Description of a new *Barbourofelis* species (Carnivora, Mammalia) from the Dalles
Formation of Northern Oregon

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Abstract

Description of a new *Barbourofelis* species (Carnivora, Mammalia) from the Dalles
Formation of Northern Oregon

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A new specimen of the nimravid *Barbourofelis* from northern Oregon is described

and compared with other nimravids and felids. The Oregon specimen, *Barbourofelis*

oregonensis, is similar in size and morphology to *Barbourofelis fricki*, the largest

Barbourofelis, but differs in a number of features, including more prominent ridges on

the frontal bone, a longer brain case, a relatively higher occipital region, and a smaller

depression anterior to the orbit. These differences affected facial, temporalis, and neck

muscle volume. The occipital region in *B. oregonensis*, as in *B. fricki*, is perpendicular to

the carnassial plane of occlusion. The larger volume of temporalis and neck musculature

in *B. oregonensis* enabled more powerful movement of the skull and mandible, and both

species had a larger angular range of skull rotation than other nimravids and felids. The

unique canine shape in *Barbourofelis* provided reduced friction between the tooth and the

surrounding tissue during stabbing, slicing, and withdrawl. P3 and M1 are absent in *B.*

oregonensis, leaving the enormous carnassial, which is 5% longer than the P4 in *B.fricki*,

the only cheek tooth.

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INTRODUCTION

Saber-toothed cats are one of the most recognizable and exhibited kinds of fossil vertebrates, yet despite their popularity, many aspects of their phylogeny and functional morphology remain debated. Some of the past confusion about relationships among saber-toothed cats involves the feature they are famous for: their elongate canines. Later it became evident that elongated canines arose many times independently in different canivore lineages as it did in non-carnivores, such as marsupials. Within the Order Carnivora, two families, Felidae and Nimravidae, evolved the saber-tooth morphology. Felids, "true cats", and nimravids, "false cats", can be distinguished by features of the auditory bulla and brain (Martin, 1980; Flynn *et al*., 1988).

The two types of canine morphology evolved in both groups of cats are dirk-toothed canines, more elongate and finely serrated, and scimitar-toothed canines, shorter and coarsely serrated. These two morphologies arose independently in true cats and false cats (Martin, 1998). The most extreme examples of dirk-tooth canines occur in the genera *Smilodon*, a felid, and *Barbourofelis*, a nimravid .

This study describes the skull of a new *Barbourofelis*, UWBM 72291, collected in the Dalles Formation of northern Oregon by Steve Nelson. The boundaries of the Dalles Formation are not well constrained, although the age is thought to be between 7.5 and 11 Ma in the Clarendonian or early Hemphillian North American Land Mammal Age (Smith *et al*., 1989). The genus

Barbourofelis belongs to the subfamily Barbourofelinae, a group of nimravids that appeared in North America about 12 million years ago, after an almost 11 million year absence of nimravids in the North American fossil record (Hunt and Tedford, 1993). The subfamily Barbourofelinae differs from other cats in possessing canines with a groove on labial and lingual sides, a complete postorbital bar, and an occipital region close to or perpendicular to the occlusal plane of the carnassial (Schultz et al., 1970). Five species of *Barbouofelis* have been described, the youngest (Hemphillian North American Land Mammal Age) and largest of which is *B. fricki* (Woodburne *et al.*, 1987; Schultz *et al.*, 1970). The Oregon specimen described here is the only known occurrence of this subfamily west of the Great Plain in North America.

MATERIALS AND METHODS

Specimens examined in this study are from the vertebrate paleontology and mammalogy collections of the Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington (UWBM and UWBM-M respectively), the University of Nebraska State Museum, Lincoln Nebraska (UNSM), and the Los Angeles County Museum (LACM). *Barbourofelis oregonensis* (UWBM 72291) was compared with *B. fricki* (UNSM 76000), *Panthera leo* (UWBM 87708), *Smilodon californicus* (LACM A-7360.5), *Neofelis nebulosa* (UWBM-M 35741), *Dinictis* (UWBM 53321), and *Hoplophoneous* (UWBM 87094). Differences between the skulls were noted and described. A dissection of the head and neck region of *Felis domesticis* was also preformed to examine origin and insertion points of head and neck musculature. These points were then used to infer the location of the head and neck musculature on the skull of *B. oregonensis*.

SYSTEMATIC PALEONTOLOGY

Class: MAMMALIA

Order: CARNIVORA

Family: NIMRAVIDAE Cope, 1880

Subfamily: BARBOUROFELINAE Schultz *et al.*, 1970

Emended Diagnosis - nimravidae with grooved upper canines; upper canines finely serrated, P4 with parastyle; lower cheek tooth row extended lateral to central axis of mandibular ramus. Origin for superficial masseter enlarged; ossified, nonseptate auditory bulla. Distal segment of limbs short; all feet plantigrade.

Included Genera - *Barbourofelis*, *Sansanosmilus*, *Prosansanosmilus*, *Syrtosmilus*, *Afrosmilus*, and *Ginsburgsmilus*.

Genus *BARBOUROFELIS* Schultz *et al.*, 1970

Type species - *Barbourofelis fricki* (UNSM 76000) Schultz *et al.*, 1970

Emended Diagnosis - Ranging from size of small mountain lion to that of African lion. Extremely narrow upper canines compared with anterioposterior length. Large mandibular flange. Dental formula I^3/$_3$, C^1/$_1$, P$^{1 or 2}$/$_2$, M^1 or 0/$_1$; P3 reduced if present, protocone absent on P4; P4 with preparastyle; metaconid absent on M1. Cranium short (brachycephalic) with the occiput nearly perpendicular to plane of occlusion; postorbital bar present; brain small with large olfactory lobes.

BARBOUROFELIS OREGONENSIS, sp. nov. (Figs. 1, 2, 4, 5, 7, 8)

Holotype - UWBM 72291, skull with right and left I1-2, incomplete right and left C1, right and left P4.

Type Locality - Arlington 16, C0195

Stratigraphic occurrence - Dalles Formation, 7.5-11 Ma (Smith *et al.*, 1989)

Diagnosis - Similar in size and morphology to *Barbourofelis fricki*; skull with larger postorbital bar; occipital plane nearly perpendicular to occlusal plane of upper carnassial; enlarged sagittal and lambdoidal crest; enlarged mastoid process. Differs from *Barbourofelis fricki* in transverse broad ridge on the frontal bone; much less prominent pit in front of the orbit; absence of P3 and M1 and alveoli; canine bears two grooves on both the lingual and labial sides; less brachycephalic: distance from the middle of the postorbital bar to the midpoint of the lambdondial crest 2 cm greater.

DESCRIPTION

Skull

The premaxillary region and other parts of the skull of *Barbourofelis oregonensis* have been distorted as a result of compression during fossilization. The left side of the skull is moved anteriorly and the right side posteriorly.

The premaxilla-maxilla suture appears to resemble that in *Barbourofelis fricki* and connects with the nasofrontal suture just lateral to the nasal bone (Schultz *et al.*, 1970). The suture in *B. fricki* continues ventrally, whereas the suture in *B. oregonensis* is like the condition in *Panthera leo*, is not well defined ventrally.

Anteriorly, the premaxilla is parallel to the palate, but for much of its length under the nares it is inclined dorsoposteriorly from the plane of the palate at an angle of 50°-60° (Figs. 1 & 2). The profile of the premaxilla under the nares in lateral view is similar to that in *B. fricki* (Fig. 3). In *P. leo*, the anterior of the premaxilla slopes ventrally at a steeper attitude than in *B. oregonensis* or *B. fricki*. In *Smilodon* the premaxilla slopes at a smaller angle under the nares; the anterior portion is almost horizontal, but not as flat as in *B. fricki* or *B. oregonensis*. The premaxilla in *Dinictis* is highly compressed vertically. The premaxilla in *Hoplophoneus* is more nearly horizontal under the nares than in the other specimens examined.

The shape of the maxilla is distinctive in *B. oregonensis* and *B. fricki*. In *B. oregonensis* it is laterally convex over the canine root, a feature that continues

dorsally as far as 4.5 cm above the canine alveolus. The canine convexity is less prominent in the similar sized *Smilodon*, but extends farther dorsally, almost to the union of the maxilla with the frontal bone. A similar expansion is present in *P. leo* but is not as prominent: 2 cm expansion in 1.5 cm in *B. oregonensis* versus 2 cm expansion in 4.5 cm in *P. leo*.

