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Chapter 12

New Felid Material from the Ulaan Tologoi Locality, Loh Formation (Early Miocene) of Mongolia

TOM ROTHWELL

ABSTRACT

Herein I describe new felid material from the early Miocene, Ulaan Tologoi locality of Mongolia. A dentary fragment and a metapodial are the first large felid fossils to be recovered from the early Miocene of Asia. Both specimens are referred to the genus *Pseudaelurus*. Comparisons of these Asian specimens to previously described European, Asian, and North American species provide insights into the size and form of this cat. I review the Asian literature on early felids and discuss possible causes for fossil felid scarcity in the early Miocene of Asia.

INTRODUCTION

The fossil evidence documenting early aeluroids from the Oligocene of Asia is poor. However, early lineages of Aeluroidea have been recovered from Oligocene localities in the Hsanda Gol Formation, Mongolia (Mellet, 1968; Hunt, 1996, 1998), suggesting that some early members of Aeluroidea were distributed throughout Europe and Asia by the end of the Oligocene. The earliest appearance of an Asian fossil possibly belonging to the family Felidae is in dispute. A single lower jaw fragment (AMNH 21674) from the Oligocene Tatal Gol locality has been assigned alternatively to the felid genus *Proailurus* (Mellet, 1968; Hunt, 1998) and to the nimravid genus *Eofelis* (Peigné, 1999). While specimens referred to the nimravid subfamily Nimravinae are present throughout the Oligocene of Asia, this lower jaw fragment from Hsanda Gol is, at present, the only candidate for felid presence in Asia prior to the end of the Oligocene.

Peigné's assignment of this specimen to the Nimravidae is based largely on the absence, or extreme reduction, of the metaconid of AMNH 21674. Peigné (1999: 131) stated, ''Tous les spécimens observés attribués à *Proailurus,* ainsi que les spécimens atribués aux *Pseudaelurus* les plus primitifs portent un métaconide.'' (All specimens observed referred to *Proailurus*, as well as the specimens attributed to the most primitive *Pseudaelurus* bear a metaconid.) Although all known specimens currently referred to *Proailurus* may indeed have a metaconid (there are only 28 specimens described from 6 localities), variability of m1 morphology within fossil Felidae is the norm.

The earliest specimens of *Pseudaelurus* appear in the early Miocene (MN3) of Europe in the Wintershof-West locality of Germany. Dehm (1950) described 18 lower jaws and one maxillary specimen from this locality as elements of a species transitional between *Proailurus* and the more derived *Pseudaelurus* reported from the La Grive–Saint-Alban (Isère) locality in France. Of the 18 lower jaws from Wintershof-West, 15 could be scored for the metaconid character. Of these 15, 12 had a metaconid and 3 did not. In North America, the earliest felids are referred to two species of *Pseudaelurus* found primarily in early Miocene localities of Nebraska (Rothwell, 2003). All seven lower jaws of the smaller species have a distinct metaconid and a talonid. Of seven lower jaw specimens assigned to the larger *P. validus*,

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four possess a detectable metaconid and three do not.

I have examined AMNH 21674. The m1 of this specimen has a tall protoconid whose shearing blade is directed dorsoposteriorly. The posterior border of the m1 is therefore vertical. This form of the lower carnassial protoconid is seen also in the type specimen of the middle Miocene Asian felid *Pseudaelurus cuspidatus* (Wang et al., 1998). The m1 of AMNH 21674 has a deep, yet closed, carnassial notch and is highly compressed both mediolaterally and anteroposteriorly, characters seen also in *P. cuspidatus*. Inspection of the well-worn m1 of AMNH 21674 under magnification reveals evidence of a reduced, yet distinct metaconid. This is consistent with the observations of Hunt (1998: 49): ''the metaconid is lost, its place represented by only a weak swelling at the base of the protoconid.'' This weak swelling has been captured by the illustrator in Hunt (1998: 50, fig. 22).

What is unusual about the m1 in AMNH 21674 is the relative large size of the talonid in the presence of such a reduced metaconid. This is an unusual character combination for a felid but is seen in some species of nimravids (H.N. Bryant, personal communication). Nonetheless, the mediolateral compression of this carnassial, its shortened length, and the similarities of the protoconid and carnassial notch to the type specimen of the Asian *P. cuspidatus* suggest an assignment to the family Felidae.

