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A new miniature saber-toothed nimravid from the Oligocene of Nebraska

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The Eusmilini are miniature saber-toothed cats that usually did not exceed the size of a bobcat, *Lynx rufus.* They occur in both Europe and North America, although North America contains the more primitive form. In spite of their small size, their cranial specializations approximate those of *Barbourofelis.* A new genus and species, *Nanosmilus kurteni,* is described from the Oligocene of Nebraska.

1. Introduction

The saber-toothed adaptation has been independently acquired at least four times by mammalian carnivores (nimravids, felids, creodonts, and marsupials). The function of saber-teeth has been surprisingly controversial. Bohlin (1940) considered them tools for scavenging and Hough (1950) restricted them to courtship battles between males. Saber-toothed carnivores have been used as examples of overspecialization leading to extinction, but most workers have considered saber-toothed carnivores to have been active and successful predators. Differences of opinion exist on how the canines were used. Martin (1980a) favored a throat bite as did Kurtén (1952), while Akersten (1985) indicates that they attacked the stomach. Most functional arguments have been made on giant taxa like *Smilodon* (Akersten 1985) and *Barbourofelis* (Martin 1980a).

Barbourofelis was the most remarkable saber-toothed carnivore known. Only the marsupial saber-tooth *Thylacosmilus* rivals it in unusual adaptations and in many respects their adaptations are similar.

Both *Barbourofelis* and *Thylacosmilus* are short-legged, plantigrade animals with large heads and long saber-like canines. They both have vertical occiputs; postorbital bars on the skull, and large dependent flanges on the rami. They were geological contemporaries as both occurred in the late Miocene with one in North America and the other in South America. The upper canines of *Barbourofelis* are bladed and about 21 cm long. The lower jaw has developed an immense dependent flange to receive the sabers. The whole skull has been remodeled to permit the jaw rotation (115°) required to clear the sabers for use. The upper canines are grooved, the incisors are prognathic and posteriorly recurved and the carnassials are among the most enlarged and specialized sectoral teeth known. The postcranial skeleton is also unusual with very short limbs (the tibia of *B. fricki* is shorter than the upper canine) and plantigrade feet. The endocranial casts indicate a relatively small brain with enlarged olfactory lobes.

It seems likely that *Barbourofelis fricki,* a lion-sized animal, was the top predator in the late Miocene savanna community of North America. On the other hand, some species of eusmilin cats were no larger than a large modern domestic cat. This suggests a very different position in the trophic structure of the community.

The Eusmilini are probably not phylogenetically close to the Barbourofelini and *Eusmilus* was already extinct before the earliest known occurrence of a barbourofelin. The earliest North American eusmilin is lower-middle Oligocene (Orellan) in age. The youngest is late Oligocene. All known eusmilins are small (Bryant 1984) and range in size from that of large domestic cats, *Felis catus,* to large bobcats, *Lynx rufus.* Cranially they share with *Barbourofelis* a number of features of skull shape, carnassial enlargement, and premolar reduction. Also, like *Barbourofelis* there is development of an enormous flange on the ramus. Because of their small size, some of the scenario's suggested for the origin of these structures in larger predators may not be applicable to *Eusmilus.* In that sense, *Eusmilus is* a unique subject for examination of the sabertooth adaptation.

The taxonomy of saber-toothed carnivores has been addressed in a number of papers (Martin 1980a, Tedford 1978, Baskin 1981, Flynn & Galiano 1982, Hunt 1987). There is general agreement that the Barbourofelini are distant from modern felids, as are the other nimravids.

The two families Felidae and Nimravidae may be further subdivided into subfamilies. I recognize three for the Nimravidae: Nimravinae, Hoplophoneinae and Barbourofelinae. The ossified auditory bulla and grooved upper canines (Schultz et al. 1970) readily distinguish the Barbourofelinae from all other nimravids.

The Eusmilini including *Nanosmilus* new species but excluding *"Eusmilus" sicaris* Sinclair & Jepson and *"E." dakotensis* Hatcher can be distinguished from other Hoplophoneinae by advanced dental features including the presence of a distinct parastyle on P^4 and the reduction of the talonid of M_1 to a small basal projection. The Eusmilini do not elevate the apex of the occiput as do other hoplophonine carnivorans, but the latter feature is almost certainly primitive and also found in the Nimravinae.

The geographic distribution of the Eusmilini and the Barbourofelini is similar, with contemporaneous populations of *Eusmilus* in Europe and the western United States. This distribution implies the existence of Holarctic populations at the latitude of Beringia. At some point portions of these population reached middle latitudes and evolved in some degree of isolation. This is certainly the case with the Barbourofelini where the European and North American members have had very different evolutionary histories.