Posterior to the canine convexity, the maxilla in both *B. oregonensis* and *B. fricki* again expands laterally, to form a bump-like convexity over the anterior margin of the P4 root.   As in *B. oregonensis* and *B. fricki*, there is a slight bulge dorsal to the anterior root of P4 in *P. leo*. The maxilla of *Neofelis nebulosa* is similar to that of *P. leo* but the undulations dorsal to the premolar roots are more defined. The premolar root indentations are much more sharply defined on *Hoplophoneus* than in *B. oregonensis* and *B. fricki*.

The anterior orifice of the infraorbital canal faces more anteriorly in *B. oregonensis* than in *B. fricki* and is much less circular in shape (Table 1). The foramina in *P. leo*, *Neofelis nebulosa*, *Smilodon*, and *Dinictis* face forward even more than the condition in *B. oregonensis*. In *Smilodon*, the foramen is somewhat triangular with less anteroposterior compression than in the other felids. In *B. oregonensis*, a groove runs anteroventrally from the foramen toward the posterior margin of the canine alveolus. The groove is absent in *P. leo*, *Smilodon*, and *Dinictis*.

As in *P. leo*, *Smilodon*, and *Hoplopheous*, the maxilla of *B. oregonensis* expands laterally between the foramen and the tooth line but, unlike those taxa,

the abrupt expansion of the maxilla over the anterior root of P4 dominates the shape of the bone in this region. Near the maxillonasal suture, the maxilla has a rugose texture with many small pits. The bone in this area is also rugose in *B. fricki* (Fig. 2, Schultz, *et al.*, 1970) and *Dinictis*, but is smooth in *P. leo, Hoplophoneus*, and *Smilodon*.

There is a small depression anterior to the orbit, just in front of the lacrimal tubercle. The tubercle is triangular and lies at the dorsoventral midpoint of the orbit in the form of a narrow triangular flange. The depression in front of the orbit in *B. fricki* is much larger (1 cm by 1.5 cm and a little over 1 cm deep) than in *B. oregonensis*. *B. fricki* has a similar lacrimal tubercle behind a more distinct pit (Fig. 2, Schultz *et al.*, 1970). In *P. leo* there is only a slight depression in front of the orbits and the lacrimal tubercle is smoother than in *B. oregonensis* or *B. fricki*. *Smilodon* has a defined depression in front of the orbit, like *B. oregonensis*, but the lacrimal tubercle is thinner and smaller. There is no lacrimal tubercle or pit in *Dinictis*. A lacrimal tubercle is visible in *Hoplophoneus*, but there is no depression anterior to it.

The suture between the maxilla and frontal bone is straight and transverse, as in *B. fricki*, but lacks the slight posterior convexity of the latter. The suture in *P. leo* and *Hoplophoneus* is a rounded V-shape.

A transverse ridge extends across the frontal bone above the centers of the orbits in *B. oregonensis*. This ridge begins at the lateral corners of the bone and runs slightly posterior to the midline of the bone, about 3 cm behind its anterior

margin. A ridge in this position in *B. fricki* is not as prominent as it is in *B. oregonensis*. This transverse ridge is absent in the other felids; however in *P. leo*, the frontal is elevated just posterior to its suture with the nasal bones. A similar elevation is present and more pronounced in *N. nebulosa*. The region in *P. leo* and *N. nebulosa* posterior to this dorsal expansion is flat.

The supraorbital ridge posterior to the transverse ridge rises sharply perpendicular to the dorsal plane of the frontal. The anterior face of the supraorbital ridge does not rise as abruptly in *B. fricki*. The posterior surface of the supraorbital ridge in both *B. oregonensis* and *B. fricki* is coincident with the posterior surface of the postorbital bar and forms the anterior margin of the temporal fossa. The supraorbital ridge in *P. leo* is acute medially but smooth laterally. In *Smilodon*, the ridge is faint and the posterior portion is flattened. A minute ridge exists in the posterior part of the frontal in *Dinictis*. In *Hoplophoneus*, the supraorbital ridge is confined to the posterior portion of the frontal bone.

There is a small medial ridge beginning at the supraorbital ridge and running anteriorly along the suture between the left and right frontals. The ridge is more prominent posteriorly but extends forward to the transverse ridge. The ridge in *B. fricki* is even smaller than in *B. oregonensis*. The medial ridge is absent in the other felids examined.

B. oregonensis, like other members of the genus, differs from the other nimravids and felids in the presence of a complete postorbital bar joined to the

zygomatic arch (Figs. 1, 2, & 3). The anteroposterior thickness of the postorbital bar in *B. oregonensis* is 13 mm at the midline of the orbit. The smoothness of the anterior side of the postorbital bar varies, but the posteroventral edge of the postorbital bar and adjoining zygomatic arch consistently forms a narrow edge.

There is a distinct, 0.5 – 1 cm deep depression on the ventral portion of the jugal bone, as well as on the maxillary, above the posterior part of the carnassial (Fig. 4). The excavation ends abruptly just above the midpoint of the carnassial. The dorsal boundary of the excavation forms a horizontal ridge on the jugal bar. There are muscle scars within the excavation. A similar depression is present on *B. fricki* (Schultz *et al.*, 1970), but its anterior boundary is not as abrupt as in *B. oregonensis* (Figs. 3 & 4). In *P. leo*, the ventral portion of the jugal and a small adjoining portion of the maxillary bear a depression that is less extensive than that in *B. oregonensis* or *B. fricki*. In *N. nebulosa* and *Smilodon*, a smaller depression is present and confined to the jugal. In *Dinictis*, there is a pit dorsal to the midpoint of the carnassials along with a slight indentation on the ventral portion of the jugal bar. *Hoplophoneus* has a depression in the maxilla above the midline of the carnassial and a slight indentation on the anterior portion of the jugal.

Posteriorly, where the zygomatic arch is composed solely of the squamosal, the arch flares laterally, then turns medially toward the braincase. The angle of this turn is approximately 120° in *B. oregonensis*, as it is in *B. fricki* and *P. leo*. In *Smilodon* and *Hoplophoneus*, the angle is close to 90°.

At the posterior most extent of the zygomatic arch as in *B. fricki*, the squamosal bone almost touches the slightly anteriorly slanting mastoid process (Figs. 1, 2, & 3), a condition present in *Smilodon* but not in the other nimravids and felids.

The glenoid surface is unusual compared to most feliforms in that it is in the same plane as the occlusal surface of the carnassial (Fig. 2). The glenoid process of the other taxa in this study ranges from 1-5 cm above the occlusal surface of the carnassial. The glenoid fossa of *B. oregonensis* is 2.5 cm wide, 4.5 cm long, and 1.2 cm deep. The glenoid surface of *P. leo* is longer than that of any of the other felids studied (Table 1).

The squamosal joins the parietal and frontal bones at a level of about two-thirds of the depth of the skull from the top. The posteroventral section of the squamosal is dominated by a broad ridge that begins at the base of the squamosal and continues dorsally, then broadens onto the parietal bone where it becomes less distinct. At the dorsal border of the squamosal, the ridge measures 4.5 cm anteroposteriorly. This ridge is also present on *B. fricki* but does not broaden on the parietal. None of the other taxa in this study have this ridge. The squamosal and parietal bones in both *B. oregonensis* and *B. fricki* appear less inflated than in the other felidforms, probably owing to the more massive sagittal and lambdoidal crests in these barbourofelines.

Posterior to the squamosal-parietal ridge there is a vertically elongate sulcus of approximately 1 cm width containing small depressions and ridges that

represent muscle scars. The posterior border of the sulcus is the lambdoidal crest. The sulcus in both *B. oregonensis* and *B. fricki* flattens halfway up the parietal as it becomes a smooth, sloped transition to the lambdoidal crest (Figs. 2 & 3). This sulcus is present but more poorly defined in the other felidiforms. In *P. leo* there are several shallow depressions, one on the squamosal, another near the ventral margin of the parietal, and one in the dorsoposterior corner of the parietal. *Smilodon* has a fairly broad depression that is less well defined and more anterior than that in *B. oregonensis* and *B. fricki*. *Dinictis* has a small depression in the position of that in *Smilodon*. *Hoplophoneus* has a large depression on its parietal that is shorter and more anterior than that in *B. oregonensis*. Like *B. oregonensis* and *B. fricki*, *Smilodon* has pits within the depression representing muscle scars. The lambdoidal crest on *P. leo* rises at an angle of 40°-50° to the parietal bone and an even larger angle to the squamosal. In *N. nebulosa*, the crest rises at 70° to the parietal, making the crest morphology similar to that of *B. oregonensis*. The crest in *Smilodon* is 75° to the plane of the parietal. The lambdoidal crest in *Dinictis* is confined to the parietal and forms an angle of 30° with the anterior part of the parietal bone. The lambdoidal crest on the squamosal of *Hoplophoneus* is small and rises at about 60° from the squamosal.

