

# 内蒙古中新世通古尔组 *Tungurictis* (*Carnivora : Hyaenidae*) 的新材料<sup>1)</sup>

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**摘要:** 斯氏通古尔鼬 (*Tungurictis spocki*) 是 1939 年 Colbert 描述的一个采自内蒙古中新世通古尔组的小型食肉类的新属、新种。他最初认为通古尔鼬属于灵猫科,但最近 Hunt (1989) 及 Hunt 和 Solounias (1991) 提出通古尔鼬具有一些鬣狗科耳区的特征(如水平方向的听泡隔板等)但缺少典型鬣狗科强壮的用来咬碎骨骼的前臼齿。Werdelin 和 Solounias (1991) 对鬣狗科分支系统的研究也进一步证实通古尔鼬实际上是一种鬣狗科较为原始的成员。因此通古尔鼬成为研究鬣狗科初期演化关系的重要一环。

*Tungurictis spocki* 的正型标本 (AMNH 26600) 是一件相当完整的头骨,但这是美国自然历史博物馆第三次中亚考查团在狼营地点 (Wolf Camp) 获得的惟一标本。缺少下颌骨和非常关键的下裂齿对于研究鬣狗科关系总是一件憾事。因此在通古尔台地南缘首次发现的出自同一个体的斯氏通古尔鼬上、下颌骨,对加深该种形态特征的认识和对鬣狗科系统关系的研究都具有一定意义。

新发现的材料 (IVPP V 13784) 包括很可能属同一个体头骨的前半部分以及下颌骨,并保存了 P3 ~ M2 及 m1 ~ m2。V 13784 采自内蒙古苏尼特左旗 IVPP 346 地点西 1.5 km (美国自然历史博物馆中亚考查团推饶木诺尔地点 Tairum Nor locality, 又称南营地 South Camp), 属通古尔组下部的推饶木动物群 (Tairum Nor fauna), 其时代比狼营地点正型标本层位的稍早 (邱铸鼎、王晓鸣, 1999; Wang et al., 2003)。

新材料的头骨及牙齿形态与正型标本基本相似。上牙只有微小的区别,例如个体稍小, P3 舌侧齿带及后附尖稍强, P4 原尖稍靠前等。V 13784 的下臼齿与一般鬣狗类的特征一致, 特别与一些原始鬣狗类 (如, *Proictitherium*、*Plioiverrops*、*Herpestides*) 的特征相似。一个相对较短并向唇侧稍弯曲的 m1 三角座, 以及在下前尖唇侧带有一个明显的小脊是所有这些原始鬣狗类的共同特征。而原始鬣狗类的 m1 跟座都拥有一对位置靠两边的下内尖与下次尖围成的一个宽大的跟座盆, 这个盆由于下后尖与下内尖之间的一个深洼而向唇侧敞开。V 13784 的 m2 也具有典型原始鬣狗类的特征。下原尖、下后尖、下内尖及下次尖都在牙齿的边缘, 并把牙齿的中间围成一个较宽的低谷。斯氏通古尔鼬没有 m3。

新材料弥补了斯氏通古尔鼬缺失下颌骨的遗憾。其下臼齿形态与原始鬣狗成员的相像, 进一步证实了斯氏通古尔鼬属鬣狗科。这对今后深入探讨鬣狗类的起源及演化将起到很大的作用。

**关键词:** 内蒙古通古尔, 中新世, 鬣狗科

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## NEW MATERIALS OF TUNGURICTIS (HYAENIDAE, CARNIVORA) FROM TUNGGUR FORMATION, NEI MONGOL

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**Abstract** New materials of *Tungurictis spocki*, a basal hyaenid (Hyaenidae, Carnivora), from the Tairum Nor locality in Tunggur Formation is described. For the first time, associated upper and lower teeth are available for this species, which is previously established on a single skull. The newly available lower molars corroborate current beliefs that *Tungurictis* is a primitive hyaenid. A relatively low metaconid and an equal height for m1 hypoconid and entoconid further establish its difference from hypocarnivorous forms such as *Plioviverrops*. *Tungurictis spocki* is probably closely related to European and western Asian *Proictitherium gaillardi*.