I have recently completed a review of almost all of the known material of eusmilin cats, both in Europe and North America. Because the genus was first described from Europe there is a tendency to think of it as a European genus. However, it has a long record in North America. The new form described in this paper from Nebraska is the most primitive known member of the tribe.

2. Systematic description

Order **Carnivora** Bowdich, 1821

Suborder **Feliformia** Kretzoi, 1945

Superfamily **Aeluroidea** Flower, 1869

Family **Nimravidae** Cope, 1881

Subfamily **Hoplophoneinae** Kretzoi, 1929

Tribe **Eusmilini** Ginsburg, 1979

Included genera: *Eusmilus* and *Nanosmilus* gen. n.

Diagnosis: Dirk-toothed carnivores with a parastyle on P^4; talonid nearly absent on M_1; cranium nearly horizontal with low saggital and occipital crests; shortened nasals and a very anteriorly placed posterior palatal foramen.

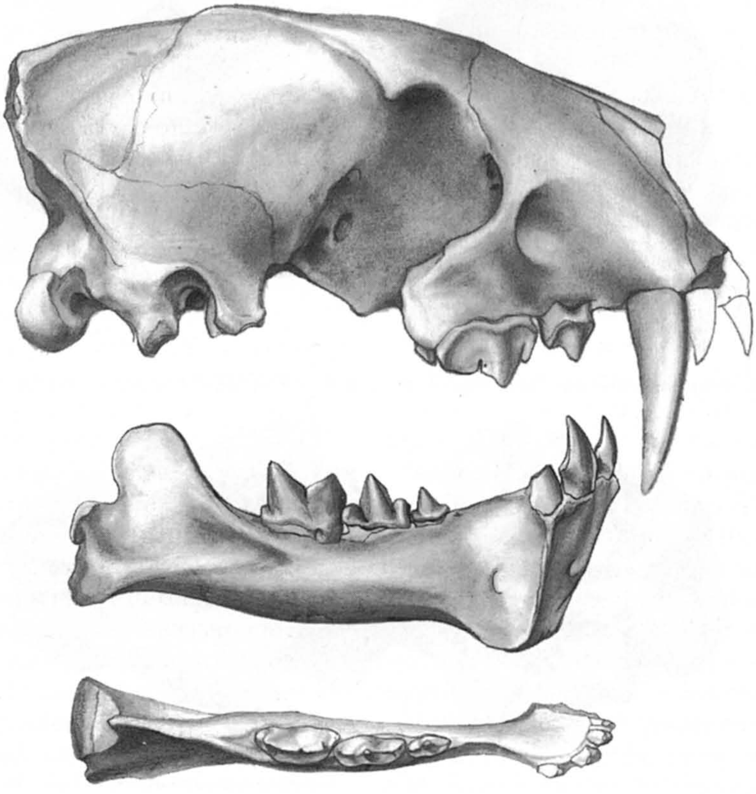

Fig. 1 *Nanosmilus kurteni*, holotype, UNSM 25505. From top to bottom: skull, lateral view; right ramus, lateral view(partly restored from left side), and dorsal view. Natural size.

Nanosmilus gen. n.

Type species: *Nanosmilus kurteni* sp. n.

Distribution: Lower Oligocene (Orellan) of Nebraska, U.S.A.

Etymology: Greek *nanos* = dwarf and *smile* = carving knife.

Nanosmilus kurteni sp. n.

Figs. 1–3.

Holotype: University of Nebraska State Museum (UNSM) 25505, skull and mandible (Figs. 1–3).

Type location and horizon: UNSM Collecting Locality SX–17 in Sec. 8, T 33 N., R 53 W., 11 1/2 miles north and 8 3/4 miles west of Crawford, Sioux County, Ne-

