

Figure 3. Developmental lethality in *stm A^{PEL}* alleles.

reported to produce complex rearrangements by random and often imprecise rejoining of breaks at or near P excision sites¹⁰. The absence of chromosomal rearrangements suggests that our P lines do not carry multiple inserts.

stm A is a developmentally interesting gene with mutant alleles affecting behaviour, embryonic neurogenesis and susceptibility to neuropoisons⁵⁻⁷. In this report on a study of P excision lethals derived from two independent P insertion alleles of *stm A*, it has been demonstrated that (i) *stm A* function is needed throughout development, (ii) homozygous viable ts paralytic alleles of *stm A* are not simple hypomorphs, but are very likely semi-dominant neomorphs, and (iii) not all lethal *stm A* alleles show embryonic neural hypertrophy. In this post-genomic sequence era, it is imperative to characterize *stm A* at the molecular level, to learn what the genetic limits of *stm A* are, what are its products and their effects on fly development. The *stm A^{P1}* and *stm A^{P4}* lines are being used for isolating genomic DNA flanking the P insert, by inverse PCR or by conversion of the Birm-2 insert to a lacZ plasmid rescuable enhancer trap line by targetted transposition¹¹.

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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 desuii*, 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 Mongolia^{1,2}. Characters diagnosing *Leptarctus* as a mustelid include absence of M² 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 P⁴, 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 Bowditch, 1821

Family Mustelidae Fischer von Waldheim, 1817

Subfamily Leptarctinae Gazin, 1936

Genus *Leptarctus* Leidy, 1856

Leptarctus desuii sp. nov.

Holotype: BHI (Black Hills Institute of Geological Research) 1571 (Figure 1), an anterior portion of skull with left P²-M¹, right P³-M².

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

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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; P² is round and thicker at the base, with a prominent posterior cingulum; P³ has double cusps and round ridges at both anterior and posterior faces; P⁴ has a well-developed parastyle, a sharp paracone and a well-

developed hypocone; M¹ is longer than wide; diastemata is between canine and P² and between P² and P³; 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* species. 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 M¹ distance, is the longest among *Leptarctus* species (Table 1). The alveolus for the upper canine is large. The width is 6.9 mm, while in *L. martini* (UNSM, University of Nebraska State Museum, Vertebrate Paleontology, 20843) and *L. ancipidens* (UF, University of Florida Natural History Museum, Vertebrate Paleontology, 5706), canine width is 4.8 mm and 4.4 mm respectively.

Two diastemata are present, one between canine and P² and the second between P² and P³ (Figure 2). The former is longer (4.8 mm) than the latter (2.5 mm). This is reversed compared to other known *Leptarctus*. The P² is very thick with a cingulum on the postero-lingual face. It is different from that of *L. martini* in having a sharp cusp and a posterior cingulum. In P³, an accessory cusp is present at the lingual side of the main cusp (Figure 2). This second cusp is almost as large as the main cusp. The anterior cingulum is on the lingual side. The second cusp divides the two cingula. The shape of the tooth is roundly triangular in form. The parastyle on the P⁴ are well-defined and the protocone is sharp at the tip. The hypo-



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*

	<i>L. desuii</i> (BHI 1571)	<i>L. primus</i> (KUVP 9153)	<i>L. ancipidens</i> (UF 5706)	<i>L. martini</i> (UNSM 20843)
P ² ; length	3.4	3.4	4.0	3.9
P ² ; width	3.5	2.6	2.2	2.9
P ³ ; length	6.6	4.1	5.0	5.4
P ³ ; width	5.4	3.8	3.9	4.8
P ⁴ ; length	9.1	7.9	9.0	8.8
P ⁴ ; width	8.2	7.7	7.0	9.5
M ¹ ; length	10.1	8.3	8.0	8.9
M ¹ ; width	9.1	7.2	8.6	10.2
M ¹ ratio: length/width	1.11	1.15	0.93	0.87
Tooth row (C-M ¹)	41	28.2	38.2	33.6

cone is enormously enlarged. The blade between paracone and metacone is not very sharp-edged. The anterior edge of P^4 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 M^1 are prominent and the protocone forms an elevated ridge. The metacone is as high as the protocone. The postero-lingual corner to M^1 forms a strong edge.

L. desuii is much larger and more robust than *L. primus* and *L. martini*. The distance between left M^1 and right M^1 in *L. desuii* is 38.8 mm and that of *L. primus* (KUV 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* (KUV 9153). The maximum diameter within the nasal opening of *L. desuii* is 21.4 mm and that of *L. primus* (KUV 9153) is 11.3 mm.

