Phylogenetic Systematics of North American *Pseudaelurus* (Carnivora: Felidae)

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ABSTRACT

I review the fossil felid literature, researching the early history of the genus *Pseudaelurus* in Europe. I examine type *Pseudaelurus* specimens from Europe, Asia, and North America and emend the generic diagnosis. A large body of new material from the Frick Collection of the American Museum is described and specimens are assigned to one of six species. One species is new and one is transferred from *Lynx*. New material includes two partial skeletons assigned to two separate species, several skulls, one skull with associated lower jaws and intact basicranium, numerous maxillary and lower jaw specimens, and isolated postcranial items. Cranial, basicranial, and postcranial material of the Frick specimens is compared to that of European taxa as well as to modern felids. A cladistic analysis of 10 taxa and 23 characters produces hypotheses of felid relationships.

INTRODUCTION

Felids attract a great deal of scientific and popular attention for many reasons. Their inherent charisma, fragile status in the global environment, and role as domesticated companion animals have resulted in numerous studies on their anatomy, behavior, physiology, pathology, and phylogeny. Their survival in the wild is an important goal of many worldwide conservation efforts. However, an essential component of conservation technique is an understanding of the species relationships and their evolutionary history (O'Brien, 1996).

The earliest fossil record of Felidae is restricted to Europe and Asia. The occurrence of the felid *Proailurus lemanensis*, in the late Oligocene (MP 30) of Europe and Asia, marks the earliest fossil evidence of the family. The fossil record of this early felid is more complete in Europe, extending into the early Miocene. *Proailurus* is represented by a small amount of cranial, dental, and postcranial material. Beginning in the later part of the early Miocene of Europe and Asia, fossils of *Pseudaelurus*, a second felid taxon, begin to appear. A common ancestry of the late Oligocene *Proailurus lemanensis*, the Miocene *Pseudaelurus*, and living felids has been suspected since before the turn of the last century (Adams, 1897).

In North America, the Miocene epoch with its cooling and drying climate, marks a transition point between the equable and stable climate of the Mesozoic and early Cenozoic and the more variable conditions experienced in the Pleistocene (Wright et al., 1992). The climate, tectonic status, and faunal composition of North America were reasonably stable throughout the Oligocene. There was little faunal interchange between Eurasia and North America during the Oligocene (Van Valkenburgh, 1999). New World mammalian carnivores were primarily members of the feliform carnivoran family Nimravidae, hyaenodont members of the extinct order Creodonta, and canids. The earliest fossils of Aeluroidea (Viverridae, Hyaenidae, Felidae, and Herpestidae) are found in Europe and Asia in sediments that are late Eocene to early Oligocene in age (Hunt, 1998). However, there were no aeluroids in North America throughout the Oligocene (Hunt, 1996). Globally, sea level had been dropping steadily throughout the Tertiary, from a mid-Cretaceous maximum. The arrangement of the continents in the Atlantic theatre began to force the long-term cooling of North America that would characterize the Miocene (Mesolella et al., 1969). As the Oligocene ended, continental landmass was increasing, surrounded by smaller, more complexly related oceans.

The North American climate steadily became cooler and drier throughout the Miocene. Various tectonic influences have been credited with causing or contributing to this climatic phenomenon: the opening of the Drake Passage between South America and Antarctica at the Eocene-Oligocene border; the commencement of deep water circulation across the Greenland-Scotland ridge in the early Miocene; the Eastern Tethys Sea closing in the early Miocene; India colliding with the Asian continent, causing Tibetan uplift in the early Tertiary; Antarctica beginning or continuing to ''ice''; and the formation of the Rocky Mountain rain shield in the early Cenozoic. Various permutations of the possible currents connecting the ocean gateways have

been hypothesized as being the "major player" in the Miocene cooling (Wright, 1998). The evidence for the Miocene cooling trend in the North America and Atlantic ocean arena has been documented by benthic foraminifer stable isotopes (Mesolella et al., 1969) and by examination of the vertebrate fauna of this epoch (Webb, 1984).

Concurrent with the transition in climate, the geology of the area was also changing. The mountains of western North America were being eroded, and the sand and clay sediments were carried eastward by mid-Cenozoic rivers. As the rivers approached the interior of the continent, the gradient decreased, the current slackened, and sediments were deposited. The great interior plain of North America was formed (Skinner et al., 1977). Alluvial aprons of sediment extended from the mountain ranges of the West to the Mississippi River in the east and Gulf of Mexico to the south (Clark and Stearn, 1960). As the erosional gradient changed, the Oligocene clays were overlain by the sands of the Miocene. It is the formation of these alluvial Miocene sand sediments that established many of the classical localities described in this manuscript. As local rivers developed on the intercontinental plain, periodic flooding and drainage of the area resulted in sediments accumulating in paleovalleys. Fossils of the contemporary fauna and flora were deposited in these sediments (Webb, 1969).

But what was the makeup of the contemporary fauna of North America? The variation in climate, sea level, and habitat altered the local fauna of North America in a new and important manner. As stated earlier, there was little faunal interchange between Eurasia and North America during the Oligocene. As the Miocene began, the mammalian carnivorous guilds were changing: the nimravids and the creodonts became extinct in North America. The ursids, amphycyonids, and the borophogine canids were now the major terrestrial carnivorans on this continent (Van Valkenburgh, 1999). With the regional extinction of the feliform Nimravidae at the end of the Oligocene, and with members of Aeluroidea still restricted to Eurasia, North America was now without a hypercarnivorous family of mammalian carnivores. For the next seven million years, the North American continent would experience a so-called "cat-gap" (Van Valkenburgh, 1999).

Soon, however, the cooling climate and lowering sea level would provide multiple opportunities for intercontinental dispersal throughout the Neogene. A major dispersal from Eurasia to North America through Beringea occurred at approximately 20 m.y. This immigration marked the beginning of the Hemingfordian land mammal age (Tedford et al., 1987). Within the mammalian order Carnivora, this North American Land Mammal Age (NALMA) has been defined by the earliest appearance of *Amphicyon*, *Hemicyon*, and *Ursavus* as well as by certain mustelids and procyonids (Tedford et al., 1987). A second immigration occurred at the start of the late Hemingfordian at approximately 18.5 m.y. (MacFadden and Hunt, 1998). Among the immigrants defining the late Hemingfordian is North America's first felid, *Pseudaelurus* (Tedford et al., 1987), thus ending North America's "cat-gap".

From 1932 to 1965, Childs Frick sent numerous collecting parties into the fossiliferous terrestrial localities of Tertiary North America. The Frick Laboratory assembled a magnificent collection of fossil mammals as a result of these expeditions. Now referred to as the Frick Collection, this assemblage of fossil mammals is housed in the collections of the Division of Paleontology of the American Museum of Natural History. Within the Frick Collection is the world's most comprehensive fossil felid collection. Fossils of the first felids to arrive in North America, in the late Hemingfordian, were collected in localities of the Sheep Creek Formation of Nebraska and the Tesuque Formation of New Mexico. The Sheep Creek material includes dentary and maxillary specimens of the large *Pseudaelurus validus* (Rothwell, 2001) as well as a new, small North American felid. The earliest known partial felid skeleton was recovered from the Nambé Member of the Tesuque Formation of New Mexico (Rothwell, 2001).

In the following pages, I perform an anatomical study and systematic review of North American early and middle Miocene felids. Most of these specimens are part of the Frick Collection. In addition, I provide an overview of the genus *Pseudaelurus* outside of North America. I examined more than 600

specimens of felid fossils. Eighty lower jaws and 33 maxillary fragments were assigned to one of six North American species. I establish one new species of *Pseudaelurus* and I reassign one species of *Lynx* to the genus *Pseudaelurus*. Additional skulls referred to the genus *Pseudaelurus* are described and assigned to three separate species. Two partial skeletons provide information on the cranial and postcranial anatomy of Barstovian *P. intrepidus* and *P. marshi*. This is the first comprehensive review of North American Miocene fossil felids since W.D. Matthew published his ''Third contribution to the Snake Creek fauna'' (Matthew, 1924).

INSTITUTIONAL ABBREVIATIONS

AMNH	Department of Vertebrate Paleontology, American Museum of Natural History, New York
ANSP	Academy of Natural Sciences of Philadelphia
Basel S.O.	Museum of Basel, Switzerland
F:AM	Frick Collection, Division of Paleontology, American Museum of Natural History, New York
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing
LACM	Natural History Museum of Los Angeles County, Los Angeles
LACM	(CIT) California Institute of Technology, now in the collection of LACM
MHNL	Muséum Guimet d'Histoire Naturelle, Lyon
MNHN	Muséum National d'Histoire Naturelle, Paris
SBCM	San Bernardino County Museum, Redlands, California
SDSM	Museum of Geology, South Dakota School of Mines and Technology, Rapid City
UCMP	Museum of Paleontology, University of California at Berkeley
UNSM	Nebraska State Museum, University of Nebraska, Lincoln
USNM	United States Natural History Museum, Smithsonian Institution, Washington, DC
UKMNH	The University of Kansas Natural History Museum
YPM	Yale Peabody Museum of Natural History, Yale University, New Haven
YPM-PU	Princeton University Natural History Museum, now in the collection of the YPM

EARLY TAXONOMIC HISTORY OF THE GENUS *PSEUDAELURUS*

The earliest history of fossil felids is enshrouded in confusion. Édouard Lartet has been given credit by many authors (Kretzoi, 1929; Thenius, 1949; Ginsburg, 1961b) for describing the first fossil felid, *Felis hyaenoides*, in 1838. A careful search of Lartet's letters in the 1838 volume of *Compte Rendu de l'Académie de Sciences* reveals no reference to *hyaenoides*. The only mention of a felid in the 1838 letters is on page 1157, where Lartet stated: ''De deux têtes de carnassiers dont l'une, dans un état de conservation peu ordinaire, lui paraît être celle d'un grand *Felis* se rapprochant du Guépard par la forme de ses dents. C'est probablement une espèce voisine du *Felis* fossile à grand menton d'Auvergne. (''Concerning two heads of carnivores of which one, in an unusual state of preservation, appears to be that of large *Felis* approaching the cheetah in the shape of its teeth. It is probably a species close to the fossil *Felis* with the large chin of Auvergne.'') This citation error was first noticed by Heizmann (1973: 49) in his European review of *Pseudaelurus*: ''In der 'Notice sur la colline de Sansan' von 1851 dieses Autors findet sich auf Seite 18 das Zitat: '*Felis hyaenoides* Lart. C.R.Ac.Sc. 1838'. In Wirklichkeit gibt es in den Comptes rendus von 1838 nirgendwo eine solche Angabe. (''In the Notice sur la colline de Sansan from 1851, these authors wrote on page 18: *Felis hyaenoides* Lart. C.R.Ac.Sc. 1838. In reality there is nowhere such statement in the Comptes rendus of 1838.'')

It is in 1839 that Lartet made the first mention of a fossil felid mandible. He described it as being in the primitive state of being hyenalike, having an additional tooth. This important fact was also mentioned by Heizmann (1973: 49): ''Lediglich in den Comptes rendus des folgenden Jahres (1839) findet sich unter dem Titel 'Nouvelles espèces fossiles découvertes dans le département du Gers' die Beschreibung eines Felidenkiefers, die mit der Feststellung endet, dieser besitze 'une certaine tendance cers les Hyènes', ein Hinweis, der natürlich nomenklatorisch nicht relevant ist. (''In the Comptes rendus from the following year (1839) there is merely an
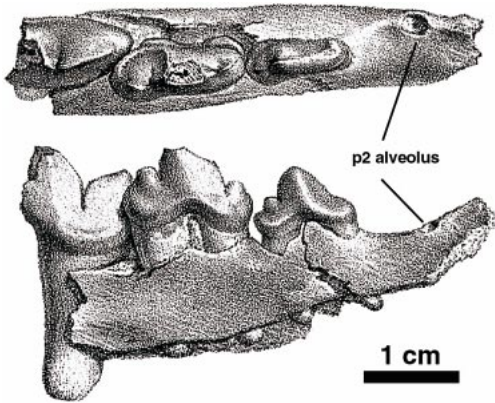
Fig. 1. *Pseudaelurus quadridentatus* Blainville (MNHN Sa 601), right ramus fragment, type specimen. Drawing from Blainville (1843).

article with the title Nouvelles espèces fossiles découvertes dans le département de Gers in which there is a description of a felid mandible which ends with the words une certaine tendence vers les Hyènes, a citation that clearly has no nomenclatural value.'') Therefore, Lartet discussed fossil felids in 1838 and 1839, but in neither paper did he assign a name.

In 1843, H.M. Ducrotay de Blainville published *Ostéographie des Mammifères.* On pages 155–157, under the heading *F. quadridentata*, he described a felid cranium and a lower jaw fragment from the middle Miocene of Sansan, France. The cranium (MNHN Sa 451) is illustrated on plate 15 and is labeled *F. quadritenta* (sic). The lower jaw fragment mentioned in the description (MNHN Sa 601) (fig. 1) is labeled on plate 16 as *F. tetraodon*. This appears to be the same dentary mentioned by Lartet in 1839. Most of Blainville's description (1843: 155) was spent, however, on the cranium: ''Le crâne proprement dit, est remarquable par la saillie des condyles occipitaux qui sont comme pédonculés, par l'étroitesse des basilaries qui sont presque cachés par le grand renflement des caisses très-avancées. . . (''The cranium itself is remarkable by the projection of the occipital condyles which are pedunculate, by the narrowness of the basioccipitals which are almost hidden by the great bulge of the bullae which are very advanced. . . '') Blainville suspected that this cranium had affinity

with modern large cats of the *Panthera* radiation due to the specimen's large size and presence of three upper premolars. The cranium was subsequently assigned to *Felis megantereon* (Lartet, 1851) and today is referred to *Sansanosmilus palmidens* within the nimravid subfamily Barbourofelinae (Ginsburg, 1961b).

While briefly describing the lower jaw fragment, Blainville (1843: 157) speculated that the cranium and the dentary might be from the same species: ''Comme le système dentaire du crâne étudié plus haut nous a également offert plus de rapprochement avec celui du *F. jubata* qu'avec tout autre, ne peut on pas-en induire comme ayant quelque probabilité que ce fragment de mandibule a appartenu à la mème espece animale que le crâne, et par consequent, ce Chat était une grande espèce de Guépard ayant quatre molaires en haut comme en bas, et passant ainsi encore d'avantage que celui-ci vers les *Canis*? (''As the dental system of the cranium studied suggests closer affinity with *F. jubata* than with the others, cannot one induce that this fragment of mandible belonged to the same animal species as the cranium, and therefore, that this cat was a great species of cheetah having four molars above as below?'') Blainville correctly focused on the unique and important character of this lower jaw fragment, the additional premolar (p2), but he seems to give credit for this character to Lartet: ''Ce qui frappe d'abord, comme l'avait très bien remarqué M. Lartet, c'est qu'au milieu, à peu près, sans doute, de la barre assez étendue qui sépare la canine de la première molaire, se trouxe une alvéole petite, ronde, qui indique une première avant molaire que nous n'avons encore observée dans aucune des espèces de Felis connues jusqu'ici. (''What strikes me at first, like Mr. Lartet had noticed quite correctly, is that in the middle of the rather wide bar (diastema) which separates the canine from the first premolar, is a small round alveolus, which indicates a first premolar that we have observed in none of the known species of *Felis* to date.'') It is not clear as to whether Blainville was referring to the 1839 letter of Lartet, but it is reasonable to assume this. Therefore, Blainville did not choose to ignore seniority in nomenclature that Lartet might

have deserved. The fact is that Lartet did not suggest a name for the felid mandible prior to 1843. Blainville then concluded with the following statement, perhaps the earliest use of biological nomenclature for a fossil felid: ''C'est pour indiquer la particularité la plus remarquable de cette mandibule que j'ai donné à le espèce à laquelle je le attribue le nom de *F. quadridentata*.'' (''It is to indicate the most remarkable characteristic of this mandible that I gave to the species the name of *F. quadridentata*.'') Therefore, regardless of how the dentary is labeled in plate 16, Blainville clearly named the cranium and the lower jaw fragment *F. quadridentata*, based on the lower jaw character of presence of p2.

By 1850, Paul Gervais recognized the generic significance of the primitive felid character of presence of p2. He erected the genus *Pseudaelurus*, distinguishing it from the genus *Felis* by a single character, ''par suite de la présence de une petite avant-molaire infériure de plus que dans les *Felis ordinaires* (''by the presence of an additional inferior premolar than in *Felis ordinaires*.'') Gervais recognized the confusion created by the labeling of the lower jaw illustration as *F. tetraodon* in Blainville's (1843) *Ostéographie*. Gervais introduced the new genus as: ''*PSEUDAELURUS*, Gerv. 68. *Pseudaelurus quadridentatus Felis quadr.* ou *tetraodon*, Blainv., Ostéogr., G. *Felis*, p. 155. pl. 15 et 16. Fossile à Sansan (Gers.).'' Gervais made a choice between the two species names and he gave priority to the one mentioned by Blainville in the text (*quadridentata*). Gervais correctly assigned it the masculine ending (*quadridentatus*) to agree with its new genus. Therefore, the type species for the genus *Pseudaelurus* is *P. quadridentatus* (MNHN Sa 601), the dentary fragment first mentioned by Lartet in 1839 as being hyenalike, described by Blainville in 1843 as *Felis quadridentata*, and illustrated in plate 16 of Blainville's *Ostéographie* as *F. tetraodon*.

The confusion concerning the synonymy of *Pseudaelurus quadridentatus* began in 1851 when Lartet published ''Notice sur la colline de Sansan.'' In this paper, Lartet began the felid section with the following, ''1. *Felis hyoenoides* Lartet C. R. Ac. Sc. 1838. Cat. Man. *Felis quadridenta* (pars) Blainville Ost. Fasc. 12. Grande espèce à formes ro-

bustes, de la taille de la Panthère, ayant à la mâchoire inférieure une dent de plus que les autres espèces du genre, ce est-à-dire, quatre comme les Hyènes. (''Large species with robust forms, of the size of the Panther, having in the lower jaw a tooth more than the other species of the genus, that is to say, four like the Hyenas.'' This was a mistake by Lartet. There was no mention of *Felis hyoenoides* or *Felis hyaenoides* in any paper that I am aware of prior to this one. Therefore, as Heizmann (1973: 50) pointed out: ''Da es also richtig heißen muß '*Felis hyaenoides* Lartet 1851', hat Blainvilles Veschreibung unter den Namen quadridentatus bzw. tetraodon eindeutig die Priorität. (''Since the correct citation must be '*Felis hyaenoides* Lartet 1851', Blainville's description of the name *quadridentatus* or *tetraodon* has priority.'') And, as explained above, it was Gervais' choice of the species name used in the text by Blainville over the one placed beneath the drawing that awards priority to *quadridentatus*. In conclusion, some authors have published variations on the spelling of the generic name. For example, *Pseudaelurus quadritentatus* Blainville was suggested by Viret (1951: 87). *Pseudailurus quadritentatus* Blainville was used by Abel (1919: 742, 743) and Ginsburg (1961b: 137). The correct species name comes from Blainville (1843: 155) *Ostéographie*: *F. quadridentata*. The correct spelling of the genus *Pseudaelurus* appears in Gervais (1850: 127) along with the new masculine suffix for the species.

REVIEW OF THE GENUS *PSEUDAELURUS* IN EUROPE, ASIA, AND AFRICA

Specimens of *Pseudaelurus* first appear in the early Miocene (MN3) of Europe (Dehm, 1950). The specimens are numerous in comparison to the earlier *Proailurus*. However, the overwhelming majority of the material reported in the literature consists of isolated lower jaws. Four species have been named from the Miocene of Europe: *Pseudaelurus quadridentatus* Blainville, 1843 (fig. 1), *Pseudaelurus turnauensis* Hoernes, 1882 (fig. 2), *Pseudaelurus lorteti* Gaillard, 1899 (fig. 3), and *Pseudaelurus romieviensis* Roman-Viret, 1934 (fig. 4). All four species were originally based on mandibular and
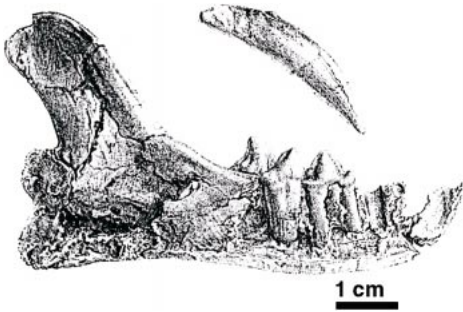
Fig. 2.   *Pseudaelurus turnauensis* Hoernes (no catalogue no.), type specimen. Drawing from Hoernes (1882).

maxillary fragments. There have been no European skulls yet described. Charles Depéret (1892) described a small specimen, *Pseudaelurus transitorius*, from the La Grive-Saint-Alban (Isère) locale of France (Depéret, 1892). This species was placed in synonymy with *Pseudaelurus turnauensis* Hoernes by G. de Beaumont (1961). The proposed synonymy was confirmed by Heizmann (1973) and Wang et al., (1998), but ignored by Ginsburg (1983).

The first postcranial bone of *Pseudaelurus* was described in 1899: a right humerus of *P. transitorius* = *P. turnauensis* from the middle Miocene La Grive-Saint-Alban locality in France (Gaillard, 1899). G. de Beaumont (1961) described 19 postcranial bones from La Grive-Saint-Alban and the early Miocene Wintershof-West localities, but none was accompanied by a skull nor alleged to be from the same individual. L. Ginsburg (1961b) reported an even larger assortment of isolated mandibular, maxillary, and postcranial material from the middle Miocene of Sansan in France, again without a skull.

Elmar Heizmann (1973) published a review of the European *Pseudaelurus* radiation recognizing four species in increasing size order: *Pseudaelurus turnauensis* Hoernes, *Pseudaelurus lorteti* Gaillard, *Pseudaelurus romieviensis* Roman and Viret, and *Pseudaelurus quadridentatus* Blainville. In Asia, three species of *Pseudaelurus* have been described, all from mandibular, maxillary, or dental material. *Pseudaelurus guangheensis* Cao et al., 1990 is from the middle Miocene Guanghe District of Gansu, China. *Pseudae-*
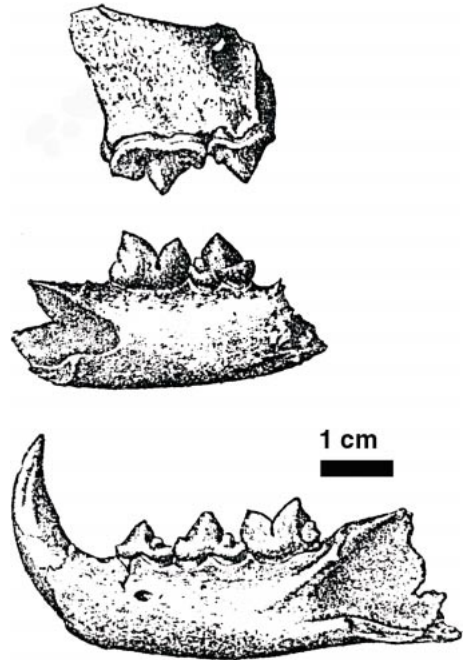

Fig. 3.   *Pseudaelurus lorteti* Gaillard (MHNL 1379) (cast AMNH 103397),type specimen. Drawing from Gaillard (1899).
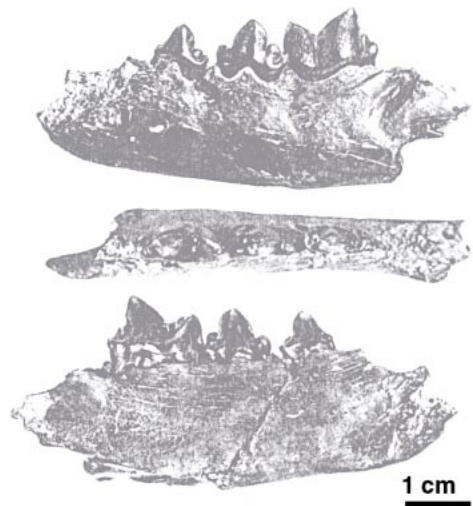

Fig. 4.   *Pseudaelurus romieviensis* Roman and Viret (Basel S.O. 6417), type specimen. Drawing from Roman and Viret (1934).

lurus cuspidatus Wang et al., 1998 is a new species from the early middle Miocene Halamagai Formation in northern Junggar Basin, in the Xinjiang Autonomous Region, China. A left ramus and dental fragments referred to *P. lorteti* were reported from the middle Miocene of Xiacaowan, Sihong County, in Jiangsu Province, China (Qiu and Gu, 1986).

From Africa, a m1 and tibia fragment were assigned to *P. turnauensis* from the Al-Sarrar locality (early Miocene, MN4a) in what is now Saudi Arabia (Thomas et al., 1982).

NORTH AMERICAN REVIEW

In 1857, the United States Army Corps of Engineers sent out exploring expeditions to seek railroad and military routes to the west. Under the direction of Lt. G.K. Warren, and accompanied by geologist Dr. F.V. Hayden, one expedition performed reconnaissance in the area of north-central Nebraska in the valley of the Niobrara River in Cherry and other counties. Hayden collected many fossils during two exploring swings through the valley. Most of these specimens were collected in October of that year near the present town of Merriman, Nebraska (Webb, 1969). All of the specimens collected by Hayden were turned over to Joseph Leidy, who worked on them until 1870, at which time the specimens were transferred to E.D. Cope (Schuchert, 1939).

Soon after the return of the first Nebraska expedition, Joseph Leidy (1858) described a new species of Miocene cat, *Felis intrepidus*, from "the loose sands of the Niobrara River" in western Nebraska. This fossil possessed evidence of p2, but Leidy did not recognize the generic value of this character at first. He interpreted the jaw at a meeting of the Philadelphia Academy of Natural Sciences in 1858 and mentioned "a well preserved specimen of the lower jaw." However, he apparently was referring to two rami of this "lower jaw."

In 1869 Leidy published a more extensive work, "The extinct vertebrates from the valley of the Niobrara River". He described 28 new species, including the *intrepidus* jaw with its new generic appellation, *Pseudaelurus intrepidus*. However, in this work Leidy referred to a left and a right ramus, while in the 1858 presentation, only a left ramus was mentioned: "On one side of the specimen, the left ramus is represented in figure 8, plate1. It contains the sectorial molar, the two premolars in advance, the canine tooth, and the lateral incisor. The right ramus contains the same teeth with the addition of the second incisor, but the canine tooth and lateral incisor are much mutilated. In both rami the premolar, considered as the chief character of the genus, is absent, but its alveolus remains midway in the hiatus back of the canine tooth" (Leidy, 1869: 52). The type specimen status is therefore consigned to the left lower jaw ramus (USNM 124) (fig. 5), whose measurements are listed in Leidy's 1858 paper.

The right ramus (ANSP11297) is lost. It was examined at the Frick Laboratory in New York ca. December, 1952, on loan from the Academy of Natural Sciences, Philadelphia. Unpublished Frick Archive notes mention the "similarity of wear on the m1" of each ramus (Toohey, 1951). However, mention is also made of matrix on the symphyseal region which did not permit articulation. There is actually no proof that these two rami were found together. Hayden's field notes, apparently lost, could provide some information regarding the relationship of these two specimens. I am unaware of any illustration or photograph of the right ramus of *Pseudaelurus intrepidus* Leidy (ANSP 11297).

The two rami of *Pseudaelurus intrepidus* were most likely collected from the lower Valentine Formation (Webb, 1969). The key is the mention by Hayden of "the loose sands of the Niobrara River". This description best fits the "fine unconsolidated light gray sands" (Webb, 1969: 8) of the Valentine Formation. The other sediments are more consolidated and are less exposed in the area visited by Hayden. This would make the holotype (USNM 124) late Barstovian in age.