**Key words** Tunggur, Nei Mongol, Miocene, Hyaenidae

### 1 Introduction

In his report on the Carnivora of the Tunggur Formation, Colbert (1939) described a new genus and species, *Tungurictis spocki*, collected from the late Middle Miocene of Nei Mongol (Inner Mongolia) during the American Museum Central Asiatic Expedition in 1930. Based on a nearly complete skull from the richly fossiliferous "Wolf Camp" locality, *Tungurictis* was initially thought to be a member of the family Viverridae. Recent studies by Hunt (1989) and Hunt and Solounias (1991), however, established it to be a basal hyaenid with a characteristic horizontal intrabullar septum but without the heavy bone crushing dentition typical for most later hyaenids. Cladistic analysis by Werdelin and Solounias (1991) also placed it as a transitional form between *Plioviverrops* and *Ictitherium* near the beginning of the hyaenid clade. It is thus increasingly clear that *Tungurictis*, having a truly hyaenid basicranium but possessing only a rudimentary hyaenid dentition, plays a critical role in the understanding of the origin and early evolution of hyaenids.

Although the type material for *Tungurictis* is based on a nearly complete skull, our knowledge about this rare form is handicapped by the lack of materials for lower jaws, especially the critically important lower molars. Here I report the first discovery of associated upper and lower jaws from the Tunggur Formation. The new materials were recovered from a stratigraphically lower position from the type locality of *Tungurictis*, and display a smaller size and slightly more primitive morphology. This added temporal dimension permits a sense of evolutionary trends of this primitive hyaenid.

Institutional Abbreviations: AMNH, American Museum of Natural History, New York; BSP, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing; UCPE, University of Colorado Paleontological Expeditions to Tunisia, Boulder.

### 2 Systematics

#### Hyaenidae Gray, 1821

#### *Tungurictis* Colbert, 1939

#### *Tungurictis spocki* Colbert, 1939

**Holotype** AMNH 26600, nearly complete skull from Wolf Camp.

**Referred specimen** IVPP V 13784 (Figs. 1 ~ 2; Table 1), rostral part of skull with left I1 ~ P2 alveoli, P3 ~ M1 broken, and M2, right I1 ~ P1 alveoli, P2 ~ M2, left and right ramal