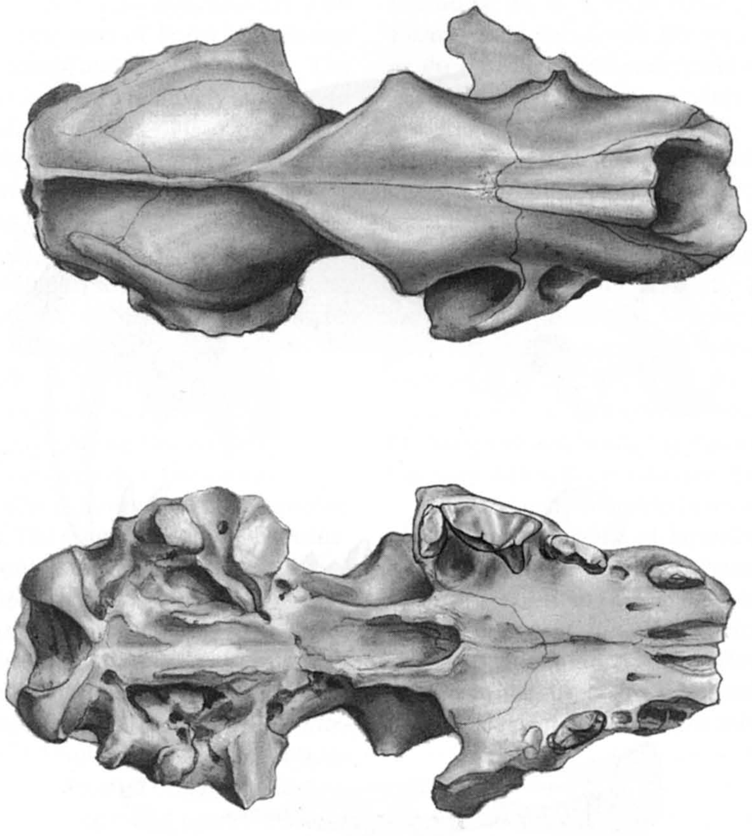

Fig. 2. *Nanosmilus kurteni*, holotype, UNSM 25505. From top to bottom: skull, dorsal and ventral views. Natural size.

braska. From the Orella Member of the Brule Formation, White River Group, Oligocene.

Description: About the size of a small bobcat *(Lynx rufus);* skull narrow (broad in *Eusmilus);* saggital crest separating into a "V" above the glenoid facet (diverging anterior to the glenoid facets in *Eusmilus* and *Hoplophoneus);* apex of the occipital crest about level with the frontals (much higher in *Hoplophoneus);* frontals not broadened as much as in either *Hoplophoneus* or *Eusmilus;* posterior margin of nasals nearly even with the frontal-maxillary sutures as in *Eusmilus;* premaxillaries terminating posteriorly above the posterior edge of the canine (resembling North Arnerican species of *Eusmilus* in this respect), *Hoplophoneus* has a more elongated premaxillary terminating well posterior to the canine; orbits large; infraorbital canal large and roofed by only a slender bone bar; the incisive foramina extend from the front to the back of the canine alveoli;

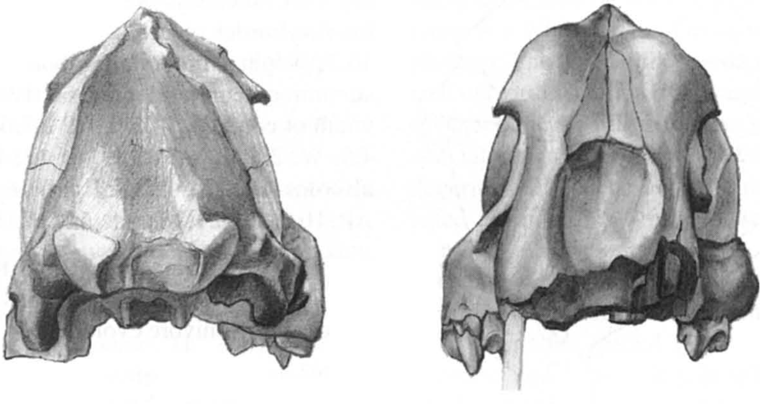

Fig. 3. *Nanosmilus kurteni*, holotype UNSM 25505. From left to right: skull, posterior and anterior views. Natural size.

groove for posterior palatal foramina across from posterior margin of incisive foramina, with the foramen across from P^2; internal narial opening across from anterior margin of M^1; deep embrasure pit anterior to M^1 and extending forward to about the carnassial notch on P^4; anterior margin of premaxillaries missing along with the incisors and incisor alveoli; canine long and slender; P^1 not present; P^2 alveolous single rooted; P^3 large and double rooted, small protocone, paracone tilted posteriorly, distinct notch between paracone and metacone, metacone bladed as in the carnassial; carnassial with a distinct parastyle, protocone reduced but supported by a root, carnassial notch about at middle of tooth; carnassial notch shallow and narrow; M^1 reduced and tilted with an "amphicone" and low protocone; glenoid fossa even with the "gum line" and the ventral border of the paramastoid process (even with the carnassial crown in *Eusmilus);* paramastoid process long and paraoccipital process reduced; optic foramen and orbital fissure separate (in a common opening in *Eusmilus);* foramen rotundum small and located in the posterior ventral margin of the orbital fissure; alisphenoid canal present; foramen ovale opens anteroventrally; postglenoid foramen large; posterior lacerate and condyloid foramina separate and carotid foramen ("inferior petrosal sinus") present.

