

INTRODUCTION

Lanzhou Basin in central Gansu Province, northern China, is relatively unknown in vertebrate paleontology but has attracted considerable attention during the 1990s because of its potential to fill a critical gap in fossil record in the early Miocene and because of its location along the northeastern rim of the Tibetan Plateau. Located just north of the city of Lanzhou (Figure 1), the Lanzhou Basin received terrestrial sediments during a substantial part of the early through late Cenozoic, although vertebrate fossils are mainly found in the early Oligocene through middle Miocene part of the section. A multinational, multidisciplinary team led by the Institute of Vertebrate Paleontology and Paleoanthropology investigated the vertebrate paleontology and magnetostratigraphy of the Lanzhou Basin for several field seasons (Qiu et al. 1997; Flynn et al. 1999; Qiu et al. 2001). Vertebrate

records during the early Miocene are rather scarce in Asia, and this is especially true for carnivorous mammals (creodonts and carnivorans). Our newly acquired Lanzhou carnivore collections, although still far too sketchy to permit a full picture of the community, appear to represent a unique assemblage, including either first records in China or last record of a lineage. Various groups of fossils vertebrates and invertebrates from the Lanzhou Basin have been described (Qiu and Xie 1997; Qiu et al. 1998; Qiu and Wang 1999; Xie 1999; Qiu 2000; B. Wang and Qiu 2000a, 2000b; Qiu 2001a, 2001b; Wang et al. 2001). This report is part of this effort and presents a systematic description of these carnivorous mammals.

Abbreviations: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing; PIN, Institute of Paleontology, Russian Academy of Sciences, Moscow; PSS, Paleontology and Stratigraphy Section of Geological Institute, Mongolian Academy of Sciences, Ulaanbaatar.

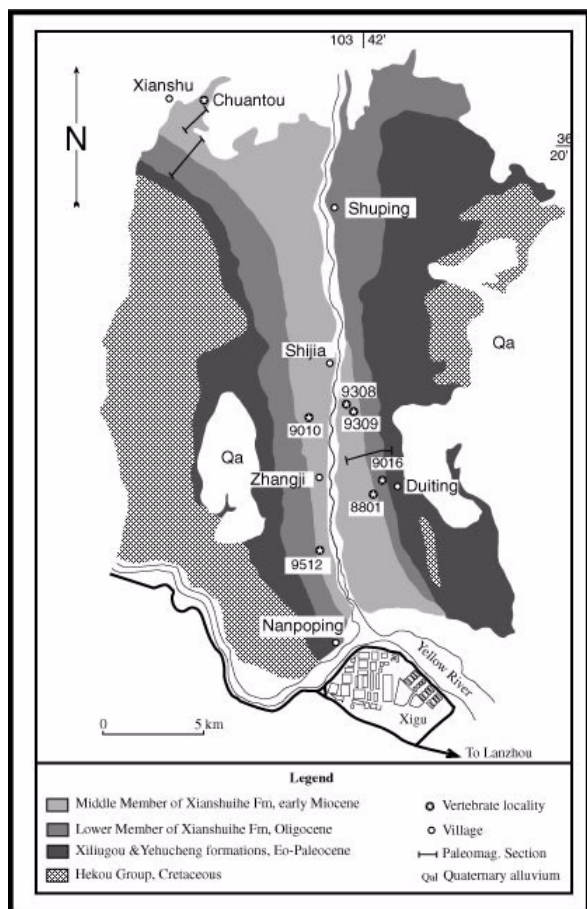


Figure 1. Map of the Lanzhou Basin and fossil carnivore localities cited in this paper. Map drawn by Will Downs.

SYSTEMATIC PALEONTOLOGY

Order CREODONTA Cope, 1875
 Family HYAENODONTIDAE Leidy, 1869
 Genus *HYAENODON* Laizer and Parieu, 1838
Hyaenodon weilini new species
Hyaenodon sp.: Qiu et al. 1997, p. 186;
 Qiu et al. 2001, p. 378.

Holotype: IVPP V12186, isolated left P4 and M2, right P3, P4, and M2, and root of left C (Figure 2).

Type Locality: IVPP V12186 was acquired from a villager in Zhangjiaping, by Qiu Zhanxiang, Yan Defa, and Xie Junyi on 19 April, 1987, about 10 km north of Lanzhou along the highway to the Lanzhou Airport (Figure 1). Loc. #2 of Zhangjiaping, probably from one of several sand quarries within the first white sandstones in the Middle Member of the Xianshuihe Formation, Zhangjiaping l.f., correlated to magnetic Chron C6n (about 19–20 Ma) in early Miocene (see Qiu et al. 1997; Qiu et al. 2001).

Although the holotype of *Hyaenodon weilini* was acquired from a farmer living near a “white sands” quarry (see below), our own independent collecting has yielded records (referred specimens) of this species in the “white sands,” increasing our confidence that the holotype is from the “white sands” as well.

