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A Partial Skeleton of *Pseudaelurus* (Carnivora: Felidae) from the Nambé Member of the Tesuque Formation, Española Basin, New Mexico

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ABSTRACT

I describe a partial felid skeleton of *Pseudaelurus validus*, new species, from the early Miocene, late Hemingfordian of New Mexico. This is the earliest known felid from North America having cranial, upper, and lower dentition as well as postcranial information. A nearly complete set of limb bones provides the first insight into the morphometry of this lynx to puma-sized cat. The skull, similar to that of the earlier European *Proailurus lemanensis*, displays a high and thin sagittal crest with prominent nuchal crests. In the auditory region, the tympanic bulla architecture resembles that of *Proailurus* and relates to modern felids. The skeleton includes an articulated manus and pes with an apparently functional first metatarsal bone, hitherto unknown in the genus *Pseudaelurus*. Log-ratio diagrams are used to compare this skeleton with various extinct and modern felids. Dental morphology, as well as the new postcranial information revealed by this skeleton, is contrasted with that of other felids.

INTRODUCTION

Pseudaelurus is a felid taxon that has been reported from the early Miocene of Europe, Asia, and North America. Most of the specimens described in the literature consist of mandibular and maxillary fragments. Postcrania, largely from Europe, are uncommon and consist for the most part of isolated elements. Only three skulls of *Pseudaelurus* have been mentioned in the literature; all are from North America, and none have been associated with postcranial material.

The relationship of modern cats to extinct Felidae has been under study since the work of Cope (1880). A common ancestry of the late Oligocene *Proailurus lemanensis*, the Miocene *Pseudaelurus*, and living felids has

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been suspected since before the turn of the last century (Adams, 1897). Although a small amount of cranial and postcranial material has been described of the earliest genus *Proailurus* (Filhol, 1888; Helbing, 1928), the postcrania of *Pseudaelurus* have been largely unknown. Considerable cranial and postcranial material for *Felis* is found throughout the fossil record from its earliest appearance in the late Miocene of Europe (de Beaumont, 1961b) and Asia (Heintz, 1981; Qi, 1985) (fig. 1). Information on the postcrania of *Pseudaelurus,* linked to a skull, is therefore needed to further the understanding of the relationships among these three felid genera.

ABBREVIATIONS

Anatomical

a-p	anterior to posterior
c	lower canine tooth
C	upper canine tooth
d-v	dorsal to ventral
i1	lower first incisor
I3	upper third incisor
m1	lower first molar
mm	millimeter
Mc1	first metacarpal bone
Mt1	first metatarsal bone
M1	upper first molar
p1	lower first premolar
ph1	first phalanx
P3	upper third premolar

Institutional

AMNH	American Museum of Natural History, New York
F:AM	Frick Collection, American Museum of Natural History
MHNL	Muséum Guimet d'Histoire Naturelle, Lyon
USNM	United States Natural History Museum, Washington, DC

HISTORY OF THE GENUS *PSEUDAELURUS*

In 1843, H. M. Ducrotay de Blainville described a maxillary fragment and a lower jaw fragment of a ‘‘highly specialized machairodont’’ from the medial Miocene of Sansan, France. The ramus contained three lower premolars (p2, p3, p4), whereas modern cats normally have only two (p3, p4). He gave this specimen the name *Felis quadridentata.* In 1850, Paul Gervais established the genus *Pseudaelurus* for the Blainville specimen. He distinguished it from the genus *Felis* by a single character: ‘‘possessing an additional inferior premolar (p2) in advance of the others’’. This was the first recognition of an ancestral state, or plesiomorphic anatomical condition of a fossil specimen, with respect to extant members of Felidae.

In North America, Joseph Leidy (1858) described another new species of Miocene cat, *Felis intrepidus,* from ‘‘the loose sands of the Niobrara River’’ in western Nebraska. This fossil also possessed evidence of the lower second premolar, but Leidy apparently did not immediately recognize the generic value of this character. By the time he had published a drawing of the left ramus (Leidy, 1869) however, he had designated it as *Pseudaelurus intrepidus.* He explained the significance of the additional tooth: ‘‘In both rami the premolar (p2), 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).

Filhol (1879) proposed a new genus, *Proailurus,* to accommodate specimens from the early Miocene (Aquitanian) of France with characters more plesiomorphic and fossils stratigraphically older than those already assigned to *Pseudaelurus. Proailurus lemanensis* mandibles, dating back to the late Oligocene Quercy fissures of France, possessed four lower premolars where *Pseudaelurus* had three. When E.D. Cope (1880) published his treatise: ‘‘On the Extinct Cats of North America’’, he clearly suggested that *Proailurus* and *Pseudaelurus* were ancestral felids.

Pseudaelurus specimens first appear in the early Miocene (MN3) of Europe (Dehm, 1950). The specimens are numerous in comparison to *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: (1) *Pseudaelurus quadridentatus* Blainville, 1843; (2) *Pseudaelurus turnauensis* Hoernes, 1882; (3) *Pseudaelurus lorteti* Gaillard, 1899; and (4) *Pseudaelurus romieviensis* Roman-Viret, 1934.

Charles Depéret (1892) described a small specimen, *Pseudaelurus transitorius* from the La Grive-Saint-Alban (Isere) locale of France. This species was placed in

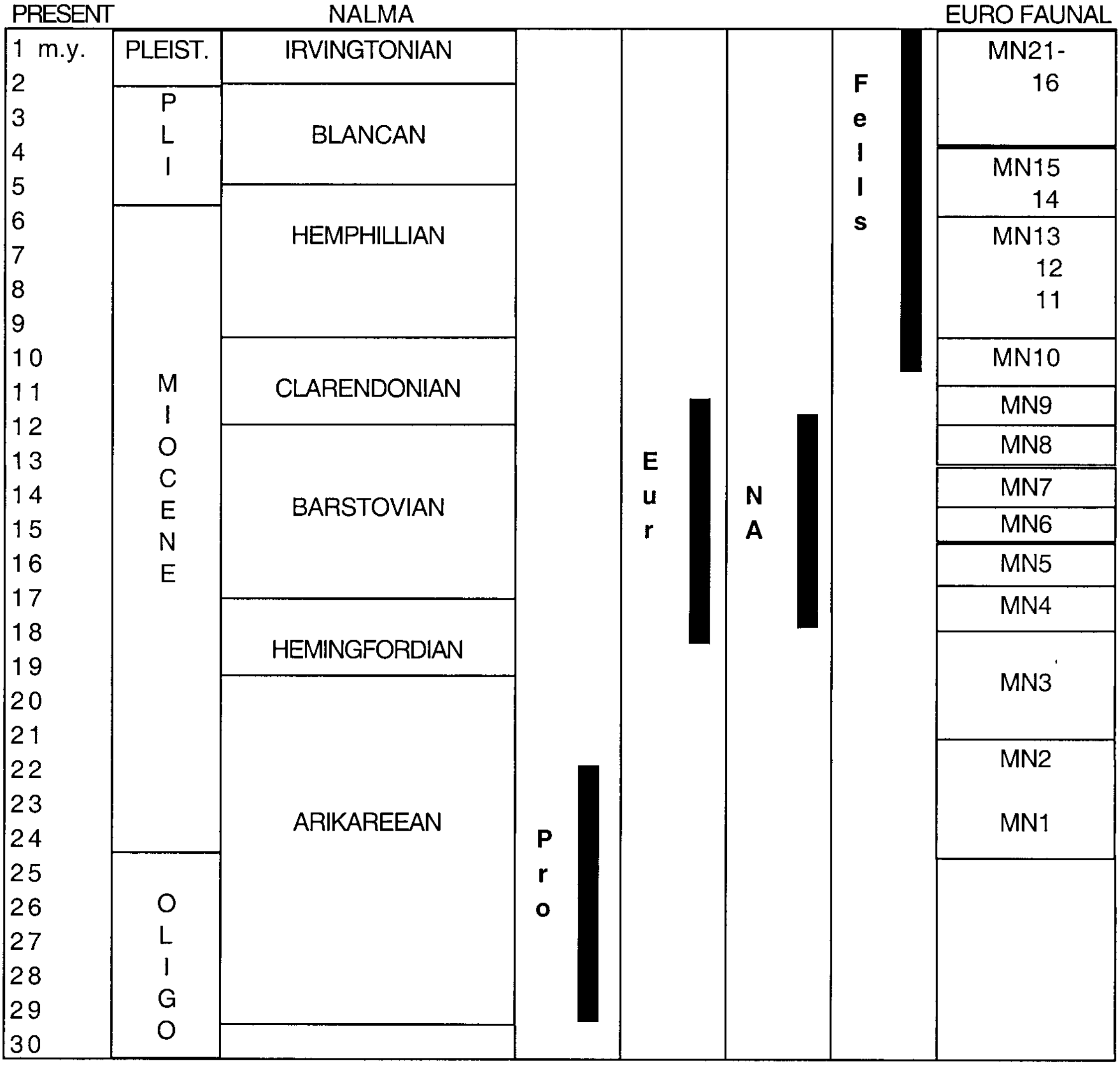

Fig. 1. Stratigraphic ranges for *Proailurus* spp. (Pro), *Pseudaelurus* spp. in Europe (Eur), *Pseudaelurus* spp. in North America (NA) and *Felis* (Felis). There appears to be no overlap in the fossil record among these three genera of Felidae. *Proailurus* is not found after MN2b. European *Pseudaelurus* range is that of the smallest species, *P. turnauensis*: MN3 to MN9. Correlation references: McKenna and Bell (1997), MacFadden and Hunt (1998).

synonymy with *P. turnauensis* Hoernes by G. de Beaumont (1961). The synonymization was confirmed by Heizmann (1973) and Wang (1998), but ignored by Ginsburg (1983). All four species was originally described based on mandibular and maxillary fragments. There have been no European skulls yet described. The first postcranial bone was described in 1899: a right humerus of *P. transitorius* (= *P. turnauensis*) from the medial Miocene La Grive-Saint-Alban locality in France (Gaillard, 1899). G. de Beaumont (1961) described 19 separate postcranial bones from La Grive-Saint-Alban and the early Miocene Wintershof-West localities, but none was alleged to be from the same individual. L. Ginsburg (1961b) reported an even larger assortment of isolated mandibular, maxillary and postcranial material from the medial Miocene of Sansan in France, again without a skull.

Richard Dehm (1950), in his seminal report on the carnivores from Wintershof-West in Germany, described 18 lower jaws and 1 maxillary specimen. These are early Miocene specimens of Burdigalian (MN3) age. Dehm assigned them to *P. transitorius* Depéret (= *P. turnauensis* Hoernes). Dehm described these specimens as elements from a transitional species between *Proailurus* and the more derived specimens of *Pseudaelurus* reported from La Grive-Saint-Alban in France. What Dehm considered most interesting in this collection was the variable key lower jaw characters: (1) presence or absence of p1; (2) presence or absence of p2; (3) one or two roots of p2; (4) presence or absence of m2; (5) presence or absence of m1 metaconid; (6) length of m1.

Elmar Heizmann (1973) published a review of the European *Pseudaelurus* radiation and recognized four species in order of increasing size: (1) *Pseudaelurus turnauensis* Hoernes; (2) *Pseudaelurus lorteti* Gaillard; (3) *Pseudaelurus romieviensis* Roman and Viret; (4) *Pseudaelurus quadridentatus* Blainville. He suggested that *Pseudaelurus* evolved from *Proailurus* with the following character changes: (1) loss of p1; (2) loss of m2; (3) reduction of p2 to one root; (4) lengthening of canines; (5) reductions in height of lower premolars such that p3 and p4 became similar in height; (6) reduction of m1 protoconid height; (7) movement of m1 metaconid from a position on the posterior surface of the protoconid, lingual of median, to a median position; (8) reduction of m1 talonid.

