New evidence for plant-eating in a Miocene mustelid

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A new species of *Leptarctus* is described on the basis of a partial skull from the North American Miocene. The new species, *Leptarctus desui*1,2, has typical leptarctine characteristics, including heavy zygomatic arches, well-developed hypocones on the fourth upper premolars, wide muzzle and broad skull. The third upper premolar differs from those of other known *Leptarctus* in having double cusps and a cingulum on the lingual side. Cranial and dental morphology suggests that *Leptarctus* had a less carnivorous diet than any other mustelid.

*LEPTARCTUS* is one of the rarest of the known fossil carnivores. The genus ranges through the Miocene of North America and Inner Mongolia1,2. Characters diagnosing *Leptarctus* as a mustelid include absence of M3 and absence of the notch between the blades of the upper carnassial. Though *Leptarctus* is a mustelid, the teeth bear many similarities to the teeth of the procyonids, *Procyon lotor* and *Nasua nasua*3. Unlike other mustelids, *Leptarctus* has prominent double sagittal crests, heavy zygomatic arches, a prominent occipital crest, a well-developed hypocone on P3, grooved lower canines, raccoon-like mandibles and unique bony projections on the tympanic bullae. Its unusual anatomy invites comparison with a unique herbivorous marsupial, the koala bear. Geologically, species of *Leptarctus* range from the basal Hemingfordian (Early Miocene) to the top of the Hemphillian (Late Miocene).

Systematic paleontology

Class Mammalia Linnaeus, 1758
Order Carnivora Bowdich, 1821
Family Mustelidae Fischer von Waldheim, 1817
Subfamily Leptarctinae Gazin, 1936
Genus *Leptarctus* Leidy, 1856
*Leptarctus desui* sp. nov.

Holotype: BHI (Black Hills Institute of Geological Research) 1571 (Figure 1), an anterior portion of skull with left P3–M3, right P3–M3.

Type locality: Carlson Quarry, SW1/4, Sec. 14, T. 1N, R. 32W, Hitchcock County, Nebraska, USA.

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References


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Geologic formation and age: Republican River Beds, 
Early Hemphillian, Late Miocene.

Etymology: Named after Desui Miao, who is one of our 
best mammalian paleontologists.

Diagnosis: The skull and dentition are larger than Leptarctus primus; 
alveolus for the canine is round and 
enlarged; P^2 is round and thicker at the base, with a 
prominent posterior cingulum; P^3 has double cusps and 
round ridges at both anterior and posterior faces; P^3 has a 
well-developed parastyle, a sharp paracone and a well-

described hypocone; M^1 is longer than wide; diastemata 
is between canine and P^2 and between P^2 and P^3; enlarged 
nasal opening; postorbital process of frontal is prominent 
and robust; muzzle is wide; infraorbital foramen is big 
and round.

Description: The incomplete skull preserves the anterior 
portion of the zygomatic arch. The deep zygomatic arch 
is typical of leptarctines. The zygomatic arch is thick 
(7.2 mm at the postorbital process while that of L. primus 
(KUVP, University of Kansas Natural History Museum, 
Vertebrate Paleontology, 9153) is 4.5 mm. The robust 
skull is much larger than those in L. primus and L. martini. 
The nasal opening is unusually enlarged and the 
infraorbital foramen is the largest among Leptarctus spe-
cies. The superior portion of the maxilla is depressed for 
muscle attachment. The postorbital processes are well-
developed, which is a synapomorphy for Leptarctus.

The overall construction of the upper dentition is more 
similar to L. primus than to other species. The maxillary 
Tooth row, canine to M^1 distance, is the longest among 
Leptarctus species (Table 1). The alveolus for the upper 
ocanine is large. The width is 6.9 mm, while in L. martini 
(UNSM, University of Nebraska State Museum, Verte-
brate Paleontology, 20843) and L. ancipidens (UF, Uni-
v 
g 
v
v


cmv
r


Figure 1. Leptarctus desuii (BHI 1571); dorsal view and ventral 
view.

Table 1. Comparative measurements (in mm) of upper dentition of L. desuii and other Leptarctus

<table>
<thead>
<tr>
<th></th>
<th>L. desuii (BHI 1571)</th>
<th>L. primus (KUVP 9153)</th>
<th>L. ancipidens (UF 5706)</th>
<th>L. martini (UNSM 20843)</th>
</tr>
</thead>
<tbody>
<tr>
<td>P^2: length</td>
<td>3.4</td>
<td>3.4</td>
<td>4.0</td>
<td>3.9</td>
</tr>
<tr>
<td>P^2: width</td>
<td>3.5</td>
<td>2.6</td>
<td>2.2</td>
<td>2.9</td>
</tr>
<tr>
<td>P^3: length</td>
<td>6.6</td>
<td>4.1</td>
<td>5.0</td>
<td>5.4</td>
</tr>
<tr>
<td>P^3: width</td>
<td>5.4</td>
<td>3.8</td>
<td>3.9</td>
<td>4.8</td>
</tr>
<tr>
<td>P^4: length</td>
<td>9.1</td>
<td>7.9</td>
<td>9.0</td>
<td>8.8</td>
</tr>
<tr>
<td>P^4: width</td>
<td>8.2</td>
<td>7.7</td>
<td>7.0</td>
<td>9.5</td>
</tr>
<tr>
<td>M^1: length</td>
<td>10.1</td>
<td>8.3</td>
<td>8.0</td>
<td>8.9</td>
</tr>
<tr>
<td>M^1: width</td>
<td>9.1</td>
<td>7.2</td>
<td>8.6</td>
<td>10.2</td>
</tr>
<tr>
<td>M^1 ratio: length/width</td>
<td>1.11</td>
<td>1.15</td>
<td>0.93</td>
<td>0.87</td>
</tr>
<tr>
<td>Tooth row (C–M^1)</td>
<td>41</td>
<td>28.2</td>
<td>38.2</td>
<td>33.6</td>
</tr>
</tbody>
</table>
cone is enormously enlarged. The blade between paracone and metacone is not very sharp-edged. The anterior edge of P₄ is shorter than the posterior one. The fourth premolar is similar to that of L. primus, while the molar is more elongated than in other species of Leptarctus. The labial side is longer than the lingual side. The major cusps on the M¹ are prominent and the protocone forms an elevated ridge. The metacone is as high as the protocone. The postero-lingual corner to M¹ forms a strong edge.