Dorsally on the parietal, the sagittal crest is extremely prominent (Figs. 1 & 2). It is approximately 2 cm high and 3 mm posteriorly in transverse thickness. The crest continues to maintain a 3 mm thickness on the frontal, where it splits into two ridges that connect with the postorbital ridges. The sagittal crest in *B.*

fricki is very similar. The sagittal crest of *P. leo* is also about 2 cm high on the parietal, but on the frontal is only 2 mm wide and at the most posterior part of the parietal is 13 mm high. The crest in *Smilodon* is similar to that in *P. leo*. The sagittal crest in *Dinictis* and *Hoplophoneus* is confined to the posterior of the parietal.

The anteroposterior length of the temporal fossa, measured as the distance from the dorsoventral midpoint of the postorbital bar to the dorsoventral midpoint of the lambdoidal crest is about 2 cm greater in *B. oregonensis* than in *B. fricki* (10.3 cm and 8.25 cm, respectively). The dorsal and posterior most regions of the temporal fossa of *B. oregonensis*, *B. fricki*, *P. leo*, and *Smilodon* have a rugous surface containing many small (about 1 mm diameter) pits. These pits are not as distinct in the other taxa.

In posterior view, the occipital bone in *B. oregonensis* and *B. fricki* has a semi-oval shape, with the mastoid processes at the widest part (Figs. 5 & 6). The occipital of *Smilodon* has a similar shape. In contrast, the dorsal most portion of the occipital in *P. leo* and *Hoplophoneus* is triangular and the mastoid processes are positioned farther laterally, giving the bone an arrow-shaped appearance.

The occipital in *B. oregonensis* and *B. fricki* has a larger area than in other similarly sized feliforms examined (Table 1). At the dorsal midline, the occipital in both *B. oregonensis* and *B. fricki* bears a posteriorly facing circular protuberance. *Smilodon*, *P. leo*, and the other feliforms bear a more angular expansion in the same position.

B. oregonensis and *B. fricki* have a 1.5-2 cm long ridge aligned dorsoventrally on either side of the circular protuberance. The midline of the occipital in both taxa is marked by a small ridge running from the dorsal protuberance down to a broad intercondylar ridge above the lip of the foramen magnum. Except for *Hoplophoneus*, the other feliforms examined have two lateral ridges on the dorsal portion of the occipital bone that are absent in *B. oregonensis* and *B. fricki*. As a result of these ridges the occipital in those felids has a more undulating appearance than that in *B. oregonensis*.

Two large circular depressions representing muscle scars are evident on each side of the occipital condyles (Fig. 5). The dorsal-most indentation is deeper, while the more ventral is broader. These two depressions are confluent in *B. fricki*. A single, larger and deeper depression is present in this position in *P. leo* and *N. nebulosa*. The depressions are separate in *Smilodon*, though not to the extent in *B. oregonensis*, and are deeper and wider.

The left occipital condyle is broken but the right occipital condyle is intact and its long axis appears to be more horizontal than in *P. leo* or *Smilodon*. It has the same orientation as in *B. fricki*, *Dinictis*, and *Hoplophoneus*.

The foramen magnum is 21 mm high and 30 mm wide, which is approximately the size of that in *P. leo*, but larger than in *Smilodon* (18 mm high and 28 mm wide). The dorsal margin of the foramen magnum is defined in *B. oregonensis* by the intercondylar ridge that forms a lip at the top. While this ridge

is apparent on all the felids, it is more massive and protrudes farther posteriorly in *B. oregonensis*.

The mastoid process is extremely large, about 41 mm wide at the base and 24 mm in anteroposterior diameter. The base of the process slopes medioventrally. The ventral margin of the process is a small lip-like cingulum around the base of the process, and anteriorly is in contact with part of the squamosal bone. The mastoid process of *B. fricki* is similar but does not come into contact with the squamosal. The mastoid process in *P. leo* is smaller than that in *B. oregonensis*, 10 mm wide laterally at its base. The anterior surface of the process runs dorsoventrally approximately parallel to the squamosal and is about 15 mm from the bone above the basal contact. As in *B. oregonensis* and *B. fricki*, the mastoid of *Smilodon* is also quite large, measuring 35 mm laterally and 20 mm anteroposteriorly at its base.

Like *B. fricki*, there is no paraoccipital process in *B. oregonensis*. There is a moderately elevated ridge on the mastoid process that begins at the base of the condyles and continues dorsolaterally to the lateral extent of the occipital bone, becoming most prominent just lateral to the depressions (Fig. 5). This ridge is very slight on *B. fricki*.

On *P. leo*, the paraoccipital process is thin and extends posterior to and below the mastoid process. It has a "hook" on its ventral end that juts anteriorly. On *N. nebulosa*, the process is thin, points to the posterior and has a groove in the distal end. On *Smilodon*, there is a small, ridge like paraoccipital process high on

the mastoid process. This ridge is similar to, but more defined than the ridge present on the mastoid process in *B. oregonensis*. On *Dinictis*, the paraoccipital process is a sharp point that protrudes posteriorly. On *Hoplophoneus*, the paraoccipital process is an elevated ridge that points posterior.

The bulla is merged with the mastoid process, appearing as only a convex surface on its medial side just ventral to the condyles. It continues anterior to the posterior margin of the squamosal. The bulla in *B. fricki* is similar to that of *B. oregonensis*, but is more inflated (Fig. 5 & 6). Bullae are absent in *Dinictis* and *Hoplophoneus*.

The basisphenoid, which is convex in the other felids, is depressed in both *B. oregonensis* and *B. fricki*.

Teeth

Only two incisors are present on either side in *B. oregonensis*. There is possibly an alveolus for a third incisor anteromedial to the other two, but distortion due to preservation makes it difficult to assess.

The canine is approximately 160 mm long. Only two thirds of the canine is present in *B. fricki*, so an extrapolation of its length is not as accurate. At the alveolus, the tooth is 47 mm in anteroposterior diameter and 11 mm in transverse width. The canine is almost as thin transversally in *B. fricki*: the ratio of the anteroposterior to transverse cross-sectional dimension is about 4:1 (Fig. 7). *Hoplophoneus* also has a thin canine but it is much thicker for its length (1:7.5) than that of *B. oregonensis* (1:13.3) and for its anteroposterior diameter

(anteroposterior to transverse ratio 2:1). The anteroposterior to transverse ratios in *P. leo*, *Smilodon*, and *Dinictis* are about 1.5:1, 2.5:1, and 2.5:1 respectively.

The cross-sectional canine shape in *B. oregonensis* is unique to this species. The canine bears two longitudinal grooves on both labial and lingual surfaces, with the posterior groove the more pronounced. In *B. fricki* there is mainly an anterior groove (Schultz, *et al.*, 1970). The anterior ridge is slightly larger than the posterior, 10 mm and 8 mm respectively. Behind the posterior groove the canine narrows again and forms a sharp posterior edge. While none of the other feliforms share this shape, their canines form a sharp edge, with the exception of the *P. leo*. Although all other felids studied have dirk teeth (knife blade-like), they do not have the unique shape seen in *B. oregonensis* and *B. fricki*.

The canines of bear 4 tiny serrations per millimeter on the posterior side. There are about 4.7 serrations per millimeter in *B. fricki*, 3.5 per millimeter in *Hoplophoneus*. The enamel on the anterior portion of the canine is slightly worn where not damaged, leaving the presence of serrations in doubt. However, *B. fricki*, *Hoplophoneus*, and *Smilodon* all possess anterior as well as posterior serrations.

P3 is absent in *B. oregonensis*, but a small one is present in *B. fricki*. A large diastema separates the canine and P4. The P4 is longer (67 mm) than that in *B. fricki* (63.5mm)is the only cheek tooth (Fig. 8). There is no protocone on the

carnassial. The paracone, metacone, and parastyle make up the shearing blade of both *B. oregonensis* and *B. fricki*.