In North America, three species have been described from the medial Miocene. Again, all species determinations were based on mandibular and maxillary fragments. *Pseudaelurus intrepidus* Leidy, 1858, and *Pseudaelurus marshi* Thorpe, 1922, are both late Barstovian specimens from the Valentine Formation in western Nebraska. *Pseudaelurus aeluroides* Macdonald, 1954, is from the early Barstovian Olcott Formation in Sioux County, Nebraska. J. R. Macdonald (1948a, 1948b) described two large Clarendonian *Pseudaelurus* species that have enlarged mental ridges on the ventral margins of the mandibles: *Pseudaelurus pedionomus* from the Minnechaduza Fauna of Nebraska and *Pseudaelurus thinobates* from the Black Hawk Ranch Local Fauna of California. David Kitts (1958) erected a new genus, *Nimravides*, for this material and made *Pseudaelurus thinobates* its type species.

Some North American cranial material has been described. Chester Stock (1934) described the first *Pseudaelurus* skull in a report on five individuals from the early Barstovian Tonopah, Nevada locality. He assigned all to *P. intrepidus* Leidy. MacDonald (1948a) described seven assorted postcranial bones referenced to *P. pedionomus*, but material referred to this species has subsequently been shifted into the genus *Nimravides* (de Beaumont, 1990). Shotwell and Russel (1963) also described some assorted postcranial fragments of *Pseudaelurus*, which they thought ‘‘apparently represent a single individual’’, but no species determination was made.

In Asia, three species of *Pseudaelurus* have been reported. All are described from mandibular, maxillary, or dental material: *Pseudaelurus guangheensis* Cao, Du, Zhao, and Cheng, 1990, is a new species from the medial Miocene Guanghe District of Gansu, China. *Pseudaelurus cuspidatus* Wang, 1998, is a new species from the early medial Miocene Halamagai Formation in northern Junggar Basin, in the Xinjiang Autonomous Region, China. *P. lorteti* left ramus and dental fragments were reported from the medial Miocene of Xiacaowan, Sihong County in Jiangsu Province, China (Qiu and Gu, 1986).

From Africa, an m1 and tibia fragment from the Al-Sarrar locality in what is now Saudi Arabia were assigned to *P. turnauensis* (Thomas et al., 1982). This formation is early Miocene (MN4a) in age. There are no other reports of any nonmachairodont members of Felidae from the African Miocene.

The Nambé skeleton (F:AM 62128) described in this paper was collected in 1939 by J. C. Blick of the Frick Laboratory. The specimen was recovered from the late Hemingfordian Nambé Member locality (Galusha and Blick, 1971) in the Tesuque Formation, Española Basin, near East Cuyamunque, New Mexico.

SYSTEMATIC PALEONTOLOGY

ORDER CARNIVORA BOWDICH, 1821

SUBORDER FELIFORMIA KRETZOI, 1945

FAMILY FELIDAE FISCHER DE WALDHEIM, 1817

Genus *Pseudaelurus* Gervais, 1850

DISTRIBUTION: Early to medial (MN3 to MN9) Miocene of Europe; early to medial (late Hemingfordian to late Barstovian) Miocene of North America; early medial Miocene of Asia; early (MN4a) Miocene of Africa.

GENERIC DIAGNOSIS: Members of Felidae with the unique combination of the following derived and primitive characters: presence of p2 with the usual absence of p1 and m2, m1 with reduced metaconid and talonid, P2 with one root, alisphenoid canal present, paroccipital process cupped about the posterior surface of an enlarged caudal entotympanic. Differing from extant felid genera by c cross section showing flattened inner surface and posterior trenchant edge, presence of p2, m1 with variable metaconid and reduced talonid, presence of alisphenoid canal. Differing from *Metailurus* by presence of alisphenoid canal and p2, absence of enlargement of mental ridge. Differing from *Nimravides* by smaller size and absence of any ventral mandibular mental ridge enlargement. Differing from *Proailurus* by absence of p1 and m2.

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

INCLUDED SPECIES: *Pseudaelurus intrepidus* Leidy, 1858; *Pseudaelurus turnauensis* Hoernes, 1882; *Pseudaelurus lorteti* Gaillard, 1899; *Pseudaelurus marshi* Thorpe, 1922; *Pseudaelurus romieviensis* Roman-Viret, 1934; *Pseudaelurus aeluroides* Macdonald, 1954; *Pseudaelurus guangheensis* Cao, Du, Zhao, and Cheng, 1990; *Pseudaelurus cuspidatus* Wang, 1998.

Pseudaelurus validus, new species

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.

TYPE LOCALITY: Nambé Member, Tesuque Formation, Española Basin near East Cuyamunque, New Mexico.

AGE: Late Hemingfordian (Galusha and Blick, 1971).

ETYMOLOGY: *validus,* Latin for strong, robust, able.

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 tibia 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: Differing from other species 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, and can be differentiated from these species by the longer c-p3 distance in *P. validus*, which exceeds the length of its m1, and by its large, erect, and rectangular coronoid process.

DESCRIPTION AND COMPARISON

SKULL

The skull (figs. 2a, 2b) has been crushed, giving it a low and wide appearance. This compromises the integrity of some skull measurements, especially those of height and width. However, the upper dentition survived, and can be associated with the lower teeth for only the second time in this genus. The premaxillary bones possess a pair of fragmented I3, the I1–2 having been lost. A short and smooth diastema separates I3 from C. The left C is separated from the skull, revealing a large, cavernous alveolus. The right C root is in situ; however its crown is fractured and missing. These two C are more elliptical than round in cross-section and lack any longitudinal grooves. Posterior to the alveolus for the left C are a preserved P1 and an alveolus for P2, both single-rooted. This agrees with the presence of these teeth in the skull described by Stock (1934) from Tonopah, although the presence of P1 was interpreted by Stock as being ‘‘a rather unusual feature’’.

The lengths of P3 and P4 in *P. validus* agree with the Tonopah skull but are smaller than the *P. quadridentatus* type. These two teeth are aligned parallel to the maxillary axis and do not exhibit any overlap, obliqueness, or crowding as seen in some extant species (Salles, 1992). The left P3 is wider and more robust when compared to P3 in the *P. lemanensis* type skull (MNHN1903–20). On the right P4 (fig. 2b) can be seen a prominent protocone that projects in an anterolingual direction. The morphology of P4 in F:AM 62128 resembles the P4 in the *P. quadridentatus* maxillary fragment from la Grive-Saint-Alban (Isère) (cast = AMNH 103396) described by Gaillard (1899). In the *P. lemanensis* type specimen, the protocone of P4 is at a slightly more obtuse angle to the lingual surface of P4. In modern felids, the protocone is closer to the lingual surface of the tooth, resulting in a narrower, compressed P4. The P4 of F:AM 62128 has a parastyle on the anterior surface which does not differ from the condition in *P. lemanensis*, other species of *Pseudaelurus*, or modern felids.

Both M1 are present with two roots. The M1 are compressed in the a-p direction, but are elongate transversely. Individual cusps can be seen on the left M1. The buccal end of this tooth is formed by the parastyle wing. The nearly conjoined paracone and metacone are midway along the occlusal surface. The lingual margin of M1 is formed by a distinct protocone. The parastyle of F:AM 626128 M1 is as tall as the caudal surface of the metastyle blade of P4 and appears to extend the carnassial blade. The left M1 of F:AM 62128 compares favorably with the M1 in the *P. lemanensis* skull (MNHN1903–20), but is in sharp contrast to the rudimentary M1 of modern cats.

The skull has a high, thin sagittal crest which is joined by equally large nuchal crests that unite at the occiput to form a protuberance that projects to a point caudal to the level of the occipital condyles. This area of the skull is very similar to the type skull of *P. lemanensis* (MNHN1903–20) from the early Miocene of France. The basicranial anatomy of F:AM 62128 is somewhat distorted, but much information endures (figs. 2b, 3). On the right side of the skull, much of the ossified bulla is lost, but the close approximation of the mastoid and paroccipital process to the bulla can be appreciated. The paroccipital process displays a concavity on its anterior surface where it cradled the posterior surface of the tympanic bulla in typical aeluroid fashion (Cope, 1880; Hunt, 1987, 1989, 1998; Werdelin, 1996; Wyss and Flynn, 1993). Medially, the ridge formed by the caudal entotympanic indenting the basioccipital bone can be seen (fig. 3). On the lateral margins of the right bulla, just proximal to the mastoid process, is the external acoustic meatus surrounded by most of the ectotympanic. This evidence of the anterolateral compartment of the bulla gives a strong signal as to the inflated size of the caudal entotympanic. This is further evi-

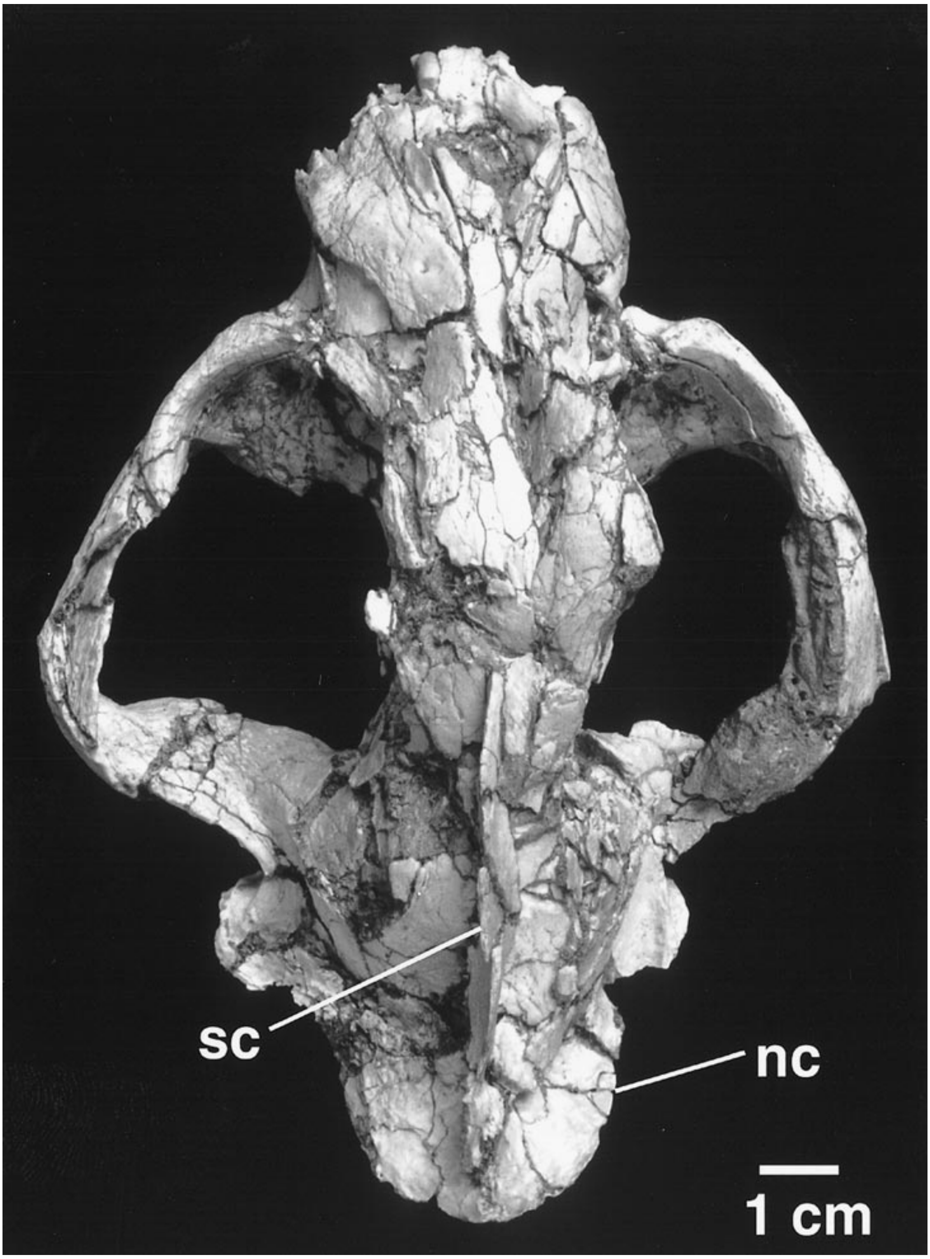

Fig. 2a. Dorsal view of F:AM 62128 skull. The morphology of the cranium resembles that of the *P. lemanensis* skull (MNHN S.G. 3509a) from Europe and the early North American Ginn Quarry skull (F:AM 61847) from Nebraska. sc = sagittal crest, nc = nuchal crest.

dence that this Nambé *Pseudaelurus* specimen possessed felid characters in the basicranial area (Hunt and Tedford, 1993).

