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1970


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BULLETIN OF
The University of Nebraska State Museum

VOLUME 9, NUMBER 1
OCTOBER, 1970

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A New Tribe of Saber-Toothed Cats
(*Barbourofelini*) from the Pliocene
of North America





Frontispiece.—*Barbourofelis tricki*, new genus and species, holotype, U.N.S.M. 76000, skull and mandibular ramus, from the Kimball Formation (very late Pliocene), Frontier County, Nebraska. X 1/2.

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ABSTRACT

A New Tribe of Saber-toothed Cats (Barbourofelini) from the Pliocene of North America

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A new genus of Pliocene Saber-toothed felid, *Barbourofelis*, is proposed and two new species *B. fricki* and *B. morrisoni* are described. These two forms and other described material represent an unusual lineage of felids with long sabers, shortened crania, and massive postorbital bars. The tribal name Barbourofelini is proposed for this lineage which is presently known in North America from deposits ranging in age from Clarendonian through Kimballian. The Barbourofelini apparently migrated from Eurasia to North America in the Late Miocene or Early Pliocene. *Sansanosmilus* of the French Vindobonian appears to represent the ancestral stock of these cats. The following genera of other saber-toothed felids are discussed: *Hoplophoneus*, *Eusmilus*, *Dinictis*, *Nimravus*, *Ekgmoiteptecela*, *Machairodus*, *Ischyrosmilus*, *Homotherium*, *H. (Dinobastis)*, *Megantereon*, and *Smilodon*. The two generic names *Albanosmilus* and *Grivasmilus* also are considered. The continued usage of the provincial age terms Valentinian and Kimballian is recommended, and a faunal list for these units in Nebraska is provided.

CONTRIBUTION OF the Department of Geology, College of Arts and Sciences, and the Division of Vertebrate Paleontology of the Museum.

A New Tribe of Saber-toothed Cats (Barbourofelini) from the Pliocene of North America⁴

INTRODUCTION

The Kimballian fauna from a fossil locality along Medicine Creek, a tributary of the Republican River in southwestern Nebraska, was first brought to the attention of paleontologists by Erwin H. Barbour (1927, 1929), when he published on a new genus and species of longirostral mastodont, *Amebelodon fricki*. The fossil locality was discovered by Alex Keith, a local farmer, who lived along Lime Creek, a tributary of Medicine Creek in Frontier County. He reported it to the State Museum of the University of Nebraska. Phillip Orr,⁵ Chief Preparator at

the Museum at that time, made the first excavations with the cooperation of Alex Keith in April of 1927. During the summer of the same year, Bertrand Schultz, an undergraduate assistant in the Museum, did further preliminary investigation of the fossil locality, and since that time the Museum has done extensive work in the Tertiary and Quaternary deposits of the Medicine Creek region. The faunal evidence was so different from that of other Nebraska localities known to Barbour that he was not sure of the geologic age, i.e., whether it was late Pliocene or early Pleistocene. Later geological work by the Museum's field parties has shown that the sediments, which produce the faunal evidence, are very late Pliocene or Kimballian in age. (See p. 23, this paper, for detailed discussion of the Kimballian.)

The most extensive work in the Medicine Creek area was commenced in 1946, when it was learned that the U.S. Bureau of Reclamation planned to build a dam on Medicine Creek as part of the Missouri Basin Development Program, and that some of the important fossil-producing areas along Lime Creek would be inundated, and the fossil evidence would be forever lost to science. A paleontological salvage program on a large scale was started in 1946 under the direction of W. D. Frankforter and C. Bertrand Schultz. The salvage work was intensified the following year, and the first offi-

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² Member of various paleontological expeditions of the University of Nebraska State Museum and Museum Volunteer since August, 1931.

³ Research Assistant, Department of Geology and University of Nebraska State Museum (1969-1970); field party leader, Division of Vertebrate Paleontology of the Museum (1965-1969).

⁴ The research for this paper has been supported by grants from the University of Nebraska Research Council, including a Research Assistantship (September, 1969, to June, 1970) for the junior author. The Board of Regents, University of Nebraska, also granted the senior author a leave of absence from his regular duties for six months (1969-1970) for paleontological research in Europe and U.S.A.

⁵ Later associated with the Field Museum of Natural History and the Santa Barbara Museum of Natural History, and now living in Santa Barbara, California.

cial vertebrate paleontological and archaeological salvage agreement was drawn up with the Smithsonian Institution (River Basin Survey). Allan Graffham was put in charge of the U.N.S.M. field party, which salvaged the fossils along Medicine Creek. The local staff of the U.S. Bureau of Reclamation furnished a bulldozer and other equipment to speed up the salvage program. Vertebrate fossils were salvaged from both the upper part of the Ash Hollow Formation and the lower part of the Kimball Formation. Three important Early Man sites—Lime Creek Site (= University of Nebraska State Museum Collecting Locality, Ft-41), Red Smoke Site (= Ft-42), and Allen Site (= Ft-50)—were discovered in the immediate proximity of the *Amebelodon fricki* Quarry, (= Ft-40). The Early Man sites were in the lower portion of Late Pleistocene Terrace-2 fills and dated from some 8,200 to 10,000 years before the present. A summary of some of the salvage work from 1946 to 1951 has been reported by the following: Schultz, Lueninghoener, and Frankforter (1948); Schultz and Frankforter (1948); Davis and Schultz (1952); and Schultz and Stout (1961). The Bureau of Reclamation completed work on the Medicine Creek Dam in 1949. Several of the paleontological and archaeological sites had been destroyed in the course of construction work, and many others had been inundated by the reservoir waters behind the Medicine Creek Dam. The normal pool level of the reservoir was reached in 1951, but the Museum has continued to salvage additional fossils and archaeological evidence. Further extensive excavations of Pliocene and Pleistocene localities along Medicine Creek and the main stem of the Republican River are planned for 1970 and 1971.

SYSTEMATIC DESCRIPTIONS

Class: MAMMALIA
 Order: CARNIVORA
 Family: FELIDAE
 Subfamily: Machairodontinae
 Barbourofelini, new tribe

Diagnosis.—Dirk-toothed cats with the following characteristics: skull with postorbital

bar; elongated and flattened saber-like canine with labial and lingual grooves, canine very finely serrated on anterior and posterior edges; longitudinal axes of carnassials parallel to each other (not directed inward as in most felids), longitudinal axes of canines and carnassials parallel to each other; palate considerably expanded laterally, posterior to canines; maxillary bone deeply excavated above carnassial (P^4) and extending posteriorly on zygomatic arch; alisphenoid canal present; ramus with large dependent flange; P_3 - M_1 sloping outward and posteriorly; carnassial notch broad and shallow.

Barbourofelis,⁶ new genus

Genotypic Species.—*Barbourofelis fricki*

Diagnosis.—Skull with postorbital bar; elongated and flattened saber-like canine with labial and lingual grooves; postorbital portion of the cranium shortened resulting in a decidedly brachycephalic skull; bullae flattened posteriorly to form part of the occipital region; posterior lacerate foramen opening on occipital region; ramus expanding in depth anteriorly, with a broad U-shaped dependent flange; symphysis of rami united almost down to ventral border of flange; pronounced convexity on labial side of ramus in area of cheek teeth with P_3 - M_1 sloping outward and posteriorly; P^3 and P_3 greatly reduced.

Barbourofelis fricki,⁷ new species

Holotype.—Skull (essentially uncrushed and complete) with I^1 - I^3 alv., C/(br.), P^3 - P^4 (br.), M^1 (alv.), and associated right ramus with I_1 (alv.)-

⁶ Named in honor of Dr. Erwin H. Barbour, Director of the University of Nebraska State Museum from 1891 to 1941, who did so much to promote research in vertebrate paleontology in Nebraska. The holotype of *Barbourofelis fricki* was discovered only a few days after Dr. Barbour's death in 1947.

⁷ Named in honor of the late Mr. Childs Frick, who planned and cooperated with the University of Nebraska State Museum from 1932 to 1965. Dr. Erwin H. Barbour and Mr. Childs Frick entered into a cooperative research and collecting agreement in August, 1932, and many cooperative projects in stratigraphic paleontology were carried on between their respective institutions during the following thirty-three years.

/ C, P₃-M₁ (P₄ br.),⁸ U.N.S.M. 76000 (Figs. 2-6, Tables 1 and 2).

Referred Specimens from Type Locality.—Left I², U.N.S.M. 76002 (Fig. 7); left P₃, U.N.S.M. 76003 (Fig. 7); axis vertebra, U.N.S.M. 76004; right pelvis, U.N.S.M. 76005; right tibia, U.N.S.M. 76006; right scapho-lunar, U.N.S.M. 76007.

Type Locality.—U.N.S.M. Coll. Loc. Ft-40, = "Amebelodon fricki Quarry," (E. ½, SW. ¼, SE. ¼, Sec. 15, T. 5N., R. 26W.), 8 mi. N. and 8½ mi. W. of Cambridge in Frontier County, Nebraska.

Stratigraphic Occurrence.—Upper Pliocene, Ogallala Group, Kimball Formation, Sidney Member (see Fig. 8), from channel deposits which rest on upper part of Ash Hollow Formation.

Diagnosis.—Largest known species of the genus; skull with massive postorbital bar; cranium much shorter proportionately than in other species; mastoid process almost touching zygomatic arch above post glenoid process; mastoid process and auditory bulla coalesced with tympanic bulla appearing uninflated; longest sabers of genus; P³ reduced to a small tooth with a single root; P⁴ greatly lengthened.

Description.—Skull about size of African lion (*Felis leo*) or Pleistocene saber-toothed cat (*Smilodon californicus*); extremely brachycephalic (resulting from shortening of cranium without comparable reduction of muzzle); markedly triangular in shape (when viewed from above); occipital region decidedly elevated with a smooth slope of about 30° running from tip of nasal to occipital crest (contrasting with convex profiles shown by dorsal margins of skulls in most cats); bone is light and cancellous, but very strong; muzzle broad and robust (slightly swollen anterior to orbits to accommodate alveoli for canines, but not inflated as in the marsupial saber-tooth, *Thylacosmilus*); infraorbital foramen, oval in shape, situated just above anterior border of carnassial (larger than infraorbi-

tal foramen in *Smilodon*); large deep pit above infraorbital foramen (not observed in other felids); premaxillary forming continuous curve with maxillary; jugal and maxillary excavated above carnassial; nasals broad and massive, similar to those of *Smilodon*; lower margin of anterior nasal opening roundish as in *Smilodon*; nasal region slightly concave medially with superior margins of frontals almost flat; frontals very broad with postorbital processes overlapping and joining jugals, forming a heavy postorbital bar (feature not approximated by any other felid genus but similar to condition in *Thylacosmilus*); postorbital process of frontal expanding outward and downward forming a partial wall to posterior-dorsal portion of orbit; sagittal crest unusually high and convex, bifurcating anteriorly to form a continuous crest along the frontal and downward along posterior border of post-orbital bar to zygomatic arch; numerous small but prominent foramina or pits along inferior margin of sagittal crest; parietals are roughened; occipital crest prominently developed and extending downward to tips of mastoid processes; occipital region fairly flat and expanding laterally at level of condyles, incorporating posterior borders of mastoid processes and auditory bullae; occipital region nearly perpendicular to horizontal plane of skull rather than being inclined as in most other felids (*Thylacosmilus* similar to *Barbourofelis fricki* in this respect); posterior lacerate foramen opening just below condyles on occipital region, rather than ventrally (due to angle of occipital and shortening of cranium); occipital condyles and neural canal nearly perpendicular to occipital; prominent condyloid fossa above, lateral and below occipital condyles (not deeply excavated ventrally as in *Smilodon*); two prominent pits located just above condylar foramina and below buttresses for condyles; pits for *rectus capitis anticus major* muscle at apex of occiput represented by two shallow depressions on either side of external occipital protuberance (not two deeply incised grooves as in *Smilodon*); mastoid process and auditory bulla coalesced so that the bulla appears uninflated (mastoid process extensively excavated and invaded by tympanic cavity); external auditory

⁸ Abbreviations used in descriptions: alv., alveolus or alveoli; br., broken; rt., root or roots; U.N.S.M., University of Nebraska State Museum; F.A.M., Frick Collection, American Museum of Natural History; U.C., University of California Museum of Paleontology.

meatus moderately ellipsoidal, and located between mastoid process and glenoid fossa; mastoid process large but not strongly inclined anteriorly (almost in contact with glenoid fossa due to extreme shortening of cranium); paraoccipital process absent; condylar foramen having a common groove with posterior lacerate foramen, extending vertically downward to about mid-point of bulla; tympano-hyal a narrow groove; basioccipital between bullae bearing two deeply incised grooves separated by a high median septum, with grooves roughened, probably for insertion of *rectus capitis anticus major* muscle (neither *Smilodon* nor *Felis leo* show such deep grooving and such a high median ridge); basisphenoid more narrow and trough-like than in *Smilodon*; ventral margins of mastoids roughened (not grooved as in *Smilodon*); deeply incised groove anterior to postorbital bar, descending along inner margin of orbit, enclosed as alisphenoid canal posterior to foramen rotundum; optic foramen and orbital fissure above groove; foramen rotundum below orbital fissure but separated by a narrow septum; foramen ovale posterior and ventral to alisphenoid canal; deep pit just ventral to eustachian canal; postglenoid foramen absent; tympano-hyal pit long and narrow, directly adjacent to the small stylomastoid foramen; carotid canal and related foramina not evident; sphenopalatine opening apparently absent; palate short but very broad; premaxillary and maxillary deeply sculptured anterior to and between canines; two grooves running from anterior portion of premaxillaries to palatine fissures; median ridges and grooving of palate (typical of *Smilodon*) absent; two large palatine foramina behind canines and at posterior margin of rugose area of palate; upper incisors uncrowded; canines wide anterior-posteriorly but unusually long and thin; shallow grooves on inner and outer margins of canine just anterior to midline (*Sansanosmilus* has similar grooves); anterior and posterior margins finely serrated; P³ vestigial having one root and two cusps (directed posteriorly and abutting against P⁴); P⁴ only functional upper cheek tooth; paracone and metacone form an unusually long, thin, shearing blade; protocone absent; minute pit present

posterior to P⁴ on lingual side (perhaps alveolus for vestigial M¹).

