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Newly described specimens of leptarctine mustelids expand their geographic range in the western United States

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Cover: Dentaries of the mustelids *Leptarctus wortmani* from Nevada (UCMP 315187) and South Dakota (UCMP 29194) and *L. primus* from Nebraska (UCMP 29582)

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Newly described specimens of leptarctine mustelids expand their geographic range in the western United States

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Leptarctus is a morphologically distinctive carnivoran mammal occurring in Miocene deposits of North America and East Asia. In North America *Leptarctus* is mostly known from the Great Plains and Florida, but a single occurrence in China and recent description of well-preserved specimens in Oregon indicate that the western North American distribution of the genus is understudied. Here I document previously unreported specimens of *Leptarctus* and review other leptarctines housed in the collections of the University of California Museum of Paleontology (UCMP). Dental materials of at least four species of *Leptarctus* are present in the UCMP collections, encompassing occurrences from the Barstovian to Hemphillian North American Land Mammal Ages, adding to known records in the Great Plains, and expanding the paleogeographic range of *L. wortmani* into Nevada. Materials representing the genus in California are fragmentary but confirm the presence of *L. wortmani* in the Black Hawk Ranch locality in the coastal ranges of northern California, and *L. ancipidens* in the Cajon Valley in the southern Great Basin region of southern California.

Keywords: Neogene, Mammalia, Carnivora, California, Nevada, Oregon

INTRODUCTION

Leptarctus Leidy, 1856 is a morphologically distinctive taxon of mustelid carnivoran found in Neogene deposits of North America and from a single occurrence in Asia. Its bunodont dentition which resembles that of hypocarnivores such as procyonids (ringtails and raccoons) is combined with uniquely well-developed parasagittal crests unmatched by extant carnivorans exhibiting dual crests such as badgers and gray foxes. These characteristics contributed to much uncertainty in reconstructions of the ecological niche occupied by *Leptarctus*, with interpretations ranging from herbivore, carnivore, to omnivore, and possibly arboreal (Lim et al. 2001; Lim and Martin 2003; Korth and Baskin 2009; Prybyla et al. 2018). The taxonomic history of the genus is similarly unresolved, with around 15 species recognized in recent treatments (Baskin 2005; Bever and Zakrzewski 2009; Korth and Baskin 2009). The fossil record of *Leptarctus* in North America spans the Hemingfordian North American Land Mammal Age (NALMA) to the Hemphillian NALMA. For most of this temporal range their geographic distribution spans western North America as far west as the Basin and Range and/or Coastal provinces, to the Gulf coast in Florida (Fig. 1).

With the goal of adding new morphological and occurrence data towards painting a fuller picture of this lineage, in this report I review dental and jaw materials referrable to leptarctines housed in the University of California Museum of Paleontology. The studied localities are concentrated in the western U.S. and the Great Plains (Fig. 1, Table 1). Two specific objectives are to (1) provide high-resolution 3D models for further research use into this interesting taxon, and (2) update the paleozoogeographic distribution of the genus *Leptarctus* in the states of California and Nevada.

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MATERIALS AND METHODS

All specimens were digitized using micro-computed tomography on a GE Phoenix Nanotom M system (Waygate Technologies, Pennsylvania, USA). Voxel resolution ranged from 16 to 40 microns depending on specimen size (smaller specimens were imaged with smaller voxel sizes). Scanning voltage ranged from 100-135 kV and current ranged from 95-350 mA to achieve reasonable X-ray penetration patterns. The resulting projection images were reconstructed using Phoenix Datos reconstruction software (Waygate Technologies, Pennsylvania, USA) into 16-bit TIFF image stacks. The image stacks were then imported into 3D Slicer (Fedorov et al. 2012) and a segmentation for each specimen scan generated using automatic thresholding in the 'segment editor' module. The segmentation was then converted to a 3D mesh and exported as an *.stl file. The mesh file was further processed in Geomagic Wrap 2020 (Hexagon AB, Stockholm, Sweden), where all mesh models were aligned to a single global axis system. The anteroposterior axis was aligned with the x axis, lateral direction with y axis, and dorsoventral direction with the z axis, respectively. Two-dimensional images of specimen layouts were exported from Geomagic Wrap as *.png files for generating figures, and measurements were taken digitally on the mesh models to the nearest 0.01 mm. 3D PDFs of specimens discussed in this study are available to view and download via FigShare (10.6084/m9.figshare.29199431); 3D mesh files are also available on MorphoSource (Table 1).

Institutional Abbreviations—AMNH: American Museum of Natural History, New York, New York; **ANSP:** Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania; **CM:** Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; **F:AM**: Frick Fossil