The petrosal bone and its promontorial process are preserved in the tympanic bulla region on the left side (figs. 2b, 3). Although the petrosal has been nudged in a caudal direction by the crushing, facets for its articulation with the ectotympanic can be seen on its ventral surface. The grooving of the an-

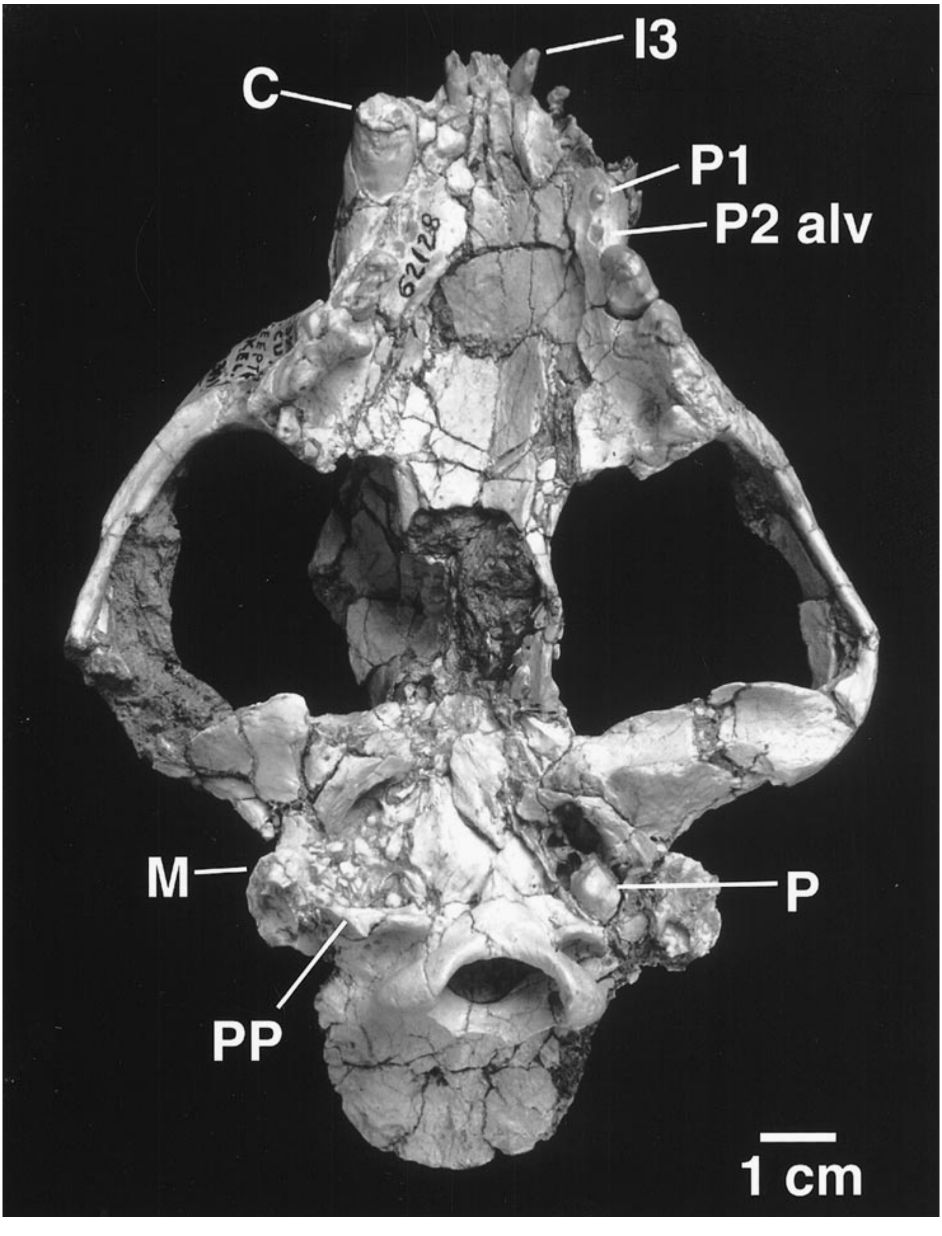

Fig. 2b. Ventral view of F:AM 62128 skull containing four upper premolars with P2 evidenced by a single-rooted alveolus. PP = paroccipital process, P = petrosal part of the temporal bone, M = mastoid bone.

terodorsal roof of the tympanic bulla, formed by the anterior invasion of the caudal entotympanic to the level of the squamosal bone, can also be seen. The hypoglossal foramina are visible bilaterally, within the depression where the posterior lacerate foramina would be.

LOWER JAW

The two rami of the lower jaw were cemented together during early, cursory preparation (fig. 4). The size of this jaw is smaller than Leidy's *P. intrepidus* type, and is more similar in size to *P. marshi* (table 1). How-

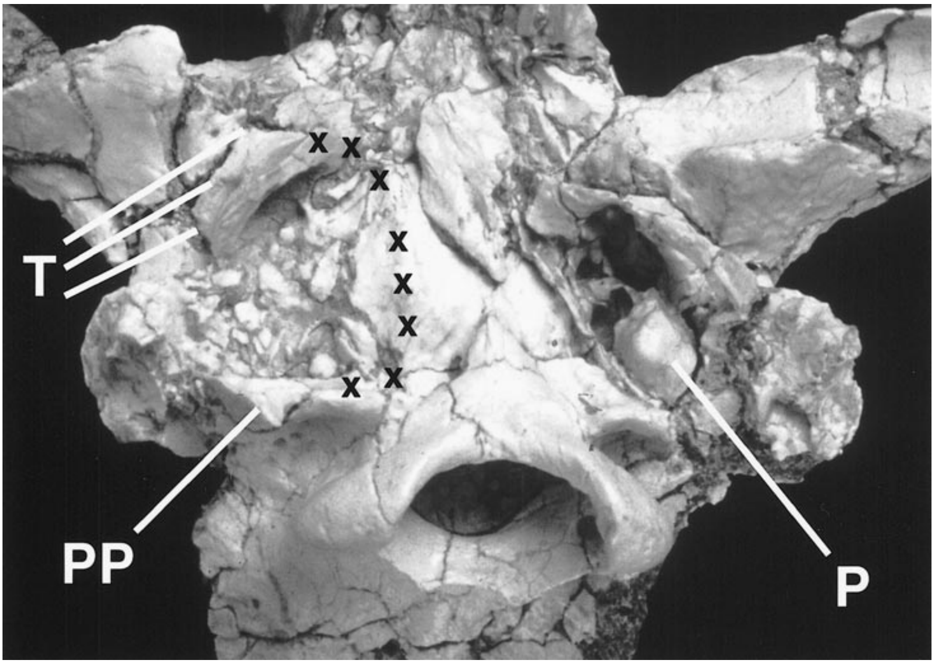

Fig. 3. Close view of basicranial area of skull. The x markers delineate the medial emargination of the basioccipital caused by an enlarged caudal entotympanic. Also seen: the concavity of the paroccipital process (PP) where it contacts the caudal surface of the expanded caudal entotympanic. T = ectotympanic, P = petrosal bone, PP = paroccipital process.

ever, it is obvious that this jaw was reconstructed from multiple fragments, thus compromising its measurements. The mandibles are not slender, as described in Thorpe's *P. marshi* specimen, but rather display considerable depth below the tooth row. The ventral surface of the lower jaw is slightly convex, but the area immediately below the tooth row is essentially straight. There is no ventral bulge in this location.

Both of the large lower canines are preserved. The inner surface of each is more flattened than the outer surfaces. Their crowns do not possess any grooves. In the space between c and p3 on both rami is an alveolus for p2, located not at the midpoint in the diastema as in Leidy's description (Leidy, 1869), but considerably closer to p3 (fig. 4). This single alveolus is also located medial of the line of the tooth row, a character first described by Thorpe (1922) in the *P. marshi* type specimen. This medial location of p2 is a consistent feature in the North American specimens, and can be seen in the *P. intrepidus* and *P. intrepidus sinclair*i types (Matthew, 1918; Thorpe, 1922). Although the number of roots of p2 varied in early European specimens (Dehm, 1950), I am unaware of any references, in North America, to a double-rooted p2.

The anterior mental foramina are located beneath the posterior portion of the c-p3 diastema, and are best seen on the left ramus of this jaw (fig. 4). The left posterior mental foramen is underneath the posterior root of the third lower premolar. This location agrees well with Stock's (1934) description of the Tonopah specimens that he assigned to *P. intrepidus* and is in slight contrast to the more anterior location in the *P. marshi* specimen (Thorpe, 1922). The coronoid process is wider and more erect than in the Leidy or Marsh types and is much taller than in *P. lemanensis.* There is no terminal ''hook'' in the coronoid process as is seen in modern felids. The deep masseteric fossa of F:AM 62128 extends anteriorly to a point just below the talonid of m1. The F:AM 62128 condyle has a mediolateral articular surface that is 20% longer than the Leidy type, and sits higher

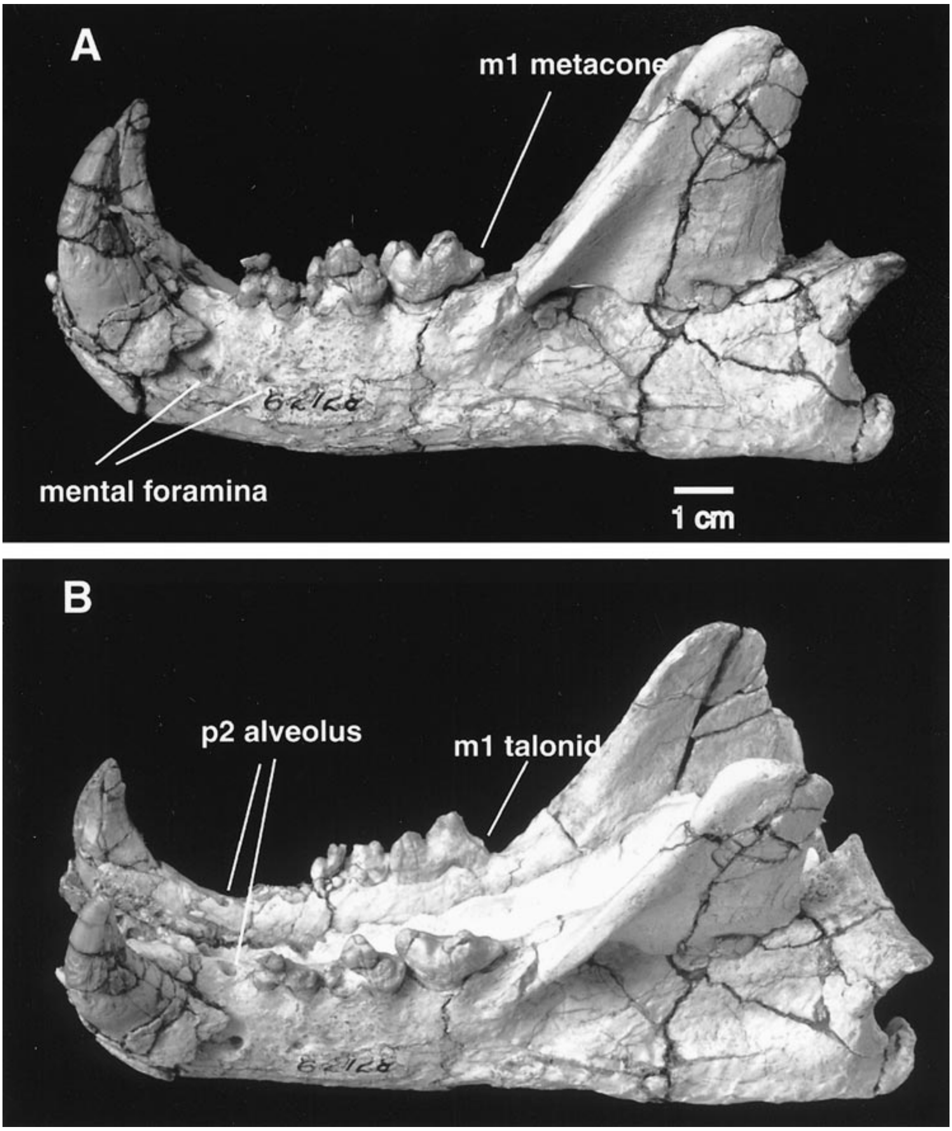

Fig. 4. Lateral **(A)** and oblique **(B)** views of lower jaw indicating dental characters of generic significance: presence of p2, lack of p1 and m2, and reduced metaconid and talonid on m1.

by an equal amount above the angular process.