Ramus proportionally larger and more massive than in other felids, becoming progressively deeper anteriorly, and widening into a flange for protection of saber; four small mental foramina scattered on surface of dependent flange; mandibular symphysis extending downward almost to ventral border of flange (Fig. 6); coronoid process with upper margin flattened (lower than in any other felid); mandibular condyle and angular process of ramus extremely close together; oval masseteric fossa small but deeply depressed; three lower incisors compressed but still in line; I₁ much reduced; lower incisors and canine serrated posteriorly; lower canine incisoriform; cheek-teeth inclined posteriorly; P₃ single-rooted and extremely reduced, with crown consisting of two small rounded cusps; paraconid of P₄ with a long shearing surface (anterior margin damaged); protoconid of P₄ high and very long; M₁ long and thin; paraconid and protoconid of M₁ combined to form a single knife-edge with a shallow carnassial notch.

Discussion.—*Barbourofelis fricki* represents the extreme of adaptation in this group of saber-toothed felids. These felids had evolved adaptations for the dirk-toothed existence by very late Pliocene times, even exceeding those of the saber-tooth *Smilodon* of the Late Pleistocene. However, the adaptations of *Barbourofelis* are along different lines than those present in *Smilodon*, which retains the more "normal" felid contours to its skull. In *Smilodon* the braincase remains long and inflated with the occipital region inclined. The sabers are robust, the ramus is weak, and there is no postorbital bar. These characters also are in part shared by *Sansanosmilus*, the probable Miocene ancestor of *Barbourofelis*. In *B. fricki* the braincase is shortened and its capacity is relatively small (Figs. 1 and 4). The occipital is extraordinarily elevated with a high sagittal crest permitting the attachment of powerful temporal muscles. The skull is additionally strengthened by a postorbital bar and the back of the orbit is partially closed off in a way analogous to some primates, perhaps to protect the orbit from the contracted temporal muscles. In front of the orbit is a large pit or

lacrimal fossa which is absent in all other felids examined. The palate between and just posterior to the canines is sculptured, but the ridges and grooves, typical of *Smilodon*, are absent. Merriam and Stock (1932, p. 36) regarded *Smilodon* as a bloodsucker because of the presence of these. The maxillary bone is very deeply excavated for the superficial masseter muscle, and this forms a common "pocket" with the masseteric fossa on the ramus.

In *Smilodon* the cheek teeth, the glenoid fossa, the ventral border of the mastoid process, and the occipital condyles are all approximately in the same horizontal plane. In *B. fricki* the ventral border of the mastoid process occurs well above the glenoid fossa and the occipital condyles are well above the ventral border of the mastoid process. The zygomatic arch and glenoid fossa form an angle of about 68° with the skull giving it a triangular appearance when viewed from above. The post-glenoid process is well developed, but the anterior process is nearly absent. The distance between the glenoid fossa and the upper carnassial is about the same as in *Smilodon*. The internal wall of the left bulla has been opened by the preparators so that the interior can be examined. It appears that the septum dividing the bulla into two parts is absent. This also seems to be true in many of the other early felids including *Nimravus* (Hough, 1953, p. 106). The presence of the alisphenoid canal is another feature characteristic of many of the early felids but has been lost in the Felinae, and also in most of the later machairodonts.

The only upper incisor recovered is a left I², U.N.S.M. 76002 (Fig. 7), which is strongly recurved and more caniniform than the upper incisors of *Smilodon*. Two wear facets on the incisor show that the upper incisors interlocked with the lower incisors as in *Smilodon* (Miller, 1969, Fig. 1). The proximal one-fourth of the right upper canine is present, and the left one is represented by the proximal two-thirds. The latter has been restored by projecting the anterior and posterior curves of the saber until they meet (Fig. 2). With this restoration the sabers project slightly past the protective flange on the mandible when the mouth is closed. It is pos-

sible that the restoration makes the sabers a few millimeters too long. In any case they are thinner in cross-section, wider anteroposteriorly, and relatively longer than the upper canines of *S. californicus*. The anterior and posterior margins of the saber are finely serrated. There are approximately 47 serrations per centimeter. The alveolus of the canine extends up to the posterior margin of the nasals. The bone is expanded around it as in *Smilodon*, and is not inflated as in *Thylacosmilus* (Fig. 10). It cannot presently be determined if the roots of the canines were closed as in all other cats, or open and ever-growing as in *Thylacosmilus* (Riggs, 1934, p. 17). The pulp cavity was very large and the walls of the tooth comparatively thin. It seems likely that the root was closed but matured very slowly.

The palate of the *Barbourofelis fricki* is broad with the cheek tooth row parallel to the long axis of the skull. In all other felids we have examined, the cheek tooth row is inclined anteriorly towards the long axis of the skull. This accounts for an unusual contour of the ramus where the cheek tooth row is set away from the main body of that bone. The P³ is vestigial, having only one root, and is directed posteriorly, abutting against the P⁴. The P⁴ is perhaps the most remarkable example of carnassial specialization known in any carnivore. It is the only functional cheek tooth in *B. fricki*, and has a restored length of 63 mm. The right P⁴ is missing but shows alveolae for the two broad thin roots. The anterior one-fourth of the left P⁴ is restored and the protocone is absent. The paracone and the metacone form a long, thin shearing blade with a knife-edge. The labial margin shows vertical wear striations indicating an almost straight up and down motion. The maxillary has a ventral buttress of bone along the posterior margin of the carnassial. This buttress contains a small round shallow pit which might have been the alveolus for the M¹. If so, this tooth had been lost fairly early in life. The premaxillary is narrower than in *Smilodon* but forms a continuous curve with the margin of the maxilla rather than being set apart by a constriction just in front of the canines as in non-machairodont cats.

TABLE 1
Barbourotelis, NEW GENUS
 COMPARATIVE MEASUREMENTS¹ OF SKULLS

SKULLS	<i>B. fricki</i> , n. sp.	<i>B. morrissi</i> , n. sp.
	Holotype U.N.S.M. 76000	Holotype F:A.M. 79999
Length from anterior end of alveolus of I ¹ to posterior end of condyles.....	298	209
Basal length from anterior end of alveolus of I ¹ to inferior notch between condyles.....	280	196
Length from anterior end of premaxillary to end of posterior inion.....	293	220
Length from anterior end of alveolus of I ¹ to anterior end of posterior nasal opening.....	84
Length of palate from anterior end of premaxillary to line tangent to posterior surfaces of maxillary parapets	168	101
Anteroposterior diameter of nasals.....	85	59
Width of anterior nares.....	35
Greatest width across muzzle at canines.....	(90) ²	69
Least width between superior borders of orbits.....	105	68
Width across postorbital processes.....	(160)	119
Least width of postorbital constriction.....	61	47
Greatest width across zygomatic arches.....	204	147
Anterior palatal width (minimum) between superior canines.....	50	43
Width across palate between posterior ends of alveoli for superior carnassials.....	130	87
Greatest width across mastoid processes.....	132	99
Greatest width across condyles.....	68	51
Length from anterior end of canine alveolus to posterior end of P ⁴	134	80
Length from anterior end of P ³ to posterior end of P ⁴	69	49
Length of diastema from posterior end of alveolus for C/ to anterior end of alveolus for P ³	10
Width of incisor series measured between outer sides of alveolae for third upper incisors....	50	40
I ¹ greatest transverse diameter.....	4.8
I ² greatest transverse diameter.....	5
I ³ greatest transverse diameter.....	6
C/ anteroposterior diameter at alveolus.....	51	25
C/ transverse diameter at alveolus.....	12.5	9
P ³ anteroposterior diameter.....	7.4
P ³ greatest transverse diameter.....	5.6
P ⁴ anteroposterior diameter.....	(63)	42.1
P ⁴ greatest transverse diameter.....	13	11.5
P ⁴ anteroposterior diameter of base of paracone.....	20	16
P ⁴ length from anterior base of paracone to anterior end of tooth.....	12
P ⁴ length of metacone blade (at base).....	25.6	16.5
M ¹ anteroposterior diameter.....	4.7 ³
M ¹ greatest transverse diameter.....	8.4

¹ The measurements are taken to the nearest millimeter except on dentition where they are measured to the nearest one-tenth of a millimeter.

² () = approximate

³ The M¹ is actually tilted so that the top of the crown of the tooth is facing anteriorly, and the long axis runs dorsoventid. The antero-posterior diameter given is that which we feel would be comparable with similar measurements in *Hoplophoneus* and *Dinictis*.

TABLE 2
Barbourofelis, NEW GENUS
 COMPARATIVE MEASUREMENTS OF MANDIBULAR RAMI

MANDIBULAR RAMI	<i>B. tricki</i> , n. sp. Holotype U.N.S.M. 76000	<i>B. morrisi</i> , n. sp. Referred F.A.M. 79999	<i>B. osborni</i> (Merriam) Holotype U.C. 19476	? <i>B. whitfordi</i> (Barbour and Cook) Holotype U.N.S.M. 25546
Length from anterior end of symphysis to posterior end of condyle.....	257	160	129
Length from anterior end of outer flange to posterior end of condyle.....	239	142	126
Length from anterior end of /C to posterior end of M ₁	160	92	83	81
Distance from alveolus of /C to ventral border of flange.....	155	(67)	45	48
Length of diastema measured between alveoli for /C and P ₃	68	32	28	25
Length from anterior end of P ₃ to posterior end of M ₁	76.9	50.7	46.4	(47.5)
Length of symphysis measured along anterior border.....	130	69	(50)	39
Least depth of ramus below diastema.....	67	45	(33)	29
Depth of ramus below posterior end of M ₁	58	35	(30)	29
Depth of ramus anterior to M ₁	68	41	32	33
Thickness of ramus below M ₁	26	19	(17)	15
Height from inferior border of angle to summit of condyle.....	33	31	23
Height from inferior border of angle to summit of coronoid process.....	73	52	43
Transverse width of condyle.....	49	32	28
Greatest depth of condyle.....	21	15	12
I ₁ greatest anteroposterior diameter at base.....	(10.5)	7.2	(6.5)
I ₁ greatest transverse diameter.....	(2.5)	3.5	(2.5)
I ₂ greatest anteroposterior diameter at base.....	10	8.5	(8)	(5.5)
I ₂ greatest transverse diameter.....	7	5	(4)	(3)
I ₃ greatest anteroposterior diameter at base.....	12	9.8	(8.5)	(7.5)
I ₃ greatest transverse diameter.....	7.4	5.8	(5)	(4.5)
/C greatest anteroposterior diameter at base of enamel.....	12	8.6	(10)	(10)
/C greatest transverse diameter.....	8	6.1	(6.5)	(5.5)
P ₃ anteroposterior diameter.....	7.7	5.8	7.3	(5.8)
P ₃ greatest transverse diameter.....	5.8	4.7	5.8	4.5
P ₄ anteroposterior diameter.....	(26.4)	17.4	18	16.8
P ₄ greatest transverse diameter.....	11.2	8.3	8	7.4
M ₁ anteroposterior diameter.....	38.5	26.5	24	25.2
M ₁ greatest transverse diameter.....	14.5	10	11	9.5
M ₁ length of protoconid blade.....	16.6	10.9	10.7	11.4