The P4 is aligned anteroposteriorly as in *B. fricki* and unlike the slightly oblique alignment in the other felids. The posterior margin of P4 curves medially 90° to the labial surface, following the curvature of the maxilla. There is no M1 in *B. oregonensis*; there is a possible alveolus for M1 in *B. fricki*.
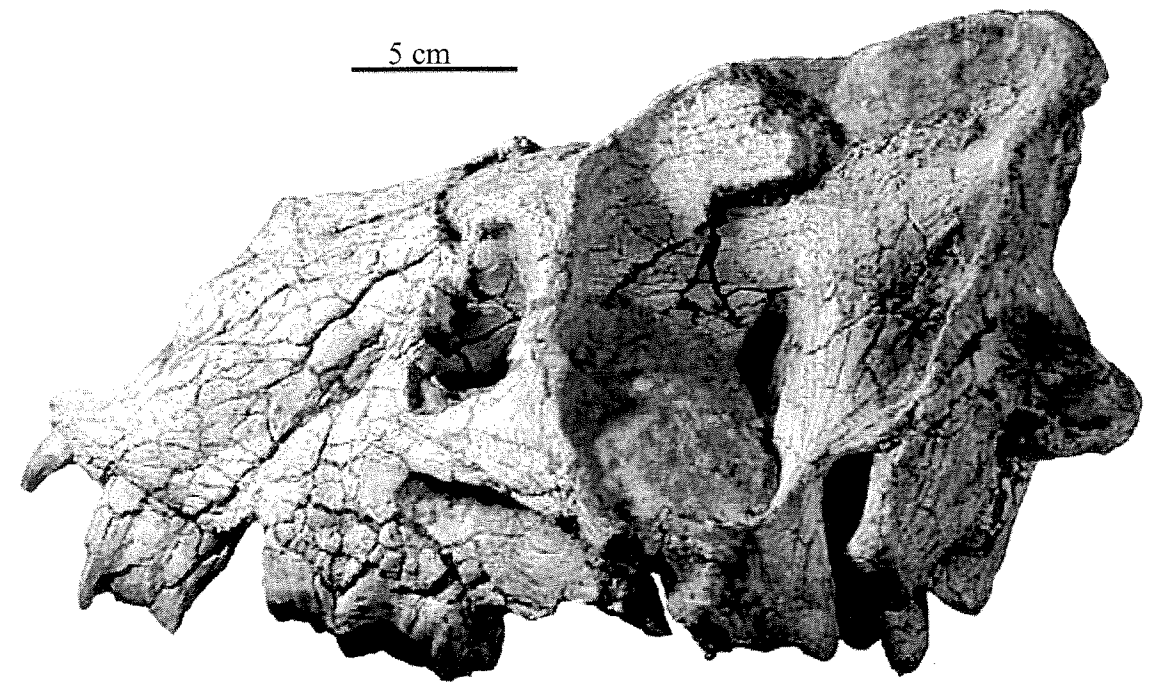
5 cm

FIGURE 1. *Barbourofelis oregonensis* (UWBM 72291) left lateral view.
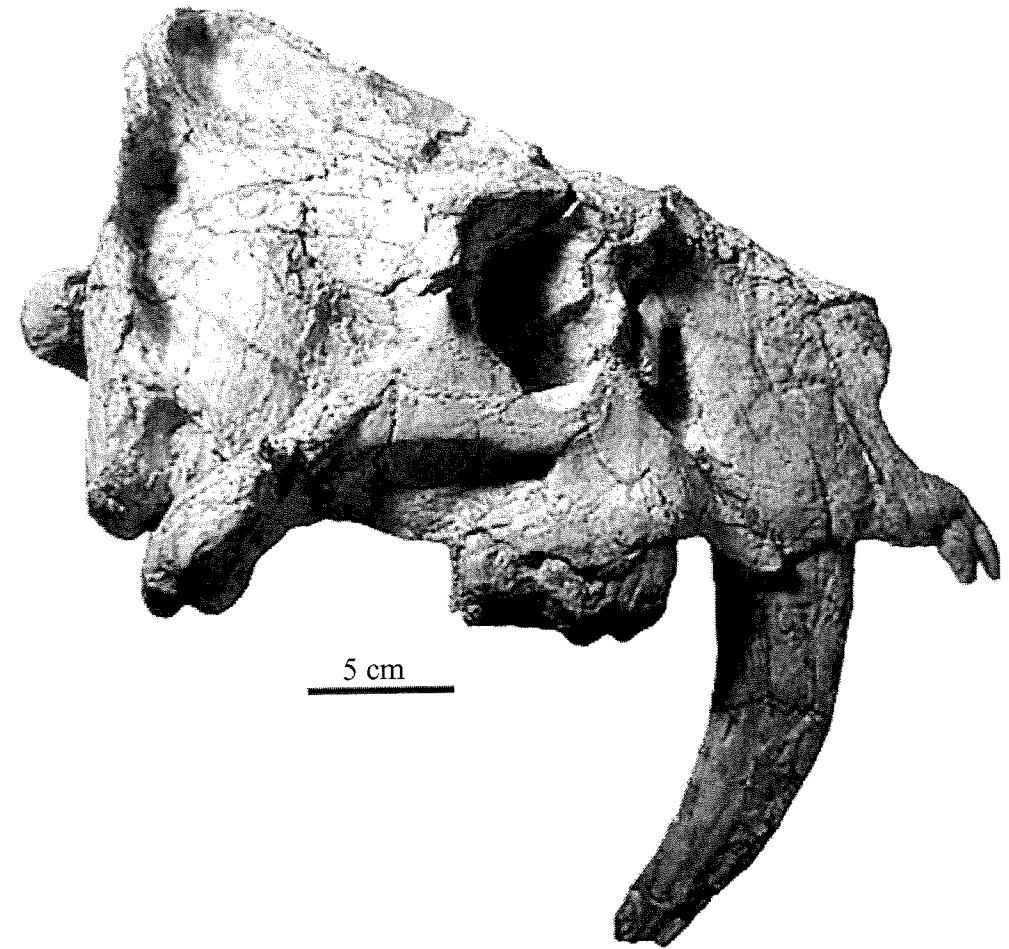
5 cm

FIGURE 2. *Barbourofelis oregonensis* (UWBM 72291) right lateral view.

5 cm
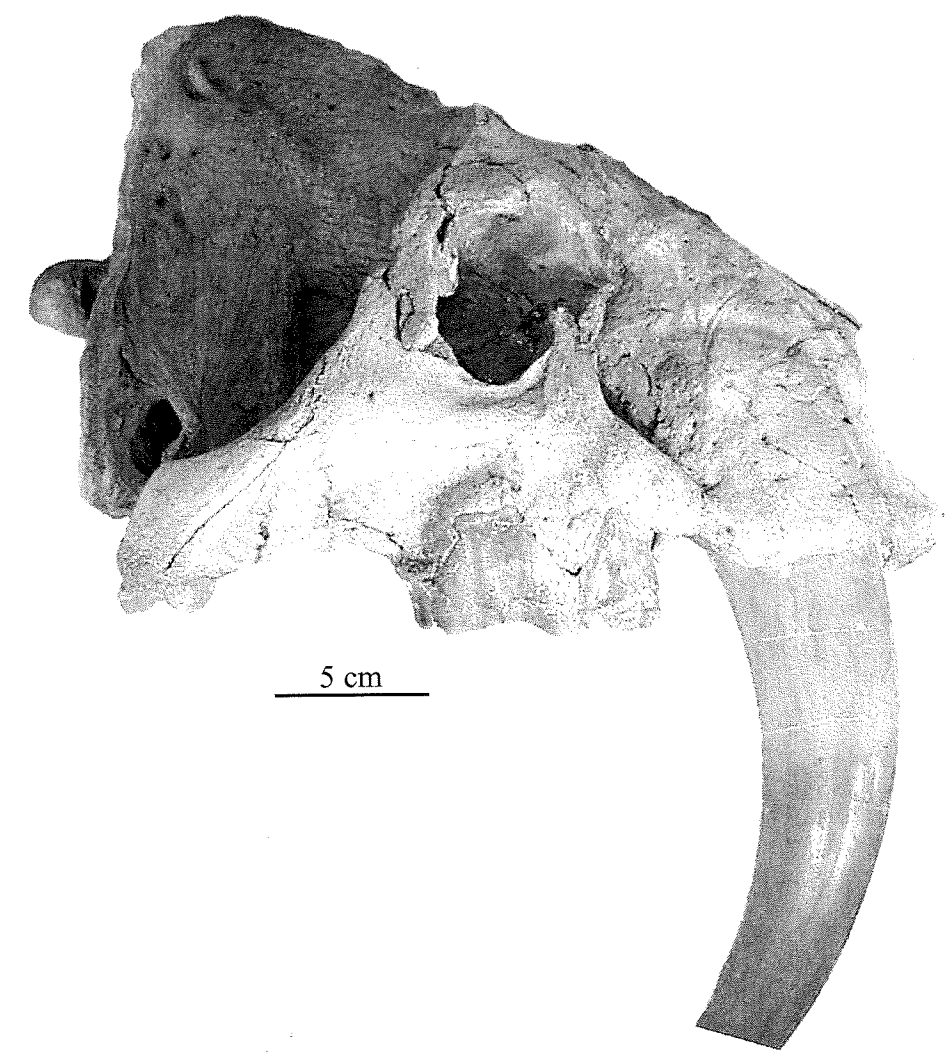
FIGURE 3. *Barbourofelis fricki* (UNSM 76000) right lateral side.

