geodiversitas

2020 • 42 • 3

A new species of *Tunguricts* Colbert, 1939 (Carnivora, Hyaenidae) from the middle Miocene of Junggar Basin, northwestern China and the early divergence of basal hyaenids in East Asia

Xiaoming WANG, Z. Jack TSENG, Wen-yu WU,
Jie YE, Jin MENG & Shundong BI

art. 42 (3) — Published on 20 February 2020
www.geodiversitas.com

MUSÉUM
NATIONAL D'HISTOIRE NATURELLE
PUBLICATIONS
SCIENTIFIQUES

Couverture / *Cover* :
Made from the figures of the article.

Geodiversitas est indexé dans / Geodiversitas *is indexed in:*
- Science Citation Index Expanded (SciSearch®)
- ISI Alerting Services®
- Current Contents® / Physical, Chemical, and Earth Sciences®
- Scopus®

Geodiversitas est distribué en version électronique par / Geodiversitas *is distributed electronically by:*
- BioOne® (http://www.bioone.org)

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Geodiversitas* sont référencés par /
Articles and nomenclatural novelties published in Geodiversitas *are referenced by:*
- ZooBank® (http://zoobank.org)

Geodiversitas est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Geodiversitas *is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:*
Adansonia, ***Zoosystema***, ***Anthropozoologica***, ***European Journal of Taxonomy***, ***Naturae***, ***Cryptogamie*** **sous-sections** ***Algologie***, ***Bryologie***, ***Mycologie.***

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

ISSN (imprimé / *print*) : 1280-9659/ ISSN (électronique / *electronic*) : 1638-9395

A new species of *Tungurictis* Colbert, 1939 (Carnivora, Hyaenidae) from the middle Miocene of Junggar Basin, northwestern China and the early divergence of basal hyaenids in East Asia

Xiaoming WANG
Department of Vertebrate Paleontology
Natural History Museum of Los Angeles County
900 Exposition Blvd
Los Angeles, CA 90007 (United States)
xwang@nhm.org

Z. Jack TSENG
Department of Pathology and Anatomical Sciences
Jacobs School of Medicine and Biomedical Sciences
University at Buffalo
Buffalo, NY 14203 (United States)
jacktsen@buffalo.edu

Wen-yu WU
Institute of Vertebrate Paleontology and Paleoanthropology
Chinese Academy of Sciences
Beijing 100044 (China)
wuwenyu@ivpp.ac.cn

Jie YE
Institute of Vertebrate Paleontology and Paleoanthropology
Chinese Academy of Sciences
Beijing 100044 (China)
yejie@ivpp.ac.cn

Jin MENG
Department of Vertebrate Paleontology
American Museum of Natural History
Central Park West at 79th Street
New York, NY 10024 (United States)
jmeng@amnh.org

Shundong BI
Department of Biology
Indiana University of Pennsylvania
Indiana, Pennsylvania 15705 (United States)
shundong.bi@iup.edu

Submitted on 23 January 2019 | accepted on 1 July 2019 | Published on 20 February 2020

urn:lsid:zoobank.org:pub:344FC2F5-A395-449E-915A-EAC53F366764

Wang X., Tseng Z. J., Wu W.-Y., Ye J., Meng J. & Bi S. 2020. — A new species of *Tungurictis* Colbert, 1939 (Carnivora, Hyaenidae) from the middle Miocene of Junggar Basin, northwestern China and the early divergence of basal hyaenids in East Asia, *in* Bonis L. de & Werdelin L. (eds), Memorial to Stéphane Peigné: Carnivores (Hyaenodonta and Carnivora) of the Cenozoic. *Geodiversitas* 42 (3): 29-45. https://doi.org/10.5252/geodiversitas2020v42a3. http://geodiversitas.com/42/3

ABSTRACT

We document new materials of *Tunguricts* Colbert, 1939, a basal hyaenid (hyena family), from the Junggar Basin in northern Xinjiang Uygur Autonomous Region, northwestern China, and recognize a new species, *T. peignei*, n. sp., from the top of the Suosuoquan Formation through the top of the overlying Halamagai Formation. Associated upper and lower teeth, plus isolated lower jaws, are described, and collectively these span *c.* 17-14 Ma in local stratigraphic sections. The new species represents the smallest and most primitive form of *Tunguricts*, which gave rise to *T. spocki* Colbert, 1939 in the middle Miocene Tunggur Formation of Inner Mongolia. These two species of *Tunguricts* form an East Asian clade with slightly more hypercarnivorous dentition, in contrast to hypocarnivorous species of *Protictitherium* Kretzoi, 1938 in Europe and western Asia. This geographic divergence may reflect environmental differences between Europe and western Asia, on the one hand, and East Asia, on another.

KEY WORDS
Hyaenidae,
China,
Asia,
Junggar Basin,
Miocene,
evolution,
new species.

RÉSUMÉ

Une espèce nouvelle de Tunguricts *Colbert, 1939 (Carnivora, Hyaenidae) du Miocène moyen du bassin de Junggar, Chine du nord-ouest, et le début de la divergence des hyénidés basaux en Asie de l'est.*
Nous rapportons du nouveau matériel de *Tunguricts* Colbert, 1939, un hyénidé basal du bassin de Junggar dans le nord de la Région autonome de Xinjiang Uygur, au nord-ouest de la Chine, et reconnaissons une nouvelle espèce, *T. peignei*, n. sp., du sommet de la formation de Suosuoquan jusqu'à celui de la formation sus-jacente de Halamagai. Nous décrivons des dents inférieures et supérieures associées ainsi que des mandibules isolées collectées dans un intervalle de 17 à 14 Ma dans des sections stratigraphiques locales. La nouvelle espèce représente la forme la plus petite et la plus primitive de *Tunguricts* qui a donné naissance à *T. spocki* Colbert, 1939 du Miocène moyen de la formation de Tunggur en Mongolie intérieure. Ces deux espèce de *Tunguricts* constituent un clade est-asiatique avec une dentition légèrement plus hypercarnivore qui contraste avec celle des espèces hypocarnivores de *Protictitherium* Kretzoi, 1938 en Europe et en Asie occidentale. Cette divergence géographique peut refléter des différences environnementales entre l'Europe et l'Asie occidentale d'un côté et l'Asie orientale de l'autre.

MOTS CLÉS
Hyaenidae,
Chine,
Asie,
bassin de Junggar,
Miocène,
évolution,
espèce nouvelle.

INTRODUCTION

The hyena family, Hyaenidae, is a diverse group of carnivorans found in the Old World and North America during much of the late Cenozoic. Often featuring large body sizes, strong, bone-crushing teeth, and being top predators of their communities, hyaenids have relatively good fossil records in many Neogene localities of Europe, Asia, and Africa (Werdelin & Solounias 1991). These large predators evolved from small fox-sized ancestors in the early to middle Miocene. The fossil records of the primitive ancestors, however, are far less abundant, partly due to preservational bias toward larger fossils more resistant to weathering, and also to possible differences in habitat. As a result, their morphology, geographic range, and age relationship are all poorly known. This is especially true for the Chinese (and East Asian in general) records. Fossils of small, stem hyaenids trickle into the published record slowly.

With the exception of fossils from the middle Miocene Tunggur Formation in Inner Mongolia (Nei Mongol), East Asian records of early hyaenids lag behind those from Europe and western Asia. Therefore, new records add significantly to our knowledge of the anatomy and geography. We previously mentioned the presence of *Protictitherium* Kretzoi, 1938 in the middle Miocene of the Junggar Basin (Fig. 1), Xinjiang Uygur Autonomous Region, northwestern China (Wang *et al.* 1998), but did not describe it. Since then, additional materials, including upper cheek teeth, have been collected. We take this opportunity to fully describe these specimens, recognizing a new species belonging to the *Tunguricts* Colbert, 1939 clade in East Asia.

MATERIAL AND METHODS

Specimens described in this paper are deposited in the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing. For comparison, we have examined the following specimens: *Tunguricts spocki* Colbert, 1939: AMNH 26600 and IVPP V 13784; *Tunguricts punica* Kurtén, 1976: UCPE T-1601.

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York;
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing (IVPP V numbers);
MNHN	Muséum national d'Histoire naturelle, Paris;
NMB	Naturhistorisches Museum Basel, Basel;
SNSB-BSPG	Staatliche Naturwissenschaftliche Sammlungen Bayerns – Bayerische Staatssammlung für Paläontologie und Geologie, Munich;
UCPE	University of Colorado Paleontological Expeditions to Tunisia, Boulder.

Fig. 1. — Map of *Tungurictis* Colbert, 1939 localities in Junggar Basin of northern Xinjiang.

HISTORY OF STUDY

Colbert (1939) first named *Tungurictis spocki* from the late middle Miocene Tunggur Formation in Inner Mongolia. This initial discovery by the American Museum of Natural History Third Central Asian Expeditions was based on two specimens: AMNH 26600, a nearly complete skull (holotype) from the Wolf Camp Site, and AMNH 26610, a dentary fragment with premolars (paratype) from "twenty-five miles northeast of Gur Tung Khara Usu" (possibly the same as IVPP Huerguolajin Locality, see Wang *et al.* 2003). Colbert (1939) thought that *Tungurictis* was a viverrid. Beaumont (1967) was doubtful of such an assignment, and Qiu *et al.* (1988) referred it to Hyaenidae. Hunt (1989) forcefully argued that *Tungurictis* was a hyaenid, followed up with a detailed documentation on its basicranial morphology (Hunt & Solounias 1991).

A second Chinese record of basal hyaenids, *Protictitherium*, was reported by Li *et al.* (1983) from Songlinzhuang (IVPP locality 82027) of Xiacaowan Formation in Sihong region, Jiangsu Province. Represented by a maxilla fragment with P2-M1, the Songlinzhuang form was designated as "*Protictitherium* sp. nov.", which is "small in size and morphologically different from known species" (Li *et al.* 1983: 319). Unfortunately, this taxon was neither described nor figured. In their recent summary of Sihong faunas, Qiu & Qiu (2013) continued to regard this *Protictitherium* record as unconfirmed.

