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Evolution of the Aeluroid Carnivora: Hyaenid Affinities of the Miocene Carnivoran Tungurictis spocki from Inner Mongolia

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Evolution of the Aeluroid Carnivora: Hyaenid Affinities of the Miocene Carnivoran *Tungurictis spocki* from Inner Mongolia

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ABSTRACT

Among the mammalian fossils discovered in 1930 by the Central Asiatic Expedition of the American Museum of Natural History (New York) in the Tung Gur Formation of Inner Mongolia were crania and mandibles of rare carnivorans, including the first complete skulls of several Asian mid-Miocene lineages. Most of these fossils came from a single locality termed Wolf Camp Quarry

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that produced, among other striking finds, a small fox-sized cranium referred to a new genus and species *Tungurictis spocki* Colbert 1939. Today this remains the only known cranium of *Tungurictis* yet discovered.

Preparation and reinterpretation of the auditory region demonstrate that *Tungurictis* belongs to an early lineage of Hyaenidae, although it has long been regarded as a viverrid. The Wolf Camp Quarry cranium of *Tungurictis* combines a hyaenid auditory bulla structure with incipient hyaenid specializations of the cheek teeth, indicating that the typical bulla pattern evolved prior to the robust, bone-crushing dentitions that characterize living species of *Crocuta* and *Hyaena*. Previously undescribed remains of left and right hindfeet found in Wolf Camp Quarry near the skull are attributed to the same species, if not the same individual, and indicate that a digitigrade paraxonic stance characterized this small Asian carnivore.

Tungurictis has been identified only in the Tung Gur Formation of Mongolia, with the exception of a doubtfully referred upper jaw fragment from north Africa. However, a survey of dentitions of small mid-Miocene European hyaenids indicates that the cheek teeth of *Tungurictis spocki* are comparable to the holotype dentition of *Protictitherium gaillardi* (Forsyth-Major, 1903) from the mid-Miocene of La Grive, France. So similar is the dental morphology that hyaenid basicranial structure can be reasonably inferred for *P. gaillardi*, and for *Protictitherium* for which no basicranium was known. Thus, at least three lineages of small hyaenids with plesiomorphic dentitions (lacking durophagous specializations of the premolars and carnassials) lived in Eurasia during the Miocene: (1) a *Protictitherium* (*Tungurictis*) lineage, with hypercarnivorous dentition and hyaenid auditory region; (2) a *Protictitherium* (*Protictitherium*) lineage, known chiefly from dentitions in which the m1 entoconid is emphasized—an intact auditory region is not yet identified; (3) a *Plioviverrops* lineage, with hypocarnivorous dentition and hyaenid auditory region.

Two additional early hyaenid lineages (*Miohyaena*, *Percrocuta*) of the mid-Miocene cannot be confused with *Protictitherium* or *Plioviverrops* because they show a precocious development of durophagous dental specializations, heralding the large bone-crushing species of the later Cenozoic of Eurasia.

Old World Miocene hyaenids parallel New World Miocene canids in body size, skull form, dental specialization, and diversity. Small, intermediate, and large-sized digitigrade canid and hyaenid ecomorphs are known during the Neogene, some with plesiomorphic skull form and dentition, others with derived "hyaenoid" cranium and teeth, including durophagous animals of large body size within both Hyaenidae (*Dinocrocuta*, *Pachycrocuta*, *Adcrocuta*) and Canidae (*Epicyon*, *Borophagus*, *Osteoborus*).

INTRODUCTION

In 1930 the Central Asiatic Expedition of the American Museum of Natural History discovered important fossil remains of previously unrecognized mid-Miocene carnivorans in the Tung Gur Formation of Inner Mongolia. In particular, a single locality known as Wolf Camp Quarry produced superb skulls of the ursid *Hemicyon teilhardi* and the hyaenid *Percrocuta tungurensis*, upper and lower jaws of the rare amphicyonid *Gobicyon macrognathus*, and a small, foxsized cranium attributed to a new genus and species, *Tungurictis spocki*. This well-preserved cranium (AMNH 26600), and the other Tung Gur Formation Carnivora, were described by E. H. Colbert in 1939.

Tungurictis was initially classified as a true viverrid, based upon (1) the arrangement of basicranial foramina; (2) a resemblance in general appearance and structure of the skull to the living *Viverra zibetha*; (3) the damaged auditory bulla said to resemble that of the paradoxurine civets. Only two additional fossils were subsequently assigned to the genus: a partial lower jaw with premolars, also found in 1930 by the Central Asiatic Expedition along the Tung Gur escarpment about 30 mi (48 km) northeast of Wolf Camp Quarry, and a partial maxilla with P3-M2 (UCM 43627) discovered in April 1968 in the lower Beglia Formation of Tunisia (Locality 18, Bled Douarah), and assigned to the Viverridae (*Tungurictis punica*, Kurten, 1978).

Recent cleaning and careful preparation of the Wolf Camp Quarry cranium of *Tungurictis* (AMNH 26600) allowed us to reinterpret its auditory region in the light of new insights into the morphology and ontogenetic development of the aeluroid basicranium (Hunt, 1987, 1989). The structure of the remnant auditory bulla was critical to our reassessment, providing compelling evidence that establishes the hyaenid affinities of this small mid-Miocene carnivoran (Tunggurian, late middle Miocene, zone MN8, Li et al., 1984; Qiu et al., 1988a). Although the teeth display incipient derived hyaenid traits (such as the form and elongation of the upper carnassial,

reduction of the posterior molars, and prominent P2–3 relative to small P1), they are nevertheless broadly plesiomorphic within Hyaenidae by virtue of their small size, presence of relatively narrow premolars not yet specialized for crushing, and retention of M2. We also believe that the long, slender skull, gracile rostrum, and narrow palate are plesiomorphic hyaenid traits retained by *Tungurictis spocki,* possibly reflecting skull proportions of the ancestral hyaenid stock.

ABBREVIATIONS

Anatomical

A	alisphenoid
AC	posterior opening of alisphenoid canal
BO	basioccipital
BS	basisphenoid
E	caudal entotympanic
EC	caudal entotympanic (posterior) chamber of bulla
EO	paroccipital process of exoccipital
FO	foramen ovale
FM	foramen magnum
GF	glenoid fossa of squamosal
L	middle lacerate foramen
M	mastoid
P	petrosal promontorium
PLF	posterior lacerate foramen
R	rostral entotympanic
S	hyaenid intrabullar septum
SB	septum bullae
SE	sediment filling posterior chamber of bulla
SMF	stylomastoid foramen
SQ	squamosal
T	ectotympanic

V	ventral process of petrosal
VF	vestigial postglenoid foramen

Institutional

AMNH	Vertebrate Paleontology, American Museum of Natural History, New York
FAM	Vertebrate Paleontology, American Museum of Natural History (Frick Collection)
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing
MGL	Musée Guimet d'Histoire Naturelle, Lyon
UCM	University of Colorado Museum, Boulder
UNSM-ZM	University of Nebraska State Museum (Zoology), Lincoln

DISCOVERY OF THE CRANIUM OF *TUNGURICTIS*

The fossil remains of *Tungurictis spocki* described by Colbert (1939) include the holotype cranium (AMNH 26600) and a referred lower jaw fragment (AMNH 26610) designated as paratype. Colbert attributed the skull to Wolf Camp Quarry, a locality also designated as Quarry 2 by Osborn and Granger (1932), who described fossils of the proboscidean *Platybelodon* from the same site (fig. 1). Insofar as we can determine, no detailed account of the collection of the holotype (and only known) skull of *Tungurictis* exists. Here we present our attempt to reconstruct the discovery.

The Tung Gur Formation of Inner Mongolia was initially discovered by L. E. Spock and R. C. Andrews during the 1928 Central Asiatic Expedition of the American Museum of Natural History. The first fossils from the Tung Gur beds were found on June 19, 1928, on a reconnaissance of the region, and later in the summer more extensive explorations resulted in discovery of the first remains of the shovel-tusked *Platybelodon grangeri* on both north and south escarpments of the vast Tung Gur tableland (Spock, 1929). Discovery of these platybelodont mastodonts stimulated a return visit to the tableland by the American Museum expedition two years later in June 1930.

