palaeogeography, Palaeoclimatology, Palaeoecology* 108: 537–555.

Furlong, E.L. 1932. A new genus of otter from the Pliocene of the northern Great Basin province. *Carnegie Institution of Washington Publication* 418: 93–103.

Gazin, C.L. 1934. Upper Pliocene mustelids from the Snake River Basin of Idaho. *Journal of Mammalogy* 15: 137–149.

Gervais, F.L.P. 1848–1852. *Zoologie et paléontologie françaises. Nouvelles recherches sur les animaux vertébrés dont on trouve les ossements enfouis dans le sol de le France et sur leur comparaison avec les espèces propres aux autres regions du globe*. 544 pp. Arthur Bertrand, Paris.

Ginsburg, L. 1999. Order Carnivora. *In*: G.E. Rössner and K. Heissig (eds.), *The Miocene Land Mammals of Europe*, 109–148. Verlag Dr. Friedrich Pfeil, München.

Ginsburg, L. and Morales, J. 1996. *Larteticti*s et *Adroverictis*, nouveaux genres de Melinae (Mustelidae, Carnivora, Mammalia) du Miocène de l'Ancien Monde. *Bulletin du Muséum National d'Histoire Naturelle, Section C, Sciences de la Terre, Paléontologie, Géologie, Minéralogie* 18: 663–671.

Ginsburg, L., Morales, J., Soria, D., and Herraez, E. 1997. Découverte d'une forme ancestrale du Petit Panda dans le Miocène moyen de Madrid (Espagne). *Comptes Rendus de l'Academie des Sciences* 325: 447–451.

Glass, G.E. and Martin, L.D. 1978. A multivariate comparison of some extant and fossil Felidae, Carnivora. *Carnivore* 1: 80–88.

Graham, A. 1999. *Late Cretaceous and Cenozoic History of North American Vegetation North of Mexico*. 350 pp. Oxford University Press, Oxford.

Gray, J.E. 1843a. Descriptions of some new genera and species of Mammalia in the British Museum Collection. *Annals and Magazine of Natural History, Series 1* 11: 117–119.

Gray, J.E. 1843b. *List of the Specimens of Mammalia in the Collection of the British Museum*. 216 pp. British Museum (Natural History), London.

Hall, E.R. 1930. Three new genera of Mustelidae from the later Tertiary of North America. *Journal of Mammalogy* 11: 146–155.

Hall, E.R. 1935. A new mustelid genus from the Pliocene of California. *Journal of Mammalogy* 16: 137–138.

Hall, E.R. 1944. A new genus of American Pliocene badger, with remarks on the relationship of badgers of the Northern Hemisphere. *Carnegie Institution of Washington Publications* 551: 9–23.

Helbing, H. 1927. Zur definition des genus *Trochictis*. *Eclogae Geologicae Helvetiae* 20: 302–307.

Helbing, H. 1935. *Cyrnaonyx antiqua* (Blainv.), ein Lutrinae aus dem europäischen Pleistocaen. *Eclogae Geologicae Helvetiae* 27: 443–457.

Hibbard, C.W. 1941. New mammals from the Rexroad fauna, upper Pliocene of Kansas. *American Midland Naturalist* 26: 337–368.

Kaup, J.J. 1832. Vier neue Arten urweltlicher Raubthiere, welche im zoologischen Museum zu Darmstadt aufbewahrt werden. *Archiv für Mineralogie, Geognosie, Bergbau- und Hüttenkunde* 5: 150–158.

Kadić, O. and Kretzoi, N. 1927. Vorläufiger bericht über die Ausgrabungen in der Csákvárer Höhlung. *Barlangkutatás* 14–15: 1–21.

Kinzey, W.G. 1992. Dietary and dental adaptations in the Pitheciinae. *American Journal of Physical Anthropology* 88: 499–514.

Kormos, T. 1931. *Pannonictis pliocaenica*, n. gen., n. sp., a new giant mustelid from the late Pliocene of Hungary. *Annalibus Instituti Regii Hungarici Geologici* 29: 1–16.

Kundrát, M. 2011. Phenotypic and geographic diversity of the lesser red panda *Parailurus*. *In*: A.R. Glatston (ed.), *Red Panda: Biology and Conservation of the First Panda,* 43–60. Elsevier/Academic Press, Amsterdam.