In 1870, O.C. Marsh from Yale University began to work in the Loup River and Niobrara River valley areas of Nebraska, the first of the Yale Student Expeditions. On July 7, 1873, in what is today Cherry County, Nebraska, the expedition collected a set of lower carnivore jaws "near mouth of Minnechaduza Creek" (Thorpe, 1922). This is the fos-
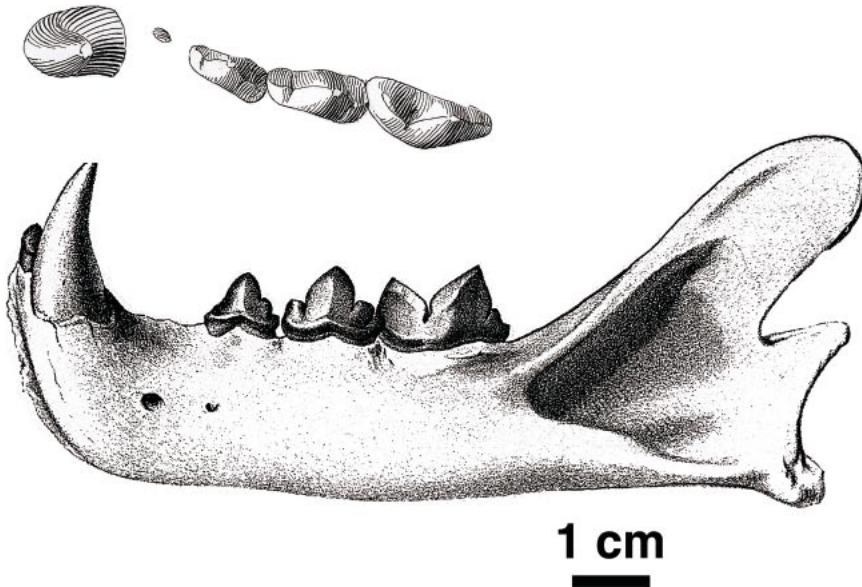
Fig. 5.   *Pseudaelurus intrepidus* Leidy (USNM 124), left lower jaw, type specimen. Drawing from Leidy (1869).

sil that was described by Thorpe in 1922 as the type specimen of a new North American species, *Pseudaelurus marshi* (YPM12865) (fig. 6). It is a partially restored felid lower jaw and is stored in Yale's Peabody collection as articulated left and right rami. *Pseudaelurus marshi* Thorpe was collected from the ''lower part of the Valentine Formation and pertains to the Niobrara River Fauna''

(Johnson, 1936). This would make this second North American *Pseudaelurus* type specimen a late Barstovian fossil. Thorpe also described a paratype (YPM 12815), a left ramus collected from Gerry's Ranch in Weld County, northeast Colorado, during the Yale Student Expedition in 1870. This locality would be part of the Ogallala Group, making the specimen Barstovian in age.
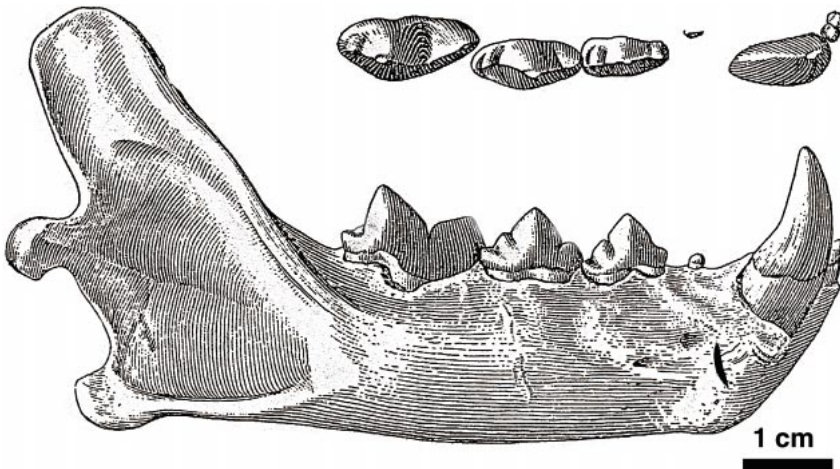

Fig. 6.   *Pseudaelurus marshi* Thorpe (YPM 12865), right ramus, type specimen. Drawing from Thorpe (1922).
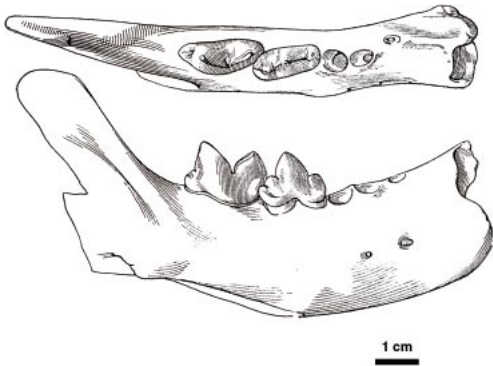
Fig. 7. *Pseudaelurus intrepidus* Leidy *sinclairi* (AMNH 17212), right ramus fragment, type specimen. Drawing from Matthew (1918).

William J. Sinclair (1915) of Princeton University reported on fossils from the ''Snake Creek Formation'' collected in Nebraska during the preceding year. He described a ''*Pseudaelurus* near *intrepidus* Leidy'' right lower jaw fragment (Sinclair, 1915). This fragmented specimen was stored in the Princeton museum and is now in Yale's Peabody collection (YPM PU 12081). W.D. Matthew (1918) in the first of his ''Contributions to the Snake Creek fauna'' described a much more complete lower jaw ramus, *Pseudaelurus intrepidus sinclairi,* new variety (fig. 7). This specimen (AMNH 17212) is thought to be from the same locality as the one described by Sinclair. Matthew labeled it as coming from Sinclair Draw, 1916 expedition (Matthew, 1918). The exact location where the specimen was found is not known, but the quarry would be part of the Lower Snake Creek Fauna, making the specimen early Barstovian in age (Skinner et al., 1977).

In 1934, two new felids from the late Miocene of Kansas were described by Claude Hibbard in the published version of his Master's thesis. The first is *Pratifelis martini* (UKMNH 3156), a partial left lower jaw collected by H.T. Martin in 1911 from the late Hemphillian Lost Quarry locality, Wallace Co., Kansas. This species was subsequently assigned to the genus *Pseudaelurus* (Macdonald, 1954). The type specimen was redescribed as *Pratifelis martini* in a faunal review of the locality (Bennett, 1979). McKenna and Bell (1997) also referred this species to the genus *Pratifelis*.

I have examined casts of this dentary fragment (AMNH 38905). The m1 length is 19.3 mm. The distance between the c and p3 is small, measuring only 8.8 mm. The missing piece of the protoconid of the m1 on the specimen has exaggerated the size of the talonid. Only p3 is intact. UKMNH 3156 is a large, late Miocene felid lower jaw lacking information on the anterior end of the dentary. Specimens such as UKMNH 3156 resemble specimens in the Frick-AMNH collection assigned to the genus *Nimravides*. Examination of the original specimen may possibly result in assignment of UKMNH 3156 to the genus *Nimravides*.

The second specimen described by Hibbard (1934) was an anterior skull fragment of a large felid, *Adelphailurus kansensis* (UKMNH 3462). This specimen was collected by H.T. Martin and party from the late Hemphillian Edson Quarry, Sherman Co., in 1924 (Hibbard, 1934). This species was subsequently assigned to the genus *Pseudaelurus* (Simpson, 1945). The type specimen, with some new referred postcrania, was redescribed as *Adelphailurus* (Harrison, 1983). I have examined casts of this fossil (AMNH 38901). The long upper canines (43 mm), large size of P4 (23 mm), and the very short distance between C and P3 (7.5 mm) put this specimen outside the morphological range of the genus *Pseudaelurus*.

In 1934, Chester Stock reported on five specimens from an early Barstovian locality near Tonopah, Nevada. He described cranial and upper and lower dental material and referred all to *P. intrepidus* Leidy (Stock, 1934). Included in this material was the first skull assigned to the genus *Pseudaelurus* as well as the first upper dentition in North America. Stock noted that the *Pseudaelurus* skull retained the primitive condition of having alisphenoid canals. This skull, LACM (CIT) 791, has undergone considerable plaster restoration in the areas of hard palate, zygomatic arches, and frontal bones. The size of the skull has been therefore compromised. I examined this skull and it will be described later in this paper.

In 1948, J.R. Macdonald described *Pseudaelurus pedionomus* (UCMP 29186) from
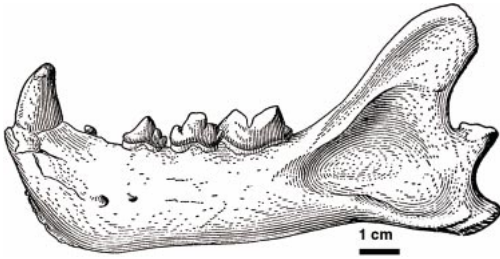
Fig. 8. *Nimravides pedionomus* (UCMP 29186), left ramus, type specimen. Drawing from Macdonald (1948a).

Fig. 9. *Pseudaelurus aeluroides* Macdonald (SDSM 3248), right ramus fragment, type specimen. Drawing from Macdonald (1954).

UCMP locality V-3327 (early Clarendonian), in Cherry County, Nebraska, of the Minnechaduza Fauna. Material described consisted of a left jaw ramus, right femur, left tibia, distal half of a right tibia, distal left humerus, lumbar vertebra, fifth left metatarsal, and right calcaneus. The lower jaw is distinguished by its large size and a ventral bulge along the anterior portion of the dentary beneath the mental foramina (fig. 8). Macdonald suggested that this species occupied "a terminal North American position similar to that of *Metailurus major* Zdansky and *Metailurus minor* Zdansky in the Asiatic fauna" (Macdonald, 1948a).

In the same year Macdonald described another new, even larger species, *Pseudaelurus thinobates*. This specimen is from the late Clarendonian Black Hawk Ranch quarry in Contra Costa Co., California. It consists of a lion-sized right mandible (UCMP 34513), a crushed skull, and a distal humerus (Macdonald, 1948b). The lower jaw resembled *P. pedionomus* in also having a ventral bulge along the anterior portion of the dentary. The length of m1 in this jaw is 28 mm, 50% larger than the largest m1 thus far assigned to *Pseudaelurus*. This large species was removed from the genus *Pseudaelurus* in 1958 when David Kitts described two large felid lower jaws from the Arnett local fauna from Ellis County, Oklahoma. He stated that these early Clarendonian felids bore "marked resemblances to the lower jaw of *Pseudaelurus*" (Kitts, 1958). Nevertheless, he made a valid claim for their generic separation. Kitts erected a new genus, *Nimravides*, for this material and made *Pseudaelurus thinobates* its type species. Kitts assigned the new genus
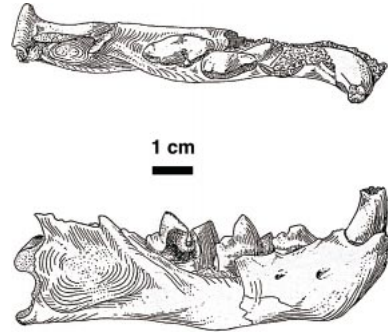
to the subfamily Nimravinae and referred to the similarities between the dentary of *Nimravides thinobates* and some specimens in the genus *Nimravus*. Subsequently, *P. pedionomus* was also removed from the genus *Pseudaelurus* in a review of the genus *Nimravides* (de Beaumont, 1990). Therefore, the affinity of both *Pseudaelurus* and *Nimravides* to Felidae and their separation from the Nimravidae was reaffirmed (Baskin, 1981).

In 1954 Macdonald described his third North American *Pseudaelurus* species, *Pseudaelurus aeluroides* (SDSM 3248), based on a much smaller right lower jaw fragment from the Northeast Rim of Sinclair Draw, Sioux Co., Nebraska (fig. 9). This specimen is a part of the early Barstovian Lower Snake Creek Fauna (Macdonald, 1954). I have not been able to examine either this specimen or a cast of it. From the illustration, it appears to be a juvenile with erupting teeth. The m1 is listed at 15.6 mm in length, and the distance between the lower canine and p3 is 7.3 mm. I have examined 21 lower jaws referred to *Pseudaelurus* from the Lower Snake Creek Fauna. Of these, I have assigned seven to *P. marshi* Thorpe. None of the characters or dimensions mentioned by Macdonald would distinguish SDSM 3248 from this group. I will not reassign a specimen without seeing it, but *Pseudaelurus aeluroides* (SDSM 3248) appears to be synonymous with *P. marshi*.

In 1963, Clarendonian material from locality UO 2343 of the Upper Juntura Formation in Malheur County, Colorado, was described that included "fragmentary teeth

and skeletal elements of the cat *Pseudaelurus*'', apparently from a single individual (Shotwell and Russell, 1963). A species determination was not possible. Material referred to *Pseudaelurus* was upper right canine, left P4, left p4, right p4, right ectocuneiform, right navicular, and various fragments. Disregarding material originally assigned to *Nimravides pedionomus*, this was the first description of North American postcranial material assigned to *Pseudaelurus*.

In 1969, W. Dalquest described some Hemphillian material from the Coffee Ranch locality in Hemphill County, Texas. On page 11 he illustrated a left dentary fragment which he called *Pseudaelurus hibbardi*, new species. This specimen is of the size of *Nimravides pedionomus*. The author justified specific separation based on a character of the symphyseal region (''swollen'') and the presence of just one mental foramen (Dalquest, 1969). I assign this specimen to the genus *Nimravides*. In 2001, T. Rothwell described *Pseudaelurus validus* (F:AM 62128), based on a partial skeleton from the Nambé Member (late Hemingfordian), Española Basin, near East Cuyamunque, New Mexico (Rothwell, 2001). This large species is the earliest known felid from North America having cranial, upper, and lower dentition as well as postcranial information.

SYSTEMATIC PALEONTOLOGY

CLASS MAMMALIA LINNAEUS, 1758

ORDER CARNIVORA BOWDICH, 1821

SUBORDER FELIFORMIA KRETZOI, 1945

FAMILY FELIDAE FISCHER DE WALDHEIM, 1817

Genus *Pseudaelurus* Gervais, 1850

TYPE SPECIES: *Pseudaelurus quadridentatus* (Blainville, 1843) (= *Felis quadridenta* Blainville, 1843)

INCLUDED SPECIES: Type species and *Pseudaelurus intrepidus* Leidy, 1858; *Pseudaelurus turnauensis* Hoernes, 1882; *Pseudaelurus lorteti* Gaillard, 1899; *Pseudaelurus marshi* Thorpe, 1922; *Pseudaelurus romieviensis* Roman and Viret, 1934; *Pseudaelurus aeluroides* Macdonald, 1954; *Pseudaelurus guangheensis* Cao et al.1990; and *Pseudaelurus cuspidatus* Wang et al., 1998; *Pseudaelurus validus*, Rothwell, 2001.

DISTRIBUTION: Early to middle (MN3 to MN9) Miocene of Europe; early to middle (late Hemingfordian to late Barstovian) Miocene of North America; early to middle (Xiejian to Shangwangian) Miocene of Asia; early Miocene of Africa.

GENERIC DIAGNOSIS: Members of Felidae with the following derived characters: absence of p1 and m2, m1 with reduced metaconid and talonid, P2 with one root, paroccipital process cupped about the posterior surface of an enlarged caudal entotympanic, tall coronoid process, hypoglossal foramen sharing a common depression with the posterior lacerate foramen, and a blunt and rectangular-shaped metacarpal 1. These derived characters are seen in combination with the primitive characters of presence of p2 and alisphenoid canal. *Pseudaelurus* differs from extant felid genera in c cross section showing flattened inner surface and posterior trenchant edge, presence of p2, m1 with variable metaconid and reduced talonid, and alisphenoid canal present. Differs from *Metailurus* in presence of alisphenoid canal and p2, absence of enlargement of mental ridge. Differs from *Nimravides* in smaller size and absence of any ventral mandibular mental ridge enlargement. Differs from *Proailurus* in absence of p1 and m2.

Pseudaelurus validus Rothwell, 2001

HOLOTYPE: F:AM 62128, skull with left and right I3, left C, broken right C, single-rooted alveoli for P1 and P2, left and right P3–M1. Articulated lower jaws with left i3, left and right c, left and right single-rooted alveoli for p2, left and right p3–m1. Postcrania: right and left humeri, right and left radii, right and left ulnae, left manus, articulated right manus, distal fragment of left femur with patella, left tibia, right tibial fragment, left and right fibular fragments, right pes, articulated left pes, partially prepared elements in plaster jacket, including exposed scapulae, ribs, vertebrae.

REFERRED SPECIMENS: Sheep Creek Fauna, Sheep Creek Formation (late Hemingfordian), Sioux County, Nebraska: F:AM 61827, right ramus with c, alveolus p2, p3, p4, broken m1, Greenside Quarry; F:AM 61837, left maxillary fragment with I3, C–M1, right tib-

ia and fibula, partial right radius, partial right ulna, astragalus, vertebrae and right fourth metatarsal, Head of Pliohippus Draw.

Lower Snake Creek Fauna, Olcott Formation (early Barstovian), Sioux County, Nebraska: F:AM 61834, complete skull with upper dentition, zygomatic arches, intact basicranium and associated lower jaws (F:AM 61829), Humbug Quarry; F:AM 61803, left maxilla with I3 alveolus, C, alveolus P1 and P2, P3–M1, Humbug Quarry; F:AM 61833, partial skull with upper dentition and partial right zygomatic arch, Quarry 3 (Far Surface Quarry); F:AM 61832, left ramus with i3, c, p2, broken p3, p4 and broken m1, East Wall Quarry; F:AM 61830, partial left ramus with p4, m1, Quarry 3 (Far Surface Quarry); F:AM 61828, left and right rami with left and right c, p2 alveoli, p3–m1, right humerus, left radius, left and right tibiae, Echo Quarry; F:AM 61835, a nearly complete skull with upper dentition and intact basicranium, Echo Quarry; F:AM 61836, skull fragment with left P4, left and right partial rami with partial dentitions, maxillary fragment with canine tooth, left radius, Echo Quarry.

DISTRIBUTION: Late Hemingfordian of New Mexico, late Hemingfordian and early Barstovian of Nebraska.

DIAGNOSIS: Differs from other species of *Pseudaelurus* by the combination of large size, long distance between c and p3, extremely reduced or absent metaconid on m1, and robust dentary with large and erect rectangular-shaped coronoid process. *P. validus* overlaps in size with *P. intrepidus* and *P. marshi* in North America and *P. quadridentatus* in Europe but can be differentiated from these species by the longer c–p3 length in *P. validus*, which exceeds the length of its m1, and by its large, erect, and rectangular coronoid process.

DESCRIPTION AND COMPARISONS: The holotype has been previously described in detail (Rothwell, 2001). The dentary bone of *P. validus* is taller and wider than similar-sized specimens of *P. marshi* or *P. intrepidus*. The coronoid process is wider and more erect than *P. marshi* or *P. intrepidus* and is much taller than in the earlier European taxon *Proailurus lemanensis* (fig. 10). The size and erectness of the coronoid process of *P. vali-*

dus resembles more the temporally equivalent *P. skinneri*.

F:AM 61829 (fig. 11) has the large distance between c and p3 that is distinctive of *P. validus*. In every observed lower jaw of *P. validus*, except for the crushed and restored holotype, the c–p3 distance exceeds the length of m1. Lower jaws assigned to *P. intrepidus* have c–p3 length ranging from 68% to 98% of the m1 measurement. In *P. marshi*, the type lower jaw (YPM 12865) has a c–p3 length 54% of the m1 length, and in the paratype (YPM 12815) it is 66%. In my study of modern felids, both male and female lions (*Panthera leo*) have an average c–p3 length that measured 110% of the m1 length (see tables 4, 5), a proportion similar to *P. validus*. In the puma, *Felis concolor*, the average c–p3 length was 66% of the m1 length in females, and 69% in males, corresponding more to the condition in *P. intrepidus* and *P. marshi*.

The lower dentition of *P. validus* is similar to that in other species within the genus. None of the specimens has p1. The p2 is usually indicated by a single-rooted alveolus positioned medial of the line of tooth row, as in the type. The left lower jaw of F:AM 61829 (fig. 11) has a two-rooted p2. This is the earliest example of a two-rooted p2 in North America. The number of roots of p2 varied in early European felid specimens (Dehm, 1950). A two-rooted p2 is routinely seen in the European taxon *Proailurus* (Filhol, 1888; Peigné, 1999), generally accepted as the earliest member of Felidae (Hunt, 1989).

The height of p3 in *P. validus* is consistently lower than p4. The primitive condition of equal-sized p3 and p4 can be seen in the European aeluroid taxa *Stenogale* and *Haplogale* (Peigné, 1999). The derived condition of p3 smaller than p4 is present in *Proailurus*, *Pseudaelurus*, and modern felids. The p4 of *P. validus* has a large posterior accessory cusp. The m1 metaconid is more reduced than in other early and middle Miocene felids. In seven lower jaw specimens assigned to *P. validus* that have m1 present, four have a greatly reduced (for *Pseudaelurus*) metaconid (fig. 12) and three have no detectable metaconid. The derived condition of a reduced metaconid contrasts with the m1
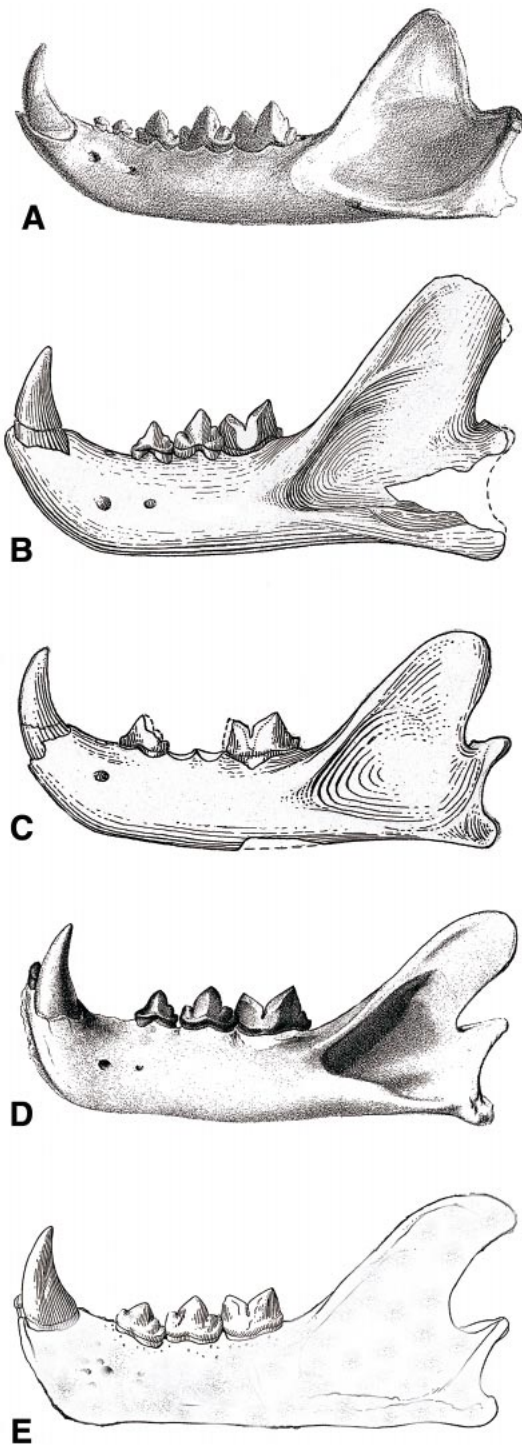
Fig. 10. Lower jaw rami of five felid species. The size of each specimen has been equilibrated to compare coronoid process morphology. **A,**

of *Pseudaelurus skinneri*, n. sp. which has a very distinct metaconid accompanied by an abridged talonid. The reduced metaconid morphology also differs from the later *P. intrepidus*, *P. marshi* and *P. stouti*, species whose m1 have a varying incidence of a more distinct metaconid.

The upper dentition of *P. validus* has been described for the type specimen, but is better preserved in many of the referred specimens (figs. 13–15). P3 of *P. validus* is large, with a primary cusp that is approximately the same size as the paracone of P4 (fig. 15). The posterior accessory cusp of P3 is also large and distinct and is approximately the same height and size as the parastyle of P4. Posterolateral to the posterior accessory cusp of P3 is a prominent cingular cusp. This cingular cusp is at the same level and of the same height and size as the anterior accessory cusp of the adjacent P4. These corresponding cusps of P3 and P4 can be seen in the lateral view of figure 15. The P4 of *P. validus* is wide, not compressed mediolaterally, as in modern felids. The P4 has a prominent protocone that projects anterolingually from the lingual surface of the paracone of P4 (fig. 14). In all referred specimens that have M1, the parastyle blade is contiguous with the metastyle blade of P4. This morphology elongates the upper carnassial blade in this species.

The ventral aspect of the skull of F:AM 61835 is in excellent state of preservation (fig. 16). Portions of the basicranium of this specimen have been described and illustrated previously (Neff, 1983; Hunt, 1998). The ectotympanic is thick and massive. The anterior crus have two components. There is a large

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Proailurus lemanensis (late Oligocene, early Miocene), drawing from Filhol (1888); **B,** *Pseudaelurus validus* (F:AM 61829) (early Miocene); **C,** *Pseudaelurus skinneri* (F:AM 61812) (early Miocene); **D,** *Pseudaelurus intrepidus* (USNM 124) (middle Miocene), drawing from Leidy (1869); **E,** *Felis concolor* (AMNH 11082), recent, drawing from Matthew (1910). The coronoid process is short and erect in *Proailurus*, still somewhat erect in *P. validus* and *P. skinneri*, but slender and sloping in *P. intrepidus* and modern felids.
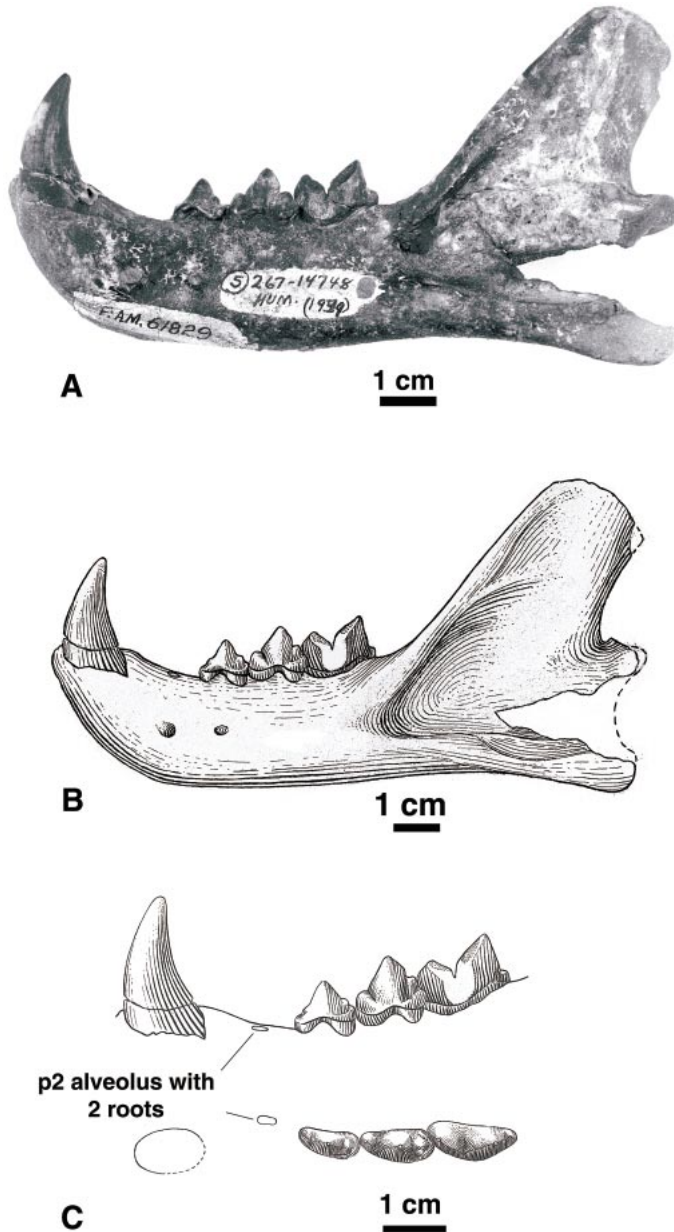
Fig. 11. **A,** *Pseudaelurus validus* (F:AM 61829), left ramus, lateral view; **B,** *P. validus* (F:AM 61829), left ramus, lateral view, line drawing; **C,** *P. validus* (F:AM 61829) left and right rami, oblique occlusal view, line drawing.

anterolateral attachment to the squamosal and a thick and wide medial articulation with the lateral margins of the basioccipital and basisphenoid. The suture between the basioccipital and basisphenoid cannot be identified. The left auditory bulla has been dissected (fig. 17). The course of the septum bullae can be seen to run diagonally, along the posterior wall of the ectotympanic, across the crest of the promontorium, from a point just medial to the vagina processus hyoideus, anteromedially to a position considerably
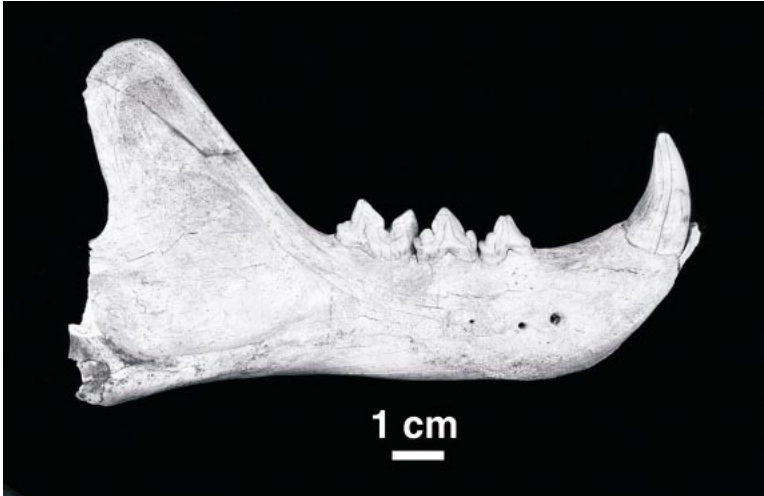
Fig. 12. *P. validus* (F:AM 61828), right ramus, lateral view. The m1 metaconid is positioned very low on the posterior surface of the protoconid, just above a very reduced talonid.

posterior to the anteromedial process of the auditory bulla. The course of the septum bullae demonstrates the level of anterior expansion of the caudal entotympanic in *P. validus*. The caudal entotympanic has advanced anteriorly to a level slightly posterior to the most anterior limit of the ectotympanic chamber. The caudal entotympanic chamber terminates posterior to the anteromedial process. This morphology is similar to the condition seen in *Proailurus lemanensis* (Hunt, 1998), but contrasts with modern felids whose thin-walled caudal entotympanic has advanced farther anteriorly. Posteriorly, the caudal entotympanic has invaded and emarginated the paroccipital process to a degree seen only in modern felids. For a more in-depth analysis of the structures of the auditory region of this specimen, see Hunt (1998: 46).