In a study of Junggar Basin carnivorans, we listed a third Chinese record as two species of *Protictitherium* (Wang *et al.* 1998). The materials consisted of only a few jaw fragments and our taxonomic assessment was tentative. With better materials in hand, we now realize they belong to *Tungurictis*, and we fully describe these specimens herein.

By the 1990s, a consensus emerged that the small fox-sized *Protictitherium* played a central role in the origin of Hyaenidae. Between three to nine species of *Protictitherium* are recognized in Europe and western Asia by different authors (Werdelin & Solounias 1991, 1996; Ginsburg 1999; Turner *et al.* 2008; Fraile 2016, 2018). The best records are from middle to late Miocene localities in several European countries, such as Greece (Bonis & Koufos 1991; Koufos 2011), Turkey (Schmidt-Kittler 1976; Andrews & Tobien 1977; Kaya *et al.* 2005; Mayda *et al.* 2015; Koufos *et al.* 2018), Spain (Ginsburg *et al.* 1981; Peigné *et al.* 2006; Fraile 2016, 2018), France (Filhol 1883; Ginsburg & Bulot 1982), and Hungary (Werdelin 2005). More recently, Bonis (2004) referred yet another form, from late Miocene of Turkey, to *Protictitherium arambourgi* (Ozansoy 1965). However, Bonis *et al.* later (2010) referred this species to *Ictitherium*, whereas Werdelin & Peigné (2010) synonymized it with *P. crassum* Filhol, 1883.

Schmidt-Kittler (1976) described multiple species of *Protictitherium* from the middle to late Miocene of Turkey. Kaya *et al.* (2005) named a new species, *P. aegaeum*, from western Turkey. In an unpublished Ph.D. dissertation, Fraile (2016) described a large sample of excellently preserved *Protictitherium crassum* from the late Miocene Spanish site of Cerro de los Batallones in Madrid Basin. This material was partially

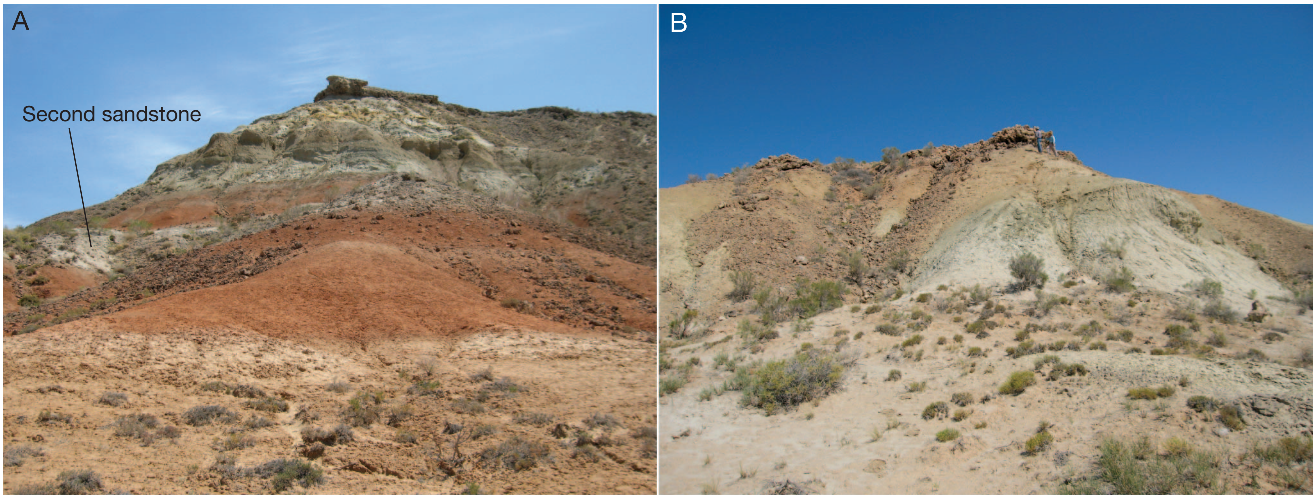

FIG. 2. — Two Junggar Basin localities that produce *Tungurictis* Colbert, 1939: **A**, Duolebulejin section showing contact of sandstones of Halamagai Formation and red mudstones of Suosuoquan Formation; the Duolebulejin locality is the only section where Suosuoquan and Halamagai formations are in continuous deposition with a superpositional relationship (Ye *et al.* 2012). XJ 200910 locality is from the second sandstone lens within Suosuoquan Formation. **B**, XJ 200815 locality in Dingshanyanchi section, upper siltstones of Halamagai Formation. Photos by Wenyu Wu.

described in Fraile (2018). But most recently, Morales *et al.* (2019) placed *P. crassum* at the base of their lophocyonid clade.

The African record of *Protictitherium* is limited. In North Africa, Kurtén (1976) described the species, *Tungurictis punica*, from the Beglia Formation of Bled Douarah, Tunisia. Werdelin & Solounias (1991) argued that it really belonged to *Protictitherium*, a decision Werdelin & Peigné (2010) reaffirmed. A second African record of *Protictitherium*, *P. crassum*, is from Beni Mellal, Morocco (Werdelin & Peigné 2010), and variously referred to *Ictitherium* (Bonis *et al.* 2010). A third possible record, *Protictitherium* sp. from Kenya, was mentioned (Werdelin & Peigné 2010) but its true nature remains unclear.

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821
Family HYAENIDAE Gray, 1821

Genus *Tungurictis* Colbert, 1939

TYPE SPECIES. — *Tungurictis spocki*, original designation by Colbert (1939).

INCLUDED SPECIES. — *Tungurictis spocki* Colbert, 1939 and *Tungurictis peignei*, n. sp.

EMENDED DIAGNOSIS. — A small feliform, *Tungurictis* has acquired the hyaenid ear region characters of a posteriorly reclined intrabullar septum and a posterodorsal chamber of the bulla floored by the intrabullar septum. *Tungurictis* is more hypercarnivorous than *Protictitherium* and *Plioviverrops* Kretzoi, 1938 in its more elongated upper and lower carnassials (P4 and m1), relatively reduced M2, less high-crowned m1 entoconid, and more reduced m1-2 hypoconulid.

REMARKS

After Colbert's (1939) initial recognition of *Tungurictis spocki*, Kurtén (1976) named a second species, *T. punica*, from the Beglia Formation of Bled Douarah, Tunisia. Werdelin & Solounias (1991) made a detailed comparison of this second species. They suggested that it really should belong to *Protictitherium*, and emended the species name to *P. punicum*, an opinion later upheld in Werdelin & Peigné (2010).

Hunt & Solounias (1991) suggested that *Tungurictis* is a junior synonym of *Protictitherium* Kretzoi, 1938 and predicted that, when lower cheek teeth become available, the m1 entoconid should not be emphasized over the hypoconid and its talonid reduced relative to trigonid. Continued explorations in the Tunggur area in the last 25 years did eventually produce an associated partial skull and dentaries (IVPP V 13784) from the Tairum Nor locality in the lower part of the Tunggur Formation (Wang 2004), which largely confirmed Hunt & Solounias' prediction. The Tairum Nor section is substantially older than the Wolf Camp section (Qiu *et al.* 2013) and IVPP V 13784 is smaller and slightly more primitive than that of the Wolf Camp individual (holotype), permitting a sense of an evolutionary trend within a single geologic formation.

Tungurictis peignei n. sp.
(Figs 4-6; Tables 1, 2)

urn:lsid:zoobank.org:act:993B1CF7-DBC3-45C5-8546-00DD0DF80E02

Protictitherium intermedium – Wang *et al.* 1998: 221, figs 3A, B.

HOLOTYPE. — IVPP V 25222, isolated upper third incisor, isolated right upper canine, right maxillary fragment with P1 and P3-4 (broken), left maxillary fragment with P1, P3-4, partial right dentary with p1 alveolus and p2-m2 (Figs 4; 5A, C, D), all apparently of the same individual; the locality was discovered by Jin Meng on July 5, 2009 and the specimen was obtained by screen washing.

TYPE LOCALITY. — IVPP XJ 200910 locality, 46°33.993'N, 87°46.965'E, Duolebulejin area, south bank of the Ulungu River,