5 cm
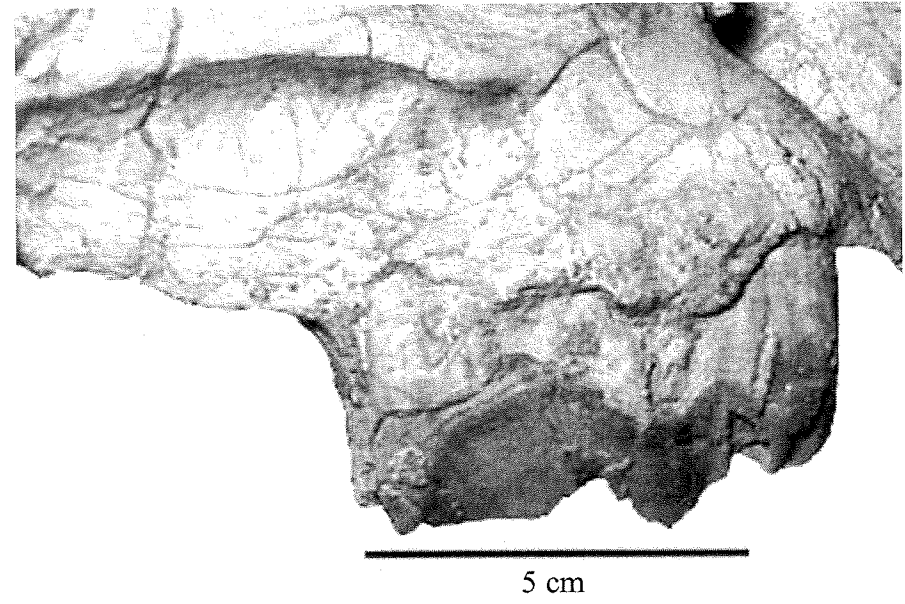
FIGURE 4. *Barbourofelis oregonensis* (UWBM 72291) masseter scar.

5 cm
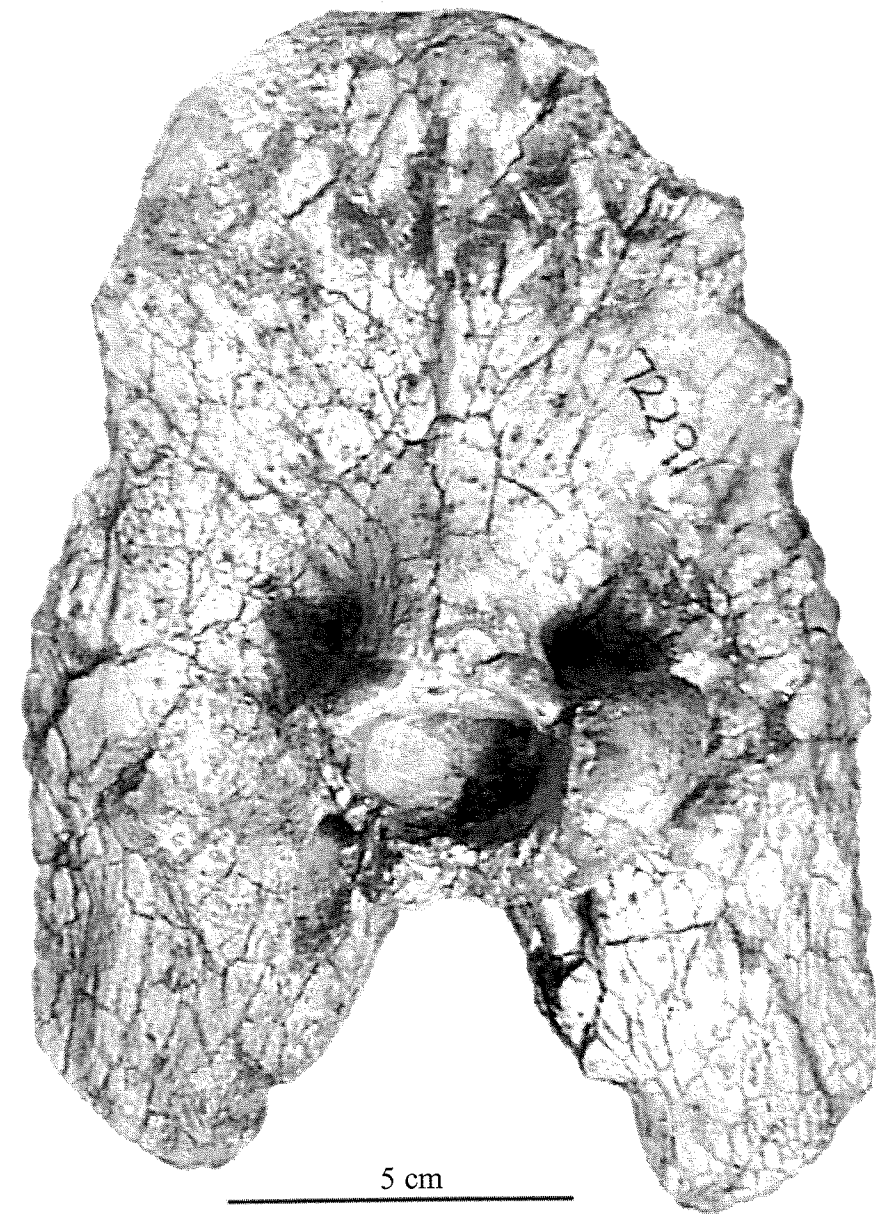
Fig. 5. *Barbourofelis oregonensis* (UWBM 72291) occipital region.
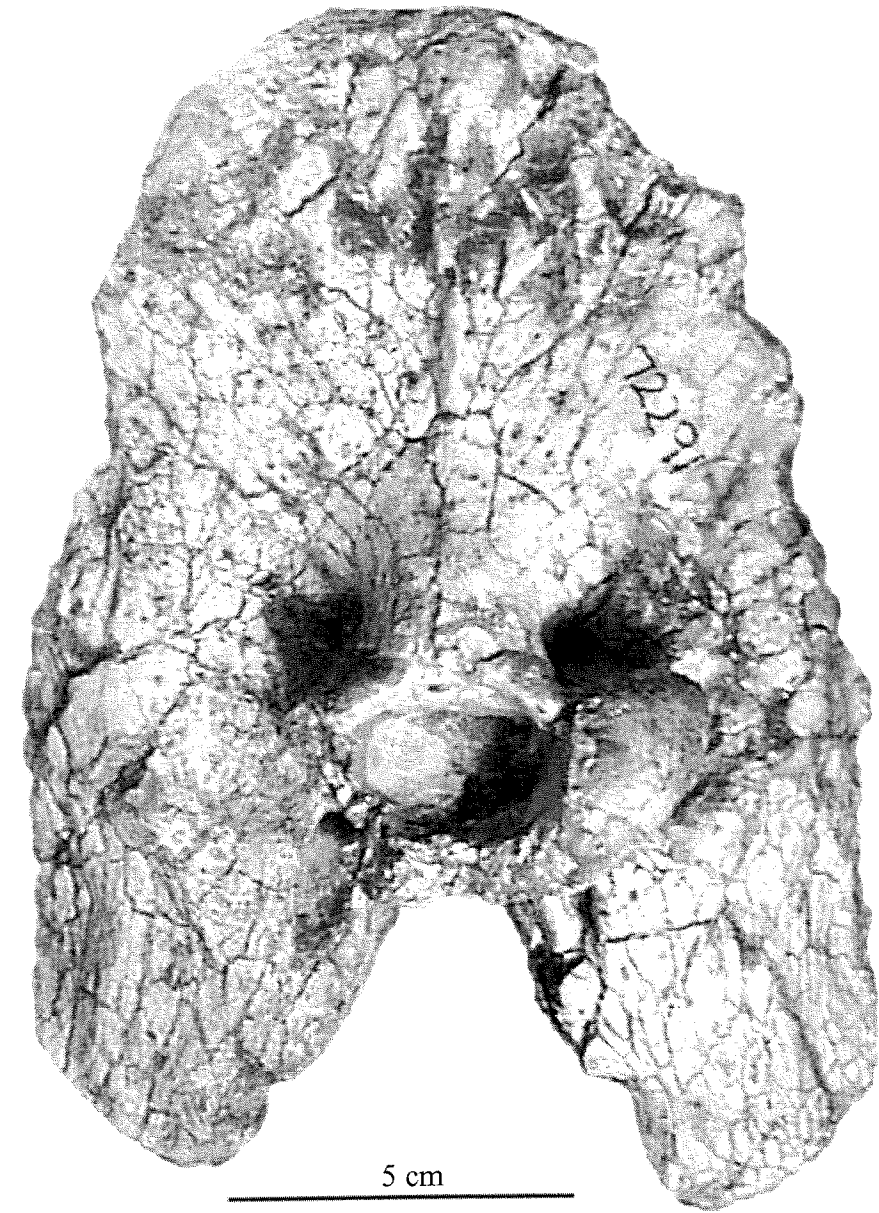
Fig. 5. *Barbourofelis oregonensis* (UWBM 72291) occipital region.