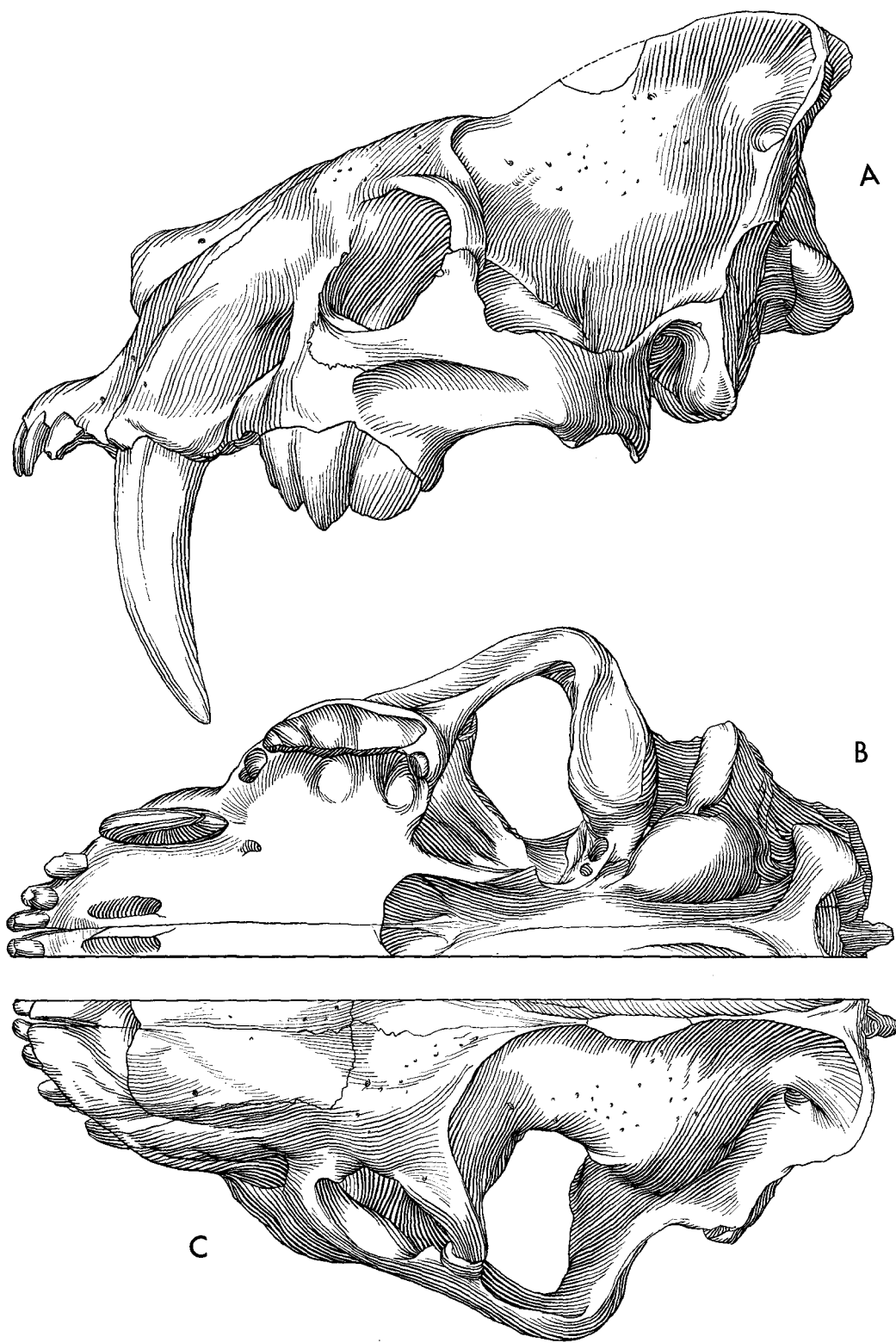
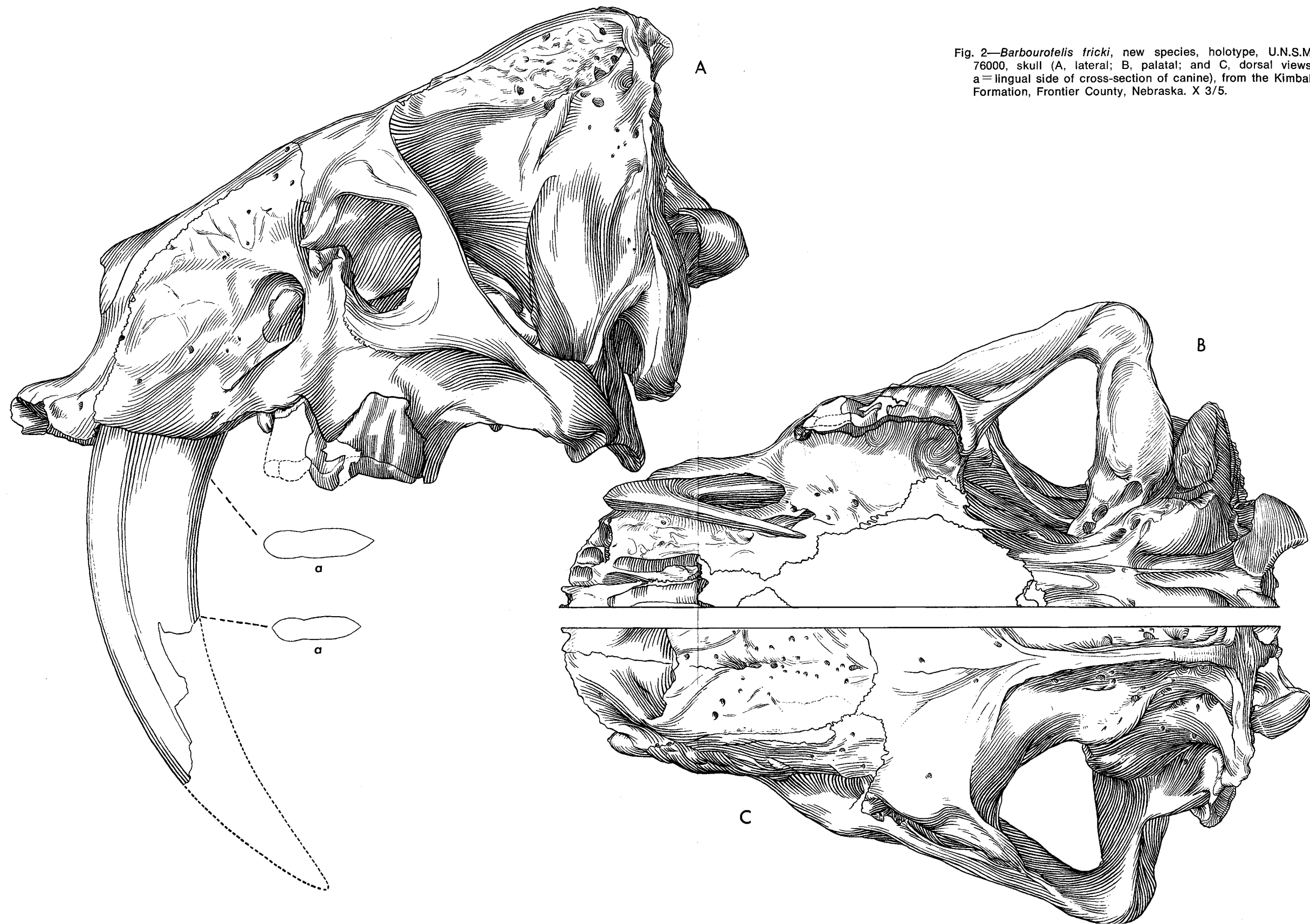


Fig. 1—*Barbourofelis morrisoni*, new species, holotype, F.A.M. 79999, skull (A, lateral; B, palatal; and C, dorsal views), from the middle part of the Ash Hollow Formation, Cherry County, Nebraska. X 3/5.

Fig. 2—*Barbourofelis fricki*, new species, holotype, U.N.S.M. 76000, skull (A, lateral; B, palatal; and C, dorsal views; a=lingual side of cross-section of canine), from the Kimball Formation, Frontier County, Nebraska. X 3/5.



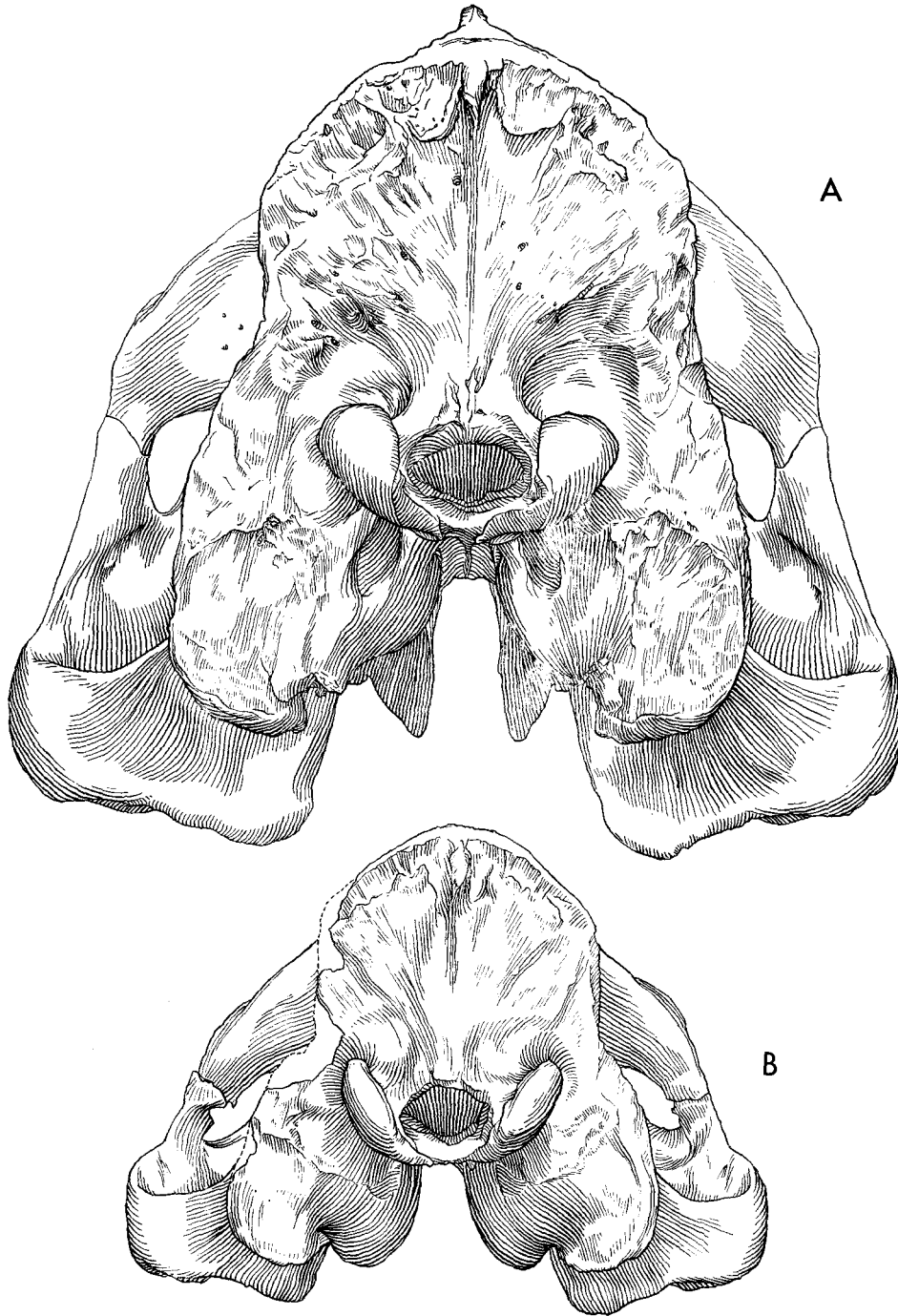


Fig.3—Occipital views of skulls: A, *Barbourofelis tricki*, new species, holotype, U.N.S.M. 76000, from the Kimball Formation, Frontier County, Nebraska. B, *B. morrissi*, new species, holotype, F.A.M. 79999, from the middle part of the Ash Hollow Formation, Cherry County, Nebraska. X 3/5.