Established on June 8, 1930, the initial base camp on the tableland was the North Camp of Osborn and Granger (1932: fig. 1), or
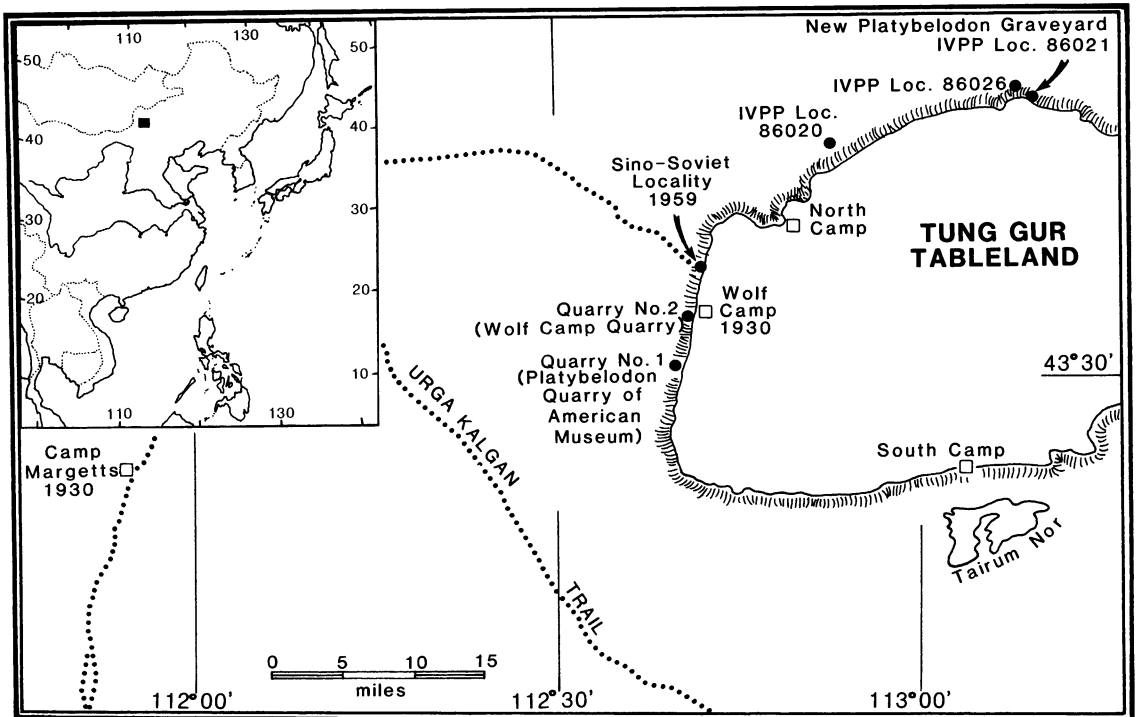
Fig. 1.   Miocene fossil localities of the Tung Gur escarpment, Inner Mongolia, based on Osborn and Granger (1932) and Qiu et al. (1988a). *Tungurictis* is known from two sites along the escarpment of the Tung Gur tableland: Wolf Camp Quarry and IVPP Loc. 86026. Wolf Camp Quarry produced a complete cranium (AMNH 26600) and postcranial remains (AMNH 99146), primarily bones of the hind feet. IVPP Loc. 86026 has yielded undescribed *Tungurictis* fossils to Chinese paleontologists in 1986, and may also be at or near the source of the American Museum paratype dentary fragment (AMNH 26610).

Mastodon Camp of Andrews (1932: 429–430). The following day (June 9), a small party comprising R. C. Andrews, P. Teilhard, C. C. Young, and W. Granger reconnoitered the western escarpment and discovered a promising area rich in bones and bone fragments (at the same time also locating the lower jaw of a rare zygolophodont proboscidean, "Serridentinus" *gobiensis,* AMNH 26461, recently placed in *Zygolophodon* by Tobien et al., 1988). On June 10, the expedition moved to this area, making camp on the rim of the western escarpment where Andrews shot a large wolf, hence the name Wolf Camp (fig. 1).

The discovery site of *Tungurictis* can be deduced from Andrew's (1932) narrative of the work in the vicinity of Wolf Camp. On June 13, 1930, Andrews reported that "Granger started all the Chinese collectors at work on the bone-bearing hillocks just below

the tents," where they discovered "skulls of small carnivores and artiodactyls. The bones were mixed in a heterogeneous mass. . . ." This locality became Wolf Camp Quarry, eventually designated Quarry No. 2 by Osborn and Granger (1932).

Collecting at Wolf Camp Quarry was delayed by the discovery of the great *Platybelodon* Quarry (Quarry No. 1 of Osborn and Granger), found by Teilhard on or about June 18. On June 21, intensive excavation of the numerous shovel-tusked proboscideans in this quarry began and continued for six weeks, producing as many as twenty individuals. By mid-July, however, work at the *Platybelodon* Quarry was reaching a conclusion and, according to Andrew's (1932: 444) account, "work had been resumed at the quarry just below [Wolf] camp where baby mastodons [=*Platybelodon*], deer, foxes [probably *Tungurictis*], and other small mammals had been

entombed." On July 15, Thomson discovered a female *Platybelodon* below Wolf Camp with a fetal young in the pelvic cavity, a remarkable find. Andrews believed this was a bog deposit, and in writing about the pregnant female, commented that "Except for the pregnant female mastodon, most of the animals that had been trapped in this ancient bog were small." Many of the rare carnivorans described by Colbert in 1939 came from these beds below Wolf Camp, including the cranium of *Tungurictis spocki*.

On August 2, Andrews, in his last entry mentioning Wolf Camp Quarry, wrote: "The big mastodon quarry [Quarry No. 1] had been exhausted and efforts concentrated upon the deposit just below the tents [Quarry No. 2]. This has yielded a really good fauna of the region: giraffe, four genera of carnivores, bovids, rodents, rhino, deer, and several skulls of baby shovel-tusked mastodons. . . ." Shortly thereafter, the work at Wolf Camp ended for the season, and the expedition moved westward.

In April 1989, while examining unpublished carnivoran material in the American Museum collected "below Wolf Camp" by the 1930 expedition, a small, nearly complete left hindfoot and associated right metatarsus (AMNH 99146) were found embedded in fine-grained gray sandy matrix like that still adhering to the holotype cranium of *Tungurictis spocki*. Preparation revealed a number of striking features that suggest these feet belong to *Tungurictis*. The presence of parts of both hindfeet, the distal tibia and fibula, and what appears to be the proximal humerus indicate that much of the skeleton may have been present at the site, but was not collected. We do not know if the postcranial bones were found in proximity to the cranium, but they must have been found in the vicinity, because all fossils collected by the 1930 party from "below Wolf Camp" or "Wolf Camp Quarry" are from the same general locality.

The paratype dentary fragment (AMNH 26610) was not collected at Wolf Camp Quarry but was found along the same escarpment about 30 mi (48 km) northeast of Wolf Camp. It may have been collected from a site at or near newly reported localities (fig. 1, IVPP Locs. 86021, 86026) on the north escarpment of the tableland recently worked by the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing (Qiu et al., 1988a). The paratype dentary fragment and its two premolar teeth correspond in size to the upper teeth of the holotype cranium, but caution should be exercised in attributing the paratype to *Tungurictis spocki* until associated upper and lower jaws are found. Qiu et al. (1988a) recently reported the presence of *Tungurictis* from locality 86026; these fossils will be of much interest when eventually described.

AUDITORY REGION OF *TUNGURICTIS SPOCKI*

The only known cranium (AMNH 26600) of *Tungurictis* is the size of a swift fox (*Vulpes velox*) cranium, with a basilar length, as preserved, of about 107 mm. On the basis of its cranioskeletal dimensions, the animal must have been similar in body size to the smaller foxes, thus under 5 kg in weight. Its hypercarnivorous dentition and small size combine to suggest a diet of small vertebrates and insects. The three-dimensional form of the cranium (fig. 2) is largely intact, although when seen in dorsal view evidently somewhat skewed to the right by crushing. Crushing has produced a mosaic of small polygonal bone fragments still in contact with each other, yet slightly to moderately displaced. The cracks between the fragments are filled with either very fine sediment or calcite. Unfortunately, the fragmentation of the cranium obscures the sutures between bones in most areas.

Postorbital length of the cranium (measured from the lacrimal foramen on the anterior orbital rim to the occipital condyle) is nearly twice the preorbital length, a primitive carnivoran trait. Pronounced constriction of the cranium behind the postorbital processes, noted by Colbert, and the prominent lambdoidal and sagittal crests are the result of small brain volume relative to skull size. In more advanced carnivorans a larger brain often fills out the cranial cavity, thereby minimizing the expression of these bony crests and the amount of postorbital constriction. The marked development of the postorbital process is reminiscent of living hyaenids and the small Turolian hyaenid *Plioviverrops orbignyi* (Dietrich, 1927; Beaumont, 1969). Only