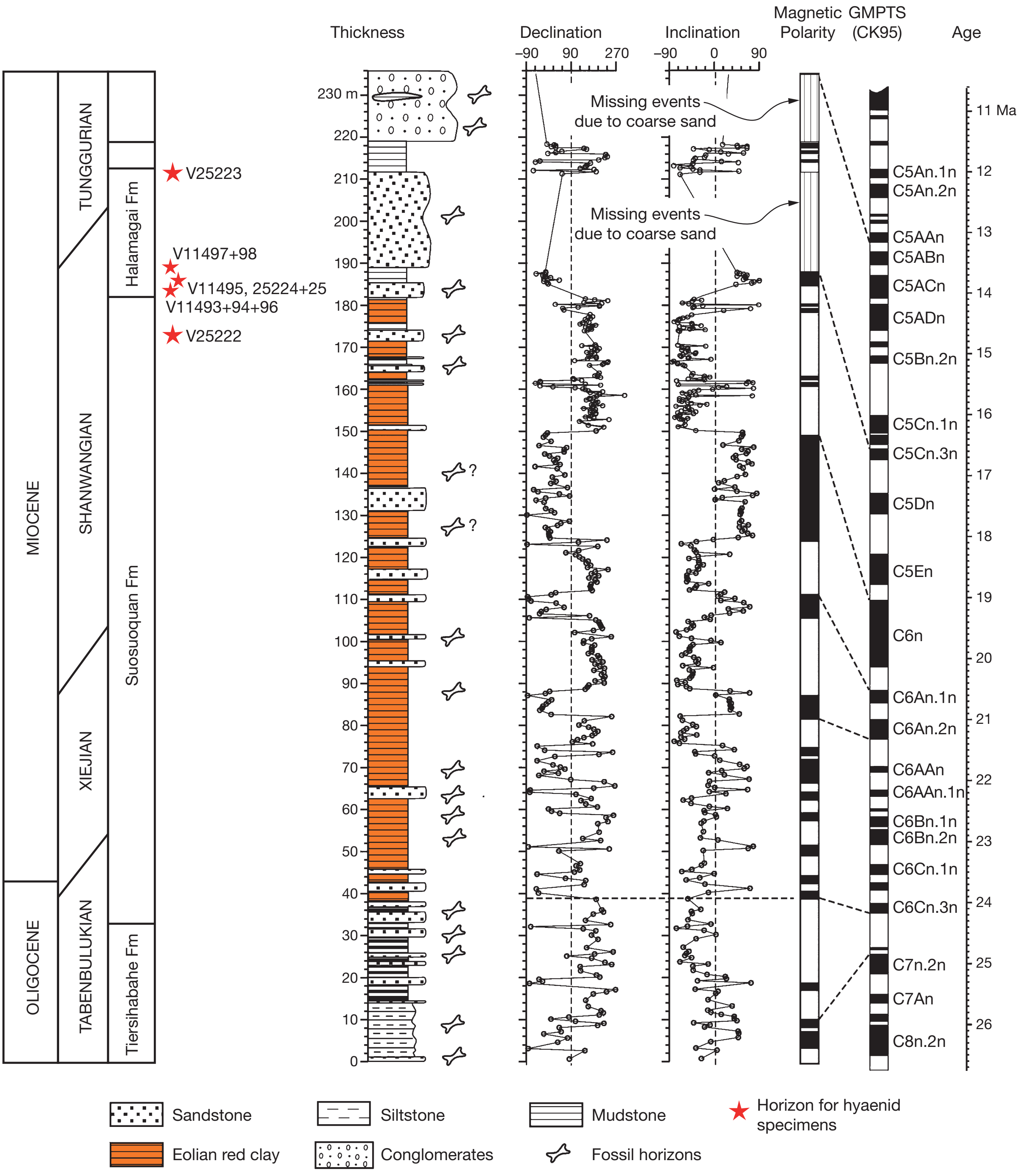

FIG. 3. — Bio- and magnetostratigraphy of basal hyaenids from Junggar Basin.

second sandstone layer from top of the Suosuoquan Formation, Junggar Basin, Xinjiang Uygur Autonomous Region (Fig. 2A).

DIAGNOSIS. — The most primitive known species of *Tungurictis*, *T. peignei*, n. sp. is smaller than *T. spocki* and has a more distinct lingual bulge on P3, a more distinct notch on M1 parastyle, and an m1 hypoconulid enclosing the talonid basin. *Tungurictis peignei*, n. sp. is similar in size to *Protictitherium intermedium* but has less well developed m1-2 hypoconulid.

ETYMOLOGY. — In memoriam of Stéphane Peigné for his contribution to the understanding of fossil carnivorans.

REFERRED SPECIMENS. — IVPP V 25223, isolated right P2 (posterior part only; not figured), P3, and M1, from XJ 200815 intermedium

TABLE 1. — Comparative measurements of upper teeth of *Tungurictis* Colbert, 1939 from Junggar Basin. Those for *Tungurictis spocki* Colbert, 1939 follow Wang (2004: table 1).

Taxa	**Catalogue number**	**P3 length**	**P3 width**	**P4 length**	**P4 width**	**M1 length**	**M1 width**
Tungurictis peignei, n. sp.	IVPP V 25222	8.0	4.1	11.0	6.0	–	–
	IVPP V 22523	7.9	3.9	–	–	4.3	9.5
Tungurictis spocki	AMNH 26600	10.0	4.8	14.7	7.4	5.7	10.7
	IVPP V 13784	8.6	3.9	13.2	7.1	4.5	10.5
Protictitherium punicum Kurtén, 1976	UCPE T-1601	9.6	5.4	14.3	7.7	5.8	11.2

TABLE 2. — Comparative measurements of lower teeth of *Tungurictis* Colbert, 1939 from Junggar Basin. Those for *Protictitherium* Kretzoi, 1938 from Turkey are from Schmidt-Kittler (1976) and those for *Tungurictis* follow Wang (2004: table 1).

Taxa	**Catalog number**	**p2 length**	**p2 width**	**p3 length**	**p3 width**	**p4 length**	**p4 width**	**m1 length**	**m1 width**	**m2 length**	**m2 width**
Tungurictis peignei, n. sp. from Junggar	IVPP V 11493	6.0	2.3	7.7	2.7	8.2	3.7	9.5	4.5	–	–
	IVPP V 11494	–	–	–	–	9.0	4.0	10.4	5.0	–	–
	IVPP V 22522	5.7	2.4	7.7	3.1	8.3	3.9	9.8	4.7	3.7	3.0
	IVPP V 25224	–	–	–	–	–	–	9.4	5.1	–	–
	IVPP V 25225	–	–	8.6	3.8	9.5	4.7	–	–	–	–
	uncatalogued	–	–	8.2	3.4	8.7	4.0	–	–	–	–
Tungurictis spocki Colbert, 1939	IVPP V 13784	–	–	–	–	–	–	10.6	3.6	4.0	3.3
Tungurictis small species	IVPP V 11497	–	–	–	–	–	–	8.0	3.7	–	–
Protictitherium intermedium Schmidt-Kittler, 1976 from Turkey	SNSB-BSPG 1968 VI 736	6.1	2.5	–	–	–	–	10.5	4.4	4.9	3.7
	SNSB-BSPG 1968 VI 738	–	–	–	–	–	–	9.1	4.0	–	–
	SNSB-BSPG 1968 VI 735	5.5	2.6	–	–	–	–	10.3	4.9	–	–
	SNSB-BSPG 1968 VI 737	6.1	2.4	7.0	2.8	7.9	3.5	9.4	–	–	–
	SNSB-BSPG 1968 VI 739	–	–	–	–	7.1	2.8	–	–	–	–
Protictitherium aff. *gaillardi* (Forsyth-Major, 1903)	SNSB-BSPG 1968 VI 745	–	–	–	–	–	–	11.3	5.1	–	–
	SNSB-BSPG 1968 VI 746	–	–	–	–	9.0	4.2	–	–	–	–

(Fig. 2B), 46°24.281'N, 87°25.991'E, at 45 km mark of West Main Irrigation Channel (Xi-gan-qu), southwest of Dingshan Salt Lake (Dingshanyanchi), upper siltstones of Halamagai Formation, 13.3 m below the boundary of Halamagai-Dingshanyanchi formations; some of the carnivoran materials were obtained by screen washing (Fig. 6). — IVPP V 11493, left dentary with c-p1 roots, p2-m1, from Tieersihabahe, lower part of Halamagai Formation (Wang *et al.* 1998: fig. 3A) (Fig. 5B, E, F). — IVPP V 11494, left dentary fragment with p3 alveolus and p4-m1, from Tieersihabahe, Halamagai Formation, collected on August 14 (Wang *et al.* 1998: fig. 3B). — IVPP V 11495, right dentary fragment with c-p4 alveoli, from Tieersihabahe, Halamagai Formation. — IVPP V 11496, right dentary fragment with p1-m1 (all broken), from Tieersihabahe, Halamagai Formation. — IVPP V 25224, left dentary fragment with m1, and p4 and m2 alveoli, from Tieersihabahe, Halamagai Formation. — IVPP V 25225, right dentary fragment with p3-4 and m1 alveolus, from Tieersihabahe, Halamagai Formation. — IVPP uncatalogued, left dentary fragment with p3-4 and p2 and m1 alveoli, from Tieersihabahe, second sandstone layer of Halamagai Formation.

GEOLOGIC SETTING, FAUNA, AND AGE. — Extensive exposures of middle to late Cenozoic sediments in northern Junggar Basin and its western extension in Kazakhstan produce a rich record of fossil vertebrates (Fig. 1). Explorations of the Junggar Basin by Chinese geologists began in the 1950s. Although Chow (1957, 1958) was first to report fragmentary mammal fossils from several Cenozoic localities in Xinjiang, all collected by local geological survey and petroleum teams, dedicated explorations by vertebrate paleontologists did not begin until 1982 and 1984, when a joint IVPP and Xinjiang Bureau of Petroleum team worked in the Ulungu River region. A basic stratigraphic framework of the Suosuoquan Formation and Halamagai Formation, plus associated vertebrate fossils, was first established by Tong *et al.* (1990). Since then various efforts have focused on the regional stratigraphy and chronology (Wu *et al.* 1998; Ye *et al.* 2000; Ye *et al.* 2001a, b; Ye *et al.* 2003; Meng *et al.* 2006; Meng *et al.* 2008; Ye *et al.* 2012; Meng *et al.* 2013), paleoenvironment and paleoclimate (Sun *et al.* 2010), small mammal taxonomy (Bi 1999; Bi *et al.* 1999; Wu *et al.* 2004, 2006; Bi *et al.* 2009; Wu *et al.* 2009; Maridet *et al.* 2011; Bi *et al.* 2013), and descriptions of large mammals (Ye 1989; Wu *et al.* 2003; Ye *et al.* 2005).

REMARKS

Carnivorans from the Junggar Basin are generally rare. From collections made during the early expeditions, Qi (1989) reported two fossil carnivorans, *Amphicyon ulungurensis* Qi, 1989 and *Ictitherium* cf. *I. gaudryi* (de Beaumont & Mein, 1972), from three localities (IVPP loc 82501, 82503, 82513, plus a reworked locality 82505) in the Halamagai beds. The

FIG. 4. — *Tunguricts peignei*, n. sp., IVPP V 25222, holotype, isolated right I3, mesial view (**A**), right upper canine, buccal view (**B**), left P1, and left maxilla with P3-4 (**C**, stereo photos of occlusal view; **D**, buccal view). Scale bar: 10 mm.

next major expeditions that saw a large increase in carnivoran diversity were led by another IVPP team in 1995 and 1996, and were summarized by Wu *et al.* (1998). Carnivoran collections made in the 1990s from the Halamagai Formation were described by Wang *et al.* (1998). These include *Nimravus*? sp., *Pseudaelurus cuspidatus* Wang, Ye, Meng, Wu, Liu & Bi, 1998, *Protictitherium intermedium* Schmidt-Kittler, 1976 (*Tunguricts* herein), *Protictitherium* small species, *Thalassictis chinjiensis* (Pilgrim, 1932), *Gobicyon*? sp., *Oligobunis*? sp., *Alopecocyon goeriachensis* (Toula, 1884), and *Simocyon* Wagner, 1858 small form. Although Wang *et al.*'s (1998) report represents a substantial increase of carnivoran diversity, fragmentary jaws and isolated teeth were the main basis of most taxa. Not surprisingly, many of the above identifications are tentative, or even speculative, and await confirmation (or rejection) by better materials. Continued collecting from the Halamagai

Fig. 5. — *Tunguríctis peignei*, n. sp., IVPP V 25222, holotype, right dentary with p2-m2 (**A**, stereo photos, occlusal view, **C**, lingual, and **D**, buccal views) and IVPP V 11493, left dentary with p2-m1 (**B**, stereo photos, occlusal view; **E**, lingual view; **F**, buccal views). Scale bars: 10 mm.