Three small species of *Pseudaelurus* have been reported from early and middle Miocene localities of Asia. A left ramus and some dental fragments assigned to *Pseudaelurus* cf. *P. lorteti* were reported from the early Miocene of Xiacaowan, Sihong County in Jiangsu Province, China (Qiu and Gu, 1986). *Pseudaelurus guangheensis* Cao, Du, Zhao, and Cheng, 1990, is represented by a maxillary fragment from the middle Miocene Guanghe District of Gansu, China (Cao et al., 1990). *Pseudaelurus cuspidatus* Wang et al., 1998, is represented by a dentary fragment from the early middle Miocene Halamagai Formation in northern Junggar Basin, Xinjiang Autonomous Region, China (Wang et al., 1998). This small amount of material from the early and middle Miocene of Asia is in contrast to the well-documented, temporally equivalent felid faunas of Europe and North America. In Europe, abundant felid material from the early and middle Miocene has been assigned to four species of *Pseudaelurus*: (1) *P. quadridentatus* Blainville, 1843; (2) *P. turnauensis* Hoernes, 1882; (3) *P. lorteti* Gaillard, 1899; and (4) *P. romieviensis* Roman-Viret, 1934 (Heizmann, 1973). In North America, an extensive collection of early and middle Miocene felid fossils, for the most part housed in the Frick Collection at the American Museum, are assigned to six species of *Pseudaelurus* (Rothwell, 2001, 2003).

Asian fossil felids, other than *Pseudaelurus*, from early and middle Miocene localities include the first fossil felid described from that continent, a maxillary fragment from the middle Miocene Chinji Formation of Pakistan originally assigned to *Pseudaelurus chinjiensis* Pilgrim, 1910. That specimen was subsequently redescribed and identified as the type specimen of a new genus, *Sivaelurus* Pilgrim, 1915. The first felid cranial material described from Asia, a fragmented skull also from the middle Miocene Chinji Formation, was also assigned to a new genus, *Vishnufelis* Pilgrim, 1932.

By the late Miocene of Asia the diversity of felids seemingly increased, the majority of forms being machairodont. Felid specimens assigned to the genera *Dinofelis*, *Machairodus*, *Metailurus*, *Paramachaerodus*, and *Pontosmilus* have been described from the late Miocene of Asia (Werdelin and Lewis, 2001; Tedford and Qiu, MS).

The new material described in this paper was collected by Malcolm C. McKenna and party during the Mongolian American Expeditions of 1991 and 1994. McKenna attributed 196 specimens collected during these expeditions to the order Carnivora. Of these, 182 fossils are from the Oligocene Hsanda Gol formation and 13 were recovered from early Miocene Ulaan Tologoi localities. Two specimens from the Ulaan Tologoi locality of the Loh Formation are identified as felids.

The Loh Formation consists of cross-bedded sands and gravels mixed with silt and clay of both fluvial and aeolian origin. Based on geochronological and biostratigraphic data, its age has been estimated at 28 Ma

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(early late Oligocene) to 13 Ma (middle Miocene) (Höck et al., 1999; Daxner-Höck et al., 1997). Ulaan Tologoi is located at 45°20′ 39″N; 101°50′01″E, 4.7 miles NNE of Camp Loh at or near a site called ''Wild Ass Camp''. The locality occupies an interval in the Asian Shanwangian (early Miocene) and is earlier than the middle Miocene Tung Gur (McKenna et al., MS.).

INSTITUTIONAL ABBREVIATIONS

AMNH	Department of Vertebrate Paleontology, American Museum of Natural History, New York
F:AM	Frick Collection, Department of Vertebrate Paleontology, American Museum of Natural History, New York
MAE	Mongolian American Expedition
MHNL	Museum Guimet d'Histoire Naturelle, Lyon

SYSTEMATICS

CLASS MAMMALIA LINNAEUS, 1758

ORDER CARNIVORA BOWDICH, 1821

SUBORDER FELIFORMIA KRETZOI, 1945

FAMILY FELIDAE FISCHER DE WALDHEIM, 1817

Genus *Pseudaelurus* Gervais, 1850

DISTRIBUTION: Early to middle Miocene (MN3 to MN9) of Europe; early to middle Miocene (late Hemingfordian to late Barstovian) of North America; early to middle Miocene (Xiejian to Shanwangian) 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 primitive characters: presence of p2 and an alisphenoid canal. *Pseudaelurus* differs from extant felid genera in cross section of c showing flattened inner surface and posterior trenchant edge, presence of p2, m1 with variable metaconid and reduced talonid, and presence of alisphenoid canal. Differs from *Metailurus* in presence of alisphenoid canal and p2, and 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.