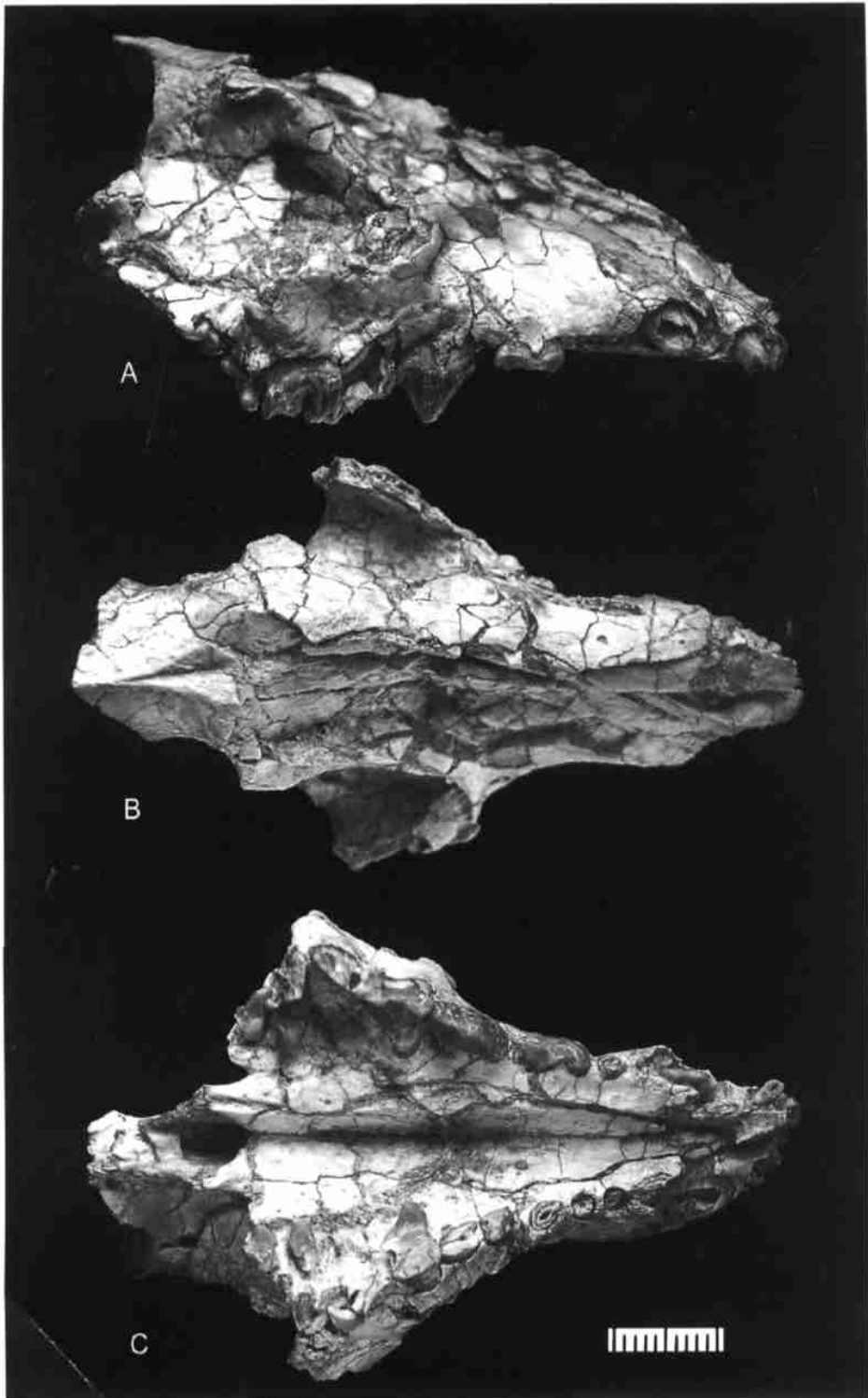


Fig. 1 Skull of *Tunguictis spocki* with P2~M2, V 13784, scales are in mm  
A. lateral view; B. dorsal view; and C. occlusal view

fragments with left m1 ~ 2 and right m1, probably belonging to the same individual; AMNH 26610, right ramal fragment with premolars, from 25 miles northeast of Gur Tung Khara Usu (probably the same as IVPP Huerquolajin Locality, see Wang et al., 2003).

**Locality of new material** Approximately 1.5 km west of IVPP road mark 346 locality (AMNH Tairum Nor locality or South Camp) (Wang et al., 2003). The skull and jaws are separately embedded in calcareous nodules within one meter of each other in the same nodular layer on a bench formed by erosion of the soft red mudstones above. It is in the lower-most paleosol immediately above the prominent channel sandstones that divide the upper and lower red beds at Tairum Nor. Collected by X. Wang on August 27, 1996.

**Associated Tairum Nor fauna and age determination** The Tairum Nor area along the southern margin of the Tunggur Tableland is traditionally included in a broad Tunggur Fauna that include materials from all exposures of the Tableland (Osborn and Granger, 1931; Qiu et al., 1988b; Spock, 1929). Based on small mammals, Qiu and Wang (1999) proposed a Tairum Nor Fauna to be distinguished from the Moergen Fauna (including the majority of the classical Tunggur materials) from the northern rim of the Tunggur Tableland. The Tairum Nor Fauna include the following small mammals: *Mioechinus? gobiensis*, *Atlantoxerus orientalis*, *Anchitheriomys tungurensis*, *Tachyoryctoides* sp., *Distylomys tedfordi*, *Heterosminthus orientalis*, *Gobicricetodon flynni*, *Plesioidipus leei*, *Megacricetodon* sp., *Desmatolagus? moergenensis*, *Alloptox gobiensis*, and *Bellatona forsythmajori*. Although the majority of these are known in the Moergen Fauna (Qiu, 1996), *Tachyoryctoides* sp. and *Distylomys tedfordi* occur only in the Tairum Nor, and they are normally seen in the Oligocene and early Miocene of central and eastern Asia. The Tairum Nor record thus represents their latest occurrence. *Atlantoxerus*, *Heterosminthus*, and *Gobicricetodon* from Tairum Nor also show somewhat more primitive morphologies as compared to those from the Moergen locality (Qiu and Wang, 1999).