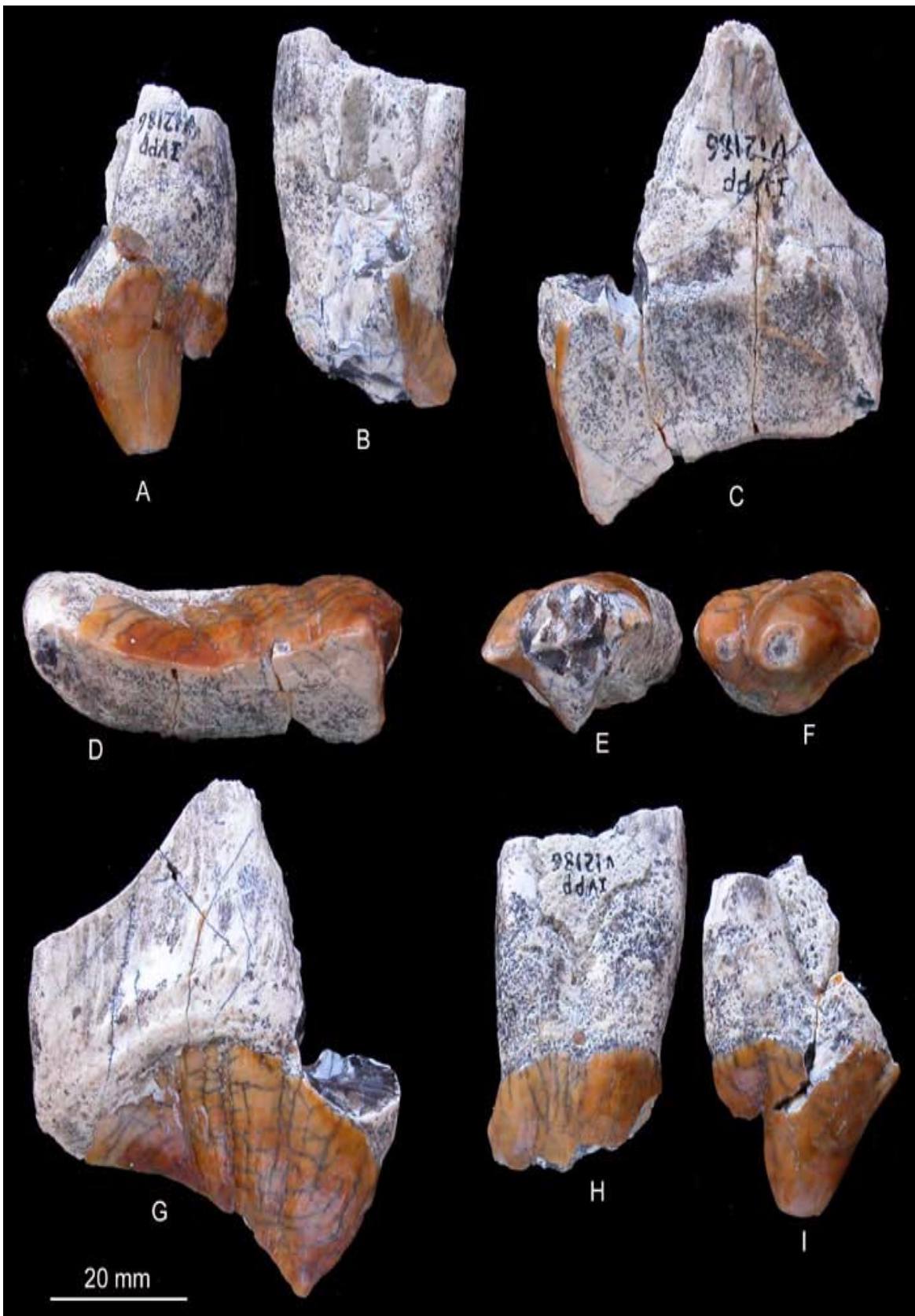


Figure 2. *Hyaenodon weilini* new species, IVPP V12186, holotype. Right P3 (A, lingual, F, occlusal, I, labial views), partial P4 (B, lingual, E, occlusal, H, labial views), and M2 (C, lingual, D, occlusal, G, labial views).

Referred Specimens: IVPP V12187, isolated left P4 and anterior half of M1, probably from IVPP loc. 8801 in Duitinggou area, Middle Member of the Xianshuihe Formation; IVPP V12188, isolated left P3, from IVPP loc. 9512, near the village of Huangyangtuo, basal white sandstone in a sand quarry, Middle Member of the Xianshuihe Formation; and IVPP V12189, isolated left m1, from IVPP loc. 9010, Yangtonggou, basal white sandstone, Middle Member of the Xianshuihe Formation (Figure 3).

Associated Fauna and Age: We here attempt to demonstrate this species to be the last known *Hyaenodon* in Eurasia, and thus it is a matter of some importance to establish the age of the Middle Member of the Xianshuihe Formation. Vertebrate fossils in the Zhangjiaping local fauna are mostly collected from sediments in and around several light colored coarse sandstones and fine gravels that are concentrated at the lower part of the Middle Member of the Xianshuihe Formation (Qiu et al. 1997; Qiu et al. 2001). Locally known as the “white sands,” in contrast to the “yellow sands” at the bottom of the Lower Member of the Xianshuihe Formation, the channel sandstones are useful as prominent stratigraphic marker beds in geologic mapping, although the sandstones tend to be thinner and less stable laterally toward the upper part of the Middle Member. The Zhangjiaping l.f., first proposed by Qiu (1990) and further elaborated on by Qiu et al. (1997; 2001), includes such early Miocene elements as the primitive ochotonid *Sinolagomys pachygnathus* and a large-tusked Asiatic rhino *Aprotodon lanzhouensis* (Qiu and Xie 1997). In particular, the Zhangjiaping l.f. appears to document the first Chinese appearance of proboscideans (see Qiu et al. 2001 for full faunal list). Constrained by the so-called Proboscidean Datum Event (Tassy 1990), Qiu et al. (2001) correlated the “white sands” beds in the Duitinggou section with magnetic Chrons C6n (in part) through C5Cr, approximately 17–20 Ma.

Diagnosis: The Lanzhou creodont is distinguished from the contemporaneous *Hyainailouros* in having more reduced protocones and metastyle notches in M1-2 with thin shearing blades. *Hyaenodon weilini* is substantially larger than all known species of *Hyaenodon* except *H. gigas*. It differs from the latter in its relatively smaller and lower crowned P4 with more distinct anterior accessory cusp and lingual cingulum, and its distinct anterior ridge on the paracone of M2.

Etymology: In fond memory of Will Downs, whose adopted Chinese name is Dong Weilin, a Chinese approximation of “Downs William,” and who enthu-

siastically participated in the Lanzhou Basin fieldwork.