The presence of a cingulum and double cusps on P^3 distinguishes it from other known *Leptarctus*. The double-cusped P^3 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 P^4 , but the second cusp is present posteriorly. The second cusp of P^3 in *L. desuii* is located on the lingual side of the main cusp. *Pteropus rodricensis* (KUMA 146855), a fruit-eating bat,

has a similar P^3 to that of *L. desuii*. The size of P^3 is the largest among *Leptarctus* species.

In P^4 , the paracone is the highest cusp and the hypocone is well-developed as in *L. primus*. The general shape of P^4 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* (KUV 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 P^3 , the molariformed P^4 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.

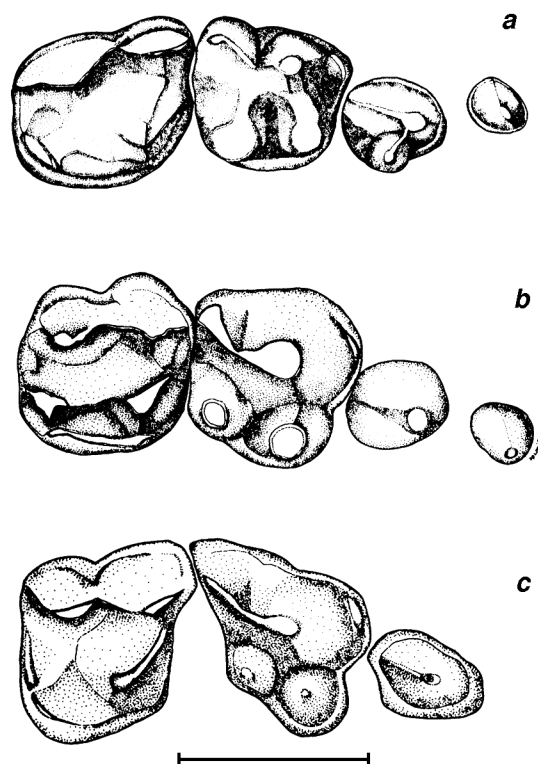
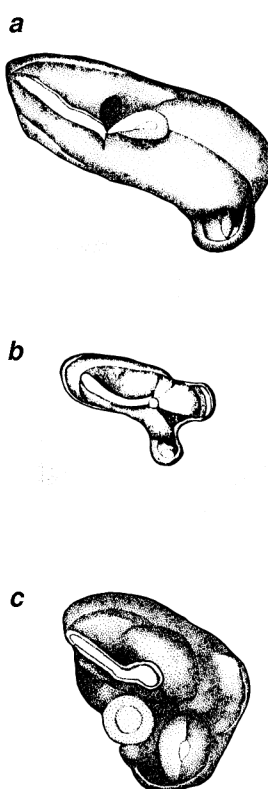


Figure 2. Occlusal view of leptarctine teeth (upper right, scale bar equals 1 cm). *a*, *L. desuii* (BHI 1571): P^2 - M^1 ; *b*, *L. martini* (UNSM 20843): P^2 - M^1 ; and *c*, *L. ancipidens* (UF 5706): P^3 - M^1 .

Carnivorous diet



Omnivorous diet

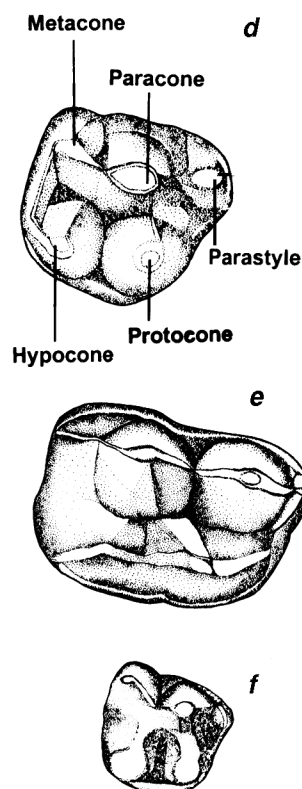


Figure 3. Comparison of the first molar of *Ursus americanus* and the fourth upper right premolar of other carnivores. *a*, *Canis latrans* (KUMA 2154): Coyote; *b*, *Martes pennanti* (KUMA 23066): Fisher; *c*, *Taxidea taxus* (KUMA 89194): American badger; *d*, *Procyon lotor* (KUMA 2099): Common raccoon; *e*, *Ursus americanus* (KUMA 151981): American black bear (M^1); 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* (P⁴) 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*⁴. The enlarged molariform surface of P⁴ in *L. desuii* suggests an omnivorous diet, with a strong plant component. Olsen⁵ 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*³. 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 leptarctines. 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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