

The first Old World occurrence of the North American mustelid *Sthenictis* (Mammalia, Carnivora)

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Tseng Z. J., O'Connor J. K., Wang X. & Prothero D. R. 2009. — The first Old World occurrence of the North American mustelid *Sthenictis* (Mammalia, Carnivora). *Geodiversitas* 31 (4): 743-751.

ABSTRACT

The Tunggur Formation in Inner Mongolia has produced a well-known middle Miocene *Platybelodon* fauna; this fauna has provided some evidence of intercontinental

KEY WORDS

Mammalia,
Carnivora,
Mustelidae,
Old World,
China,
Inner Mongolia,
middle Miocene,
Tunggur Formation,
new species.

exchanges of carnivoran taxa during that time. Here we describe a new immigrant mustelid from the Tunggur Formation. The new material, composed of two partial dentaries, belongs to the genus *Sthenictis*. A new species, *S. neimengguensis* n. sp., is named after the dentaries which represent the first occurrence of this genus outside North America. *Sthenictis neimengguensis* n. sp. is closest in size and morphology to the North American *S. dolichops*, but the former has a more slender dentition and mandible. In terms of carnassial morphology, the less trenchant m1 talonid and a well-developed m1 metaconid in *S. neimengguensis* n. sp. are plesiomorphic characters of the Mustelinae. The relatively elongated tooth row and simple premolar morphology, however, unites it with other species of *Sthenictis*. This combination of characters excludes *Sthenictis* from both the highly hypercarnivorous *Hoplictis-Ischyriactis-Eomellivora* group and *Iberictis-Plesiogulo* group, and seems to represent that of a basal lineage with intermediate morphology.

RÉSUMÉ

Première occurrence du mustélidé nord-américain Sthenictis (Mammalia, Carnivora) dans l'Ancien Monde.

La formation Tunggur en Mongolie intérieure a fourni une faune bien connue à *Platybelodon* du Miocène moyen ; cette faune a montré des preuves d'échanges intercontinentaux de taxons de carnivores durant cette époque. Un nouveau migrant mustélidé de la formation Tunggur est décrit. Ce nouveau matériel, constitué par deux dentaires partiels, est rattaché au genre *Sthenictis*. Une nouvelle espèce, *S. neimengguensis* n. sp., est érigée à partir de ces dentaires qui représentent la première occurrence de ce genre hors d'Amérique du Nord. *Sthenictis neimengguensis* n. sp. a une taille et une morphologie très proches du taxon nord-américain *S. dolichops*, mais possède une dentition et une mandibule plus minces. Concernant la morphologie de la carnassière, le tranchant moins prononcé du talonide de la m1 et la présence d'un métacônide sur la m1 bien développé chez *S. neimengguensis* n. sp. sont des caractères plésiomorphiques des mustélidés. Toutefois, la rangée dentaire relativement allongée ainsi que la morphologie simple de la prémolaire rattachent ce taxon aux autres espèces de *Sthenictis*. Cette combinaison de caractères exclut *Sthenictis* des groupes hautement hypercarnivores *Hoplictis-Ischyriactis-Eomellivora* et *Iberictis-Plesiogulo*, et semble plutôt représenter celle d'une lignée basale de morphologie intermédiaire.

MOTS CLÉS

Mammalia,
Carnivora,
Mustelidae,
Ancien Monde,
Chine,
Mongolie intérieure,
Miocène moyen,
Formation Tunggur,
espèce nouvelle.

INTRODUCTION

Mammal fossils from the Tunggur Formation of Inner Mongolia were first documented by the American Museum of Natural History's Central Asiatic Expedition in 1928 (Andrews 1932), and are well known for its middle Miocene *Platybelodon* Fauna. Particularly noteworthy is the presence of North American immigrants (e.g., *Leptarctus*

Leidy, 1856) as well as taxa that emigrated to North America (such as *Sansanosmilus* Kretzoi, 1929 and *Pliohocyon* Ginsburg, 1955) (Wang *et al.* 2003). Here we describe another immigrant, *Sthenictis* Peterson, 1910, from North America, and demonstrate once again a modest exchange between Asian and North American continental biota.