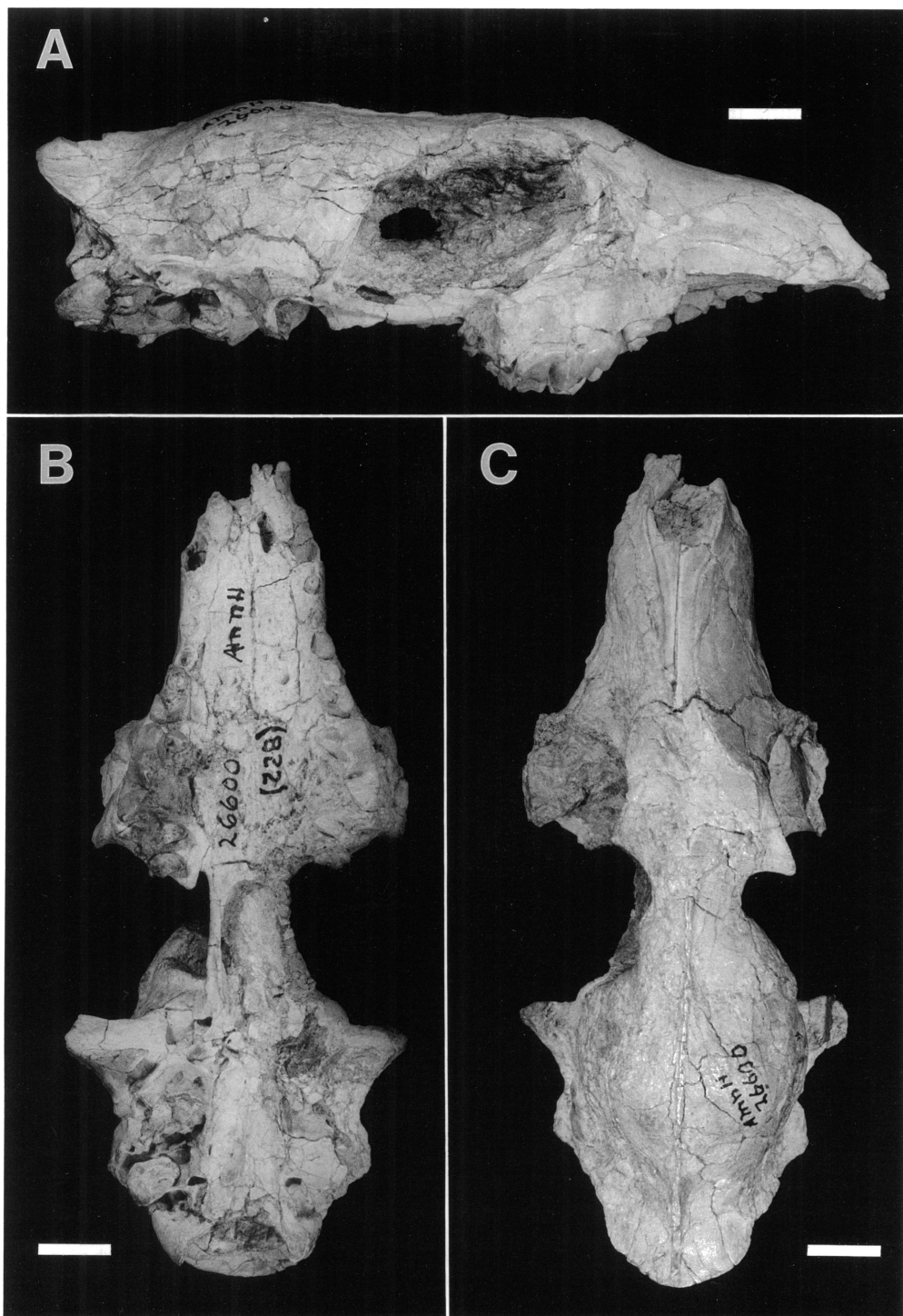Fig. 2. The holotype and only known cranium of the early hyaenid *Tungurictis spocki* Colbert, AMNH 26600, from Wolf Camp Quarry, mid-Miocene (MN8), Tung Gur Formation, Inner Mongolia, collected by the Central Asiatic Expedition, American Museum of Natural History, 1930, **A,** lateral; **B,** ventral; **C,** dorsal views. Natural size. White scale bar in this figure and all subsequent photographs is 1 cm in length.

Fig. 3. Basicranium of the hyaenid *Tungurictis spocki,* AMNH 26600, Wolf Camp Quarry, Tung Gur Formation, Inner Mongolia, ventral view, ×1. Although both auditory bullae are broken open, a bony plate representing a remnant of the hyaenid intrabullar septum is still present on both right and left sides (for detail, compare figs. 4 and 5, S). For all abbreviations not defined in figure captions, see p. 3. Stereopair.

minimal anatomical detail can be discerned within the orbits because the interorbital region has been badly damaged and little but matrix remains. The palatal region is not widened as in large durophagous hyaenids; the rostrum is slender and gracile, much like the snout of the living swift fox. In its skull proportions, there is no evidence of the dimensional idiosyncrasies that characterize the robust, wide-skulled, bone-crushing hyaenids often considered typical of the family.

The basicranium of AMNH 26600 is illustrated at natural size in figure 3: the crushing mentioned by Colbert in his original description is evident, particularly the bones surrounding the posterior choanal opening. However, the basicranium itself shows little distortion. Unfortunately, both auditory bullae have been broken open, and so the external form of the bulla must be reconstructed. Closer inspection reveals that the left auditory region (fig. 4) lacks nearly the entire bony bulla, yet retains an intact petrosal promontorium. In the right auditory region (fig. 5), the anterior part of the bulla is largely intact; some bone belonging to the posterior bulla also remains, but the petrosal promontorium that lies between these two bulla remnants has been damaged. By combining fea-

tures of both right and left sides, the architecture of the auditory region can be restored.

Left auditory region (fig. 4): A mosaic of small bone fragments occupies the roof of the anterior part of the auditory region; they are unidentifiable but appear to be pieces of the bulla and sphenoid bones. Posterior to this mosaic, and partly covered by a few bone fragments, is the petrosal, intact except for the loss of the tip of its ventral promontorial process (fig. 4, V). The base of the promontorial process is robust and thick, about 5 mm in anteroposterior length, indicating that the process in *Tungurictis* was well developed. It was strongly applied to the lateral margin of the basioccipital, as in aeluroid carnivorans in general (Hunt, 1989).

The ventral surface of the intact petrosal promontorium is marked by a transverse ridge. Against the posterior face of this ridge abuts the anterior edge of a slightly concave bony plate (fig. 4, S) that curves ventrad to meet the paroccipital process (fig. 4, EO: the process is broken, hence has a roughened edge). At first glance, this concave plate appears to be the roof of the posterior chamber of the bulla but, on closer inspection, fine sediment (fig. 4, SE) can be seen to fill the

true posterior chamber of the bulla dorsal to the concave plate. The plate in fact is a bony intrabullar septum of the type found only in hyaenids. This relationship is confirmed by examination of the right auditory region, where a remnant of the septum is also present (fig. 5, S), and has collapsed dorsad to contact the actual bony roof of the posterior chamber (formed by the caudal entotympanic).

In fossil and living hyaenids (fig. 6), the intrabullar bony septum lies posteroventral to the promontorium, its anterior edge either in contact with the promontorium, or situated immediately below its ventral eminence (fig. 6B, also Hunt, 1974: figs. 36, 38–42). However, the true dorsal roof of the posterior chamber (fig. 6A, E), formed by caudal entotympanic, lies deep within the posterior auditory region where its anterior margin covers the posterior part of the petrosal, mantling the base and posterior face of the promontorium. The presence and configuration of this intrabullar bony septum and its relationship to the posterior chamber of the bulla formed by caudal entotympanic are important diagnostic features that identify *Tungurictis spocki* as an early hyaenid.

Right auditory region (fig. 5): The anterior part of the auditory bulla is fortuitously preserved on the right side, permitting reconstruction of the geometry of the anterior chamber of the bulla. The anterior chamber was formed by a well-inflated ectotympanic element, configured as in hyaenids or canids in which ectotympanic is strongly chambered, subhemispherical, and firmly attached to the surrounding basicranial bones. There is no evidence of the smaller, less-inflated, loosely attached ectotympanic crescent of true viverrids. For comparison, figure 7 illustrates the nature of the ectotympanic in a fossil viverrid (AMNH 18725, Pleistocene, Szechuan province, China) referred to *Viverra zibetha*, the species believed by Colbert (1939) to be most like *Tungurictis spocki*. Note that the ectotympanic of *Viverra* (AMNH 18725) is not as inflated as the ectotympanic of *Tungurictis*, nor does it contact the bones (basisphenoid, basioccipital) of the basicranial axis. In the viverrid, the ectotympanic is a small discrete crescentic element separated from the basicranial axis by a space for the rostral entotympanic (fig. 7, R). Rostral en-

totympanic is ventrally exposed in *Viverra zibetha*, but is covered by (and probably fused to) the ectotympanic in *Tungurictis spocki*, just as it is in all hyaenids.

In addition, in *Viverra zibetha* the ectotympanic (T) and caudal entotympanic (E) persist as discrete structural elements from early ontogeny into adult life (fig. 7): they remain separate bony elements during the anterior migration of caudal entotympanic over ectotympanic, an ontogenetic growth process demonstrated by the observed change in relative position of these two elements from neonate through juvenile to adult. The two bulla elements are only in contact where they join to form the septum bullae (fig. 7, SB), and the two do not unite to form a single subhemispherical chamber. Rather, in all viverrids, they maintain an imbricated or overlapping relationship that reflects the anteriorly directed growth trajectory of the caudal entotympanic element. In contrast, when we examine the anterior bulla remnant (fig. 5, T) of *Tungurictis spocki*, the broken posterior edge of the ectotympanic is directed posteroventrad, suggesting that the bone continued as the smoothly confluent floor of a subhemispherical bulla: there is no suggestion of the indentation (where ectotympanic and caudal entotympanic join) that would be expected in a viverrid bulla, nor is there adequate space to accommodate the enlarged anterior end of the viverrid caudal entotympanic. Thus the anterior remnant of the auditory bulla in *Tungurictis spocki* is not configured as in true viverrids.