Fig. 6. *Barbourofelis fricki* (UNSM 76000) occipital region.

FIGURE 7.   a. *Barbourofelis oregonensis* (UWBM 72291) right canine and cross-section.
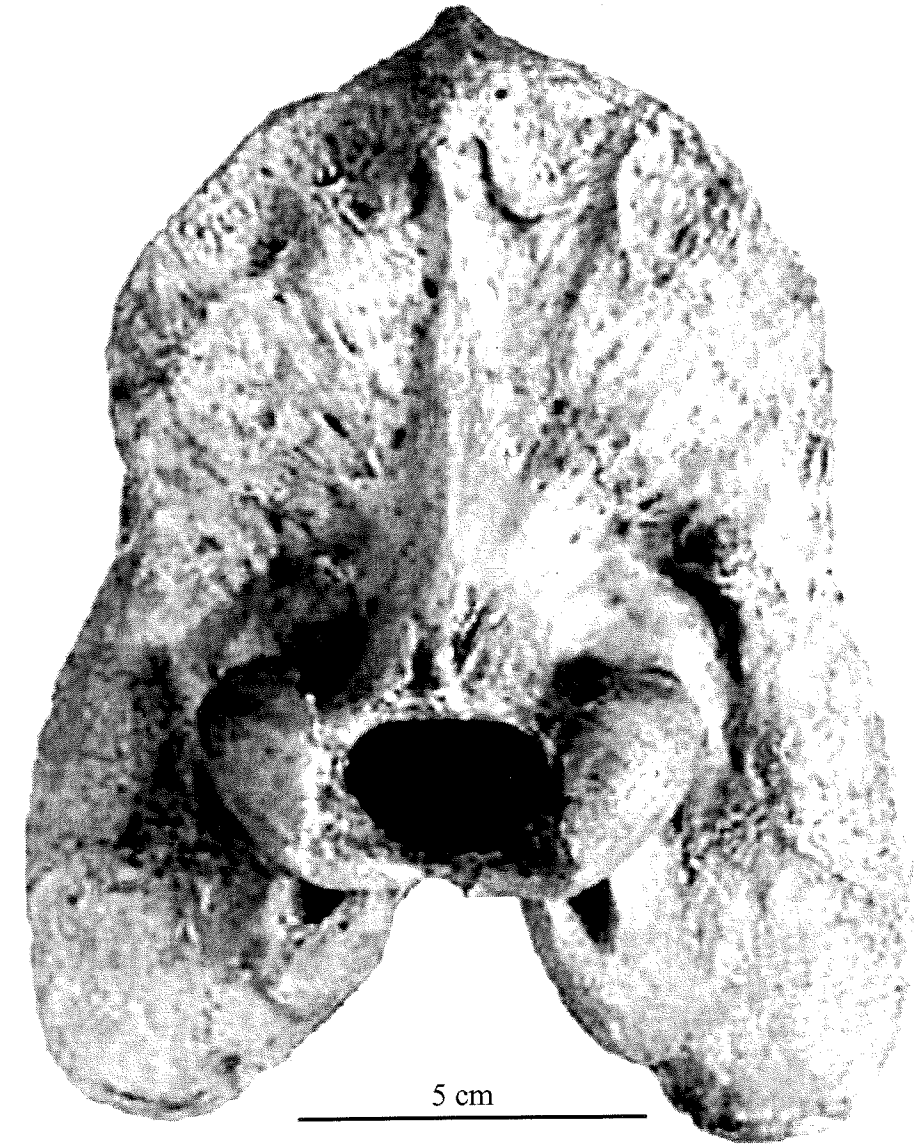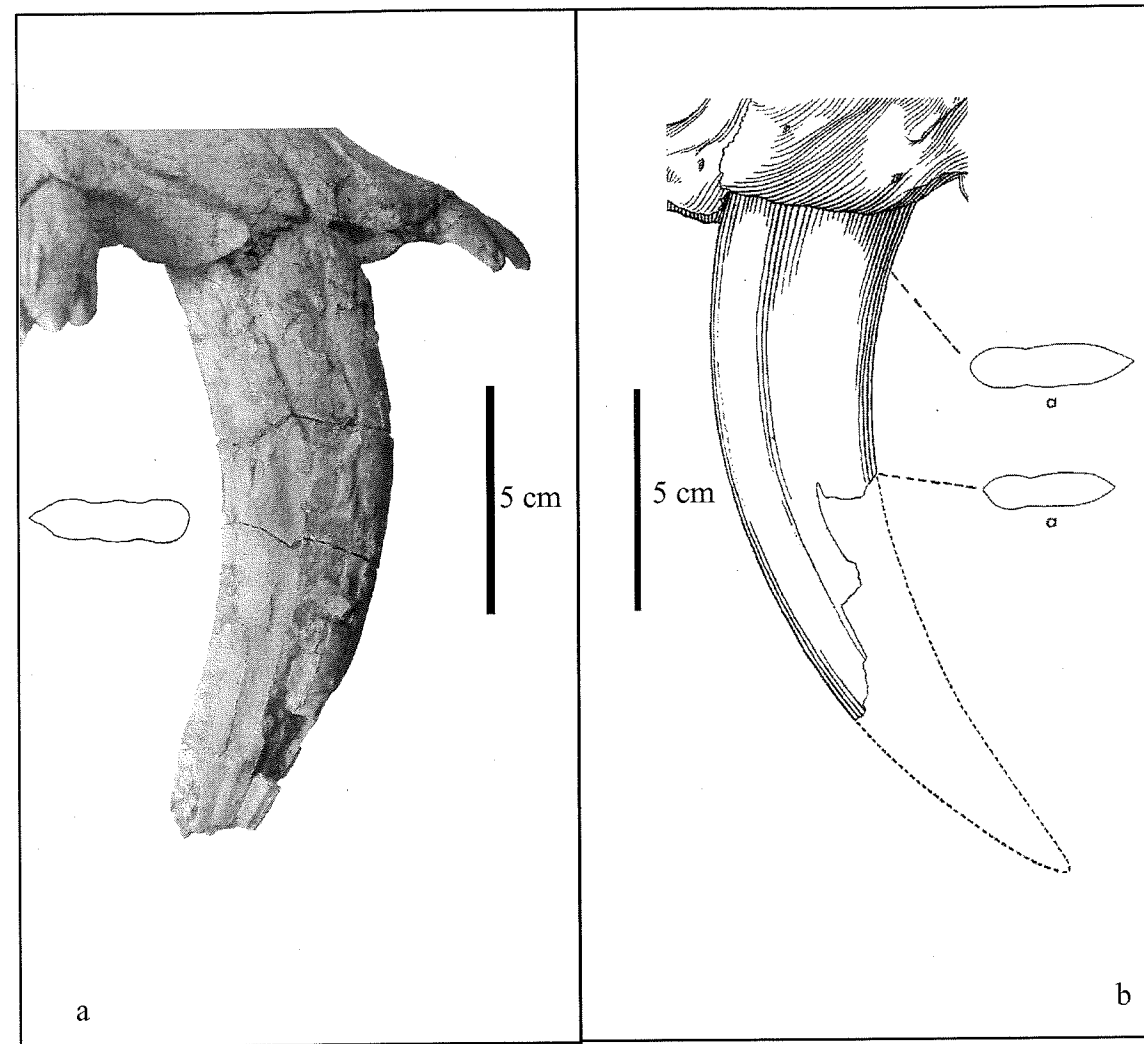
b. *Barbourofelis fricki* (UNSM 7600) canine and cross-section, from Schultz *et al.*, 1970.
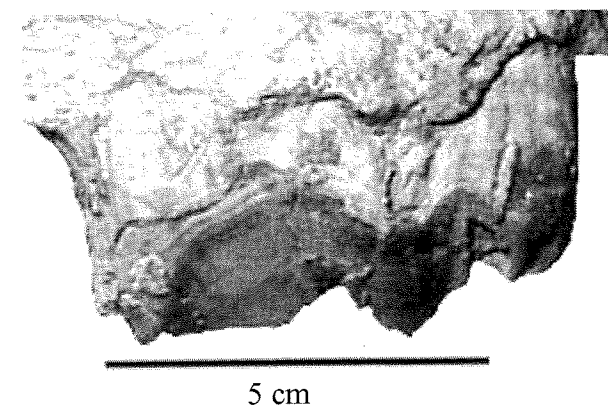
5 cm