L. desuii is much larger and more robust than L. primus and L. martini. The distance between left M¹ and right M¹ in L. desuii is 38.8 mm and that of L. primus (KUVP 9153) is 33.2 mm.

The infraorbital foramen is round and the nasal opening is at least 1.5 times larger than that of L. primus (KUVP 9153). The maximum diameter within the nasal opening of L. desuii is 21.4 mm and that of L. primus (KUVP 9153) is 11.3 mm.

The presence of a cingulum and double cusps on P³ distinguishes it from other known Leptarctus. The double-cusped P³ is only found in this skull; living mustelids and procyonids do not have this feature. Ursus americanus (KUMA, University of Kansas Natural History Museum, Mammalogy 151981) has a double-cusped P³, but the second cusp is present posteriorly. The second cusp of P³ in L. desuii is located on the lingual side of the main cusp. Pteropus rodricensis (KUMA 146855), a fruit-eating bat, has a similar P³ to that of L. desuii. The size of P³ is the largest among Leptarctus species.

In P⁴, the paracone is the highest cusp and the hypocone is well-developed as in L. primus. The general shape of P² is more similar to that of L. primus than other Leptarctus. However, the hypocone of L. desuii is more enlarged than its protocone and there is a separation between these two cusps.

The first molar has a strong ridge lingually. The tooth is much longer than wide (Table 1), while L. ancipidens and L. martini have wider molars.

The skull has large depressions anterior to and slightly below the orbits, while those of L. primus (KUVP 9153) are not as deep and clear as in L. desuii. The depressions are the areas for attachment of the levator nasi that moves the nose. Unlike other leptarctines, the skull has an enlarged fossa for the origin of the masseter superficialis. The double-cusped P³, the molariformed P⁴ and enlarged chewing muscle indicate this mustelid had a diet requiring more efficient chewing than extant mustelids, and that chewing forces were more increased anteriorly.

**Figure 2.** Occlusal view of leptarctine teeth (upper right, scale bar equals 1 cm). a, L. desuii (BHI 1571): P°–M¹; b, L. martini (UNSM 20843): P°–M¹; and c, L. ancipidens (UF 5706): P°–M¹.

**Figure 3.** Comparison of the first molar of Ursus americanus and the fourth upper right premolar of other carnivores. a, Canis latrans (KUMA 2154): Coyote; b, Martes pennanti (KUMA 23066): Fisher; c, Taxidea taxus (KUMA 89194): American badger; d, Procyon lotor (KUMA 2099): Common raccoon; e, Ursus americanus (KUMA 151981): American black bear (M¹); and f, Leptarctus desuii (BHI 1571).
In Carnivora, the upper carnassial blade (between paracone and metacone in the last upper premolar) is indicative of diet. *Canis latrans* has sharp upper carnassial blades for a carnivorous diet, while *Ursus americanus* (M1) and *Procyon lotor* (P3) have a crushing surface for an omnivorous diet (Figure 3). In *P. lotor*, the hypocone of the P4 is expanded posteriorly, making the surface of occlusion larger (Figure 3). A well-developed hypocone on the P4 is a characteristic of *Procyon* and *Nasua*. The enlarged molariform surface of P4 in *L. desuii* suggests an omnivorous diet, with a strong plant component. Olsen considered *Leptarctus ancipidens* as a badger-like mustelid. However, the lower dentition of *L. ancipidens* (UF 5655) shows it differs from that of *Taxidea taxus* and is more similar to *P. lotor*. The first lower molar of *L. ancipidens* has a relatively long talonid, similar to that of *P. lotor*, while the talonid and the trigonid of the first lower molar in *T. taxus* are of similar length. This increased length of the talonid in *Leptarctus* and *Procyon* indicates that the anterior part of the first upper molar, which is occluded with the talonid, is also increased in its surface area. The dental similarity is regarded as convergence resulting from adaptation to a similar diet. The diet of *P. lotor* includes frogs, fish, birds, eggs, fruits, nuts, insects and small rodents. The teeth of *L. desuii* indicate that it was even more herbivorous and bear-like. This raises the question of the overall lifestyle of leptartines. We suggest that they were not badger-like, but more closely resembled the arboreal procyonids or even the bear-like marsupial, the koala, thereby describing a new niche for mustelids.


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