In the *Tungurictis* cranium, an alisphenoid canal is preserved on the right side. The canal itself was only 3–4 mm in length. Its posterior opening (fig. 5, AC) was very close to and nearly confluent with the foramen ovale. Five mm posterior to the alisphenoid canal is a prominent middle lacerate foramen (fig. 5, L), 1.7 mm in length by about 1.5 mm in width, nearly entirely surrounded by the basisphenoid. The foramen was not covered by the bulla as it is in living hyaenids. Whether it transmitted an internal carotid artery equal in diameter to the foramen is uncertain: the foramen is large relative to the size of the skull, and a groove in the anterior bulla wall adjacent to the foramen closely corresponds to its diameter, suggesting that a large internal
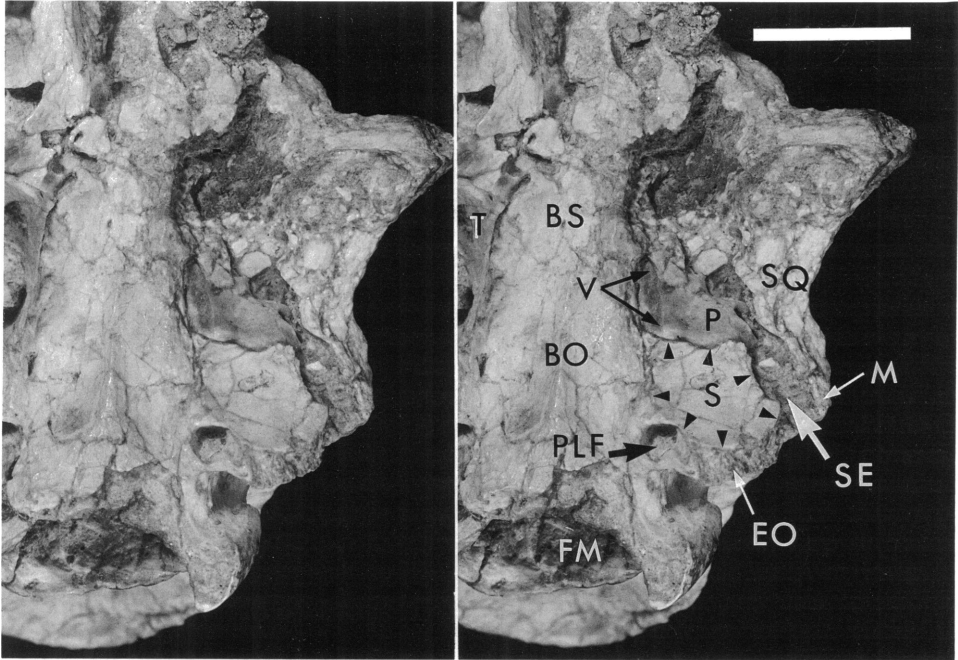
Fig. 4. Basicranium and left auditory region of the hyaenid *Tungurictis spocki* (AMNH 26600), Wolf Camp Quarry, Inner Mongolia, ventral view. Most of the auditory bulla has been destroyed, revealing the petrosal and the posterodorsal chamber of the bulla floored by an intact hyaenid intrabullar septum (S). The limits of this septum are indicated by black triangles. Note that the bulla abutted the paroccipital process of the exoccipital (EO) as in living hyaenids. The largely intact posterodorsal chamber is still filled with sediment (SE) that supported the intrabullar septum, thereby preventing its collapse (the sediment has been removed from the posterodorsal chamber in fig. 5, revealing an open cavity constructed as in living hyaenids). A large ventral petrosal process (V) was present in this primitive hyaenid, but the tip has been broken off. Petrosal form and the relationship of the intrabullar septum to the petrosal in *Tungurictis* is comparable to those of Pleistocene and living hyaenids (fig. 6). Stereopair.

carotid artery could have been present. However, the portion of the bulla wall through which the artery must pass (via the posterior carotid foramen) to enter the middle ear is not preserved on either the right or left side and, therefore, the full extent of the internal carotid pathway in this small hyaenid remains to be determined.

Posterior to the anterior bulla remnant, the right petrosal promontorium of *Tungurictis* has been destroyed. A low transverse ridge running somewhat obliquely across the roof of the auditory region is all that remains of its posterior face. Behind this ridge the bony roof of the posterior bulla chamber is formed by caudal entotympanic (fig. 5, EC and asterisks); the anterior edge of this roof contacts the transverse ridge and, in so doing, covers the posterior margin of the petrosal.

The posterior chamber of the bulla invades and thereby creates a bony pocket within the mastoid region (fig. 5, EC) as in living hyaenids, so that the roof of the chamber lies at two levels: (a) a dorsally deep, laterally placed mastoid pocket, and (b) a more shallow, flatter, bony roof (fig. 5, asterisks) internal (medial) to the pocket. This lateral pocketing of the roof formed by caudal entotympanic is typical of the posterior bulla chamber of hyaenids: it is exaggerated in the living aardwolf *Proteles cristatus* (Hunt, 1974: fig. 39), and is also present in late Miocene (*Ictitherium*, FAM 117490, China) to Pleistocene fossil hyaenids (fig. 6A). In figure 6A, the characteristic dual levels of the roof of the chamber, indicated by the letters E and M, are particularly evident.

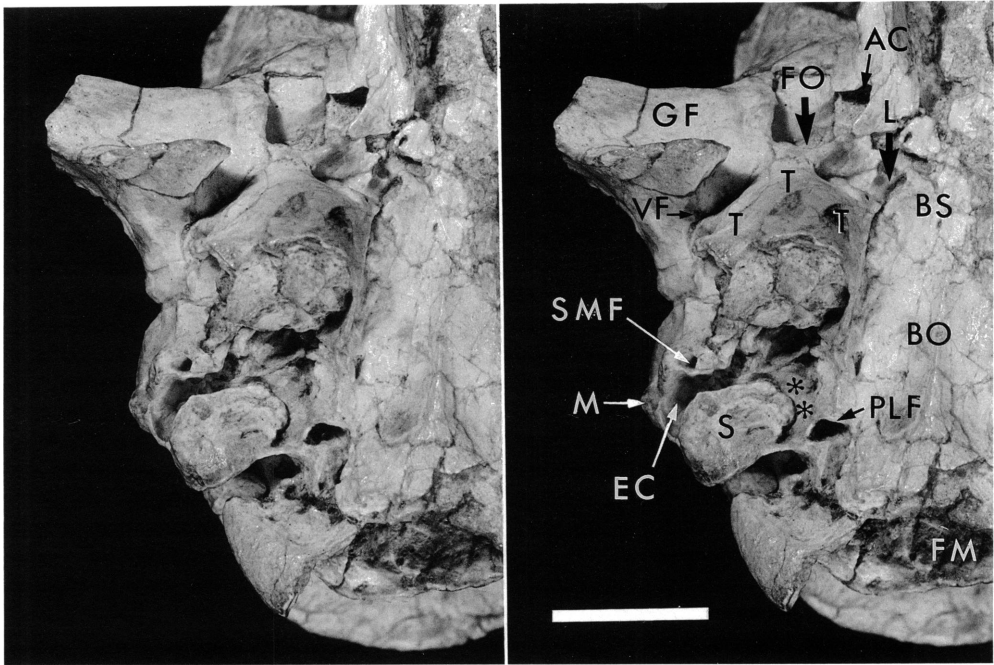Ventral to the bony roof of the posterior

Fig. 5. Basicranium and right auditory region of the hyaenid *Tungurictis spocki* (AMNH 26600), Wolf Camp Quarry, Inner Mongolia, ventral view. The anterior part of the auditory bulla formed by ectotympanic (T) is intact; the posterior bulla was crushed and broken open, fortuitously exposing the posterodorsal chamber (EC) formed by caudal entotympanic. The medial extent of this chamber is indicated by two black asterisks; the lateral and deepest part of the chamber (EC) invades the mastoid bone (M) and is visible posterior to the stylomastoid foramen (SMF). Pleistocene and living hyaenids display the same configuration of the roof of the posterodorsal chamber (compare fig. 6). A part of the hyaenid intrabullar septum (S) still remains in place in the posterior auditory region where it forms the floor to the posterodorsal chamber (EC) of the bulla. A vestigial postglenoid foramen (VF) demonstrates that the postglenoid venous drainage is already reduced in this early hyaenid, yet the large diameter of the middle lacerate foramen (L) suggests that the internal carotid artery may be functional, and not reduced as in living hyaenids. Stereopair.

chamber of the *T. spocki* bulla is a slightly concave, nearly rectangular plate of bone (fig. 5, S). This plate is a remnant of the intrabullar bony septum, which is more completely preserved and in its normal life orientation in the left auditory region of figure 4. This bony septum in figure 5 at first appears to be in direct continuity with a thin lamina of the exoccipital bone medial to it. Because the internal bony septum of hyaenids is not part of the exoccipital, this observation at first seems to contradict its identification as the hyaenid septum. However, when examined under a microscope, a line of separation can be traced around the periphery of the plate of bone, indicating it is not part of the exoccipital, but in fact has nearly fused with it

as the skull plastically deformed and fractured during postburial diagenesis. As a result, sutures in this part of the skull are extremely difficult to identify.