Ramus with a very small dependent flange, with a single small anterior foramen; single mental foramen on the lateral side of the flange; diastema a thin ridge; deep masseteric fossa with a forward projection under the M_1; coronoid short and rounded; angular process reduced and turned medially; I_1 very reduced; I_{2-3} pointed and posteriorly recurved; lower canine similar to incisors; P_{1-2} not present; P_3 double rooted with two cusps; P_4 overlapping the antero-lateral margin of M_1, cusps compressed; carnassial with a narrow carnassial notch, protoconid of M_1 higher than paraconid, very small metaconid present on M_1; M_2 absent.

Measurements: Skull and jaws, U.N.S.M. 25505; Anterior posterior lengths (AP), widths (W); all measurements are in millimeters. — Skull measurements: length from posterior end of canine alveolus to posterior margin of condyles, 108.5; length from posterior end of glenoid fossa to posterior end of the condyles, 35.6; minimum width between superior borders of orbits, 26.8; width across postorbital processes, 33.8; minimum width of postorbital constriction 19.2; minimum anterior palatal width between superior canines, 17.3; width between posterior ends of alveoli for superior carnassials, 43.1; maximum width across paramastoid processes, 44; maxi-

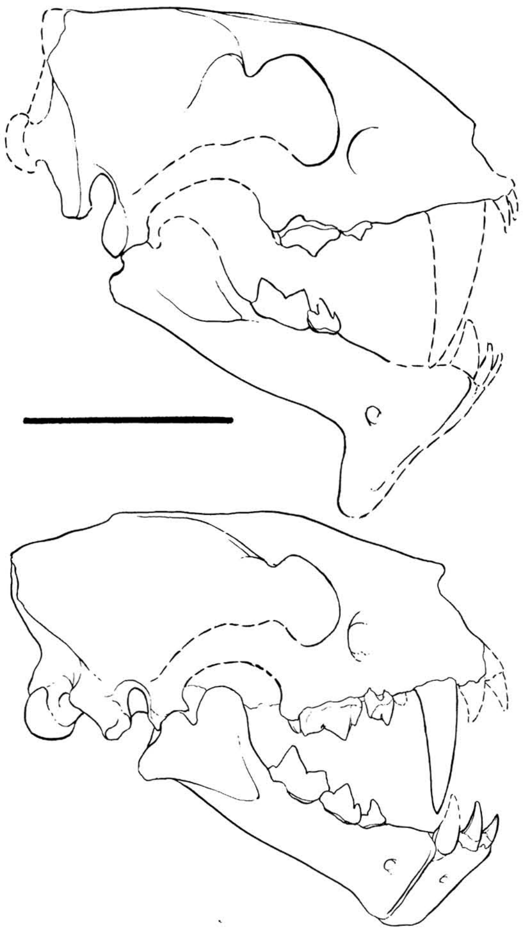

Fig. 4. Restoration of skulls. From top to bottom: *Eusmilus olsontau* (Macdonald), based on Frick American Museum (FAM) 98199, and *Nanosmilus kurteni* (holotype, UNSM 25505). Line = 5 cm.

mum width across the occipital condyles, 28; height of skull from apex of occipital crest to dorsal border of foramen magnum, 32.1; width of foramen magnum 13.7; height of foramen magnum 11.5; length from anterior end of alveolus for superior canine to posterior end of alveolus for P^4, 41.8; length from anterior end of alveolus of P^3 to posterior end of P^4, 26.8; canine AP at alveolus, 10; W, 4.6; P^3 AP, 9.4; W, 3.9; P^4 AP, 16.4; W, 7.9; M^1, AP, 4.3; W, 10.2. — Ramus: total length 85.8; distance from alveolus of canine to ventral border of flange, 22.3; length of distance, 11.5; minimum depth of ramus below diastema 17.9; depth below posterior border of M_1, 14.9; thickness below M_1, 9.2; height from interior border of angle to summit of condyle, 15.7; height from inferior border of angle to summit of coronoid process, 17.1; transverse width of condyle, 13.7; I, AP 2.7, W 1.5; I2, AP 4.5, W, 2.4; I3, AP, 5.1, W, 4.1; lower canine, alveolus AP, 5.7; W, 3.1; P_3, AP, 6.8, W, 3.1; P_4, AP, 10.6, W, 5.1; M_1, AP, 5.8, W, 14.6.