Description: Isolated teeth in the holotype IVPP V12186 are regarded as belonging to the same individual because of their consistency of coloration and approximately same stage of wear. However, the possibility exists that they belong to more than one individual because there are moderate size differences between the left and right sides (Table 1).

The P3 is double rooted, and its posterior root is substantially larger than the anterior one, supporting a lingual swelling of the main cusp. The main cusp is slightly recumbent and followed behind by a low posterior accessory cusp. There are faint ridges on the anterior and posterior faces of the main cusp.

The P4 is about the same size as the P3 (in anteroposterior length) and is triple rooted. The lingual root forms the base of a swelled lingual cingulum. This lingual swelling is only slightly more pronounced than that on the P3, and there is no discrete protocone despite the additional root. The P4 main cusp and posterior accessory cusp are more recumbent than in the P3. In addition, the P4 has an incipient anterior accessory cusp that is not present on the P3 (more pronounced in IVPP V12187).

The two upper molars of the holotype are here regarded as M2s because of their considerably larger (anteroposterior length) size than the P4. A prominent M2 is a characteristic of the subfamily Hyaenodontinae, and the M1 is usually about the same size or only slightly larger than the P4. The M2 is highly hypercarnivorous with its long (anteroposteriorly) and thin (transversely) shearing blade and reduced protocone. Although there are three shallow grooves on the labial surface of the M2 (more distinctly displayed on the left M2), none seems to represent a notch between the paracone and metacone, because these grooves extend all the way to the base of the crown. It is likely that the paracone and metacone are fully fused into a single cusp. Instead, the grooves appear to be part of the tooth ornamentation since finer wrinkles are interspersed between the grooves. Wear on the metastyle has eliminated any trace of a metastyle notch (“carnassial notch”). The M2 protocone is extremely reduced (much of its crown was worn off); its existence is only suggested by a small root, which is closely compressed to the larger, labial root below the paracone, and by a shallow notch immediately behind the protocone, which produces a V-shaped enamel edge after wearing. This notch is visible on the left M2. The anterior border of the protocone is behind the anterior ridge of the para-

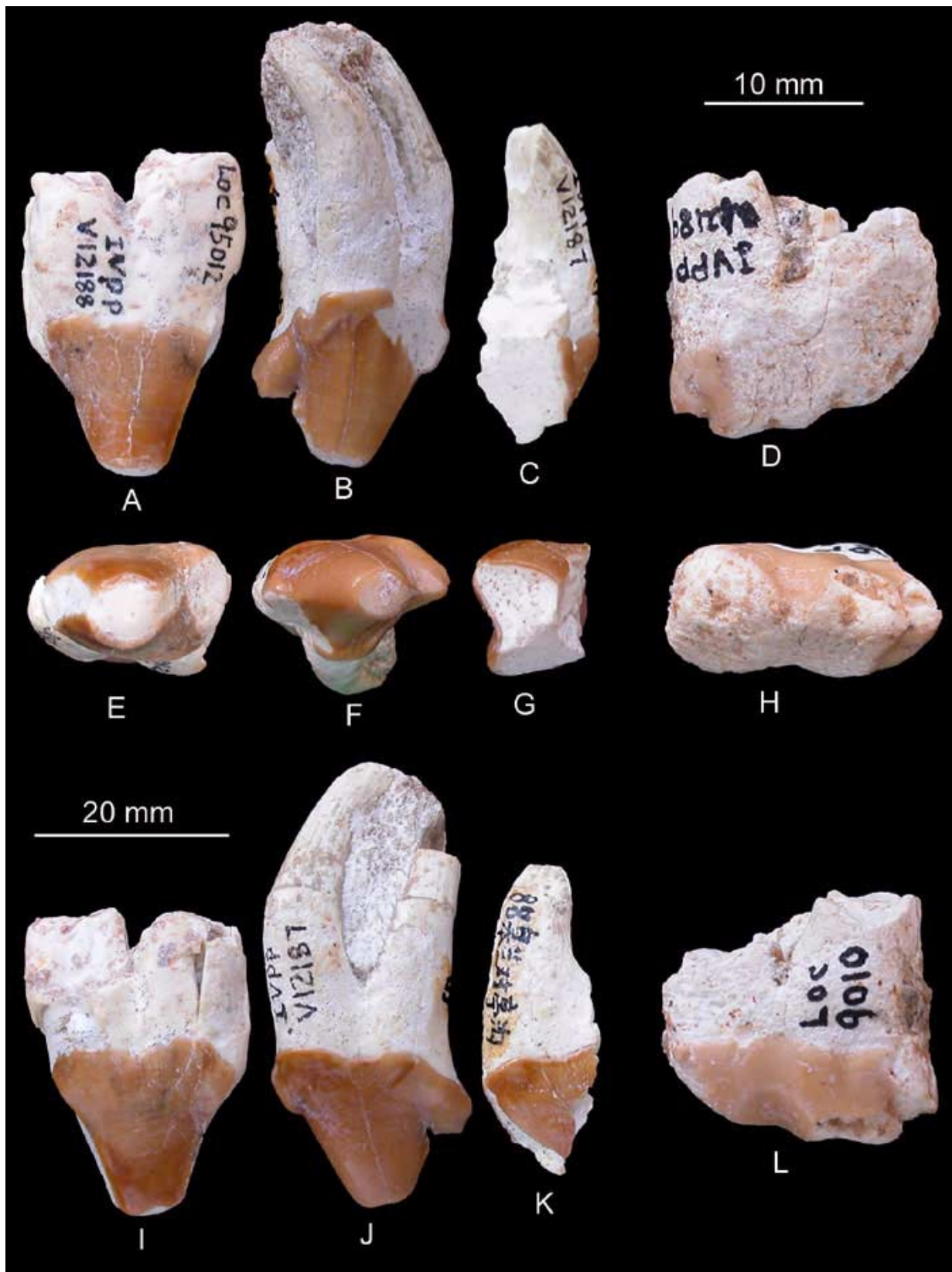


Figure 3. *Hyaenodon weilini* new species. Left P3, IVPP V12188 (A, lingual, E, occlusal, I, labial views); left P4, IVPP V12187 (B, lingual, F, occlusal, J, labial views); partial left M1, IVPP V12187 (C, lingual, G, occlusal, K, labial views); and right m1, IVPP V12189 (D, lingual, H, occlusal, L, labial views). Large scale (20 mm) is for A, B, C, E, F, G, I, J, K, and small scale (10 mm) is for D, H, and L.