Formation since the 1990-2000s has yielded five species of bear dogs, recently described by Jiangzuo *et al.* (2018), but isolated teeth and jaw fragments are still mostly what are known at the moment.

A newly described specimen herein, IVPP V 25223, is from IVPP XJ 200815 locality (Fig. 2B) in the Dingshanyanchi area (Meng *et al.* 2008; Wu *et al.* 2009). Ye *et al.* (2012) described the Duolebulejin section and produced a magnetostratigraphy. Unfortunately, much of the Halamagai Formation are sandstones, coarse-grained sediments unsuitable for magnetic studies. Only two short segments of fine-grained sediments at the top and bottom of the Halamagai Formation yielded

Fig. 6. — *Tungurictis peignei*, n. sp., IVPP V 25223, isolated right P3 and M1: **A**, posterior view of M1; **B**, buccal view of P3; **C**, stereo photos of occlusal view of P3 and M1. Scale bar: 5 mm.

useful magnetic results (Ye *et al.* 2012: fig. 3), consisting of just a few short magnetic chrons in a busy part of the magnetic time scale, not enough to offer much constraint in correlation. Nevertheless, as constrained by fossil mammals within, such as *Anchitherium gobiense* Colbert, 1939 (Ye *et al.* 2005), Ye *et al.* (2012) placed the Halamagai Formation roughly in C5Cn.3n through somewhere in C5A, or about 16-14 Ma.

In contrast to the fluviatile sandstones of the middle Miocene Halamagai Formation, the underlying Suosuoquan Formation is mainly a fine-grained red bed of late Oligocene to early Miocene age (Ye *et al.* 2003; Meng *et al.* 2013). So far, no carnivoran has been reported in the Suosuoquan Formation. Specimen IVPP V 25222 described in this paper is from IVPP XJ 200910 locality (Fig. 2A) in the Duolebulejin area at the top of the Suosuoquan Formation. This is known as the "Top of Suosuoquan Fauna" (Ye *et al.* 2001a, b). Constrained by small mammal faunas, Meng *et al.* (2013: pl. 3.1) magnetically correlated the lower half (up to the S-III assemblage) of the Suosuoquan Formation to C6Cn.3n-C6An.1n, spanning 23.30 Ma of GTS2012 (Vandenberghe *et al.* 2012) to 20.04 Ma of ATNTS2012 (Hilgen *et al.* 2012) (Fig. 3). The top part of the Suosuoquan Formation can be as young as 16.8 Ma (Ye *et al.* 2012). IVPP V 25222 falls within the reversed chron C5Cr (Fig. 3) with a duration of 16.72-17.24 Ma of ATNTS2012. This specimen thus represents the oldest record of *Tungurictis* in East Asia.

DESCRIPTION

The maxilla fragments and right dentary of IVPP V 25222 have associated upper and lower teeth. These form the main basis of description, supplemented by additional specimens to evaluate variation. Dental measurements are provided in Tables 1 and 2.

Maxilla and upper teeth

We interpret the isolated teeth of IVPP V 25222, collected by screen washing from a single site, as belonging to a single individual because they all have the same stage of wear (a young adult) and there are no duplicate teeth from the same side. The left and right maxillae do not preserve much beyond where the cheek teeth are rooted. The floor of the left infraorbital foramen is preserved, and it appears that the anterior opening of this foramen is approximately at the anterior edge of P4.

An isolated upper incisor (Fig. 4A) is here identified as a right I3 because of its relatively rounded root, as opposed to the more mesiodistally compressed roots of I1-2, as seen on *Tungurictis spocki* (IVPP V 13784) (Wang 2004: fig. 1). The crown surface is simple and single-cusped, but with a mesial and distal crest converging toward the tip of the main cusp. The maximum mesiodistal length at the base of the crown is 2.13 mm.

A well-preserved right upper canine (Fig. 4B) preserves the entire crown, but much of its root is missing. The cross section at the base of the crown is oval, with a mesiodistal length of 4.72 mm, linguobuccal width of 3.69 mm, and crown height of 13.45 mm. The surface of the crown is smooth, lacking crenulations or grooves. A thin but distinct posterior and anterolingual ridge runs along the entire length of the tooth.

An isolated left P1 (Fig. 4C, D) is double-rooted, as in *Tungurictis spocki*. It measures 5.50 mm in mesiodistal length and 2.33 mm in linguobuccal width. A single main cusp leans forward with a distinct ridge both anterior and posterior to the cusp. An incipient posterior cingular cusp is present and the posterior cingulum is confined to the posterior end of the tooth.

The left and right P3s (Fig. 4C, D; Table 1) are well-preserved. As in P1, the main cusp of P3 is flanked by an anterolingual ridge and a posterior ridge. At the anterior end of the anterolingual ridge is a small cingular cusp, and similarly, the posterior ridge is also terminated by a posterior cingular cusp. Immediately anterior to the posterior cingular cusp is an incipient posterior accessory cusp, more distinct on the left side, at the base of the posterior ridge. There is no buccal cingulum. On the lingual side, there is a distinct bulge just posterior to the main cusp and a cusp-like lingual cingulum. This bulge did not result in a lingual root above the lingual cingulum, as confirmed by an isolated P3 in IVPP V 25223 (Fig. 6B, C) (on *Tungurictis spocki*, a lingual bulge also does not result in a third root).

The left P4 (Fig. 4C, D; Table 1) is essentially unworn except the very tip of the paracone. This tooth is slender with a long shearing blade. The paracone is the most dominant cusp not only in crown height but also in cusp size. An anterior ridge on the paracone leads up to a small but distinct parastyle separated from the paracone by a notch. There is no buccal cingulum, but a narrow but distinct lingual cingulum. The protocone protrudes forward, its anterior edge being anterior to that of the parastyle. The protocone is slightly taller than the parastyle and is formed by the rising anterior and lingual cingula, i.e., a distinct ridge leads from the protocone tip and continues with the anterior and lingual cingula. There is also a sharp ridge connecting the protocone to the paracone, a condition also seen in *Tungurictis spocki*. The metastyle blade is of similar height to the protocone and there is a deep carnassial notch separating it from the paracone.

An isolated right M1 is present in IVPP V 25223 (Fig. 6A, C; Table 1) It is unworn. The paracone dominates as the tallest cusp and has a distinct lingual crista extending toward the protocone. A parastyle protrudes buccally, forming a prominent lateral bulge. The metacone is about half the size of the paracone and is located in a posterior and lingual position relative to the paracone. The protocone is located at the lingual border and features distinct pre- and postprotocristae. A very indistinct swelling along the buccal end of the postprotocrista indicates the presence of a metaconule. A paraconule is not present. There is no cingulum surrounding any part of the tooth.

M2 is not preserved.

Dentary and Lower Teeth

Several fragmentary dentaries are available, but IVPP V 25222 (Fig. 5A, C, D) and V 11493 (Fig. 5B, E, F) are the best preserved with the most lower teeth. The unworn nature of these teeth permits a clear view of cusp morphology. The following descriptions are mainly based on these two specimens, with additional comments on variations in other specimens where warranted.

Overall construction of the horizontal ramus of the dentary is modestly robust and it gently tapers anteriorly, forming a curved lower border. The deepest point of the lower jaw is at the m1. Both IVPP V 25222 and V 11493 preserve two mental foramina. The anterior foramen is located below the anterior root of the p2 and is more than twice as large as the posterior one. The smaller posterior mental foramen is below the anterior root of the p3 in V 11493 and between the roots of the p3 in V 25222.

The p1 is only present as a single root in IVPP V 25222 and V 11493. The p2 is double-rooted. It has a single main cusp with a small (V 11493) or indistinct (V 25222) posterior cingulum. Distinct anterior and posterior ridges flank the main cusp and there is very vague bulge to suggest an incipient posterior accessory cusp. There is no cingulum on either side of the tooth. The p3 is similar to p2 with the exception of a more distinct posterior accessory cusp, a better-developed posterior cingulum, and an incipient anterior accessory cusp. On IVPP V 25225, the p3 accessory cusps are more prominent than seen in other specimens. The p4 has a distinct anterior accessory cusp, a very strong posterior accessory cusp, and a widened posterior cingulum.

The m1 has a much wider trigonid than talonid. The protoconid is the largest and tallest cusp. The paraconid is the second largest and tallest cusp. The posterolingual aspect of the paraconid has a gentle ridge flanking the lingual side and enclosing a slightly concave groove. The metaconid is slightly lower than the paraconid and jutting toward the lingual side. The hypoconid is approximately equal in size to the entoconid in occlusal view, but it is only slightly taller than the latter. A sharp ridge flanks the anterior face of the hypoconid enclosing the labial side of the talonid basin. This ridge connects to a posterior ridge on the posterior face of the protoconid, but is separated from the latter by a thin notch. Posterolingual to the hypoconid is a posterior ridge running down the apex of the hypoconid. This posterior ridge forms an obtuse angle with the anterior ridge of the hypoconid. The entoconid, by contrast, is more cusp-like and pointing somewhat lingually, such that the tip of the entoconid protrudes outside the lingual border of the talonid in occlusal view in IVPP V 11493 (Fig. 5B, E, F). Slightly taller-crowned than the hypoconid, the entoconid flanks the lingual side of the talonid but does not fully enclose the talonid basin. Instead, there is a V-shaped notch anterior to the entoconid such that the basin is open lingually. This notch runs deep to sharply divide the base of the metaconid from that of the entoconid in lingual view. This condition is more pronounced in IVPP V 25222 than in V 11493. The anterior face of the entoconid is mostly rounded, with a vague ridge on its anterolingual surface, but posteriorly the entoconid has a sharp ridge oriented in the posterolabial direction. This posterior ridge continues to the hypoconulid in IVPP V 25222 but is separated from the hypoconulid in IVPP V 11493. Posterolingual to the hypoconid, the hypoconulid forms a thin, ridge-like structure enclosing the posterior aspect of the talonid basin. The hypoconulid is either an independent cusp (V 11493) or a ridge continuous with the entoconid (V 25222).