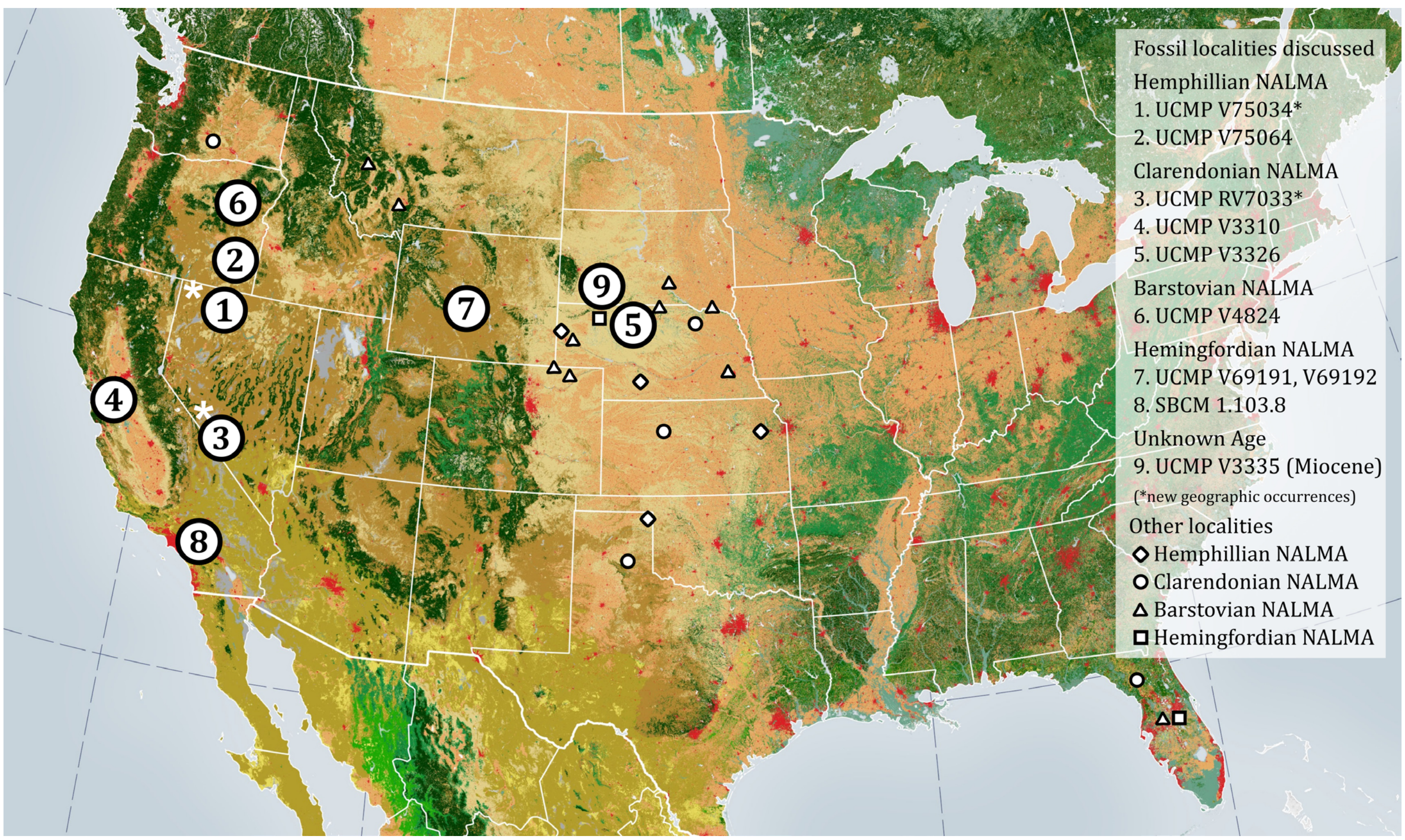

Figure 1. Fossil localities of leptarctine genera discussed in this study. Localities from which specific specimens are described are numbered; all other localities are indicated by geological age only. Abbreviations: **NALMA**, North American Land Mammal Age; **RV**, locality prefix for the former UC-Riverside collection now in the University of California Museum of Paleontology; **SBCM**, San Bernardino County Museum; **UCMP**, the University of California Museum of Paleontology; **V**, prefix for vertebrate localities in the University of California Museum of Paleontology collections. Satellite image from NASA Earth Observatory Program. Locality information retrieved from New and Old Worlds Database of fossil mammals (https://nowdatabase.org/).

Mammal Collection of the AMNH; **LACM (CIT)**: Natural History Museum of Los Angeles County specimens and localities formerly at the California Institute of Technology, Los Angeles, California; **SBCM**: San Bernadino County Museum, Redlands, California; **UCMP**: University of California Museum of Paleontology, Berkeley, California; **UF,** Vertebrate Paleontology Collection, Florida Museum of Natural History, University of Florida, Gainesville, Florida; **UNSM**, University of Nebraska State Museum, Lincoln, Nebraska.

Anatomical Abbreviations—c: lower canine; **d**: deciduous tooth; **m**: lower molar; **p**: lower premolar (upper case for upper premolar); **PAC**: posterior accessory cusp.

SYSTEMATIC PALEONTOLOGY

CARNIVORA Bowdich, 1821
MUSTELIDAE Fischer von Waldheim, 1817
LEPTARCTINAE Gazin, 1936
LEPTARCTUS Leidy, 1856
LEPTARCTUS OREGONENSIS Stock, 1930
Figs. 2A, O, & Z; Table 2

Leptarctus primus Leidy 1856, p. 311; Matthew, 1924, p. 139, figs. 37-38.
Leptarctus oregonensis Stock 1930; Stock 1930, Pl. I, fig. 1a-b, text figs 1-2.
Leptarctus oregonensis Stock 1930; Downs 1956, p. 239, fig. 13.
Leptarctus oregonensis Stock 1930; Olsen 1957, p. 2, fig. 2A.
Leptarctus oregonensis Stock 1930; Baskin 1998, p. 158.
Leptarctus primus Leidy 1856 (in part); Lim and Martin 2001, p. 636.
Leptarctus primus Leidy 1856 (in part); Lim et al. 2001, p. 1044, fig. 1.
Leptarctus primus Leidy 1856 (in part); Lim and Martin 2002, p. 271, fig. 2B.
Leptarctus oregonensis Stock 1930; Baskin 2005, p. 431.
Leptarctus oregonensis Stock 1930; Korth and Baskin 2009, p. 29.
Leptarctus oregonensis Stock 1930; Calede et al. 2018, figs 1-6.
Leptarctus oregonensis Stock 1930; Baskin 2020, p. 223.

Holotype—LACM (CIT) 206, maxillary fragment with left P4-M1, right P4, and several cranial fragments.

Referred Specimen—UCMP 39102, right P4.

Occurrence of Referred Specimen—UCMP Locality V4824 (UCMP 39102; Mascall 10, Mascall Formation, Grant County, Oregon, Barstovian NALMA). Maguire et al. (2018) placed locality V4824 in the upper unit of the Mascall Formation, below the "Kangaroo Tuff Bed" which has been dated at 13.564 ± 0.08 Ma.