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

INCLUDED SPECIES: Type species and *Pseudaelurus intrepidus* Leidy, 1858; *P. turnauensis* Hoernes, 1882; *P. lorteti* Gaillard, 1899; *P. marshi* Thorpe, 1922; *P. romieviensis* Roman and Viret, 1934; *P. aeluroides* Macdonald, 1954; *P. stouti* (Schultz and Martin, 1972); *P. guangheensis* Cao et al. 1990; and *P. cuspidatus* Wang et al., 1998; *P. validus* Rothwell, 2001; *P. skinneri* Rothwell, 2003.

Pseudaelurus sp.

Specimen MAE-LO-94-14131 is a right dentary fragment with an exposed posterior root of p3 and fractured crowns of p4 and m1 (fig. 12.1). This is a large felid with an m1 length approximately 15.1 mm. The size and form of the teeth, as well as the height and width of the dentary below the carnassial, agree well with *Pseudaelurus validus* from the early and middle Miocene of North America (Rothwell, 2003), *P. intrepidus* and *P. marshi* from the middle Miocene of North America (fig. 12.2), and the large European species, *P. quadridentatus* (table 12.1). Based on the length and width of the lower carnassial, its body mass can be estimated at approximately 26.8 kg (Legendre and Roth, 1988), similar in size to a small adult female puma (*Felis concolor*).

The anterior portion of the dentary is lost at the level of the exposed posterior root of p3. The dentary fragment extends posteriorly to the exposed root of m1. At the base of the exposed m1 root, a fragment of ascending ramus is preserved. Although the crown of m1 is missing, the lingual surface is entirely intact at the level of the cingulum, from its contact with p4 to its posteromedial margin. Here, the exposed posterior root of m1 is contiguous with the fractured base of the talonid.

A large posterior root of p4 can be seen in

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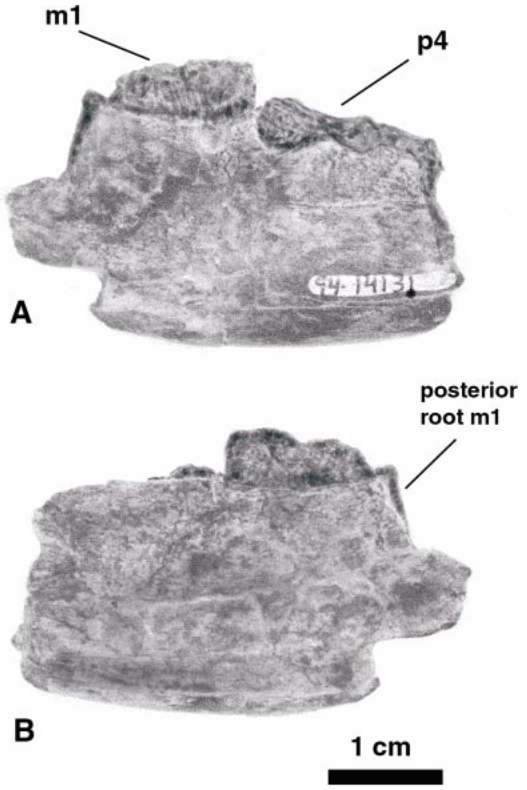


Fig. 12.1. Lateral (**A**) and medial (**B**) views of MAE-LO-94-14131 dentary fragment.