The Tunggur Formation has a paleomagnetic age of 13 to 11.8 Ma (Wang *et al.* 2003; but see

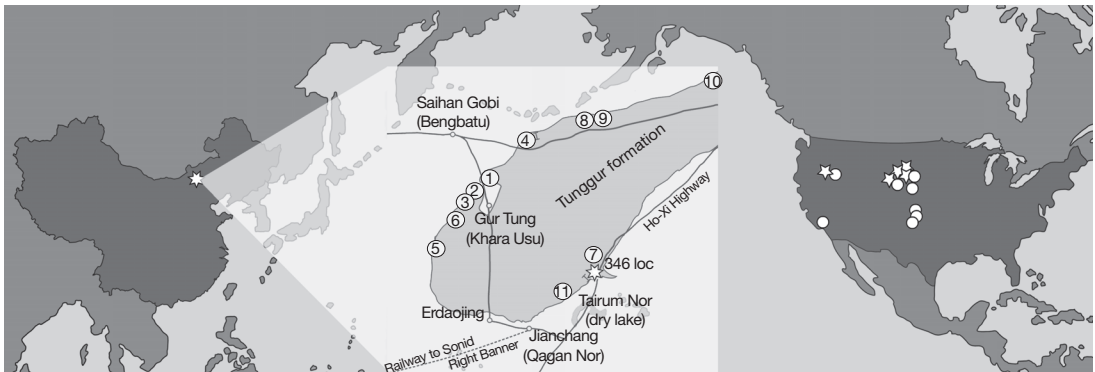


FIG. 1. — Locality map of *Sthenictis neimenguensis* n. sp. (IVPP V15873) and known occurrences of the genus *Sthenictis* Peterson, 1910 in North America: ☆, locations of holotype specimens of species of *Sthenictis*; ○, localities of specimens referred to the genus; ○, locality of occurrence in Inner Mongolia; 1, Mandelin Chabu; 2, Aoershun Chaba; 3, Zhunwuguer; 4, Moergen loc; 5, *Platybelodon* Quarry; 6, Wolf Camp; 7, 346 locality; 8, Aletexire loc; 9, Huerquolajin loc; 10, PM-08 loc; 11, South Camp.

Deng *et al.* 2007 for an alternative interpretation). Informally, the formation is divided into two sedimentary units; the upper unit produces the Tunggur Fauna (= *Platybelodon* Fauna) and the lower unit produces the Tairum Nor Fauna (Fig. 1). The Tairum Nor section can be further subdivided into an upper red mudstone, a middle channel sandstone, and a lower red mudstone. For a more comprehensive review of the Tunggur Formation and a complete faunal list see Wang *et al.* (2003) and Qiu *et al.* (2006).

The new material described here is referred to the genus *Sthenictis*, an extinct lineage of Mustelidae with a temporal range extending from the late Hemingfordian (~17.5 Ma) through the Clarendonian (~9 Ma) North American Land Mammal Ages (NALMAs) (Baskin 1998; Tedford *et al.* 2004). This genus shares a suite of symplesiomorphic characters, such as slender and simple lower premolars and moderately developed m1 talonid basin, with basal mustelines; these musteline characteristics combined with larger body size are diagnostic features of the genus. *Sthenictis* has previously only been described from North American localities. The genus includes six named species: *S. bellus* Matthew, 1932, *S. dolichops* Matthew, 1932, *S. robustus* Cope, 1890, *S. jun-turensis* Shotwell & Russel, 1963, *S. lacota* Matthew & Gidley, 1904, and *S. campestris* Gregory,

1942 (Baskin 1998). Holotype specimens of all species, with the exception of *S. campestris*, and a majority of referred specimens consist of isolated and/or fragmentary mandibles. Postcranial material is almost completely unknown, the exception being an undescribed skeleton (F:AM 25235) from the Burge Fauna of Nebraska (Dingus *et al.* 1994). The genus itself requires taxonomic revision, which goes beyond the scope of this paper and thus most referred specimens are omitted from comparison here, pending further investigation (see Baskin 2005, for additional discussion).