The p3 and p4 are damaged by crushing. However, their size is recoverable (table 1). The posterior accessory cusps of the left p3 and both p4 can be seen on the posterior surface of the primary cusps. These posterior accessory cusps are separate from a well-defined posterior cingulum. This condition of a conspicuous posterior accessory cusp on p3 and p4 is present in specimens of *Proailurus lemanensis* and persists, with little change, in modern felids. The left m1 is well preserved and demonstrates a much-reduced metaconid that blends smoothly into an abridged talonid. The protoconid is taller than the paraconid and the carnassial notch is open and deep. This description of the carnassial would fit the diagnosis of any of the previously described large *Pseudaelurus* species

TABLE 1

Comparison of Lower Jaws of Five North American Type Specimens of *Pseudaelurus*

	P. validus[a]	*P. intrepidus* Leidy[b]	*P. marshi* Thorpe[c]	*P. intrepidus sinclairi*[d]	*P. aeluroides* MacDonald[e]
Length of m1	15.17	19.6	16.0	17.0	15.6
Length of p4	11.2	14.8	12.5	13.8	11.4
Length of p3	9.3	11.6	9.5	11.0	9.4
p3 to m1	38.0	44.5	36.0	40.3	35.5
Height of jaw at P4/m1	24.8	23.2	17.0	24.0	?
Width of jaw at P4/m1	9.6	?	9.0	13.3	9.5
c-p3 diastema	14.6	14.8	8.6	16.0	7.3
Diastema index	0.96	0.76	0.5	0.94	0.47
Jaw length, condyle to incisor	120.0	122.7	97.0	?	?

[a] F:AM 62128.
[b] USNM 124.
[c] YPM 12865.
[d] AMNH 17212.
[e] SDSM 3238.

of North America: *P. intrepidus*, *P. marshi*, or Matthew's *sinclairi* variety of *P. intrepidus*.

Because of the predominance of lower jaw material in the fossil felid literature, this portion of the skeleton must be given special consideration with respect to diagnosis and species referrals. Most species within the genus *Pseudaelurus* are represented only by lower jaws. A recent study utilizing bivariate analysis (Glass and Martin, 1978) concluded that mandibular dentition is useful in differentiating extant felid species. However, to rely on lower jaw material for purposes of specific diagnosis is at present problematic. In table 1 and in the log-ratio diagram (Simpson, 1941) of figure 5, the lower jaw of the Nambé skeleton is compared with four North American type specimens.

HUMERUS

In the first description of a postcranial *Pseudaelurus* specimen, Claude Gaillard (1899) compared a *P. turnauensis* right humerus from La Grive-Saint-Alban with that of a domestic cat (*Felis catus*) and of a lynx (*Lynx lynx*). The *Pseudaelurus* humeri from the Nambé Member are 50% larger than the specimen from France. The shaft of the F: AM 6128 right humerus (fig. 6) is thinner when viewed from the anterior or posterior perspective. Its lateral and medial surfaces appear broad and flat. The proximal end of each humerus consists of a convex arthral surface that is visible only from the posterior view. This articular surface blends into a deep bicipital groove between greater and lesser tubercles of equal height. The greater tubercle continues down the anterior surface of the shaft of the humerus as a sharp, but low, deltoid ridge, very typical of a cursorial carnivore (Ginsburg, 1961a; Wang, 1993). In the dog, this ridge is more exaggerated, and is better termed the deltoid tuberosity. In the domestic cat, this deltoid ridge blends into the humeral shaft by midpoint. In this specimen, however, the deltoid ridge extends well into the distal half of the humerus. This agrees with Ginsburg's description of this character in the *P. quadridentatus* humerus from Sansan. On the lateral surface of the proximal end of the right humerus, the pectoral ridge extends down from the posterior surface of the greater tubercle (fig. 6).

Modern felid humeri are most cylindrical just distal to the midpoint of the diaphysis, and this is true of F:AM 62128. From this midpoint in the humeral diaphysis, the supracondyloid ridge extends down the lateral margin of the shaft to the point of the lateral epicondyle. This feature is large in this specimen, forming a shelf that curls in the ante-

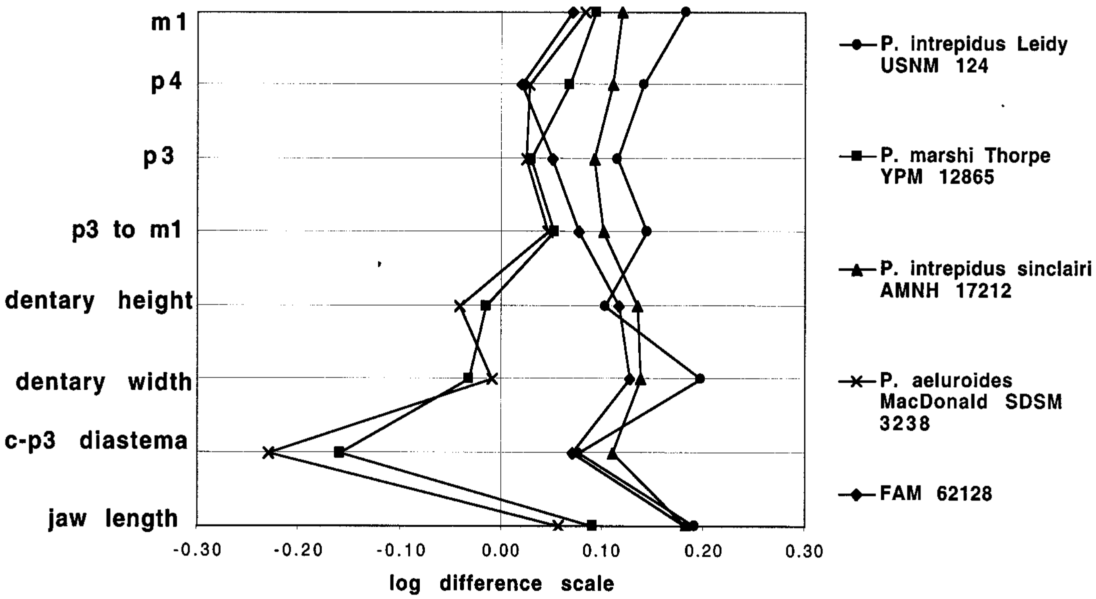

Fig. 5. Log-ratio diagram of lower jaw characters and measurements featured in table 1. The standard specimen on the y axis is *P. lemanensis,* an early Miocene felid from Europe. The five *Pseudaelurus* specimens fall into two categories of jaw types based on size of jaw and the c-p3 diastema character. The two *P. intrepidus* species and F:AM 62128 have larger jaws than *Proailurus,* but still have a relatively shortened c-p3 diastema when compared to their European relative. The other two *Pseudaelurus* species (*P. marshi, P. aeluroides*) have a greater reduced c-p3 diastema in comparison to *Proailurus.*

rior direction. This shelf forms a ridge with a cupped appearance when viewed from the anterior perspective. Forming the medial edge of this distal end of the bone is the medial condyloid ridge. The supracondlyoid foramen is located here. This oval shaped foramen, which carries the brachial artery and the median nerve in Felidae, is somewhat smaller in this specimen when compared to similar sized modern specimens. This is due to the crushing. In other, better preserved *Pseudaelurus* sp. humeri specimens in the Frick-AMNH collection, these foramina agree in size and shape with modern specimens such as *Panthera pardus* or *Felis concolor.*

The distal end of the *P. validus* humeri, while extremely similar to modern felids, possesses certain characters that resemble the humerus of *Proailurus.* Differing in the proportions of the medial epicondyle, depth of olecranon fossa, and the distally projecting medial margin of the trochlea, the *Pseudaelurus* humerus maintains a position intermediate between *Proailurus* and modern felids. The two *P. validus* humeri possess large, bulbous, and convoluted medial epicondyles, deep olecranon fossae, and robust medial margins of the trochleae. This morphology agrees well with Ginsburg's (1961b) description of *Pseudaelurus quadridentatus,* which he stated was closer morphologically to *Proailurus* than to modern felids. The large and rough-surfaced medial epicondyles, typical of animals that climb (or dig) (Taylor, 1976; Heinrich and Rose, 1997) are in contrast to the smaller and smoother epicondyles in modern felids. This combination of enlarged medial epicondyle and deep olecranon fossa suggests that this species was a reasonably cursorial cat (Wang, 1993). The capitulum on the humeral trochlea is convex and faces primarily in an anterior direction. Medially, the arthral surface becomes concave and terminates in a distally projecting, robust trochlea. Just proximal to these structures, on the anterior surface is the radial fossa adja-

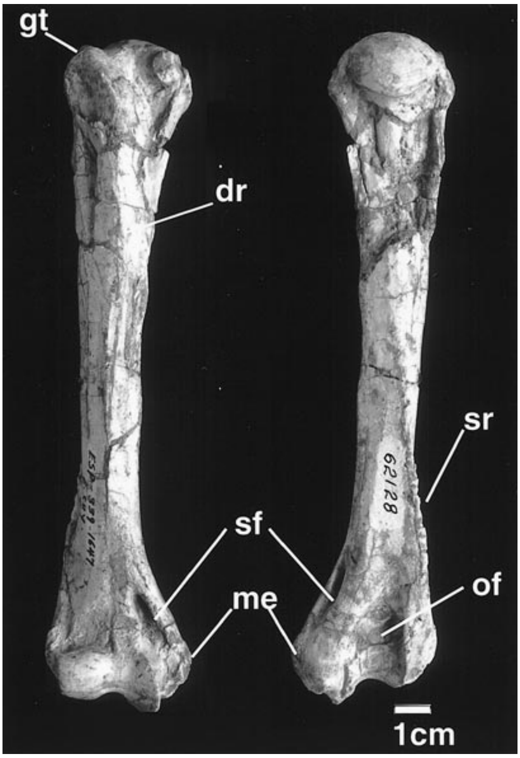

Fig. 6. Right humerus: dorsal view (left) and ventral view (right). The deltoid ridge (dr) can be seen extending beyond midpoint into the distal half of the diaphysis. gt = greater tubercle, sf = supracondyloid foramen, sr = supracondyloid ridge, of = olecranon fossa, me = medial epicondyle.

Fig. 7. A Medial view of right ulna, B: dorsal view of right radius.

cent to the more lateral and slightly smaller ulnar fossa.

RADIUS

The right radius (fig. 7) has a proximal surface that is oval in shape. The bone immediately narrows into a brief neck area just prior to the bicipital tuberosity that lies on the posteromedial surface. The shaft is roughly cylindrical and is convex in the lateral and cranial direction. All of these characters agree with modern Felidae. The radius increases in diameter distally. Unless this is due to crushing, it agrees with the description of *Proailurus* (Ginsburg, 1961b), and may establish a plesiomorphic character state for felid radii.