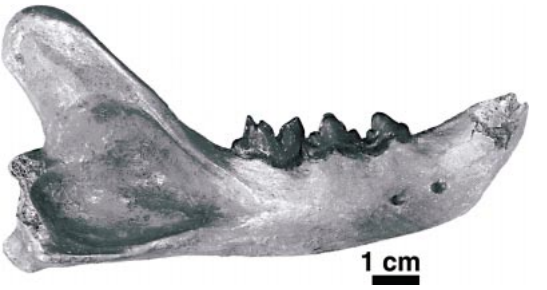


Fig. 12.2. *Pseudaelurus intrepidus* (F:AM 61804), right ramus, from Quarry 2 of the Lower Snake Creek Fauna in Sioux County, Nebraska. The available morphology of the dentary fragment from Ulaan Tologoi (MAE-LO-94-14131) agrees strongly with this specimen.

the occlusal view (fig. 12.3). A posterior root of p4 larger than the anterior root is primitive for felids and is exhibited in all species of *Pseudaelurus* (Heizmann and Kubiak, 1992). This p4 morphology persists in modern felids. Also seen in the occlusal view is the considerable overlap, or crowding, that occurs between the posterior border of p4 and the anterior margin of m1. The base of the paraconid of m1 rests upon the posteromedial border of p4. This morphology is also primitive for Felidae, but persists in modern felids. Other than the larger size, the morphology of the Ulaan Tologoi dentary fragment compares well with the other specimens of *Pseudaelurus* reported from Asia.

The fractured crowns of the dentary fragment offer the opportunity to study some internal structure of this early felid's teeth. In the close occlusal view (fig. 12.4) the exposed roots of the premolars have been prepared to reveal the pulp cavity and the thick layer of surrounding dentine. These same structures are also evident in the robust lower carnassial tooth. The relative thickness of

TABLE 12.1

Comparison of Lower Carnassial Measurements and Estimated Body Masses of Felids[a]

Specimen	Taxon	m1 length	m1 width	Estimated body mass (kg)
MAE-LO-94-14131	*Pseudaelurus* sp.	15.3	7.23	26.8
F:AM 61804	*P. intrepidus*	15.5	7.19	27.1
F:AM 62128	*P. validus*	15.2	6.9	24.8
IVPP V11491	*P. cuspidatus*	12.6	5.6	13.4
V 8070	*P.* cf. *lorteti*	12.5	?	?
AMNH 103395	*P. quadridentatus*	17.4	7.1	31.8

[a]Includes MAE-LO-94-14131 (*Pseudaelurus* sp. from the early Miocene of Asia), F:AM 61804 (*P. intrepidus* from the middle Miocene of North America), F:AM 62128 (*P. validus* from the early Miocene of North America), IVPP V11491 (*P. cuspidatus* From the middle Miocene of Asia), V 8070 (*P.* cf. *lorteti* From the early Miocene of Asia), and AMNH 103395 (cast of *P. quadridentatus* from the middle Miocene La Grive-Saint-Alban [Isère] locality of France).

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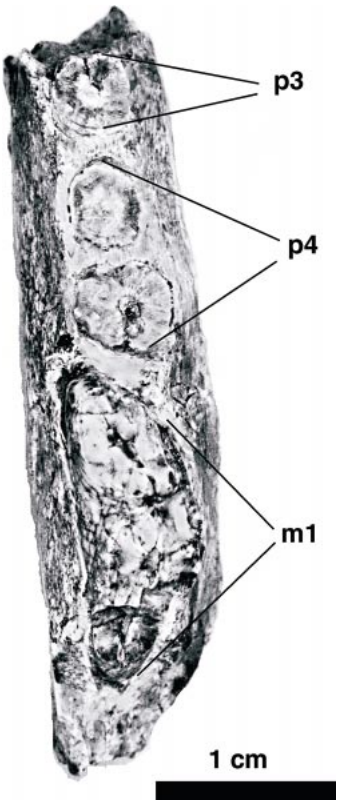


Fig. 12.3. MAE-LO-94-14131 dentary fragment, occlusal view.