In summary, the auditory region of *Tungurictis spocki* possesses a group of basicranial features that, when considered together, identify the animal as an early hyaenid: (1) the subhemispherical anterior bulla chamber and its relationship to surrounding bones; (2) structure and relationships of the petrosal; (3) form and position of the intrabullar bony septum; (4) configuration of the posterior bulla chamber. To these points of evidence derived from the auditory region, we next add relevant observations on the hyaenid features of its teeth.
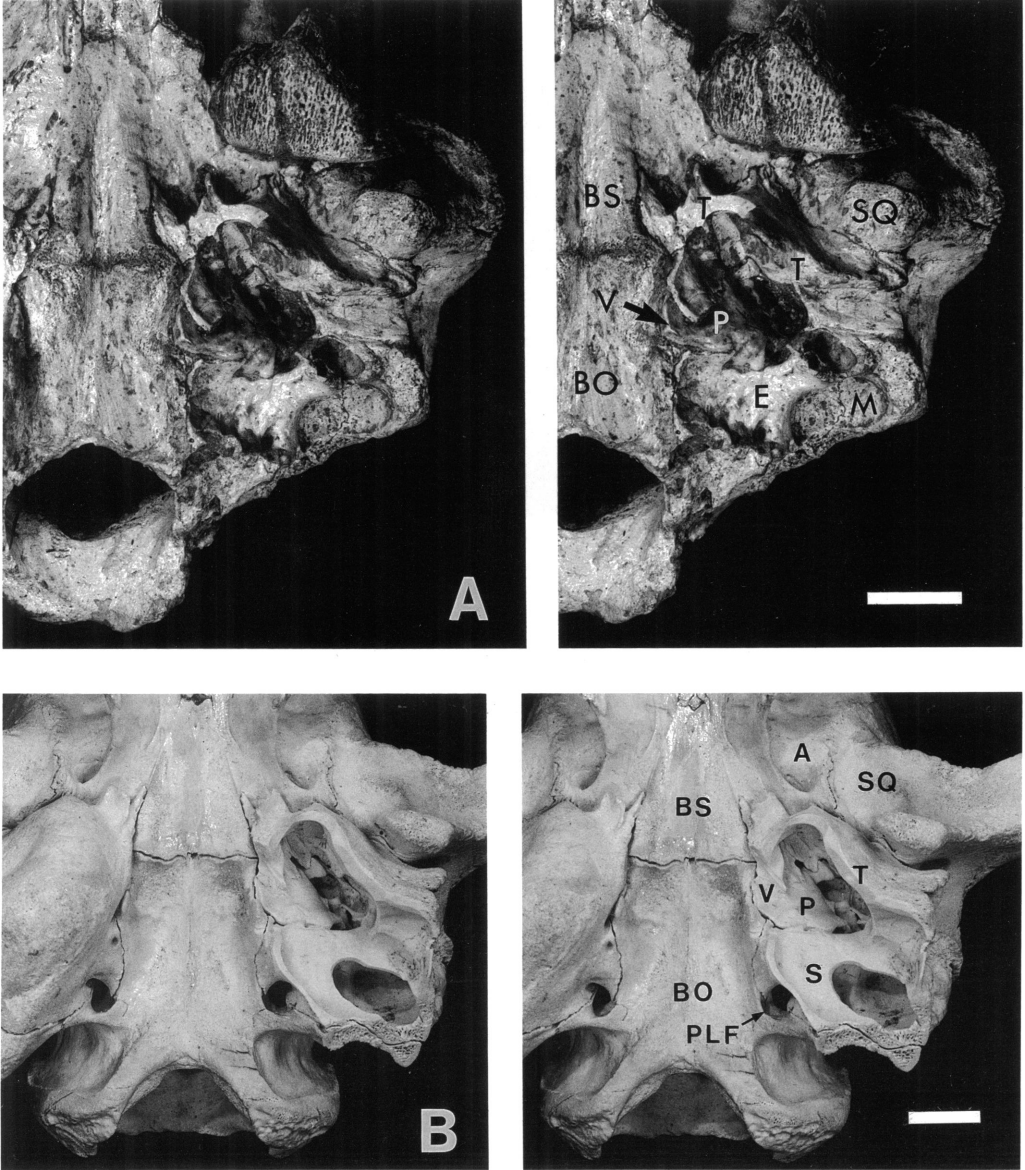
Fig. 6. Basicranium of the hyaenid *Crocuta* demonstrating the internal architecture of the auditory bulla: **A,** Left auditory region of Pleistocene *Crocuta* (AMNH 18730), China, ventral view. The ventral bony floor of the bulla has been removed (including the hyaenid intrabullar septum) to reveal the configuration of the roof of the posterodorsal bulla chamber formed by caudal entotympanic. Note that the roof lies at two levels: a dorsally deep mastoid pocket (M), and a medial platform (E). In life, both levels are veneered by caudal entotympanic but in this individual the entotympanic covers only the medial platform and has been removed from the mastoid pocket to reveal the petrosal-mastoid suture. **B,** Left auditory region of living *Crocuta crocuta* (UNSM-ZM 5012), Africa, ventral view. Ventral bony floor of bulla removed, showing relation of hyaenid intrabullar septum (S) to petrosal promontorium (P) and ventral petrosal process (V). An opening has been cut in the hyaenid septum to reveal the posterodorsal chamber of the bulla (equivalent to EC in fig. 5) dorsal to the septum. Stereopairs.

Fig. 7. Basicranium of the viverrid *Viverra zibetha* (AMNH 18725), Pleistocene, Szechuan, China, collected by W. Granger, 1923. The left auditory r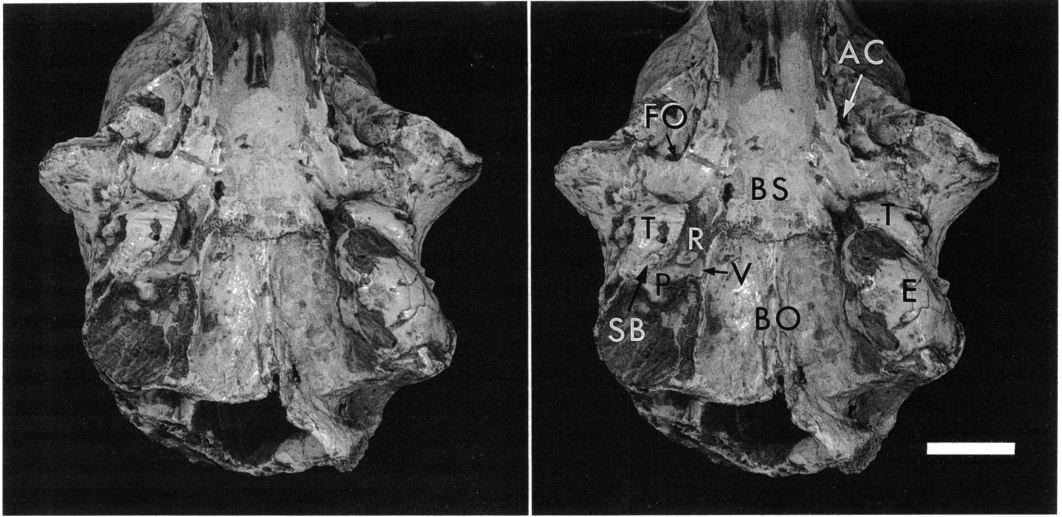egion is largely intact, showing the small crescentic ectotympanic (T) forming the anterior chamber of the bulla, and the caudal entotympanic (E) forming the posterior chamber. The anteriorly directed overgrowth of ectotympanic by the inflated caudal entotympanic is a hallmark of true viverrids and does not occur in hyaenids. Most of caudal entotympanic has been removed from the right auditory region, revealing the lack of an intrabullar septum of hyaenid type in this and all true viverrids. Note the rostral entotympanic (R) in the anterointernal corner of the auditory region, the transversely ridged petrosal (P) dividing the middle ear into anterior and posterior chambers, and the ventral petrosal process (V) characteristic of aeluroid carnivorans. Stereopair.

DENTITION OF
TUNGURICTIS SPOCKI

Measurements of the dentition and cranium of *Tungurictis spocki* are presented in table 1.

Incisors: Only the left I1–3 are preserved, arranged in a transverse row (fig. 2). Although slightly damaged, I1 and I2 are nearly the same size, I2 being slightly larger. I3, however, is significantly larger than I2, as in living hyaenids. There are no evident accessory cusps (Nebenzacken) on the incisor teeth, but these teeth are broken and worn.

Canines: Only the alveoli for the two canines are preserved (fig. 2). Their shape suggests that the canines were slender, laterally compressed teeth. The best preserved (right) canine alveolus measures 7.3 mm in length by 3 mm in width.

Premolars: The left P1 is a single-rooted, peglike tooth (fig. 2). The right P1 is broken off at the level of the alveolus. P2 is a double-rooted, laterally compressed tooth (fig. 8), much larger than P1: on the right, only roots broken at the alveolar margin remain, but on

the left, the posterior part of the tooth is present and is wider than the anterior part, but otherwise without distinguishing traits. P3 is broken on both right and left sides; only the heel of the tooth with a posterior basal accessory cusp is present. P3 shows a slight internal expansion of its posterior lingual margin, as is present in living viverrids and hyaenids.