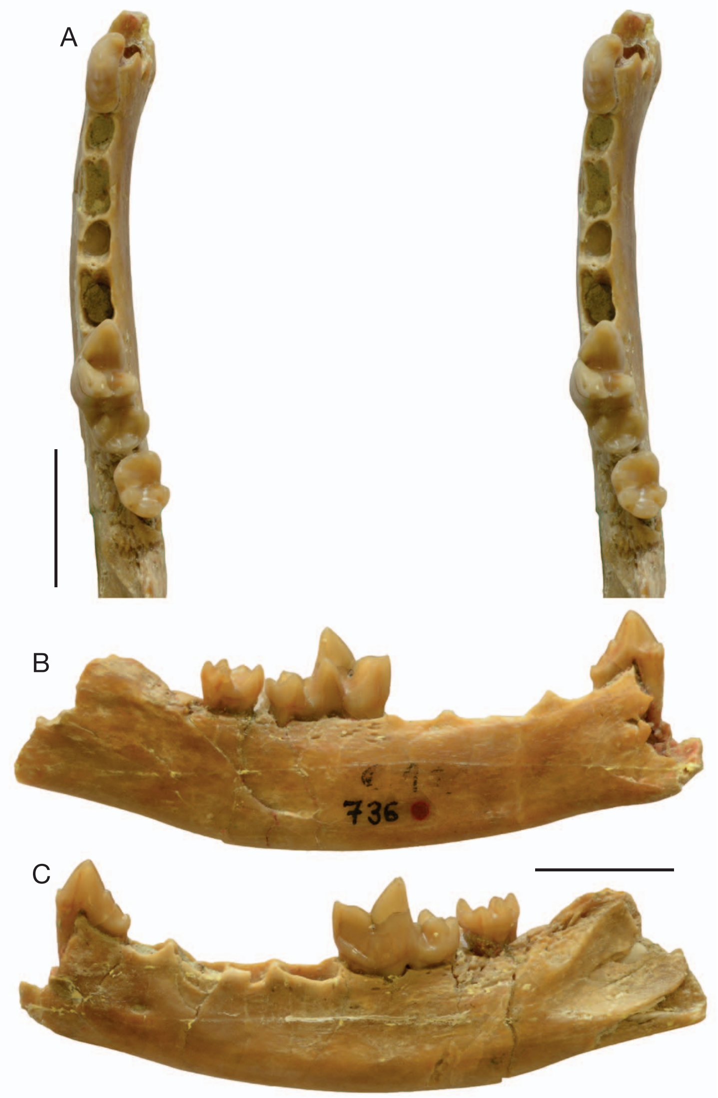

FIG. 7. — *Tunguritis* small sp., IVPP V 11497, left dentary fragment with m1 and m2 alveolus. **A**, stereo photos of occlusal view; **B**, lingual view; **C**, buccal view. Scale bars: 10 mm.

The m2 is only preserved in IVPP V 25222. The m2 crown forms an elongated basin rimed by its trigonid and talonid cusps. The paraconid is absent. The protoconid forms a ridge-like structure along the buccal rim. The ridges fall away from the tip of the protoconid and are oriented longitudinally. Located at the anterolingual corner of the tooth, i.e., more anterior than the protoconid, the metaconid is taller but not much larger than the protoconid. On its buccal side, there is a vague ridge toward the base of the metaconid. Like the protoconid, the hypoconid is a ridge-like structure and is essentially continuous with the protoconid but separated by a notch. As in the m1, the entoconid is taller-crowned than the hypoconid but is much larger in occlusal view. The entoconid is also more posteriorly located at the posterolingual corner of the tooth. This more posteriorly located entoconid, combined with the more anteriorly located metaconid, permits a wider separation between these cusps, resulting in a broad valley on the lingual side that opens into the talonid. On the posterior face of the entoconid, a transversely oriented ridge encloses the posterior aspect of the talonid basin. At the base of this ridge, a slight bulge seems to indicate the presence of a hypoconulid.

Tunguritis small sp.
(Fig. 7)

Protictitherium small sp. – Wang *et al.* 1998: 221, 236.

REFERRED SPECIMENS. — IVPP V 11497, left dentary fragment with m1 and m2 alveolus from Botamoyin, lower part of Halamagai Formation (Wang *et al.* 1998: fig. 3C) (Fig. 7). — IVPP V 11498, left dentary with c-p1 alveoli, p2 broken, p3-m2 alveoli, from Tieersihabahe, lower part of Halamagai Formation.

COMPARISON WITH JUNGGAR *TUNGURICTIS PEIGNEI*, N. SP.
Only two dentary fragments are available for this taxon. The length of m1 is only 80% of the average for Junggar *Tunguritis*

Fig. 8. — *Protictitherium intermedium* Schmidt-Kittler, 1976, SNSB-BSPG 1968 VI 736, holotype, left dentary with p2 and m1-2. **A**, stereo photos of occlusal view; **B**, lingual; and **C**, buccal view. Scale bar: 10 mm.

peignei, n. sp. specimens (Table 2), much too small to be comfortably included in the latter. Although overall consistent with the latter in dental morphology, this small form stands out for its relatively more cuspidate and lingually slanted entoconid and much smaller hypoconulid, which is consistent with assigning this taxon to *Tungurictis*. Furthermore, the ramus height at the position of m1 appears to be visibly shallower in this unnamed taxon relative to m1 crown height, compared to *T. peignei*, n. sp.

Intraspecific variations and sexual dimorphism in extinct basal hyaenids are difficult to evaluate when most species from any single locality amount to no more than a handful of specimens. For the present, the small size and dental morphology seems to suggest a different species, pending additional material.

COMPARISON AND DISCUSSION

Comparison of Chinese records

As shown in Tables 1 and 2, the Junggar *Tungurictis* form (*T. peignei*, n. sp.) is the smallest among all Chinese basal

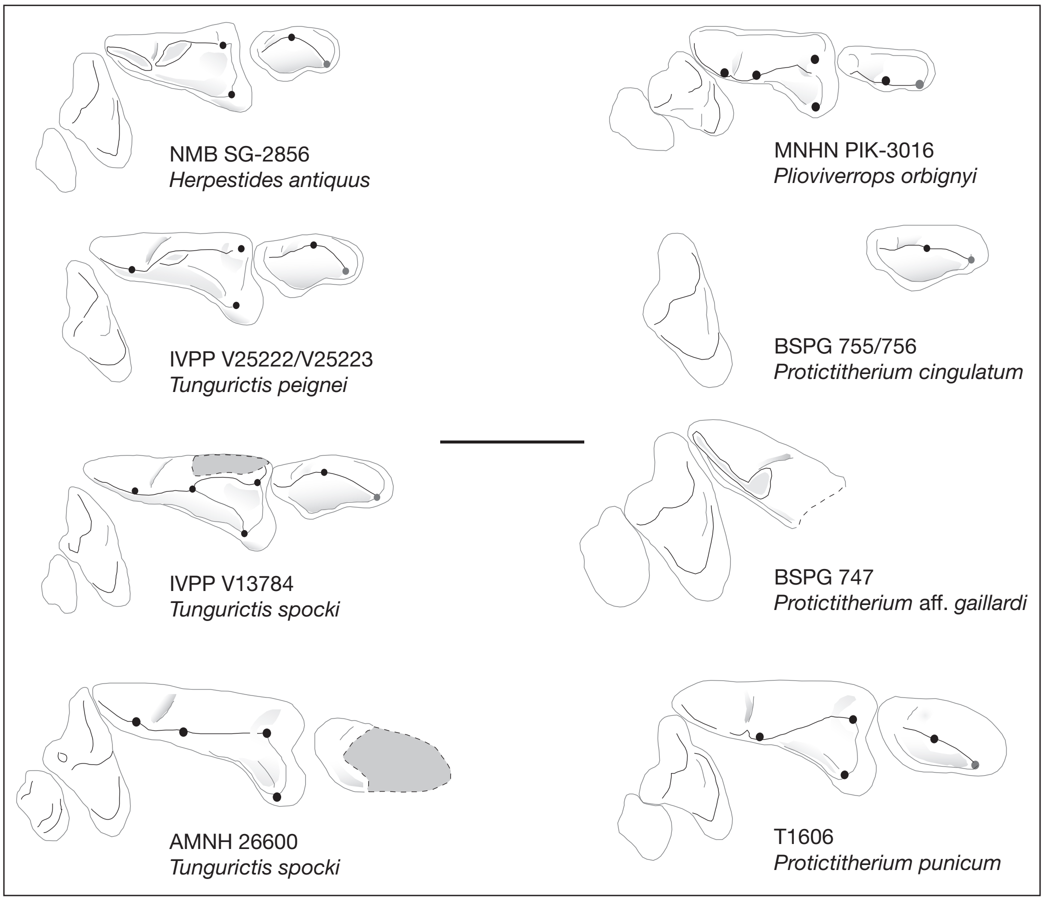

FIG. 9. — Comparisons of upper P4-M2 of selected basal hyaenids. Scale bar: 10 mm.

hyaenids. The Tairum Nor form (IVPP V 13784) from the lower part of the Tunggur Formation is slightly larger. Available upper teeth indicate a 20% (13.2/11.0 for lengths of P4) difference between the Tairum Nor and Junggar Basin forms but only about 8% (10.6/9.775, the latter being the mean of four individuals in Table 2) for lower carnassial length, when larger sample of lower jaws is available. By contrast, the holotype of *Tunguricts spocki* from Wolf Camp in the upper part of the Tunggur Formation is by far the largest, 34% (14.7/11.0 for P4 lengths) larger than the Junggar form.