ULNA

The right and left ulnae of F:AM 62128 are complete. The right (fig. 7) was selected for description. There is considerable width or surface area of the trochlear notch, more so than in extant felids. This joint surface is interrupted only by the laterally excavated radial notch that accepts the head of the radius. This laterally positioned radial notch has been shown to be a consistent character within modern felids (Gonyea, 1978), contrasting with the more cranially located notch in canids and hyaenids. This ulna has a maximum width just below the olecranon fossa and tapers towards its distal termination as the styloid process. Below the olecranon, in the next one-third of the diaphysis, the shaft changes from the two-sided olecranon to a three-surfaced bone. In the final one-third of this bone, the shaft tapers and loses a sense of surfaces.

CARPUS

The F:AM 62128 scapholunar proximal surface consists of a dome-shaped convexity for articulation with the distal radius. Its distal surface is extremely complicated, containing facets for articulation with all components of the next row of carpal bones. Most anterior and medial is the facet for articulation with the trapezoid. Moving posteriorly and laterally, there are facets for the trapezium and the magnum, and, on the posteriormost margin of this carpal bone there is the surface for articulation with the unciform. This complicated articulation can be seen in a photograph of a European specimen assigned to *P. lorteti* (de Beaumont, 1961b, plate 2, #7), and agrees well with modern felids.

The lateral member of the proximal row of carpal bones is the cuneiform. Its lateral surface consists of two equal-sized concave facets for articulation with the ulna and the pisiform. This ulnar articulation is often lacking in modern felids (Merriam and Stock, 1932), but can be clearly seen in this specimen. The pisiform of F:AM 62128 contains a deeper groove on its proximal end than is seen in extant felids, but agrees in this respect with illustrations of *Felis atrox* and *Smilodon californicus* (Merriam and Stock, 1932). Otherwise, the cuneiform and the pisiform do not differ from these same elements in modern felids.

In the distal row of carpal bones, most medial, is the trapezium articulating with Mc1. Lateral to the trapezium and articulating with Mc2 is the trapezoid. It is clear that both articulate with the scapholunar proximally, and therefore distribute load to and from the radius. Completing the distal row of carpal bones, the magnum and unciform articulate with the proximal ends of metacarpals 3, 4 and 5.

METACARPUS

The compressed and compact appearance of the articulated metacarpals (fig. 8) coordinates with the hind foot's digitigrade appearance. All five metacarpal bones are present. In this early Miocene specimen, we see metacarpal proportions like those of the living felids: The length decreases from the third to the fifth and the second is shorter than the fourth. The proximal ends of these metacarpals articulate together and with the distal row of carpal bones in a unique and characteristic manner that can be traced through the fossil record into today's modern Felidae (Helbing, 1928; Merriam and Stock, 1932; Ginsburg, 1961a; Wang, 1993).

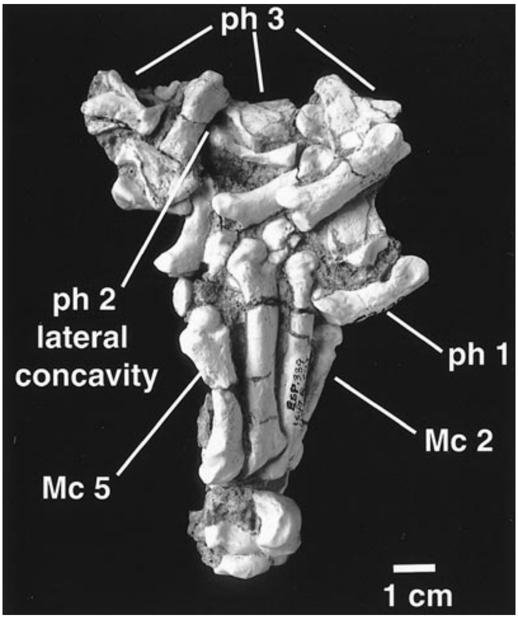

Fig. 8. Articulated left manus: third phalanges (ph3), lateral concavity in the second phalanges (ph2) for retractile claws.

The first *Pseudaelurus* Mc1 reported in the literature was from Sansan, France assigned to *P. quadridentatus* (Ginsburg, 1961b). The F:AM 62128 Mc1 is nearly identical in shape to the drawing on page 143 of that paper. A second *P. quadridentatus* Mc1, from Los Valles in Spain (Ginsburg et al., 1981), was neither described nor drawn. Both the Nambé Mc1 and the Sansan Mc1 have the morphology of a vestigial metacarpal bone. The distal end of the F:AM 62128 Mc1 has an oblique, medially directed axis with respect to the other four metacarpals (fig. 9). The lateral condyle extends considerably further distally than the

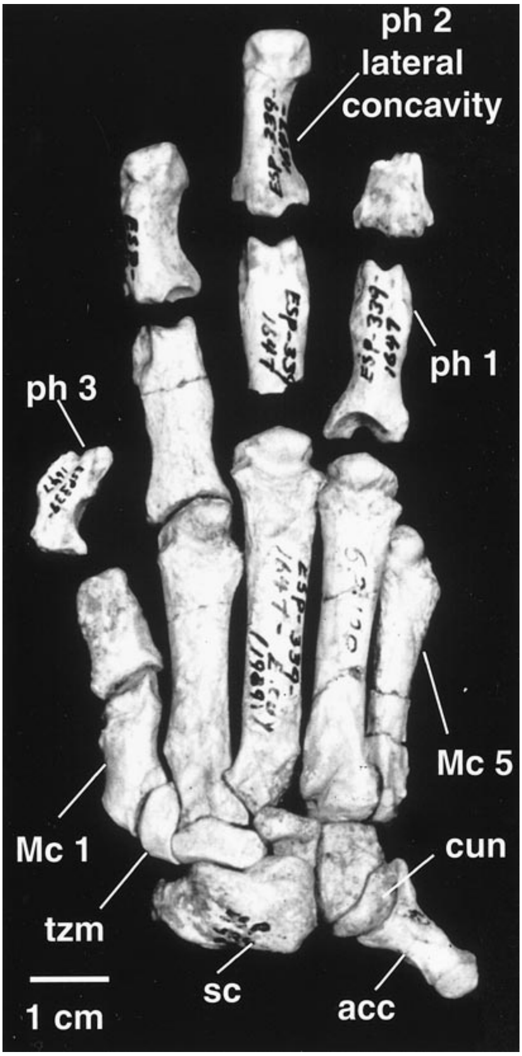

Fig. 9. Disarticulated and prepared right manus. The vestigial state of Mc1 is almost identical to that seen in modern members of Felidae. sc = scapholunar carpal bone, acc = accessory, cun = cuneiform, tzm = trapezium. Greatest length measurements of metacarpal bones: first Mc, 20.9 mm; second Mc, 41.0 mm; third Mc, 49.5 mm; fourth Mc, 47.0 mm; fifth Mc, 38.1 mm.

medial does. This distorts the distal articular surface, allowing the first phalanx of this digit to articulate in a medial direction. The bone has a blunt and rectangular shape, having lost the length of the other four metacarpals. This shared derived character of vestigial Mc1 persists in all extant Felidae. There is only one accurate reference to a Mc1 in the *Proailurus* literature (Helbing, 1928). In this paper, Helbing illustrated a Mc1 labeled *Proailurus sp.* that is in the primitive, unreduced state. The *Proailurus* Mc1, unlike those in the *Pseudaelurus* specimens, resembles the other four metacarpals. It has a slender, axial diaphysis and a distal articular surface that is parallel to the ground.

The remaining metacarpals, 2 through 5, are robust precursors of their counterparts in modern Felidae (figs. 8, 9). Articulated metacarpals 2, 3, and 4, assigned to the large European species *P. quadridentatus,* were described and illustrated by Ginsburg (1961b). Their proximal articular surfaces are identical to those of the Nambé specimen. F:AM 62128 metacarpals 1, 2, 3 and 5 are accompanied by first phalanges in the prepared right manus (fig. 9). Only two of the second phalanges and one of the third phalanges are present in this front foot. The articulated left manus (fig. 8) contains a more complete set of phalanges. Clearly evident in both mani are lateral concavities in the second phalanges necessary for a retraction and protraction claw mechanism (Bryant et al., 1996). The degree of concavity in the F:AM 62128 second phalanges is not distinguishable from modern felids.

FEMUR AND PATELLA

Only the distal 39 mm of the left femur and the patella has survived. Although slightly distorted by crushing, the internal condyle can be identified by its greater length. The condyles' articular surfaces fuse anteriorly to form the concave patellar groove. This patellar groove is constrained by heightened edges with distinct margins. The maximum width of the patella occurs just below the upper margin of this sesamoid bone. It is shaped like a teardrop, ending in a blunt distal end. Its dorsal surface is smooth and uniformly convex. However, the ventral surface, which articulates with the femur, consists of a pair of equal-sized concave surfaces that register with the corresponding femoral condyles.

TIBIA

The intact left tibia (fig. 10) strongly resembles a modern felid tibia. In the only pri-

Fig. 10. Left tibia, a-p view.

or North American description of *Pseudaelurus* postcranial material, Shotwell and Russell (1963) mentioned ‘‘tibia and vertebrae fragments’’, but did not describe or illustrate these bones. G. de Beaumont (1961) described tibial material assigned to *P. turnauensis,* and L. Ginsburg (1961b) described a distal tibial fragment assigned to the larger *P. quadridentatus.* Of the distal fragment assigned to the *P. quadridentatus* specimen from Sansan, Ginsburg stated it ‘‘differs not from the size or shape of *Felis.*’’

The tibia is the longest bone in the domestic cat, *F. catus* (Mivart, 1881), but it is exceeded in length by the femur in the *Panthera* radiation. Both the *Proailurus* skeleton (Filhol, 1888) and F:AM 62144, a partial *Pseudaelurus* skeleton in the Frick-AMNH collection from the late Barstovian Rincon Quarry in New Mexico, have femora that exceed their tibiae in length. The tibia of F:AM 62128 has been compressed laterally by crushing. The proximal end displays two large, concave articular condyles that are separated at their cranial and caudal boundaries by depressions for insertion of menisci and collateral ligaments. Dividing these two oval articular surfaces in a sagittal manner is a large intercondylar eminence.

FIBULA

Approximately the distal two-thirds of the left fibula and a small distal fragment of the right fibula are present in F:AM 62128. There is no information on the proximal end of this bone. The medial surface of this robust hind limb element is concave, contrasting with the convex lateral surface. The cross section of the shaft of the left fibula is triangular, and terminates in a lateral malleolus with a deep groove for the passage of the peroneus brevis muscle. All of this is in strong accord with modern felids.