Leidy, J. 1858. Notice of remains of extinct Vertebrata, from the valley of the Niobrara River, collected during the exploring expedition of 1857, in Nebraska, under the command of Lieut. G.K. Warren, U.S. Topographical Engineers, by Dr. F.V. Hayden. *Proceedings of the Academy of Natural Sciences, Philadelphia* 1858: 20–29.

Lesson, R.P. 1827. *Manuel de Mammalogie, ou Histoire Naturelle des Mammifères*. 441 pp. Roret, Paris.

Lichtenstein, H. 1827–1834. *Darstellung neuer oder wenig bekannter Säugethiere in Abbildungen und beschreibungen von fünf und sechzig arten auf funfzig colorirten steindrucktafeln nach den originalen des zoologischen museums der Universität zu Berlin* [not paginated; text page is headed "*Mustela frenata* Licht. Das gezäumte Wiesel." plus plate 42]. C.G. Lüderitz, Berlin.

Lucas, P.W. and Luke, D.A. 1984. Chewing it over: basic principles of food breakdown. *In*: D.J. Chivers, B.A. Wood, and A. Bilsborough (eds.), *Food Acquisition and Processing in Primates*, 283–301. Plenum Press, New York.

Lucas, P.W. and Teaford, M.F. 1994. Functional morphology of colobine teeth. *In*: A.G. Davies and J.F. Oates (eds.), *Colobine Monkeys: Their Ecology, Behaviour and Evolution*, 173–203. Cambridge University Press, Cambridge.

Macdonald, J.R. 1954. A new *Pseudaelurus* from the lower Snake Creek fauna of Nebraska. *Journal of Paleontology* 28: 67–99.

Major, C.I.F. 1903. New Carnivora from the middle Miocene of la Grive-Saint-Alban. *Geological Magazine* 10: 534–538.