On the ventral surface of the basioccipital of F:AM 61835, between the two bullae, are two round rugose areas of attachment for the paired rectus capitus ventralis muscles (fig. 16). These two muscle insertion areas are much larger and more expanded than on skulls of other species of *Pseudaelurus*. This increased area of attachment is seen also in
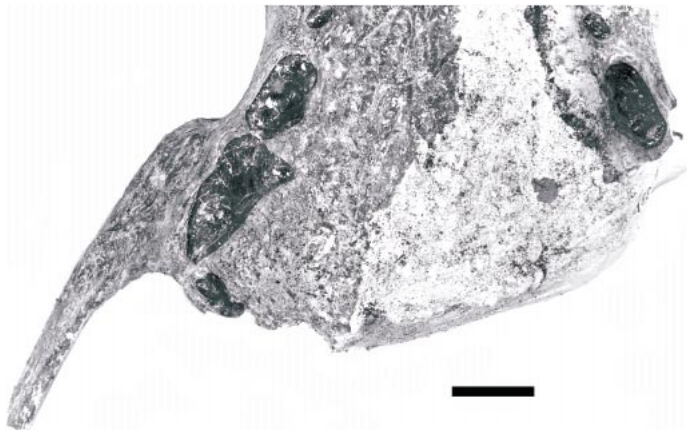

Fig. 13. *P. validus* (F:AM 61833), maxilla, occlusal view, anterior is to the top.
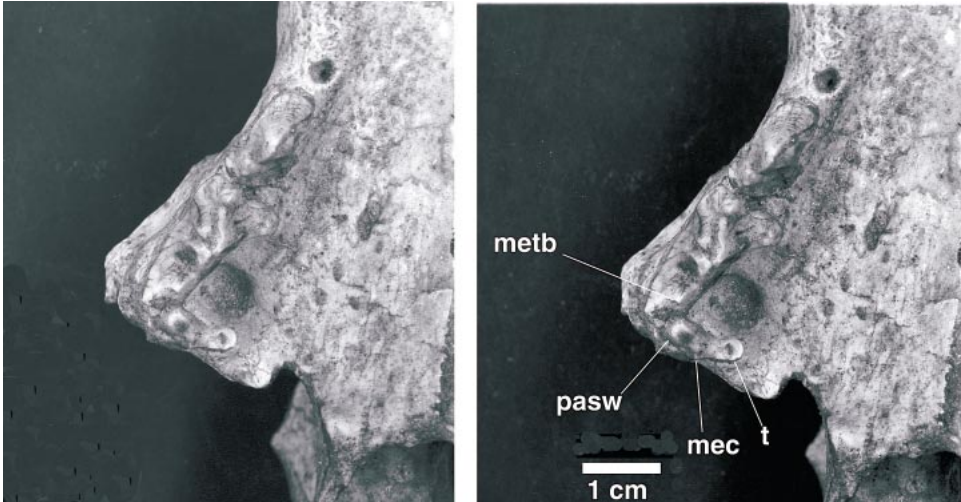
Fig. 14. *P. validus* (F:AM 61835), partial right upper dentition, occlusal view, anterior is to the top, stereo pair. The teeth in this specimen exhibit considerable wear. The parastyle wing (pasw) of M1 is contiguous with the metastyle blade (metb) of P4. Visible on M1 are a distinct metacone (mec) and a talon basin (t).

F:AM 61834 skull (fig. 18). There is no evidence of a postglenoid foramen in either F:AM 61834 or F:AM 61835. The postglenoid foramen is present in the type skull of the earlier European felid *Proailurus lemanensis* (MNHN 1903–20). In the skulls of four species of extant felid that I studied (*Panthera leo*, *Felis* concolor, *Lynx canadensis*, *Lynx rufus*), the postglenoid foramen was variably present, although minute.

The foramen ovale in F:AM 61834 and F:AM 61835 is located at the level of the anteroventrally facing glenoid fossa (figs. 19, 20). This agrees with the location of this foramen in the type specimen (F:AM 62128) and does not differ from modern species. The three skulls assigned to *P. validus* (F:AM 61834, 61835, 62128) have distinct anterior and posterior alisphenoid foramina, with the anterior alisphenoid foramen positioned anterodorsally to the posterior alisphenoid foramen. Careful examination of F:AM 61834
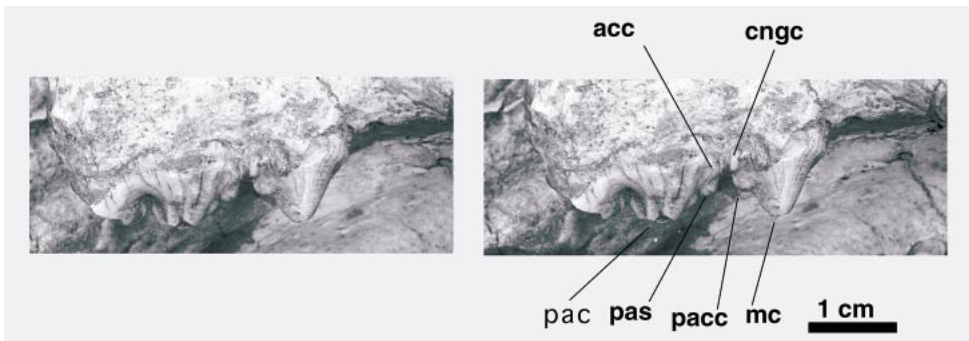
Fig. 15. *P. validus* (F:AM 61835), partial right upper dentition, close lateral view of P4 and P3, anterior is to the right, stereo pair. The primary cusp of P3 (mc) is of the same size and height as the slightly damaged paracone (pac) of P4. The posterior accessory cusp of P3 (pacc) is of the same size and height as the parastyle cusp of P4 (pas). The posterior cingular cusp of P3 (cngc) is also evident, and it is of the same size and height as the adjacent accessory parastyle cusp (acc) of P4.

Fig. 16. *P. validus* (F:AM 61835), ventral view of skull, stereo pair.
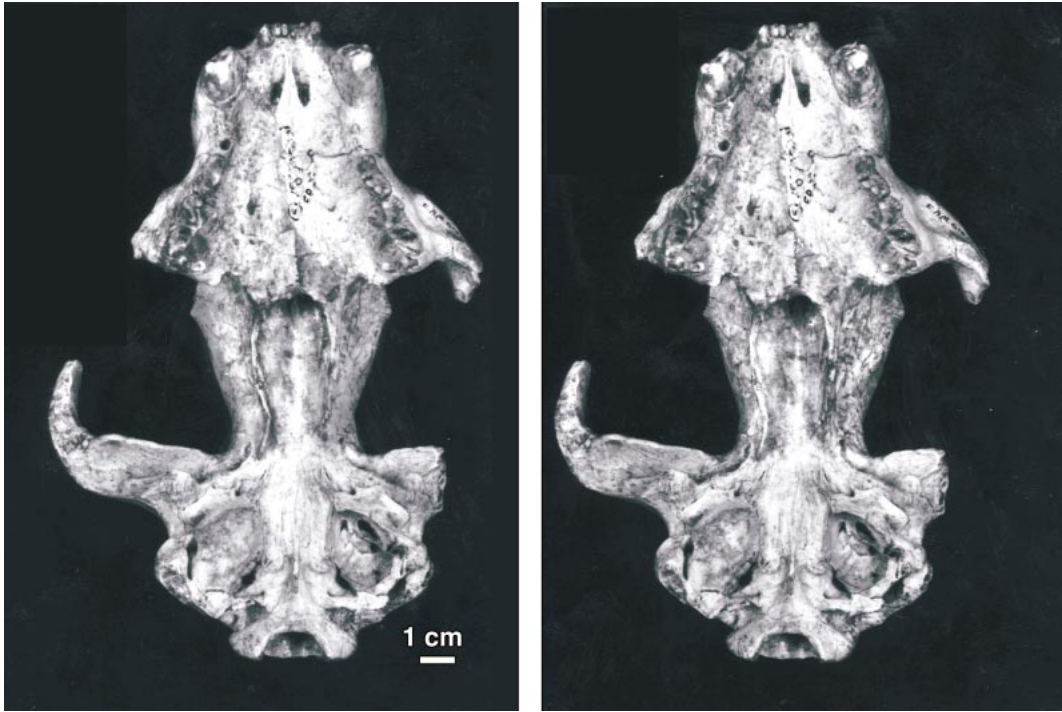
and F:AM 61835 reveals a patent foramen rotundum within the alisphenoid canal. The foramen rotundum opens in the general direction of the anterior alisphenoid foramen. This contrasts with the condition in modern felid skulls, in which the alisphenoid canal is absent. In extant felid species, the foramen ovale retains its position medial to the glenoid fossa, while the foramen rotundum is positioned farther anteriorly.

In both F:AM 61834 and F:AM 61835, a well-developed external pterygoid fossa can be seen immediately ventral to the alisphenoid canal. Both of these skulls also have well-preserved palatine and pterygoid bones. The paired vertical plates of the palatine bones are parallel to each other when viewed from the ventral aspect. However, the paired pterygoid bones are not parallel, but rather reflect medially toward each other posteriorly, thus giving an oval shape to the area between the corresponding plates.

Some extremely well-preserved postcranial bones from the early Barstovian Echo Quarry are referred to *P. validus* (F:AM 61828 and F:AM 61828-A). However, they do not differ in size or morphology from the type specimen (see Rothwell, 2001).

DISCUSSION: *P. validus* has a dentition that is for the most part primitive for felids, but some states are derived relative to *Proailurus*. P1, P2, and p2 of *P. validus* are vestigial and peglike. These teeth do not occlude. There is a great difference in size between the upper and lower second and third premolars. The third premolars (p3, P3) are robust and possess accessory cusps that assist in mastication. The well-preserved F:AM 61834 skull and its associated lower jaws (F:AM 61829) (figs. 11, 18) provide insight into early felid occlusion. The carnassial activity is centered at the carnassial notches of P4 and m1, as in all Carnivora. The shear activity of F:AM 61834 extends anteriorly to the anterior surface of P3, which occludes with the posterior surface of p3. This morphology is identical to the condition in modern felids. Posteriorly, the upper carnassial activity continues to the parastyle blade of M1 (M1 missing in F:AM 61834 skull, present in F:AM 61835 skull), which occludes with the reduced metaconid and talonid of m1. Mod-
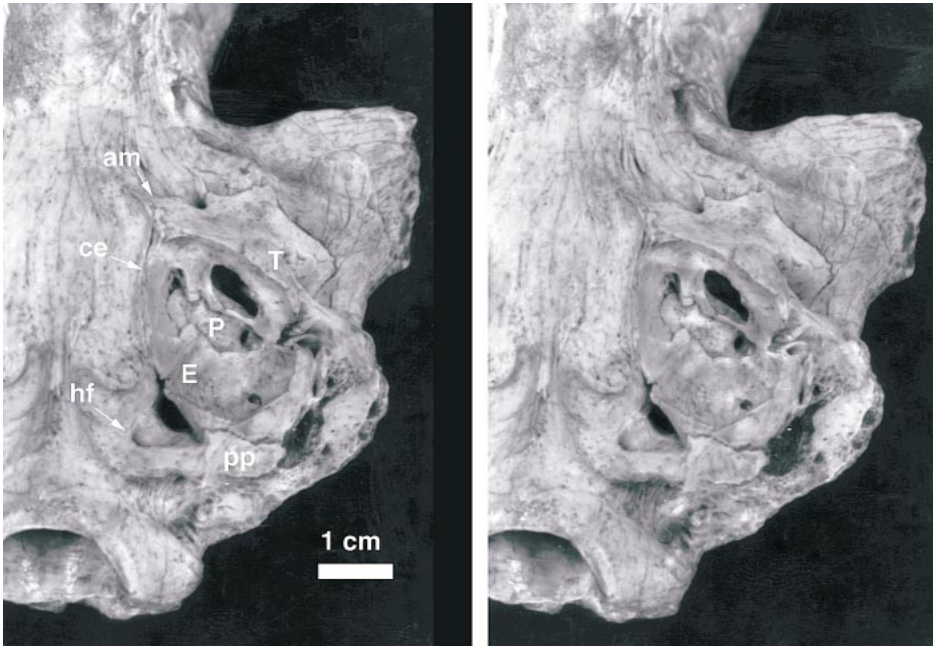
Fig. 17. *P. validus* (F:AM 61835), auditory region, stereo pairs. The ectotympanic (T) is thick and massive. The caudal entotympanic chamber (ce) has advanced anteriorly to a level slightly posterior to the anteriormost limit of the ectotympanic chamber. Posteriorly, the caudal entotympanic (E) has invaded and emarginated the paroccipital process (pp). Abbreviations: anteromedial process of the auditory bulla (am), hypoglossal foramen (hf), petrosal (P).

ern felids, in which M1 is vestigial and the metaconid and talonid of m1 are absent, have lost the occlusal ability of M1. The erect coronoid process of *P. validus* agrees with the condition in the smaller, but temporally equivalent species, *P. skinneri*. Outgroup comparison to earlier fossil aeluroids such as *Proailurus*, *Stenogale*, *Haplogale*, and *Stenoplesictis* establishes this erect morphology of the ascending ramus as a plesiomorphic condition for the family Felidae.

In both F:AM 61834 and F:AM 61835 the alisphenoid foramina are nearly perfectly preserved. Both skulls show evidence of the alisphenoid canal, foramen rotundum, and foramen ovale (figs. 19, 20). The primitive eutherian condition for these foramina (Novacek, 1986; Rougier, Wible et al. 1992) and their role in circulation (Davis and Story, 1943) have been previously described and illustrated. In a hypothetical primitive aeluroid, the mandibular branch of cranial nerve V exits the cranium via the foramen ovale. Entering the foramen ovale from outside of

the skull is a branch of the carotid circulation via the maxillary artery. This branch of the maxillary artery enters the cranium and forms an anastomosis with the internal carotid circulation (Davis and Story, 1943). In this hypothetical aeluroid, the maxillary branch of cranial nerve V exits the cranial cavity via the neomorph foramen rotundum and enters the alisphenoid canal. The maxillary branch of the trigeminal nerve (V) then proceeds anteriorly in the alisphenoid canal and exits the skull via the anterior alisphenoid foramen. As it leaves the anterior alisphenoid foramen, the nerve branch is accompanied by the maxillary artery, which has just traversed the alisphenoid canal after entering the posterior alisphenoid foramen. This is the condition in *Pseudaelurus validus*. On the floor of the cranial cavity in F:AM 61835 (fig. 21) are seen three separate grooves associated with the three branches of the trigeminal nerve (ophthalmic, maxillary, and mandibular) as they exit the braincase via separate foramina.
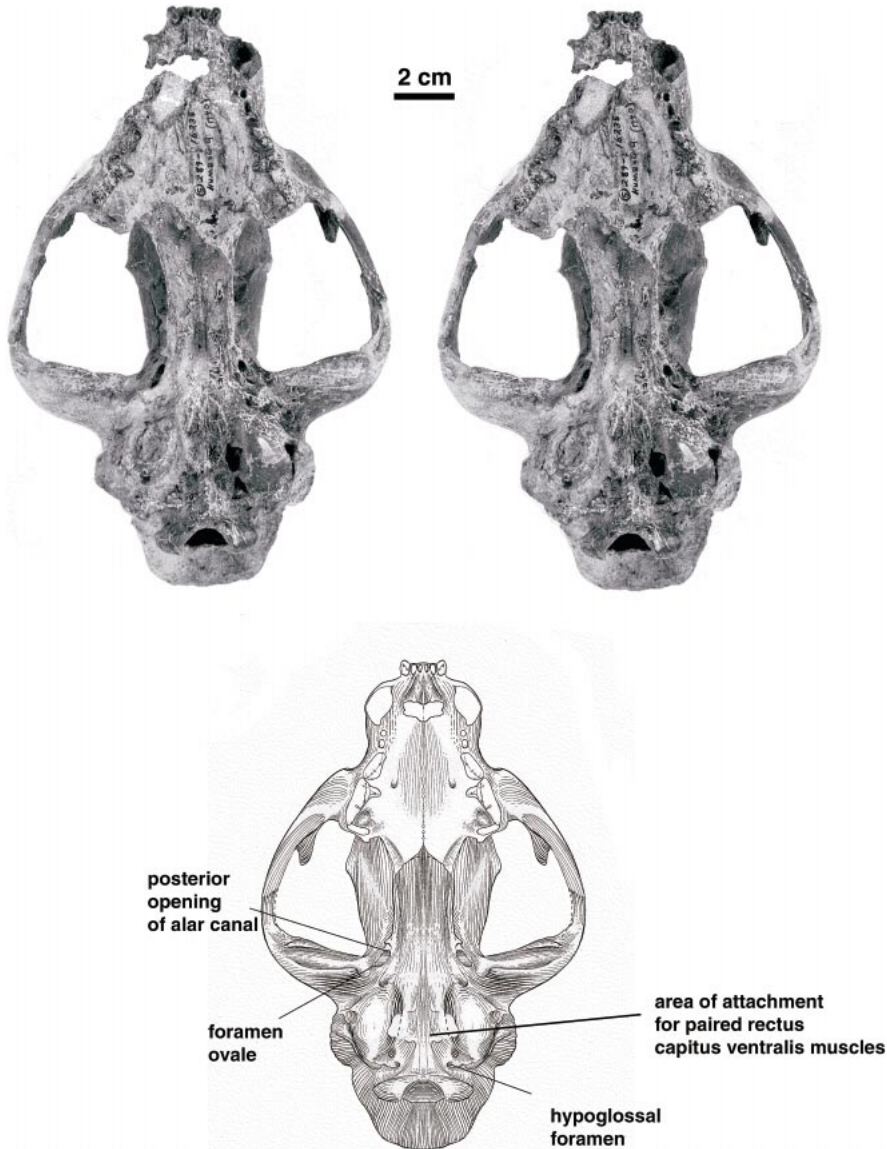
Fig. 18. *P. validus* (F:AM 61834), skull, ventral view, stereo pair and interpretive drawing.

Modern felids have greatly increased the degree of anastomosis of the external and internal carotid circulations over the primitive condition, decreased the role and size of the internal carotid artery, and incorporated the maxillary artery into a complicated rete externum. However, in the area of the alisphenoid foramina, modern felids differ from *P. validus* only by lacking external evidence of passage of the maxillary artery—the alisphenoid canal. The primitive condition of an ali-

sphenoid canal present in *Pseudaelurus validus*, and the derived state of absence of alisphenoid canal in *Felis*, supports the hypothesis that loss of the alisphenoid canal developed in parallel in the family Hyaenidae (Werdelin, 1996). Loss of the alisphenoid canal is another example of a character that should not be considered a synapomorphy for these two aeluroid families, as previously suggested (Wyss and Flynn, 1993).

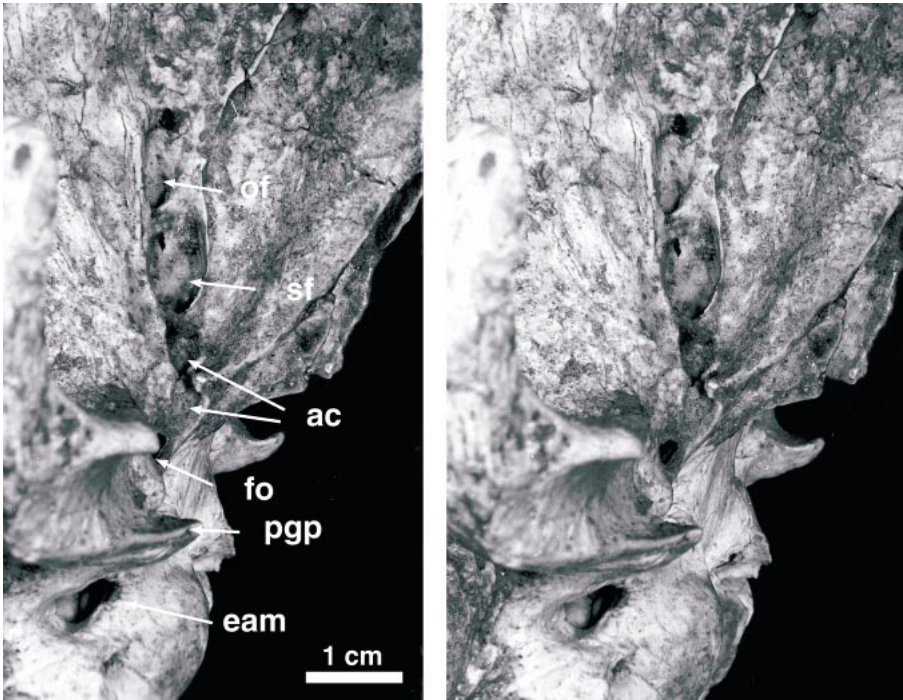In the auditory region of *Pseudaelurus*

Fig. 19. *P. validus* (F:AM 61835), oblique view of right basicranial foramina, stereo pair. Anterior is up and to the right, to expose the foramina. Abbreviations: optic foramen (of), sphenorbital fissure (sf), alisphenoid canal (ac), foramen ovale (fo), postglenoid process (pgp), external acoustic meatus (eam).

validus, the caudal entotympanic chamber has expanded slightly beyond that seen in *Proailurus* (see Hunt, 1998: 35). This anterior expansion of the caudal entotympanic can be monitored by the emargination of the adjacent basioccipital (Hunt, 1998). Although the emarginated basioccipital ridge in *P. validus* and *Proailurus lemanensis* is similar, a greater percentage of the caudal entotympanic lies anterior to the petrosal in *P. validus* (fig. 17). In *P. validus*, the anteromedial process is formed by robust medial crus of the ectotympanic. This area of the basicranium in *P. lemanensis* is unknown. In modern felids, the caudal entotympanic has advanced farther anteriorly, invading the medial crus of the ectotympanic and leaving the anteromedial process to be formed mostly of thin-walled caudal entotympanic.

Pseudaelurus skinneri, new species

HOLOTYPE: F:AM 61812, left ramus with c, p2 alveolus, p3, p4 alveolus and m1.

TYPE LOCALITY: Hilltop Quarry, Sheep Creek Formation, Sioux Co., Nebraska.

REFERRED SPECIMENS: Sheep Creek Fauna, Sheep Creek Formation (late Hemingfordian), Sioux County, Nebraska: F:AM 61814, left partial ramus with c, alveolus of p2, p3–m1, Thistle Quarry; F:AM 61816, left partial ramus with broken c, alveolus of p2, p3–m1,Thistle Quarry; F:AM 61818, left partial ramus with broken alveolus c, alveolus of p2, p3, p4, broken m1, Hilltop Quarry; F:AM 61817, right partial ramus with broken alveolus of c, p3–m1, Long Quarry; F:AM 61810, left partial ramus with broken alveolus of c, alveolus of p2, p3–m1, Greenside Quarry; F:AM 61819, left partial ramus with broken alveolus of c, alveolus of p2, p3–m1, Buck Quarry; and F:AM 61813, maxillary fragment with alveolus of P2, P3–P4, Ashbrook Quarry.

AGE: Late Hemingfordian (Galusha, 1975; Skinner et al., 1977; Tedford et al., 1987).

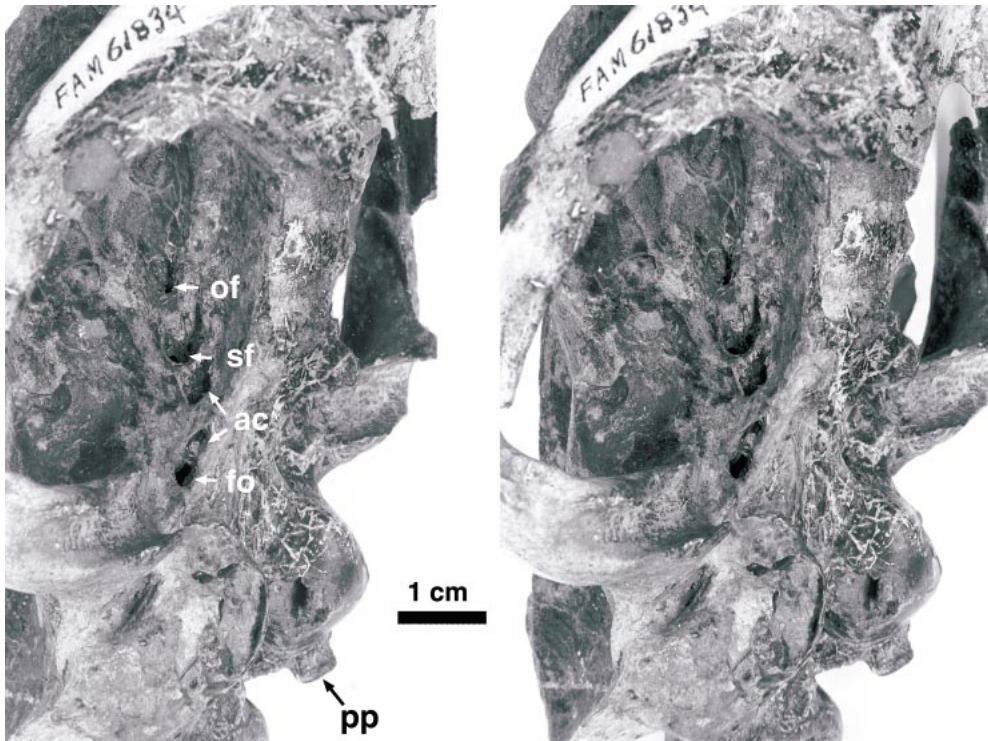DISTRIBUTION: Late Hemingfordian of Nebraska.

Fig. 20. *P. validus* (F:AM 61834), oblique view of right basicranial foramina, stereo pair. Anterior is up and to the right to display the foramina. In this specimen the ''roof'' of the alisphenoid canal (ac) is intact. The left paroccipital process (pp) can be seen projecting posteroventrally away from the posterior surface of the caudal entotympanic. Abbreviations: optic foramen (of), sphenorbital fissure (sf), foramen ovale (fo).