Table 1. Measurements (in mm) of *Hyaenodon weilini* from Lanzhou Basin. Measurements for *H. gigas* are estimated from a combination of Dashzeveg's measurements and his figure 12 (1985), because he apparently adopted an unconventional system of measuring the dimensions of the roots at the points of contact with the maxilla.

	Lanzhou Basin <i>Hyaenodon</i>			<i>H. gigas</i> PSS	
	IVPP		IVPP		
	V12186		V121		
	left	right	V1218		
			87	8	27–10
P3 length		27.1		20.6	
P3 width		16.0		13.1	
P4 length	24.5	25.6	21.3		38.0
P4 width		18.0	14.5		24.0
M2 length	45.7	50.3			54.0
M2 width	18.8	18.3			22.0

cone, and there is a weak indentation between the protocone and paracone. A sharp ridge is present on the anterior surface of the paracone.

A heavily worn m1 (IVPP V12189), measuring 18.5 mm in length and 8.8 mm in width, reveals little more than the presence of a large protoconid-paraconid blade and a small talonid with a single trenchant hypoconid.

Discussion: The Lanzhou *Hyaenodon* represents the last survivor of this ancient lineage in northern and central Asia. Of the Miocene forms (see Zoo-geographic Remarks below), only *Hyainailouros* and *Hyaenodon* achieved the giant size and high degree of hypercarnivory (Helbing 1925; Koenigswald 1947; Ginsburg 1999b) seen in the Lanzhou specimens. Recent phylogenetic analyses suggest that these two genera may represent terminal members of two distinct clades within the family Hyaenodontidae (Polly 1993, 1996), and many of their hypercarnivorous characters (such as the loss of metaconids on lower molars) are independently acquired within the two clades.

Five nominal species of *Hyainailouros* were recognized by Ginsburg (1980): *H. sulzeri*, *H. bugtiensis*, *H. fourtaui*, *H. nyanzae*, and *H. napakensis*. All whose upper cheek teeth are known (including unpublished materials referable to *H. bugtiensis* from Chinji Formation of Pakistan, Barry, personal commun., 2004) still primitively retain a large (relative to those in *Hyaenodon*), lingually positioned protocone on the M1-2, and the shearing blade of the M1-2 is still relatively thick (mediolaterally) with a deep metastyle notch. Such primitive morphology of the M1-2 in *Hyainailouros* is in sharp contrast to the far more hypercarnivorous “carnassials” of *Hyaenodon*. In the Lanzhou materials, the degree

of hypercarnivory far exceeds that seen in *Hyainailouros* in terms of elongation of shearing blade, reduction of metastyle notch (“carnassial notch”), and reduction of protocone on the M2. The Lanzhou form is thus more readily referable to *Hyaenodon*.

Numerous species from Africa, Europe, Asia, and North America have been referred to *Hyaenodon* (37 by Lange-Badré 1979; 42 by Polly 1993). Most of them, however, are from the Eocene to Oligocene and are small to medium-sized predators. By early Miocene time, only a few relics are left. The last North American *Hyaenodon* (such as *H. brevirostris*) is found in the early Arikareean (late Oligocene) of California and the northern Great Plains (Mellett 1977; Gunnell 1998; Tedford et al. 2004). None of the North American *Hyaenodon* achieved the giant size of the Lanzhou taxon. In Europe, the last *Hyaenodon* are represented by such late Oligocene (Chattian) species as *H. milloquensis*, *H. bavaricus*, and *H. leptorhynchus*. They are small in size, their m1 being in the range of 7–8 mm (see summary in Dehm 1935) in contrast to the 18.5 mm of the Lanzhou *Hyaenodon*. Three species of *Hyaenodon* (*Isohyaenodon*) described by Savage (1965) from the Miocene of Africa, *H. andrewsi*, *H. matthewi*, and *H. pilgrimi*, were based on fragmentary lower jaws (and a single referred M1 of *H. pilgrimi*). Even the largest of the three species, *H. andrewsi* (8.9 mm in length), is considerably smaller than the Lanzhou *Hyaenodon*.

In Asia, *Hyaenodon* is present in the Paleogene of Mongolia, China, and Kazakhstan (e.g., Matthew and Granger 1924; Teilhard de Chardin 1926; Young 1937; Huang 1982; Dashzeveg 1985; Russell and Zhai 1987; Lange-Badré and Dashzeveg 1989; Huang 1993; Kordikova 1994; Lavrov 1999). Of these, the Mongolian records are the most complete, both in diversity and stratigraphic representation. As summarized by Lange-Badré and Dashzeveg (1989, figure 3), a pattern of declining diversity can be observed from about 3–4 species in the late Eocene to 1–2 species in the Oligocene.