The upper carnassial (P4) is a specialized cutting tooth, with an elongate planar shear surface formed by the confluent internal faces of the paracone and metastylar blade (fig. 8). Anterior to the paracone is a strong parastylar cusp, which anteriorly extends the shearing surface. The considerable length of the carnassial tooth is best demonstrated by the right P4, in which the thin delicate metastylar blade, paracone, and parastyle remain largely intact (the left P4 is slightly damaged). Lingual to the parastylar cusp is a prominent cuspid protocone (deuterocone), separated from the shearing face of the tooth by a shallow depression. In hyaenids, the prominent P4 protocone occludes with an enlarged heel of p4 in the lower jaw, forming a mortar-and-

Cranial and Dental Measurements (in mm) of the mid-Miocene Hyaenids *Tungurictis spocki* Colbert, Wolf Camp Quarry, Tung Gur Formation, Inner Mongolia, and *Protictitherium gaillardi* (Forsyth-Major), La Grive, France

	T. spocki AMNH 26600	P. gaillardi MGL 1352
Basilar length	107.0	
Basioccipital-basisphenoid length	(34)	
Preorbital length	43.1	
Postorbital length	75.0	
Palatal length	58.5	
Palatal width across M1 parastyles	36.0	
Width across mastoid processes	37.9	
Toothrow length, I3 to M2	59.4	
Toothrow length, C to M2	52.6	*56
Toothrow length, P1 to M2	42.9	
Width, left I1–3	5.6	
Length and width, right canine	(7.3 × 3.0)	*6.0 × 4.5
Length, right P1–4	37.0	*39
Greatest length and width, left P1	1.8 × 1.6	
Greatest length and width, left P2	7.8 × —	
Greatest length and width, left P3	9.4 × 4.5	
Greatest length and width, left P4	(14.1) × 7.4	
Greatest length and width, left M1	5.7 × 10.7	5.7 × (10.6)
Greatest length and width, left M2	(2.6 × 5.2)	3.3 × (5.0)
Greatest length and width, right P1	(1.8) × —	*3
Greatest length and width, right P2	(8) × —	7.6 × 3.1
Greatest length and width, right P3	9.4 × 4.5	9.5 × 4.7
Greatest length and width, right P4	14.7 × 7.4	13.9 × 7.9
Greatest length and width, right M1	5.1 × (10.5)	
Greatest length and width, right M2	3.0 × 5.2	

( ) = estimated or alveolar measurement.
* = from Gaillard, 1899.

pestle crushing mechanism that is especially developed in bone-crushing species.

The most striking aspect of P4 is its elongate, bladelike character, quite different from the short P4 in the small (<5 kg) late Miocene hyaenid *Plioviverrops orbignyi*, yet reminiscent of the upper carnassial in the much larger hyaenid *Thalassictis wongii* (fig. 9, for comparison of skulls of *Tungurictis* and *Thalassictis*).

Molars: Both right and left M1–2 are present (fig. 8). M1–2 are both anteroposteriorly narrow teeth, a trait that distinguishes them from the wider M1–2 seen in *Plioviverrops orbignyi* (Beaumont, 1969). In addition, M1–2 are triangular in occlusal view, with prominent parastyle lobes. M1 is simple in form, lacking a prominent cingulum, but has a small paraconule and weak pre- and postcingula. The left M2 is intact and indicates a tooth anteroposteriorly narrower than in any other

small Miocene hyaenid, but not greatly different from the M2 of the holotype of *Protictitherium gaillardi* from La Grive.

Comparison of dental proportions with those of the swift fox (*Vulpes velox*) shows that *Tungurictis spocki* has relatively larger carnassials and smaller molars. Despite its small body size, premolars (P2–3) of the Mongolian hyaenid are more robust, longer, and thicker than those of the fox. The canines of the hyaenid are larger and somewhat more laterally compressed, judged by alveolar dimensions. The dentition of *Tungurictis spocki* is distinguished by the shearing carnassials, incipiently enlarged premolars, and prominent canines as its primary features, and indeed this is the direction taken by later hyaenid dental evolution in many lineages, here foreshadowed in a small fox-sized progenitor.

These same dental traits are found in the Turolian hyaenid *Thalassictis* (fig. 9). In fact,
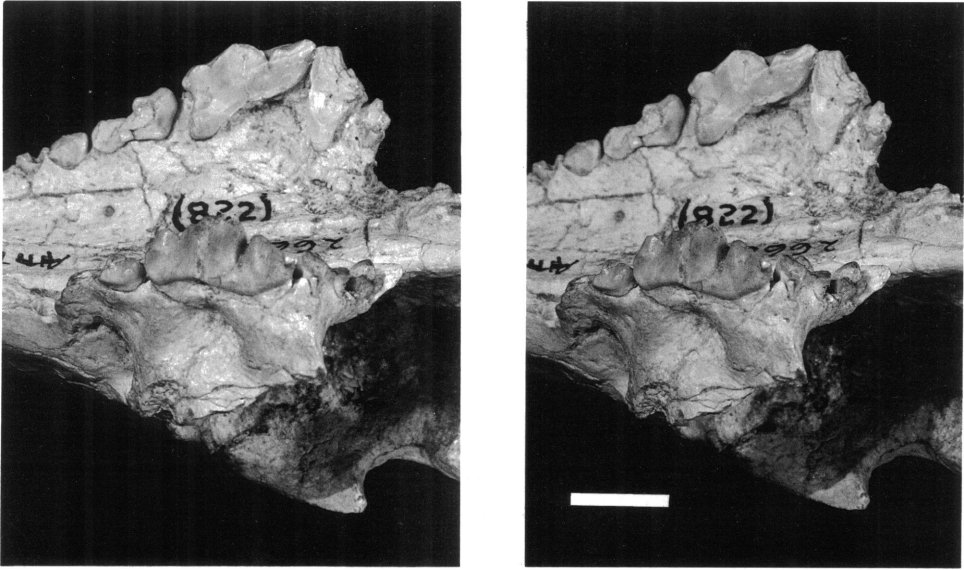
Fig. 8. Upper dentition of the hyaenid *Tungurictis spocki* (AMNH 26600), Wolf Camp Quarry, Tung Gur Formation, Inner Mongolia. Premolars are laterally compressed yet robust, the elongate upper carnassial is specialized for shearing, with developed parastylar cusp and prominent protocone. Molars are triangular with prominent parastylar lobe; M2 is much reduced and M3 is lost. The teeth are very similar in morphology and proportion to those of the larger late Miocene hyaenid *Thalassictis* and the contemporaneous mid-Miocene hyaenid *Protictitherium gaillardi*. Stereopair.

there is a particularly striking correspondence in skull proportions, morphology, and dental features between the late Miocene *Thalassictis* and mid-Miocene *Tungurictis,* suggesting that the Mongolian species is a plausible ancestor for the *Thalassictis* lineage. *Tungurictis spocki* from Wolf Camp Quarry (zone MN8) and *Thalassictis wongi* from Quarry 4 at Samos (zone MN12) are separated by about 5 million years.

Among small contemporaneous European hyaenids, the upper dentition of *T. spocki* is most similar to the upper dentition of the holotype of *Protictitherium gaillardi* (Forsyth-Major, 1903) from La Grive (Gaillard, 1899; Viret, 1951).

ANTIQUITY OF THE HYAENID AUDITORY PATTERN

The cranium of *Tungurictis spocki* demonstrates that the typical hyaenid auditory pattern was already well developed in small fox-sized hyaenids of the Eurasian mid-Miocene. True hyaenids of very small body size (5 kg or less) are restricted to Miocene sites in the Old World, and occur primarily as den-

tal remains. Some of these small Miocene fossil species, such as *Tungurictis spocki,* probably reflect the body size, general skull form, and basicranial structure of the ancestral hyaenid stock. Later multiple radiations of large, bone-crushing hyaenids of the late Miocene, Pliocene, and Pleistocene are plausibly derived from lineages of these small hyaenids.

Prior to 1988, the hyaenid auditory pattern had been identified and traced from the present to the late Miocene (Hunt, 1987). No skulls of mid-Miocene age that certainly possessed the hyaenid auditory region had been described. In 1988 it became apparent to us that *Tungurictis spocki* was, in fact, a small hyaenid based on reinterpretation of its auditory anatomy. Also, in the same year, Qiu et al. (1988b) published photographs of a small skull of mid-Miocene age from the Tongxin Basin of China that preserves a hyaenid bulla. These two skulls represent widely divergent lineages within the Hyaenidae, and conclusively demonstrate the existence of the hyaenid bulla pattern in the mid-Miocene.