To the above list of small mammals, the following large mammals can be added to the Tairum Nor Fauna: *Leptarctus neimenguensis*, *Sthenictis* sp. n., *Tungurictis spocki*, *Platybelodon grangeri*, *Acerorhinus zernowi*, and *Dicrocerus* sp. Of these *Leptarctus neimenguensis* and *Sthenictis* sp. n. are not found in the northern and western exposures of the Tunggur Tableland. These two carnivorans apparently represent immigrants from the North America, and based on the stage of evolution, seem to correspond to North American forms from the Burge Member of the Valentine Formation around the Barstovian-Clarendonian boundary. Paleomagnetic studies further indicate a correlation of the Tairum Nor section to the magnetic chrons C5Ar.3r to C5An.2n around 13~12.15 Ma (Wang et al., 2003). According to this correlation scheme, the top of the channel sandstone in the Tairum Nor section, where V 13784 was collected, is around 12.5 Ma, probably 0.2~0.4 million years older than the Wolf Camp section that produced the holotype of *Tungurictis spocki*.

**Description** V 13784 represents a young adult with permanent dentition fully erupted that acquired minimum wear. Although the skull and lower jaws were found in separate nodules nearby, their similarity in wear and compatibility in occlusal fits suggest that they belong to the same individual. Only the anterior half of the skull is preserved. The skull suffered severe crushing. The left and right halves are sheared along the sagittal plane near the center line such that the right half is shifted ventrally relative to the left half. As in the holotype, the rostrum of the new specimen is slender. Much of the nasals are crushed to small pieces. The orbital area on the left is relatively intact. The tip of the postorbital process of frontal is broken off, and as commented by Colbert (1939), the postorbital constriction is deep. The temporal crests converge to the single sagittal crest about 12 mm behind the postorbital process.

The upper dentition includes three incisors, one canine, four premolars, and two molars. Although the left and right premaxillae are disjointed, the tip of the snout is preserved along with roots of all upper incisors. The roots of the incisors are highly compressed mediolaterally, especially so toward the medial (I1) side of the incisor row. Both upper canines are broken off at the base and



Fig. 2 Lower jaw and upper dentition of *Tungurictis spocki*, V 13784, scales are in mm  
 A. occlusal view of lower teeth, stereo photograph; B. occlusal view of upper dentition, stereo photograph;  
 C. lingual view of lower jaw; and D. labial view of lower jaw

only their roots are left. The same is true for the single-rooted P1s. There is a 2.8 mm diastema between the C and P1 and a shorter one, less than 1 mm, between the P1 and P2. The main cusp of the right P2 is missing but enough of the base of the crown is preserved to allow reliable measurement of its dimension. The cingulum is very weak, almost nonexistent in the anterior part and slightly better developed in the posterolabial aspect of the tooth. There is a sharp posterior ridge that ends nearly horizontally at the base of the crown. The right P3 is complete and is unworn. Its main cusp has a sharp anterior ridge around the anterolingual aspect of the tooth and stops at the anterior cingulum. The anterior cingulum is slightly swelled at this juncture and is elevated to form a cusp-like structure. The anterior cingulum is otherwise poorly developed. The posterior ridge is also sharp and has a tiny notch near the base of the tooth. The posterior ridge is abruptly turned to a horizontal orientation to give it an appearance of a posterior accessory cusp. As in the P2, the posterior cingulum is generally poorly developed except at the posterolingual side where it is suddenly swelled up.