ETYMOLOGY: Species name in honor of Morris Skinner, a charter member of the Society of Vertebrate Paleontology who worked for the Frick Laboratory from 1927 to 1973 as a field worker, preparator, and curator.

DIAGNOSIS: Differs from all North American species by its unique size. *P. skinneri* has an m1 length range of 11.5–13.8 mm, larger than *P. stouti*. The next largest North American species, *P. aeluroides*, known only by the type specimen, has an m1 length of 15.6 mm. In size, *P. skinneri* overlaps only the European species *P. lorteti* and the Asian species *P. cuspidatus* and *P. guangheensis*. *Pseudaelurus skinneri* can be differentiated from these species by the following combination of characters: shorter c–p3 length, m1 with tall protoconid and reduced metaconid and talonid, P4 protocone projecting at an obtuse angle anterolingually. *P. skinneri* differs from the European species *P. lorteti* by

a taller m1 protoconid which is consistently much taller than the paraconid. *P. skinneri* differs from the Asian *P. cuspidatus* by a shorter c–p3 length, lacking the pronounced anterior cingular cusps on p3 and p4, and by presence of a gently sloping posterior edge of m1. *P. skinneri* differs from the Asian *P. guangheensis* by P4 protocone projecting at an obtuse angle anterolingually.

DESCRIPTION AND COMPARISONS OF HOLOTYPE: F:AM 61812, the type specimen of *P. skinneri*, has a dentary that is a well preserved (figs. 22–24). It is slender and gracile. Medially, fine details of a small mandibular symphysis can be seen along the anterior border of the ramus. A large mandibular foramen is positioned medially, beneath the origin of a slender, yet erect, coronoid process (fig. 23). This upright morphology of the coronoid compares favorably with the much larger *P. validus*, but contrasts with the more
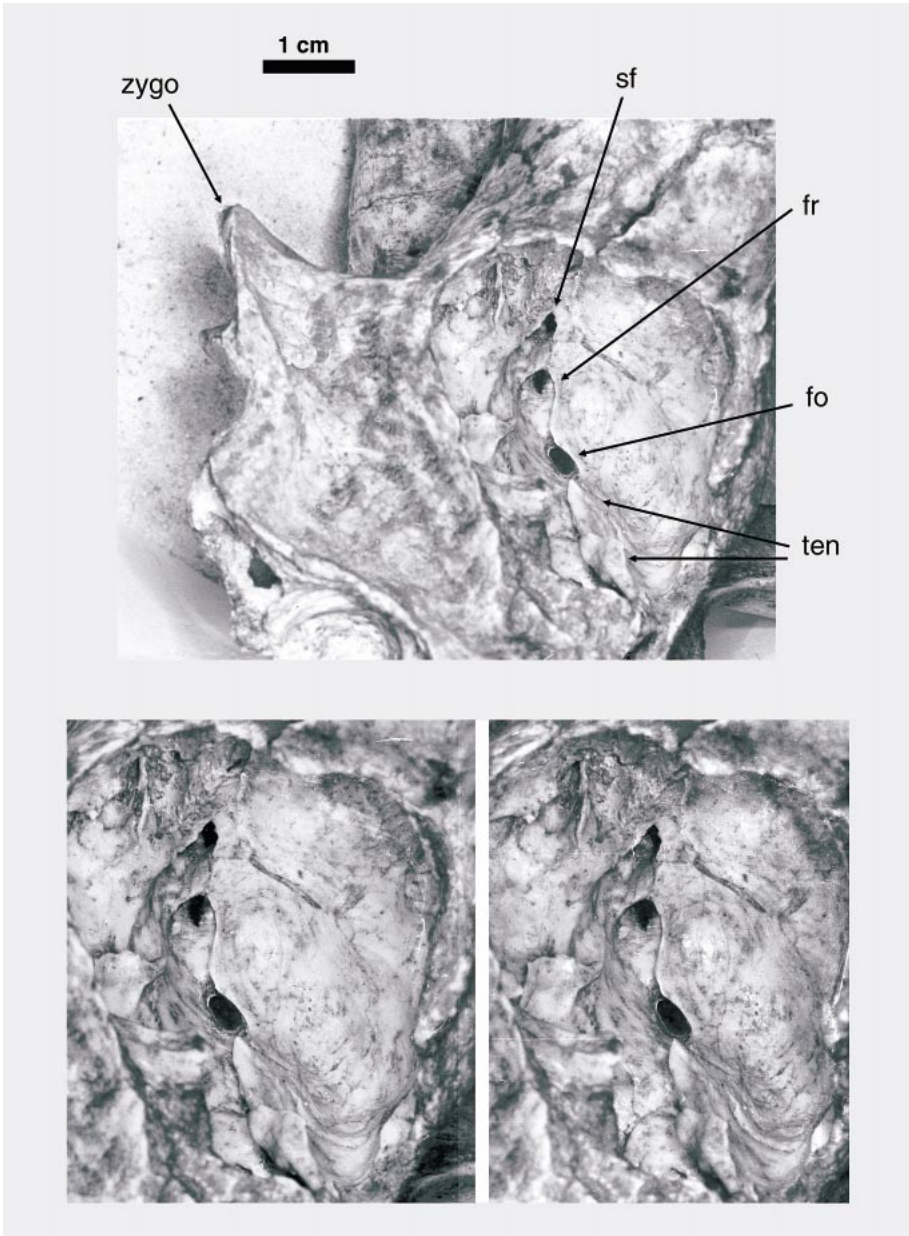
Fig. 21. *P. validus* (F:AM 61835), dorsal oblique view of cranium, stereo pair. Anterior is to the top. View is anterolateral, from the left side, through the opening in the left parietal bone. On the right side of the floor of the cranial cavity can be seen three separate grooves for the three branches of the trigeminal nerve (optic via sphenorbital fissure (sf), maxillary via foramen rotundum (fr), and mandibular via foramen ovale (fo)), which exit the braincase via separate foramina. The broken edge of the osseous tentorium (ten), separating the middle and posterior cranial fossae, can be seen. On the lateral wall of the cranial cavity, lateral and dorsal to the foramina, distinct impressions for cerebral convolutions can be seen. The left zygomatic arch (zygo) is labeled.

Fig. 22. Holotype of *P. skinneri* (F:AM 61812), left ramus, lateral view. This specimen displays the erect coronoid process and the distinct metaconid and talonid that are typical of this species.

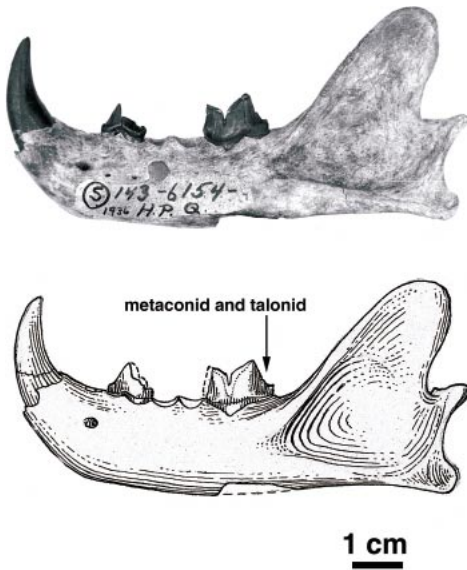Fig. 23. *P. skinneri* (F:AM 61812), left ramus, medial view.

sloping processes seen in the later *P. intrepidus* and *P. marshi*. The lower canine has a posterior ridge, but the cross section is more elliptical and symmetrical than the medially flattened canine of *P. validus*. There is no evidence of a p1 as in the specimen of *P. cuspidatus* (Wang et al., 1998). A large single-rooted alveolus for p2 is between c and p3. The alveolus of p2 is slightly closer to p3 than it is to c, and is situated lingual of an axis between c and p3. The distance between c and p3 is short. A short c–p3 length is also seen in *P. marshi* and *P. aeluroides*, but contrasts with the long c–p3 length seen in *P. validus*. The p3 of F:AM 61812 has a fractured crown, but the anterior and posterior cingular cusps are present. The anterior cingular cusp is minute, which differs from the more prominent anterior cusp described in *P. cuspidatus* but agrees with other species of *Pseudaelurus*. The large two-rooted p4 alveolus has a posterior root that is much larger than the anterior. Three mental foramina are present on the lateral surface. The largest and most anterior of these is at the level of the p2 alveolus.

The m1 is well preserved, missing only a

sliver of the anterior border of the paraconid. The carnassial notch is deep, narrow, and open to a level that is even with the reduced talonid. The protoconid is much taller than the paraconid, which agrees with the condition in *P. cuspidatus*. This degree of disparity in the height of paraconid and protoconid is not seen in other North American species. On the posterior margin of the paraconid is a reduced but distinct metaconid, aligned with the axis of the protoconid (fig. 22). The
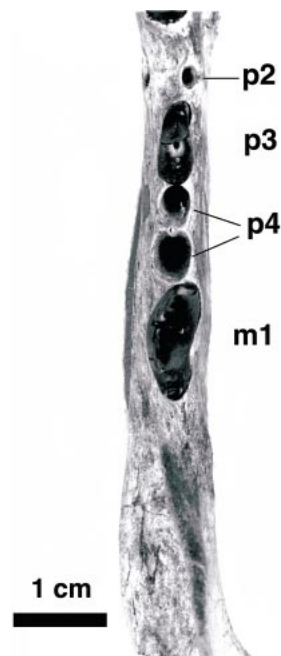
Fig. 24. *P. skinneri* (F:AM 61812), left ramus, occlusal view; the location of the p2 alveolus, lingual to a line between c and p3, is typical of North American *Pseudaelurus*.

Fig. 25. *P. skinneri* (F:AM 61816), left partial ramus, lateral view; the protoconid is much taller than the paraconid.

Fig. 26. *P. skinneri* (F:AM 61817), right partial ramus. The greater height of m1 protoconid described in the type specimen is seen also in this specimen. All of the lower jaws assigned to *P. skinneri* have m1 with a prominent metaconid and a distinct talonid.

reduced metaconid is not lingually positioned as in *P. cuspidatus*, and it blends into a reduced but prominent talonid.
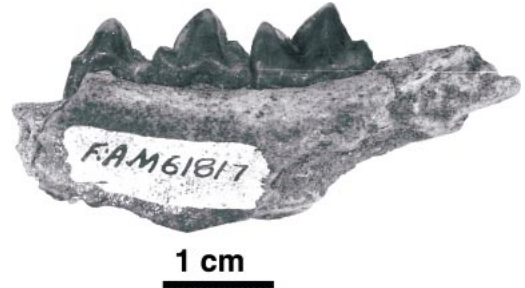
DESCRIPTION AND COMPARISONS OF RE-FERRED MATERIAL: The greater height of m1 protoconid described in the type specimen (F:AM 61812) is seen also in F:AM 61816 (fig. 25) and F:AM 61817 (fig. 26). All of the m1s have a prominent metaconid and distinct talonid. The presence of a metaconid in other North American species of *Pseudaelurus* is variable. F:AM 61813, the maxillary fragment, is the only upper dentition known for the species (fig. 27). P3 has a prominent posterior accessory cusp as well as a basal cingular cusp. On the labial side of P4 there is a small accessory cusp at the base of the parastyle. This morphology of P3 and P4 agrees with *P. validus*. The P4 of F:AM 61813 has a prominent protocone (fig. 28). The slenderness and the angle of the P4 protocone are similar to the P4 in the type skull of *Proailurus lemanensis* (MNHN1903–20) (fig. 29). The protocone lies at a more obtuse angle anterolingually than is seen in *P. intrepidus* and *P. marshi*. This less acute angle formed by the protocone of P4 compares well with *P. validus*. M1 of F:AM 61813 is fragmented. Only the lingual half of the tooth remains. However, it is obvious that this M1 was multicusped. This agrees with the condition in *P. validus*, in contrast to the vestigial M1 seen in modern felids.

DISCUSSION: Material referred to *P. skinneri* is restricted to lower and upper jaw specimens from late Hemingfordian localities of North America. Without cranial and postcranial information, it is difficult to hy-
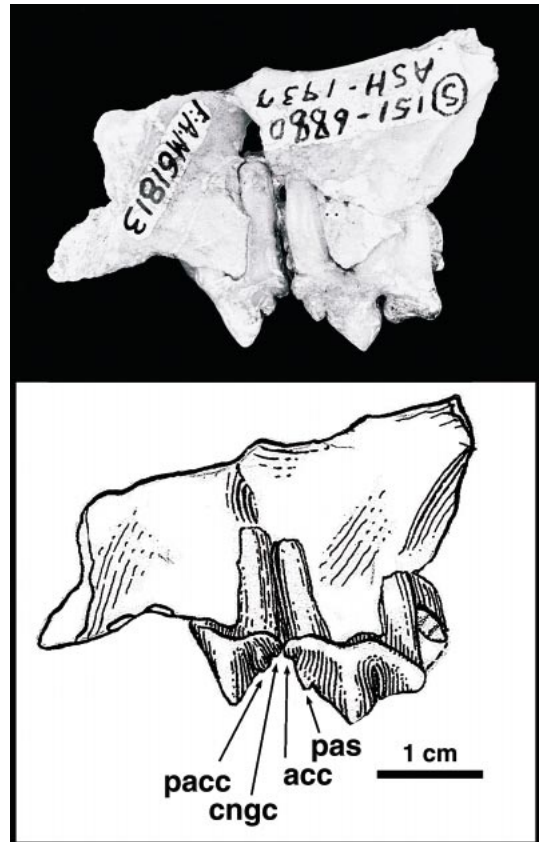

Fig. 27. *P. skinneri* (F:AM 61813), left maxillary fragment, lateral view. P3 has both the posterior accessory cusp (pacc) and the cingular cusp (cngc). P4 contains a prominent parastyle (pas) and an anterolateral accessory cusp (acc).
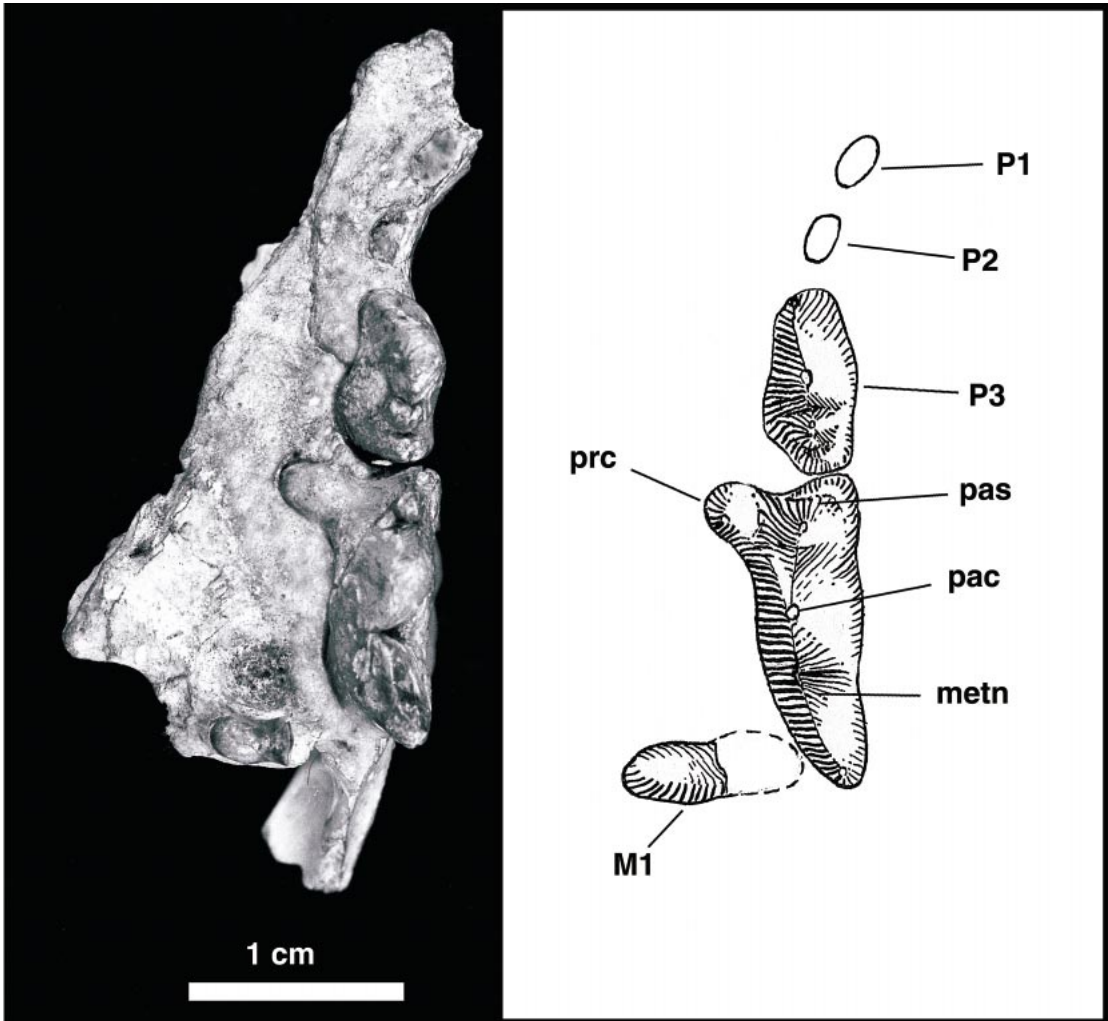
Fig. 28. *P. skinneri* (F:AM 61813), left maxillary fragment, occlusal view, anterior is to the top. P1 and P2 are represented by single-rooted alveoli. The slender protocone of P4 (prc) projects in an anterolingual direction. A deep metastyle notch (metn) lies posterior to a large and prominent paracone (pac). On the anterior surface of P4, a distinct parastyle (pas) is present.

pothesize the relationship of *P. skinneri* with other felids. One possibility is that it is most closely related to the other similar-sized species found on other continents. Fossils of *P. lorteti* of Europe are similar in size and morphology and are temporally equivalent to *P. skinneri*. This is not unlike the situation seen today with *Lynx lynx* of Europe and *Lynx canadensis* of North America. In Asia, *Pseudaelurus cuspidatus*, *P. guangheensis*, and *P. lorteti* are all similar in size to *P. skinneri* and all have been reported from middle Mio-

cene localities. Conversely, there is no reason to expect the diversity of early felids in North America to reflect the situation in Europe or Asia. *P. skinneri* along with *P. validus* are among the earliest felids to arrive in North America. It is possible that *P. skinneri* is more closely related to *P. validus* than to Eurasian species. Perhaps *P. skinneri* and *P. validus* represent part of an early North American radiation of felids. Without additional material (e.g., basicrania and postcrania) however, it will be difficult to determine

Fig. 29. *Proailurus lemanensis* skull (MNHN 3509a), ventral view, stereo pair. The hypoglossal foramen opens in a ventral direction in this specimen. Abbreviations: alisphenoid canal (ac), medial process of the promontorium (fp), hypoglossal foramen (hf).
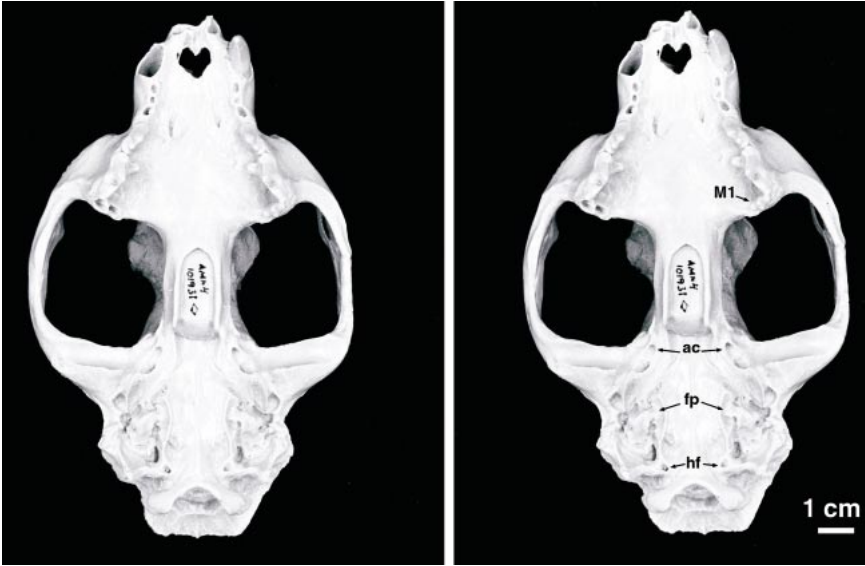
the relationship of *P. skinneri* to other Miocene felids.

Pseudaelurus intrepidus Leidy, 1858

HOLOTYPE: USNM 124 (AMNH cast 10396), left ramus with i3, alveolus p2, p3–m1 from the Valentine Sands, Bed F, ''Loup Fork'', Valentine Formation (late Barstovian (Webb, 1969), Cherry County, Nebraska (fig. 5).

REFERRED SPECIMENS: Lower Snake Creek Fauna, Olcott Formation (early Barstovian), Sioux and Dawes counties, Nebraska: YPM PU 12081, right partial ramus with broken c, alveolus p2, p3–broken m1, Sinclair Draw; AMNH 17212, right partial ramus with broken c alveolus, alveoli of p2 and p3, p4–m1, Sinclair Draw; F:AM 61806, left ramus with broken c, p2 alveolus, p3–m1, Humbug Quarry; F:AM 61804, right ramus with alveolus of I3, broken canine, and p2–m1, Quarry 2; F:AM 61805, right ramus with alveolus of canine and p3–m1, Quarry 2; F: AM 61831, right ramus with alveolus of canine, alveolus of p2, broken p3, and p4–m1, Echo Quarry; F:AM 61564, left partial ramus with p3–broken m1, Version Quarry; AMNH 18271, with broken c, alveolus of p2, broken p3–m1, East Surface Quarry.

Trinity River Local Fauna, Fleming Formation (early Barstovian), San Jacinto County, Texas: AMNH 18271, right partial ramus with alveolus of c, alveolus of p2–p4 and m1, pit no. 1.

Tonopah Local Fauna, Siebert Formation (early Barstovian), San Antonio Mountains, Nye County, Nevada: LACM (CIT) 791, partially restored skull with upper dentition and basicranium, locality 172; LACM (CIT) 1233, maxillary fragment with C–M1, and right ramus with i3–c, p2–m1, locality 172; LACM (CIT) 772, left partial ramus with p3–m1, locality 172; LACM (CIT) 1234, left partial ramus with p3–m1, locality 172.

Green Hills Fauna (early Barstovian), Barstow Formation, San Bernardino County, California: F:AM 61923, right partial ramus with broken c, p2–p3, broken p4, and m1, Upper Steepside Quarry; F:AM 27331, right crushed ramus with c, p2–m1 and left ramus with broken c, p2–m1, ''Green Hills, Box 72, 1926''; F:AM 27327, left partial ramus with c, p2–m1, ''Green Hills, Box 59, 1925''.

Pawnee Creek Formation (early Barstovian), Big Springs Pit, Weld County, Colorado:

F:AM 61842, left partial ramus with alveolus p3, p4–m1.

Second Division Fauna, Barstow Formation (early Barstovian), San Bernardino County, California: F:AM 61933, left and right rami with i3–c, p2–m1, Mayday Quarry.

First Division Fauna, Barstow Formation (late Barstovian), San Bernardino County, California: F:AM 61910, partial skeleton with left and right rami with i3, c, p2–m1, right humerus, radius, tibia, and partial femur, left articulated forearm (radius, ulna, and manus) with prepared metapodials, left tibia, left partial humerus and femur, partial axis, metatarsal fragments, unprepared vertebrae, and partial scapulae, 6 ft under New Year Quarry; SBCM L1816–5224, crushed skull with broken I1–M1, and left and right rami with broken I–c, p2–m1, Robbins Quarry.

Valentine Formation (late Barstovian), Elliot Place, Brown County, Nebraska: AMNH 25209, right partial ramus with alveoli of i1–i3, c, alveolus of p2, p3–m1;

Valentine Formation (late Barstovian), Cherry County, Nebraska: ANSP 11297, right ramus with i2, broken i3 and c, alveolus of p2, p3–m1 (paratype), ''Valentine Sands, Bed F, Loup Fork'' (Webb, 1969).

DISTRIBUTION: Early Barstovian of Texas, Colorado, and Nevada, early and late Barstovian of Nebraska and California.

DIAGNOSIS: Differs from similar-sized species of *Pseudaelurus* by the c–p3 length and coronoid process morphology. *P. intrepidus* has an m1 length range of 15–20 mm, overlapping only with *P. validus* and *P. marshi* in North America and *P. quadridentatus* in Europe. *P. intrepidus* can be differentiated from *P. validus* by its shorter c–p3 length and by its slender and sloping coronoid process. *P. intrepidus* can be differentiated from *P. marshi* by its longer c–p3 length and by a taller and wider dentary. *P. intrepidus* can be differentiated from *P. quadridentatus* by its longer c–p3 length, and by having an m1 with larger talonid and a better developed, larger metaconid.

DESCRIPTION AND COMPARISONS: In Leidy's (1858) original description, he described the type lower jaw ramus (USMN 124, AMNH 10396) (fig. 5) as being ''intermediate in size

Fig. 30. *P. intrepidus* (F:AM 61804), a right ramus from East Surface Quarry in Sioux County, one of the earliest specimens of *Pseudaelurus intrepidus*.

to the Panther (*Felis concolor*) and the Lynx (*Felix canadensis*).'' This specimen is longer, wider, and deeper than a modern lynx (*Lynx canadensis*). Its dentition is closer in size to that of the puma (*Felis concolor*). The dentary is wide and deep below the tooth row. The lower dentition of *P. intrepidus* is similar to that of other species within the genus. The c is flattened medially and has a distinct posterior trenchant edge. The p2 alveolus was single-rooted and was positioned midway in the diastema between c and p3 (fig. 5). The distance between c and p3 is long, measuring 76% of the m1 length. This is in contrast to *P. marshi*, which has a shorter c–p3 length that measures 54% of its m1 length in the type specimen, and *P. validus*, which has a c–p3 length that exceeds the length of m1. The slender coronoid process extends posterodorsally from a deep masseteric fossa. This contrasts with the larger, wider, and more erect coronoid process in *P. validus*, but is indistinguishable from *P. marshi* specimens.

The earliest specimens of *P. intrepidus* are seven rami from various early Barstovian localities of the Lower Snake Creek Fauna of Nebraska. F:AM 61804 (fig. 30) is a right ramus from East Surface Quarry in Sioux County from this early group. These early Barstovian *P. intrepidus* differ from the late Barstovian holotype in lacking the pronounced chin or thickening of the dentary below the canine. Matthew's ramus of *P. intrepidus sinclairi* (AMNH 17212) (fig. 31) is another early Barstovian lower jaw of *Pseudaelurus intrepidus*. In spite of its historical
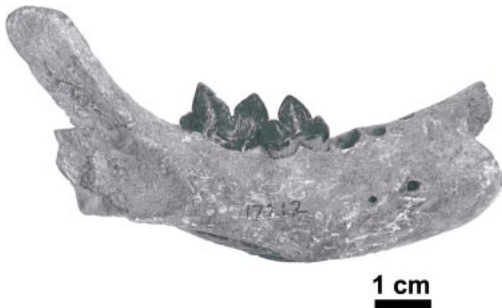
Fig. 31. *Pseudaelurus intrepidus sinclairi* Matthew (1918) (AMNH 17212).

status and ''variety'' designation, it does not differ appreciably from the type specimen.

I am unable to differentiate *P. intrepidus* and *P. marshi* material that is unaccompanied by a lower jaw. Therefore, diagnosed upper dentitions of *P. intrepidus* are not common. I am aware of only three. The earliest is from the Tonopah locality reported by Stock (1934): a maxillary fragment with an associated partial ramus (LACM CIT 1233) (fig. 32). P1 and P2 are both single-rooted. The P4 has a prominent protocone that projects anterolingually. As in *P. validus* and *P. skinneri*, the anterior surface of P4 has a prominent parastyle with a small but distinct accessory cusp. The P4 morphology of *P. intrepidus* is better seen in F:AM 61910 (fig. 33), but this crushed specimen lacks M1. The third *Pseudaelurus intrepidus* specimen with upper dentition is SBCM L1816–5224, a late Barstovian partial skull from the Barstow Formation. It does not differ from the other two *P. intrepidus* skulls.