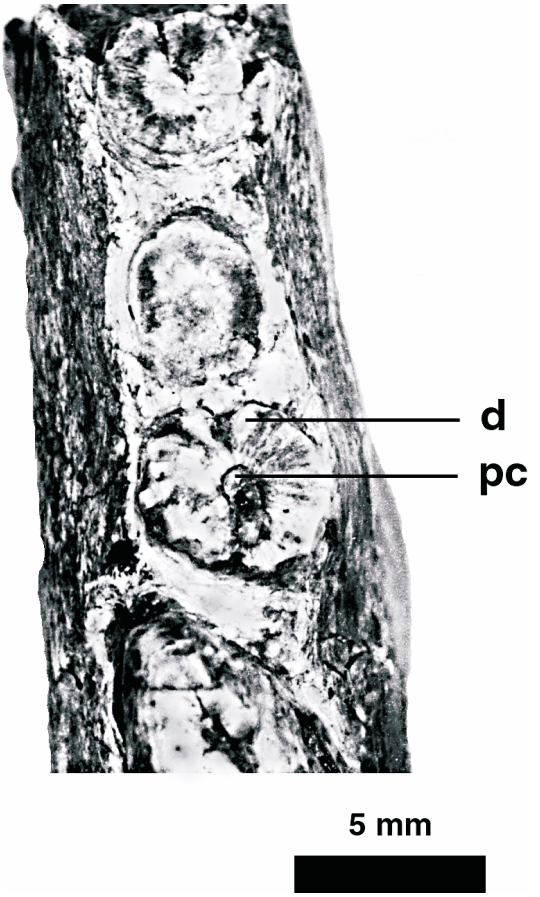


Fig. 12.4. MAE-LO-94-14131 dentary fragment, close occlusal view of fractured crown of p4, smaller anterior root is to the top. The relative thickness of dentine (d) and pulp cavity (pc) is indicated.

these structures is similar to that of North American specimens that I have previously studied. In m1, midway between the two pulp cavities, lies evidence of the lower limits of the carnassial notch.

The metapodial, MAE-LO-91-14117, is a left second metatarsal measuring 55 mm in length. It is in an excellent state of preservation and is extremely gracile in appearance (fig. 12.5). In size and form it is comparable to F:AM 61840-D, an early Miocene metatarsal from the Rhino Quarry in the Sheep Creek Formation of North America referred to *Pseudaelurus* (fig. 12.6). The shaft of the Mongolian metatarsal, however, arches more strongly than does that of the North American metatarsal. When viewed from the lateral perspective, the Mongolian metatarsal has a ventral concavity and a dorsal convexity. This morphology resembles that seen in many large, extant felids. Specimen MAE-LO-91-14117 is a metatarsal of a large digitigrade and cursorial felid (see Ginsburg, 1961; Wang, 1993). Its slender and concave form contrasts with the robust and stout metatarsals referred to the early Miocene North American species *Pseudaelurus validus* (Rothwell, 2001).

On the posteromedial surface of the proximal end of the metatarsal is an oval depression for articulation with the proximal end of the first metatarsal (fig. 12.5). This small, roughened basin is extremely similar, if not identical, to that of extant forms. Although the first metatarsal of an extant felid is vestigial, its articular surface is equivalent in size to its early Miocene predecessor. The length of the MAE-LO-91-14117 metatarsal

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Fig. 12.5. MAE-LO-91-14117, the metatarsal from Ulaan Tologoi assigned to *Pseudaelurus* sp.

(55 mm) can be used to estimate this cat's size by comparing it with that of other fossil felids, because the percentage of rear limb length contributed by the metatarsals has remained constant in felids from the early Miocene to the present (Rothwell, 2001). The length of this second metatarsal is close in size to that of a *Proailurus lemanensis* skeleton, which was compared in size to *Cryptoprocta ferox*, the modern fossa (Filhol, 1888). F:AM 62128, a partial skeleton from the late Hemingfordian Nambé Member in New Mexico, previously described as resembling a small female mountain lion (*Felis concolor*) weighing approximately 26 kg, has a second metatarsal measuring 62.9 mm (Rothwell, 2001).