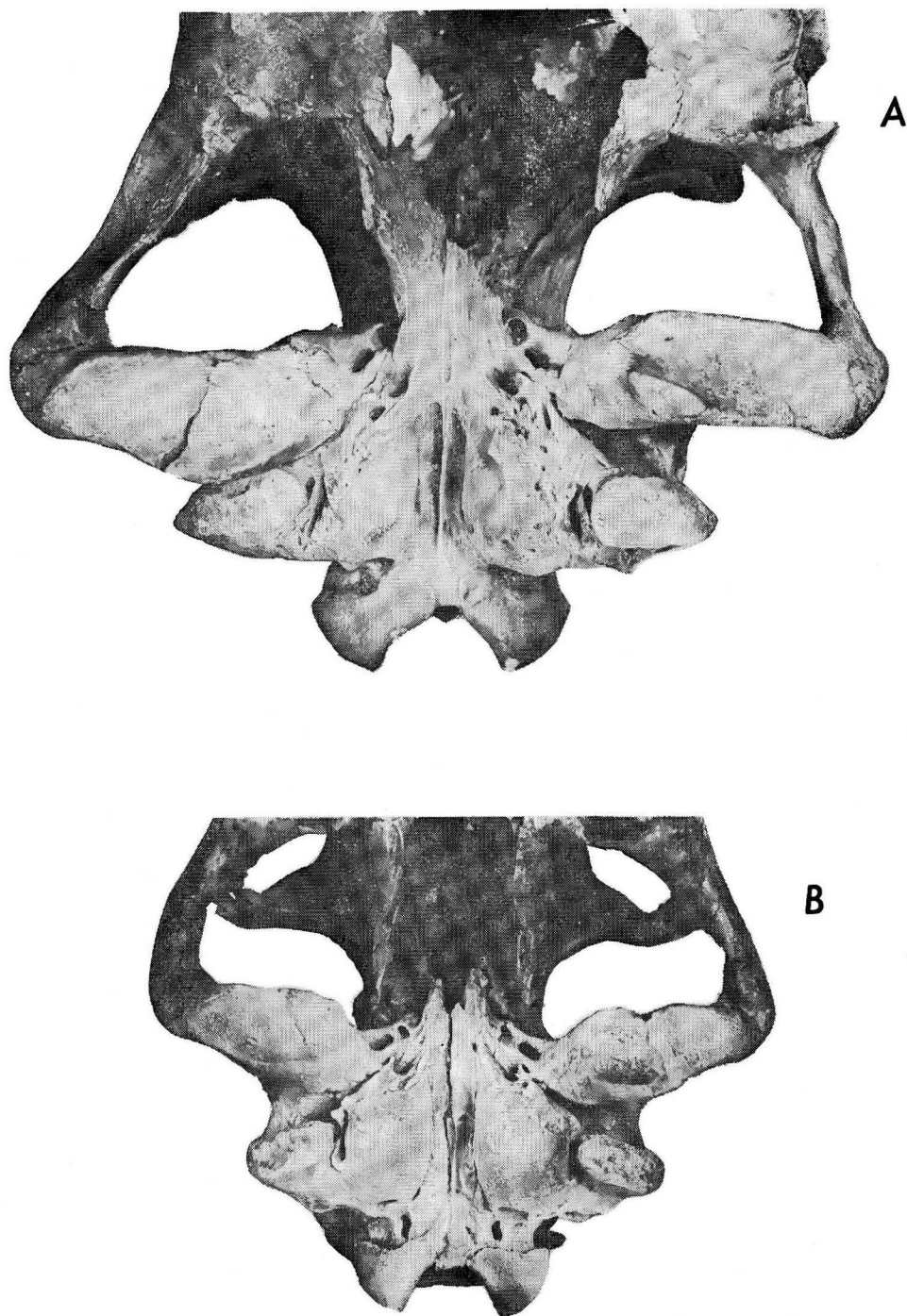


Fig. 4—A, *Barbourofelis fricki*, new species, holotype, U.N.S.M. 76000, ventral view of basicranium; B, *Barbourofelis morrissi*, new species, holotype, F:A.M. 79999, ventral view of basicranium. X 3/5.

The ramus is exceptionally large and powerful contrasting with the relatively weak ramus of *Smilodon* which may be somewhat constricted posterior to the flange. The loss of the flange in *Smilodon* may be a specialization, as it might permit that form to slash with its sabers with the mouth shut. The only other flanges really comparable to those of *Barbourofelis fricki* are those of *Eusmilus* the middle to late Oligocene felid and *Thylacosmilus* (Fig. 10), the Pliocene saber-toothed marsupial from South America. The flange of *B. fricki* bears a shallow groove on its surface which approximates the contour of the upper canine. Each incisor consists of a single cusp and I^1 - I^3 are more caniniform than the incisors of *Smilodon*. The incisors and the canine are serrated posteriorly. The incisors show sharp wear facets on their lingual and labial margins, where they interlocked with the upper incisors. The canine is of about the same size and shape as the incisors. The lower carnassial (M_1) and P_4 jointly form the shearing blade which is opposite to the upper carnassial, and both show the same vertically striated wear as the upper carnassial. The diastema between the lower canine and P_3 is 68 mm. in *B. fricki*. The dorsal edge of the diastema is thin and extends directly back from the lower canine to a point just anterior to P_3 where it swings sharply to the labial side. The mandible swings back into the same vertical plane as the diastema behind the carnassial causing the cheek teeth to be on a sort of lateral "island" away from the ramus. The symphyseal suture is constricted slightly below the mid-line of the ramus, and just posterior to this point is a pit containing a foramen, and a ridge extends downward from the alveolus of the canine around the symphysis and up onto the area below P_3 , where it merges with the side of the ramus just below the mid-line. Gregory (1942, p. 356) also reported this condition for ?*B. whittfordi*. The mandible of *B. fricki* is deeply pocketed and roughened between the posterior crest of the flange and the body of the mandible.

The axis vertebra (U.N.S.M. 76004) referred to *Barbourofelis fricki* has a high thin neural spine similar to that on the axis of *Hoplophoneus*. It is unusually short and broad with trans-

verse processes extending back past both the postzygapophyses and the centrum. The referred pelvis (U.N.S.M. 76005) is narrow and massive as it is in *Hoplophoneus* (Hough, 1949, p. 131). The referred tibia (U.N.S.M. 76006) is shorter than in *Smilodon* and is very heavily built indicating a powerful animal with short limbs.

Barbourofelis morrissi,⁹ new species

Holotype.—Skull (essentially uncrushed and complete) with I^1 -C/(I^3 br.), P^3 (alv.)- M^1 ; F:A.M. 79999 (Figs. 1, 3, 4; Table 1); collected by Morris F. Skinner and associates, 1936.

Type Locality.—F:A.M. Coll. Loc., "Leptarctus Quarry," (NE. $\frac{1}{4}$, NE. $\frac{1}{4}$, sec. 28, T. 34N., R. 25W., 3 mi. S. of Sparks P.O., Cherry County, Nebraska.

Stratigraphic Occurrence.—Pliocene, Ogallala Group, Middle Ash Hollow (see Fig. 8). From a channel deposit which rests unconformably on the Cap Rock Member (Skinner, Skinner, and Gooris, 1968, p. 409) of the Ash Hollow Formation.

Referred Example.—Right ramus with I_1 (br.) -/C, P_3 - M_1 ; F:A.M. 80000 (Figs. 5-6; Table 2); collected by Morris F. Skinner and associates, 1936.

Locality.—F:A.M. Coll. Loc., "Hans Johnson Quarry," SE. $\frac{1}{4}$, NW. $\frac{1}{4}$, sec. 26, T. 34N., R. 25W., $1\frac{1}{2}$ mi. E. and $3\frac{1}{4}$ mi. S. of Sparks P.O., Cherry County, Nebraska.

Stratigraphic Occurrence.—Same as holotype.

Diagnosis.—Postorbital bar felid having a skull decidedly smaller than that of *Barbourofelis fricki*, with less brachycephaly and proportionately smaller sabers; P^3 and P_3 less reduced than in *B. fricki*; ramus less expanded anteriorly and flange proportionately less deep than in *B. fricki*.

⁹ Named in honor of Mr. Morris F. Skinner, Frick Assistant Curator, Department of Vertebrate Paleontology, American Museum of Natural History. Morris Skinner and his associates have contributed much to a better understanding of the Tertiary deposits in Nebraska during the past 40 years.



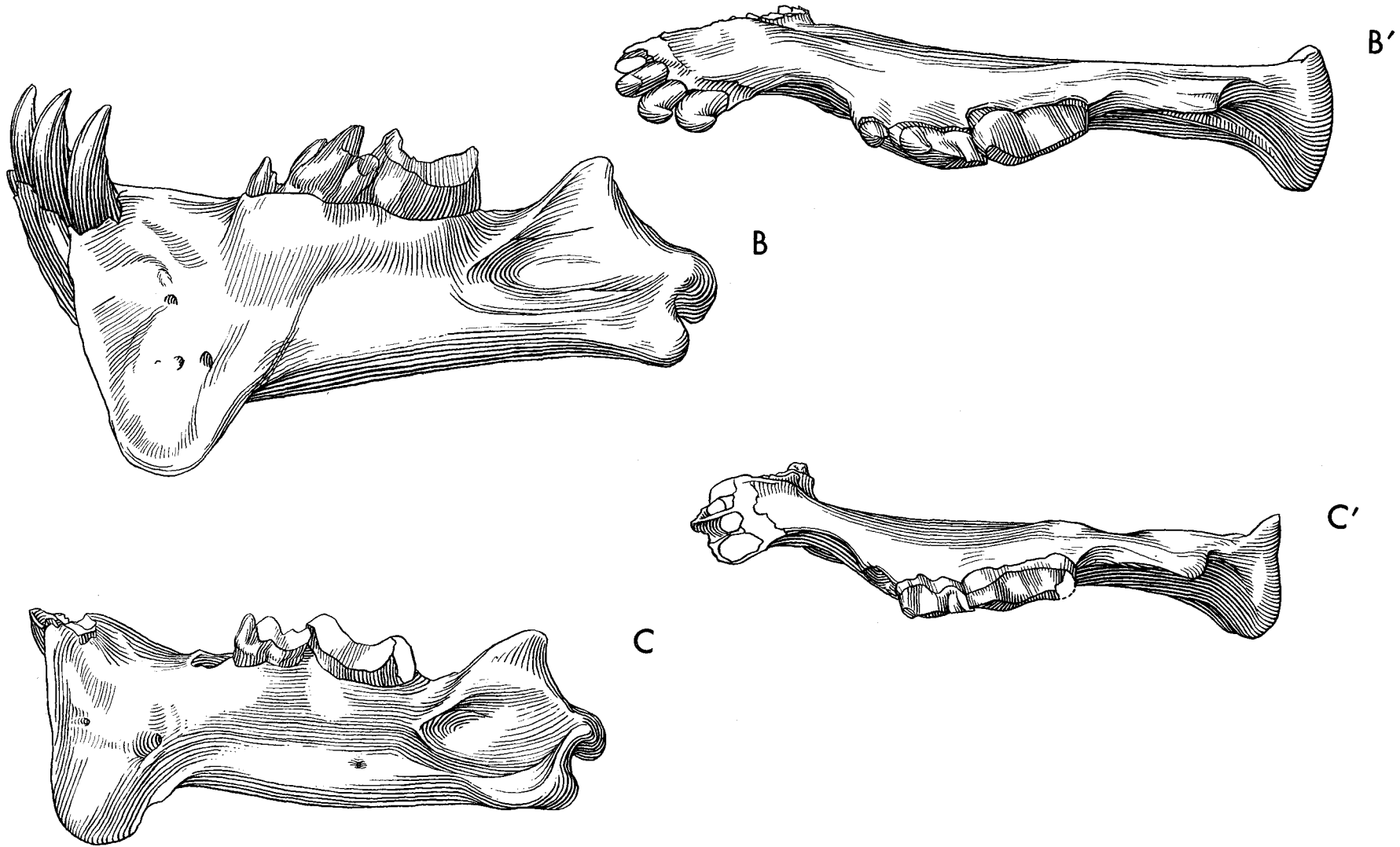


Fig. 5—Mandibular rami: *Barbourofelis fricki*, new species, holotype, U.N.S.M. 76000 (A, lateral view; A¹, occlusal-both reversed), from the Kimball Formation, Frontier County, Nebraska; *B. morrisoni*, new species, referred left ramus, F:A.M. 80000 (B, lateral view; B¹, occlusal), from the middle part of the Ash Hollow Formation, Cherry County, Nebraska; ?*B. whitfordi* Barbour and Cook, holotype, U.N.S.M. 25546 (C, lateral view; C¹ occlusal-both reversed), from the lower part of the Ash Hollow Formation, Brown County, Nebraska. X 3/5.



Fig. 6—A, *Barbourofelis fricki*, new species, holotype, U.N.S.M. 76000, lingual view of right ramus; B, *Barbourofelis morrisoni*, new species, referred, F:A.M. 80000, lingual view of left ramus (reversed). X 3/5.