TARSUS

The entire right pes of this specimen is articulated (fig. 11). The left rear foot (fig. 12) was disarticulated and prepared. The proximal end of the left calcaneus begins with a shallow groove for the flexor tendons and quickly narrows into a neck much deeper anteroposteriorly than it is wide. The calca-

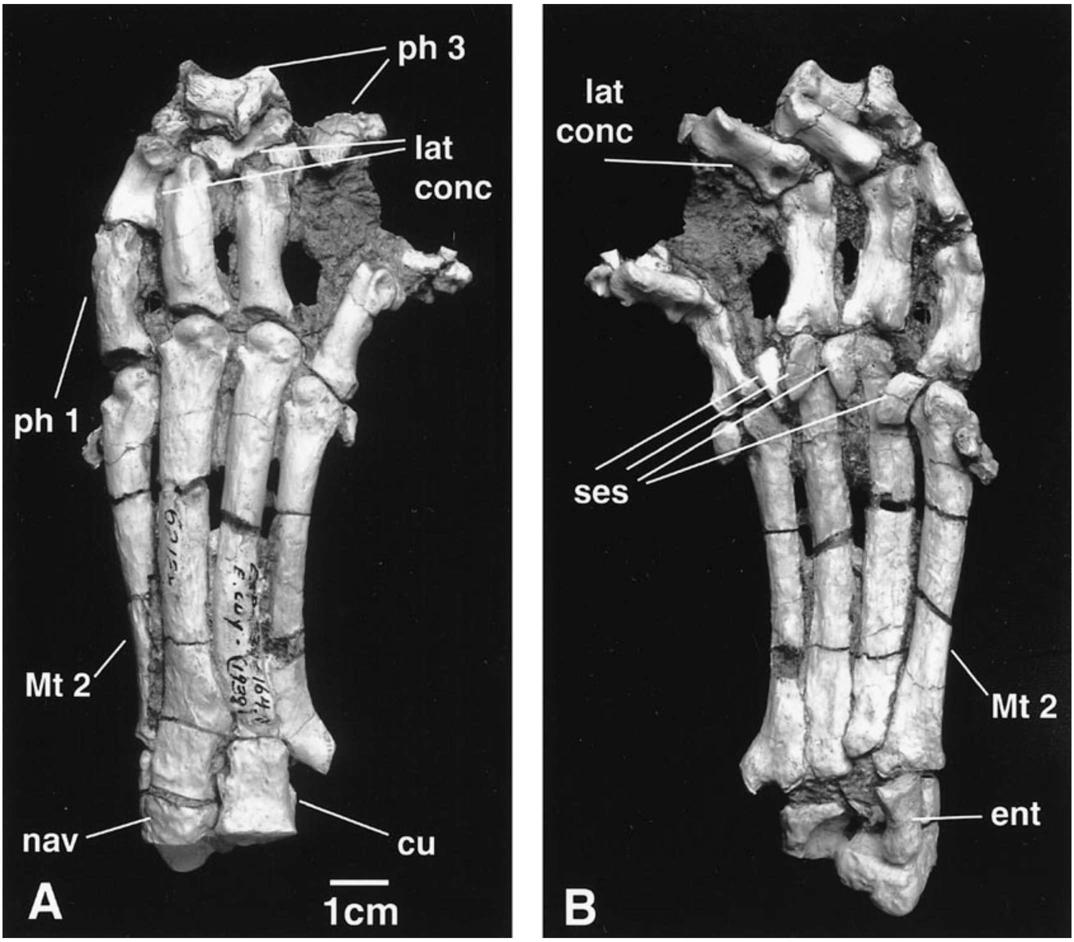

Fig. 11. Articulated right pes in dorsal (**A**) and ventral (**B**) views. In the dorsal view, the more stout third metatarsal bone can be appreciated. The ventral view shows sesamoid bones (ses) in situ. nav = navicular, cu = cuboid, ent = entocuneiform, lat conc = lateral concavity of second phalanx.

neal facets are distinct and separate. Halfway down the calcaneus length, the bone quickly widens to form the tight *s*-shaped articulation with the astragalus. This *s*-shaped articulation, a character of cursoriality (Ginsburg, 1961a) seen in all modern felids, is well displayed in this specimen.

The right astragalus possesses a large and deeply grooved trochlea. There is no evidence of an astragalar foramen. This smooth joint surface appears to offer little restriction or limitation to tibial rotation. It describes a circular arc that extends nearly from the proximal to the distal margin of this tarsal bone. All of these characters of the astragalus demonstrate that *P. validus* was fully digitigrade (Wang, 1993). There is a short and strong neck, which terminates in a rounded, convex articular surface.

Immediately below and articulating with the astragalus is the navicular bone (fig. 12). Shotwell and Russell (1963) listed a right navicular, but did not provide illustration or description of this Clarendonian specimen from Oregon. The Nambé navicular contains a deeply concave proximal surface for articulation with the astragalus. This articular area occupies most of the proximal surface of this rectangular bone. On the distal surface of the navicular are separate facets for articulation with all three members of the distal row of tarsal bones. This navicular, including its typ-

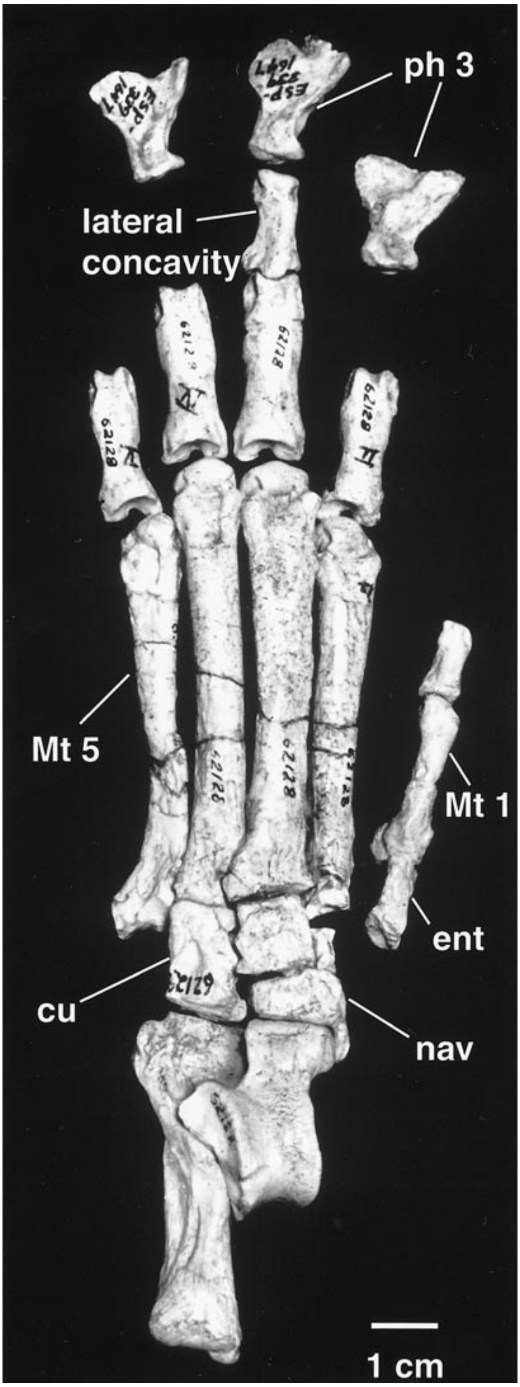

Fig. 12. Left pes, dorsal view. With the exception of the hallux, this rear foot is virtually identical to that of today's felids. nav = navicular, cu = cuboid, ent = entocuneiform, lateral concavity = lateral concavity in second phalanx.

ical caudal projection, strongly resembles its complement in large, extant felids.

Lateral to the navicular is the cuboid, which articulates with the astragalus proximally. The remainder of the third row consists of the three smallest tarsal bones. Superior to Mt3, and therefore the most lateral of the three, is the ectocuneiform. Medial to this is the mesocuneiform, which articulates with the second metatarsal. The third of these, most medial and positioned more caudal to the navicular, is the entocuneiform. All of this tarsal anatomy can be observed in situ in the articulated rear foot (fig. 11) and agrees with modern felids.

METATARSUS AND PHALANGES

The articulated right pes shows four primary metatarsals tightly compressed side to side, indicating a digitigrade hindfoot (Ginsburg, 1961a; Wang, 1993). These four main metatarsals, numbered 2 through 5, are approximately equal in length. Each bone's diameter varies little throughout its length. However, as in modern felids, the third metatarsal is considerably stouter than the others (fig. 12). The distal ends of the metatarsals widen to form large, prominently displayed arthral surfaces. When viewed from the ventral surface, their articulations with the proximal phalanges are linked by paired sesamoids that are separated by a midline trochlea (fig. 11).

The first metatarsal did not survive in the articulated specimen, but is intact and in place in the prepared left pes (fig. 12). F:AM 62128 Mt1 is plesiomorphic, is not vestigial, and articulates with a proximal phalanx. The Nambé Mt1 has proximal and distal articular surfaces, a slender diaphysis, and an accompanying first phalanx (fig. 13). The proximal end of F:AM 62128 Mt1 is very broad, with an asymmetric arthral surface that articulates with the accompanying entocuneiform. The lateral condyle of the proximal end of this bone is enlarged and extends further proximally. The result of this asymmetry is to direct the digit medially, at an angle from the foot, not parallel with the other metatarsals that point toward the ground. On the ventral surface of the proximal end of Mt1 is a groove for passage of a flexor tendon. Dis-

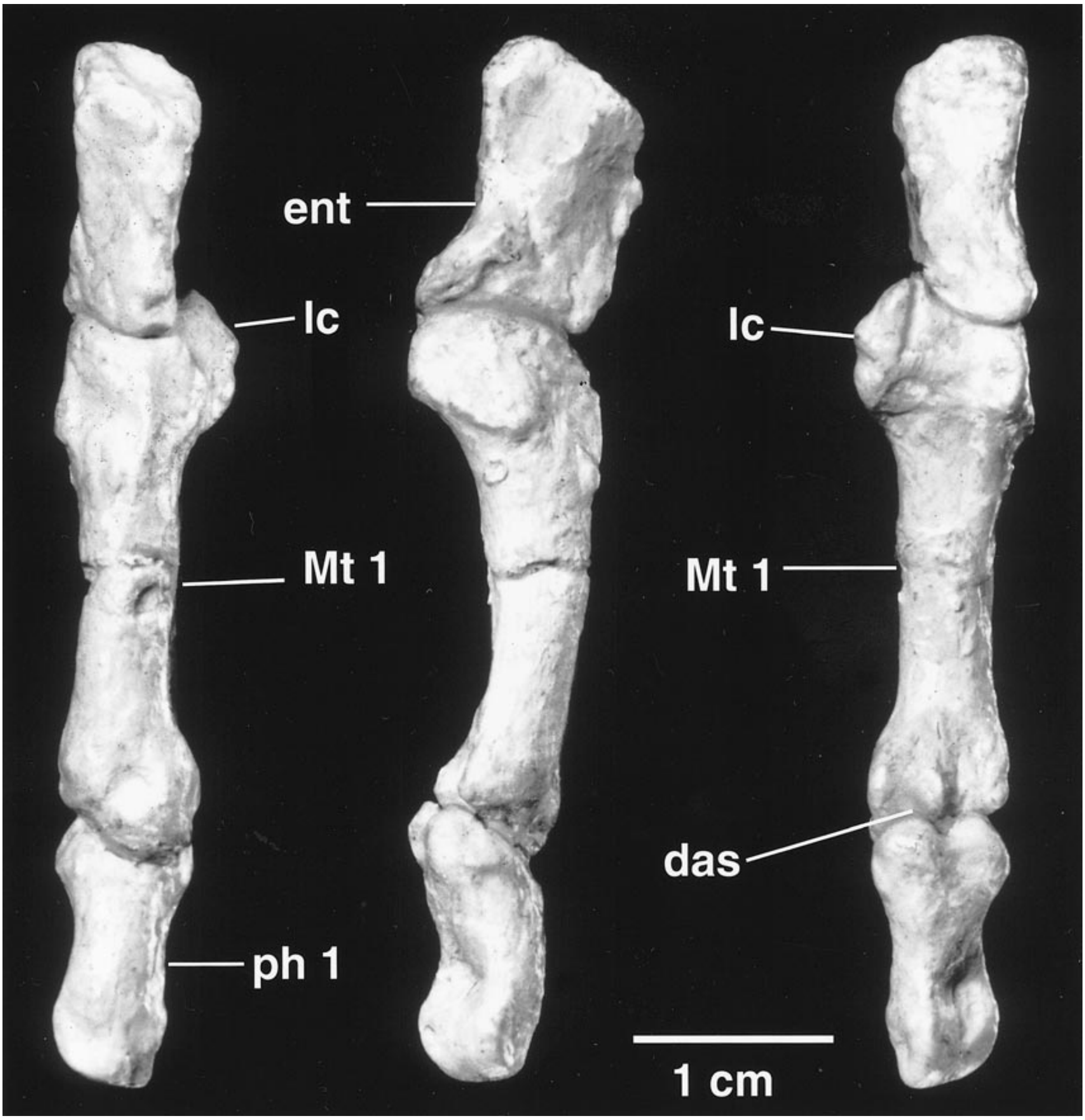

Fig. 13. Left Mt1 articulating with entocuneiform (ent) proximally and its first phalanx distally. From left to right: dorsoventral, medial, and ventral views. The shape of this metatarsal bone is extremely similar to that seen in early Tertiary members of Carnivora. das = distal articular surface with midline trochlea, lc = lateral condyle of first metatarsal bone.

tally the shaft narrows considerably, reaching its minimal diameter in the middle of the diaphysis. The termination of this Mt1 is similar to the four main metatarsals: It enlarges to form an articulation with a proximal phalanx. Ventrally, it displays a central trochlea similar to the four adjacent metatarsals. This distal articular surface is not perpendicular to the bone's axis. The shaft is longer on its lateral margin and this results in a medial deviation of the first digit. This first digit on the rear foot of F:AM 62128 is unlike that in any living member of Felidae. I am unaware of any Mt1 bones in the *Pseudaelurus* literature. Helbing (1928) published an illustration of a Mt1 (fig. 14) assigned to *P. lemanensis* which is extremely similar to the F:AM 62128 bone just described. However,

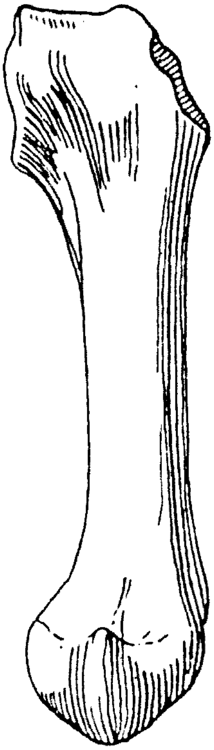

Fig. 14. Mt1, *Proailurus* sp. Helbing (1928). This illustration suggests a more midline, sagittal axis than F:AM 62128, especially on the distal articular surface.