Currently, seven species of *Hyaenodon* are recognized in the late Paleogene of Asia: *H. pervagus* Matthew and Granger 1924 from the Loh locality, early Oligocene Hsanda Gol Formation, *H. eminus* Matthew and Granger 1925 from the late Eocene Ergilin Dzo Formation, *H. yuanchensis* Young 1937 from middle Eocene Heti Formation of Yuanqu Basin, *H. mongoliensis* (Dashzeveg 1964) from Khoer Dzan and Bayan Tsav localities of the Ergilin-Dzo Formation, *H. incertus* Dashzeveg 1985 and *H. (=Neohyaenodon)* in Lavrov, 1999) *gigas* Dashzeveg 1985 from Khoer Dzan locality,

and *H. chunkhtensis* Dashzeveg 1985 from Chunkht locality of the Hsanda Gol Formation (see Russell and Zhai 1987 for a summary of these localities).

Only *Hyaenodon gigas* and *H. mongoliensis* approach the size of the Lanzhou *Hyaenodon*. *H. mongoliensis* is based on lower jaw and teeth only, and thus cannot be directly compared with the Lanzhou materials. Given that *H. gigas* and *H. mongoliensis* co-occur in the Khoer Dzan locality of the Ergilin-Dzo Formation, and even allowing that these two giant *Hyaenodon* species are distinct, it is likely that they are closely related (either sister species or anagenetically successive forms). If so, the following substantial differences of *H. gigas* from *H. weilini* also likely to apply to *H. mongoliensis*.

Based on Dashzeveg's (1985, figure 12) illustration, the P4 of *Hyaenodon weilini* differs from *H. gigas* in the following features: somewhat smaller M2 (Table 1), substantially smaller P4 (i.e., relatively small P4 compared to M2), and P4 with more distinct anterior accessory cusp and a lingual cingulum. Perhaps the most prominent difference between these two species is the considerably higher crowned P4 in *H. gigas* (see especially Dashzeveg 1985, figure 12b). Considering the fact that PSS 27-10, holotype of *H. gigas*, has suffered far more wear on the tip of the main cusp of the P4, the crown height of PSS 27-10 may be twice as tall as that of IVPP V12187. The P4 in PSS 27-10 shows substantial apical wear, in contrast to the shearing wear on the M1-2, indicating its primary function as a bone-crushing tooth. The M2 has gone through extensive wear on PSS 27-10 and shows signs of lingually bent shearing blades typical for many late adult individuals of *Hyaenodon*. PSS 27-10 appears to lack a distinct anterior ridge on the anterior face of the paracone, which is present in IVPP V12186. This ridge is present in earlier and more primitive species from North America (such as in some individuals of *H. vetus*, *H. montanus*, and *H. horridus*, see Mellett 1977, figures 6, 7, 10), and its absence in *H. gigas* may be another derived character.

A new genus and species, *Macropterodon zelenovi* Lavrov 1999, was named on a lower jaw fragment, PIN 3110/630, also from the Khoer Dzan locality in the Ergilin Dzo Formation. This taxon is mainly diagnosed on the basis of a large, high-crowned p4 that is relatively larger than the m1. Although lacking comparable materials of *Hyaenodon gigas* and *Macropterodon zelenovi*, we cannot help but note the similar giant size and robustness, as well as a similarly massive P4 in both species. The possibility of that these two species are synon-

ymous should be explored when additional materials become available.

The size difference between the P3s in IVPP V12186 (25.6 x 18.0 mm) and V12187 (21.1 x 14.3 mm) is substantial (more than 20%), but is well within the documented variation (16 to 23 mm for P3s, or more than 40%) in *Hyaenodon horridus*, the largest species in North America (Mellett 1977). At the present our sample size is too small to evaluate intraspecific variations and we treat this size difference as variation within species.

Overall, the above outlined features seem to indicate a somewhat more primitive stage of evolution in *Hyaenodon weilini*, and considering the long hiatus (more than 10 m.y.) between *H. weilini*, on the one hand, and *H. gigas* and *H. mongoliensis*, on the other, it seems unlikely that the Lanzhou *Hyaenodon* is conspecific with the Ergilin Dzo forms. Instead, it represents the last survivor of this genus in Eurasia, one that developed gigantism independently from its earlier Asian relatives.

Hyaenodon pervagus

Matthew and Granger, 1924

Material: IVPP V13573, an isolated left p4, from IVPP loc. 9016, 100 m west of the village of Duitinggou from basal yellow conglomeratic sandstones, Lower Member of the Xianshuihe Formation, Nanpoping local fauna, in magnetic Chron C11r (about 30.3–30 Ma) in late early Oligocene (Qiu et al. 2001).

Comments: IVPP V13573 (Figure 4) has a tall, slightly recumbent main cusp, a thin anterior ridge along its anterior face, and a posterior ridge reaching down to the posterior accessory cusp. The posterior accessory cusp is well developed. A very weak lingual cingulum is present on the anterior and posterior half of the tooth.

Measuring 17.4 x 7.2 mm, IVPP V13573 is nearly identical in size to the holotype of *Hyaenodon pervagus* Matthew and Granger 1924 (17.3 x 8.4 mm) from the Hsanda Gol Formation, although the latter falls in the upper range of the species (Lange-Badré and Dashzeveg 1989, table 2). The size and shape of IVPP V13573 easily distinguish it from other Hsanda Gol species (p4 of *H. chunkhtensis* measuring 7.0 x 3.0 mm, p4 of *H. eminus* measuring 11.0 x 5.5 mm, and *H. incertus* having a robust and broad p4 measuring 17 x 11 mm).