Description.—Skull about size of jaguar (*Panthera onca*); cranium brachycephalic; occiput elevated with high thin sagittal crest; superior contour of skull more like *Smilodon* than that of *B. fricki*; muzzle broad and robust; infra-orbital foramen large, opening into a groove running to posterior margin of alveolus of canine; maxillary slightly expanded to accommodate saber; premaxillary projects anterior to canines in a smooth curve; nasals broad and massive, ending very abruptly anteriorly; external nasal opening large and similar in shape to that of *Smilodon*; frontal joining jugal to form a postorbital bar (posterior portion of orbit similar to that in *B. fricki*); lacrimal foramen small; maxillary bone excavated for superficial masseter muscle just above carnassial; frontal region slightly depressed; occipital region more inclined from horizontal plane of skull than in *B. fricki*; pits for *rectus capitu longicus* muscles narrow, paired and deep as in *Smilodon*; occipital narrow dorsally, widening considerably at condyles; auditory bulla well inflated and elongated dorsoventrally; external auditory meatus large and oval in shape; posterior sides of bulla and mastoid processes flattened to form part of occipital region; ventral border of mastoid process well below glenoid fossa; occipital condyles lower than mastoid process; mastoid process forming a thin, flat protuberance fused to auditory bulla, not excavated for tympanic sinus as in *B. fricki*; condylar foramen well separated from posterior lacerate foramen; posterior lacerate foramen forming a large triangular opening on occipital region of skull; posterior carotid foramen entirely separate from and just medial to posterior lacerate foramen; basioccipital region between bulla not so excavated or roughened as in *B. fricki*, and median ridge not so high; tympano-hyal pit small and tear-shaped; stylomastoid foramen just anterior and lateral to tympano-hyal pit; eustachian canal with single large opening; foramen ovale just anterior and lateral to eustachian canal; foramen for alisphenoid canal anterior to foramen ovale; alisphenoid canal in a deep groove containing foramen rotundum, orbital fissure, and optic foramen; no postglenoid foramen present; posterior narial opening wider and more anterior

than in *Smilodon* or *Felis leo*; anterior border of posterior nares slightly anterior to posterior edge of carnassial; pterygoid processes at about same level as glenoid fossae; palate very short and broad; small palatine foramina located just posterior to canines; palate without grooves or ridges as in *Smilodon*, with two grooves running from posterior margin of incisors to palatine fissures; palate excavated for inferior cheek teeth along P⁴; anterior edge of premaxillaries broad and rounded; incisors sharply recurved posteriorly and caniniform; I¹ through I³ increasing in size; canine long, thin, and finely serrated; canine not extending past lower edge of flange of ramus when jaw closed; P³, two-rooted; P⁴, large trilobate tooth with a small anterior cusp and a moderately large parastyle, a prominent paracone, and a distinctly elongated metacone (these cusps forming a long shearing blade); protocone absent on P⁴; maxillary swinging up to buttress posterior margin of carnassial and bearing a small elongated M¹.

Ramus expanding dorsoventrally toward symphysis with a prominent flange for saber at anterior end; V-shaped crest on margin of flange running from alveolus of canine along flange and extending up on the ramus to posterior of P₄; two mental foramina on flange, one located centrally and a larger one posteriorly and ventrally; ramus constricted before and after cheek teeth; diastema between the P₃ and /C, 31 mm; coronoid process small and very low with dorsal margin rounded; deep oval masseteric fossa just below and anterior to coronoid process; lateral edge of mandibular condyle connected by a continuous crest extending to angular process; mandibular foramen small, and opening posteriorly just anterior to mandibular condyle; mandibular symphysis extending from incisor alveolae nearly to ventral border of flange (Fig. 6), and constricted about at midpoint with a very shallow depression posterior to the constriction; incisors caniniform strongly recurved; first incisor very compressed; no accessory cusps present on incisors; canine similar to incisors, but posterior margin serrated; cheek teeth all inclined posteriorly; P₃ single rooted with one large cusp and an accessory small one; P₄

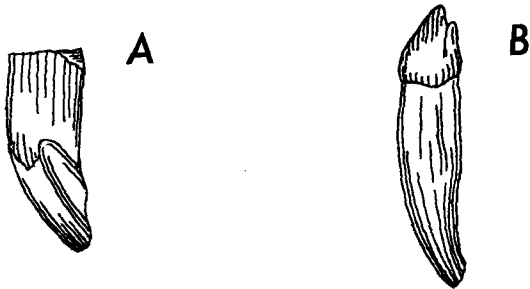


Fig. 7.—*Barbourofelis fricki*, new species, referred, from type locality, U.N.S.M. 76002, left I², and U.N.S.M. 76003, left P₃. X 1.

abutting against carnassial with the two teeth sharing a single shearing surface; paraconid on P₄ small, and closely pressed against and overlapping M₁; large protoconid on P₄ equal in height to paraconid on M₁; metaconid of P₄ with small talonid; M₁, a long shearing carnassial consisting of paraconid and elongated metaconid; carnassial notch not so well defined as in other felids; all cheek teeth with short tracts of serrations.

Discussion.—*Barbourofelis morrisoni* is a much smaller dirk-toothed felid than is *B. fricki* and probably could prey on smaller game. On the whole, the skull of *B. morrisoni* is less modified especially in terms of the elevation of the occipital and the shortening of the cranium. There is no pit anterior to the orbit, and the palate, between and anterior to the canines, is not sculptured as in *B. fricki*. The embrasure pits of *B. morrisoni*, however, are well defined as they are in *B. fricki*. The mastoid processes of *B. morrisoni* are large but separated from the posterior root of the zygomatic arch. The bullae are well inflated (Figs. 1 and 4) although not as much as shown by Ginsburg (1961, Pl. 8, Fig. 1) for *Sansanosmilus*. The cranial foramina of *B. morrisoni* resemble those of *B. fricki*, except that in the former the condyloid foramen and posterior lacerate foramen are well separated, and there also is a small sphenopalatine opening. The strongly recurved upper incisors consist of a single cusp (Fig. 1). The upper canines are complete but crushed. They do appear to have the internal and external grooves characteristic of the Barbourofelini, and are very finely serrated on the anterior and posterior margins. The P³

is missing from both sides of F:A.M. 79999 but the alveoli show that it had two roots. The P⁴ is a large trilobate trenchant tooth with a small prostyle,¹⁰ moderately large parastyle, large paracone and metacone. The cusps are arranged in a nearly straight line and are elongated, flattened lingually, and rounded labially. The buttress behind P⁴ bears a small M¹ which is tilted vertically and worn flat by the posterior margin of M₁ as in *Eusmilus*.

The ramus is not as expanded in depth as in *Barbourofelis fricki*, and the flange is not so well developed. The flange bears three small mental foramina. The coronoid process is not quite so reduced as in *B. fricki*. The mandibular foramen is small and opens posteriorly into the groove between the angular process and the mandibular condyle. The lower incisors are unicuspid and recurved posteriorly, and the lower canine is incisoriform.

Ozansoy (1965, pp. 41–43, Pl. 4, Figs. 6, 8, and 9) described a new felid, "*Megantereon piveteaui*," from the middle Sinap ("Pliocene superior") sediments located at 50–60 km. NW. of Ankara, Turkey. Examination of Ozansoy's figures and description of this felid leads the writers to the conclusion that "*M.*" *piveteaui* should be tentatively referred to *Barbourofelis*. Although the ramus of ?*B. piveteaui* (Ozansoy) is approximately the same size as that of ?*B. whitfordi* from the Clarendonian of North America, the teeth (see Fig. 12) are similar in morphology and size to those of *B. morrisoni* from the early Hemphillian of Nebraska. There is a small anterior cusp on P₃ of ?*B. piveteaui*, but it is absent in *B. morrisoni*. The coronoid process of the Turkish species appears to be more elevated than that of the Nebraska form.

***Barbourofelis osborni* (Merriam)**

Ischyrosmilus osborni Merriam, 1919, p. 545, Fig. 155; Burt, 1931, p. 273.

"*Megantereon*" *osborni* (Merriam): Gregory, 1942, p. 358.

Albanosmilus? *osborni* (Merriam): Kitts, 1957, p. 14.

¹⁰ Merriam and Stock, 1932, p. 48.

Sansanosmilus? osborni (Merriam): Mawby, 1965, p. 576.

Holotype.—Partial left ramus with I_1 - I_3 br./C alv., P_3 rt., P_4 - M_1 , Univ. of Calif. Museum of Paleo. No. 19476.

Type Locality.—New Red Rock Canon, Mohave Desert, California.

Stratigraphic Occurrence.—Upper part of Ricardo Formation, middle Pliocene.

Diagnosis.—Ramus significantly smaller than that of *B. morrisoni*; incisors proportionately smaller and more compressed than in *B. morrisoni*, but other characters similar.

Discussion.—Gregory (1942: 354–359) pointed out the close similarity between "*Ischyrosmilus? osborni* (Merriam) and "*Eusmilus? whitfordi* (Barbour and Cook) and suggested that both might be placed in the genus *Megantereon*. However, he did note the possibility of relationship to *Sansanosmilus*. *Barbourofelis osborni* is closest to *B. morrisoni* in all respects but is considerably smaller than that species. It differs from *?B. whitfordi* primarily in the shape of the ramus which widens rapidly anteriorly, and forms the characteristically deep symphysis of the Barbourofelini. The general shape of the ramus of *?B. whitfordi* follows a more typical machairodont pattern with a much smaller symphysis. The P_4 is slightly larger and more recurved posteriorly in *B. morrisoni* than in *B. osborni*. The I_1 is preserved in the holotype, showing it to be a very small compressed tooth.

The geologic ages of the two forms, *B. osborni* and *B. morrisoni*, are approximately the same, although the California deposits may be slightly younger in age than the middle Ash Hollow sediments of Nebraska. The smaller size of *B. osborni* may be attributed to geographic isolation. However, the range of sexual variation is unknown in the genus so that the value of the size difference is uncertain. A cat allied to *B. osborni* also occurred in the Black Hawk Ranch fauna (Richey, 1948, p. 2; Macdonald, 1948, p. 75–76, Fig. 15). This material, consisting of a deciduous upper canine and an upper carnassial, needs to be re-examined. Merriam (1905, 1918) described two other felids, *Ischyrosmilus*

ischyrus and *I. idahoensis*, but these are both Early Pleistocene scimitar-toothed forms, and are not closely related to the Barbourofelini.

?Barbourofelis whitfordi (Barbour and Cook)

Eusmilus whitfordi Barbour and Cook, 1915, p. 236, Pl. 1; Burt, 1931, p. 273.

Eusmilus? whitfordi Barbour and Cook: Sinclair and Jepsen, 1927, p. 405; Jepsen, 1933, p. 368.

"*Megantereon? whitfordi* (Barbour and Cook): Gregory, 1942, p. 354, Figs. 13–14.

Albanosmilus? whitfordi (Barbour and Cook): Kitts, 1957, p. 15.

Sansanosmilus whitfordi (Barbour and Cook): Mawby, 1965, p. 576.

Holotype.—Right ramus with I_2 -/C rts., P_3 (alv), P_4 - M_1 ; U.N.S.M. 25546 (= field no. 7-2-11-13W); collected by A. C. Whitford, 1913.

Type Locality.—U.N.S.M. Coll. Loc. BW-102, head of Quinn Canyon (also known as "William's School" locality), on S. side of Plumb Creek (sec. 5,¹¹ T.31 N., R.22 W.), 9½ mi. N. and 3¼ mi. W. of Ainsworth, Brown County, Nebraska.

Stratigraphic Occurrence.—Middle Pliocene, Ogallala Group, lower part of Ash Hollow Formation.

Diagnosis.—This is the smallest North American member of the Barbourofelini with the following characteristics; ramus not expanding anteriorly as in other Barbourofelini; dependent flange U-shaped and smaller than in other barbourofelins; cheek teeth not projected so far labially; P_3 single rooted; P_4 smaller than in *B. osborni* and less inclined posteriorly.

Discussion.—The resemblance of the ramus of *?B. whitfordi* to that of *Sansanosmilus palmidens* (Filhol) is quite remarkable, especially

¹¹ Morris F. Skinner has investigated the locality and reported that the *?B. whitfordi* holotype possibly came from the SW.¼, NE.¼, sec. 5 (personal communication, March 10, 1970). Skinner had corresponded with Whitford and obtained additional detailed information concerning the locality of the holotype.

NEBRASKA PLEISTOCENE CORRELATION CHART						
By C. Bertrand Schultz and Thompson M. Stout						
Provincial Ages	PLEISTOCENE-Blancan above				European Standard	
KIMBALLIAN	OGALLALA GROUP	KIMBALL	FM.	UPPER MEMBER Dalton L.F.		A
			KIMBALL	Cambridge L.F. Oshkosh L.F. SIDNEY MEMBER		
HEMPHILLIAN		FORMATION	Feldt Ranch L.F.		B	
			Xmas and Kat Quarries L.F.			
CLARENDONIAN		ASH HOLLOW	LOWER PT., ASH HOLLOW	Upper Snake Creek L.F.		C
				Minnechaduza L.F. Complex (?) CAP ROCK BED		
VALENTINIAN	VALENTINE	FM.	BURGE MEMBER Burge L.F. Devil's Gulch L.F.		MESSINIAN	
		VALENTINE	Fort Niobrara L.F. Railroad Quarry L.F. Crookston Bridge L.F.			
	MIOCENE- Hemingfordian below					

Fig. 8—Pliocene correlation chart showing the stratigraphic distribution of the Barbourfelini in Nebraska. A = *Barbourfells fricki*, new species, Early Kimballian; B = *B. morrissi*, new species, Early Hemphillian; C = ?*B. whitfordi* Barbour and Cook, Early Clarendonian. Modified after Schultz and Stout, 1961, p. 9, Fig. 3. Note: The lower part of the Valentine Formation below the Burge Member, is now the Devil's Gulch Member; and the "Cap Rock Bed," or lower part of the Ash Hollow Formation, is now the Cap Rock Member (Skinner, Skinner, and Gooris, 1968, p. 406, 409).