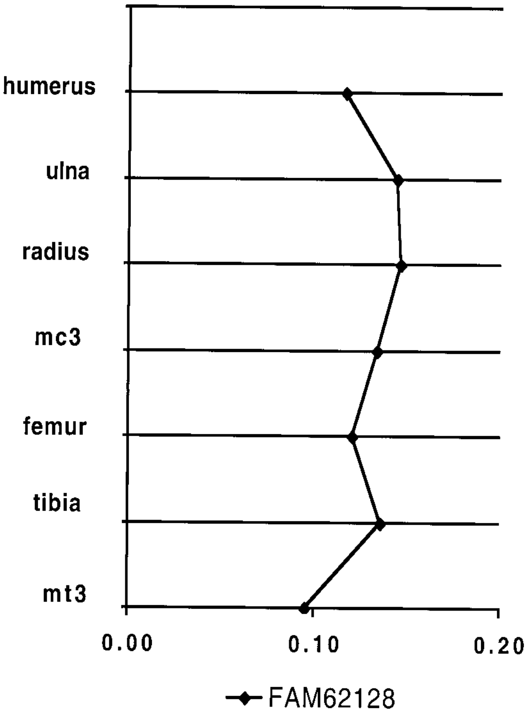

Fig. 15. Postcranial log-ratio diagram comparing front and rear limb measurements of *Proailurus* and *Pseudaelurus.* The standard specimen on the y axis is *P. lemanensis,* the earliest recognized member of Felidae. Contrasted to this taxon is F:AM 62128, the early Miocene Nambé skeleton described in this paper. The length of the fragmented femur of F:AM 62128 was estimated. The data curve of the Nambé skeleton is reasonably vertical (similar in proportion to *Proailurus*). For the characters featured, the North American *Pseudaelurus* appears to be a larger version of the earlier *P. lemanensis.* A data point of 0.1 to the right of the y axis on this log difference scale represents an increase in size of approximately 25%.

the *Proailurus* Mt1 is more plesiomorphic. It has a more midline sagittal axis than the *Pseudaelurus* specimen.

The first phalanges of F:AM 62128 do not differ from modern felids. The second phalanges of digits 2 through 4 are roughly half the length of their respective first phalanges. Two of these second phalanges are present in the prepared left pes (fig. 12) while all four can be observed in the articulated right rear foot (fig. 11). The three proximal facets of each second phalanx allow for a strong articulation between the first two phalanges and would appear to minimize torque between the two bones. The second phalanges are asymmetric; their diaphyses are laterally concave. The degree of this concavity is equal to that in the second phalanges of the manus. Both groups of second phalanges of F:AM 62128, those of the manus and those of the pes, resemble those in large, modern felids. The concave lateral surfaces of these second phalanges demonstrate that *Pseudaelurus* possessed a passive claw retraction and protraction mechanism (Wang, 1993; Bryant et al., 1996). Both the first and second phalanges of metatarsals 2 through 4 possess a groove on their ventral surface, as in extant felids, for passage of the flexor tendon of the claw.

The third phalanges of the pes are large and laterally compressed (fig. 12). On their proximal surfaces is a circular concave area for articulation with the second phalanx. The

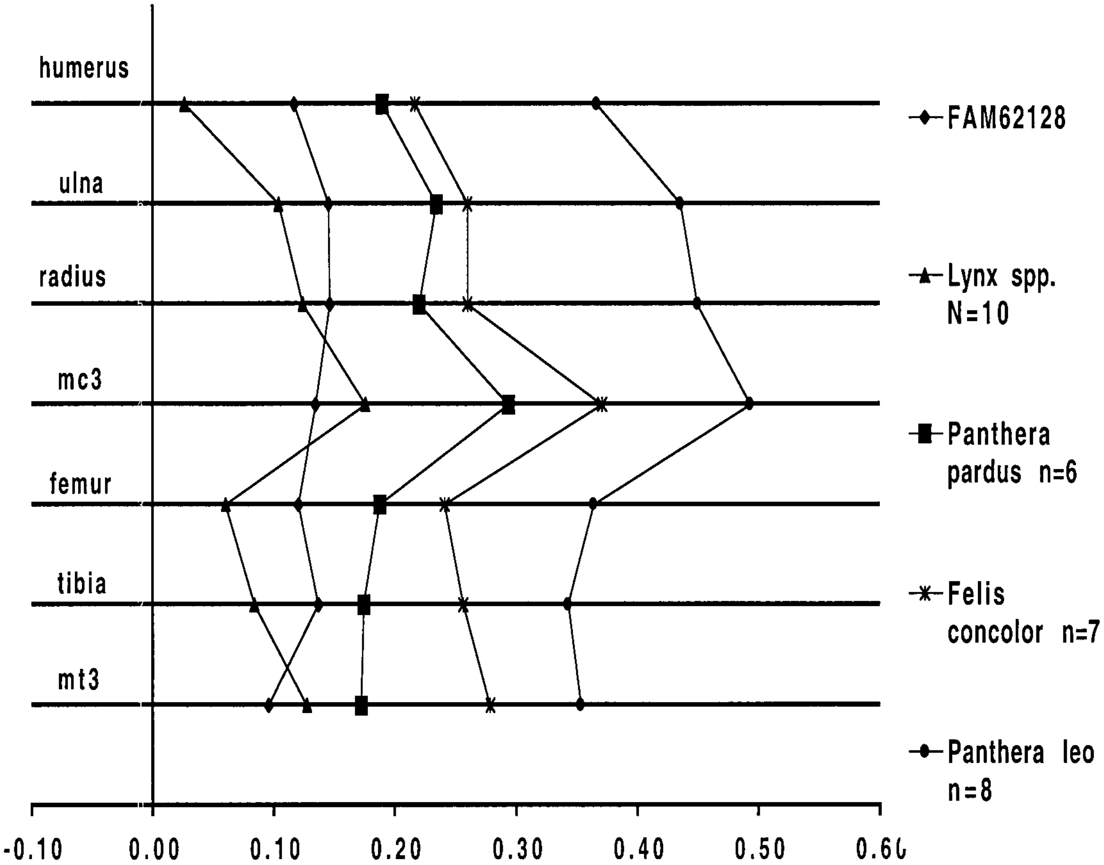

Fig. 16. Postcranial log-ratio diagram of figure 15 with inclusion of four extant species of Felidae. All four of the extant species display a characteristic lengthening spike in their data curves at Mc3. Note how all six felids featured on this chart have proportionate (all curves parallel to each other) rear limb components. The rear limb of felids has changed little from the early Miocene *P. lemanensis* to today's modern species.

ventral termination of this joint ends at the plantar process. The beak-like ungual process or bony claw core projects distally, forming the foundation for the keratinous claw. All of this morphology of the third phalanx in *P. validus* resembles that of large, extant felids. In the third digit of the articulated right pes (fig. 11) can be seen an example of a third phalanx with an intact ungual crest and hood.

DISCUSSION

All students of Felidae become frustrated, at some time, with the homogeneity of the anatomy within this family. In both extant and extinct species of felids, morphological characters are more often shared by species than differentiated by them. Early and medial Miocene felid lower jaws that overlap in size are distinguished only by the absence or presence of p1, p2, or m2 and the morphology of the lower carnassial. If we look only at specimens from the early and medial Miocene of North America, dental variations are restricted to p2 and m1. Partly because of this phenomenon of homogeneity, *Pseudaelurus* has been referred to as a wastebasket taxon for Miocene felids. Species within the genus *Pseudaelurus* are based on different sizes of lower jaws that rarely differ otherwise. In North America, virtually 100% of all early and medial Miocene felid fossils are

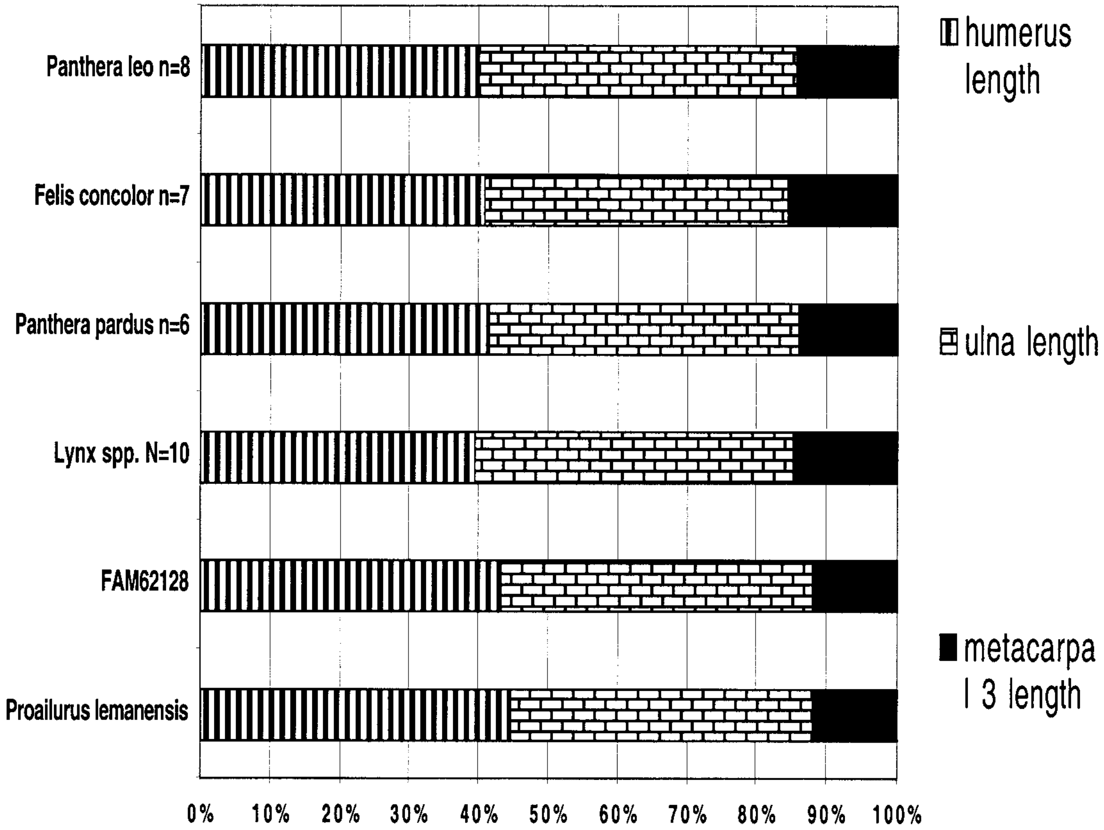

Fig. 17. Bar-graph presentation of front limb data seen in figure 16. From left to right, each species' bar is segmented into the humerus, ulna, and metacarpal 3 contribution to the front limb length. The percentage of the front limb length contributed by the metacarpal bone has increased in the modern radiation of Felidae.