In dental morphology, however, there is very little difference among individuals from these three samples. The main difference between the Junggar and Tairum Nor forms is that the latter's m1 talonid basin is more open toward the posterior end. The hypoconulid in IVPP V 13784 (*T. spocki*) is greatly reduced and no longer forms a posterior wall surrounding the talonid basin. Additionally, the P3 in IVPP V 25222 (*T. peignei*, n. sp.) has a slightly more distinct lingual bulge than in IVPP V 13784.

Therefore, although the Junggar form may be grouped with the Tairum Nor specimens in terms of body size (with 8-20% size difference as part of variations), there do seem to be indications of geographic or temporal (or both) differentiation between samples from Xinjiang and Inner Mongolia. Until better samples from both areas become available, we treat these as two separate species. However, the overall similarities among Chinese forms suggest that they belong to the same evolutionary lineage (Fig. 8), for which the name *Tunguricts* is appropriate. This East Asian lineage has a known duration of about 5 million years (17-12 Ma) in Chinese records, and mainly evolved in the direction of moderately increasing body size and reduced hypoconulid of the lower carnassial.

COMPARISON WITH EURASIAN RECORDS

A relatively short, lingually bent m1 trigonid with a posterolingual ridge leading down from the tip of paraconid is typical of all forms referred to *Protictitherium*, *Tunguricts*, *Plioviverrops*, and *Herpestides* de Beaumont, 1967 from Europe, "Asia Minor" (portions of modern day Turkey), and Africa. Upper teeth of the above genera differ in relative length of upper carnassial and size of M2 (Fig. 8), characters commonly associated with hyper- vs. hypocarnivory. These basal hyaenids ("ictitheroid" of Schmidt-Kittler 1976) have yet to develop the strong premolars for crushing bones so typical of later "hyaenoid" forms. As remarked by Hunt & Solounias (1991), this suggests that basal hyaenids acquired their ear region characteristics before the dental adaptations began.

Turkish middle and late Miocene sites, such as Çandır, Paşalar, Yeni Eskihisar, Sofça, Esendere, etc., are known to produce the most diverse *Protictitherium* forms (Schmidt-Kittler 1976; Mayda

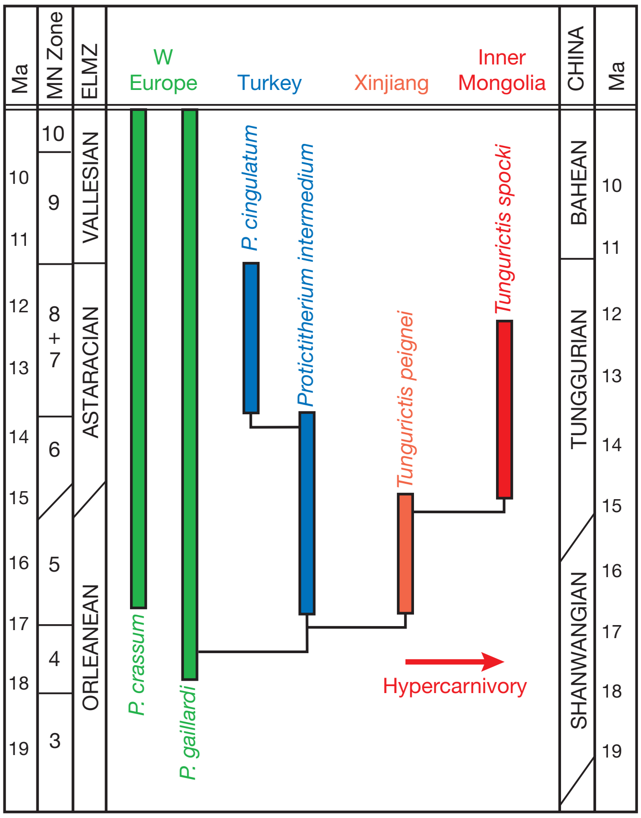

Fig. 10. — Chronologic and geographic distribution of selected basal hyaenids from Eurasia.

et al. 2015; Koufos *et al.* 2018). Currently included species are *P. crassum* (Filhol, 1883), *P.* aff. *gaillardi* (Forsyth-Major, 1903), *P. intermedium* Schmidt-Kittler, 1976, *P. cingulatum* Schmidt-Kittler, 1976, and *P. aegaeum* Kaya, Geraads & Tuna, 2005. The Turkish records offer clues to the initial diversification of stem hyaenids.

Relationships within *Protictitherium* were depicted as an unresolved multichotomy at the base of hyaenid clade (Werdelin & Solounias 1991, 1996; Turner *et al.* 2008), whereas *Tungurictis*, together with *Tongxinictis* Werdelin & Solounias, 1991, has been placed in a more derived position as a sister to *Ictitherium* (Werdelin & Solounias 1991) or *Thalassictis* (Turner *et al.* 2008). Fraile (2016) attempted to resolve a genus-level relationship and placed *Protictitherium*, *Plioviverrops*, and *Tungurictis* in a clade on their own. As currently recognized, *Protictitherium* is in a more basal position in hyaenids and likely paraphyletic, or even polyphyletic, given its stem position. In fact, Morales *et al.* (2019) singled out *P. crassum* to be a stem species to their newly elevated family, Lophocyonidae, one of the most hypocarnivorous feliform clades. Indeed, *P. crassum* has a distinct "talonid" on its p3-4 in the Turkish materials (SNSB-BSPG 1968 VI 760).

Hunt & Solounias (1991) proposed a classification of two subgenera, *Protictitherium* (*Protictitherium*) and *Protictitherium* (*Tungurictis*). They envisioned the former to be a hypocarnivorous clade that includes *P.* (*P.*) *crassum*, *P.* (*P.*) *intermedium*, *P.* (*P.*) *cingulatum*, and *P.* (*P.*) *gaillardi*, whereas the latter was thought to be a hypercarnivorous lineage that contains *P.* (*T.*) *spocki*. We retain generic level classification for species of *Tungurictis* because we suspect that the genus *Protictitherium* (excluding those classified under *Tungurictis*), as currently understood, may represent more than one monophyletic clade or stem taxa of paraphyletic arrangements. This dichotomous division between hypo- versus hypercarnivorous morphological tendencies is more readily visible in the upper teeth (Fig. 8), whereas the lower teeth are not always easy to distinguish. Where comparable materials are available, such as in the case of *P. intermedium* (e.g., SNSB-BSPG 1968 VI 736; Fig. 9), the Çandır specimen has more upright m1 entoconid and m2 protoconid and hypoconulid, characters commonly associated with hypocarnivory.

With the help of the new Junggar Basin records described above, we recognize a paleogeographic divergence. A hypocarnivorous *Protictitherium* (may also include *Plioviverrops* in the views of some researchers) clade is restricted to Europe and western Asia, whereas a slightly more hypercarnivorous *Tungurictis* lineage is found in East Asia (Fig. 10). Such a distribution may be the result of an eastward expansion of a Tunggurian Chronofauna through time (Mirzaie Ataabadi *et al.* 2013; Wang *et al.* 2013), i.e., basal hyaenids first diversified in western Europe and expanded into East Asia as environments became suitable. Alternatively, the dichotomous relationship of the hypercarnivorous forms in the East and hypocarnivorous forms to the West may have been tracking a paleoenvironmental dichotomy with the East Asian clade favoring more open environments in Chinese Xinjiang and Inner Mongolia, as is consistent with the digitigrade posture of *Tungurictis* (Hunt & Solounias 1991).

CARNIVORAN DIVERSITY AND MIDDLE MIOCENE CLIMATIC OPTIMUM

As shown in Figure 10, the *Tungurictis peignei*, n. sp. materials described in this paper straddle the Suosuoquan and Halamagai formations in the Junggar Basin. However, *Tungurictis* may be exceptional in this regard because of the otherwise drastic difference in carnivoran faunal diversity across those formations. There is a marked increase in carnivoran diversity within the middle Miocene Halamagai Formation, with as many as 13 forms currently recognized (see Geologic Setting section above) (Wang *et al.* 1998; Jiangzuo *et al.* 2018). This is in contrast to the predominantly small mammal assemblies (rodents, lagomorphs, insectivores and bats) found in the early Miocene Suosuoquan Formation below (Meng *et al.* 2006; Meng *et al.* 2013) and late Miocene Dingshanyanchi Formation above (Meng *et al.* 2008; Wu *et al.* 2009). Depositionally, the Halamagai Formation is essentially a sequence of greenish or grey fluvial sandstones whereas the Suosuoquan and Dingshanyanchi formations are largely a sequence of fine-grained red siltstones or mudstones.

Geochemical and grain-size analyses suggest that the Suosuoquan Formation is mainly comprised of fine eolian dust interbedded with occasional fluvial sandstones (Sun *et al.* 2010; Ye *et al.* 2012). These wind-blown deposits were the basis to push back the onset of Chinese loess sedimentation to around 24 Ma with the implicit linkage of winter monsoon intensities in East

Asia. Sedimentary structures in the Dingshanyanchi Formation is also consistent with an eolian origin (Meng *et al.* 2008).

Within the above depositional framework of fluvial sandstones sandwiched within red loess deposits in the Neogene of the Junggar Basin, the Halamagai Formation seems to stand out as an episode of relatively high-energy sedimentation with implications for a relatively wet period. If our current understanding of its biochronology is correct (i.e., the early Tunggurian Chinese Land Mammal Age for the Halamagai Formation), this places the Halamagai Formation within the Mid-Miocene Climatic Optimum (Flower & Kennett 1994), a period of warm climate in mid latitudes. Across much of North China, this middle Miocene Tunggurian Chronofauna, also popularly known as the *Platybelodon* Fauna, is often obtained from high energy sandstones or gravel beds, such as in the Tongxin Basin (Ningxia Province), the Linxia Basin (Gansu Province), and to some extent the Tunggur Basin (Inner Mongolia).