ABBREVIATIONS

Lp1-Lm1	maximum length of the respective tooth;
Wp1-Wm1	maximum width of the respective tooth;
Ltgm1	length of the trigonid of m1;
Ltdm1	length of the talonid of m1;
AMNH	American Museum of Natural History, New York;
F:AM	Frick collection, AMNH;
IPHG	Institut für Paläontologie und historische Geologie, Ludwig-Maximilian-Universität, Munich;
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing;
MNHN	Muséum national d'Histoire naturelle, Paris;
UOMNH	University of Oregon Museum of Natural History, Eugene, Oregon;
UPM	University of Uppsala Museum of Evolution, Uppsala.

SYSTEMATICS

Class MAMMALIA Linnaeus, 1758
 Order CARNIVORA Bowdich, 1821
 Family MUSTELIDAE
 Fischer von Waldheim, 1817
 Subfamily MUSTELINAE
 Fischer von Waldheim, 1817
 Genus *Sthenictis* Peterson, 1910

Sthenictis neimengguensis n. sp.
 (Table 1; Figs 2; 3)

"*Sthenictis* n. sp." – Wang *et al.* (2003): 26.

HOLOTYPE. — IVPP V15873, partial right mandible with p1-m1 and partial left mandible with m1 and partial m2 from the same individual. Collected by Xiaoming Wang on 4 August 1998.

ETYMOLOGY. — *Neimengguensis* refers to Inner Mongolia (Neimenggu in Chinese), where the new species was discovered.

TYPE LOCALITY. — Locality 346 (formerly 356) of the Tairum Nor locality area (43°24'45.3"N, 113°06'50.9"E), middle channel sandstone of the Tunggur Formation, Inner Mongolia, China.

AGE. — ~12.2 Ma, middle Miocene Tunggur Formation (Wang *et al.* 2003).

DIAGNOSIS. — A medium-sized species of *Sthenictis*; most similar in morphology to *S. dolichops* but with narrower p4 and m1, and shallower jaws; larger in overall size than *S. bellus*, *S. robustus*, and *S. jurentensis*; smaller than *S. lacota*, with narrower premolars and first molar; p1-p4 simple as in other species of *Sthenictis*; p4 posterior accessory cusp present.

DESCRIPTION

The holotype specimen (IVPP V15873) is best represented by the right mandible which has complete p1 to m1 preserved. The total mandibular length is 84.83 mm; the tooth row length is 44.61 mm from p1 to m1. The mandible is close to twice the m1 crown height immediately ventral of the m1 (Fig. 2). The p1 is reduced to one small, simple cusp. The p2 is small and slender, the anterior half reduced. The p3 is nearly symmetrical; p1 through p3 are unornamented. The p4 is larger than the p3 and very similar in shape with the exception of a

well-developed posterior accessory cusp. The m1 of *S. neimengguensis* n. sp. shows greater lateral compression relative to other species of *Sthenictis* (Fig. 3). The m1 talonid is slightly trenchant, with the labial border higher than the lingual side; the posterior slope of the protoconid and the anterior slope of the hypoconid form an angle slightly less than 90° while the posterior slope of the metaconid forms a U-shape with the lingual margin of the talonid. The m1 hypoconid is moderately developed. The partial left mandible bears a complete m1 which is the only tooth preserved in the specimen. There are two roots exposed at the position of the p4. The m2 is poorly preserved but is clearly single-rooted. The examination of tooth enamel using the method outlined in Stefen (2001) showed undulating Hunter-Schreger bands throughout the dentition.

COMPARISON AND DISCUSSION

Based on dental characteristics, *Sthenictis neimengguensis* n. sp. and its congeneric species are at a morphological stage intermediate between and probably basal to the *Iberictis* Ginsburg & Morales, 1992-*Plesiogulo* Zdansky, 1924 and *Hoplictis* Ginsburg, 1961-*Ischyriictis* Helbing, 1930-*Eomellivora* Zdansky, 1924 morphological groups, a phylogenetic framework proposed by Ginsburg & Morales (1992). Its overall evolutionary position is discussed below.