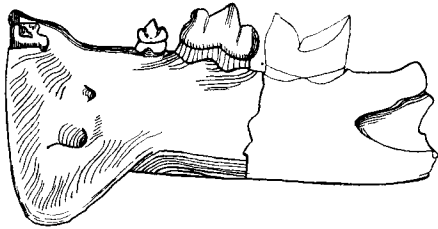


Fig. 9—*Sansanosmilus palmidens* Blainville, referred specimens, Paleontologie du Museum National d'Histoire Naturelle (Paris) catalogue no. 456, restoration of posterior portion of ramus (reversed) based on specimen, no. 454, left carnassial based on no. 459, and P_3 based on holotype, no. 553. (After Ginsburg, 1961, Pl. 15, Fig. 2a; Pl. 14, Fig. 4; Pl. 12, Fig. 13a; Pl. 14, Fig. 3a) X 3/5.

in terms of the shape of the flange, the P_4 , and the shallow notch on the carnassial (Fig. 9). *?B whitfordi* is larger and has the P_3 more reduced with only one foot rather than two as in *Sansanosmilus palmidens*. *Albanosmilus*¹² *jourdani* is known only from the ramus of a kitten and isolated teeth, but in the size and characters of the lower cheek teeth it is very close to *?B whitfordi*. Whether or not *?B whitfordi* or *Albanosmilus* has postorbital bars cannot presently be ascertained. However, if skull material of both are found they may prove to be at least congeneric.

Gregory (1942, p. 354) reported a left ramus of *?B whitfordi* as well as a maxillary of an immature sabertooth from Big Springs Canyon in South Dakota. The ramus shows alveoli for three lower incisors. The holotype only shows alveoli for two incisors with the first incisor absent. This is undoubtedly an aberrant condition with the tooth having been lost in life and the alveolus closed. The maxillary shows the characteris-

¹² The names *Albanosmilus* and *Sansanosmilus* were proposed by Kretzoi (1929, p. 1306) for *Machairodus jourdani* Fihol and *Felis palmidens* Blainville respectively. Simpson (1945, p. 120) considers the two genera congeneric, and selects *Sansanosmilus* (Kretzoi, 1929, p. 1307) as the valid genus since the type is better known, although *Albanosmilus* has page priority (Kretzoi, 1929, p. 1306). Villalta and Crusafont (1952, p. 308) propose *Grivismilus* to replace *Albanosmilus*. The present writers do not wish to undertake a revision of these European felids and for this paper use both *Albanosmilus* and *Sansanosmilus* since the material at hand does not permit a conclusive decision as to the two genera being congeneric.

tically deep fossa for the superficial masseter muscle of the Barbourofelini. The deciduous carnassial shows the long-thin shearing tooth characteristic of this group.

Ustatochoerus profectus, was reported by Gregory (1942, p. 362, Fig. 17) from the Big Spring Canyon local fauna in South Dakota. This species is typical of the Cap Rock Member of the Ash Hollow in Nebraska.

SUMMARY AND CONCLUSIONS

The presence of a postorbital bar separates *Barbourofelis* from the following genera of machairodont cats: *Hoplophoneus*, *Eusmilus*, *Machairodus*, *Megantereon*, *Homotherium*, *Paramachairodus*, *Sansanosmilus*, and *Smilodon*.

The material of *Albanosmilus* available (Villalta and Crusafont, 1943a and 1943b) is much too incomplete to be adequately compared with *Barbourofelis*. However, it does have the long, flat grooved sabers and the shallow carnassial notch on the M_1 as found in *B. fricki*. The upper carnassial is also somewhat similar. The only ramus known to us of *Albanosmilus* is the juvenile specimen illustrated by Villalta and Crusafont (1943a). *Sansanosmilus* lacks the postorbital bar, but does resemble *Barbourofelis morrisoni* in some of the skull proportions. The resemblance between the ramus of *Sansanosmilus* and that of *?Barbourofelis whitfordi* is striking (see Figs. 5 and 9), especially in the relative shape of the flange and P_4 . The P_3 of *Sansanosmilus* is larger and has two roots while that of *?B whitfordi* is more reduced, and has only a single root. Ginsburg (1961, p. 154) regards *Albanosmilus* as congeneric with *Sansanosmilus*, and states that *Albanosmilus jourdani* is larger, with wider and longer canines and the $P^3/3$ more reduced. *Sansanosmilus* would make an acceptable ancestor for *Albanosmilus*. *Sansanosmilus* does have the grooves found on the outer and inner sides of the saber (Ginsburg, 1961, p. 159) as in the *Barbourofelini*.

It seems likely that the *Sansanosmilus-Albanosmilus* group gave rise to the Barbourofelini. In this case a representative of the group probably invaded North America in the Late

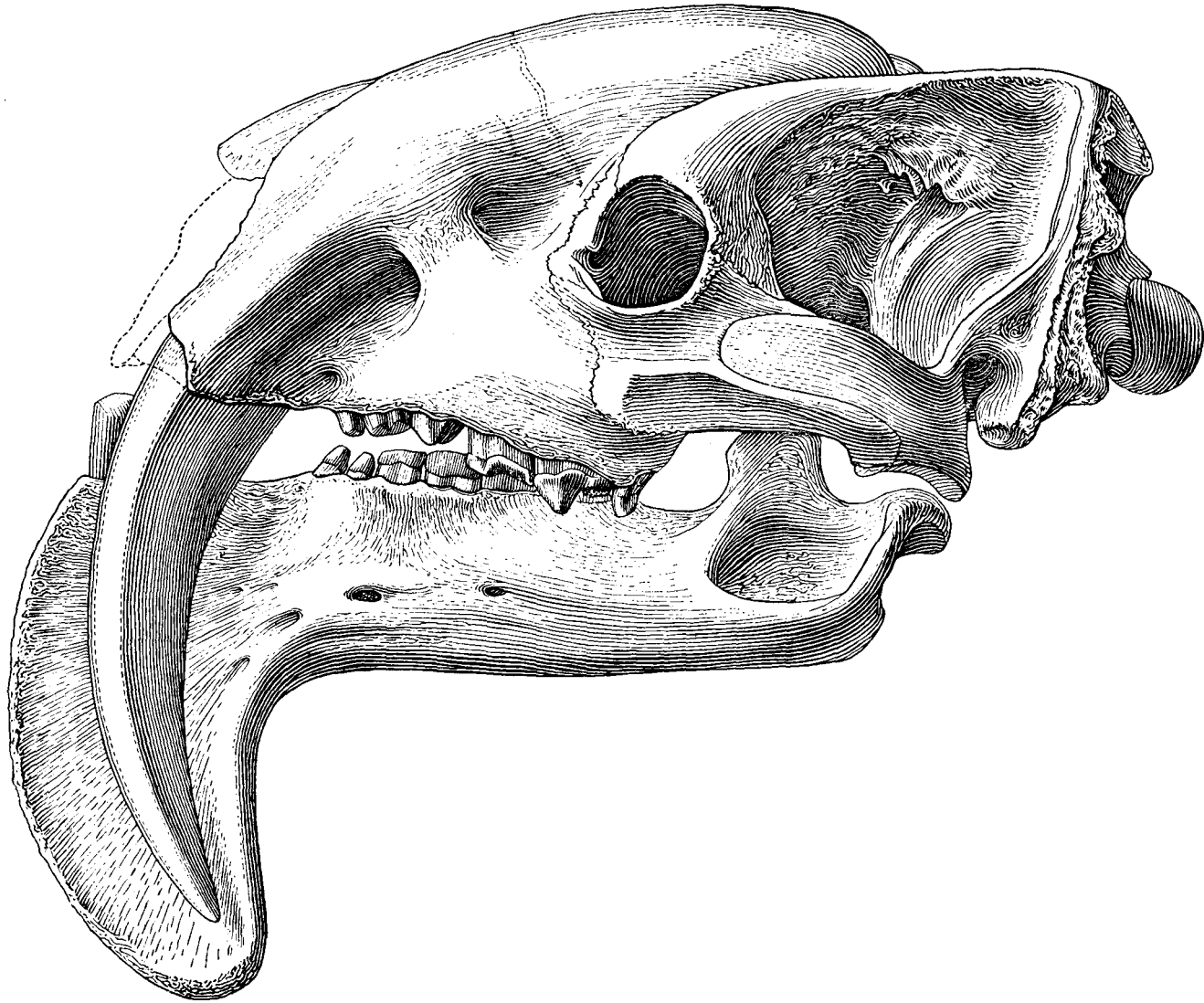


Fig. 10—Lateral view of the skull of *Thylacosmilus atrox*, a Pliocene marsupial from Argentina, holotype, Field Museum of Natural History, cat. no. P14531 (from Riggs, 1934, pl. 1). X 3/5.

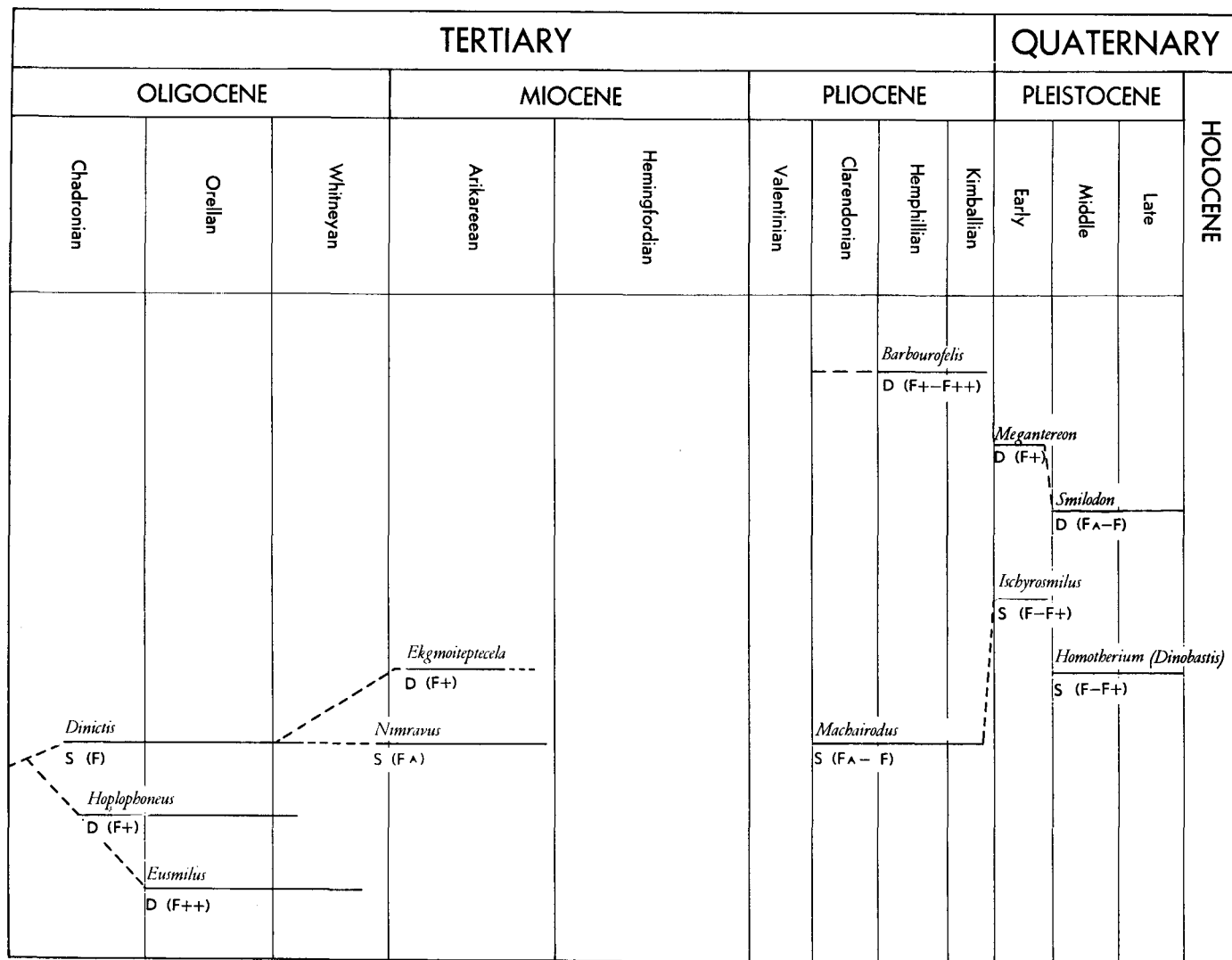


Fig. 11—Stratigraphic distribution of saber-toothed felids in North America. Some relationships are suggested by dashed lines. D = Dirk-tooth; S = Scimitar-tooth; FA = Flange absent; F = small flange; F+ = medium-sized flange; F++ = very large flange. (The presence of *Megantereon* in North America is based on material from the Broadwater Local fauna soon to be reported by Schultz and Martin.)