Order CARNIVORA Bowdich, 1821

Infraorder ARCTOIDEA Flower, 1869

Family AMPHICYONIDAE Haeckel, 1866

Genus *ICTIOCYON* Crusafont-Pairó et al., 1955

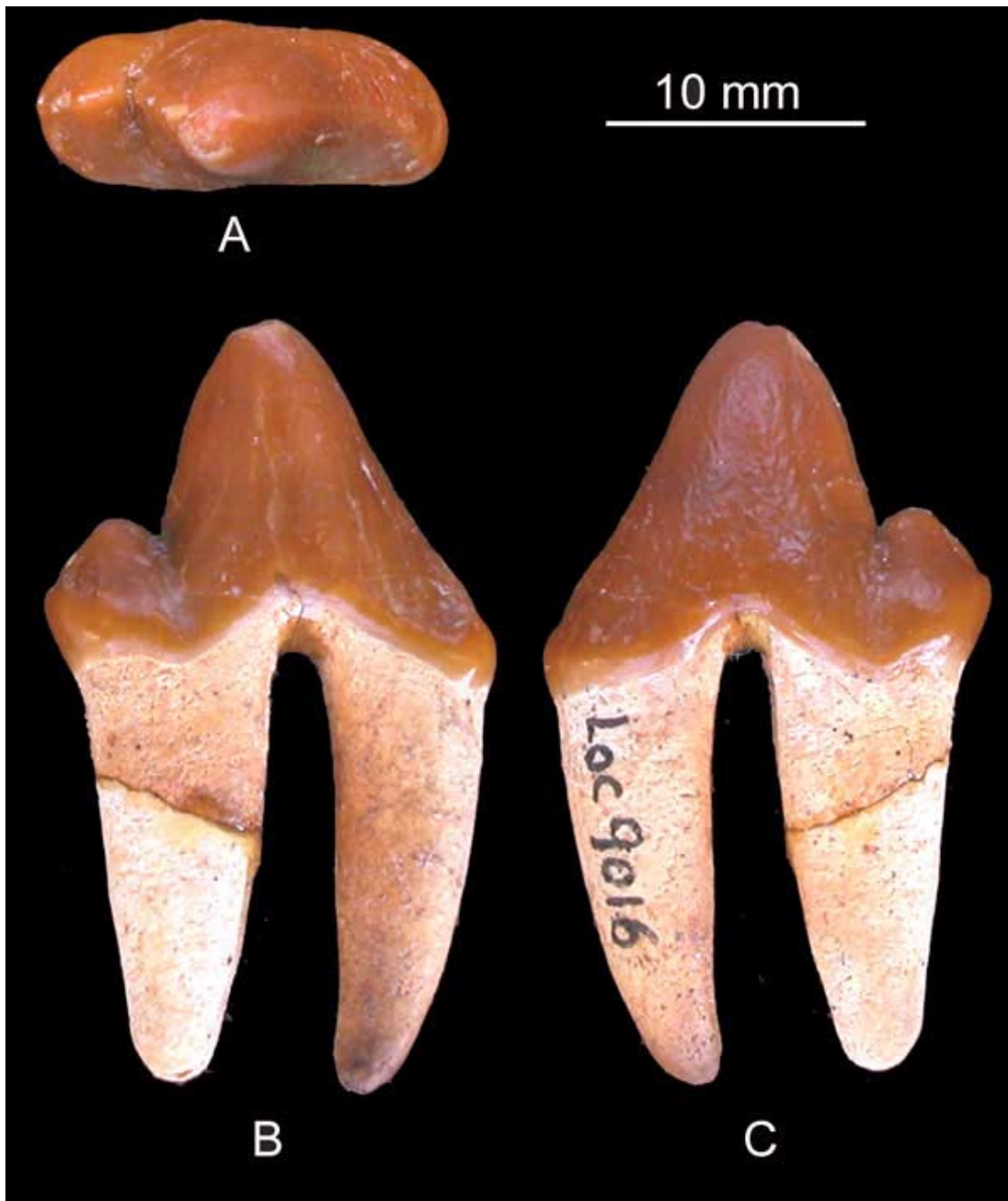


Figure 4. *Hyaeodon pervagus* Matthew and Granger 1924, IVPP V13573, left p4 (A, occlusal, B, lingual, C, labial views).

Ictiocyon cf. *I. socialis* (Schlosser 1904)

?*Ictiocyon* sp.: Qiu et al. 1997, p. 186.

Ictiocyon cf. *I. socialis* (Schlosser 1904): Qiu et al. 2001, p. 378.

Materials: IVPP V12185, partial right horizontal ramus with anterior half of p4 and alveoli of c1-m3, collected from IVPP locality 9308, N 36° 13' 52.1" E 103° 36' 23.9", south of the village of Qujiachuan, on a small road cut in the first white sands,

Middle Member of the Xianshuihe Formation, Zhangjiaping l.f., early Miocene (see further discussion in Associated Fauna and Age under *Hyaeodon weilini*).

Description: This large fox-sized carnivoran has a robust horizontal ramus (Figure 5), which is rather deep relative to its length. The jaw depth is 22.8 mm below the talonid of m1 (on the lingual side). The anteroventral corner of the masseteric fossa is preserved and located rather high, about 10 mm



Figure 5. *Ictiocyon* cf. *I. socialis* (Schlosser, 1904), IVPP V12185, right horizontal ramus with broken p4 (A, occlusal, and B, labial views).

above the ventral border of the ramus. There are two mental foramina: one below the anterior root of the p2 and the other below the posterior root of the p3. The premolar tooththrow is short, and the p3-m1 are apparently in close contact or even imbricate slightly. There is a short diastema between the p2 and p3. The p1 and m3 are single rooted, whereas the p2-m2 are all double rooted. The anterior half of the p4 indicates a short but rather high-crowned tooth, its anterior ridge of the main cusp being rather erect as compared to the more recumbent anterior ridges in many amphicyonids. Its anterior cingulum swells slightly to form a low, cingulum cusp. Alveoli of the corresponding teeth indicate a robust lower canine, a broad m1-2, an elongated m2, and a reduced m3.

Measurements of IVPP V12185 (all in alveolar length and in mm): p1 = 2.9, p2 = 7.9, p3 = 7.3, p4 = 9.8, m1 = 16.8, m2 = 8.7, m3 = 3.8, and p1-m3 = 62.3.