Fig. 8. *Barbourofelis oregonensis* (UWBM 72291) right carnassial.
P4 is the only post-canine tooth and is very enlarged.

TABLE 1. Measurements (in mm) of felids studied. Where a measurement is not given, it could not be obtained.

Measurement (in mm)	B. oregonensis UWBM 72291	B. fricki UNSM 76000	P. leo	N. nebulosa UWBM-M 35741	Smilodon LACM A-7360.5	Dinictis UWBM 53321	Hoplophoneus UWBM 87094
anterior alveolus I1 to posterior condyles	330	298	334	150	280	194	189
greatest width across mastoid	126.5	132	150	67	130	69	66
greatest width across condyles	68	68	67	33	62	44	43.5
length anterior alveolus C to posterior P4	124	134	115	54	104	71	63.5
length C to P4	29	33	49	21	25	33.5	15
width of I3	15	14.5	15	6.5	13	4.5	7
length I3	22.5			6	24	11	11
width I2	13	13.5		2.5	9	2.5	6
length I2	22.5			9.5	21	5	8
length canine	47	51	28	15	41	17	19
width canine	11	12.5	19	9	23	8	10
height canine	160	180	56	36.5	14.2	38.5	64
length P4	67	63.5	38	14	41	29.5	21
width P4 (shearing surface)	13	11.9	16	9.5	19		10
height P4	35	36	25	13	20.5	14	12
tip of carnassial to palate	35	36	35	21	30		19
glenoid length	45	53.3	57	25	45		27
glenoid width	25	27	25	8	2		14
glenoid depth	12	16	15	5	1		9
orbit length	57	52	65	36	50	40	35
orbit width	41	40	52	29	38	30	31
skull length	330	298	380	155	310	215	205
skull width	190	201	245	116.5	193	140	131
skull height		121	133	73	138	76	88
occipital (mastoid included) height	175	175	135	53	150	55	95
occipital width (mastoid to mastoid)	126.5	132	150	67	130	69	75
occipital width (at center of foramen magnum)	110	115	115	50	106	47	54
top of skull to top of condyles	97	91	79.5	35	70	39	42
top of condyles to end of mastoid process	86	86	51	18	85	19	37
width of postorbital process	13	15.5		7			
M1 length across alvelous			9	8	7	13	13
diastema C-P3	25		24	14	8	17	15
length P3	7	25	25	8	14	19	10
width P3	6	7	13	13		9	5
height P3	9	6	17		13	13	8.5
infraorbital canal long dimension	30	9	22			22	14
infraorbital canal perpendicular to long dimension	13	29	13	25	22	12	10
Mandibular fossa length	45	25	57	8	12	45	27
Mandibular fossa width	25	53	25	25	45	20	14
Mandibular fossa depth	12	27	15	5	20	10	9

DISCUSSION

Although there are five previously recognized *Barbourofelis* species
(Table 2), this study has focused its comparison especially on *Barbourofelis fricki*
because of the similar ages and sizes of these specimens. The other *Barbourofelis*
species are smaller and older, but their characteristics are also compared with
those of *B. oregonensis* (Table 2).

B. oregonensis differs from *B. fricki* in its frontal ridges, maxilla
depression, cross-sectional shape of the canine, and absences of P3 and M1.
Differences in ridge and depression sizes can be related to morphologic diversity
in different populations or sexes. However, one specimen is known from either
species, so one cannot conclude that these differences are the result of drift in
populations or sexual dimorphism. The significance of the absence of vestigial
teeth in classifying species is controversial. Teeth, especially vestigial teeth, can
be highly variable in Felidae (Dayan *et al.*, 2002). However, a study by Fenton *et
al.* (1998) showed that the frequency of missing teeth in Felidae is very low, and
the larger carnassial in *B. oregonensis* correlates with trends in which selection is
shifting function from P3 to M1 to the carnassial alone. Dental morphology of
individual teeth, however, is less variable in mammals.

Barbourofelis oregonensis shares all of the following features with
Barbourofelis fricki: complete post-orbital process; enlarged mastoid; absence of
a paraoccipital process; and enlarged, shearing carnassial. *B. oregonensis* has
taken some of these traits to an extreme level of development compared to other

members of the genus. The enhancement of some of these traits in both *B. oregonensis* and *B. fricki* probably relates to the extreme size of both species in comparision with other *Barbourofelis* species.

The morphological differences between *B. oregonensis* and *B. fricki* suggest some functional differences in predation and mastication.

Although P3 and M1 are greatly reduced in *B. fricki*, these teeth are completely gone in *B. oregonensis*, leaving the carnassial as the only posterior tooth (Table 2). With the loss of the other posterior teeth, all the forces associated with biting converge on the carnassial, maintaining very high occlusal stresses in spite of the enlargement of the tooth and providing improved efficiency in fracturing thick tendons and ligaments of large herbivores. In addition, muscle scars in both *B. oregonensis* and *B. fricki* indicate large mastication muscles. The masseter scar in both large *Barbourofelis* species extends to the midpoint of the carnassial, much farther anterior than in other fossil cats.

Whereas true felids and most nimravids have a posteriorly slanted occipital this region in both *B. oregonensis* and *B. fricki* is nearly perpendicular to the palatal plane of the skull (Figs. 1, 2 & 3). This construction of the skull is unique to *B. oregonensis* and *B. fricki* within *Barbourofelis* and only seen in a few other genera of nimravids and in the marsupial *Thylacosmilus*. With the occipital region perpendicular to the palatal plane the skull could rotate farther back before conflicting with the vertebral column. An occipital region perpendicular to the palatal plane also allows for longer muscle fibers and greater muscle mass in the

neck, much of which attaches to the enlarged occipital region. The combination of larger neck muscles than in similarly sized feliforms and the ability to rotate the head father back would allow a stronger forward thrust of the skull when stabbing.

Enhanced muscle attachment area is also made possible by the increased size of the mastoid area in all *Barbourofelis* species. The digastric originates on the mastoid and the sternomastoid inserts on the mastoid. The digastric lowers the lower jaw, while the sternomastoid turns and depresses the head. The larger mastoid process is related to an increase in the size of both of these muscles. The increase in the digastric probably relates to a need to open the mouth widely so that the lower jaw can clear the plane of the canines. The digastric also acts as an antagonist to the massetaer and temporalis, which themselves are enlarged. It also might have been involved in disengaging the long canines. Much of the musculature probably related to control of the massive head of these animals. The large extended mastoid processes added leverage beneath the condyle, powering this flexion.