The oldest species of *Sthenictis* is *S. bellus* of the late Hemingfordian (Matthew 1932), about 5 Ma older than *S. neimengguensis* n. sp. The lower tooth row of *S. bellus* is similar to *S. neimengguensis* n. sp. in overall morphology, but *S. bellus* is smaller than all other congeneric species, including the contemporaneous *S. dolichops* (Hemingfordian-Barstovian; Matthew 1932), which is closest to *S. neimengguensis* n. sp. in overall size (Table 1). *Sthenictis dolichops*, however, has wider p4 and m1 than *S. neimengguensis* n. sp., which gives it a more robust appearance. In addition, the depth of the mandibular corpus is close to 2.5 times the height of m1 protoconid in *S. dolichops*, whereas in *S. neimengguensis* n. sp. the mandibular depth is just under two times

TABLE 1. — Lower dentition measurements (in mm) of *Sthenictis neimengguensis* n. sp., related North American species, and the European *Iberictis buloti* Ginsburg & Morales, 1992, *Ischyriictis zibethoides* Blainville, 1841 and *Ischyriictis anatolicus* Schmidt-Kittler, 1976. Unless noted, measurements were taken with a vernier caliper. Abbreviations: see text; l, left dentition; r, right dentition. Notes: 1, Shotwell *et al.* 1963; 2, Matthew & Gidley 1904; 3, Ginsburg & Morales 1992.

	<i>Sthenictis neimengguensis</i> (V15873)		<i>Sthenictis junturensis</i> (UOMNH F-6694 ¹)	<i>Sthenictis lacota</i> (AMNH 10810 ²)	<i>Sthenictis dolichops</i> (AMNH 18264)	<i>Iberictis buloti</i> (MNHN LRM1044 ³)	<i>Ischyriictis zibethoides</i> (MNHN Sa4078)	<i>Ischyriictis anatolicus</i> (IPHG 1967.VI.646)
	r	l						
Lp1	2.9							4.4
Wp1	2.9							3.1
Lp2	6.5		5.7	9.0	6.9		7.9	6.6
Wp2	3.6		3.7	4.0	3.7		4.5	3.9
Lp3	7.8		6.6	10.0	8.1	7.5	8.7	7.9
Wp3	4.0		4.0	5.0	4.3	4.1	4.8	4.4
Lp4	10.1		7.7	13.0	10.1	10.2	12.7	11.7
Wp4	4.7		4.3	6.5	5.6	5.1	6.4	5.6
Lm1	15.6	15.7	12.7	18.5	16.9	14.7	17.4	16.1
Wm1	5.8	5.9	5.8	7.0	7.7	6.2	8.1	7.8
Ltgm1	11.5	11.7			11.2		12.3	12.1
Ltlm1	4.1	4.0			5.6		5.1	4.0

the protoconid height. The mandible of the late Barstovian *Sthenictis robustus* has four mental foramina, whereas in *S. neimengguensis* n. sp. only two are present (Fig. 2). In addition, the m1 length in *S. neimengguensis* n. sp. is 30% larger than in *S. robustus* (Cope 1890). The late Barstovian to Clarendonian *Sthenictis junturensis* has two mental foramina on the lower jaw (Shotwell *et al.* 1963) just as in *S. neimengguensis* n. sp.; however, *S. junturensis* lacks ap4 posterior accessory cusp which is well-developed in *S. neimengguensis* n. sp. (Fig. 2). *Sthenictis junturensis* also has anteroposteriorly shorter teeth than *S. neimengguensis* n. sp. (Fig. 3). *Sthenictis lacota*, a Clarendonian species, is larger but possesses a more slender dentition than the slightly older *S. robustus* (Matthew & Gidley 1904). Compared to *S. neimengguensis* n. sp., *S. lacota* is not only larger but also has a relatively broader p4 and m1 (Fig. 3). The sixth species, *Sthenictis campestris*, another Clarendonian form but only known by a partial right maxilla, shares certain craniodental features with the European *Trochictis* von Meyer, 1842 (Gregory 1942). Gregory (1942) noted that the lateral flaring of the snout in *S. campestris* is similar to the extent seen in *Trochictis*, although the palate width is close to that of *Plesiogulo* and *Gulo* Pallas, 1780. Furthermore, the M1 paracone and