Etymology: Named for Björn Kurtén in recognition of his many contributions to the understanding of carnivore evolution.

Discussion: North American *Eusmilus* is confined to the late Oligocene (late Whitneyan and Geringian). *Nanosmilus* is significantly older (Orellan). It is also much more primitive. Comparison between the two genera (Fig. 4) shows the following changes from *Nanosmilus* to *Eusmilus:* development of a vertical occiput; lowering of the glenoid fossa; enlargement of the paramastoid process at the expense of the paraoccipital process; loss of P^2; reduction of P^3; loss of P_3; lowering of the coronoid process and the development of a huge dependent flange on the ramus. These are all typical evolutionary changes in dirk-toothed Carnivora lineages (Martin 1984).

The smallest species of *Hoplophoneus* presumably would be *Hoplophoneus oreodontis* Cope. Unfortunately, the type of that species (American Museum No. 5337) is a fragment of a ramus with deciduous dentition. It must be regarded as a *nomen vanum*. According to Simpson (1941:14) small specimens sometimes referred to this species are small female *H. primaevus*. All other described *Hoplophoneus* are clearly much larger than *Nanosmilus*, and are more derived in terms of premolar reduction and flange development.

3. Conclusions

The large species generally assigned to *Eusmilus* in North America seem to be very different nimravids that may belong to a different tribe (possibly the Hoplophonini). This was recognized by Toohey (1959) and also by Martin

(1980a). North American true *Eusmilus* has been described as small species of *Hoplophoneus* (*H. belli* Stock and *H. cerebralis* Cope) or as a distinct genus *Ekgmoiteptecela olsontau* Macdonald). I am presently studying the validity of these species. The association of the holotype of *Nanosmilus* with *Eusmilus* was recognized as early as Schultz et al. (1970) where *Eusmilus* is shown as having a tentative association with *Dinictis*. *Nanosmilus* is, in many characters of its dentition, skull and lower jaw, at a *Dinictis* level of saber-toothed cat evolution, and it is in many respects more primitive (weak dependent flange, strongly inclined occiput, well developed premolars) than *Hoplophoneus*. The ear region and well-developed paramastoid processes clearly show its affinities with the hoplophonine cats. It is in some ways the most primitive known member of that subfamily and the eusmilin line must have separated very early as more advanced species of *Hoplophoneus* are known from the Chadronian.

The relationship of the North American and European *Eusmilus* presents several problems. The nominate species, *Eusmilus bidentatus* Filhol is from the fissure deposits of Quercy that are normally regarded as lower Oligocene and equivalent to the Chadronian of North America. *Eusmilus* occurs with *Nimravus* in these deposits (Piveteau 1931). The first appearance of this combination in North America is in the Whitneyian. Neither genera are known from Orellan age deposits in North America. It might be possible that *Eusmilus*-level dirk-toothed cats evolved independently in North America and Eurasia. In that case, the generic name, *Ekgmoiteptecela* might be valid for the North American form. I find this hard to accept considering the detailed resemblances between *Eusmilus bidentatus* and the North American specimens. It is possible that *Nanosmilus* is not directly related to *Eusmilus*, but it has the features that I would expect to find in an early form from this lineage. Another possibility concerns a revision of the correlations between North America and Europe. Prothero & Swisher (1989) suggest that the Chadronian is Eocene and the Orellan through Whitneyian lower Oligocene. That would bring together the first appearance of *Eusmilus* and *Nimravus* in North America and Europe.

Because the European *Eusmilus bidentatus* Filhol is comparable in morphology to the late Oligocene North American *Eusmilus,* it seems likely that *Eusmilus* became part of the European fauna at a Whitneyan or Geringian level of morphology. The base of the Geringian is characterized in North America by the earliest appearance of other typically European taxa such as sicistines and talpine moles (Martin 1980b). The North American Oligocene ungulate fauna was dominated by an extinct group of selenodont artiodactyls, the oreodonts. It seems likely that they formed a significant portion of the prey of all nimravid carnivores in North America and must have been the special prey of the miniature *Eusmilus* and *Nanosmilus*. In spite of their small size, it seems likely that *Eusmilus* and *Nanosmilus* were ferocious predators that were able to take animals the size of a domestic pig or deer. The larger *"Eusmilus" sicaris* Sinclair & Jepson and *"E." dakotensis* Hatcher probably included larger prey like entelodonts and rhinoceroses in their diet.

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