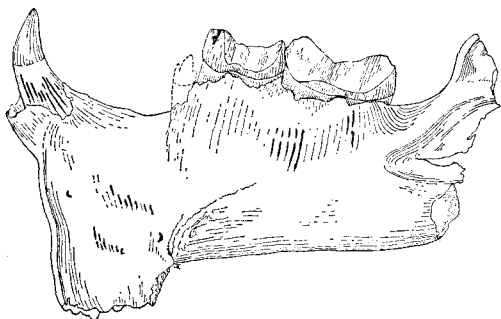


Fig. 12—?*Barbourofelis piveteaui* (Ozansoy), holotype, partial mandible (P_3 restoration from right side of mandible) from the middle Sinap ("Pliocene superieur"), 50-60 km. NW. of Ankara, Turkey. (After Ozansoy, 1965, Pl. IV, Figs. 8 and 9.) x 3/5.

Miocene or Early Pliocene, at which time the ecological niche for dirk-toothed cats appears to have been vacant and a unique opportunity for rapid evolution prevailed. Whether the American Tertiary scimitar-toothed cats, belonging to the genus *Machairodus*, were also immigrants from Asia or developed in North America out of *Nimravus* is uncertain at present. The earliest occurrences of which we are aware are not much older than those of the *Barbourofelini*. In any case, it seems to have been normal for dirk-toothed and scimitar-toothed cats to occur together as in the case of *Barbourofelis* and *Machairodus*, *Megantereon* and *Homotherium*, and *Dinobastis* and *Smilodon* (Churcher, 1965; Kurten, 1965). In the Pleistocene this paired arrangement is reflected in the tribes Homotherini for the scimitar-toothed cats and Smilodontini for the dirk-toothed cats (Churcher, 1965). This division is probably more fundamental and should be reflected at the subfamily level. However, such a comprehensive revision is too extensive to be undertaken in the present report.

Ozansoy's (1965) record from Turkey is the only evidence, known to the writers, of *Barbourofelis*-like cats in Eurasia. This occurrence indicates that two phylogenetic lines of these felids apparently were evolving in Eurasia and North America at the same time. It is not known, however, if the Eurasian forms had closed orbits.

The theoretical classification proposed by Hough (1953, p. 113) for the Felidae is based on

adaptive features highly subject to convergence and does not correspond to the evidence we have at hand. The machairodont cats and the Felinae are certainly more closely related to each other than either is to any other family of carnivores. Characters given for the superfamily Machairodontoidea, including the shape of the incisors, reduction of the lower canine, high degree of carnassialization, inclination of the carnassial, and size of the upper canine, are all adaptive features related to the mechanics of the saber-toothed condition, and can be found to a greater or less extent in *Dinictis*, *Nimravus*, and *Thylacosmilus* (the saber-toothed marsupial). The highly inflated bulla is just as apparent in *Sansanosmilus* (Ginsburg, 1961, Pl. 8, Fig. 1) as it is *Dinictis*, and the Machairodontoidea differ no more from the Felidae in the characteristics of the interior of the bulla than do the Canidae. Probably *Sansanosmilus* should be included in the *Barbourofelini* in that it seems to represent the stock from which the tribe is derived. *Sansanosmilus* may in turn be derived from the *Nimravinae* (Ginsburg, 1961, p. 172).

Barbourofelis was even more specialized for a saber-toothed niche than was *Smilodon*. However, independent solutions had been developed for many of the mechanical problems involved with stabbing. *Thylacosmilus*, the saber-toothed marsupial from the Pliocene of South America (Riggs, 1933, 1934), had many similar adaptations in the skull and mandible, including the perpendicular occipit, shortened cranium, post-orbital bar, and large flange on the ramus (Fig. 10). This is an excellent example of convergence in evolution. It should be noted, however, that these two forms could not have been very similar in the way that they stabbed. In *Barbourofelis* the elongated canines are parallel and were probably both imbedded in the animal's prey. In *Thylacosmilus* the upper canines diverge ventrally (Riggs, 1934, Pl. 3, Fig. 1) and could not have been embedded at the same time without being spread apart. The canine also is triangular in shape, being strengthened by a median ridge on its labial side. This is suggestive of the canines of some peccaries, and indicates that the canines may have been used to slash laterally as is the case in many pigs.

Barbourofelis seems to have been a purely stabbing cat whose canines were too long and poorly serrated to have been effective slashing weapons. The shortening of the cranium and development of a postorbital bar may have resulted from adaptation to the enormous stresses these skulls must have undergone when stabbing prey.

The dirk-toothed cats typically are heavily built with short legs and powerful forequarters. Apparently they depended on ambushing their prey, immobilizing it with the powerful front limbs just long enough to dispatch it with the long sabers. The sabers bear only very fine crenulations and are clearly adapted for stabbing as was shown by Simpson (1941).

The scimitar-toothed cats, on the other hand, are more lightly built, with longer legs, and were possibly able to catch more agile prey. Their sabers are short, wide, and coarsely crenulated much like a steak knife. They must have slashed their prey as well as stabbing it. The dirk-toothed cats could probably handle larger and thicker-skinned prey but would have been at a disadvantage if only small agile animals were available. It appears to be no coincidence that the extinction of the Barbourofelini corresponds with the extinction of the large Pliocene rhinoceroses and mastodonts.

During the Tertiary the saber-toothed cats were the "typical" felids, and the modern cats (Felinae) appear to have achieved their present abundance and dominance comparatively recently. Taking this into consideration it still seems useful to compare the two major types of machairodont cats with the Holocene predators whose hunting habits are well known. When this is done we find that in all respects the scimitar-toothed felids seem more "normal" and similar to modern cats than are the dirk-toothed felids, which are, in contrast, highly specialized. When we examine Fig. 11 we see that this specialization is reflected in a high vulnerability to extinction, and at each epochal boundary, except for the Miocene-Pliocene boundary, we have extinction of the dirk-toothed cats. There is at the present an almost complete dearth of machairodont material from the North American Middle Miocene through Early Pliocene, which

accounts for the apparent anomaly. The scimitar-toothed cats, evolving more slowly, were less effected by the environmental changes at these boundaries, and probably existed as a continuous line until the end of the Pleistocene. The scimitar-toothed line probably formed the ancestral stock for several separate lineages of dirk-toothed cats, including the Barbourofelini, and also for the Felinae. In the Oligocene we have two dirk-toothed forms, *Eusmilus* and *Hoplophoneus* (Scott and Jepsen, 1936), both of which become extinct before the Miocene. At the same time the small scimitar-toothed cat *Dinictis* probably gave rise to a larger scimitar-toothed cat *Nimravus* (Matthew, 1910; Toohy, 1959). Small specimens of *Dinictis* in the U.N.S.M. collections are similar to *Ekgmoiteptecela belli* (Stock) and suggest that this tiny aberrant dirk-toothed cat may be derived from *Dinictis* (a more adequate discussion of these cats is given in Macdonald, 1963, p. 221). The nimravine cats may have led to both *Machairodus* and the Barbourofelini. The latter became extinct at the end of the Pliocene but *Machairodus* may have given rise to *Homotherium*, and *Ischyrosmilus* of the Early Pleistocene, both of these forms are scimitar-toothed as is *Homotherium (Dinobastis)*, (Meade, 1961). The origin of the Pleistocene dirk-toothed felids, *Megantereon* and *Smilodon*, is presently uncertain.

THE KIMBALLIAN AND VALENTINIAN PROVINCIAL AGES

The present writers encourage the continuation of the use of the provincial age terms, Kimballian and Valentinian, as used by Schultz and Stout (1961, p. 9, Fig. 3).¹³

The term Valentinian was proposed by Schultz and Stout (*in* Wilson, 1960, p. 14), and Kimballian by Schultz and Stout (1961, Fig. 3). As more precise faunal and stratigraphic evidence are collected it is very apparent that these additional provincial age terms are needed for a

¹³ The chart (Fig. 3) published by Schultz and Stout represented work which had been done for the Society of Vertebrate Paleontology's Cenozoic Correlation Committee. The chart was published in a preliminary form by Wilson (1960), who was at that time Chairman of the Miocene Subcommittee. (See Fig. 8, present paper.)

OGALLALA FORMATION		
VALENTINE FLORAL ZONE	ASH HOLLOW FLORAL ZONE	KIMBALL F. ZONE
	<i>Stipidium intermedium</i>	
	<i>Stipidium variegatum</i> and <i>S. elongatum</i>	
	<i>Stipidium breve</i> and <i>S. coloradense</i>	
<i>Stipidium commune</i>		
	<i>Prolithospermum johnstoni</i>	
	<i>Panicum eliasi</i>	
<i>Krynitzkia coroniformis</i>	<i>Panicum elegans</i>	
<i>Celtis</i>	<i>willistoni</i>	
	<i>Biorbia fossilis</i> and <i>B. papillosa</i>	
	<i>Berrichloa tuberculata</i>	
	<i>Berrichloa minuta</i> and <i>B. maxima</i>	
	<i>Berrichloa amphoralis</i> and <i>B. conica</i>	

Fig. 13—Chart showing floral zones of the Ogallala Formation (from Frye and Leonard, 1959, p. 23, Fig. 3). Zone of principal occurrence shown by the wide bar. The Kilgore flora of MacGinitie (1962, p. 68) from the Valentinian deposits, 22 miles west of Valentine, Nebraska (or 14 miles south of Kilgore) reported some 53 species. MacGinitie (p. 77) listed the following genera under the title, "Megafossils": *Chamaecyparis*, *Populus*, *Carya*, *Pterocarya*, *Quercus*, *Celtis*, *Ulmus*, *Mahonia*, *Cocculus*, *Ribes*, *Platanus*, *Crataegus*, *Prunus*, *Cladrastis*, *Robinia*, *Cedrela*, *Acer*, *Meliosma*, *Vitis*, *Nyssa*, *Fraxinus*, *Diospyros*, and *Cordia*. The following genera were listed under the title, "Microfossils": *Quercus*, *?Ulmus*, *Celtis*, *Lycopodium*, *Picea*, *Pinus*, *?Sequoia*, *Salix*, *Carya*, *Juglans*, *Pterocarya*, *Alnus*, *?Betula*, *?Sarcobatus*, *Liquidambar*, *Cedrela*, *Ilex*, *Acer*, *Meliosma*, *Tilia*, *Ambrosia*, and *Artemisia*.

better understanding of faunal comparisons. It is gratifying to note that Skinner, Skinner, and Gooris (1968, p. 404) support the recognition of Valentinian.

The Valentinian provincial time term is based on local faunas from north-central Nebraska in the vicinity of Valentine (Cherry County) and Ainsworth (Brown County), which occur in the Valentine Formation of the Ogallala Group. The local faunas of Valentinian age are derived from collecting localities and quarries in the Crookston Bridge, Devil's Gulch, and Burge members of the Valentine Formation, including Railway Quarry A,¹⁴ Crookston Bridge Quarry, Devil's Gulch Horse Quarry, Norden Bridge Quarry, Fairfield Falls Quarry, Jones Canyon Quarry, Nenzel Quarry, Midway Quarry, and Burge Quarry.¹⁵

Schultz and Stout (1961, Fig. 3) were very explicit as to what was to be included in the Valentinian, and the Burge Member (including the Burge Local Fauna) was shown to be part of the Valentinian on the chart, although Webb (1969, p. 15) reported: "Possibly it [Valentinian] was intended to include the Burge Fauna." Webb (1969) considered Valentinian as preoccupied because of the usage of "Valentine floral zone" by Frye and Leonard (1959), but it is difficult to see that the provincial age term could be preoccupied by an essentially informal floral assemblage zone.

Much of the confusion concerning the usage of the provincial age terms Barstovian, Clarendonian, and Hemphillian undoubtedly will be clarified when the report of the Society of Vertebrate Paleontology's Cenozoic Correlation Committee (by Bryan Patterson, George Gaylord Simpson, and associates) is published. Unfortunately the old correlation of the North Ameri-

can continental Tertiary (Wood, *et al.*, 1941) is too far out of date, and the usage of Barstovian is greatly misunderstood. The present writers have avoided using Barstovian because this provincial age includes a variety of faunal assemblages representing both the Hemingford and Ogallala groups.

Elias (1931, 1932, 1935, 1942), Chaney and Elias (1936), Lugn (1938, 1939a, 1939b), Frye, Leonard, and Swineford (1956), and Frye and Leonard (1959, 1964) have contributed much to a better understanding of the floral zones of the Ogallala in the Great Plains Region. Various floral zones have been established, the most recent of which is by Frye and Leonard (1959, p. 23). In the latter report, Frye and Leonard have indicated a Valentine floral zone, an Ash Hollow floral zone, and a Kimball floral zone (Fig. 13, this paper). Certainly these zones would agree in general with the faunal evidence at hand. The Valentine floral zone would be of Valentinian provincial age, the Ash Hollow floral zone would be of Clarendonian and Hemphillian ages, and the Kimball floral zone would be of Kimballian age.