A relatively high diversity carnivoran fauna from the Halamagai Formation, as also reflected in the greater abundance of *Tunguricti*s materials described in this study, is likely a result of favorable depositional environments, in contrast to the less richly fossiliferous red beds above and below, especially in terms of large mammals. To what extent this can be attributed to the Mid-Miocene Climatic Optimum remains to be demonstrated when collections biases can be teased out. In the Tianshan foreland deposits, which form the southern rim of the Junggar Basin, Sun & Zhang (2008) identified a similarly warm climate from 18-15 Ma based on pollen records with high abundance of thermophilous broadleaved trees such as *Juglans* and *Quercus*. While future discoveries will undoubtedly enrich our knowledge of carnivoran biodiversity in the red beds, the Halamagai Formation seems to stand out as representing a period of time when both predators and prey thrived.

Acknowledgements

Stéphane Peigné was a close friend and colleague of the senior author (XW), going back to Stéphane's Ph.D. student days in the 1990s. His untimely death was a great loss to the small community of carnivore paleontologists. We are grateful to have this opportunity to write in Stéphane's memory and we thank Louis de Bonis for an invitation to contribute this paper.

We greatly appreciate the efforts by numerous members of the Xinjiang field team, who painstakingly accumulated materials described in this paper. We thank Yanping Song for assistance in photographic manipulations. Gertrud Rössner of Bayerische Staatssammlung für Paläontologie und Geologie gave permission to study materials from Turkey under her care. We are grateful to three reviewers, Lars Werdelin, Qiu Zhanxiang, and Camille Grohé, for their excellent suggestions, which greatly improved this paper. We are also in debt to the editorial efforts by Louis de Bonis and Lars Werdelin, and for translation of French resume by the former. Field works were supported by Chinese National Natural Science Foundation (40872032) and National Basic Research Program of China (973 Program, 2012CB821904).

REFERENCES

ANDREWS P. & TOBIEN H. 1977. — New Miocene locality in Turkey with evidence on the origin of *Ramapithecus* and *Sivapithecus*. *Nature* 268: 699-701. https://doi.org/10.1038/268699a0

BEAUMONT G. D. 1967. — Observations sur les Herpestinae (Viverridae, Carnivora) de l'Oligocène supérieur avec quelques remarques sur des Hyaenidae du Néogène. *Archives des Sciences* 20: 79-108.

BI S.-D. 1999. — *Metexallerix* from the early Miocene of north Junggar Basin, Xinjiang Uygur Autonomous Region, China. *Vertebrata PalAsiatica* 37: 140-155.

BI S.-D., WU W.-Y., YE J. & MENG J. 1999. — Erinaceidae from the Middle Miocene of north Junggar Basin, Xinjiang Uygur Autonomous Region, China, *in* WANG Y.-Q. & DENG T. (eds), *Proceedings of the Seventh Annual Meeting of the Chinese Society of Vertebrate Paleontology*. China Ocean Press, Beijing: 157-165.

BI S.-D., MENG J., WU W.-Y., YE J. & NI X. 2009. — New distylomyid rodents (Mammalia: Rodentia) from the early Miocene Suosuoquan Formation of northern Xinjiang, China. *American Museum Novitates* 3663: 1-18. https://doi.org/10.1206/665.1

BI S.-D., MENG J., MCLEAN S., WU W.-Y., NI X.-J. & YE J. 2013. — A new genus of aplodontid rodent (Mammalia, Rodentia) from the late Oligocene of northern Junggar Basin, China. *PLoS ONE* 8: e52625. https://doi.org/10.1371/journal.pone.0052625

BONIS L. DE 2004. — Carnivores hyaenidés du Miocène supérieur de Turquie, *in Zona Arquaeologica, Miscelanea en homenaje a Emiliano Aguirre, Volume 2, Paleontologia*. Museo Arqueologico Regional, Madrid: 108-117.

BONIS L. DE & KOUFOS G. D. 1991. — The late Miocene small carnivores of the lower Axios valley (Macedonia-Greece). *Geobios* 24: 361-379. https://doi.org/10.1016/S0016-6995(09)90015-8

BONIS L. DE, PEIGNÉ S., GUY F., MACKAYE H. T., LIKIUS A., VIGNAUD P. & BRUNET M. 2010. — Hyaenidae (Carnivora) from the late Miocene of Toros-Menalla, Chad. *Journal of African Earth Sciences* 58: 561-579. https://doi.org/10.1016/j.jafrearsci.2010.06.003

BOWDICH T. E. 1821. — *An Analysis of the Natural Classifications of Mammalia, for the Use of Students and Travellers*. Paris, J. Smith, 115 p.

CHOW M.-C. 1957. — Notes on some mammalian fossils from the late Cenozoic of Sinkiang. *Vertebrata PalAsiatica* 1: 33-41.

CHOW M.-C. 1958. — New material of Tertiary mammals from Sinkiang. *Vertebrata PalAsiatica* 2: 289-293.

COLBERT E. H. 1939. — Carnivora of the Tung Gur Formation of Mongolia. *Bulletin of the American Museum of Natural History* 76: 47-81. http://hdl.handle.net/2246/374

FILHOL H. 1883. — Notes sur quelques mammifères fossiles de l'époque miocène. *Archives du Muséum d'Histoire naturelle de Lyon* 3: 1-97.

FLOWER B. P. & KENNETT J. P. 1994. — The middle Miocene climatic transition: East Antarctic ice sheet development, deep ocean circulation and global carbon cycling. *Palaeogeography, Palaeoclimatology, Palaeoecology* 108: 537-555. https://doi.org/10.1016/0031-0182(94)90251-8

FORSYTH-MAJOR C. I. 1903. — New Carnivora from the middle Miocene of La Grive Saint-Alban, Isère, France. *Geological Magazine New Series* 10: 534-538. https://doi.org/10.1017/S0016756800115365

FRAILE S. G. 2016. — *Estudio de* Protictitherium crassum *del Cerro de los Batallones (Torrejón de Velasco, Madrid): aportación a la filogenia y evolución de la familia hyaenidae*. Facultad de Ciencias Geológicas, Departamento de Paleontología, Universidad Complutense Madrid, Madrid, 378 p.

FRAILE S. G. 2018. — *Protictitherium crassum*, la pequeña hiena de 9 milliones de años del Cerro de los Batallones, *in* CIFUENTES C., DURÁN E., BAQUEDANO E. & MORALES J. (eds), *La Colina de los Tigres Dientes de Sable: Los Yacimientos Miocenos del Cerro de los Batallones (Torrejón de Velasco, Comunidad de Madrid)*. Museo Arqueológico Regional, Cosmocaixa, Museo Nacional de Ciencias Naturales, Madrid: 221-234.

Ginsburg L. 1999. — Order Carnivora, *in* Rössner G. E. & Heissig K. (eds), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München: 109-148.

Ginsburg L. & Bulot C. 1982. — Les carnivores du miocène de Bézian près de la Romieu (Gers, France). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B* 85: 53-76.

Ginsburg L., Morales J. & Soria D. 1981. — Nuevos datos sobre los Carnivoros de los Valles de Fuentidueña (Segovia). *Estudios Geologicos* 37: 383-415.

Gray J. E. 1821. — On the natural arrangement of vertebrose animals. *London Medical Repository* 15: 296-310.

Hilgen F. J., Lourens L. J., Van Dam J. A., Beu A. G., Foyes A. F., Cooper R. A., Krijgsman W., Ogg J. G., Piller W. E. & Wilson D. S. 2012. — The Neogene Period, *in* Gradstein F. M., Ogg J. G., Schmitz M. D. & Ogg G. M. (eds), *The Geologic Time Scale 2012, Volume 2*. Elsevier, Amsterdam: 923-978.

Hunt R. M. Jr. 1989. — Evolution of the aeluroid Carnivora: significance of the ventral promontorial process of the petrosal, and the origin of basicranial patterns in the living families. *American Museum Novitates* 2930: 1-32. http://hdl.handle.net/2246/5145

Hunt R. M. Jr. & Solounias N. 1991. — Evolution of the aeluroid Carnivora: hyaenid affinities of the Miocene carnivoran *Tungurictis spocki* from Inner Mongolia. *American Museum Novitates* 3030: 1-25. http://hdl.handle.net/2246/5059

Jiangzuo Q.-G., Li C., Zhang X., Wang S., Ye J. & Li Y. 2018. — Diversity of Amphicyonidae (Carnivora, Mammalia) in the Middle Miocene Halamagai Formation in Ulungur River area, Xinjiang, northwestern China. *Historical Biology*: 1-16. https://doi.org/10.1080/08912963.2018.1477142

Kaya T., Geraads D. & Tuna V. 2005. — A new late Miocene mammalian fauna in the Karaburun Peninsula (W Turkey). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 236: 321-349.

Koufos G. D. 2012. — A new protictithere from the late Miocene hominoid locality Ravin de la Pluie of Axios Valley (Macedonia, Greece). *Paläontologische Zeitschrift* 86: 219-229.

Koufos G. D., Mayda S. & Kaya T. 2018. — New carnivoran remains from the Late Miocene of Turkey. *Paläontologische Zeitschrift* 92: 131-162. https://doi.org/10.1007/s12542-017-0376-2

Kurtén B. 1976. — Fossil Carnivora from the late Tertiary of Bled Douarah and Cherichira, Tunisia. *Notes du Service géologique de Tunisie* 42: 177-214.

Li C.-K., Lin Y.-P., Gu Y.-M., Hou L.-H., Wu W.-Y. & Qiu Z.-D. 1983. — The Aragonian vertebrate fauna of Xiacaowan, Jiangsu. 1. A brief introduction to the fossil localities and preliminary report on the new material. *Vertebrata PalAsiatica* 21: 313-327.

Maridet O., Wu W.-Y., Ye J., Bi S.-D., Ni X.-J. & Meng J. 2011. — Earliest occurrence of *Democricetodon* in China, in the early Miocene of the Junggar Basin (Xinjiang), and comparison with the genus *Spanocricetodon*. *Vertebrata PalAsiatica* 49: 393-405.