Table 1. Locality data and Morphosource links for specimens described here. Abbreviations: NALMA, North American Land Mammal Age; p, lower premolar; P, upper premolar; R, right side; RV, locality prefix for the former UC Riverside collection now in UCMP; V, prefix for UCMP vertebrate locality.

UCMP spec. no.	Taxon	NALMA	Locality	Locality Name	County	State	Morphosource ARK id
39102	*L. oregonensis*	Barstovian	V4824	Mascall 10	Grant	OR	https://n2t.net/ark:/87602/m4/772229
29582	*L. primus*	Clarendonian	V3326	Little Beaver B	Cherry	NE	https://n2t.net/ark:/87602/m4/772221
95978	*L. wortmani*	Clarendonian	V3310	Black Hawk Ranch	Contra Costa	CA	https://n2t.net/ark:/87602/m4/772232
95979	*L. wortmani*	Clarendonian	V3310	Black Hawk Ranch	Contra Costa	CA	https://n2t.net/ark:/87602/m4/772241
29194	*L. wortmani*	Clarendonian	V3335	Lake Creek 1	Bennett	SD	https://n2t.net/ark:/87602/m4/772220
315187	*L. wortmani*	Clarendonian	RV7033	Fish Lake Valley 14	Esmeralda	NV	https://n2t.net/ark:/87602/m4/772262
113571	*L. wortmani*	Hemphillian	V75034	Bog Hot Springs E1	Humboldt	NV	https://n2t.net/ark:/87602/m4/772243
114136	*L. wortmani*	Hemphillian	V75064	Rome Beds	Malheur	OR	https://n2t.net/ark:/87602/m4/772250
162501	cf. *Craterogale*	Hemingfordian	V69192	First Bench	Fremont	WY	https://n2t.net/ark:/87602/m4/772251
163795	cf. *Craterogale*	Hemingfordian	V69191	Second Bench	Fremont	WY	https://n2t.net/ark:/87602/m4/772261