Comparison: From what little is preserved, IVPP V12185 possesses amphicyonid characters such as a high position (relative to the ventral border) of the masseteric fossa and a large m2. The Lanzhou specimen is slightly more derived than European and North American Oligocene small- to medium-sized amphicyonids (such as *Pseudocyonopsis*, *Cynelos*, *Daphoenus*, and *Temnocyon*) in its short-

ened premolar tooththrow and correspondingly broad and closely spaced premolars.

Ginsburg (1992) recognized two distinct lineages of small, short-snouted amphicyonids in the early to middle Miocene of Europe: an early Miocene *Ictiocyon* and a mostly middle Miocene *Pseudarctos*, in contrast to an earlier hypothesis of a single anagenetic lineage of *Pseudarctos* that decreases in size through time (Kuss 1965). The Lanzhou specimen readily falls in the size range of both *Pseudarctos* and *Ictiocyon*, and has similarly short and closely spaced premolars, derived characters shared by both genera. In addition, V12185 has a rather long m2 relative to its m1, a derived feature that is well-developed in *I. socialis* (Ginsburg 1992, figure 4, plate II), and still primitively retains a p1, which was lost in *Pseudarctos*. Therefore, the Lanzhou specimen is here referred to *Ictiocyon* based on its possession of a large m2 and its lack of a *Pseudarctos* synapomorphy of the loss of p1. Caution, however, must be exercised in an identification based on so little material.

A short rostrum and imbricated premolars also characterize the European Oligocene *Brachycyon*. However, *Brachycyon* is much larger and has a much more robust lower jaw than the Lanzhou specimen. In addition, the horizontal ramus of *Brachycyon* tends to expand ventrally near both its anterior and posterior ends (Ginsburg 1966) in contrast to a rather straight ventral border in the

Lanzhou specimen. Finally, the m2 of *Brachycyon* is not enlarged as in the Lanzhou specimen.

In Europe, the monotypic *Ictiocyon socialis* is known from several early Miocene localities (Ginsburg 1992; Viranta 1996; Ginsburg 1999a), Wintershof (MN3), Artenay (MN4a), Solnhofen fissures (MN4), and El Canyet (MN4). *Pseudarctos bavaricus*, on the other hand, occurs later in MN4b through MN9, and a series of three subspecies of *P. bavaricus* were recognized by Ginsburg to represent a morphocline of increasing size through time. The present recognition of a Chinese occurrence of *Ictiocyon* extends its geographic range to East Asia and suggests an early Miocene age of the first white sands in the Lanzhou strata.

Amphicyonidae gen. et sp. indet.

Material: IVPP V13574, posterior half of left p4, acquired from local villagers, specimen probably from near IVPP loc. 8801 in Duitinggou area, in basal white sandstones, Middle Member of the Xianshuihe Formation, Zhangjiaping l.f., early Miocene (see further discussion in Associated Fauna and Age under *Hyaenodon weilini*).

Comments: Although of large size, this tooth is primitive in its retention of a well-developed posterior cingulum and posterior accessory cusp, features that tend to occur in less derived species of amphicyonids (most derived amphicyonids tend to reduce and simplify their premolars through time). On the other hand, its broadened heel (11.0 mm wide) reminds us of robust forms such as *Gobicyon* (Colbert 1939), which is known only in the middle Miocene of China (a jaw from Serbia referred to *Gobicyon* by Pavlovic and Thenius [1959] was recently transferred to *Haplocyonoides* by Ginsburg [1999a]). With the scanty material available, it is not possible to further explore the identity of this form.

Musteloidea indet

?*Plesictis* sp.: Qiu et al. 1997, p. 186.

Plesictis cf. *P. vireti* Dehm, 1950: Qiu et al. 2001, p. 378.

Material: IVPP V12190, isolated right m1, from IVPP locality 9309, N 36° 13' 44.1" E 103° 36' 18.6", Daochazigou, near a sand and gravel quarry south of Qujiachuan, in the third white sands in the Middle Member of the Xianshuihe Formation, Zhangjiaping l.f., early Miocene (see further discussion in Associated Fauna and Age under *Hyaenodon weilini*).

Comments: This isolated carnassial (Figure 6), 4.6 mm long and 2.1 mm wide, is the smallest car-

nivoran from the Lanzhou Basin, smaller than any known early Miocene carnivoran in Asia. The metaconid is well developed, slightly offset (located slightly posterior to) from the protoconid in occlusal view, and of approximately the same height as the paraconid. The talonid appears to be narrow, but this is partly due to damage to the labial portion of the talonid. The talonid is dominated by a centrally located hypoconid (only the lingual half is preserved), and the entoconid is poorly differentiated. The possibility that this tooth is a deciduous p4 cannot be ruled out.

With the poor preservation, IVPP V12190 cannot be easily identified. The relatively low-crowned trigonid and well-developed metaconid suggest a caniform carnivoran (in contrast to higher crowned feliforms). Among early Miocene caniforms, certain European basal musteloids, such as *Plesictis* (Wolsan 1993; Ginsburg 1999a), are closest in size and overall morphology, although a definite match awaits discovery of additional specimens.

BIOGEOGRAPHY

Qiu (1997) listed several large mammals, mostly large herbivores, which are shared by early Miocene faunas in Lanzhou and in Bugti, Pakistan: a gomphothere proboscidean, the schizotheriine chalicothere *Phyllotillon*, giant paraceratherine rhinos, the endemic Asian rhino *Aprotodon*, and the large archaic artiodactyl *Paraentelodon*. Such faunal exchange is indicative of a lack of barriers, at least for large mammals, between the two regions in the early Miocene. This is in contrast to biogeographic differentiation observed in the middle and late Miocene of mainland Asia, commonly attributed to the uplift of the Tibetan Plateau (Qiu and Li, in press).