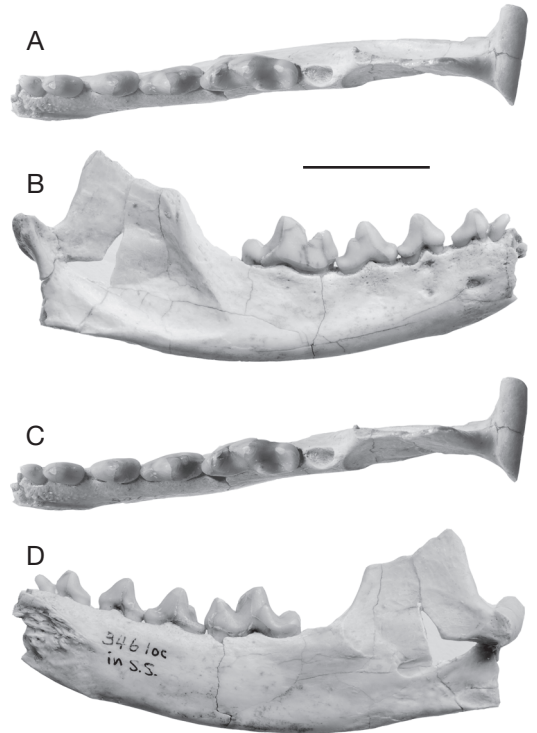


FIG. 2. — Holotype of *Sthenictis neimengguensis* n. sp., IVPV V15873, right partial dentary: occlusal (in stereo, the stereo pair is A and C), labial (B), and lingual (D) views. Scale bar: 20 mm.

metacone are more widely separated in *S. campestris* than in *Ischyriactis*; the smaller size of the M1 metacone and a more expanded lingual cingulum in *Eomellivora* also differ from *S. campestris* (Gregory 1942). There is no directly comparable material between *S. campestris* and *S. neimengguensis* n. sp., but the distinction of the upper dentition in *S. campestris* to the *Eomellivora* and *Plesiogulo* lineages does not contradict the interpretation of the position of *Sthenictis* as intermediate and basal to morphological groups represented by those taxa. Lastly, an undescribed specimen (F:AM 25235) referred to in the introduction has many similarities in its upper dentition to *S. campestris*: similar overall size, conical P4 protocone with no constriction of the connection. However, the M1 morphology in the undescribed form appears quite different; it is anteroposteriorly more compressed on both the lingual and labial sides compared to *S. campestris*. The lower dentition is intermediate in size between *S. lacota* and *S. dolichops*, and the premolars appear relatively narrower, but the m1 talonid more trenchant, than in *S. dolichops*. The undescribed form is slightly larger than *S. neimengguensis* n. sp.; no further comparisons will be made here as the specimen remains unstudied.

After the first appearance of the genus *Martes* Pinel, 1792 in Europe during the early Miocene, a group of larger-bodied mustelids diversified, beginning with the basal genus *Dehmictis* Ginsburg & Morales, 1992 (Ginsburg 1999). From an ancestral stock represented by *Dehmictis* (early Miocene of Europe, MN3), the genera *Trochictis*, *Iberictis*, *Hoplictis*, and *Ischyriactis* evolved in three different morphological directions (Ginsburg & Morales 1992; but see Ginsburg & Morales 2000 for an alternative scenario). *Trochictis* (MN4-5) is thought to represent a basal form that evolved into lutrines (otters) with subsequent evolution of a P4 lingual cingulum with enlargement of M1 for increased surface area for crushing. The genus *Iberictis* (MN4), although hypercarnivorous, showed a tendency to remain lower-crowned and develop strong cingula at the base of the premolars, giving the teeth a buttressed and robust appearance. This trend is emphasized in *Plesiogulo*