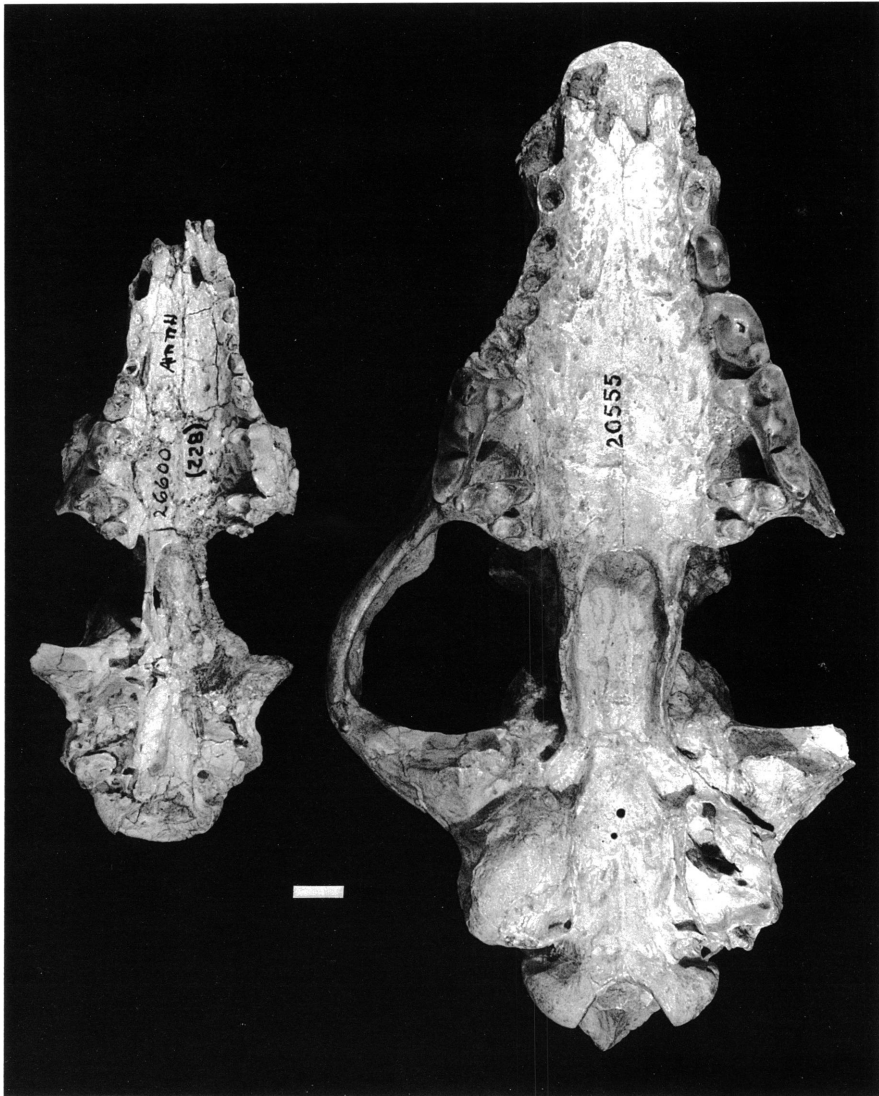At present, the oldest hyaenid auditory re-

Fig. 9. Comparison of the crania of the hyaenids *Tungurictis* and *Thalassictis,* ventral view. Left, *Tungurictis spocki* (AMNH 26600), Tung Gur Formation, Inner Mongolia; Right, *Thalassictis wongii* (AMNH 20555), Quarry 4, Samos, collected by Barnum Brown, 1924. The close correspondence in many features of skull, basicranium, and teeth suggests the possibility that *Tungurictis* is ancestral to *Thalassictis.*

gion definitely attributable to the family belongs to the small cranium (about 15 cm basilar length) recently discovered in the Tongxin Basin, described as *Percrocuta primordialis* (Qiu et al., 1988b). Qiu and his colleagues believe that Yinziling, the locality that produced the cranium, can be correlated with European Neogene mammal zone MN6. Although hyaenid dentitions are known in Eurasia from faunas as old as zone MN4b (Gins-

burg and Bulot, 1982), there are no known skulls with intact basicrania that can be attributed to Hyaenidae prior to zone MN6. We anticipate that once intact crania are discovered from zones MN4 and MN5, they will possess the typical hyaenid auditory pattern.

Based upon the similarity in auditory structure of the *Percrocuta* and *Tungurictis* lineages, we conclude that the hyaenid auditory pattern must have been present in their

common ancestor. It is improbable that the broad-skulled *Percrocuta primordialis* (MN6) is ancestral to *Tungurictis spocki* (MN8), because we regard the small Mongolian hyaenid as more plesiomorphic in skull form and dentition. Therefore, the common ancestry of these two lineages must exist prior to European mammal zone MN6 in the early Miocene or earliest mid-Miocene of the Old World.

Once *Tungurictis* is identified as a true hyaenid, it is evident from Colbert's (1939) work that the mid-Miocene Tung Gur Formation (MN8) of central Asia has produced two contemporaneous hyaenid lineages widely divergent in adaptive type: the small foxlike hyaenid *Tungurictis spocki,* and the large bone-crushing *Percrocuta tungurensis.* These two hyaenid species from Tung Gur have achieved differences in body size, skull form, and dentition approaching the maximal divergence documented in the family during its Cenozoic history. Coexistence of a small primitive carnivorous species alongside a large highly derived bone-crushing form indicates that hyaenid diversification was well underway 13–14 million years ago in the mid-Miocene of east Asia, and we can extend this inference to Eurasia based upon the diversity of hyaenid dentitions (*Protictitherium, Miohyaena, Percrocuta*) known from the mid-Miocene of Europe and Turkey.

TUNGURICTIS AND OTHER EARLY HYAENIDS

Hyaenids first occur in Europe as rare dental remains from European Neogene mammal zone MN4b (Bézian: Ginsburg and Bulot, 1982; Vieux Collonges: Mein, 1958) and MN5 (Pontlevoy: Stehlin, 1925). The earliest appearance of hyaenids in Africa occurs at Fort Ternan in Kenya where both *Proticititherium* and *Percrocuta* are dated at about 14 Ma (MN6 or MN7, Schmidt-Kittler, 1987). In Asia, the earliest record is a partial maxilla referred to *Proticititherium* from the locality of Songlinzhuang in eastern China, probably MN4 or MN5 (Li et al., 1983). None of these first occurrences includes basicranial material. Together, these records indicate that early hyaenids were small carnivorans and were widely distributed in Eurasia and Africa by

14–15 Ma in the mid-Miocene (MN6). By the later mid-Miocene (MN8), Eurasian hyaenids had achieved a remarkable diversity, evidenced by the association of small fox-sized and large bone-crushing species at Wolf Camp Quarry in the Tung Gur Formation, and in deposits of equivalent age elsewhere in Eurasia.

Three hyaenid genera are currently recognized in the MN4–MN8 interval in Eurasia: *Proticititherium, Percrocuta,* and *Miohyaena,* all named by Kretzoi in 1938. *Proticititherium* is recognized by its plesiomorphic dentition, the least specialized among mid-Miocene hyaenids, in which the premolars are not enlarged for crushing, the second upper and lower molars are present, and the small lower carnassial (less than 15 mm in length) retains the metaconid and a developed talonid. In contrast, *Percrocuta* is characterized by the earliest development of a durophagous dentition among Hyaenidae: enlarged robust premolars; reduction of the molars (M1 is small; M2 and m2 are lost); the lower carnassial is without its metaconid and the talonid is rudimentary; the dp4 has a strong metaconid and a small, narrow talonid fused to the trigonid (Schmidt-Kittler, 1976: 48). *Miohyaena* has also developed similar specializations of premolars and molars that herald a crushing hyaenid dental pattern, but these features are not as advanced as in contemporary *Percrocuta.*

Because *Tungurictis spocki* retains a plesiomorphic dentition and skull form, and does not show the enlarged premolars or reduced molars found in *Percrocuta* and *Miohyaena,* it is comparable only to *Proticititherium.* At present, *Proticititherium* includes four species: *P. intermedium* Schmidt-Kittler 1976; *P. cingulatum* Schmidt-Kittler, 1976; *P. gaillardi* (Forsyth-Major, 1903); *P. crassum* (Deperet, 1892). These species are chiefly differentiated on dental features and size (they are listed in order of increasing size). Referred fossils are entirely dental or postcranial remains: a skull of *Proticititherium* has not been recognized.

Most fossils of *Proticititherium* are geographically distributed from western Europe eastward to Asia Minor, the majority coming from Spain (Crusafont-Pairo and Petter, 1969; Petter, 1976), France (Ginsburg and Bulot,

1982; Mein, 1958; Viret, 1951; Gaillard, 1899), and Turkey (Schmidt-Kittler, 1976; Ozansoy, 1965). No more than a handful of specimens are currently reported from east Asia and Africa.

Recent studies of the European and Turkish material demonstrate a number of features of the teeth that characterize *Protictitherium*: The lower carnassial from its earliest (MN4b) occurrence has a form characteristic of primitive hyaenids. The plesiomorphic hyaenid (protictithere) m1 retains both talonid and metaconid, in contrast to their reduction or loss in more dentally derived hyaenids. A tricuspid trigonid is dominated by a tall protoconid, the paraconid is robust, and a prominent metaconid is situated directly internal to the protoconid. The talonid is commonly well developed, and has entoconid, hypoconid, and hypoconulid cusps that together form a raised posterior margin diagnostic of plesiomorphic hyaenid carnassials. In most species the entoconid is taller and more developed than the hypoconid: in the genoholotypic species, *P. crassum* (MGL 1344), the large m1 entoconid is just a somewhat smaller replica of the metaconid. A basal cingulum is developed on the external face of m1 trigonid, and it is particularly prominent at the base of the paraconid. Two upper and two lower molars are always present. In species where M2 is known, it is nearly oval in occlusal outline, anteroposteriorly broad, not narrow as in *Tungurictis*. The upper carnassial is a well-developed shearing tooth with anteriorly placed robust protocone that occludes with the heel of p4. The premolars are not converted to widened crushing teeth, remaining relatively laterally compressed.