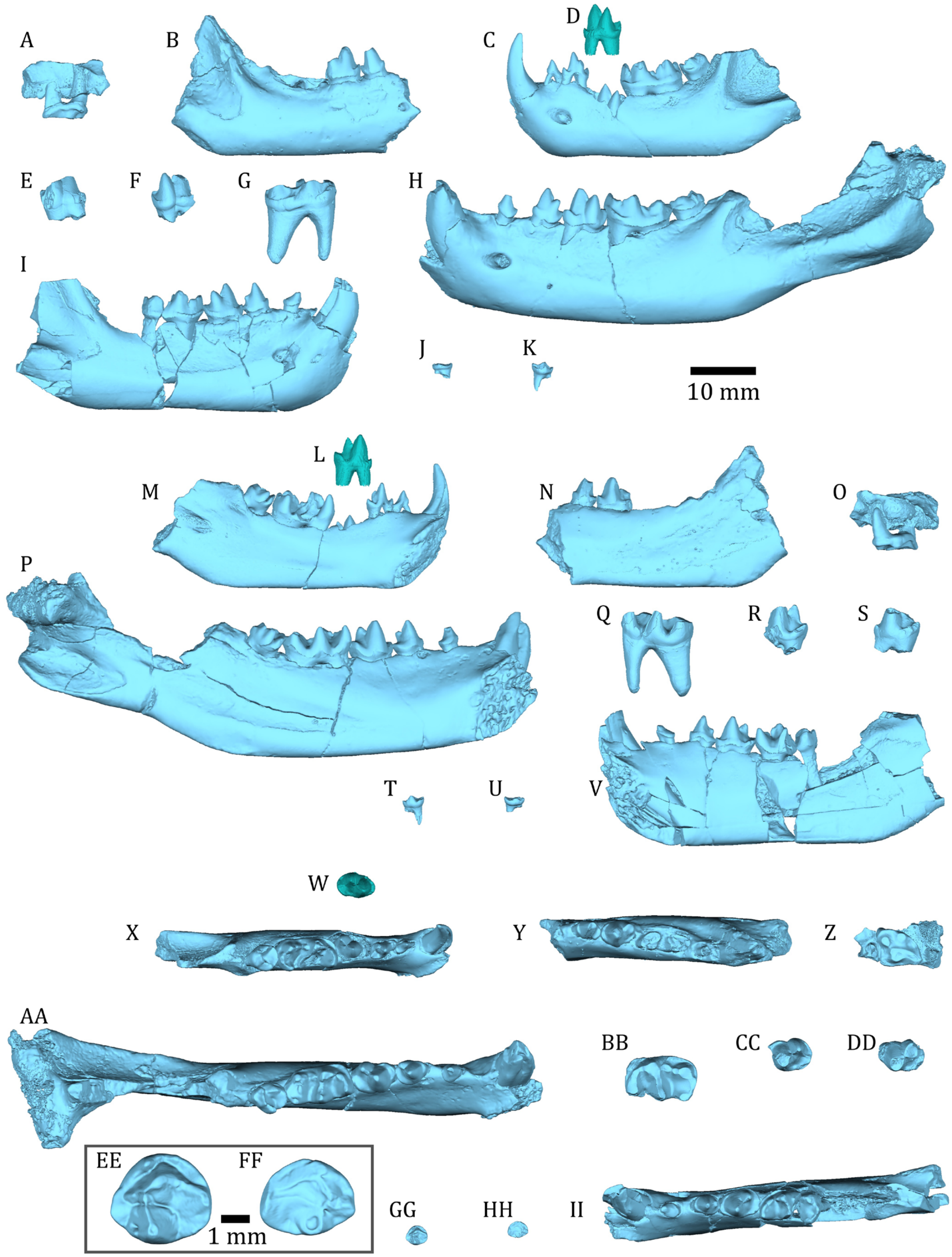

Figure 2A–II. Leptarctines described in this study. *Leptarctus oregonensis*: UCMP 39102, right upper fourth premolar, in lateral (**A**), medial (**O**), and occlusal (**Z**) views. *Leptarctus primus*: UCMP 29582, dentary fragment with right third and fourth premolars, in lateral (**B**), medial (**N**), and occlusal (**Y**) views. *Leptarctus wortmani*: UCMP 29194, left dentary with deciduous canine to second molar, in lateral (**C**), medial (**M**), and occlusal (**X**) views, with digitally segmented erupting fourth premolar in lateral (**D**), medial (**L**), and occlusal (**W**) views; UCMP 95978, right lower fourth premolar, in lateral (**E**), medial (**S**), and occlusal (**DD**) views; UCMP 95979, right lower fourth premolar, in lateral (**F**), medial (**R**), and occlusal (**CC**) views; UCMP 113571, lower right first molar, in lateral (**G**), medial (**Q**), and occlusal (**BB**) views; UCMP 114136, left dentary with lower canine to first molar, in lateral (**H**), medial (**P**), and occlusal (**AA**) views; UCMP 315187, right dentary with canine to first molar, in lateral (**I**), medial (**V**), and occlusal (**II**) views. cf. *Leptarctus*: UCMP 162501, right lower second molar, in lateral (**J**), medial (**U**), occlusal (**HH**), and enlarged occlusal (**FF**) views; UCMP 163795, left lower second molar, in lateral (**K**), medial (**T**), occlusal (**GG**), and enlarged occlusal (**EE**) views.

Description—The referred specimen was identified and illustrated in Downs (1956) and reviewed along with other specimens of *L. oregonensis* from the Mascall Formation by Calede et al. (2018). Maquire et al. (2018) listed the occurrence of *L. oregonensis* in the Mascall Formation as both lower (John Day National Monument locality 71, 262) and middle stratigraphic unit (UCMP V4824)(Maguire et al., 2018:Table 2). However, the stratigraphic positions for *L. oregonensis* localities included in their stratigraphic framework (Maguire et al., 2018: Fig. 2) indicate the taxon's occurrence in the middle and upper units, but not the lower unit. Based on available information in that study, it is unclear whether any of the remaining localities in which *L. oregonensis* occur are assignable to the lower unit of the Mascall Formation. Therefore, the lower age bound of the taxon in the Mascall Formation is interpreted here to be the base of the middle unit in the "Mascall Tuff Bed" (15.122 ± 0.017 Ma)(Maguire et al. 2018). Baskin (1998, 2020) referred *L. primus* (Matthew 1924) from the early Barstovian Olcott Formation to *L. oregonensis*. No additional information is provided in this study, other than to provide high-resolution 3D model and images of UCMP 39102.

LEPTARCTUS PRIMUS Leidy, 1856

Figs. 2B, N, Y; Table 2

Leptarctus primus Webb 1969, p. 69.
Hypsoparia bozemanensis Dorr 1954, p. 179; Baskin 1998, p. 158.
Hypsoparia timmi Lim and Martin 2002, p. 272; Korth and Baskin, 2009, p. 41.

Holotype—ANSP 11293, left P4.

Referred Specimen—UCMP 29582, right dentary fragment with p3-p4 and alveoli of m1-m2.

Occurrence of Referred Specimen—UCMP Locality V3326 (Little Beaver B, Caprock Member, Ash Hollow Formation, Cherry County, Nebraska, early Clarendonian NALMA (Skinner and Johnson 1984)). Collected by R.A. Stirton in 1933.

Description—The dentary fragment is broken anteriorly at the position of the p2 (the posterior alveolus of p2 is visible). The anterior face of the fragment preserves the posterior wall of the canine alveolus, which has a diameter of approximately 8.8 mm. There is a single, moderately sized mental foramen on the lateral side of the ramus. Two moderately worn teeth, p3 and p4, are preserved. The p3 is a single-cusped tooth with thin anterior and posterior basal cingulids. The p4 has a robust main cuspid and a labially offset posterior accessory cuspid (PAC); the PAC is roughly half the height of the main cuspid. There are low anterior and postero-lingual cingulids. The m1 and m2 positions are marked by double-rooted alveoli; the m2 alveoli sit on a slope marking the base of the ascending ramus. The remainder of the ascending ramus is broken posterior to the mandibular foramen on the medial side of the ramus; the mandibular foramen is slightly larger in diameter than the mental foramen.

Remarks—The morphology of both p3 and p4 in UCMP 29582 compares favorably with those of CM 9574 in Dorr (1954) (the holotype of *Hypsoparia bozemanensis* Dorr 1954, subsequently subsumed under *Leptarctus primus* by Korth and Baskin, 2009) in the delicate cingulids on p3-p4, absence of accessory cusps on p3, and a slightly offset PAC on p4. One of the two neotypes of *L. primus* designated by Matthew (1924), a partial lower right dentary (AMNH 18270), is assigned to *L. oregonensis* by Baskin (2020) and is thus not comparable to UCMP 29582 as *L. primus*.

LEPTARCTUS WORTMANI Matthew, 1924

Figs. 2C-I, M-L, P-S, V-X, AA-DD, II; Table 2

Leptarctus primus Leidy 1856; Wortman 1894, p. 229.
Leptarctus wortmani Matthew 1924, p. 142.
Leptarctus primus Webb 1969, p. 69.
Leptarctus (Pseudoleptarctus) genowaysi Lim and Martin 2003, p. 17; Baskin 2005, p. 425.
Leptarctus kansasensis Lim and Martin 2001, p. 634; Baskin 2005, p.426.

Holotype—AMNH 2575, right dentary fragment with canine, p3-p4.