The skull of *B. oregonensis* has more pronounced transverse and medial ridges on the frontal bone than *B. fricki*. These ridges allow for increased attachment for facial muscle groups which control ear movement (Crouch, 1969; Gest & Schlesinger, 1995; Orengo & Iyenger, 2002). *B. fricki* has a large pit on the maxilla, for the quadratus labii superioris group which raises the upper lip for snarling (Crouch, 1969; Orengo & Iyenger, 2002), suggesting these muscles were

larger than in *B. oregonensis*. The differences in the sizes of these muscles may have allowed different facial movements but probably did not affect biting and mastication.

Emerson and Radinsky (1980) argued that the masseter scar of saber cats and modern felids is in the same position and that since the zygomatic arch is shorter in saber cats, the area for the masseter muscle is smaller. However, in *B. oregonensis* and *B. fricki*, the masseter scar is more pronounced than in other feliforms and begins at the midpoint of the carnassial (Fig. 4), much farther anterior than in modern felids, indicating that the muscle is relatively larger.

A relevant question is how did *B. oregonensis* use its canines? The morphology indicates that *B. oregonensis* and *B. fricki* attacked in the same manner, but this behavior differed from that of *Smilodon*. Though all three taxa have transversely thin canines compared with modern felids, those of *B. oregonensis* and *B. fricki* are thinner relative to their anteroposterior diameter than those of *Smilodon*. *B. fricki* has a unique canine morphology among felids and nimravids, for its canines have a labial and lingual groove, giving the canine an hourglass shape. The canine of *B. oregonensis* has two grooves on each side. The grooved surfaces of the canines of *B. oregonensis* and *B. fricki* represent a mechanism that maximized the stiffness of the blade relative to its cross-sectional area, and correlates with the unusually thin canines in these taxa. The same technology (fullering) has been used in the manufacturing of swords and knives. A thinner blade provides less friction as the blade slices through the tissue

because the hole is not stretched as widely and greater stress concentration at the edge that is opening the crack in the direction of the slicing movement. *B. oregonensis*, with two grooves, represents a further specialization for this function. The canines in *Smilodon* and *Hoplophoneous*, however, are designed primarily for insertion then withdrawal, or slicing in the same motion.

The complete ossification of the post-orbital bar in *Barbourofelis* is probably a response to the stress of shearing via the carnassial. Greaves (1985) considered stresses due to mastication the sole reason for a post-orbital bar. Noble *et al.* (2000), concluded that the ossification of the bar served to overcome visual distortion resulting from muscle contraction during mastication. Their study found that ossification of the post-orbital bar in felids only occurred in cats of small size and concluded that in smaller animals the orbits are more anteriorly positioned.

However, *Barbourofelis* species are large, suggesting a different function for an ossified postorbital bar. The postorbital bar buttresses the enlarged temporalis muscle which inserts along the upper half of its posterior surface. Another possible explanation may relate to the use of the canines. A predator that keeps its canines embedded and continues slicing in a prey has a greater probability of damaging its eyes.

The placement of Barbourofelinae within the aeluroid Carnivores remains controversial (Flynn *et al.*, 1988). They are here included within the Nimravid following one widely held view (Martin, 1980; 1998; Joeckel *et al.*, 2002;

Baskins, 1981; Bryant, 1988). However, Morales *et al.* (2001) recently classified *Barbourofeli*s as a felid based on three points: the absence of nimravids from the late Oligocene to the middle Miocene, the divergences between auditory regions, and differences in dental characteristics. If Barbourofelinae are indeed nimravids, then they are the youngest members of this family, and *B. oregonensis* and *B. fricki* (from the late Miocene), the two largest species within the group and the last known of the nimravid radiation.

TABLE 2. Differences between *Barbourofelis* species. *B. whitfordi* is excluded because species is only known from mandible.

Characteristic	B. oregonensis	B. fricki (Schultz et al., 1970)	B. morrisi (Schultz et al., 1970)	B. lovei (Baskins, 1981)	B. piveteaui (Genads and Gulec, 1997)
P3	absent	vestigial – one root & 2 cuspules	two roots	-trilobed: medial larger & taller -root varies 1 or 2 roots	-3 cusps, middle highest -2 roots
M1	absent	possible alveolus	small, elongated	-unclear if present	-broader than long; recurved forward
C	-two shallow grooves on lingual and labial sides, anterior to midline -at least posterior margin finely serrated	-one shallow groove on inner and outer margins just anterior to midline -anterior and posterior margins finely serrated	-internal and external grooves present -finely serrated on anterior and posterior margins	-weak internal and external grooves -anterior and posterior serrations	adult canine not yet erupted
Incisors	only two present on each side	-Three alveoli per side -only I2 known	-I1-I3 increase in size; strongly recurved	-I1-I3 increase in size; I3 has fine serrations along its posterior edge	-I1-I3 increase in size; finely serrated
Occipital	-nearly perpendicular to horizontal plane of skull	-nearly perpendicular to horizontal plane of skull	-more inclined from horizontal plane of skull than B. fricki	-more inclined from horizontal plane of skull than B. fricki	
Auditory Bulla	-incorporated with mastoid -less inflated than in B. fricki	-mastoid and auditory bulla coalesced -bulla appears uninflated	-fused with mastoid - well inflated and elongated dorsoventrally	- forms a continuous flat surface with the mastoid and occipital -flattened medially and posteriorly	
Mastoid Process	-massive -diagonal ridge present	-large but not strongly inclined anteriorly -slight diagonal ridge present	-forms a thin, flat protuberance fused to auditory bulla	-greatly enlarged and extends below bulla	
Maxilla Pit	-present but small	-large; 1 cm by 1.5 cm; 1 cm deep	-unclear	-unclear	-unclear
Transverse Ridge of Frontal	-large	-present but not as prominent as in B. oregonensis	-unclear	-unclear	
Age of specimen	Between 7.5-11 million years	Hemphillian	Late Clarendonian, Early Hemphillian	Latest Clarendonian	Clarendonian
Number of specimens documented	One	One	Nine	Twenty-five	One

CONCLUSION

Barbourofelis oregonensis most closely resembles *B. fricki* in size and overall skull shape, but the doubly grooved canine, longer carnassial, absence of P3 and M1, the more prominent transverse ridge on the frontal bone, larger temporal fossa and less pronounced depression in front of the orbit differentiate it from *B. fricki*. *B. oregonensis* also differs from *B. fricki* in emphasis of certain groups of facial muscles.

The larger temporal fossa, reduction of the dental formula, longer carnassial and the doubly grooved canine in *B. oregonensis* probably enhanced the efficiency of this species in fracturing tough connective tissues compared to other members of *Barbourofelis*.

The skull in *Barbourofelis* is specialized in unique ways for carnivory. The orientation of the occipital region allowed greater dorsal flexion of the skull, important in use of the canine in stabbing. The area of origin of the temporalis musculature is enlarged and the portion of the masseter originating in the extensive scar above and behind the P4 was enlarged, allowing for exertion of high occlusal stresses along the elongated carnassial blade. The digastric, which originates on the enlarged mastoid and inserts on the ventral surface of the mandible, may have been larger and would have aided in opening the mouth widely. The sternomastoid, which also inserts on the mastoid and turns the head laterally, may also have been larger.

The posterior surface of the mastoid process is greatly enlarged, indicating thick ventrolateral neck musculature that would have functioned in flexing the skull downward and controlling its lateral movements, activities fundamental to use of the canine.

Control of the lateral flexure of the canine was particularly important in *Barbourofelis*, owing to the thin canine blades. The uniquely thin canines minimized the degree of stretching of prey tissue and made movement of the blade within the prey more efficient, especially during slicing movements. The grooves also reduced friction within prey tissue because the ridges separating them held the tissue away from the interior surfaces of the grooves during slicing movements. The prominent mandibular flange protected the canine from lateral bending when the mouth was closed, whereas during engagement with prey the grooved lateral and lingual surfaces resisted lateral bending by maximizing stiffness relative to overall thinness of the blade.

These attributes, especially the presence of a very thin canine blade and the unusual development of the mastoid processes, suggest that the two largest species, *B. oregonensis* and *B. fricki*, used the massive cranial and neck musculature in a different behavior than other feliforms, one involving a greater role for slicing movements of the canine. This slicing activity could have involved opening large wounds, but could also have been used in removing portions of a carcass because the ability for fine control of lateral movements of the head would be a requirement for the use of such thin canines.

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