Both upper carnassials (P4) are damaged, the right one being much better preserved. Together the remaining parts give a reasonable picture of the entire tooth. The protocone is prominently developed, its anterior edge being slightly in front of the parastyle. The apex of the protocone is high and clearly continuous with the cingula both laterally and posteriorly, giving the impression that the protocone is formed by the elevation of the internal cingulum. A parastyle is well developed, and is of nearly the same height and size as the protocone. The parastyle is connected to the protocone via the anterior cingulum. The paracone is reclined backward. The paracone-metastyle blade is quite sharp and shows no signs of wear. A very thin lingual cingulum is present but there is no labial cingulum.

The right M1 is complete and only the talon of the left M1 is preserved. The straight anterior face, constructed from the anterior ridge of the paracone and the preprotocrista, forms a sharp shearing edge against the posterior face of the m1 trigonid. A large paracone dominates over the smaller and lower metacone. The parastyle extrudes labially to give the cusp a transversely oriented appearance. The parastyle and paracone occupies about half of the entire transverse width of the M1. A posterior ridge of the paracone connects with the metacone. The much smaller metacone is located at the posterolabial corner of the tooth. The protocone is second largest cusp of the tooth and is formed from a crescent-shaped pre- and postprotocrista. There is a vague indication of a paraconule near the anterior end of the preprotocrista but there is no sign of a metaconule. The pre- and postprotocrista enclose a large basin in the talon to occlude with the hypoconid of the m1. The entire M1 is naked without a cingulum.

Both M2s are well preserved and suffered no wear. Its paracone is much smaller than that in the M1, but still dominates (about twice as large as) the metacone. In contrast to the M1, the labial half of the M2 paracone is not greatly expanded but its lingual half is more expanded. The posterior and anterior ridges of the paracone and metacone are aligned in a diagonal direction. The protocone is formed along the lingual border of the tooth, with the pre- and postprotocrista circling around.

Both horizontal rami are broken just in front of the posterior root of the p4. The remainder of the horizontal ramus is slender and curves gently below the m1. The ascending ramus on the left side is better preserved, although the tip of the coronoid process is broken. The anterior border of the ascending ramus is reclined backward. The tip of the angular process stops at the same level as the posterior edge of the condyloid process. A vague ridge divides the medial surface of the angular process into superior and inferior facets.

Only m1 ~ 2 are preserved. The protoconid on the left m1 is broken but that on the right is well preserved, so that the left and right m1s combined to permit a complete description of its morphology. The m1 trigonid is long and its shearing blade is at an angle with the longitudinal axis. The anterior border of the paraconid is slightly reclined and forms a vague ridge on the anterior facet. There is a distinct labial cingulum around the anterior half of the paraconid and it quickly disappears posteriorly. On the lingual side, there is a vague lingual cingulum around the paraconid, but none

is present around the metaconid. The paraconid has a ridge on the posterolingual aspect of the cusp and leads down from its apex to the lingual opening of the trigonid. The protoconid is slightly taller than the paraconid. In addition to the anteroposterior shearing blade anterior to the protoconid, there is also a transverse shearing blade on the posterior surface of the protoconid. This latter blade shears with the anterior edge of the M1. The metaconid is only about half as tall as the protoconid. It leans slightly lingually to occupy the posterolingual corner of the trigonid. The talonid is narrow and short. The basined talonid is formed by a hypoconid and entoconid. The hypoconid is slightly larger and taller on the left m1 but the opposite is true on the right m1. A short and steep crista obliqua connects between the hypoconid and the posterior face of the trigonid, terminating slightly lateral to the protoconid-metaconid notch. The entoconid is an isolated cusp without connection to either metaconid anteriorly or hypoconid labially. There is a deep notch between the metaconid and entoconid, allowing the talonid basin to be open lingually. A minute cuspule is present on the labial face of the entoconid just below its apex. A low hypoconulid platform is present on the left m1 but is absent in the right side.