Referred Specimens—UCMP 29194, collected by R.A. Stirton in 1933, left partial dentary with complete mandibular symphysis, canine, dp2-dp3, p4-m2, and rostral portion of ascending ramus; UCMP 95978, collected by C.T. Williams in 1971, isolated right p4 with worn cuspids; UCMP 95979, isolated right p4 with broken distal edge; UCMP 113571, collected by L. Kent in 1969, isolated right m1 with worn cuspids; UCMP 114136, collected by J. Faulhaber and C.A. Repenning in 1973, partial skeleton with mandible preserving partial right and left canines, partial right m1, complete left cheek dentition from p2-m2; UCMP 315187, collected by P. Robinson in 1970, right dentary with partial canine, p2-m1, and coronoid process and condyloid process fragments, respectively.

Occurrence of Referred Specimens—UCMP Locality V3335 (UCMP 29194; Lake Creek 1, Bennett County, South Dakota, likely part of the Ogallala Group, or

Miocene in age, based on R.A. Stirton's description of the locality as being "7 miles south of Martin near the head waters of Lake Creek on the Less Fairhead ranch" and updated geological map of South Dakota ([UCMP Archives, "R.A. Stirton 1933 Nebraska Expedition", accessed 8 September 2025]; Martin et al. 2004), V3310 (UCMP 95978, 95979; Black Hawk Ranch, Green Valley Formation, Contra Costa County, California, Clarendonian NALMA; MacDonald 1948), RV7033 (UCMP 315187; Fish Lake Valley 14, Esmeralda Formation, Esmeralda County, Nevada, Clarendonian NALMA; see Kelly et al. 2020), V75034 (UCMP 113571; Bog Hot Springs E1, Thousand Creek Formation, Humboldt County, Nevada, Hemphillian NALMA; Prothero and Davis 2008), V75064 (UCMP 114136; Line Shack 1, Rome Beds, Malheur County, Oregon, Hemphillian NALMA; Campion 1979).

Description—Dental materials of *Leptarctus wortmani* are by far the most common specimens of *Leptarctus* in the UCMP, represented by four partial dentaries from three individuals and also three isolated teeth. UCMP 29194 represents a sub-adult individual, with a complete left deciduous canine exhibiting a deep longitudinal groove on its medial face. UCMP 29194 also preserves intact dp2 and dp3: the former tooth is single-cusped with no anterior cingulid but a heel with a low posterior cingulid; the latter tooth has a main cuspid with a posterior accessory cuspid halfway up the posterior slope of the main cuspid, and both anterior and posterior cingula each with a cusp-like central tip which sits on a straight line drawn through the main cuspid. An erupting p4 shows a strong main cuspid with a laterally offset posterior accessory cupid that is only slightly smaller than the main cuspid. The p4 was digitally extracted from the alveolus to facilitate its study, and the resulting 3D model shows the presence of strong anterior and posterior cingulids, with a longitudinal ridge leading from the posterior accessory cuspid to the cingular cuspid. The m1 is nearly complete, missing only the region at and around the metaconid; the carnassial cuspids are all around the same height, with the paraconid being the largest cuspid and situated laterally across the anterior border of the tooth. The protoconid is slightly shorter than the paraconid; the two cuspids meet in the anterolabial corner of the tooth, which has a low but distinct basal cingulid. Equally sized hypoconid and entoconid sit across from each other in the medio-lateral axis, and together with a slightly lower and broader hypoconulid form a c-shaped wall on the posterior and lateral edges of the talonid basin. A strong hypoflexid is present between the protoconid and hypoconid, to the extent that the ridges almost form two small cuspids on either side of the trigonid-talonid junction, respectively. The m2 is oval-shaped and double-rooted. The m2 paraconid is positioned horizontally across the width of the tooth as in m1, and a relatively small protoconid is located on the antero-labial edge of the tooth, bracketed by a low cingular shelf similar to the

Table 2. Dental measurements of leptarctine mustelids described here. Abbreviations: c, lower canine; d, deciduous tooth; L, length; m, lower molar; p, lower premolar; P, upper premolar; W, width. All measurements are in mm.

Specimen	c L	c W	p2 L	p2 W	p3 L	p3 W	p4 L	p4 W	m1 L	m1 W	m2 L	m2 W
L. primus												
UCMP 29582					3.84	2.99	5.24	4.37				
L. wortmani												
UCMP 95978							7.36	5.12				
UCMP 95979							6.75	5.42				
UCMP 29194	4.74(d)	3.73(d)	2.82(d)	1.61(d)	4.76(d)	2.61(d)	6.34	4.19	9.89	5.13	4.62	4.35
UCMP 315187	6.44	5.23	2.84	2.44	4.17	3.12	6.79	4.69	10.06	5.45		
UCMP 113571									11.12	7.22		
UCMP 114136	6.11	5.31	3.09	2.91	4.69	3.87	7.22	4.82	11.07	5.54	5.79	5.05
cf. *Craterogale*												
UCMP 162501											3.27	2.68
UCMP 163795											3.54	3.15
L. oregonensis							**P4 L**	**P4 W**				
UCMP 39102							7.34	6.03				

morphology seen in the m1. The m2 metaconid is similar in size to the protoconid and sits directly medial to it. The talonid is reduced to a single laterally-direct cingulid with a hint of two fused cuspids; the trigonid and talonid together enclose a central basin.

UCMP 95978 is a double-rooted partial right p4. Both anterior and posterior cingulids are present; the main cuspid is roughly the same size at the base as a laterally offset posterior accessory cuspid. The cuspids are worn, and the two occlusal surfaces are connected into a figure-eight enamel surface tilting towards the postero-labial edge of the tooth. UCMP 95979 is another partial right p4 from the same locality as UCMP 95978, and both preserve similar morphological features. The main differences in UCMP 95978 are a broken anterior portion of the tooth that obscures the cingulid, and a slightly worn main cuspid and an unworn posterior accessory cuspid indicating the full height of the PAC (6.7 mm) and a main cuspid that would be higher than ~8 mm when unworn.