In addition to the maxillary fragment, Stock (1934) described a partially restored skull (LACM (CIT) 791) (fig. 34). This was the first skull of the genus *Pseudaelurus* described. It was also the only *Pseudaelurus* skull described until the description of the Nambé felid, *P. validus* (Rothwell, 2001). Other felid skulls in the Frick-AMNH collection have been featured in a basicranial study (Hunt, 1998), but there was no attempt at assigning genera and species. There is considerable plaster repair and replacement in the area of hard palate, zygomatic arches, and frontal bones of LACM (CIT) 791. There is no accompanying lower jaw. The

Fig. 32. *P. intrepidus* (LACM (CIT) 1233), maxillary fragment. Drawing is from Stock (1934).

upper dentition of the Tonopah skull (LACM (CIT) 791) agrees with the Tonopah maxillary fragment (LACM (CIT) 1233) in size and morphology. The occlusal surface of M1 is contiguous with the P4 carnassial blade (fig. 35). This characteristic of the upper carnassial apparatus in specimens of *P. intrepidus* agrees with the *P. validus* skulls.

The paroccipital process of the Tonopah skull, assigned to *P. intrepidus*, is cupped about the posterior surface of the caudal entotympanic, pointing caudoventrally away from the posterior surface of the bulla as a distinct process. The anterior portion of the sagittal crest has been estimated in plaster by
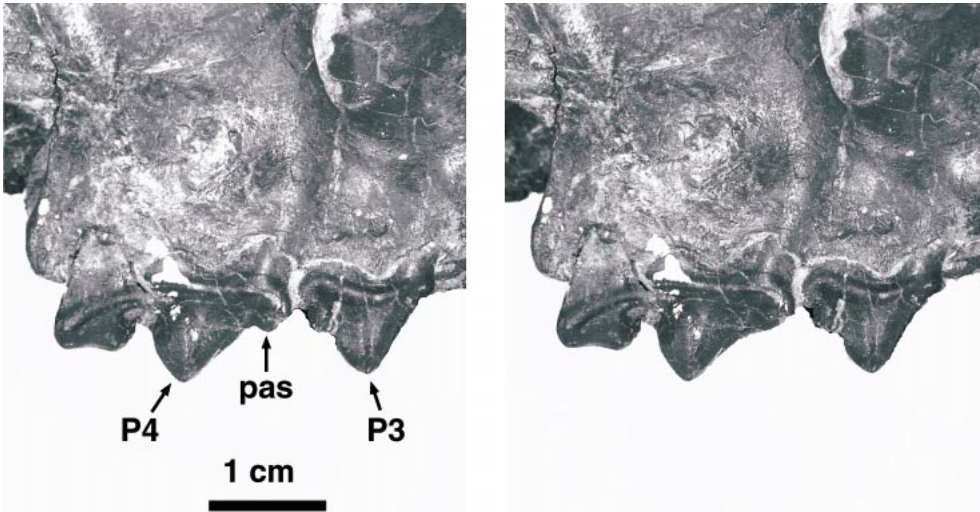
Fig. 33. *P. intrepidus* (F:AM 61910), lateral view of P3 and P4, anterior is to the right. The main cusp of P3 is similar in size to the paracone of P4. Abbreviation: parastyle of P4 (pas).

a preparator, but the caudal portion and the nuchal crest resemble *P. validus*. The alisphenoid canal can be seen on both sides of the Tonopah skull. The size and location of these foramina do not differ from those seen in other skulls assigned to *Pseudaelurus*. The other two skulls that I assign to *P. intrepidus* are F:AM 61910 and SBCM L1816–5224. The size, dentition, and cranial foramina of

Fig. 34. *P. intrepidus* (LACM (CIT) 791), ventral view. White areas represent restoration by a California Institute of Technology preparator.
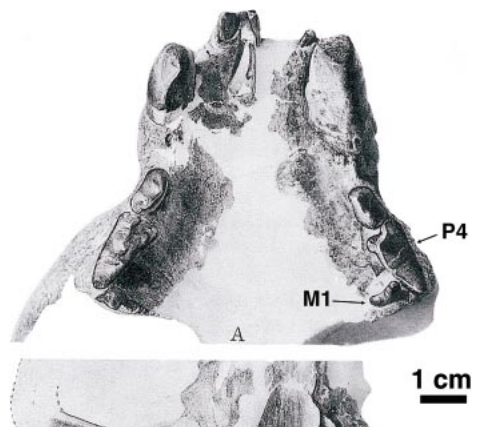
Fig. 35. *P. intrepidus* (LACM (CIT) 791), ventral view. Drawing from Stock (1934).

TABLE 1
Greatest Length Measurements (mm) of Components of F:AM 61910 Skeleton, Referred to *Pseudaelurus intrepidus* (length of metatarsal 3 has been estimated)

Humerus	187.0
Ulna	200.0
Radius	158.7
Metacarpal 3	57.2
Femur	189.1
Tibia 1	88.0
Metatarsal 3	(64.0)

Fig. 36. Log-ratio diagram, *P. intrepidus* skeleton (F:AM 61910) is contrasted with the earlier *P. validus* (F:AM 62128) skeleton. The *y*-axis or standard specimen is the *Proailurus lemanensis* skeleton described by Filhol (1888).

these crushed specimens do not differ from the skull described by Stock (1934).

Postcranial information on *Pseudaelurus intrepidus* is provided by F:AM 61910. The postcranial elements do not differ morphologically from F:AM 62128, the partial skeleton from the Nambé Member in New Mexico assigned to *P. validus* (Rothwell, 2001). However, the metacarpal measurements of the *P. intrepidus* skeleton are relatively longer than those of *P. validus* specimen (table 1). The occurrence of longer metacarpals is similar to modern felids and differs from the shorter metacarpal form seen in *Proailurus lemanensis* and *P. validus* (figs. 36–38).

DISCUSSION: *Pseudaelurus intrepidus* is the only species of *Pseudaelurus* in North America that has been described in the literature more than once (Sinclair, 1915; Matthew, 1918; Stock, 1934). Lower jaw specimens of *P. intrepidus* are abundant in the Frick-AMNH collection and come from Barstovian localities of Texas, Colorado, Nevada, Nebraska and California. I studied 22 lower jaws that I assigned to *P. intrepidus*. Only three of these lower jaws are associated with other material (e.g., cranial, maxillary, postcranial).

The dentition of *P. intrepidus* does not differ significantly from other North American species of *Pseudaelurus*. However, *P. intrepidus* is among the earliest felids to display the derived condition of a sloping and slender vertical ramus of the lower jaw. The Lower Snake Creek Fauna, in the early Barstovian of North America, has felids with the primitive coronoid process (*P. validus*) as well as three species with vertical rami that display the derived condition (*P. intrepidus*,

P. marshi and *P. stouti*). In the late Barstovian, all felids studied have the derived sloping coronoid process seen today in modern felids (fig. 10).

The prominent chin seen in late Barstovian specimens of *P. intrepidus* leads to speculation that this species could be ancestral to one or more of the many machairodont felid forms seen in the late Miocene. This prominent chin, seen also in late Barstovian *P. marshi*, is a thickening of the dentary on the ventral surface below the lower canines. The
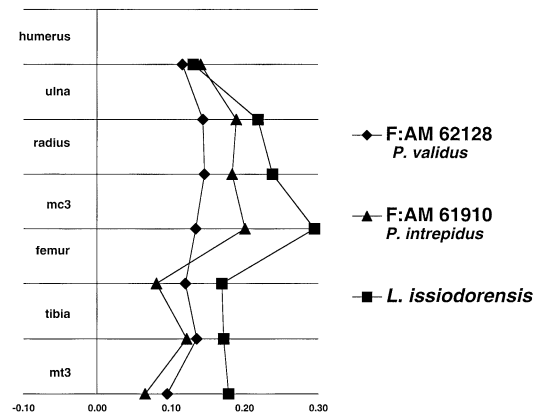
Fig. 37. Log-ratio diagram, data from the fossil taxon *Lynx issiodorensis* are added to those from specimens found in figure 10.
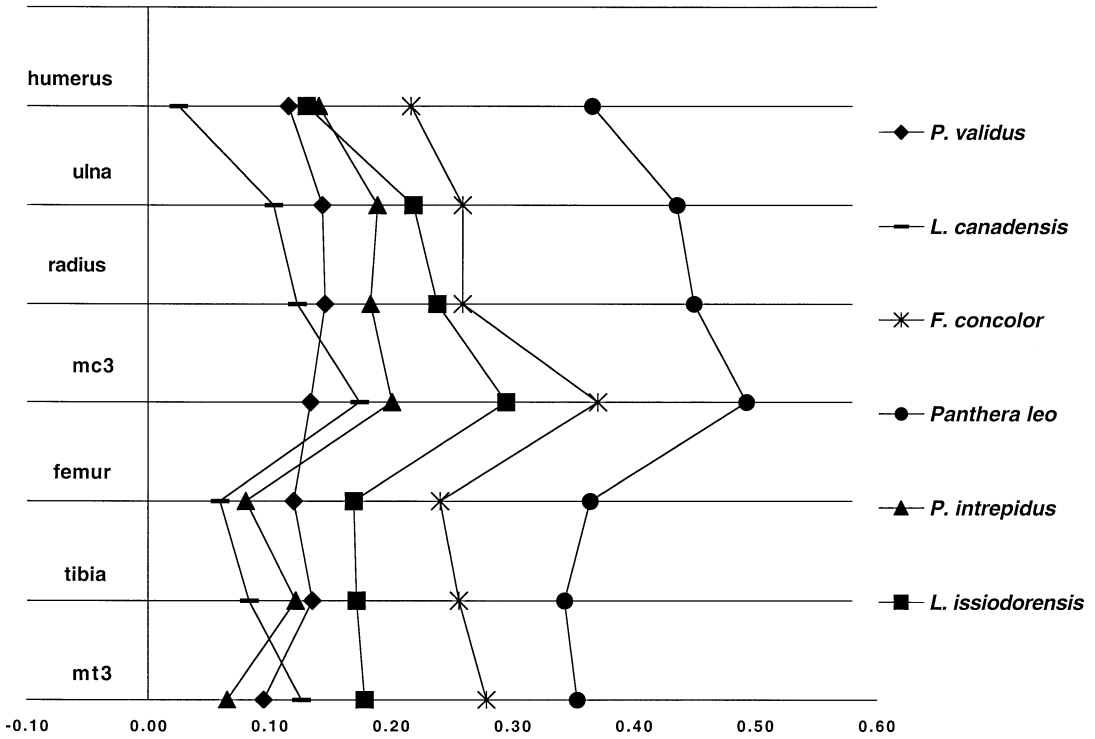
Fig. 38. Log-ratio diagram, data from modern felid skeletons are compared to the extinct taxa in figures 36 and 37. The *P. intrepidus* skeleton resembles the modern skeletal form of increased metacarpal length in the front limb and increased tibial contribution in the hind limb. The *P. validus* skeleton is more similar to the standard specimen, *Proailurus lemanensis*.

ventral thickening of the dentary is associated with an elongation of the mandibular symphysis. It is well demonstrated in the type specimens of *P. intrepidus* and *P. marshi* (figs. 5, 6). Early specimens of these two species lack these characters (fig. 30). Numerous authors have included early specimens of machairodont felids in the genus *Pseudaelurus* (Andrews, 1914; MacDonald, 1948b, 1948a; Ginsburg, 1978). Indeed, *Pseudaelurus* has been designated as a likely ancestor of the machairodont North American felid *Nimravides* (fig. 8) (Baskin, 1981; de Beaumont, 1990).

None of the three *P. intrepidus* skulls (LACM (CIT) 791, SBCM L1816–5224, F: AM 61910) is well preserved. Cranial and basicranial information on *P. intrepidus* is limited. However, the postcranium of *P. intrepidus* (F:AM 61910) does allow comparison with other taxa. Although conclusions made from one skeleton must be provisional,

it appears that late Barstovian *P. intrepidus* had different proportions of its limb bones. In figure 36, I have contrasted the *P. intrepidus* data with the earlier *P. validus* postcranium. The y-axis or standard specimen is the *Proailurus lemanensis* skeleton described by Filhol (1888). The *P. validus* data are reasonably vertical and therefore similar to *P. lemanensis*. Thus, their limb proportions are comparable. The *P. intrepidus* skeleton (F: AM 61910) is different. In the front limb, the metacarpal bone is relatively larger. In the hind limb, the femur has decreased in relative size, while the tibia has increased. This form compares favorably with modern felid skeletons. In figure 37, data from *L. issiodorensis* (Kurtén, 1978), the suspected ancestor of *Lynx lynx* and *Lynx canadensis* (Werdelin, 1981), is added for comparison. In figure 38, modern taxa are also included for comparison. *P. intrepidus* shares the modern skeletal form of greater relative

metacarpal length in the front limb and increased tibial length in the hind limb.

Pseudaelurus stouti, new combination

Lynx stouti Schultz and Martin, 1972

TYPE SPECIMEN: UNSM 25490, partial skull including articulated maxillae and premaxillae with upper dentition, articulated mandible with left and right i1–c, left p2, right alveolus of p2, left and right p3–m1, left petrosal, atlas.

TYPE LOCALITY: W2, 6 miles west and 2 miles north of Chimney Rock, SW¼, T12N, R55W, from a buff very fine sandstone just below a prominent concretionary zone, Ogallala Group (late Barstovian), Logan County, Colorado.

AGE: Late Barstovian.

ASSOCIATED FAUNA: Sand Canyon Fauna.

REFERRED SPECIMENS: Lower Snake Creek Fauna, Olcott Formation (early Barstovian), Sioux County, Nebraska: F:AM 61801, partial left ramus with broken c, alveolus p2, p3–m1, Quarry 2; F:AM 25471, partial left ramus with alveolus i3, c, alveolus p2, p3–m1, West Sinclair Draw.

Sand Canyon Formation, Dawes County, Nebraska: AMNH 140227, partial radius, Observation Quarry.

Skull Ridge Member, Tesuque Formation (early Barstovian; Tedford and Barghoorn, 1997)), Santa Fé County, Española Basin, New Mexico: F:AM 61931, left partial ramus with c, p2–broken m1; AMNH 140228, right partial ramus with broken c, alveolus of p2, broken p3–p4, broken alveolus of m1, Joe Rak Wash.

Santa Cruz sites, Tesuque Formation (late Barstovian; Tedford, 1981; Tedford and Barghoorn, 1997), Española Basin, Santa Fé County, New Mexico: F:AM 27456-A, articulated lower jaw fragment with left i1–i3, left c, broken right c, alveolus of left p2, right p2, left and right p3–broken m1, Red layer, 2nd wash locality, F:AM 27455, right partial ramus with alveoli i1–i3, broken c, p2 and p3 alveolus, p4–m1, no locality.

Cerro Conejo Member, Zia Formation (late Barstovian; Tedford and Barghoorn, 1997), Sandoval County, northern Albuquerque Basin, New Mexico: F:AM 61901, left partial ramus with c, p2–m1, Rincon Quarry.
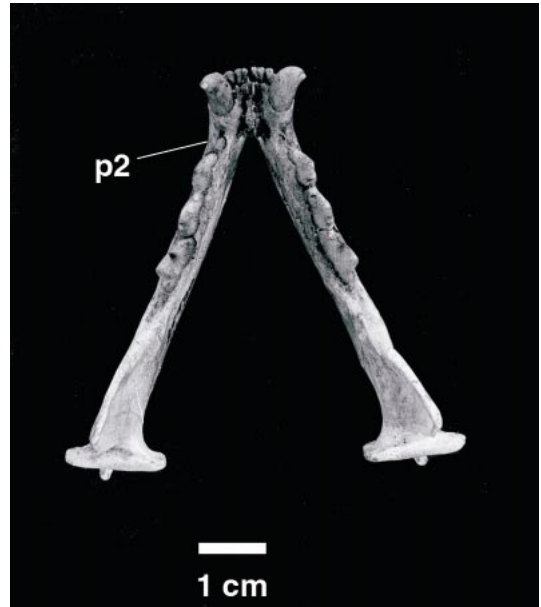
Fig. 39. *P. stouti* (UNSM 25490), holotype lower jaw, dorsal view. Except for its small size, this specimen resembles other species of North American *Pseudaelurus*. The presence of a complete set of incisors is uncommon.

DISTRIBUTION: Early Barstovian of Nebraska, late Barstovian of Colorado, and early and late Barstovian of New Mexico.

DIAGNOSIS: Differs from all other species of *Pseudaelurus* by its small size. *P. stouti* has an m1 length range of 8–9 mm, distinctly smaller than the next largest North American species, *P. skinneri*, with an m1 range of 11.5–13.5 mm. *P. stouti* is approximated in size only by the smallest and earliest European species, *P. turnauensis*, with its m1 range of 9.3–12.8 mm.

DESCRIPTION AND COMPARISONS OF TYPE SPECIMEN: UNSM 25490 (figs. 39–42). This is a very small and slender felid. The lower canine is flattened on the inner surface, and the posterior surface is rounded. This differs from the sharper rear edge seen in the lower canines of larger species. A single-rooted p2 can be seen on the left lower jaw (fig. 39). There is a single-rooted alveolus on the right side. The left p2 is closer to p3 than to c and is lingual of midline, typical of the genus. The p3 is as tall as p4, with a small posterior cingular cusp. The distance between c and p3 is 5.74 mm, which is relatively short, similar
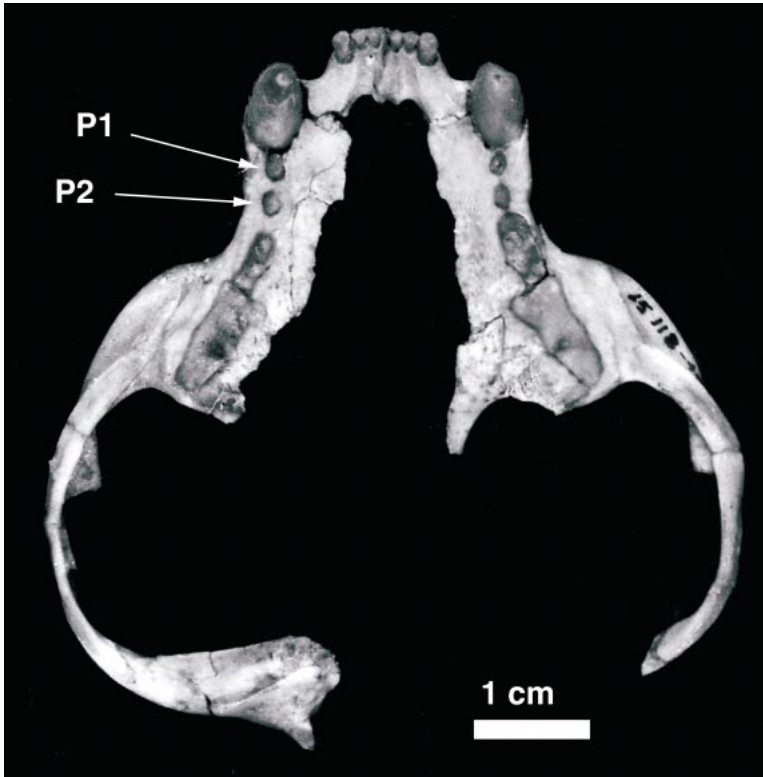
Fig. 40.   *P. stouti* (UNSM 25490), holotype rostrum and zygomatic arches, ventral view. Four upper premolars are present.

to the condition in *P. marshi* and *P. aeluroides*. A reduced metaconid is present on the posterior surface of the protoconid of m1, above a prominent talonid. The protoconid is taller than the paraconid, and the carnassial notch is open and deep to a level above that of the talonid. There is no evidence of m2 on either ramus. The dentary is convex below the tooth row. Posteriorly, the horizontal ramus terminates in a slender and pointed angular process.

The left and right maxillary bones contain a full complement of four upper premolars (fig. 40). Present also are the zygomatic arches and the squamosal fragments that contain the jaw articulations (Schultz and Martin, 1972). The upper incisors are aligned in a tight row with a slight arc (fig. 40). The third upper incisors are significantly larger than the equal-sized I1 and I2. This upper incisor morphology agrees with earlier *Pseudaelurus* skulls as well as modern felids. The left C

has a fractured crown. The right C is complete. P1 and P2 are single-rooted. In occlusal view P4 has a low protocone projecting at an acute, anterolingual angle (fig. 41). In this respect, P4 is similar to modern felids, but contrasts with the condition seen in *P. skinneri* and *P. validus*, where the P4 protocone is robust and positioned at a more obtuse angle.

The left petrosal of UNSM 25490 (fig. 42) is not as long as in modern felids (fig. 43). Its anterior portion ends more abruptly, affording a rectangular appearance. Medially, there is no evidence of a petrosal flange to rest upon the basioccipital, as is seen in *Proailurus lemanensis* and *Pseudaelurus validus*. Posteriorly, there is little or no apron caudal to the fenestra rotunda, as is seen in some primitive aeluroids such as *Stenogale julieni* (Hunt, 1998). However, a vestigial ventral process of the promontorium is present, but does not contain a facet to indicate

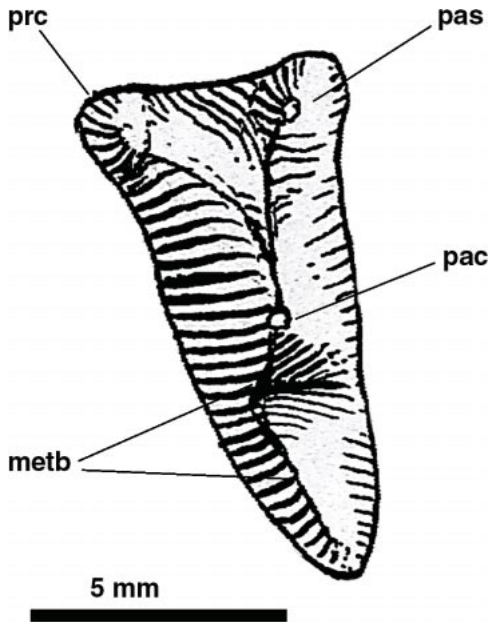Fig. 41. *P. stouti* (UNSM 25490), left P4 occlusal view, anterior is to the top, lingual is to the right. The protocone (prc) is smaller than is seen in other species of North American *Pseudaelurus*, giving the tooth a more compressed lateral to medial appearance. Abbreviations: parastyle (pas), paracone (pac), metastyle blade (metb).

Fig. 42. *P. stouti* (UNSM 25490), left petrosal, ventral view, anterior is to the top. Abbreviations: ventral process of petrosal promontorium (V) , fenestra rotundum (fr) , fenestra ovale (fov).

where the ectotympanic rested. In this respect, it agrees with the condition of modern felids.

DESCRIPTION AND COMPARISONS OF REFERRED SPECIMENS: In addition to their small size, the seven *P. stouti* lower jaws from the American Museum are distinguished by characters that are considered primitive for fossil felids. F:AM 27456A has a prominent metaconid and talonid on the m1 (figs. 44, 45). F:AM 27456a has a p3 that is tall, close in height to p4. This is a primitive state for p3 and p4 and can be seen in the holotype (UNSM 25490), F:AM 61931 (fig. 46), as well as in the early aeluroids *Stenoplesictis*, *Stenogale*, and *Haplogale* (Peigné, 1999). The advanced state of a p4 that is larger than p3 is seen in *Proailurus* as well as in modern felids. I have not seen this condition of similar-sized p3 and p4 in other North American species of *Pseudaelurus*.

None of the specimens of *P. stouti* has evidence of p1. Of 18 lower jaws from Win-

tershof-West (early Miocene, MN3) assigned to *P. transitorius* Depéret (= *P. turnauensis* Hoernes), only 2 displayed evidence of p1 (Dehm,1950). The only other reference to a p1 of *Pseudaelurus* of which I am aware is a partial right ramus from the Northern Junggar Basin, China (Wang et al., 1998). This specimen also displayed the unusual combination of presence of p1 (alveolus) and lack of p2. AMNH 140228 has a p2 alveolus with two roots (fig. 47). This is uncommon in North American felids. While studying over 100 felid lower jaw specimens of early and middle Miocene age, this is only the second North American specimen with evidence of a two-rooted p2. The type specimen of *Proailurus lemanensis* (MNHN S.G. 3509a), from the early Miocene of France, has a p2 with 2 roots. In the 18 felid lower jaws from Wintershof-West, 4 had a p2 with 2 roots and 4 had alveoli with an ''hourglass'' configuration (Dehm, 1950) (fig. 48).
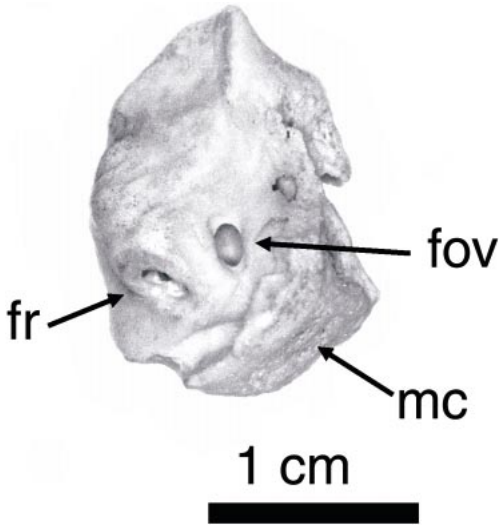
Fig. 43. Left petrosal of *Acinonyx jubatus* (AMNH 2389), modern cheetah. The ventral process of the promontorium, identifiable in specimens of *Pseudaelurus*, is not present. Abbreviations: fenestra rotundum (fr), fenestra ovale (fov), contact with mastoid (mc).

DISCUSSION: *P. stouti* is distinguished by its small size and primitive felid characters. It is the smallest species of *Pseudaelurus* described (fig. 49). This small felid, with the authors acknowledging similarities to *Pseudaelurus*, was originally assigned to the genus *Lynx* (Schultz and Martin, 1972). This was reasonable considering that the occa-

Fig. 44. *P. stouti* (F:AM 27456A), right lateral view of articulated lower jaw fragment. A prominent metaconid and talonid can be seen on the right m1. Note also the similar-sized p3 and p4.