Matthew, W.D. 1901. Fossil mammals of the Tertiary of northeastern Col-

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orado. *Memoirs of the American Museum of Natural History* 1 (7): 353–447.
Matthew, W.D. 1918. Contributions to the Snake Creek fauna with notes upon the Pleistocene of western Nebraska. *Bulletin of the American Museum of Natural History* 38: 183–229.
Matthew, W.D. 1924. Third contribution to the Snake Creek fauna. *Bulletin of the American Museum of Natural History* 50: 59–210.
Matthew, W.D. and Cook, H.J. 1909. A Pliocene fauna from western Nebraska. *Bulletin of the American Museum of Natural History* 26: 361–414.
Matthew, W.D. and Gidley, J.W. 1904. New or little known mammals from the Miocene of South Dakota. American Museum Expedition of 1903. *Bulletin of the American Museum of Natural History* 20: 241–268.
Mein, P. 1958. Les mammifères de la faune sidérolithique de Vieux-Collonges. *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon* 5: 1–122.
Meyer, H. von 1842. Mitteilungen an Professor Bronn gerichtet. *Neues Jahrbuch für Mineralogie, Geologie, Geognosie und Petrefakten-Kunde* 1842: 583–589.
Munthe, K. 1998. Canidae. *In*: C.M. Janis, K.M. Scott, and L.L. Jacobs (eds.), *Evolution of Tertiary Mammals of North America: Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals. Volume 1*, 124–173. Cambridge University Press, Cambridge.
Noble, D.C. 1972. Some observations of the Cenozoic volcanotectonic evolution of the Great Basin, western United States. *Earth and Planetary Science Letters* 17: 142–150.
Owen, P.R. 2006. Description of a new late Miocene American badger (Taxidiinae) utilizing high-resolution x-ray computed tomography. *Palaeontology* 49: 999–1011.
Peigné, S., Salesa, M.J., Antón, M., and Morales J. 2005. Ailurid carnivoran mammal *Simocyon* from the late Miocene of Spain and the systematics of the genus. *Acta Palaeontologica Polonica* 50: 219–238.
Pinel, M. 1792. Recherches sur une nouvelle méthode de classification des quadrupèdes, fondée sur la structure méchanique des parties osseuses qui servent à l'articulation de la mâchoire inférieure. *Actes de la Société d'Histoire Naturelle de Paris* 1: 50–60.
Pomel, N.-A. 1853. Catalogue méthodique et descriptif des vertébrés fossiles découverts dans les bassins de la Loire et de l'Allier. *Académie des Sciences, Belles-lettres et Arts, Clermont-Ferrand; Annales scientifiques, littéraires et industrielles de l'Auvergne* 26: 81–229.
Pilgrim, G.E. 1932. The genera *Trochictis, Enhydrictis*, and *Trocharion*, with remarks on the taxonomy of the Mustelidae. *Proceedings of the Zoological Society of London* 4: 845–867.
Qiu, Z.-X. 2003. Dispersals of Neogene carnivorans between Asia and North America. *In*: L.J. Flynn (ed.) Vertebrate Fossils and their Context: Contributions in Honor of Richard H. Tedford. *Bulletin of the American Museum of Natural History* 279: 18–31.
Ray, C.E., Anderson, E., and Webb, S.D. 1981. The Blancan carnivore *Trigonictis* (Mammalia: Mustelidae) in the eastern United States. *Brimleyana* 5: 1–36.
Riggs, E.S. 1942. Preliminary description of two lower Miocene carnivores. *Field Museum of Natural History, Geological Series* 8: 59–62.
Roman, F. and Viret, J. 1934. La faune de mammifères du Burdigalien de la Romieu (Gers). *Mémoires de la Société Géologique de France, Nouvelle Série* 21: 1–67.
Roth, J. and Wagner, A. 1854. ie fossilen Knochen-Ueberreste von Pikermi in Griechenland. *Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften, mathematisch-physikalische Klass* 7: 371–464.
Rothwell, T. 2001. A partial skeleton of *Pseudaelurus* (Carnivora: Feildae) from the Nambé Member of the Tesuque Formation, Española Basin, New Mexico. *American Museum Novitates* 3342: 1–31.
Rothwell, T. 2003. Phylogenetic systematics of North American *Pseudaelurus* (Carnivora: Felidae). *American Museum Novitates* 3403: 1–69.
Salesa, M.J., Antón, M., Peigné, S., and Morales, J. 2006. Evidence of a false thumb in a fossil carnivore clarifies the evolution of pandas. *Proceedings National Academy of Sciences of the USA* 103: 379–82.
Salesa, M.J., Antón, M., Siliceo, G., Pesquero, M.D., Morales, J., and Alcalá, L. 2013. A non-aquatic otter (Mammalia, Carnivora, Mustelidae) from the late Miocene (Vallesian, MN10) of La Roma 2 (Alfambra, Teruel, Spain): systematics and functional anatomy. *Zoological Journal of the Linnean Society* 169: 448–482.
Salesa, M.J., Peigné, S., Antón, M., and Morales, J. 2011. Evolution of the family Ailuridae: origins and Old-World fossil record. *In*: A.R. Glatston (ed.), *Red Panda: Biology and Conservation of the First Panda*, 27–41. Elsevier, Los Angeles.
Savage, D.E. and Russell, D.E. 1983. *Mammalian Paleofaunas of the World*. 432 pp. AddisonWesley, Reading.
Schlosser, M. 1899. *Parailurus anglicus* und *Urusus böckhi*, aus den Ligniten von Baróth-Köpecz, Comitat Háromszèk in Ungarn. *Mittheilungen aus dem Jahrbuch der Königlichen Ungarischen Geologischen Anstalt* 13: 66–95.
Schultz, C.B. and Martin, L.D. 1972. Two lynx-like cats from the Pliocene and Pleistocene. *Bulletin of the University of Nebraska State Museum* 9: 197–203.
Simpson, G.G. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* 85: 1–350.
Smith, C.E.H. 1842. Mammalia. Introduction to mammals. *In*: W. Jardine (ed.), *The Naturalist's Library, vol. 15*, 75–313. Chatto and Windus, London.
Smith, K.S. 2002. *Mammalian Paleontology of the Monarch Mill Formation at Eastgate, Churchill County, Nevada*. 711 pp. Ph.D. Dissertation, University of Oklahoma, Norman.
Smith, K.S., Cifelli, R.L., and Czaplewski, N.J. 2006. A new genus of eomyid rodent from the Miocene of Nevada. *Acta Palaeontologica Polonica* 51: 385–392.
Sotnikova, M.V. 2008. A new species of lesser panda *Parailurus* (Mammalia, Carnivora) from the Pliocene of Transbaikalia (Russia) and some aspects of ailurine phylogeny. *Paleontologičeskij Žurnal* 2008 (1): 92–102.
Spassov, N. and Geraads, D. 2011. A skull of *Simocyon primigenius* (Roth & Wagner, 1854) (Carnivora, Ailuridae) from the late Miocene of Karaslari (Republic of Macedonia), with remarks on the systematics and evolution of the genus. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 262: 151–161.
Stefani, C. de 1891. Sul fosfato di calce della Sardegna. *Atti della Reale Accademia Economico-Agraria dei Georgofili di Firenze* 14: 222–239.
Stewart, J.H., Sarna-Wojcicki, A., Meyer, C.E., Starratt, S.W., and Wan, E. 1999. Stratigraphy, tephrochronology, and structural setting of Miocene sedimentary rocks in the Middlegate area, west-central Nevada. *United States Geological Survey Open File Report* 99–350: 11–17.
Stock, C. 1947. A peculiar new carnivore from the Cuyama Miocene, California. *Bulletin of the Southern California Academy of Science* 46 (2): 84–89.
Swisher, C.C. 1992. *$^{40}Ar/^{39}Ar$ Dating and Its Application to the Calibration of the North American Land Mammal Ages*. 239 pp. Ph.D. Dissertation, University of California, Berkeley.
Tedford, R.H., Albright III, L.B., Barnosky, A.D., Ferrusquía-Villafranca, I., Hunt Jr., R.M., Storer, J.E., Swisher III, C.C., Voorhies, M.R., Webb, S.D., and Whistler, D.P. 2004. Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene through early Pliocene epochs). *In*: M.O. Woodburne (ed.), *Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology,* 169–231. Columbia University Press, New York.
Tedford, R.H. and Gustafson, E.P. 1977. First North American record of the extinct panda *Parailurus*. *Nature* 265: 621–623.
Tedford, R.H., Skinner, F.F., Fields, R.W., Rensberger, J.M. Whistler, D.P. Galusha, T., Taylor, B.E., Macdonald, J.R., and Webb, S.D. 1987. Faunal succession and biochronology of the Arikareean through Hemphillian interval (late Oligocene through earliest Pliocene epochs) in North America. *In*: M.O. Woodburne (ed.), *Cenozoic Mammals of North America: Geochronology and Biostratigraphy,* 153–210. University of California Press, Berkeley.
Tedford, R.H., Wang, X., and Taylor, B.E. 2009. Phylogenetic systematics