UCMP 113571 is an isolated right m1 in an advanced stage of tooth wear. The paraconid, protoconid, and metaconid are worn into a C-shaped dentine ridge opening towards the lingual side. The hypoconid, hypoconulid, and entoconid are similarly worn into a C-shaped ridge, but with the opening facing the trigonid instead. A strong hypoflexid connects the trigonid and talonid.

UCMP 114136 is a partial skeleton of *Leptarctus wortmani* whose description is beyond the scope of this paper. Only the mandibular portion of the specimen is presented here for the sake of completeness in the documentation of craniodental materials of *Leptarctus* in the UCMP. The canines are broken near the base of the crown, but nevertheless preserve evidence of prominent lingual grooves. The p2 is single-rooted and single-cusped, with a moderate posterior heel that is expanded in the postero-lingual corner of the tooth. On both sides of the mandible there are diastemata both anterior and posterior to the p2 (p2 alveolus for the right side), with the anterior diastema being twice the length of the posterior one. The p3 is a two-cusped tooth with weak anterior and posterior cingulids; the main cuspid is twice the height of the postero-labially situated posterior accessory cusp. The morphology of the p4, m1 and m2 in UCMP 114136 is consistent with those described above for UCMP 29194, 95978, 95979, and 113571.

UCMP 315187 is the right dentary of an adult individual (all preserved teeth are permanent dentition) with unworn cusp crowns. The morphology of the c1, p2-p4, and m1 are consistent with those described above for other specimens. A noticeable feature of this specimen is the slender p3 and p4 posterior accessory cuspids, which are relatively smaller and less laterally offset from the main cuspid compared to other specimens referred to *L. wortmani* in this report.

Remarks—The referred specimens of *Leptarctus wortmani* compare favorably to F:AM 49412 and UNSM 25470, specimens previously assigned to *Pseudoleptarctus genowaysi* by Lim and Martin (2003) and subsequently synonymized with *L. wortmani* by Korth and Baskin (2009). A main component of variation within the UCMP sample of *L. wortmani* includes larger overall size and better development and more lateral displacement of posterior accessory cusps on p3 and p4 in Hemphillian specimens compared to Clarendonian ones.

Macdonald (1948) illustrated UCMP 33708, a right p4, from Black Hawk Ranch and attributed it to Procyoninae. The specimen was referred to *Leptarctus wortmani* by Wagner and Reynolds (1983) and to *L. webbi* by Baskin (2005). In an attempt to re-study this material, I located UCMP 33708 in the collections. However, the specimen associated with that number is an upper P4 that should be referred to *Sthenictis* (Tseng and Wang, 2025); it is not the same specimen illustrated in Macdonald (1948). As far as I can tell, the illustrated specimen is actually UCMP 95978, which is referred to in this report as *L. wortmani* along with UCMP 95979. These two specimens are the only two dental specimens of *Leptarctus* identified from the Black Hawk Ranch collections.

cf. *Craterogale* Gazin, 1936

Figs. 2J, K, T, U, EE, FF, GG, HH; Table 2

cf. *Leptarctus* Munthe 1979, p.36.

cf. *Leptarctus* Munthe 1988, p.12.

Referred Specimens—UCMP 162501, right m2, collected by J. and K. Munthe in 1972; 163795, left m2, collected by J.H. Hutchison in 1970.

Occurrence—UCMP Locality V69191 (UCMP 163795; Second Bench locality of the Split Rock local fauna (Munthe 1979), Split Rock Formation, Fremont County, Wyoming, Hemingfordian NALMA (Tedford et. al. 2004), V69192 (UCMP 162501; First Bench, Split Rock Formation, Fremont County, Wyoming, Hemingfordian NALMA (Tedford et al. 2004)).

Description – Both m2 specimens possess a diagonally oriented paraconid connected to a laterally situated protoconid by a ridge. The metaconid is large and located postero-lingually relative to the protoconid. The trigonid cuspids collectively form a C-shaped ridge that opens lingually. A strong antero-labial cingulid is present, and the talonid is reduced to a cingular shelf that forms two low cingular cuspids at the posterior and posterolabial edges of the tooth, respectively. Both specimens are double-rooted.

Remarks – The Hemingfordian age of the two m2 specimens makes them among the early occurrences of the subfamily Leptarctinae, preceded by Arikareean *Craterogale* from the Belgrade Formation in North Carolina (MacFadden et al. 2025), early Hemingfordian *Leptarctus* and *Craterogale* from the Miller and Thomas Farm local faunas in Florida, and the fauna of the Runningwater Formation in Nebraska (Baskin 2017). The stratigraphically oldest species of *Leptarctus, L. ancipidens*, was originally described by White (1941) based on a palate with right and left P2-M1 (MCZ 3659; White 1941: pl. XIV, fig. 1), and therefore cannot be directly compared to the two referred specimens. Therefore, the referred specimens were compared to *L. ancipidens* UF 225236, lower left dentary with p3-m2 form Thomas Farm, Florida. Although the trigonid in UF 225236 is very similar in morphology to UCMP 163795 and 162501, the talonid in the Florida specimen is a broader, more flattened shelf rather than a cingular shelf as in the UCMP specimens. The overall size of the UCMP specimens falls within the range of the stratigraphically younger *L. oregonensis* (Baskin, 2020), and both the UCMP specimens and *L. oregonensis* are smaller than *L. ancipidens*. No m2 is known for *Craterogale*, but tooth lengths estimated from m2 alveoli by Baskin (2017) range from 3.2 mm (UF 246363) to 3.8 mm (AMNH 25348), which completely overlap with the referred UCMP specimens 162501 (3.27 mm) and 163795 (3.54 mm). On the other hand, m2 lengths reported for contemporaneous *Leptarctus ancipidens* range from 4.8 to 5.6 mm (Baskin, 2017), larger than the two specimens studied. Beside *Leptarctus* and *Craterogale,* the only other neomustelid with double-rooted m2 is *Miomustela*, which is much smaller in size compared to the leptarctines discussed herein (Hall 1930). Given these suggestive but inconclusive lines of evidence, in particular the matching size range of m2 alveolar lengths in *Craterogale* to the two UCMP specimens, I tentatively assign these two specimens to cf. *Craterogale*. Additional material (especially teeth) from the Split Rock Formation is needed to identify these specimens more confidently.