Fig. 45. *P. stouti* (F:AM 27456a), dorsal view.

sional appearance of primitive dental characters (m1 with metaconid and talonid, presence of m2) in modern *Lynx lynx* has created controversy concerning the phylogenetic position of that species (Kurtén, 1963; Werdelin, 1987). However, the earliest fossil evidence of the genus *Lynx* is the early or mid-
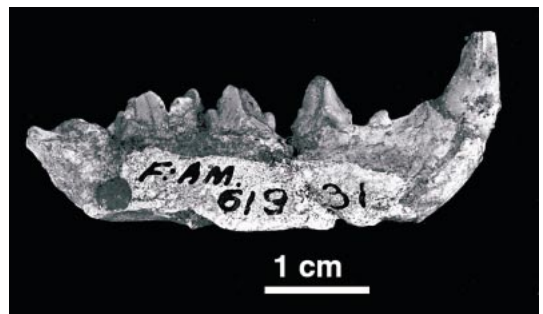
Fig. 46. *P. stouti* (F:AM 61931), right ramus fragment, lateral view. This specimen also displays similar-sized p3 and p4.
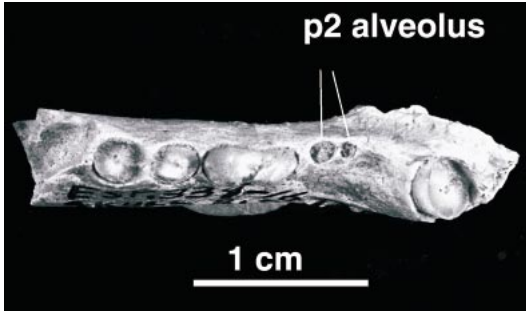
Fig. 47. *P. stouti* (AMNH 140228), right ramus fragment, occlusal view. A p2 alveolus for two roots can be seen.

dle Pliocene appearance of *L. issiodorensis* throughout the northern hemisphere. *Lynx issiodorensis* is the suspected ancestor of *L. lynx*, *L. canadensis*, *L. rufus*, and *L. pardina* (Werdelin, 1981). Early *L. issiodorensis* lower carnassials do not have a talonid-metaconid complex or m2 (Kurtén, 1978). There is no mention of any p1, p2, or m2 in *L. issiodorensis*. The dentition of *L. issiodorensis* is therefore more similar to modern *Felis*, as is the postcranial skeleton. Also, *L. issiodorensis* is a large felid. Kurtén (1978) reported m1 measurements of *L. issiodorensis* ranging from 14.6–16.3 mm in length, comparable in size to *P. intrepidus* and *P. marshi*, or the modern taxon *Felis concolor*. *L. issiodorensis* is much larger than modern *L. lynx* or *L. canadensis* specimens that I examined at the American Museum. Although the type spec-
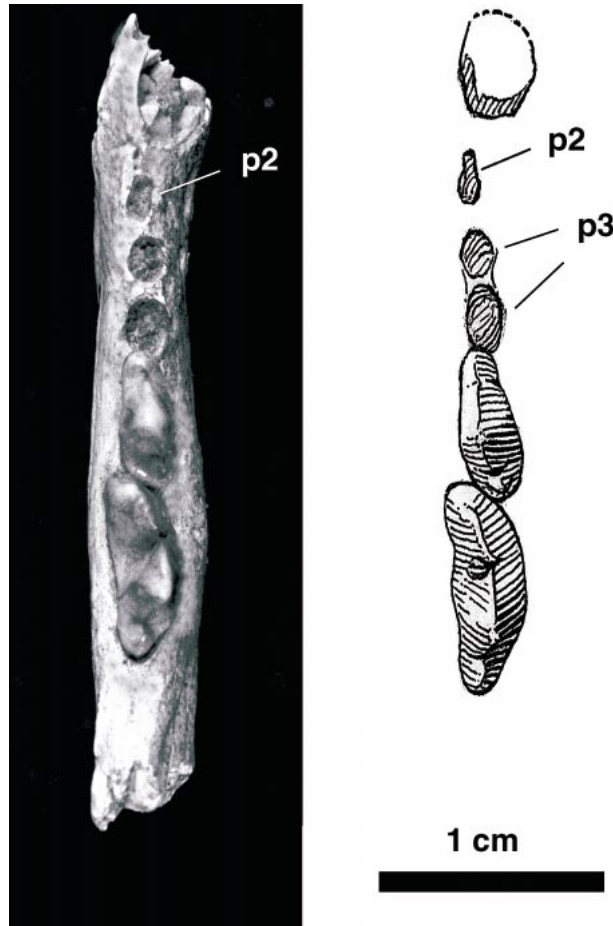
Fig. 48. *P. stouti* (F:AM 27455), right ramus fragment, occlusal view. Anterior is to the top. An ''hourglass'' alveolus for p2 can be seen where the two roots are partially conjoined.
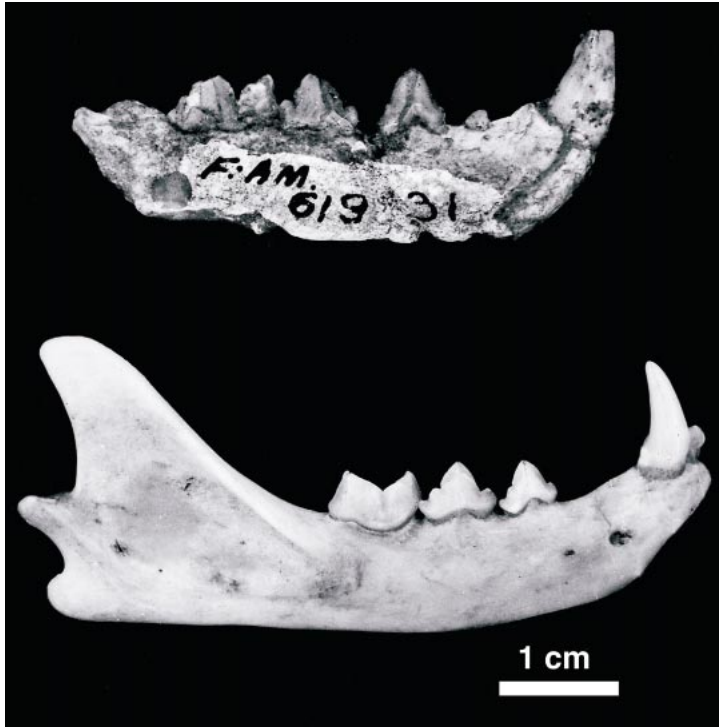
Fig. 49.   *P. stouti* (F:AM 61931), with right ramus of a domestic cat, *Felis catus*, for size comparison. Note the similarity in p3 and p4 morphology.

imen of *Lynx stouti* was originally described as "a felid the size of *Lynx issiodorensis*" (Schultz and Martin, 1972), it is much smaller with m1 length of 8–9 mm. A felid specimen with P1, P2, and m1 with a metaconid and talonid is characteristic of the genus *Pseudaelurus*. I therefore assign the type, UNSM 25490, and other specimens to the genus *Pseudaelurus* as *Pseudaelurus stouti*.

The presence of equal-sized p3 and p4 in *P. stouti* may indicate adaptation to a food source. An elongated p3 crown was considered an autapomorphy for the extant black-footed cat, *Felis nigripes* (Salles, 1992). A study of the black-footed cat revealed a diet consisting of 43% arachnids (Kitchner, 1991). *P. stouti* is the sixth species of *Pseudaelurus* to be recognized in North America. *P. stouti* increases the diversity of felids in the Barstovian of North America to five species (*P. validus*, *P. intrepidus*, *P. marshi*, *P. aeluroides* and *P. stouti*) The diversity of North American early and middle Miocene felids now resembles the more continuous

fossil felid record of Europe. In Europe, four different-sized species of *Pseudaelurus* (Heizmann, 1973; Ginsburg, 1983) are found throughout the early and middle Miocene.

Pseudaelurus marshi Thorpe, 1922

HOLOTYPE: YPM 12865 (AMNH 13506 cast), articulated left and right rami with left i2, i3, left and right c, left alveolus of p2, right p2, left and right p3–m1, from Valentine Formation, Niobrara River, near mouth of Minnechaduza Creek (late Barstovian) (Webb, 1969), Cherry County, Nebraska.

PARATYPE: YPM 12815 (AMNH 133505 cast), left ramus with broken c, alveolus of p2, p3–p4, broken m1, from Gerry's Ranch, Ogallala Group (early Barstovian), Weld County, Colorado.

REFERRED SPECIMENS: Lower Snake Creek Fauna, Olcott Formation (early Barstovian), Sioux County, Nebraska: F:AM 61808, left ramus with c, alveolus of p2, p3–m1, Echo Quarry; AMNH 22401, left partial ramus

with alveolus of c, p3–broken m1, Ashbrook Pasture; AMNH 22404, right partial ramus with alveolus c and alveolus p2, broken p3–m1, Ashbrook Pasture; F:AM 61807, left partial ramus with alveolus of c, p2, p3–m1, Quarry 2; F:AM 61809, left partial ramus with alveoli of c and p2, p3–m1, Quarry 2; AMNH 22398, partial right ramus with alveoli of i1–p4, m1, Ashbrook Pasture.

Sand Canyon Formation (Early Barstovian), Dawes County, Nebraska: F:AM 61846, partial left ramus with alveolus of i3, c, alveolus of p2, p3–broken m1, Observation Quarry.

Green Hills Fauna, Barstow Formation (early Barstovian), San Bernardino County, California: F:AM 61926, partial left ramus with p3–m1, Upper Steepside Quarry; F:AM 61921, right ramus with c, alveolus of p2, p3–m1, Upper Steepside Quarry; F:AM 61924, partial left ramus with broken c, p2 alveolus, p3–m1, Upper Steepside Quarry; F:AM 61918, partial left ramus with broken c, p3–m1, Upper Steepside Quarry; F:AM 61938, partial left ramus with i3–c, p3–m1, Turbin Quarry; F:AM 27337, left and right rami with c, p2–m1, Rak Division.

Second Division Fauna, Barstow Formation (early Barstovian), San Bernardino County, California: F:AM 18008, crushed partial skull with upper dentition, occipital fragment, left partial ramus with c, alveolus of p2, p3–m1 and partial right ramus with c, p2–m1, Valley View Quarry.

Trinity River Local Fauna, Fleming Formation (early Barstovian), San Jacinto County, Texas: F:AM 69331, partial left ramus with broken alveolus of c, alveolus p2, p3 and p4, m1, pit no. 1.

First Division Fauna, Barstow Formation (late Barstovian), San Bernardino County, California: F:AM 61934, articulated lower jaw fragment with i3, alveolus of p2, p3–m1, Leader Quarry; F:AM 61916, partial right ramus with broken c, p3–m1, Leader Quarry; F:AM 61936, partial right ramus with c, alveolus of p2, p3–m1, Black Hill Quarry; F:AM 27317, left and right partial rami with left and right c, left and right alveolus of p2, broken p3–m1, White Layer, 0.5 mile below cabin; F:AM 61940, crushed skull with left and right I1–M1 and right ramus with i1–c,

alveoli p2–p4, broken m1, Hidden Hollow Quarry.

Pawnee Creek Formation, Big Springs Pit, Weld County, Colorado: F:AM 61841, partial right ramus with c, alveolus of p2, p3–m1.

Cerro Conejo Member, Zia Formation (late Barstovian; Tedford and Barghoorn, 1997), Sandoval County, northern Albuquerque Basin, New Mexico: F:AM 62144, partial skeleton with crushed skull with I1–C, alveolus of P2, P3–M1, partial left ramus with c, alveolus of p2, p3–m1, left and right humerus, radius, ulna, femur and tibia, partial scapulae, vertebrae, articulated pelvis, left and right calcaneus, assorted left and right metatarsal bones, and assorted phalanges, Rincon Quarry.

Pojoaque Member, Tesuque Formation (late Barstovian), Santa Fé and Rio Arriba counties, NM: F:AM 27457, partial articulated lower jaw with left and right lower dentition, left and right maxillary fragments with I3, C, P1, P2–M1, right calcaneus, partial humerus, Santa Cruz; F:AM 62135, skull fragment, left ramus with i2–c, p2 alveolus–m1, right partial ramus with separated c and p3–m1, vertebrae in matrix, partial femur, and assorted metapodials, south side of the Lobato branch of the South Fork of 3 Sand Hills Wash; F:AM 27453, partial skeleton, skull with upper dentition and intact basicranium, left dentary with i3, c, alveolus of p2, p3–m1, vertebrae, one rib, partial left articulated tarsus and metatarsus, Santa Cruz, field no. 13.

DISTRIBUTION: Early Barstovian of Texas, early and late Barstovian of Nebraska, California, and Colorado, late Barstovian of New Mexico.

DIAGNOSIS: Differs from all other species by combination of large size, short c–p3 length and slender and sloping coronoid process. *P. marshi* has m1 length that ranges from 14–19 mm, overlapping only with *P. validus* and *P. intrepidus* in North America and *P. quadridentatus* in Europe. *P. marshi* can be differentiated from *P. validus* by its much shorter c–p3 length and a slender and sloping coronoid process. *P. marshi* can be differentiated from *P. intrepidus* by shorter c–p3 length and dentary that is narrower and shallower below the tooth row. *P. marshi* can
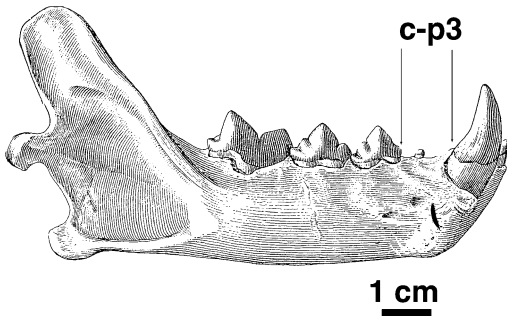
Fig. 50. Right ramus of YPM 12865, type specimen of *Pseudaelurus marshi* Thorpe (1922). The small distance between c and p3 (c-p3) distinguishes *P. marshi* from similar-sized lower jaws of *Pseudaelurus*. Drawing from Thorpe (1922).

be differentiated from the European *P. quadridentatus* by its shorter c–p3 length and m1 with larger talonid and greater incidence of metaconid.

DESCRIPTION AND COMPARISONS: Thorpe's (1922) description of the type lower jaw (YPM 12865) listed most characters that differentiate *P. marshi* from other large species in the genus: smaller size and a more slender and shallower dentary below the tooth row. However, he did not mention the shorter c–p3 length that differentiates *P. marshi* from other large species of *Pseudaelurus* (fig. 50). There is no evidence of p1 on either ramus. A single-rooted p2 can be seen on the right ramus, an alveolus on the left ramus. The p3 is smaller and shorter than p4, and both p3 and p4 have prominent posterior accessory cusps. The m1 has a reduced, yet distinct metaconid and talonid. The paratype partial left ramus (YPM 12815) was originally described as having an m2 alveolus. I examined this specimen and a cast (AMNH 133505) (fig. 51). The posterior root of the broken m1 is exposed, forming a triangular area posterior to the broken m1 crown. I suggest that the supposed m2 alveolus is this cavity formed behind the exposed portion of the m1 root.

The upper dentition of *P. marshi* does not differ appreciably from that of *P. intrepidus*. The best preserved specimen is F:AM 27453, from the late Barstovian Cerro Conejo Member of New Mexico (figs. 52–54). This skull has only three pairs of upper premolars. The
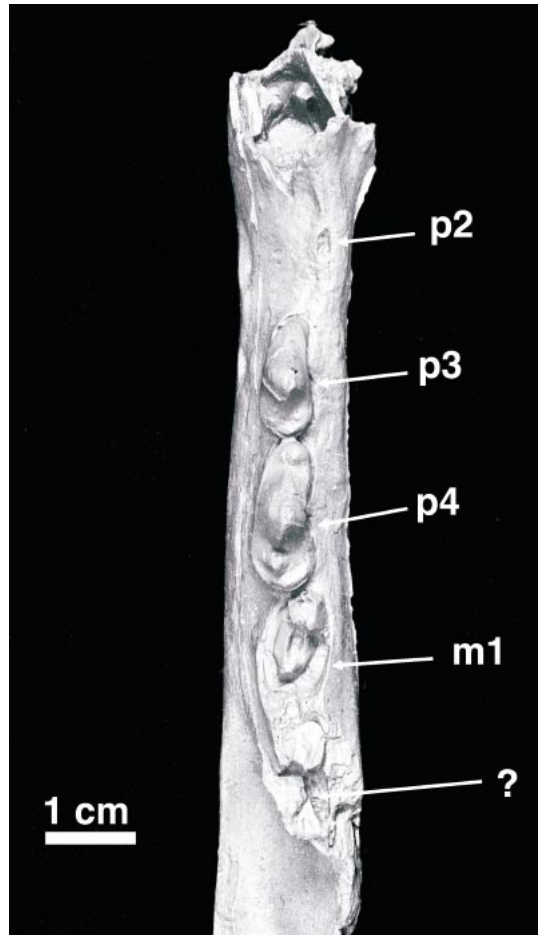
Fig. 51. *P. marshi* (YPM 12815, cast AMNH 133505), dorsal view. This specimen was described as having an m2 alveolus.

Frick-AMNH collection has five specimens of *P. marshi* with upper dentitions. F:AM 27453 is the only specimen not having evidence of four upper premolars. I think that the most anterior premolar present in F:AM 27453 is P2. The crushed skull was reconstructed by Frick Laboratory preparators who located this P2 anterior to a point midway between C and P3. The suspected P2 is long, peglike and single-rooted in F:AM 27453. P3 is large, with a primary cusp that is similar in size to the paracone of P4. The width of P3 is greater in the posterior half of the tooth. P4 is similar to that of *P. intrepidus*. There is a prominent protocone that projects anterolingually. Anteriorly, at the base of the para-
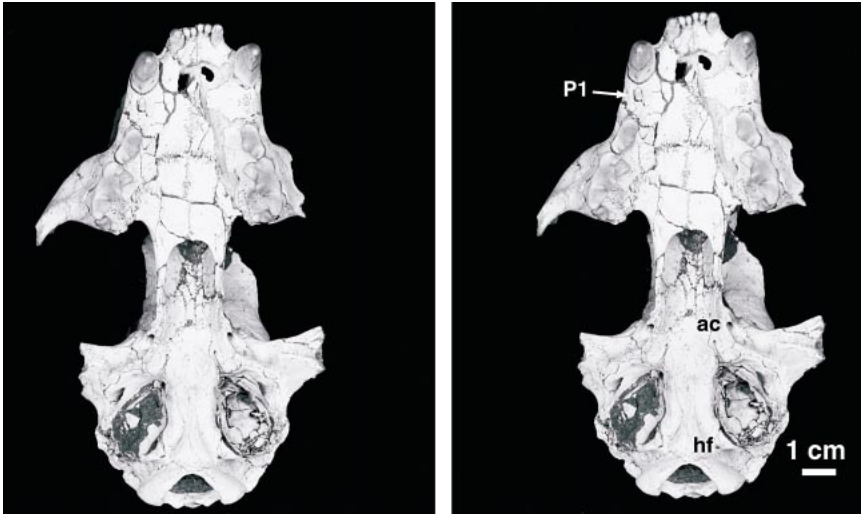
Fig. 52. *P. marshi* (F:AM 27453), ventral view, stereo pair. This skull has only three upper premolars on each side, apparently lacking P1. Abbreviations: alisphenoid canal (ac), hypoglossal foramen (hf).

cone of P4, a distinct parastyle is present, forming a deep secondary carnassial notch. On the anterolateral surface of the parastyle, a small accessory cusp is present. All of this P4 morphology resembles other species of North American *Pseudaelurus*. M1 is com-

pressed anteroposteriorly. M1 of *P. marshi* is nonvestigial. All North American specimens of *Pseudaelurus* studied have a functional, occluding, nonvestigial M1. In modern felids, however, M1 is vestigial. The upper component of the carnassial apparatus in-
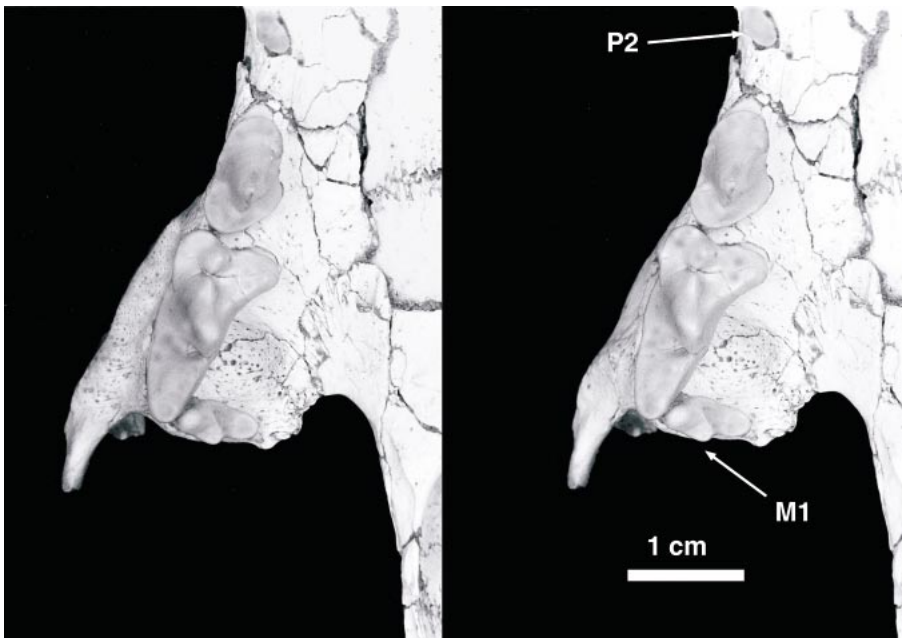
Fig. 53. *P. marshi* (F:AM 27453), right upper dentition, close view, anterior is to the top. M1 is nonvestigial, having multiple cusps.
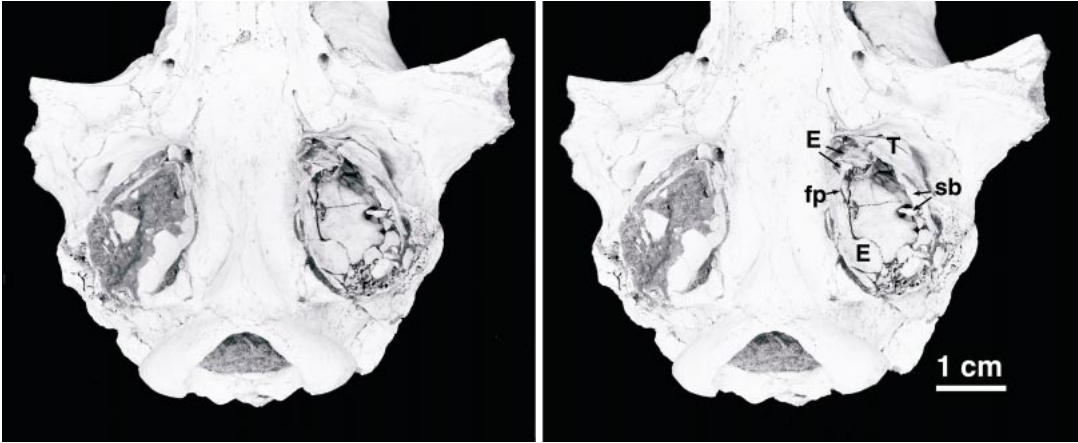
Fig. 54. *P. marshi* (F:AM 27453), auditory region, ventral view, stereo pair. The caudal entotympanic (E) has inflated anteriorly to a position even with the anterior most portion of the ectotympanic (T). Abbreviations: medial process of the promontorium (fp), septum bullae (sb).

cludes P3 and P4 in extant felids, but does not involve M1.

F:AM 27453 provides well-preserved information about the skull of *P. marshi* (figs. 52–55). However, the dorsum of the cranium has been crushed, thus losing information on the sagittal and nuchal crests. The basicranium is better preserved. The left auditory bulla was prepared (fig. 54). Anteriorly, the septum bullae can be seen at the anterior margin of the petrosal, forming the lateral wall of the most anterior portion of the caudal entotympanic chamber. Posterolaterally, a sliver of the septum bullae can be seen arching toward the petrosal promontorium. This morphology of the septum bullae and its relationship to the petrosal promontorium agrees with that of *P. validus* (Hunt, 1998; Rothwell, 2001). However, the caudal entotympanic of the *P. marshi* skull has expanded more anteriorly when compared to the *P. validus* skull. The anterior expansion of the caudal entotympanic of *P. marshi* has reached the level of the most anterior margin of the ectotympanic chamber. The caudal entotympanic chamber terminates only slightly posterior to the anteromedial process of the auditory bulla. The caudal entotympanic has invaded, emarginated, and thinned out the ectotympanic, where it articulates with the basioccipital and basisphenoid. This differs from the much thicker, less invaded ectotympanic attachment seen in *P. validus*. The

most anterior point of the *P. validus* caudal entotympanic is slightly posterior to the anterior apex of the ectotympanic chamber. This degree of anterior expansion in the *P. marshi* auditory region approaches the level seen in modern felids. On the medial surface of the petrosal, a medial extension or process of the promontorium can be seen. It rests upon the edge of the basioccipital. This process is smaller than the one described in a skull assigned to *P. validus* (Hunt, 1998). Possible correlation of depth of an expanding caudal entotympanic with disappearance of the medial process of the petrosal promontorium in modern felids has been suggested (Hunt, 1998).

The close relationships of the bullae of F:AM 27453 with the mastoid and paroccipital processes are similar to those described in the *P. validus* skeleton from the Nambé Member of the Tesuque Formation (Rothwell, 2001). Medial to each bulla, the ridge formed by the expanded caudal entotympanic indents the basioccipital. Posteromedial to each bulla, the hypoglossal foramen is visible within the same depression as the posterior lacerate foramen (figs. 54, 55). In F:AM 27453, the hypoglossal foramen is at the posteromedial border of the depression that it shares with the posterior lacerate foramen. Because of its position on the rim of a depression, the hypoglossal foramen does not open in a ventral direction as in *Proailurus*
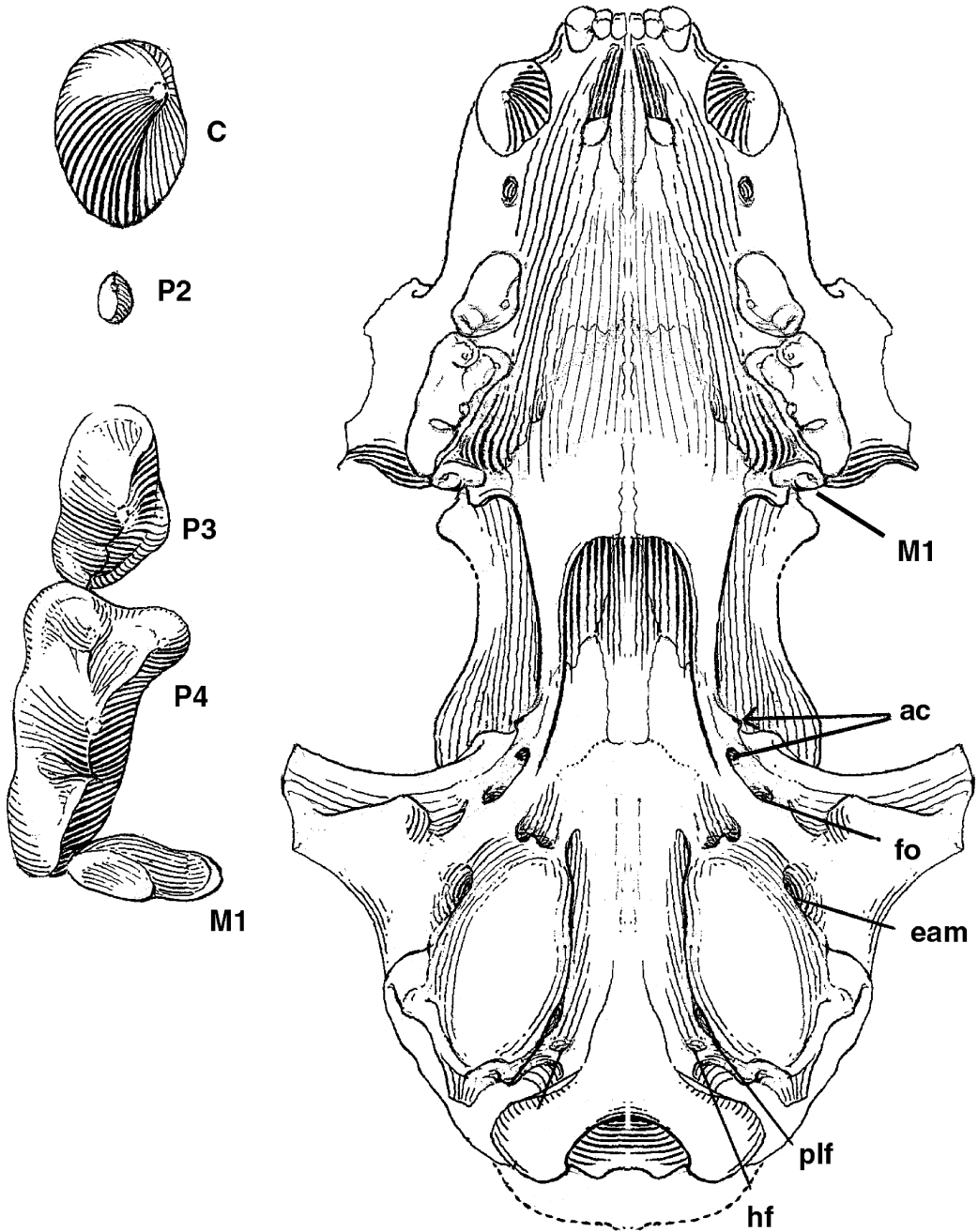
Fig. 55. Reconstruction of skull and right upper dentition of *P. marshi* (F:AM 27453). Labeled on the skull illustration from top to bottom: multi-cusped M1; alisphenoid canal (ac) composed of anterior and posterior alisphenoid foramina; foramen ovale (fo); external auditory meatus (eam); posterior lacerate foramen (plf); hypoglossal foramen (hf). Labeled on the dental illustration from top to bottom: upper canine C, P2, P3, P4, and M1.