The carnivores from Lanzhou, on the other hand, appear to be mostly Palearctic elements and no southern Asian affinity can be detected. The Lanzhou *Hyaenodon* is the only Miocene survivor of the genus outside Africa. *Hyaenodon* is a highly hypercarnivorous (almost exclusively meat eating) and cursorial predator (Morlo 1999). This highly diverse genus is one of the most wide-ranging, highly mobile predators, occupying the entire northern hemisphere. As archaic predators, creodonts are mostly dominant in the Paleogene. By Miocene time, hyaenodonts were largely replaced by carnivorans in Eurasia and North America, and were survived by only a few relicts in Africa, Europe, and southern Asia. A single species, *Hyaenailouros*, is left in the early Miocene of Europe (Ginsburg 1999b). In the early and middle Miocene of eastern and northern Africa, these archaic forms

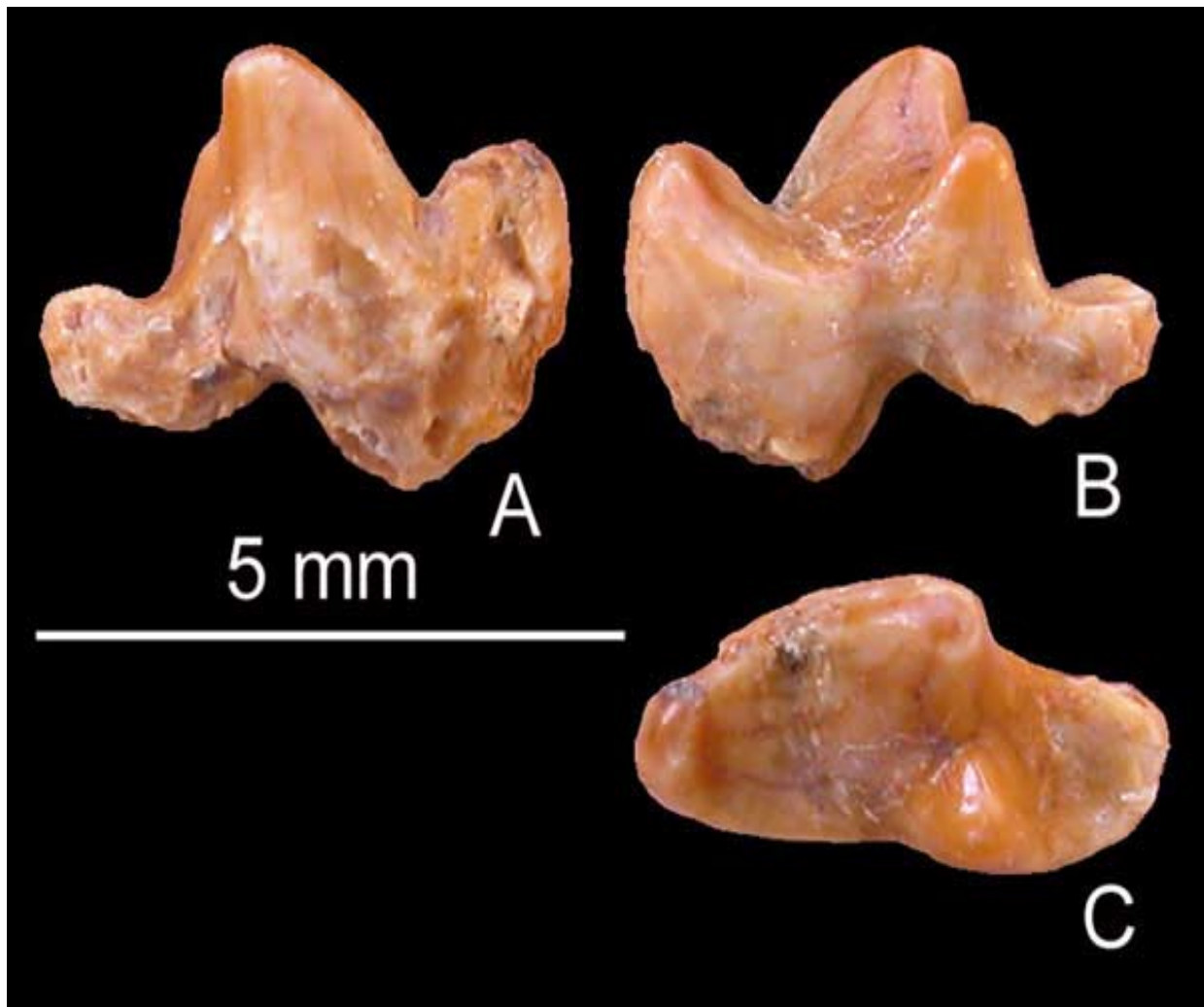


Figure 6. Musteloidea indet, IVPP V21290, right m1 (A, labial, B, lingual, and C, occlusal views).

still thrived in relative isolation and include modest generic diversity: *Teradon*, *Anasinopa*, *Metasinopa*, *Dissopsalis*, *Metapterodon*, *Leakitherium*, *Hyaenodon* and *Hyainailouros* (Savage 1965; Ginsburg 1980; Barry 1988; Morales et al. 1998). In India and Pakistan, *Dissopsalis*, *?Metapterodon*, and *Hyainailouros* are Miocene survivors, showing geographic relationships to both Africa and Europe (Pilgrim 1908, 1914; Colbert 1933; Barry 1980, 1988), but not to mainland Asia. The immediate ancestry of *Hyaenodon weilini* is unclear, for lack of a comparable form elsewhere. It seems likely that this Chinese survivor was derived from northern Eurasia stocks, instead of southern Asia.

Other taxa from Lanzhou, such as *Ictiocyon*, may also indicate European affinity, although materials are too limited to draw firm conclusions. A more definite assessment has to wait for improvement over the currently limited number of taxa available from the Lanzhou Basin.

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