DISCUSSION

This review of specimens of *Leptarctus* in the UCMP provides two insights for paleozoogeography of the genus: (1) two species, *L. wortmani* (Wagner and Reynolds 1983; this study) and *L. ancipidens* (Wagner and Reynolds 1983; Fig. 2), are confidently known from dental materials in California, and (2) *L. wortmani* occurred in Nevada in both Clarendonian and Hemphillian NALMAs (this study). Of the species recorded from the western United States, *L. oregonensis* is known from more northern localities in Oregon and Nebraska (Calede et al. 2018; Baskin 2020; Figs. 1,2). *Leptarctus ancipidens* are well-represented at the Thomas Farm locality in Florida, but otherwise rare elsewhere in North America (Olsen 1957; Wagner and Reynolds 1983; Baskin 2017). Finally, with two new occurrences in Nevada reported here, *L. wortmani* is now known from mid-latitude localities in California, Nevada, Nebraska, and Kansas (Wagner and Reynolds 1983; Baskin 2005; this study).

Together with a single occurrence of the genus outside of North America, in the middle Miocene Tunggur Formation of Inner Mongolia, China (Zhai 1964), this report reinforces the interpretation that *Leptarctus* experienced little to no barrier to dispersal across much of the North American continent. Therefore, the limits to their geographical distribution may instead lie in competitive exclusion by potentially similarly-sized hypocarnivorous procyonids along the gulf coast (Baskin, 2003). Borophagine canids such as *Cynarctoides* or smaller species of *Cynarctus* are also possible competitors, although the broad geographic distribution of both leptarctines and hypocarnivorous borophagine canids across the Great Plains and Great Basin would suggest potential niche partitioning on a community level rather than wholesale geographic exclusion (Wang et al. 1999; Baskin, 2003). Finally, one must consider the possibility of leptarctines tracking distribution of preferred prey such as mylagaulids, as noted by Calede and Samuels (2020). I concur with the assessment of Bever and Zakrzewski (2009) that a phylogenetic analysis of *Leptarctus* is necessary in order to test this and other hypotheses about paleoecological and functional morphological evolutionary trends in this fascinating lineage of carnivorans.

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LITERATURE CITED

Baskin, J. A. 1998. Mustelidae; pp. 152–173 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. Cambridge University Press, Cambridge.

Baskin, J.A. 2003. Chapter 6: New Procyonines from the Hemingfordian and Barstovian of the Gulf Coast and Nevada, Including the First Fossil Record of the Potosini. *Bulletin of the American Museum of Natural History* 279:125–146.

Baskin, J. A. 2005. Carnivora from the late Miocene Love bone bed of Florida. *Bulletin of the Florida Museum of Natural History* 45:413–434.

Baskin, J. A. 2017. Additional carnivorans from the early Hemingfordian Miller Local Fauna, Florida, *Journal of Vertebrate Paleontology* 37(2). doi: 10.1080/02724634.2017.1293069.

Baskin, J. A. 2020. Mustelidae from Observation Quarry (Early Barstovian) of Nebraska, with comments on Sheep Creek and Lower Snake Creek mustelids. *Paludicola* 12:223–246.

Bever, G., and R. Zakrzewski. 2009. A new species of the Miocene leptarctine *Leptarctus* (Canivora: Mustelidae) from the early Hemphillian of Kansas. Papers on Geology, Vertebrate Paleontology, and Biostratigraphy in Honor of Michael O. Woodburne: *Museum of Northern Arizona Bulletin* 65:465–481.

Bowdich, T. E. 1821. An Analysis of the Natural Classifications of Mammalia, for the Use of Students and Travellers. 180 pp.

Calede, J. J., W. A. Kehl, and E. B. Davis. 2018. Craniodental morphology and diet of *Leptarctus oregonensis* (Mammalia, Carnivora, Mustelidae) from the Mascall Formation (Miocene) of central Oregon. *Journal of Paleontology* 92:289–304.

Calede, J. J. M., and J. X. Samuels. 2020. A new species of *Ceratogaulus* from Nebraska and the evolution of nasal horns in Mylagaulidae (Mammalia, Rodentia, Aplodontioidea). *Journal of Systematic Palaeontology* 18(17):1395–1414. https://doi.org/10.1080/14772019.2020.1765889

Campion, K.M. 1979. Diagenetic alteration and formation of authigenic minerals in the Miocene "Rome Beds," southeast Oregon. PhD dissertation, Ohio State University, 197 p.

Dorr Jr., J. A. 1954. *Hypsoparia bozemanensis*: a new genus and species of leptarctine mustelid from the late Miocene Madison Valley Formation of Montana. *Annals of Carnegie Museum* 33:179–184.

Downs, T. 1956. The Mascall fauna from the Miocene of Oregon. *University of California Publications in Geological Sciences* 31:199–354.

Fedorov, A., R. Beichel, J. Kalpathy-Cramer, J. Finet, J.-C. Fillion-Robin, S. Pujol, C. Bauer, D. Jennings, F. Fennessy, M. Sonka, J. Buatti, S. Aylward, J. V Miller, S. Pieper, and R. Kikinis. 2012. 3D Slicer as an image computing platform for the Quantitative Imaging Network. *Magnetic Resonance Imaging* 30:1323–1341.

Fischer von Waldheim, G. 1817. Adversaria zoologica. *Memoires de La Societe Imperiale Des Naturalistes de Moscou* 5:357–472.