DISCUSSION

The fossil evidence for all carnivoran taxa is poor in the late Oligocene and early Miocene of Asia (Hunt, 1996), especially when compared to Europe and North America. One explanation for the relatively poor fossil record of early Miocene Asian felids is the longer history of paleontological investigations in Europe. The Phosphorites du Quercy of France have long provided European paleontologists with a unique opportunity to study early lineages of arctoid and aeluroid carnivorans. Nothing like the Quercy Fissures has yet to be found in Asia. Another hypothesis for explaining the difference between Asia and Europe is habitat. Small- to medium-sized felids are often arboreal, a habitat less prevalent in the early Miocene of Asia (X. Wang, personal communication). Still another premise would be that early Asian felids experienced competition from other carnivorous taxa for available prey (Van Valkenburgh, 1999). For example, creodonts became extinct in North America by the end of the Oligocene and in Europe by the early Miocene. However, in Asia hyaenodont creodonts persisted into the late Miocene. It is reasonable to speculate that felids may have been scarce in the early Miocene of Asia due to a unique combination of environment al and competitive circumstances.

The dentary fragment and metatarsal described herein are the first evidence that at least one large species of *Pseudaelurus* was present in the early Miocene of northern Asia. These two Mongolian specimens may be from a single large species of felid, a status seemingly held by *P. quadridentatus* in the middle Miocene of Europe. Alternatively, the dentary fragment and the metatarsal may be from two large but similar species, comparable to *P. intrepidus* and *P. marshi* in the Barstovian of North America. Regardless of

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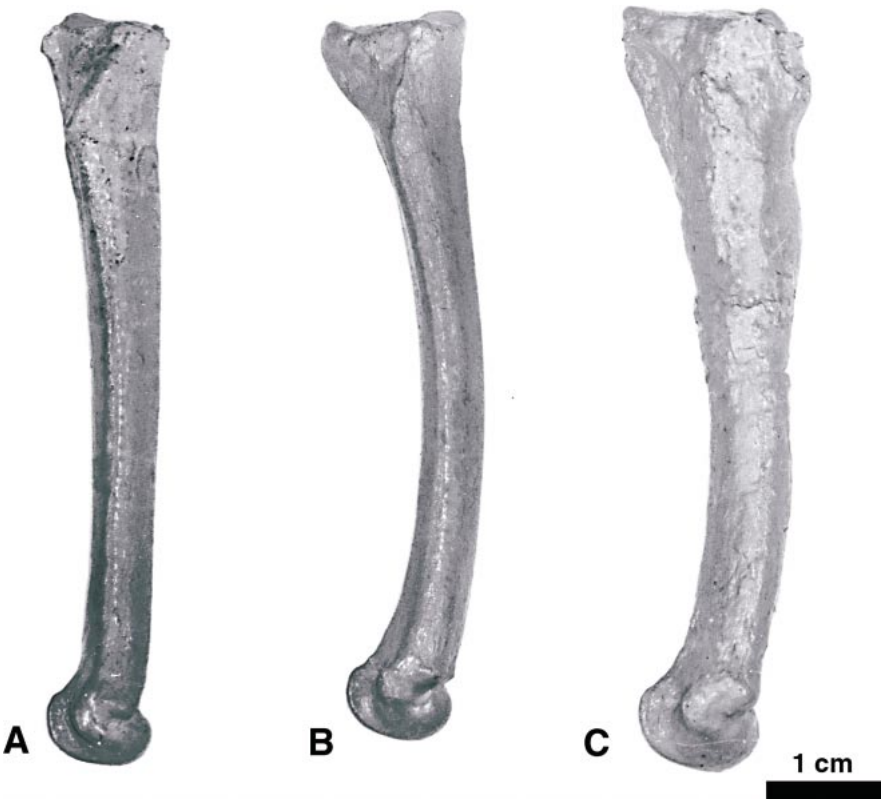


Fig. 12.6. A comparison of the left second metatarsals of **A,** *Pseudaelurus intrepidus* (F:AM 61840-D) from the Rhino Quarry (late Hemingfordian) of Nebraska; **B,** (MAE-LO-91-14117) the metatarsal from Ulaan Tologoi assigned to *Pseudaelurus* sp.; and **C,** *Pseudaelurus validus* (F:AM 62128) from the Nambé Member (late Hemingfordian) of New Mexico. The shaft of the Mongolian metatarsal arches more strongly from proximal to distal forming a greater ventral concavity than the *P. intrepidus* metatarsal. Its slender form contrasts with the robust and stout metatarsal referred to *P. validus*.

these new finds, the seeming scarcity of fossil felid specimens in Asia, large and small, is in contrast to the more abundant fossil felid record in Europe and North America.

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