Frye and Leonard (1959, p. 28) in their "Summary and Conclusions" regarding the correlation of the Ogallala Formation in Western Texas with type localities in Nebraska reported: "It also is fortunate that the type of the Clarendonian faunal zone and Clarendonian Provincial Age (Wood *et al.*, 1941) falls within the Valentine floral zone, and that the type of the Hemphillian faunal zone and the Hemphillian Provincial Age falls within the Ash Hollow floral zone." However, they also went on to say: "Although it is impossible for us to determine whether the regional extensions of these two vertebrate fossil faunal zones are coincident with the limits of the Valentine and Ash Hollow floral zones as used here, we judge that they are approximately so." Personal communication with John Frye in 1970, however, indicates that the Valentinian floral zone at Clarendon, Texas, the type locality of the Clarendonian, is very low in the geological section and apparently below the main level of the Clarendonian vertebrate fossil zone. It must be pointed out that at the Clarendon and Hemphill localities more than one

¹⁴ Johnson (1936, p. 467) established the type locality for the Valentine, which is the same locality as the Railway Quarry A Local Fauna. Railway Quarry A also has been referred to as "Valentine Quarry," "Railroad Quarry," and the "Railway Locality Quarry A."

¹⁵ These are fossil localities well known in the literature and have been excavated by field parties from the University of Nebraska State Museum, the Frick Laboratory of the American Museum of Natural History, the University of California Museum of Paleontology, the Field Museum of Natural History, the University of Notre Dame, and other institutions.

stratigraphic unit occurs, as Charles H. Falkenbach, who supervised the field work at the localities for so many years for the Frick Laboratory, pointed out to Marian and Bertrand Schultz on numerous occasions at the Texas localities.

The present writers, as well as Mylan Stout (personal communication, and Schultz and Stout, 1961), consider the Clarendonian as representing the provincial age of the lower portion of the Ash Hollow Formation of Nebraska and Hemphillian as the upper portion. Morris Skinner (personal communication, 1970) considers that the holotype of *Barbourofelis morrisoni* was derived from deposits that are Clarendonian in age, but the present writers strongly feel that *B. morrisoni* is early Hemphillian. Stout and Schultz (1961) also considered the Xmas and Kat quarries of the Frick Laboratory as Hemphillian as did Wood, *et. al.* (1941, Pl. 1).

At Clarendon the vertebrate fossils appear to be typical of the lower Ash Hollow forms from Nebraska, and deposits in the area seem to be not only of Clarendonian age, but also of Valentinian and Hemphillian. At the type locality of the Ash Hollow not only are Clarendonian and Hemphillian provincial ages involved, but also Valentinian and Kimballian.

The Kimballian provincial time term is based on faunal assemblages from the type area of the Kimball Formation in Kimball and Cheyenne counties Nebraska, and from other localities in southwestern Nebraska, especially from near Ash Hollow Canyon (the type locality of the Ash Hollow Formation) and Oshkosh in Garden County and from near Cambridge in Frontier County. There does not appear to be any Kimball Formation or deposits of Kimballian age at the type locality of the Hemphillian in Texas, and John C. Frye (personal communication, April 10, 1970) reports that there is no evidence of the Kimball floral zone near the type locality. Frye (1970) described the Kimball in a very concise manner: "The Kimball represents the final, and nearly complete coalescence of the 'plain of alluviation' that concluded the deposition of the Ogallala Formation. As the climate had become hotter and drier and the rate of deposition was greatly reduced, processes of soil formation gained ascendancy over processes of

deposition." The Kimballian was a period of climatic change and extinction. Some of the mammals which became extinct during the latest Pliocene or the Kimballian age are: the closed orbit felid, *Barbourofelis*; the Pliocene bear, *Indarctos*; the longirostrine mastodont, *Amebelodon*; the horses, *Calippus*, *Hipparion*, *Neohipparion*, *Protohippus*, and *Pliohippus*; and the horned ruminants *Cranioceras*, *Texoceros*, and *Sphenophalos*.

The following two faunal lists for the Valentinian and Kimballian provincial ages are based on evidence in the collections of the University of Nebraska State Museum and published reports.¹⁶ A study of several new genera and (or) species of vertebrates, representing the Kimballian Provincial Age, is under way by the present writers and others.

Valentinian:

Class: OSTEICHTHYES

Amia sp.
Lepisosteus sp.
Ictalurus sp.
Lepomis cf. *microlophus* (Gunther)

Class: AMPHIBIA

Andrias matthewi (Cook)
Ambystoma minshalli (Tihen and Chantell)
Scaphiopus wardorum (Estes and Tihen)
S. cf. *alexanderi* Zweifel
Bufo cf. *hibbardi* Taylor
B. valentinensis Estes and Tihen
Acris cf. *crepitans* Baird
Pseudacris cf. *clarki* Baird
Pseudacris nordensis Chantell

¹⁶ Barbour, 1927, 1929; Barbour and Schultz, 1941; Chantell, 1964, 1966; Estes and Tihen, 1964; Frick, 1933, 1937; Hibbard, 1960; Holman, 1964; Johnson, 1936, 1938; Kent, 1963, 1967; Klingener, 1968; McGrew, 1938; McGrew and Meade, 1938; Meszoely, 1966; Osborn, 1936; Schultz and Falkenbach, 1941, 1968; Schultz and Stout, 1961; Skinner, Skinner, and Gooris, 1968; Smith, 1962; Stirton and McGrew, 1935; Tanner, 1967; Tihen, 1962; Tihen and Chantell, 1963; Webb, 1963; also Schultz and Stout, 1948; Short, 1966, 1969, 1970; Martin and Tate, 1970.

Hyla cf. cinerea Schneider
H. cf. gratiosa LeConte
H. cf. squirella Sonnini and Latreille
H. cf. versicolor LeConte
Rana sp.

Class: REPTILIA

Chrysemys sp.
Geochelone orthopygia (Cope)
Trionyx sp.
Phrynosoma sp.
Gerrhonotus sp.
Paleoheterodon tiheni Holman
Elaphe nebraskensis Holman
Lampropeltis similis Holman

Class: AVES

Dissouroides milleri Short
Heterochen pratensis Short

Class: MAMMALIA

Metechinus sp.
Hypolagus sp.
Allomys stirtoni Klingener
Mylagaulus cf. monodon Cope
Eucastor cf. dividerus Stirton
Perognathoides, cf. P. cuyamensis
 Wood
Cupidinimus nebraskensis Wood
Diprionomys agrarius Wood
Plesiosminthus sp.
Megasminthus tiheni Klingener
Copemys kelloggae Hoffmeister
Aelurodon platyrhinus Barbour and
 Cook
Aelurodon taxoides Hatcher
Strobodon stirtoni Webb
Ischyrocyon gidley (Matthew)
Tomarctus euthos (McGrew)
Plionictis sp.
Leptocyon vafer (Leidy)
Hemicyon sp.
Bassariscus parvus Hall
Brachypsaloides modicus (Matthew)
Brachypsalis pristinus (Matthew and
 Gidley)
Leptarctus sp.
Eubelodon morrilli Barbour

Megabelodon lulli (Barbour)
Gomphotherium abeli (Barbour)
G. phippsi (Cook)
G. (Genomastodon) osborni (Barbour)
G. (G.) willistoni (Barbour)
G. (Tabelodon) gregorii (Frick)
Teleoceras sp.
Hypohippus affinis Leidy
Megahippus matthewi (Barbour)
Pseudhipparion retrusum (Cope)
Hipparion sp.
Neohipparion cf. coloradense Osborn
Calippus sp.
Pliohippus supremus (Leidy)
Protohippus sp.
Prosthennops xiphodonticus Barbour
P. niobrarenensis Colbert
Ustatochoerus medius Leidy¹⁷
Procamelus grandis Gregory
P. robustus Leidy
Protolabis heterodontus (Cope)
Homocamelus sp.
Aepycamelus sp.
Blastomeryx gemmifer valentinensis
 Frick
B. mefferdi Frick
Cranioceras unicornis Matthew
C. mefferdi Frick
C. (Procranioceras) skinneri Frick
Longirostromeryx wellsii (Matthew)

¹⁷ Webb (1969, p. 144) reported *Ustatochoerus profectus* from the Burge Member of the Valentine Formation but based his identification primarily on a cranium of a very old individual, and he reported that "the dentition is very heavily worn." His illustration shows this feature. Specimens such as this are difficult to identify. Schultz and Falkenbach (1941) reported numerous examples of *U. medius* from the Burge channels of north-central Nebraska. The specimens from the Burge Member are slightly larger on the average from typical *U. medius* examples from the Devil's Gulch Member below, but all fall within the expected range of variation of *U. medius*. The Valentinian *Ustatochoerus medius* gave rise to the Clarendonian species, *U. profectus* (see Schultz and Falkenbach, 1941, p. 45; 1968, p. 423, Chart 18A). Species based on progressive evolution along a single phylogenetic line are by nature arbitrary. Usually they are based on populations separated by time gaps, and subsequent populations are then grouped with those named populations they most resemble. This permits the earlier names to provide a framework for dividing up the lineage. However, as the time intervals between populations become small we can expect the overlap in characters to reduce the confidence placed in individual specimens to the point where we are forced to use statistical treatments of populations.

L. merriami Frick
Ramoceros sp.
Meryceros warreni johnsoni Frick
Cosoryx furcatus Leidy

Kimballian:

Class: AVES

Paracygnus plattensis Short
Proagriocharis kimballensis Martin
 and Tate

Class: MAMMALIA

?*Megalonyx* sp.
Hypolagus sp.
Perognathus sp.
Spermophilus kimballensis (Kent)
Thomomys sp.
Dipoides stirtoni Wilson
Dipoides williamsi Stirton
Indarctos sp.
Barbourofelis fricki, New species
Amebelodon fricki Barbour
 ?*Tapirus* sp.
Aphelops kimballensis Tanner
Teleoceras sp.
Calippus sp.
Hipparion eurystylum (Cope)
Neohipparion sp.
Protohippus sp.
Pliohippus sp.
Nannippus sp.¹⁸
 ?*Mylohyus* sp.
Procamelus sp.
Pliauchenia sp.
Cranioceras sp.
Texoceros guymonensis Frick
Sphenophalos middleswarti Barbour
 and Schultz

ACKNOWLEDGMENTS

The present writers are indebted to the following for helping to make possible the dis-

¹⁸ Morris Skinner is preparing a report on the Kimballian horses from U.N.S.M. Coll. Loc. Ft-40, the locality of the holotype of *Barbourofelis fricki*.

covery and description of this new tribe of felids and a better understanding of Kimballian faunal evidence: The late Mr. Alex Keith for the discovery of the *Amebelodon fricki* Quarry (U.N.S.M. Coll. Loc. Ft-40), in 1927; the late Dr. Erwin H. Barbour, and Prof. E. F. Schramm for their interest in and encouragement of continued work in the late Pliocene deposits of the Great Plains; the late Mr. Childs Frick for his help, sincere counsel, financial aid, and the loan of the holotype and referred specimen of *Barbourofelis morrissi*; Prof. Miguel Crusafont Pairo, Dr. C. S. Churcher, Dr. Bjorn Kurten, and the late Pierre Teilhard de Chardin, for their aid and counsel concerning the classification, phylogeny, and characteristics of the various Old World saber-toothed felids; Professors T. M. Stout, A. L. Lugin, Harvey L. Gunderson, William J. Wayne, and Vincent Dreeszen; and Messrs. Lloyd G. Tanner, King Richey, and W. D. Frankforter for their assistance and advice; the late Mr. Charles H. Falkenbach for his friendship, cooperation, and help in acquainting Marian and Bertrand Schultz with the geology and stratigraphic correlations of the Pliocene deposits and associated faunal assemblages in the Clarendon, Hemphill, and Higgins areas of Texas; Dr. John C. Frye for counsel concerning the correlation of Ogallala deposits in the Great Plains; Mr. Morris F. Skinner for geologic information regarding the stratigraphic positions of the holotypes of *Barbourofelis morrissi* and ?*B. whitfordi*; Prof. Donald E. Savage for the loan of felid types from the collections of the University of California Museum of Paleontology; and the members of the University of Nebraska State Museum's 1947 field crew, who discovered and collected the fantastic and well-preserved holotype of *B. fricki*. Members of this crew were Allen Graffham (party leader), James Allen, William H. Berninghausen, Kenneth Harding, J. Knox Jones, Richard Loomis, Richard Lugin, Neal McClymond, Maurice Mendenhall, George Scheffert, Robert Truxell, Olin Webb. The present writers also appreciate the aid of the following: Mrs. Florence Erford Sunderland for her many weeks of volunteer time in 1947 and for other assistance in making the 1947 field season a success; Mrs. Norma Wagner for typing

and editorial assistance; and Mr. Robert Miller for the preparation of illustrations of *B. fricki*, *B. morrisi*, and ?*B. whitfordi* (Figs. 1-3 and 5). Mr. Jerry Tanner for Figs. 7, 9, and 12, and the University of Nebraska Conservation and Survey Division for Fig. 11. Special thanks are due to Mr. Cecil Williams, owner of the fossil quarry (Ft-40) where the holotype of *Barbourofelis fricki* was found.

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