(late Miocene). The genera *Hoplictis* (MN4-8 and Clarendonian) and *Ischyriactis* (MN4-12), on the other hand, evolved toward hypercarnivory with reduction of m1 talonid and metaconid while retaining a more elongate profile of the premolars. *Eomellivora*, a more derived member of this group, follows this trend but with an expansion of the base of the crown to increase robustness of the premolars (MN9 and on; Ginsburg 1999). The dental morphology of *Sthenictis* has a slender profile as observed in species of *Hoplictis* and *Ischyriactis*, but *Sthenictis* retains a less trenchant talonid basin and a distinct m1 metaconid as in the *Iberictis-Plesiogulo* group (Fig. 3). In North America, the taxa included in what is called Ischyriactini by Baskin (1998) were probably derived from the European groups just discussed, which is what Ginsburg (1999) refers to as basal gulolines of Eurasia (both are considered part of the Mustelinae in this study). The most basal member of the North American representative in this group is *Plionictis* Matthew, 1924, a small, *Martes*-like form (Baskin 1998); along with the larger *Sthenictis*, these two are the earliest occurring genera of this clade in North America, showing up as early as the late Hemingfordian (Tedford *et al.* 1987, 2004; Baskin 1998).

Sthenictis neimengguensis n. sp. has a suite of plesiomorphic characters observed in early Miocene European forms. Other than larger size and the presence of a crowded p1, *S. neimengguensis* n. sp. is very close in dental morphology to *Dehmictis vorax* Ginsburg & Morales, 1992: p2 and p3 are simple and unicuspid, and p4 has a prominent posterior accessory cusp and a small anterior cingulum. The main difference in dental morphology between the two forms is the relative reduction of m1 talonid size (and thus grinding area) in *S. neimengguensis* n. sp. Furthermore, the ridge between the m1 protoconid and hypoconid is relatively gradual in *Dehmictis*, whereas the same area in *S. neimengguensis* n. sp. is interrupted by a notch, resulting in a more trenchant appearance from lateral view (Fig. 2). However, both taxa still have in common the presence of a relatively unreduced talonid basin which becomes more trenchant in the *Hoplictis-Ischyriactis-Eomellivora* group.

As mentioned above, the two hypercarnivorous groups between which *Sthenictis* falls evolved in slightly different directions towards hypercarnivory. Whereas the *Hoplictis-Ischyriactis-Eomellivora* group began with a more elongate tooth row and evolved robust premolars with a trenchant talonid, the *Iberictis-Plesiogulo* group evolved robust premolar morphology but with a prominent crushing area in the talonid. The lower dentition of the genus *Iberictis* is best known in *I. buloti* Ginsburg & Morales, 1992 (Ginsburg & Morales 1992); the dimensions of p2-m1 are similar between that species and *Sthenictis neimengguensis* n. sp. (Fig. 3). However, the relative elongation of the m1 in *S. neimengguensis* n. sp. makes it more similar to other species of *Sthenictis*, and to a certain extent, the *Hoplictis-Ischyriactis-Eomellivora* group. Interestingly, *Plesiogulo*, *Gulo*, *Eomellivora*, and *Mellivora* Storr, 1780 are among the only mustelids to evolve zigzag Hunter-Schreger Bands in the posterior premolars and molars, indicating increased capability for consuming hard food items such as shells and bone (Stefen 2001). The teeth of *S. neimengguensis* n. sp. show no such modification and remain unspecialized in this regard.

Sthenictis neimengguensis n. sp. has a relatively larger m1 metaconid compared to other known species of *Sthenictis*. This is taken to indicate the relatively less hypercarnivorous position of *S. neimengguensis* n. sp. within the genus because of the incorporation of the metaconid into a crushing occlusion with the upper molar. *Sthenictis neimengguensis* n. sp. is intermediate in overall size compared to other *Sthenictis*; the North American species of *Sthenictis* encompass a large size range from taxa smaller than *S. neimengguensis* n. sp. to taxa near the size of the larger *Ischyriactis* (Fig. 3). The m1 talonid of *Sthenictis* tends to be less trenchant than that of *Ischyriactis*, *Hoplictis*, and *Eomellivora*, in which the m1 hypoconid is more cuspidate and is positioned closer to the center of the talonid basin. Compared to *Ischyriactis*, species of *Sthenictis* tend to have relatively shorter p4 and narrower m1 (Fig. 3). These features of *Sthenictis* are again consistent with the interpretation of them being intermediate and basal to the two major groups represented by *Plesiogulo* and *Eomellivora*, respectively.