Humerus	175.00
Ulna	180.00
Radius	144.00
Metacarpal 3	
Femur	207.00
Tibia	193.00
Metatarsal	75.50

lemanensis (fig. 29). The hypoglossal canal in *P. marshi* has shifted toward the horizontal, opening in an anteroventral direction, similar to modern felids. The alisphenoid canal is present on both sides of the *P. marshi* skull. However, crushing of this specimen prevents documentation of the presence of a foramen rotundum.

Postcranial information on *P. marshi* is provided by F:AM 62144, a partial skeleton from the late Barstovian Cerro Coñejo Formation (table 2). The limb elements do not differ from those previously referred to *P. validus* and *P. intrepidus*. Unfortunately, F:AM 62144 does not include any metacarpal bones. This hinders comparison of the front limb elements of *P. marshi* with *Proailurus lemanensis*, *Pseudaelurus validus*, *Pseudaelurus intrepidus*, and modern felids (Rothwell, 2001).

DISCUSSION: *P. marshi* is the most abundant Miocene felid in the Frick-AMNH collection. I have studied 80 *Pseudaelurus* lower jaws that I have been able to assign to one of six North American species. Twenty-eight specimens, or 35%, are referred to *P. marshi*. Twenty-two are assigned to the similar-sized and temporally equivalent species *P. intrepidus*. Specimens of *P. marshi* are found in virtually every felid-producing locality in the early and late Barstovian of North America. *P. marshi* and *P. intrepidus* account for 75% of the felid lower jaws from North American Barstovian localities. *Pseudaelurus marshi*, similar in size to *P. intrepidus*, differs primarily in the c–p3 length and the height of the dentary.

The possibility that these two fossil taxa are sexually dimorphic members of the same species must be considered. One definition of sexual dimorphism is ''when the means for fully developed males and females differ in a statistically significant way. The dimorphism is partial when the standard ranges of males and females overlap, and complete when they do not'' (Kurtén, 1955: 7). One hypothesis is that lower jaw specimens assigned to *P. marshi*, based primarily on the character of short c–p3 length and dentary height, are female members of *P. intrepidus*. To test this hypothesis, I studied modern felids. I examined modern skulls of four felid species in the Department of Mammology at the American Museum. Skeletons of *Lynx canadensis*, *Lynx rufus*, *Felis concolor*, and *Panthera leo*, killed in the wild and labeled as either male or female, were examined, measured, and scored for 40 dental and cranial characters (table 6). The limited number of skeletons labeled as to sex did not make it possible to select specimens in a random manner. To facilitate comparison of c–p3 length in different-sized felids, I calculated the mean of a c–p3 index for extinct and modern felids (table 4). To compute the c–p3 index, I divided the c–p3 length by the m1 length for each specimen studied (table 5). The length of the lower carnassial tooth has been demonstrated to be a good proxy for body size in felids (Legendre and Roth, 1988).

Panthera leo and *Lynx canadensis* displayed sexual dimorphism with respect to the c–p3 length; *Felis concolor* and *Lynx rufus* did not (table 3). I then grouped *P. intrepidus* and *P. marshi* into one hypothetical extinct species. I treated the data from these two taxa as partitions of the same species. The *P. marshi* and *P. intrepidus* data present as either two separate species or as sexually dimorphic members of the same species (table 3). In other words, the data of *P. intrepidus* and *P. marshi* present as either male and female felids whose c–p3 length resembles somewhat the lion or the lynx, or as two similar-sized but separate species which have the c–p3 length form of the mountain lion or bobcat.

To further compare *P. intrepidus* and *P. marshi* with modern felids, I plotted the dentary height versus m1 length (fig. 56). The height of the dentary below the carnassial

TABLE 3
Results of Analysis of Variance Performed on c-p3 Length Data of Extinct and Living Felids

Taxon	N	p	Hypothesis
L. canadensis	21	0.008	sexual dimorphism
Female	10		
Male	11		
L. rufus	16	0.065	no sexual dimorphism
Female	8		
Male	8		
F. concolor	15	0.28	no sexual dimorphism
Female	7		
Male	8		
P. leo	18	0.043	sexual dimorphism
Female	9		
Male	9		
P. intrepidus and *P. marshi*	46	0.0001	sexual dimorphism
P. intrepidus	18		
P. marshi	28		

tooth differs significantly (p = 0.0004) in *P. intrepidus* and *P. marshi*. Again, the length of m1 was used as an analog for body size. These data can be compared to the same information from modern specimens of *F. concolor* killed in the wild (fig. 57). The male and female *F. concolor* data resemble the *P. intrepidus* and *P. marshi* chart. Data from figures 56 and 57 are combined in figure 58. *Felis concolor* does display sexual dimorphism with respect to height of the dentary (p = 0.0475). This felid does not display sexual dimorphism in the c–p3 length (p = 0.28).

TABLE 4
Data of c-p3 Length in Felid Lower Jaws

Taxon	N	Mean	Max.	Min.	SD	CV	Index
P. validus	7	17.7	19.9	14.6	1.22	6.9	1.1
P. skinneri	7	7.5	8.9	6.1	1.22	16.3	0.6
P. intrepidus	18	14.1	16.8	10.3	1.89	13.5	0.8
P. marshi	28	9.7	13.8	6.6	1.68	17.3	0.6
P. stouti	6	6.0	8.1	4.4	1.35	22.7	0.7
Panthera leo	18	24.9	29.2	21.8	2.22	8.9	1.1
Females	9	25.2	30.1	21.8	2.26	9.0	1.1
Males	9	28.6	36.3	23.5	3.96	13.8	1.0
F. concolor	15	10.8	14.0	9.0	1.58	14.6	0.7
Females	7	9.9	10.9	9.0	0.66	6.7	0.7
Males	8	11.4	14.0	9.5	1.75	15.3	0.7
L. canadensis	21	7.2	9.5	4.4	1.40	19.4	0.6
Females	10	6.4	8.2	4.4	1.21	18.8	0.5
Males	11	8.0	9.5	5.1	1.17	14.7	0.6
L. rufus	16	7.6	10.2	5.3	1.40	18.4	0.7
Females	8	7.0	8.7	5.3	1.22	17.5	0.7
Males	8	8.3	10.2	5.6	1.34	16.3	0.8

TABLE 5
Data of m1 Length in Felid Lower Jaws

Taxon	N	Mean	Max.	Min.	SD	CV
P. validus	7	16.5	17.3	15.2	0.42	2.5
P. skinneri	7	12.7	13.8	11.6	0.88	6.9
P. intrepidus	18	16.6	19.6	15	1.32	8.0
P. marshi	28	16.3	19.2	14.1	1.25	7.7
P. stouti	6	8.5	8.9	8.0	0.36	4.3
P. leo	18	24.9	29.2	21.8	2.22	8.9
Females	9	23.2	30.1	21.8	0.97	4.2
Males	9	26.5	36.3	23.5	1.78	6.7
F. concolor	15	15.6	16.7	14.1	0.97	6.2
Females	7	15.1	16.7	14.1	0.89	5.9
Males	8	15.9	16.7	14.2	0.84	5.2
L. canadensis	21	12.4	13.2	10.8	0.62	5.0
Females	10	12.3	13.1	10.8	0.68	5.5
Males	11	12.4	13.2	11.2	0.58	4.7
L. rufus	16	10.7	12.2	9.5	0.80	7.5
Females	8	10.5	11.4	9.5	0.67	6.4
Males	8	11.0	12.2	9.9	0.87	7.9

In summary, there are arguments for and against sexual dimorphism being the explanation for character differences between *P. intrepidus* and *P. marshi*. Supporting arguments include: (1) Sexual dimorphism is seen in modern felid species, at the very least in body size and skull length in small felids (Dayan and Simberloff, 1996). (2) *P. skinneri* and *P. stouti* display differences in c–p3 length that could also be interpreted as sexual dimorphism. (3) *P. intrepidus* and *P. marshi* are size and temporally equivalent. Specimens of the two species are sometimes found in the same localities. Counter arguments include: (1) A similar range in c–p3 length and dentary height and width is not seen in *P. validus*. *P. validus* and some modern species do not exhibit sexual dimorphism in the low-

TABLE 6
Character/Taxon Matrix Used to Resolve Felid Phylogeny (question marks indicate missing data)

	1	2	3	4	5	6	7	8	9	1 0	1 1	1 2	1 3	1 4	1 5	1 6	1 7	1 8	1 9	2 0	2 1	2 2	2 3
Didymictidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	?	0
Stenogale	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	1	0	1	0	?	?	?	0
Proailurus	0	0	0	1	1	1	0	0	0	1	2	0	0	0	0	2	0	1	1	0	0	0	1
Pseudaelurus validus	0	1	0&1	1	1	1	1	0	1	1	2	0	0	1	0	2	1	1	1	0	1	0	?
P. skinneri	2	1	1	1	1	1	1	0	?	1	2	0	0	1	?	?	?	?	?	?	?	?	1
P. intrepidus	1	1	1	1	1	1	1	0	1	1	2	0	0	2	0	?	1	?	1	?	?	1	2
P. marshi	2	1	1	1	1	1	1	0&1	1	1	2	0	0	2	0	2	1	1	1	?	?	?	2
P. stouti	1	1	0&1	0	1	1	1	0	1	1	2	0	0	2	?	?	?	?	?	?	?	?	0
Felis concolor	1	1	2	1	2	2	1	1	1	1	2	0	2	2	1	2	1	2	2	1	1	2	2
Lynx canadensis	0	1	2	1	1&2	2	1	1	2	1	2	1	2	2	1	2	1	2	2	1	1	2	1

TABLE 7
**Metacarpal 3 Contribution to Total length of
Front Limb in Six Felids**
Total front limb length was computed from combined
lengths of humerus, ulna, and metacarpal 3.

Proailurus front limb length	300.00
metacarpal 3 percentage	12.00%
Pseudaelurus validus front limb length	405.00
metacarpal 3 percentage	12.10%
P. intrepidus front limb length	443.31
metacarpal 3 percentage	12.90%
Lynx issiodorensis front limb length	467.00
metacarpal 3 percentage	12.30%
Felis concolor front limb length	541.20
metacarpal 3 percentage	15.61%
L. canadensis front limb length	360.80
metacarpal 3 percentage	14.91%

er jaw. (2) Modern assemblages of felids sometimes contain at least two species that are indistinguishable in jaw length (Kiltie, 1988). (3) The p error for the hypothetical *P. intrepidus–P. marshi* species (0.0001) is far outside the range of p error seen in the four modern species studied (0.28–0.008).

The results appear inconclusive, primarily because of the variability of the sexual dimorphism displayed by different species of living felids. However, if *P. intrepidus* and *P. marshi* were indeed sexually dimorphic members of the same species, the males and females differed far more than any of the four living felids. For this reason, I choose to consider these two samples as separate species.

Pseudaelurus aeluroides Macdonald, 1954

HOLOTYPE: SDSM 3248, right ramus with c, p3, p4 and m1 from northeast rim of Sinclair Draw (early Barstovian), Sioux Co., Nebraska.

REFERRED SPECIMENS: None.

DISTRIBUTION: Type locality only.

DESCRIPTION AND COMPARISONS: I have not been able to examine either this specimen or a cast of this taxon. From the illustration pro-
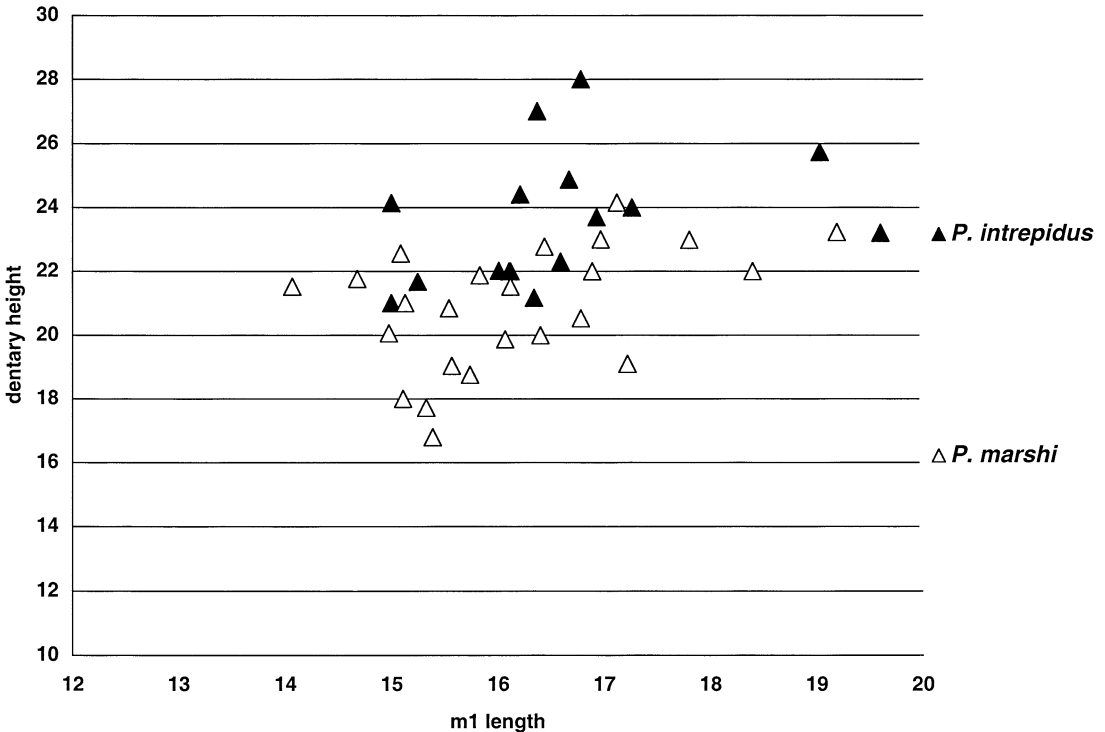

Fig. 56. Chart of dentary height versus m1 length for lower jaws of *P. intrepidus* and *P. marshi*. When specimens of *P. intrepidus* and *P. marshi* are similar-sized, *P. marshi* tends to have a shorter dentary as measured below P4/m1.
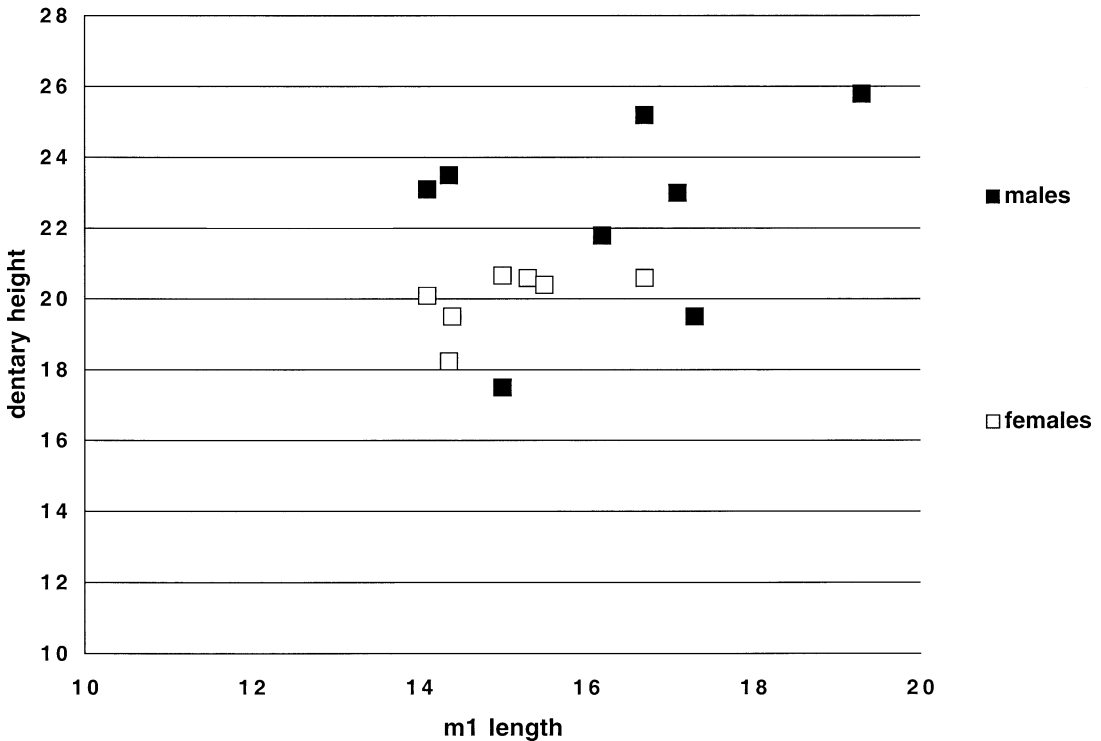
Fig. 57. *Felis concolor* data: male and female dentary height versus m1 length. Female members of this species also appear to have shorter dentaries than do similar-sized males.

vided by Macdonald (1954), it may be a juvenile with erupting teeth. The m1 is 15.6 mm long and the distance between the lower canine and p3 is 7.3 mm. I have examined 21 lower jaws referred to *Pseudaelurus* from the Lower Snake Creek Fauna. I have assigned seven of these specimens to *P. marshi* Thorpe (1922). None of the characters or dimensions mentioned by Macdonald would distinguish SDSM 3248 from this group of fossils. I hesitate to reassign a specimen without seeing it, but *Pseudaelurus aeluroides* (SDSM 3248) may be synonymous with *P. marshi*.

CHARACTER ANALYSIS

The morphology of species within the monophyletic feliform Didymictidae (Flynn and Galiano, 1982) is suggested as an approximate ancestral form of the Felidae. One species from within the Didymictidae, *Didymictis altidens* (AMNH 14781) was scored for postcranial characters. A second didym-

ictid, a skull of *Protictis schaffi* (YPM-PU 16495), provided dental and basicranial outgroup information. The European aeluroid *Stenogale* is included as an outgroup because of its status as possible sistergroup to the Felidae (Hunt, 1998). Twenty-three equally weighted characters were selected, based on their relevance across the taxa included. Character polarities were determined via comparison with the two outgroups, the *Didymictidae* and *Stenogale*. Dental features account for 62% of the characters selected. Despite the relative rarity of postcrania in the fossil record, three postcranial characters are included.

DENTITION

1. c–p3 length: Early felids have a skull with a relatively long and narrow snout. The fossil record of the family Felidae reveals a trend toward a more brachycephalic skull, shorter dentary, and reduction in the number of teeth both anterior and posterior to m1

Fig. 58. *Pseudaelurus marshi* and *P. intrepidus* data added to figure 57.

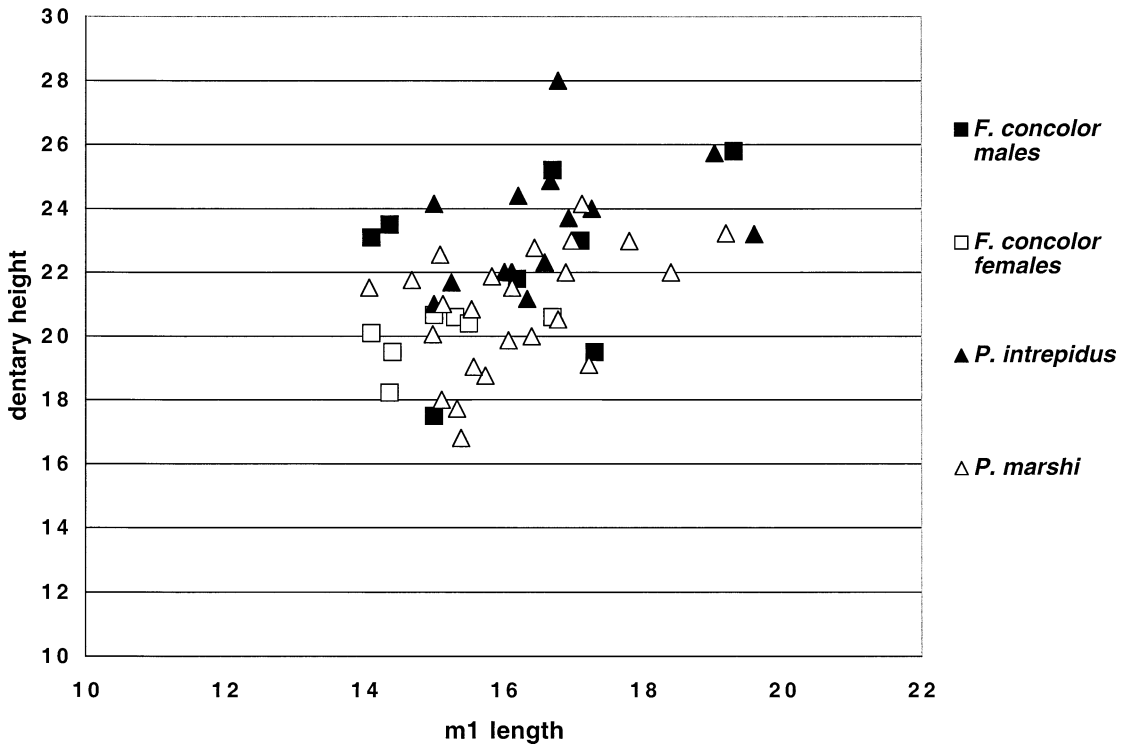(Pilgrim, 1931). Both modern and extinct felids display variation in the distance between the lower canine and p3. Some modern species display sexual dimorphism with respect to this character (table 3). A c–p3 index was calculated for modern and extinct felid species using the length of the lower first molar. POLARITY:0, c–p3 length is equal to or greater than m1 length (c–p3 index > 1.0); 1, c–p3 length is less than m1 length (c–p3 index 1.0 > 0.6); 2, c–p3 length is greatly reduced (c–p3 index < 0.6).

2. p1: Early Tertiary carnivorans, early aeluroids, and the earliest felid *Proailurus* had four lower premolars. Within Felidae, loss of p1 is first seen in *Pseudaelurus*. POLARITY:0, p1 present; 1, p1 absent.

3. p2: The condition of a two-rooted p2 occurs in European aeluroids of late Oligocene and early Miocene age (Hunt, 1998), the felid *Proailurus*, and early specimens of *Pseudaelurus turnauensis* from Europe (Dehm, 1950). Within fossil Felidae, the presence of p2 is diagnostic for the genus *Pseudaelurus*. In North American *Pseudae-lurus*, one specimen of *P. validus* and two specimens of *P. stouti* have p2 with two roots. POLARITY:0, p2 present with two roots; 1, p2 present with one root. 2, p2 absent.

4. p3 and p4 height: Early Tertiary carnivorans have p3 and p4 that are similar in size and height. This condition is also seen in the early European aeluroids *Stenogale*, *Palaeoprionodon*, and *Stenoplesictis* (Peigné, 1999). The condition of a p4 taller than p3 is seen in the felid genera *Proailurus*, most species of *Pseudaelurus*, and modern felids. POLARITY:0, p3 and p4 similar in size; 1, p3 considerably smaller than p4.

5. m1 metaconid: Within Aeluroidea, reduction of the m1 metaconid occurs in parallel in Felidae and Hyaenidae (Werdelin, 1996). Within Felidae, reduction of the metaconid is first seen in *Proailurus lemanensis*. State 2, loss of the m1 metaconid, is seen in modern felids. The variable "reappearance" of m1 metaconid and talonid in some species of *Lynx* (Kurtén, 1963) was treated as polymorphism. POLARITY:0, metaconid is distinct, large (for felids), and positioned high above

the talonid on the posterior surface of the protoconid; 1, metaconid is less distinct, positioned low, slightly above the talonid on the posterior surface of the protoconid; 2, metaconid is absent.

6. m1 talonid: Early Tertiary carnivorans had an m1 talonid with a distinct basin. Profound reduction in the talonid has been considered a synapomorphy for Felidae and Hyaenidae (Wyss and Flynn, 1993), but studies of the fossil evidence suggest parallel development in the two families (Werdelin, 1996). Within Felidae, *Proailurus lemanensis*, the earliest recognized member of Felidae, displays reduction of the m1 talonid. POLARITY:0, talonid present with basin; 1, talonid is reduced, no basin evident; 2, talonid absent.

7. m2: m2 is present in early aeluroids *Stenoplesictis*, *Stenogale*, and *Palaeoprionodon* and in the early felid *Proailurus lemanensis*. Within Felidae, absence of this tooth is seen in most species of *Pseudaelurus* and all extant felids. POLARITY:0, m2 present; 1, m2 absent.

8. P1: Early felids (*Proailurus*, *Pseudaelurus*) have P1 present. One North American *Pseudaelurus* skull, referred to *P. marshi*, exhibits the condition of P1 absent. I examined 70 modern skulls of male and female lynx, bobcat, puma, and lion. None exhibited evidence of P1. POLARITY:0, P1 present; 1, P1 absent.

9. P2: Early aeluroids, including *Proailurus lemanensis*, the earliest recognized felid, have a P2 with two roots. A vestigial P2, peglike with one root, was seen in all *Pseudaelurus* skulls examined. In the skulls of four modern species that I studied, *Panthera leo* and *Felis concolor* all had a vestigial P2 with one root. *Lynx canadensis* and *Lynx rufus* skulls lacked a P2. POLARITY:0, present with 2 roots; 1, P2 is vestigial with one root; 2, P2 is absent.

10. P3 posterior accessory cusp: The primitive carnivoran condition has been hypothesized to be P3 with no posterior accessory cusp (Wang and Tedford, 1994; Peigné, 1999). P3 with a posterior accessory cusp (fig. 15) is seen in the extinct aeluroid species *Stenogale*, the extinct felids *Proailurus* and *Pseudaelurus*, as well as in all living felids. POLARITY:0, P3 posterior accessory cusp

absent; 1, P3 posterior accessory cusp present.

11. P4 parastyle: Carnivorans classified within the Viverravidae have a small parastyle on the anterior margin of the paracone of P4. This character state has been hypothesized to be primitive for Carnivora (Flynn and Galiano, 1982). Enlargement of the parastyle cusp over the primitive state has been described as a synapomorphy for the Didymictida and Aeluroidea (Flynn and Galiano, 1982). An enlarged parastyle accompanied by a small accessory cusp on the anterolateral margin of the parastyle is seen in the extinct felids *Proailurus* and *Pseudaelurus* (figs. 15, 27). The accessory parastyle cusp on P4 was first described in the extinct felid *Sivaelurus chinjiensis* (''anterior cingular cusp'') in a specimen that was originally assigned to the genus *Pseudaelurus* (Pilgrim, 1915). This accessory cusp (''prostyle'') is also described as being very variable in the felid *Smilodon*, sometimes being present on one side only (Merriam and Stock, 1932). Modern felids retain the accessory cingular parastyle cusp, which is always located anterolabially from the parastyle. POLARITY:1, enlargement of the cusp over the primitive state; 2, present, enlarged, and accompanied by an accessory cingular cusp.

12. P4 protocone: A prominent protocone that projects far forward of the P4 paracone has been hypothesized as the primitive state for all Carnivora (Wyss and Flynn, 1993). This cusp does not vary much within fossil Felidae. All *F. concolor* specimens studied had P4 with a robust protocone, while the *L. canadensis* and *Lynx rufus* specimens had a P4 with a reduced protocone. POLARITY:0, protocone distinct, projecting anterolingually from medial surface of P4; 1, protocone is reduced, compressed as seen in some modern felids (Pilgrim, 1932; Salles, 1992).

13. M1: Reduction in size of M1 has been described as a shared derived character for Aeluroidea (Ginsburg, 1999). *Proailurus* and North American species of *Pseudaelurus* have an M1 that is reduced in size, but still contains multiple cusps (fig. 14) and appears to occlude. A vestigial M1 without multiple cusps is seen in all modern felids. POLARITY:0, non-vestigial, multicusped M1, occlud-

ing with metaconid and talonid of m1; 1, M1 is vestigial.

MANDIBLE

14. Shape of coronoid process: Early aeluroids, and particularly the early felid *Proailurus lemanensis*, have a coronoid process that is short and erect (fig. 10). All North American felids have a tall coronoid process. In *Pseudaelurus intrepidus*, *P. marshi*, *P. stouti*, and extant felids, the coronoid process slopes posterodorsally. The coronoid process has a terminal hook in extant felids. POLARITY:0, coronoid process is short, wide, and erect; 1, coronoid process is tall, wide, and yet still relatively erect; 2, coronoid process is slender and slopes posterodorsally.