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of the North American fossil Caninae (Carnivora: Canidae). *Bulletin of the American Museum of Natural History* 325: 1–218.

Tedrow, A.R., Baskin, J.A., and Robison, S.F. 1999. An additional occurrence of *Simocyon* (Mammalia, Carnivora, Procyonidae) in North America. *In*: D.D. Gillette (ed.), *Vertebrate Paleontology in Utah. Miscellaneous Publication 99-1*, 487–493. Utah Geological Survey, Salt Lake City.

Thenius, E. 1949a. Die carnivoren von Göriach (Steiermark) Beiträge zur Kenntnis der Säugetierreste des steirischen Tertiärs IV. *Sitzungsberichte der Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Abteilung I, Biologische Wissenschaften und Erdwissenschaften* 158: 695–762.

Thenius, E. 1949b. Zur Herkunft der Simocyoniden (Canidae, Mammalia). Eine phylogenetische Studie. *Sitzungberichten der Österreichischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse Abteilungen I, Biologische Wissenschaften und Erdwissenschaften* 158: 799–810.

Thomas, O.1912. Small mammals from South America. *Annals and Magazine of Natural History* 10: 44–48.

Thorpe, M.R.1921.Two new fossil Carnivora. *American Journal of Science, ser. 5*, 1: 477–483.