Only the left m2 is preserved. The m2 trigonid is slightly longer than the talonid. A sharp metaconid is located on the anterolingual corner of the trigonid, whereas the protoconid is on the opposite side on the anterolabial corner. Both cusps are placed along the margin of the tooth, and a broad valley opens up between these cusps. The metaconid is taller than the protoconid. There is no paraconid. The talonid is similarly constructed with a marginal entoconid and hypoconid on either side. The two cusps are about equal in height. As in the m1, the talonid basin opens lingually between the metaconid and entoconid. A small hypoconulid is present and projects upwards and posteriorly so that the talonid basin is closed from behind. There is no m3.

Table 1 Dental measurements\*

(mm)

	<i>T. spocki</i>		<i>P. intermedium</i>		<i>T. punica</i>	<i>P. gaillardi</i>
	AMNH	IVPP	BSP VI	IVPP	UCPE	BSP VI
	26600	V 13784	736	V 11494	T 1606	743/ 745/ 475
I3 to M2 length	59.4	55.0				
C to M2 length	52.6	49.4				
P1 to M2 length	42.9	39.2				
P1 ~ P4 length	37.0	34.1				
P2 length	7.8	7.2				
P3 length	9.4	8.6			9.6	
P3 width	4.5	3.9			5.4	
P4 length	14.7	13.2			14.3	13.6
P4 width	7.4	7.1			7.7	
M1 length	5.7	4.5			5.8	5.9
M1 width	10.7	10.5			11.2	11.6
M2 length	3.0	3.0			3.1	4.1
M2 width	5.2	4.5			5.1	6.3
m1 length		10.6	10.5	10.4		11.3
m1 trigonid length		7.5				
m1 trigonid width		4.8	4.4	5.0		5.1
m1 talonid width		3.6				
m2 length		4.0	4.9			
m2 width		3.3	3.7			

\* Those for the holotype of *Tungurictis spocki* and *Protictitherium gaillardi* follow Hunt and Solounias (1991: Table 1).

### 3 Comparison and discussion

Overall cranial and dental morphologies of the new materials are closely comparable to those of the holotype. Only minor variations can be observed. V 13784 is slightly smaller than the holotype (Table 1), averaging about 8% in differences for larger dimensions such as tooth rows. Certain dental measurements can exceed this average, such as P3 width, M1 length and M2 width, but these latter dimensions are usually the most variable in carnivorans because of their lack of physical constraints in their occlusion patterns. The small sample size does not permit evaluations of whether these size differences are the result of temporal or individual variations. Other observable differences between V 13784 and the holotype include a slightly better developed lingual cingulum and posterior accessory cusp on P3 of V 13784 and a slightly more anteriorly located P4 protocone on the holotype, differences that can easily be accounted for variations within a species. Lack of common dental elements between V 13784 and AMNH 26610, the only other known lower jaw, prevent a meaningful comparison. Overall, the reference of V 13784 to *Tungurictis spocki* is not in doubt.

The most significant contribution of the new *Tungurictis* material lies in its presence of lower molars, a crucial part of morphology that is previously unavailable. Lower molars of *Tungurictis* are reminiscent of a generalized hyaenid morphology, particularly those of certain species of *Protictitherium*, and are largely consistent with conclusions reached by Hunt and Solounias (1991) through their study of basicranium and upper teeth. The lower molar construction of *Tungurictis* is fundamentally similar to such basal, small fox-sized hyaenids as *Protictitherium*, *Plioviverrops*, and to a lesser extent, *Herpestides* from Europe, Asia Minor, and northern Africa. A relatively short and lingually bent m1 trigonid with a distinct ridge on the lingual aspect of the paraconid leading down from the apex of the cusp is typical for all of these forms. On the m1 talonid, these basal hyaenids share a marginally located hypoconid and entoconid enclosing a broad basin, which opens lingually due to a deep notch between the entoconid and metaconid. The m2s of these forms share marginally positioned main cusps such that the protoconid, metaconid, entoconid, and hypoconid more or less enclose a broad basin in the middle. A detailed analysis is under way (to be published elsewhere) to sort out these similarities and assess their significance in the origin of hyaenids. While it is beyond the scope of this paper to elaborate their relationships, I will only make the following brief comments on Chinese basal hyaenids.