BASICRANIUM

15. Alisphenoid canal: The primitive eutherian alisphenoid canal has been described as either absence or presence of an indistinct canal, with the anterior opening confluent with the sphenorbital fissure (Novacek, 1986). One study that focused on Carnivora scored the presence of the alisphenoid canal as primitive for the order (Wyss and Flynn, 1993). Although the alisphenoid canal is not mentioned in the description of the *Protictis schaffi* basicranium (Gingerich and Winkler, 1985), early European aeluroids have an alisphenoid canal. Therefore, the presence of a distinct alisphenoid canal is most likely a shared primitive character for the suborder Aeluroidea and the family Felidae. Loss of the alisphenoid canal has been described as an apparent synapomorphy for Felidae and Hyaenidae (Wyss and Flynn, 1993). However, within fossil Felidae, *Proailurus* and *Pseudaelurus* are in the plesiomorphic state (Figs. 19, 20), demonstrating homoplasy for this character in these two aeluroid families. POLARITY:0, alisphenoid canal present; 1, alisphenoid canal absent.

16. Caudal entotympanic: The negative evidence of lack of an ossified bulla in early Tertiary carnivorans has been previously discussed (Flynn and Galiano, 1982; Wang and Tedford, 1994). The late Paleocene *Protictis schaffi* (PU 13964) basicranium has evidence of a cartilaginous articulation between the petrosal and a bulla (Gingerich and Winkler,

1985). Aeluroids are defined by the placement of the posterior edge of the ectotympanic directly on the petrosal promontorium in early ontogeny (R. Hunt, Jr., personal commun.). One result of this morphology is the formation of a bony septum due to the juxtaposition of the caudal entotympanic and the ectotympanic. An obvious consequence of the development of the septum bullae is the formation of two separate chambers in the auditory region. The anterior chamber is formed by the ectotympanic. The posterior chamber is formed by the caudal entotympanic. The European aeluroid taxa *Stenoplesictis*, *Palaeoprionodon*, *Stenogale*, and *Proailurus* demonstrate this two-chambered morphology (Hunt, 1989). It is the increase in size of the caudal entotympanic chamber over the primitive aeluroid condition that characterizes the auditory region of Felidae. POLARITY:0, nonossified, single-chambered bulla; 1, ossified, two-chambered bulla with relatively small caudal entotympanic; 2, caudal entotympanic has expanded to emarginate the adjacent basioccipital.

17. Hypoglossal foramen: The hypoglossal foramen of early Tertiary carnivorans is separate from the posterior lacerate foramen (Wyss and Flynn, 1993). The hypoglossal foramen of *Proailurus lemanensis* is clearly separate from the posterior lacerate foramen and opens in a ventral direction. In all skulls of *Pseudaelurus* and modern felids studied, the hypoglossal foramen and the posterior lacerate foramen share a common depression in the basioccipital. Due to its position on the wall of a concavity, the hypoglossal foramen in *Pseudaelurus* and modern felids opens in an anteroventral direction. POLARITY:0, hypoglossal foramen separate from the posterior lacerate foramen, not sharing a common depression, opening from the basioccipital in a ventral direction; 1, positioned on the posteromedial rim of a common depression with the posterior lacerate foramen, opening anteriorly, ventrally, and laterally.

18. Ventral petrosal morphology: The petrosal of early carnivorans has been described as being isolated from surrounding bones (Wang, 1994). The auditory region of *Stenogale* and *Proailurus* displays a medial flange of the petrosal promontorium that rests upon the adjacent basioccipital (Hunt,

1998). This medial flange is seen in *Pseudaelurus validus* and *Pseudaelurus marshi*. However, it is absent in living felids. POLARITY:0, petrosal isolated from surrounding bones; 1, medial flange of promontorium rests upon basioccipital; 2, absence of medial flange.

19. Paroccipital process: The primitive mammalian paroccipital process has been hypothesized as being separate from the auditory capsule, projecting posteroventrad from the exoccipital (Wyss and Flynn, 1993). Early aeluroids have been described as having this condition (Hunt, 1989). *Proailurus lemanensis*, *Pseudaelurus validus* (fig. 20), *Pseudaelurus intrepidus* (fig. 34), and *Pseudaelurus marshi* (figs. 54, 55) have a paroccipital process that has been fully contacted by the expanded caudal entotympanic. In addition, in these four felids there is a distinct projection of the paroccipital process projecting posteroventrad from the posterior surface of the caudal entotympanic. Controversy concerning the state of this character in some taxa (Wyss and Flynn, 1993; Hunt, 1987) may be due to paucity of fossil material and a tendency for the posteroventral termination of the process to be poorly preserved in many fossil felid skulls. Nonetheless, all modern felids have a paroccipital process that is cupped about the caudal entotympanic with no posteroventral process. POLARITY: 0, paroccipital process separate from the auditory bulla, projecting posteroventrad from the exoccipital; 1, paroccipital process cupped firmly about the caudal surface of the bulla, with termination of the process projecting posteroventrad; 2, paroccipital process cupped firmly about the caudal surface of the bulla with no evidence of a terminal process projecting posteroventrad.

POSTCRANIUM

20. Metatarsal 1: The early Tertiary carnivoran metatarsal 1 is nonvestigial, having a slender diaphysis and articulating with a phalanx. This condition can be seen in AMNH 14781, a complete hind foot of the viverravid *Didymictis altidens* from the early Eocene Wind River Formation of Wyoming. The nonvestigial metatarsal 1 is known in the felids *Proailurus* (Helbing, 1928) and *Pseudaelurus*

validus (Rothwell, 2001). A vestigial metatarsal 1 is seen in all modern *Felis*. POLARITY:0, functional metatarsal 1, articulating with a phalanx; 1, vestigial metatarsal 1.

21. Metacarpal 1: The metacarpal 1 of early Tertiary carnivorans has a long, slender diaphysis. The proximal and distal articular surfaces are both parallel to each other and perpendicular to the long axis of the diaphysis. This morphology of metacarpal 1 can be seen in the viverravid *Didymictis altidens* (AMNH 14781) as well as the miacid *Vulpavus profectus* (AMNH 12626). Helbing's (1928) illustration of a *Proailurus* metacarpal 1 that is equivalent to these early Tertiary metacarpals scores *Proailurus* in the primitive state. The metacarpal 1 of *Pseudaelurus validus* has a blunt and rectangular shape, having lost the length and slender diaphysis of the other four metacarpals (Rothwell, 2001). A blunt, rectangular, and reduced Mc1 is seen also in *P. intrepidus* (F:AM 6190), *P. marshi* (F:AM 62135), and all extant Felidae. However, this character state is still unknown in many fossil species. POLARITY:0, metacarpal 1 has a long, slender diaphysis resembling the other four metacarpals; 1, metacarpal 1 has a blunt and rectangular shape.

22. Metacarpal bone length: *Proailurus lemanensis* (Filhol, 1888) and *Pseudaelurus validus* have short metacarpal bones. *P. intrepidus* and modern felids have increased the length of the metacarpals (figs. 36–38, table 7). POLARITY: 0, metacarpals relatively short, contributing approximately 12% to the front limb length; 1, metacarpals long, contributing more than 12% to the front limb length; 2, metacarpals much longer, approaching 16% of the front limb length.

23. Size: Within the anatomically homogenous family Felidae, size is an important character (table 5). *Proailurus*, the earliest recognized felid, is a medium-sized cat, whose three species are differentiated primarily by size (Peigné, 1999). Early and middle Miocene felids of North America range in size from the domestic cat-sized *Pseudaelurus stouti* to the puma-sized *Pseudaelurus validus*. Overlap in body size seems to occur only in the two large species, *P. intrepidus* and *P. marshi*. POLARITY:0, small, domestic cat-sized felid with m1 length < 9 mm as in *P. stouti*; 1, medium-sized felid

with m1 length range of 9–14 mm, as in *Proailurus* spp., *P. skinneri*, and *Lynx canadensis*; 2, large felid with m1 length exceeding 14 mm, as in *P. validus*, *P. intrepidus*, *P. marshi*, *Felis concolor*, and *Panthera leo*.

PHYLOGENY

A 10-taxa by 23-character matrix representing 55 character states was compiled for phylogenetic analysis (table 6). The matrix has 13% missing data displayed as question marks. Two species account for the majority of the missing information. *Pseudaelurus skinneri* is known only by fragmentary lower and upper jaw material. The material known from a second species, *P. stouti*, consists only of fragmentary lower and upper jaw material and one petrosal. The single lower jaw of *P. aeluroides* was not included in the matrix because of its likely synonymy with *P. marshi*. Character states for the early European aeluroid species *Stenogale* were obtained from illustrations, photographs (Filhol, 1879; Hunt, 1998), and a recently published character matrix (Peigné, 1999). Some taxa were scored as polymorphic for certain dental characters. One lower jaw of *Pseudaelurus validus* and two of *P. stouti* have evidence of p2 with two roots. One skull, assigned to *P. marshi*, had no evidence of P2.

A search for the shortest tree was performed with PAUP program (version 3.0, Swofford, 1990). An exhaustive search yielded three trees, each with 43 steps. All three trees depict the three late Barstovian species *P. intrepidus*, *P. marshi* and *P. stouti* as forming a monophyletic group with the modern felids. This clade is supported by character 14, the tall and sloping coronoid process. In all three trees, the sister group to this clade is the late Hemingfordian species, *P. skinneri*. Figure 60 is a strict consensus tree. The monophyletic status of Felidae (node 16) is supported by five synapomorphies: character 4, the condition of p4 taller than p3 with a reversal in the small taxon *Pseudaelurus stouti*; character 5, the condition of reduction of the metaconid on m1; character 11, the condition of P4 parastyle enlarged over the primitive carnivoran con-

dition and accompanied by an accessory cingular cusp; character 16, the condition of caudal entotympanic expanding to emarginate the adjacent basioccipital; and character 19, the condition of the paroccipital process cupped firmly about the caudal surface of the bulla.

Six synapomorphies support the monophyly of *Pseudaelurus* and the modern felids (node 15) (fig. 59): character 2, the loss of p1; character 7, the absence of m2; character 9, P2 with one root; character 14, a tall coronoid process; character 17, a hypoglossal foramen sharing a common depression with the posterior lacerate foramen; and character 21, a blunt and rectangular-shaped metacarpal 1.

BIOGEOGRAPHY

The extensive Frick Collection of felid fossils provides considerable insight into the felid fauna of the early and middle Miocene of North America. It appears that the diversity of felids in North America during this time differed from that in Europe. The earliest known felid immigrants to the New World are the large *P. validus* and the smaller, medium-sized *P. skinneri*. These two North American felids do not have analogous forms in the fossil record of Europe. Felid fossils of comparable age in Europe are restricted to one species, the small *P. turnauensis* (Ginsburg, 1961b). The presence of the two endemic North American species in late Hemingfordian localities suggests that early Miocene felid biogeography in the New World may not mirror the situation in Europe, but understandably may be more associated with the as yet untold story in Asia.

In the middle Miocene felid faunae of Europe, four different-sized species of felids, from small to large, have a reasonably continuous presence in the fossil record (Ginsburg, 1961b; Heizmann, 1973). The middle Miocene Barstovian of North America, however, is dominated by the presence of two large species, *P. intrepidus* and *P. marshi*. These two large felids account for almost 75% of the felid specimens from the middle Miocene in the Frick Collection. This suggests that the hypercarnivorous guilds in North America and Europe were dissimilar
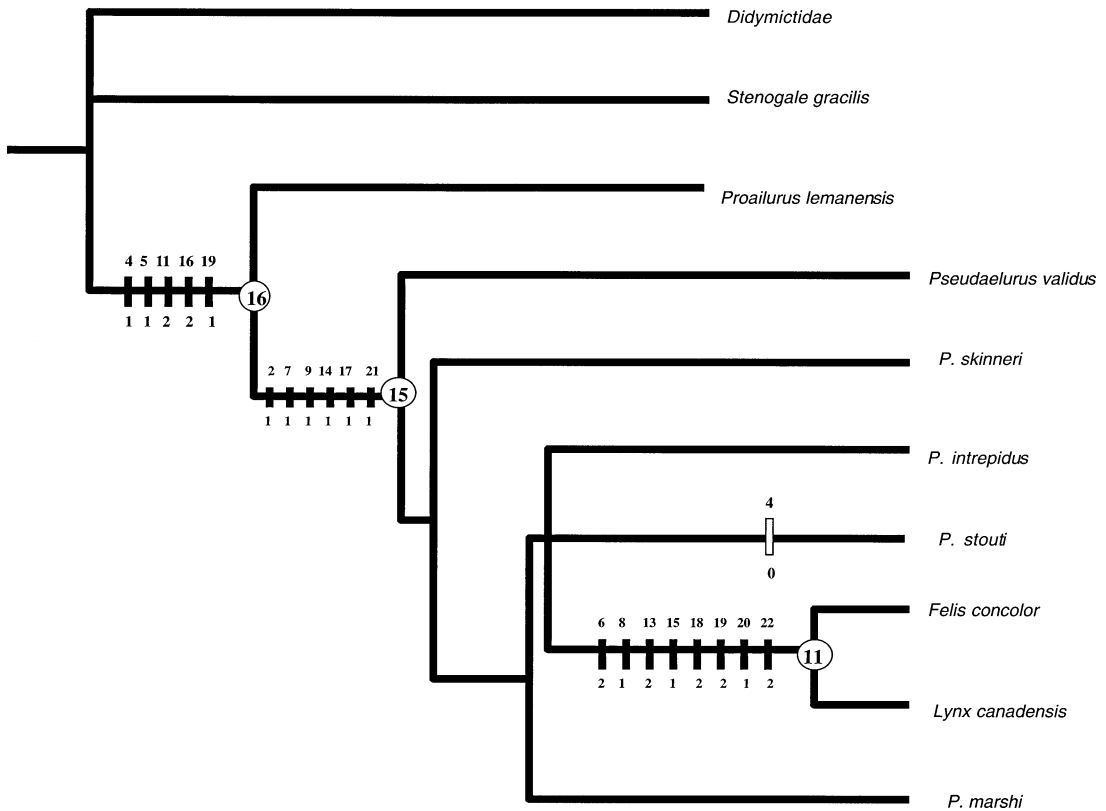
Fig. 59.   Strict consensus tree based on three equally parsimonious trees calculated by PAUP from a data matrix of 10 taxa and 23 characters. The solid bars represent synapomorphies. The empty boxes represent homoplasies (parallelisms or reversals). Numbers above the branches represent characters and those below represent character states. Tree statistics: length = 43, consistency index = 0.88, retention index = 0.86.

during this time as well. The only other North American felid known during the Barstovian, the less common and very small species *P. stouti*, appears to be unique to the New World. There are no medium-sized felids known from the middle Miocene of North America.

DISCUSSION

Classification of felids has been problematic since creation of the genus *Felis* (Linnaeus, 1758). The process has been long hampered by the homogeneity of the anatomy within the family (Salles, 1992; Rothwell, 2001; Werdelin, 2001). Most felid classifications support the recognition of 38 modern species (Collier and O'Brien, 1985), but disagreement abounds on the generic as-

sociations. Ranges of 2–19 genera have historically been suggested. The advent of molecular data studies has somewhat improved the phylogenetic resolution of the living family, but only to the level of multiple lineages (Masuda et al., 1996; Johnson et al., 1996). Additional molecular analyses have attempted to provide timetables for what appears to be a recent radiation of living felids (Collier and O'Brien, 1985; Bininda-Emonds et al., 1999), but with considerable disagreement. Morphological character analysis of modern species (Salles, 1992) has also resolved modern felid relationships only to the level of lineage.

While the monophyletic status of modern Felidae has been little questioned, the roster of its fossil members has been more dynam-

ic. It is only in the last 20 years, due in large part to morphological studies of the basicranium, that the equally hypercarnivorous Nimravidae have been excluded from close relationship with the Felidae (Baskin, 1981; Flynn and Galiano, 1982; Neff, 1983, Bryant, 1991). Description of conservative auditory region morphological characters has improved our understanding of fossil felids (Hunt, 1974; Tedford, 1978). This has led to identification and clarification of even earlier fossil felids and their sister taxa within the suborder Aeluroidea (Hunt and Tedford, 1993; Hunt, 1998). This study of the Frick Collection of early and middle Miocene North American felids, stable anatomy notwithstanding, attempts to continue this momentum and provide new information of phylogenetic importance to early felids and their aeluroid relatives. If and when cranial, basicranial, and postcranial information is available from European and Asian species of *Pseudaelurus*, some improvement in the resolution of the early felid phylogenic tree could be expected.

Early and middle Miocene felids lacking machairodont characters have historically been assigned to the genus *Pseudaelurus*. This is due largely to the phenomena of anatomical homogeneity and specimen scarcity. The same could be said of the earlier felid taxon *Proailurus*. Prior to this study, these two genera largely consisted of species based on different sizes of lower jaws that rarely differed otherwise. It is not until the late Miocene and Pliocene, when numerous machairodont lineages appeared, that the family Felidae began to display significant diversity at the generic level. As a result of this study, some nonmachairodont felids from the early and middle Miocene of North America have cranial, basicranial, and postcranial characters to complement the dental data.

In this study, the monophyletic status of Felidae is supported by only two derived nondental characters: the caudal entotympanic expanding to emarginate the adjacent basioccipital; and the paroccipital process cupped firmly about the caudal surface of the bulla. It is reasonable to consider that these two characters are linked to the same process of the expanding caudal entotympanic. But even with the conservative amount of mor-

phological character information presented here, it is possible to consider further investigations into the evolution of the family Felidae.

From its origins within the early Tertiary carnivorans, through the appearance of *Proailurus* and *Pseudaelurus*, the continued evolutionary story of the family Felidae needs to be told as it radiated in the late Miocene into *Felis* and the numerous machairodont forms. There are multiple problems to be solved within the fossil family Felidae. The relationship of this family (or any family within Carnivora) to the early Tertiary miacids and viverravids is as yet undetermined. Aeluroids are another frustrating example of a highly derived carnivoran form suddenly appearing in the fossil record of the late Oligocene. Another uncertainty is the referral of the Barbourofelinae to Nimravidae and hypotheses concerning its Miocene ''ghost lineage'' (Neff, 1983, Bryant, 1991, Morales et al., 2001). An equally compelling chapter in this felid narrative is the Pliocene and Pleistocene extinction of the many sabertoothed forms and the collateral survival of modern felids' ancestors. Likewise, the identity of a possible common ancestor of modern felids has yet to be recognized within the fossil taxa of the late Miocene.

ACKNOWLEDGMENTS

helpful in obtaining information available only in historic, archived manuscripts. Lars Werdelin is to be thanked for the many e-mail exchanges, often resolving obscure references to archaic citations of felids.

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APPENDIX 1
Measurements (mm) of 46 Felid Lower Jaws Assigned to *P. intrepidus* and *P. marshi*

ID no.	Taxon	m1 L	c-p3	c-p3 index[a]
F:AM 61806	*P. intrepidus*	15.4	12.0	0.78
F:AM 61804	*P. intrepidus*	16.1	13.0	0.81
F:AM 61805	*P. intrepidus*	16.1	11.4	0.71
F:AM 61831	*P. intrepidus*	16.8	16.1	0.96
F:AM 69331	*P. intrepidus*	15.0	12.0	0.80
AMNH 10396	*P. intrepidus*	19.6	14.8	0.76
AMNH 25209	*P. intrepidus*	15.3	13.1	0.85
AMNH 18271	*P. intrepidus*	18.4	14.9	0.81
F:AM 61933	*P. intrepidus*	15.0	13.4	0.89
F:AM 27331	*P. intrepidus*	16.9	16.0	0.94
F:AM 27327	*P. intrepidus*	16.2	15.2	0.94
F:AM 61910	*P. intrepidus*	16.6	13.7	0.82
SBCM L18165224	*P. intrepidus*	16.7	16.8	1.01
F:AM 61923	*P. intrepidus*	16.3	13.4	0.82
UNSM 83981	*P. intrepidus*	19.0	14.5	0.76
LACM (CIT) 1233	*P. intrepidus*	15.3	10.3	0.68
LACM (CIT) 772	*P. intrepidus*	16.0	15.8	0.99
AMNH 17212	*P. intrepidus*	17.3	16.7	0.97
F:AM 61808	*P. marshi*	16.9	12.3	0.72
AMNH 22401	*P. marshi*	17.0	11.2	0.66
AMNH 22404	*P. marshi*	16.4	9.6	0.59
F:AM 61807	*P. marshi*	15.1	8.7	0.58
F:AM 61809	*P. marshi*	15.1	8.5	0.56
F:AM 61841	*P. marshi*	18.4	11.5	0.63
F:AM 61846	*P. marshi*	17.4	10.1	0.58
AMNH 22398	*P. marshi*	15.4	8.1	0.53
YPM 12865	*P. marshi*	16.1	8.5	0.53
YPM 12815	*P. marshi*	15.0	10.0	0.67
F:AM 69331	*P. marshi*	15.5	8.3	0.54
F:AM 27453	*P. marshi*	14.1	10.3	0.73
F:AM 27457	*P. marshi*	15.3	7.2	0.47
F:AM 62135	*P. marshi*	15.8	9.2	0.59
F:AM 62144	*P. marshi*	15.8	10.6	0.67
F:AM 61934	*P. marshi*	16.1	6.6	0.41
F:AM 61916	*P. marshi*	18.7	11.8	0.63
F:AM 61936	*P. marshi*	16.2	8.1	0.50
F:AM 27317	*P. marshi*	17.2	10.2	0.59
F:AM 61926	*P. marshi*	16.4	9.5	0.58
F:AM 61940	*P. marshi*	15.7	7.0	0.45
F:AM 18008	*P. marshi*	17.8	8.2	0.46
F:AM 61938	*P. marshi*	19.2	10.3	0.54
F:AM 61924	*P. marshi*	16.8	13.8	0.82
F:AM 61918	*P. marshi*	17.1	11.3	0.66
F:AM 27337	*P. marshi*	15.1	11.2	0.74
F:AM 61921	*P. marshi*	14.7	9.7	0.66
UNSM 2448-87	*P. marshi*	15.6	10.1	0.65

[a] For explanation of c-p3 index, see page 44.

APPENDIX 2

Measurements (mm) of *Lynx canadensis, Lynx rufus, Felix concolor,* and *Panthera leo* Killed in the Wild and Labeled as Either Male or Female

ID no.	Taxon	m1 L	c-p3	c-p3index[a]	Sex
AMNHM137194	*Felis concolor*	14.4	9.0	0.63	female
AMNHM27239	*Felis concolor*	14.1	10.4	0.73	female
AMNHM17460	*Felis concolor*	15.0	10.9	0.73	female
AMNHM37505	*Felis concolor*	16.7	10.1	0.60	female
AMNHM17459	*Felis concolor*	15.3	9.3	0.61	female
AMNHM1339	*Felis concolor*	14.4	9.5	0.66	female
AMNH-AMNHM1323	*Felis concolor*	15.5	10	0.65	female
AMNHM17458	*Felis concolor*	16.7	12.4	0.74	male
AMNHM6677	*Felis concolor*	16.4	9.6	0.59	male
AMNHM1340	*Felis concolor*	16.0	5.6	0.35	male
AMNHM1328	*Felis concolor*	16.6	12.7	0.77	male
AMNHM1330	*Felis concolor*	16.7	11.9	0.71	male
AMNHM73221	*Felis concolor*	16.0	12.8	0.80	male
AMNHM92205	*Felis concolor*	14.2	9.5	0.67	male
AMNHM136293	*Felis concolor*	15.6	14.0	0.90	male
AMNHM239786	*Lynx canadensis*	13.0	6.6	0.51	female
AMNHM239787	*Lynx canadensis*	12.3	5.6	0.46	female
AMNHM239825	*Lynx canadensis*	12.4	5.6	0.45	female
AMNHM36992851	*Lynx canadensis*	11.7	8.0	0.68	female
AMNHM239813	*Lynx canadensis*	12.5	4.4	0.35	female
AMNHM239799	*Lynx canadensis*	10.8	7.5	0.70	female
AMNHM239785	*Lynx canadensis*	12.0	8.1	0.68	female
AMNHM239793	*Lynx canadensis*	13.1	6.5	0.50	female
AMNHM239825	*Lynx canadensis*	12.6	5.3	0.42	female
AMNHM239827	*Lynx canadensis*	12.6	6.6	0.52	female
AMNHM239795	*Lynx canadensis*	13.2	7.1	0.54	male
AMNHM239817	*Lynx canadensis*	12.3	8.1	0.66	male
AMNHM239821	*Lynx canadensis*	12.9	9.4	0.73	male
AMNHM36982850	*Lynx canadensis*	12.7	8.5	0.67	male
AMNHM56364605	*Lynx canadensis*	12.5	9.2	0.73	male
AMNHM239810	*Lynx canadensis*	12.8	5.1	0.40	male
AMNHM239784	*Lynx canadensis*	11.2	8.1	0.73	male
AMNHM239789	*Lynx canadensis*	11.6	8.5	0.73	male
AMNHM239798	*Lynx canadensis*	12.6	7.6	0.60	male
AMNHM239817	*Lynx canadensis*	12.2	8.0	0.66	male
AMNHM239833	*Lynx canadensis*	12.7	8.1	0.64	male
AMNHM174464	*Lynx rufus*	11.1	8.2	0.74	female
AMNHM13452503	*Lynx rufus*	11.4	6.3	0.55	female
AMNHM144936	*Lynx rufus*	10.6	5.7	0.54	female
AMNHM137376	*Lynx rufus*	9.5	8.7	0.91	female
AMNHM19621	*Lynx rufus*	9.9	5.3	0.54	female
AMNHM185737	*Lynx rufus*	9.8	6.4	0.65	female
AMNHM15676	*Lynx rufus*	10.8	7.6	0.70	female
AMNHM243459	*Lynx rufus*	10.7	7.6	0.71	female
AMNHM17462	*Lynx rufus*	10.0	8.8	0.87	male
AMNHM17463	*Lynx rufus*	10.3	7.8	0.75	male
AMNHM17465	*Lynx rufus*	9.9	8.3	0.84	male
AMNHM1341	*Lynx rufus*	12.2	8	0.66	male
AMNH-1347	*Lynx rufus*	10.7	10.2	0.95	male
AMNHM1344	*Lynx rufus*	11.7	9.4	0.80	male
AMNHM188957	*Lynx rufus*	11.6	5.6	0.48	male
AMNHM1607	*Lynx rufus*	11.6	8	0.69	male

APPENDIX 2
(Continued)

ID no.	Taxon	m1 L	c-p3	c-p3 index[a]	Sex
AMNHM54996	*Panthera leo*	21.8	30.1	1.39	female
AMNHM85147	*Panthera leo*	22.6	23.9	1.06	female
AMNHM85145	*Panthera leo*	22.6	24.7	1.09	female
AMNHM83618	*Panthera leo*	23	25.3	1.10	female
AMNHM30243	*Panthera leo*	24.7	23.8	0.96	female
AMNHM52075	*Panthera leo*	22.9	25.6	1.12	female
AMNHM81840	*Panthera leo*	24.4	21.8	0.89	female
AMNHM81839	*Panthera leo*	23.9	25.1	1.05	female
AMNHM70171	*Panthera leo*	22.7	26.1	1.15	female
AMNHM54995	*Panthera leo*	23.5	36.3	1.55	male
AMNHM85142	*Panthera leo*	27.4	26.4	0.97	male
AMNHM85144	*Panthera leo*	25.8	29.2	1.13	male
AMNHM83620	*Panthera leo*	25.8	23.5	0.91	male
AMNHM30248	*Panthera leo*	25.3	29.9	1.18	male
AMNHM52082	*Panthera leo*	25.7	31.4	1.22	male
AMNHM52072	*Panthera leo*	29.2	29.8	1.02	male
AMNHM81837	*Panthera leo*	27.9	24.1	0.86	male
AMNHM28151	*Panthera leo*	28.3	26.8	0.95	male

[a]For explanation of c-p3 index, see page 44.