Thorpe, M.R. 1922. Some Tertiary Carnivora in the Marsh Collection, with descriptions of new forms. *American Journal of Science* 3: 432–455.

Toula, F. 1884. Ueber einige säugethierreste von Göriach bei Turnau (Bruck a M. Nord) in Steiermark. *Jarhbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt* 34: 385–402.

Tseng, Z.J., Wang, X., and Stewart, J.D. 2009. A new immigrant mustelid (Carnivora, Mammalia) from the middle Miocene Temblor Formation of central California. *Paleobios* 29: 13–23.

Viret, J. 1929. *Cephalogale batalleri* carnassier du Pontien de Catalogne. *Bulletin de la Société d'Histoire Naturelle de Toulouse* 58: 567–568.

Viret, J. 1933. Contribution à l'étude des carnassiers Miocènes de la Grive-Saint-Alban (Isère). *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon* 21 (Memoire 18): 1–31.

Viret, J. 1951. Catalogue critique de la faune des mammifères miocènes de La Grive Saint-Alban (Isère). Première partie. Chiroptères, Carnivores, Édentés, Pholidotes. *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon* 3: 1–104.

Vogel, E.R., Woerden, J.T. van, Lucas, P.W., Utami Atmoko, S.S., and Schaik, C.P. 2008. Functional ecology and evolution of hominoid enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. *Journal of Human Evolution* 55: 60–74.

Wagner, A. 1858. *Geschichte der Urwelt, mit besonderer Berücksichtigungd er Menschenrassen und des mosaischen Schöpfungsberichtes.* Second edition. 528 pp. Leopold Voss, Leipzig.

Wallace, S.C. 2011. Advanced members of the Ailuridae (Lesser or Red Pandas—Subfamily Ailurinae). *In*: A.R. Glatston (ed.), *Red Panda: Biology and Conservation of the First Panda,* 43–60. Elsevier/Academic Press, Amsterdam.

Wallace, S.C. and Wang, X. 2004. Two new carnivores from an unusual late Tertiary forest biota in eastern North America. *Nature* 431: 556–559.

Wang, X. 1997. New cranial material of *Simocyon* from China, and its implications for phylogenetic relationship to the red panda (*Ailurus*). *Journal of Vertebrate Paleontology* 17: 184–198.

Wang, X., Flynn, L.J., and Fortelius, M. (eds.) 2013. *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology*. 752 pp. Columbia University Press, New York.

Wang, X., Tedford, R.H., and Taylor, B.E. 1999. Phylogenetic systematics of the Borophaginae (Carnivora: Canidae). *Bulletin of the American Museum of Natural History* 243: 1–391.

Webb, S.D. 1969a. The Burge and Minnechaduza Clarendonian mammalian faunas of north-central Nebraska. *University of California Publications in Geological Sciences* 78: 1–191.

Webb, S.D. 1969b. The Pliocene Canidae of Florida. *Bulletin of the Florida State Museum Biological Sciences* 14: 273–308.

Wegner, R.N. 1913. Tertiaer und umgelagerte Kreide bei Oppeln (Oberschlesien). *Palaeontographica Beitraege zur Naturgeschichte der Vorzeit* 60: 175–274.

Willemsen, G.F. 1992. A revision of the Pliocene and Quaternary Lutrinae from Europe. *Scripta Geologica* 101: 1–115.

Wolfe, J.A., Schorn, H.E., Forest, C.E., and Molnar, P. 1997. Paleobotanical evidence for high altitudes in Nevada during the Miocene. *Science* 276: 1672–1675.

Woodburne, M.O. 2004. Global events and the North American mammalian biochronology. *In*: M.O. Woodburne (ed.), *Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology*, 315–343. Columbia University Press, New York.

Woodburne, M.O. and Swisher, C.C. 1995. Land mammal high resolution geochronology, intercontinental overland dispersals, sea level, climate, and vicariance. *In*: W.A. Berggren, D.V. Kent, M.P. Aubry, and J. Hardenbol (eds.), *Geochronology, Time Scales and Global Stratigraphic Correlation, Volume 54*, 335–364. Society for Sedimentary Geology Special Publication, Tulsa.

Zachos, J.C., Dickens, G.R., and Zeebe, R.E. 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* 451: 279–283.

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