Hunt and Solounias (1991) suggested that *Tungurictis* is probably closest to Eurasian and African *Protictitherium*, particularly *P. gaillardi*, in contrast to the more hypocarnivorous *Plioviverrops*. The new lower dentition of *Tungurictis* generally bears out their conclusion—the m1 has relatively low crowned metaconid and entoconid when compared to those of *Plioviverrops* and the trigonid is also relatively long as contrasted to a short trigonid in the latter. The entoconid and hypoconid in V 13784 is essentially equal in height, a feature also seen in *Protictitherium gaillardi* (Hunt and Solounias, 1991; Schmidt-Kittler, 1976). Based on such similarities, Hunt and Solounias (1991) placed *Tungurictis* as a subgenus of *Protictitherium*.

Wang and colleagues (1998) described a few fragmentary mandibles (IVPP V 11493 ~ 6) from the middle Miocene Halamagai Formation in the Junggar Basin, Xinjiang, and lacking comparable materials to the Tunggur form at the time, referred them to *Protictitherium intermedium*. The new Tunggur lower teeth afford a direct comparison between the Tunggur and Junggar forms. As shown in Table 1, lower molars from these two localities are nearly identical in size. Overall dental morphology is also very similar, such as their nearly equal height of the hypoconid and entoconid. The Junggar form may thus belong to the same species as *Tungurictis spocki*.

In his original description of *Tungurictis*, Colbert (1939) mainly compared it with living Oriental civet (*Viverra zibetha*) from South China. Kurtén (1976) subsequently described a new species of *Tungurictis*, *T. punica*, from the late Miocene Bled Douarrah of Tunisia. Kurtén more or less followed Colbert in his assessment of the phylogenetic relationships. Although the upper car-



massial of *T. punica* is close to be the same size as the type species, its upper first molar appears to be relatively larger (Table 1), a dental proportion suggesting a slightly more hypocarnivorous dentition. Werdelin and Solounias (1991) suggested that the Tunisian form do not belong to *Tungurictis*, and instead, may be closely related to *Protictitherium cingulatum* from the middle Miocene of Turkey (Schmidt-Kittler, 1976). Since there is no lower jaw material in *T. punica* for comparison, the new Tungur material does not provide new insight into this matter.

In their monographic treatment of the phylogenetic relationships of the Hyainidae, Werdelin and Solounias's (1991: Fig. 38) proposed a phylogeny in which *Tungurictis* stands alone in a basal position immediately below *Ictitherium* and is separated from species of *Protictitherium* by *Plioviverrops* and *Proteles*. This phylogenetic scheme, however, contains an element of speculation because the majority of the basal taxa are not included in the analysis for lack of adequate materials, and the authors cautioned that things could easily change when new information becomes available. Beside their recognition of the unambiguously hyainid bullar in *Tungurictis*, Werdelin and Solounias saw nothing in its dentition to indicate any special relationship to particular clades. Hunt and Solounias (1991), on the other hand, suggested that the Nei Mongol species possesses such incipient dental characters as slightly enlarged premolars and canines and long carnassials that foreshadow durophagous dentitions of most advanced hyainids. Furthermore, their suggestion that *Tungurictis* be subsumed within *Protictitherium* contradicts the arrangement by Werdelin and Solounias (1991), a controversy that requires further investigation.

It is becoming clear that basal hyainids from China will play an increasingly important role in our understanding of the major radiations. In addition to the peculiar bone-crushing perocrotines (Chen and Schmidt-Kittler, 1983; Colbert 1939; Qiu et al., 1988a, c), basal hyainids in the Chinese middle Miocene are known from at least three localities: an undescribed *Protictitherium* from Xiacaowan of Jiangsu Province (Li and Ting, 1983), two species of *Protictitherium* from Halamagai Formation of Junggar Basin (Wang et al., 1998), a *Thalassictis* also from Halamagai Formation of Junggar Basin (Wang et al., 1998), and *Tungurictis spocki* from Tungur Formation. Such an array of diversity in East Asia suggests an important center of evolution for a group of carnivoran that later became dominant predators during much of the late Cenozoic of the entire Old World.

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