Three major Neogene carnivoran dispersal events across the Bering corridor occurred at the Arikarean-

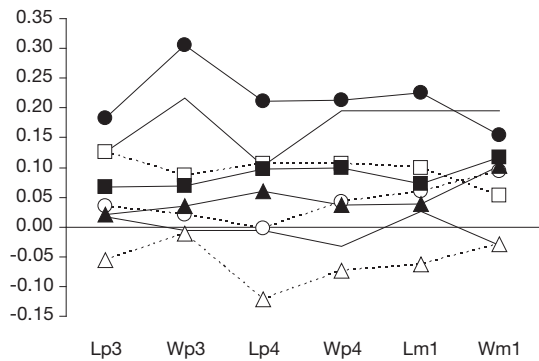


FIG. 3. — Log ratio diagram of several species of *Sthenictis* Peterson, 1910 and other compared genera. The dental measurements of *Iberictis buloti* Ginsburg & Morales, 1992 (MNHN LRM1044; Ginsburg and Morales 1992) serve as the basal hypercarnivore standard for comparison (solid line at origin). **Bold line**, *Sthenictis neimengguensis* n. sp.; **solid line with ●**, *Eomellivora wimani* Zdansky, 1924 (UPM m3693); **solid line**, *Plesiogulo brachygnathus* Schlosser, 1903 (UPM m3806); **solid line with ■**, *Ischyriactis zibethoides* Blainville, 1841 (MNHN Sa4078); **solid line with ▲**, *Ischyriactis anatolicus* Schmidt-Kittler, 1976 (IPHG 1967. VI.646; Schmidt-Kittler 1976); **dotted line with □**, *Sthenictis lacota* Matthew & Gidley, 1904 (AMNH 10810; Matthew & Gidley 1904); **dotted line with ○**, *Sthenictis dolichops* Matthew, 1932 (AMNH 18264; Matthew 1932); **dotted line with △**, *Sthenictis jurensis* Shotwell & Russell, 1963. (UOMNH F-6694; Shotwell 1963). For explanation of measurement abbreviations see text. Diagram constructed as in Simpson (1941).

Hemingfordian boundary, the middle part of the Hemphillian, and the Hemphillian-Blancan boundary, respectively (Tedford *et al.* 1987; Qiu 2003; Tedford *et al.* 2004). A minor event occurred around 13 Ma during which Eurasia received *Leptarctus* and North America *Sansanosmilus* and *Plithocyon* (Qiu 2003; Wang *et al.* 2003). The similarity in morphology between *S. neimengguensis* n. sp. and the Barstovian *S. dolichops*, and the greater diversity and earlier occurrence of *Sthenictis* (Hemingfordian) in North America, suggest that *S. neimengguensis* n. sp. was probably an immigrant from North America to Asia sometime near the Barstovian-Clarendonian boundary, based on the age of the Tunggur locality (Wang *et al.* 2003). This re-establishment of *Sthenictis* in the Old World would have occurred approximately 5 million years after its first entry into North America from Eurasia at the beginning of the late Hemingfordian (Tedford *et al.* 1987; 2004).

Acknowledgements

We thank Stéphane Peigné and Gildas Merceron for the invitation to contribute to this volume in honour of Professor Louis de Bonis; Didier Merle and the reviewers for their comments. We thank J. Baskin for freely sharing his knowledge about mustelid evolution. We also thank R. Amiot (IVPP) for translating the English abstract into French. E. Pederson (AMNH) helped with specimen preparation; S. Abramowicz (Natural History Museum of Los Angeles County) made Figure 1; field work and laboratory analysis were supported by funds from the Knowledge Innovation Program of the Chinese Academy of Sciences (KZCX2-YW-120), Major Basic Research Projects (2006CB806400) of MST of China, the CAS/SAFEA International Partnership Program for Creative Research Teams, Chinese Academy of Science Outstanding Overseas Scholar Fund (No. 2004-2-4), Chinese National Natural Science Foundation (Nos. 49872011 and 40128004), National Geographic Society (Nos. 5527-95 and 6004-97); JKO was supported by the Richter Undergraduate Grant at Occidental College and ZJT a NSF Graduate Research Fellowship.

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*Submitted on 23 January 2009;
accepted on 25 June 2009.*