assigned to *Pseudaelurus.* The problem to date has been a lack of information (cranial, basicranial, postcranial) accompanying lower jaw specimens. Because of this lack of supporting data, assignment of many of these lower jaws to genera other than *Pseudaelurus* has not been possible, or even necessary. The specimen described herein from the Nambé Member is the earliest felid skeleton from North America having information on the cranial, postcranial, and upper and lower dentition. The description of this partial skeleton provides a baseline of information for at least one species within the genus *Pseudaelurus.*

The lower jaw of the Nambé skeleton differs from the other three North American species of *Pseudaelurus* in size, c-p3 diastema, and morphology of the coronoid process. In a manner resembling modern felids, the lower dentition of all four species is similar. This can be seen in the lower jaw and dental log-ratio diagram of figure 5. In this chart I have compared characters from the lower jaws of *Proailurus lemanensis* (MNHN S.G. 3509a), the holotypes of four other North American species of *Pseudaelurus,* as well as the Nambé form (F:AM 62128). *Proailurus* is the standard specimen, represented as the vertical axis. The graph demonstrates that the *Pseudaelurus* lower jaws and teeth are similar in anatomical proportions to each other and to the Oligocene felid. The graph also demonstrates the differences in size of the lower jaw and length of the diastema between the c and p3. In comparison to the *Proailurus* specimen, the lower jaws of the *Pseudaelurus* taxa have been abbreviated by

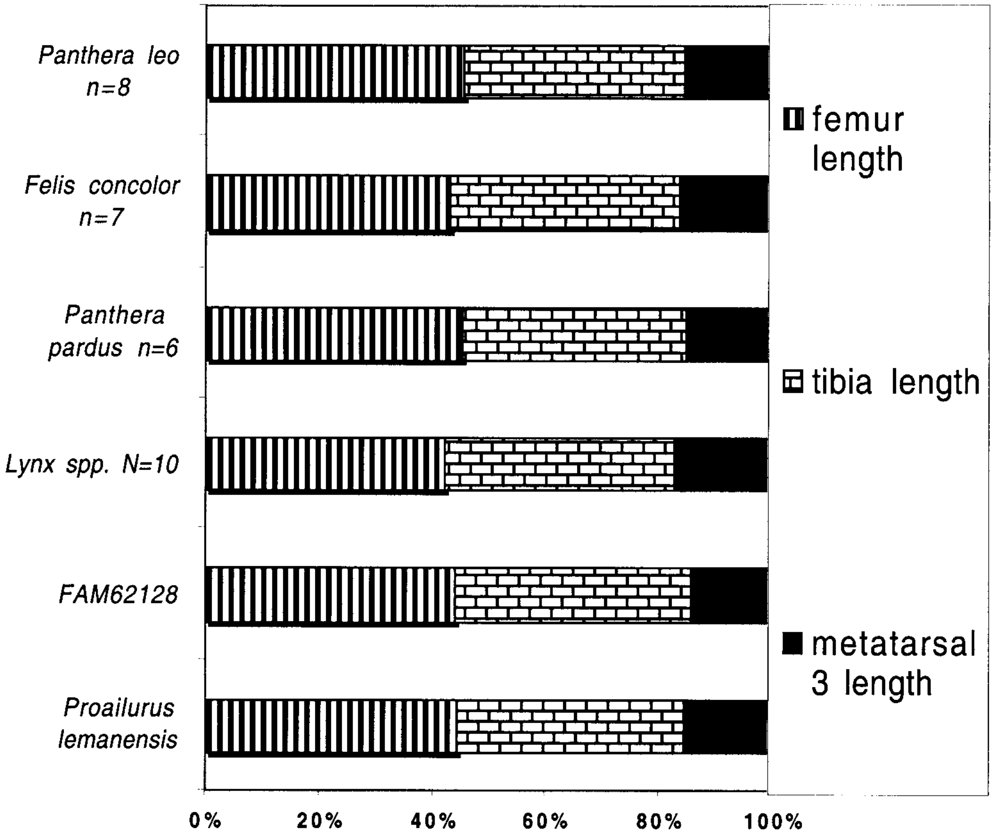

Fig. 18. Hind limb bar chart. For each species, the bar is segmented into the femur, tibia, and Mt3 contribution to rear limb length. From *Proailurus* in the early Miocene to the living members of Felidae, the proportions of the hind limb have remained constant.

shortening of the diastema space. Two species, *P. aeluroides* and *P. marshi* are distinguished by an extreme shortening of this diastema. The length of c-p3 diastema is an important tool for fossil felid-specific diagnosis. The coronoid process of *P. validus,* while larger than that seen in *P. lemanensis,* is in the primitive, erect state.

F:AM 62128 displays many primitive felid characters in the skull and upper dentition. In most instances, the Nambé felid resembles the *P. lemanensis* skull from St.-Gérand while maintaining an intermediate position anatomically between *P. lemanensis* and *Felis.* The P4 of F:AM 62128 has a prominent protocone which projects in an anterolingual direction from the lingual surface of the paracone (fig. 2b). However, the protocone projects at a more obtuse angle than is seen in later specimens of this genus such as *P. intrepidus* and *P. marshi.* This less acute angle formed by the protocone is seen also in the earlier *P. lemanensis* skull and the temporally equivalent F:AM 61847 Ginn Quarry skull (see Hunt, 1998, p. 43, fig. 19B). F:AM 62128 has a primitive (for felids) M1 with evidence of parastyle, paracone, metacone, and protocone. The M1 of the Nambé felid appears to have had carnassial function. The M1 paracone is contiguous with the metastyle blade of P4. The paracone of M1 thus provides a longer carnassial blade in this plesiomorphic state. This primitive M1 morphology can also be seen in the *P. lemanensis* skull (MNHN S.G. 3509a), but is in contrast to the vestigial condition of this tooth in modern felids.

The cranial information provided by the crushed F:AM 62128 skull is important, but limited. It is clear that this late Hemingfor-

Fig. 19. F:AM 62128, the Nambé skeleton from the Tesuque Formation near Cuyamunque, New Mexico.

dian felid was a large and primitive member of the family Felidae. The skull anatomy resembles the earlier European taxon *P. lemanensis*. Precise conclusions regarding the relationships of this specimen with other fossil felids are not possible. Fortunately, two other skulls referenced to *P. validus* (F:AM 61834 and F:AM 61835), from the early Barstovian Lower Snake Creek Fauna, are in near perfect condition. The basicranial anatomy of these two skulls, along with 10 other assorted specimens from late Hemingfordian and early Barstovian localities, will be described in more detail in a paper in preparation.

The Nambé skeleton (F:AM 62128) provides the first North American evidence for limb proportions in the genus *Pseudaelurus*. Since information is available from a *Proailurus* skeleton (Filhol, 1888), it is possible to compare both of these fossil taxa with extant felids (figs. 15, 16, 17, 18). Figure 15 demonstrates that the limb proportions of *P. validus* are similar to those of *P. lemanensis*. The Nambé felid was larger than the *Proailurus* specimen, but it still resembled the earlier European felid. In figure 16, a recognizable ‘‘signature’’ of front limb proportions for the modern cats can be seen. There has been an increase in the proportion of front limb length contributed by the metacarpals in the modern felids. These extant felids are clearly different from the standard specimen, *Proailurus*, and the North American *P. validus* skeleton. *Proailurus* and *Pseudaelurus* have similar proportions of the limb bones. The modern felids form a separate anatomical group. Equal-sized specimens of *P. lemanensis*, *P. validus*, and *L. lynx* would all be of the same approximate height at the shoulder and the hip. However, the lynx would have a longer set of metacarpals and a somewhat shorter humerus than the two Miocene felids. In figure 17, front limb data demonstrating the metacarpal contribution is compared in a bar graph.

A vestigial Mt1 is seen in all modern Felidae. The presence of the primitive, unreduced Mt1 in *Proailurus lemanensis* and *Pseudaelurus validus*, and the advanced state of vestigial Mt1 in *Felis* supports the hypothesis that this character developed in parallel in the family Hyaenidae (Werdelin, 1996). This character should not be considered a synapomorphy for these two aeluroid families as previously suggested (Wyss and Flynn, 1993). The rear limb data (figs. 16, 18) indicate that there has been little change in the proportions of these elements within the family Felidae since the early Miocene. The metatarsals did not change in proportional size, as did the metacarpal series.

SUMMARY

P. validus is the earliest felid in North America with cranial, dental and postcranial information (Galusha and Blick, 1971; Galusha, 1975; Tedford, 1981; Tedford et al., 1987) (fig. 19). This is a big cat, with a skeleton approximately 30% larger than the *P. lemanensis* skeleton described by Filhol (1888). By one method, its body mass could be estimated at 26 kg (Legendre and Roth, 1988). This would place *P. validus* between a large lynx (*Lynx canadensis*) and a small puma (*F. concolor*) in size. However, this *Pseudaelurus* skeleton clearly resembles *P. lemanensis* more so than *Felis* (figs. 15, 16). Its skull morphology, carnassial apparatus, and limb bone proportions are very similar to *P. lemanensis*. Regardless of whether *Proailurus* and *Pseudaelurus* are monophyletic groups, the fossils in these genera are early, primitive members of the family Felidae. Thus, understanding their anatomy is critical to our understanding of the phylogeny of modern cats and in determining polarity of characters within the family. This, in turn, can only improve phylogenetic resolution within the Aeluroidea.

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APPENDIX 1

Pseudaelurus validus, Type Specimen (F:AM 62128), Measurements (in millimeters)

Skull and Upper Dentition	
Basal length: anterior premaxillary to inferior notch between occipital condyles	133.2
Greatest width across muzzle at upper canines	44.3
Greatest width across zygomatic arches	124.7
Upper canine length	13.1
Upper canine width	9.5
Diastema: posterior end of C to anterior end of P3	10.3
Maxilla length: anterior end of P3 to posterior end of P4	28.8
Maxilla length: anterior end of C to posterior end of P4	55.3
P3 length	11.9
P3 width	7.1
P4 length	18.3
P4 width	6.9
M1 length	4.8
M1 width	10.5
Mandible and Lower Dentition	
Length of dentary: anterior end of symphysis to posterior end of condyle	124.9
Height of dentary bone at interface of p4-m1	24.8
Width of dentary bone at interface of p4-m1	9.6
Jaw length from anterior end of c to posterior end of m1	61.5
Jaw length from anterior end of p3 to posterior end of m1	36.4
Jaw length from anterior end of p4 to posterior end of m1	26.9
Lower canine length	11.9
Lower canine width	7.6
p3 length	9.3
p3 width	4.1
p4 length	12.7
p4 width	6.0
m1 length	15.2
m1 width	6.9
Diastema length: posterior end of c to anterior end of p3	14.6
Transverse width of condyle	30.2
Perpendicular height: ventral border of dentary to summit of coronoid process	61.3

APPENDIX 1
Continued

Postcrania, long bones:	Right humerus	Right radius	Right ulna	Left tibia	Left fibula
Greatest length	175.0	145.0		193.0	
Transverse diameter of shaft at middle	17.3	13.7	7.9	11.0	4.7
a-p diameter of shaft at middle	16.9	8.7	17.3	19.5	9.8

Postcrania, metacarpus and metatarsus:	Mc3	Mt3
Greatest length	48.6	68.4
Greatest transverse diameter of proximal end	10.5	14.8
Greatest d-v diameter of proximal end	11.0	14.8
Transverse diameter at middle of shaft	7.4	8.8
Dorsoventral diameter at middle of shaft	?	8.2
Greatest transverse diameter at distal end	12.4	13.2

Postcrania, tarsus:	Calcaneus	Astragalus
Greatest length	55.1	35.1
Greatest width	24.3	20.3

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