Mayda S., Koufos G. D., Kaya T. & Gul A. 2015. — New carnivore material from the Middle Miocene of Turkey. Implications on biochronology and palaeoecology. *Geobios* 48: 9-23. https://doi.org/10.1016/j.geobios.2014.11.001

Meng J., Ye J., Wu W.-Y., Yue L.-P. & Ni X.-J. 2006. — A recommended boundary stratotype section for Xiejian Stage from northern Junggar Basin: implications to related bio-chronostratigraphy and environmental changes. *Vertebrata PalAsiatica* 44: 205-236.

Meng J., Ye J., Wu W.-Y., Ni X.-J. & Bi S.-D. 2008. — The Neogene Dingshanyanchi Formation in northern Junggar Basin of Xinjiang and its stratigraphic implications. *Vertebrata PalAsiatica* 46: 90-110.

Meng J., Ye J., Wu W.-Y., Ni X.-J. & Bi S.-D. 2013. — Chapter 3. A single-point base definition of the Xiejian age as an exemplar for refining Chinese land mammal ages, *in* Wang X., Flynn L. J. & Fortelius M. (eds), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology*. Columbia University Press, New York: 124-141.

Mirzaie Ataabadi M., Liu L.-P., Eronen J. T., Bernor R. L. & Fortelius M. 2013. — Chapter 29. Continental-scale patterns in Neogene mammal community evolution and biogeography: A Europe-Asia perspective, *in* Wang X., Flynn L. J. & Fortelius M. (eds), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology*. Columbia University Press, New York: 629-655.

Morales J., Mayda S., Valenciano A., DeMiguel D. & Kaya T. 2019. — A new lophocyonid, *Izmirictis cani* gen. et sp. nov. (Carnivora: Mammalia), from the lower Miocene of Turkey. *Journal of Systematic Palaeontology* 17 (16): 1-12. https://doi.org/10.1080/14772019.2018.1529000

Ozansoy F. 1965. — Étude des gisements continentaux et des mammifères du Cénozoïque de Turquie. *Mémoires de la Société géologique de France (Nouvelle Série)* 44: 1-92.

Peigné S., Salesa M. J., Antón M. & Morales J. 2006. — New data on carnivores from the middle Miocene (Upper Aragonian, MN6) of Arroyo de Val area (Villafeliche, Zaragoza Province, Spain). *Estudios Geologicos* 62: 359-374. https://doi.org/10.3989/egeol.0662131

Qi T. 1989. — Miocene carnivores from Altai region, Xinjiang. *Vertebrata PalAsiatica* 27: 133-139.

Qiu Z.-D. & Qiu Z.-X. 2013. — Chapter 4. Early Miocene Xiejiahe and Sihong fossil localities and their faunas, eastern China, *in* Wang X., Flynn L. J. & Fortelius M. (eds), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology*. Columbia University Press, New York: 142-154.

Qiu Z.-D., Wang X. & Li Q. 2013. — Chapter 5. Neogene faunal succession and biochronology of central Nei Mongol (Inner Mongolia), *in* Wang X., Flynn L. J. & Fortelius M. (eds), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology*. Columbia University Press, New York: 155-186.

Qiu Z.-X., Yan D.-F., Chen G.-F. & Qiu Z.-D. 1988. — Preliminary report on the field work in 1986 at Tung-gur, Nei Mongol. *Chinese Science Bulletin (Kexue Tongbao)* 33: 399-404.

Schmidt-Kittler N. 1976. — Raubtiere aus dem Jungtertiär Kleinasiens. *Palaeontographica Abteilung A* 155: 1-131.

Sun J. & Zhang Z. 2008. — Palynological evidence for the Mid-Miocene Climatic Optimum recorded in Cenozoic sediments of the Tian Shan Range, northwestern China. *Global and Planetary Change* 64: 53-68. https://doi.org/10.1016/j.gloplacha.2008.09.001

Sun J., Ye J., Wu W., Ni X., Bi S., Zhang Z., Liu W. & Meng J. 2010. — Late Oligocene-Miocene mid-latitude aridification and wind patterns in the Asian interior. *Geology* 38: 515-518. https://doi.org/10.1130/G30776.1

Tong Y.-S., Qi T., Ye J., Meng J. & Yan D.-F. 1990. — Tertiary stratigraphy of the north of Junggar Basin, Xinjiang. *Vertebrata PalAsiatica* 28: 59-70.

Turner A., Antón M. & Werdelin L. 2008. — Taxonomy and evolutionary patterns in the fossil Hyaenidae of Europe. *Geobios* 41: 677-687. https://doi.org/10.1016/j.geobios.2008.01.001

Vandenberghe N., Hilgen F. J., Speijer R. P., Ogg J. G., Gradstein F. M., Hammer Ø., Hollis C. J. & Hooker J. J. 2012. — The Paleogene Period, *in* Gradstein F. M., Ogg J. G., Schmitz M. D. & Ogg G. M. (eds), *The Geologic Time Scale 2012, Volume 2*. Elsevier, Amsterdam: 855-921.

Wang X. 2004. — New materials of *Tunguricti*s (Hyaenidae, Carnivora) from Tunggur Formation, Nei Mongol. *Vertebrata PalAsiatica* 42: 144-153.

Wang X., Ye J., Meng J., Wu W.-Y., Liu L.-P. & Bi S.-D. 1998. — Carnivore from middle Miocene of Northern Junggar Basin, Xinjiang Autonomous Region, China. *Vertebrata PalAsiatica* 36: 218-243.

Wang X., Qiu Z.-d. & Opdyke N. O. 2003. — Litho-, Bio-, and Magnetostratigraphy and Paleoenvironment of Tunggur Formation (Middle Miocene) in central Inner Mongolia, China. *American Museum Novitates* 3411: 1-31. https://doi.org/10.1206/0003-0082(2003)411<0001:LBAMAP>2.0.CO;2

WANG X., FLYNN L. J. & FORTELIUS M. 2013. — Introduction. Toward a continental Asian biostratigraphic and geochronologic framework, *in* WANG X., FLYNN L. J. & FORTELIUS M. (eds), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology*. Columbia University Press, New York: 1-25.

WERDELIN L. 2005. — The Carnivora of Rudabánya (MN9, Late Miocene, Hungary). *Palaeontographia Italica* 90: 163-180.

WERDELIN L. & SOLOUNIAS N. 1991. — The Hyaenidae: taxonomy, systematics and evolution. *Fossils and Strata* 30: 1-104.

WERDELIN L. & SOLOUNIAS N. 1996. — The evolutionary history of Hyaenas in Europe and western Asia during the Miocene, *in* BERNOR R. L., RIETSCHEL S. & MITTMANN W. (eds), *The Evolution of Western Eurasian Miocene Mammal Faunas*. Columbia University Press, New York: 290-306.

WERDELIN L. & PEIGNÉ S. 2010. — Carnivora, *in* WERDELIN L. & SANDERS W. J. (eds), *Cenozoic Mammals of Africa*. University of California Press, Berkeley: 603-657.

WU W.-Y., MENG J. & YE J. 2003. — The discovery of *Pliopithecus* from northern Junggar Basin, Xinjiang. *Vertebrata PalAsiatica* 41: 71-86.

WU W.-Y., MENG J., YE J. & NI X.-J. 2004. — *Propalaeocastor* (Rodentia, Mammalia) from the early Oligocene of Burqin Basin, Xinjiang. *American Museum Novitates* 3461: 1-16. https://doi.org/10.1206/0003-0082(2004)461<0001:PRMFTE>2.0.CO;2

WU W.-Y., MENG J., YE J. & NI X.-J. 2006. — The first finds of eomyids (Rodentia) from the late Oligocene-early Miocene of the northern Junggar Basin, China. *Beiträge zur Paläontologie* 30: 469-479.

WU W.-Y., MENG J., YE J., NI X.-J., BI S.-D. & WEI Y.-P. 2009. — The Miocene mammals from Dingshanyanchi Formation of north Junggar Basin, Xinjiang. *Vertebrata PalAsiatica* 47: 208-233.

WU W.-Y., YE J., MENG J., WANG X., LIU L., BI S.-D. & DONG W. 1998. — Progress of the study of Tertiary biostratigraphy in north Junggar Basin. *Vertebrata PalAsiatica* 36: 24-31.

YE J. 1989. — Middle Miocene artiodactyls from the northern Junggar Basin. *Vertebrata PalAsiatica* 27: 37-52.

YE J., WU W.-Y. & MENG J. 2001a. — The age of Tertiary strata and mammal faunas in Ulungur River area of Xinjiang. *Journal of Stratigraphy* 25: 283-287.

YE J., WU W.-Y. & MENG J. 2001b. — Tertiary stratigraphy in the Ulungur River area of the northern Junggar Basin of Xinjiang. *Journal of Stratigraphy* 25: 193-200.

YE J., MENG J. & WU W.-Y. 2003. — Oligocene/Miocene beds and faunas from Tieersihabahe in the northern Junggar Basin of Xinjiang, *in* FLYNN L. J. (ed), Vertebrate Fossils and Their Context: Contributions in Honor of Richard H. Tedford. *Bulletin of the American Museum of Natural History* 279: 568-585. https://doi.org/10.1206/0003-0090(2003)279<0568:C>2.0.CO;2

YE J., WU W.-Y. & MENG J. 2005. — *Anchitherium* from the middle Miocene Halamagai Formation of northern Junggar Basin, Xinjiang. *Vertebrata PalAsiatica* 43: 100-109.

YE J., WU W.-Y., MENG J., BI S.-D. & WU S.-Y. 2000. — New results in the study of Tertiary biostratigraphy in the Ulungur River region of Xinjiang, China. *Vertebrata PalAsiatica* 38: 192-202.

YE J., WU W.-Y., NI X.-J., BI S.-D., SUN J.-M. & MENG J. 2012. — The Duolebulejin section of northern Junggar Basin and its stratigraphic and environmental implication. *Scientia Sinica Terrae* 42: 1523-1532. https://doi.org/10.1360/zd-2012-42-10-1523

Submitted on 23 January 2019;
accepted on 1 July 2019;
published on 20 February 2020.