Gazin, C. L. 1936. A new mustelid carnivore from the Neocene beds of Northwestern Nebraska. *Journal of the Washington Academy of Sciences* 26:199–207.

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

Kelly, T. S., R. A. Martin, and C. Ronez. 2020. New records of cricetid rodents from the medial Clarendonian (middle Miocene) Esmeralda Formation, Fish Lake Valley, Nevada. *Paludicola* 13:1–32.

Korth, W. W., and J. A. Baskin. 2009. A new species of *Leptarctus* (Carnivora, Mustelidae) from the late Clarendonian (late Miocene) of Kansas. *Annals of Carnegie Museum* 78:29–44.

Leidy, J. 1856. Notices of Extinct Vertebrata Discovered by Dr. F. V. Hayden, during the Expedition to the Sioux Country under the Command of Lieut. G. K. Warren. *Proceedings of the Academy of Natural Sciences of Philadelphia* 8:311–312.

Lim, J.-D., and L. D. Martin. 2001. A new species of *Leptarctus* (Mustelidae) from the Miocene of Kansas, USA. *Neues Jahrbuch Für Geologie Und Paläontologie-Monatshefte* 10:633–640.

Lim, J.-D., and L. Martin. 2002. A new fossil mustelid from the Miocene of South Dakota, USA. *Naturwissenschaften* 89:270–274.

Lim, J.-D., and L. D. Martin. 2003. New subgenus of leptarctine (Carnivora: Mustelidae) from the late Miocene of Nebraska, USA. *Proceedings of the Biological Society of Washington* 116:16–22.

Lim, J.-D., L. D. Martin, and R. W. Wilson. 2001. A new species of *Leptarctus* (Carnivora, Mustelidae) from the late Miocene of Texas. *Journal of Paleontology* 75:1043–1046.

Macdonald, J. R. 1948. The Pliocene carnivores of the Black Hawk Ranch fauna. *University of California Publications in Geological Sciences* 28:53–80.

Maguire, K. C., J. X. Samuels, and M.D. Schmitz. 2018. The fauna and chronostratigraphy of the middle Miocene Mascall type area, John Day Basin, Oregon, USA. *PaleoBios* 35. http://dx.doi.org/10.5070/P9351037578

MacFadden, B.J., D.J. Bohaska, L. Cone, S.R. Killingsworth, S.P. Zbinden, J. Pirlo, S.M. Moran, J. Baskin, and V.J. Perez. 2025. Early Miocene land mammals and chronology of the Belgrade Formation, eastern North Carolina. *Journal of Paleontology*, 1-21. https://doi.org/10.1017/jpa.2024.68

Martin, J.E., J.F. Sawyer, M.D. Fahrenbach, D.W. Tomhave, and L.D. Schulz. 2004. Geologic map of South Dakota. *South Dakota Geological Survey*, General Map G-10.

Matthew, W. D. 1924. Third Contribution to the Snake Creek Fauna. *Bulletin of the American Museum of Natural History* 50:59–210.

Munthe, J. 1979. Summary of Miocene vertebrate fossils of the Granite Mountains Basin, central Wyoming. *Rocky Mountain Geology* 18(1):33–46.

Munthe, J. 1988. Miocene mammals of the Split Rock area, Granite Mountains basin, central Wyoming. *University of California Publications in Geological Sciences* 126:1–136.

Olsen, S. J. 1957. Leptarctines from the Florida Miocene (Carnivora, Mustelidae). *American Museum Novitates* 1861:1–7.

Prothero, D.R. and E.B. Davis. 2008. Magnetic stratigraphy of the upper Miocene (early Hemphillian) Thousand Creek Formation, northwestern Nevada. *New Mexico Museum of Natural History and Science Bulletin* 44:233–237.

Prybyla, A. N., Z. J. Tseng, and J. J. Flynn. 2018. Biomechanical simulations of *Leptarctus primus* (Leptarctinae, Carnivora), and new evidence for a badger-like feeding capability. *Journal of Vertebrate Paleontology* 38:e1531290.

Skinner, M.F. and F.W. Johnson. 1984. Tertiary stratigraphy and the Frick Collection of fossil vertebrates from north-central Nebraska. *Bulletin of the American Museum of Natural History* 178(3):215–368.

Stock, C. 1930. Carnivora new to the Mascall Miocene fauna of eastern Oregon. *Carnegie Institution of Washington Publication* 404:43–48.

Tedford, R., Albright, L., Barnosky, A., Ferrusquia-Villafranca, I., Hunt, R., Storer, J., Swisher, C., Voorhies, M., Webb, S. and Whistler, D. 2004. Chapter 6. Mammalian Biochronology of the Arikareean Through Hemphillian Interval (Late Oligocene Through Early Pliocene Epochs). *In:* Woodburne, M. ed. *Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology*. Columbia University Press, New York. pp. 169-231. https://doi.org/10.7312/wood13040-008

Tseng Z. J. and X. W. Wang. 2025, in press. Late Miocene immigrant carnivorans in California, USA highlight a coastal corridor for intercontinental dispersals. *Vertebrate PalAsiatica* DOI: 10.19615/j.cnki.2096-9899.250813

Wagner, H. M., and R. E. Reynolds. 1983. *Leptarctus ancipidens* (White)(Carnivora: Mammalia) from the Punchbowl Formation, Cajon Pass, California. *Bulletin, Southern California Academy of Sciences* 82:131–137.

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

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

White, T. E. 1941. Additions to the Miocene fauna of Florida. *Proceedings of the New England Zoological Club* 18:91–98.

Wortman, J. 1894. On the affinities of *Leptarctus primus*. *Bulletin of the American Museum of Natural History* 6:229–231.

Zhai, R. J. 1964. *Leptarctus* and other Carnivora from the Tung Gur Formation, Inner Mongolia. *Vertebrata PalAsiatica* 8:27–30.