As various hyaenid lineages (*Percrocuta, Miohyaena, Adcrocuta, Dinocrocuta, Pachycrocuta*) developed durophagous dentitions in the mid- and later Cenozoic, the plesiomorphic protictithere tooth pattern underwent modification: the talonid and metaconid of m1 were gradually lost, the protoconid and paraconid become aligned to form a shearing blade, and the premolars became enlarged robust crushing teeth. M2 and m2 are lost from the dentition, and M1 becomes much reduced.

The species of *Protictitherium*, from the earliest to the most recent, are noted for con-

spicuous emphasis of the m1 entoconid relative to the hypoconid (Ginsburg and Bulot, 1982; Schmidt-Kittler, 1976). Commonly, both entoconid and metaconid are strongly developed in tandem in most species of *Protictitherium*. However, Schmidt-Kittler (1976) remarked on the lack of development of the m1 entoconid in one particular species, *P. gaillardi* (Forsyth-Major, 1903). Through the courtesy of M. Phillipe, the senior author has been able to examine the holotype palate (MGL 1352) and lower jaws (MGL 1353) of this species in the Lyon Museum, and confirms that the entoconid is not developed, and is, in fact, about the same height as the hypoconid. In addition the m1 trigonid is emphasized, and the talonid is quite small. Very little is known about the amount of variation in the La Grive population from which the type was drawn (Viret, 1951). However, because the developed entoconid and talonid are so widespread among other species of the genus, including forms of the same body size (Pontlevoy: Stehlin, 1925: fig. 13, #141) as the holotype of *P. gaillardi*, there is reason to suggest that *P. gaillardi* may represent a separate lineage of small hypercarnivorous hyaenids distinct from those lineages of *Protictitherium* with developed m1 entoconid (including the holotype species of *Protictitherium, P. crassum* [Deperet, 1892], based upon MGL 1344, 1346, 1347).

Direct comparison of the holotype palate (MGL 1352) of *Protictitherium gaillardi* with the palate of *Tungurictis spocki* demonstrates a degree of similarity between these two relatively hypercarnivorous early hyaenids— more so than previously believed. Schmidt-Kittler (1976) has briefly discussed a comparison of the P4 and M1 of these two species, apparently based upon Colbert's (1939: fig. 14) illustration of these teeth in *Tungurictis*. The M1 in Colbert's figure appears to have a backwardly directed parastylar lobe which was viewed by Schmidt-Kittler as a peculiarity of the genus. In fact, this area of the tooth is broken, and if the M1 of the opposite side is examined, its parastylar region is normally developed and identical to the M1 of *P. gaillardi* from La Grive. However, although the upper carnassials are very similar in size and general form, the P4 of *Tungurictis* is thinner and more bladelike than the P4 of *P. gail-*

lardi. Also, the M2 of the La Grive carnivore is anteroposteriorly wider than the same tooth in the Mongolian animal. Despite these differences, the remaining correspondences in the upper dentition indicate that there is a definite relationship between these two small hyaenids that can be expressed by inclusion in a single genus.

Thus we believe that (1) *Tungurictis* Colbert 1939 is a junior synonym of *Protictitherium* Kretzoi 1938; we conserve *Tungurictis* as a subgenus of *Protictitherium* for hypercarnivorous species of small Asian protictitheres; (2) the Mongolian skull of *Tungurictis* provides us with our first glimpse of the skull form and basicranial anatomy of the early hyaenid *Protictitherium*; (3) the Mongolian *T. spocki* is placed in the subgenus, *Protictitherium* (*Tungurictis*), distinguished by a more hypercarnivorous dentition in which the upper carnassial is extremely thin and bladelike, and the M2 is anteroposteriorly narrow and reduced in size relative to *P.* (*Protictitherium*); although the lower carnassial is unknown, we predict that the entoconid is not emphasized over the hypoconid, and the talonid is reduced in size relative to the trigonid; (4) the subgenus *Protictitherium* (*Protictitherium*) is created for those more typical early hyaenids, including the type species *P. crassum* (Deperet), with a more hypocarnivorous dentition in which the m1 entoconid is emphasized over the hypoconid, and the m1 talonid is not reduced in size relative to the trigonid. Species in this subgenus include *crassum* (Deperet), *intermedium* Schmidt-Kittler, and *cingulatum* Schmidt-Kittler. Many specimens classified as *P. gaillardi* (e.g., *P.* aff. *gaillardi* Schmidt-Kittler, 1976; *gaillardi* form A, Crusafont-Pairo and Petter, 1969) in fact have well developed m1 entoconids, hence belong in this group, and differ from the holotype of *P. gaillardi* from La Grive. The placement of the holotype of *P. gaillardi* remains problematic; some workers have argued that *P. gaillardi* and *P. crassum* are synonymous (Ginsburg et al., 1981), however, the morphological differences between the holotype lower dentitions of these two species from La Grive are hard to reconcile with such a conclusion. Even if one disregards size, the small m1 talonid with weak entoconid, and low p4 of *P. gaillardi* and the developed m1 talonid with strong entoconid and robust taller p4 of *P. crassum* exceed the degree of morphological variation permitted in a single contemporaneous species.

Several predictions follow from the foregoing conclusions: the skull and basicranial structure of European or African *Protictitherium*, when eventually discovered, will be similar if not identical to the skull and basicranium of *Tungurictis*; a similar digitigrade postcranial anatomy also will probably be shared by the small mid-Miocene protictitheres of the Old World, based upon the evident correspondence among presently known European Miocene hyaenid postcranials and the hindfeet of *Tungurictis spocki* described here for the first time.

DIGITIGRADE STANCE IN MIOCENE HYAENIDS

Postcranial bones of Miocene hyaenids were reported as early as 1861 by Albert Gaudry from his excavations at Pikermi where they were associated with, or could be attributed to, hyaenid dentitions and skulls in the deposits. He was able to distinguish postcranial bones belonging to three separate lineages of late Miocene hyaenids, ranging from the tiny foxlike *Plioviverrops orbignyi*, the mid-sized *Ictitherium viverrinum*, to the large durophagous *Adcrocuta eximia*. These Pikermi hyaenid skeletons were illustrated and described by Gaudry in 1862–63. The insight into hyaenid postcranial traits provided by Gaudry's discoveries at Pikermi, published only a few years after Darwin's *Origin*, was remarkable for its time, particularly in its demonstration of the digitigrade stance of all three late Miocene hyaenid lineages, despite their pronounced dental and cranial diversity.

A humerus and five articulated hindfeet of *Ictitherium viverrinum* from Pikermi indicated a cursorial, digitigrade animal with paraxonic foot and only limited ability to pronate/supinate the forelimb, paralleling the living canids. A narrow distal humerus showed little development of attachment areas for extensor/flexor muscles of the carpus; the paraxonic hindfoot contained long, slen-

der metatarsals 3–4, flanked by slightly short-
er but slender metatarsals 2 and 5—the first
metatarsal and its digit were reduced.

The large Pikermi *Adcrocuta,* the size of
the living spotted hyaena, also possessed a
cursorially adapted forelimb in which pro-
nation/supination was greatly restricted. Its
feet were also paraxonic and digitigrade, with
reduction of the first digit in both fore- and
hindfoot (the first metacarpal and metatarsal
are reduced to small bony elements). In many
carnivorans, including *Ictitherium* and *Plio-
viverrops,* the metacarpals are shorter than
the metatarsals, indicating a short forefoot
and longer hindfoot, but in *Adcrocuta eximia*
the metacarpals are equal in length to the
metatarsals as in living hyaenids.

Limb and hindfoot bones of *Plioviverrops
orbignyi* show proportions like those of *Ic-
titherium viverrinum* in which the forelimb is
somewhat shorter than the hindlimb. *Plivi-
verrops* from Pikermi is long-footed, digiti-
grade, with elongate tibia, hence a lengthened
hindlimb. Subsequent to the Pikermi discov-
eries, Gaudry (1873) reported a small car-
nivoran metatarsus from the late Miocene of
Mont Léberon, France, which he attributed
to *Plioviverrops,* but it was not until Pilgrim's
(1931) summary of the Pontian Carnivora of
Europe that associated cranial and postcra-
nial remains of this genus were made known.

In 1931, Guy Pilgrim reviewed Pikermi
carnivorans, including hyaenids, in the col-
lections of the British Museum (N.H.). Among
this material was an associated partial skel-
eton of *Plioviverrops orbignyi* that included a
skull, mandible, radius, four metacarpals, and
the greater part of the left hindlimb with tar-
sals and metatarsals. Pilgrim was able to
compare the length ratio of metacarpal
4/metatarsal 4 in this associated skeleton with
this same ratio in a number of living and
extinct carnivorans. These ratios confirmed
Gaudry's observation that the forefoot of
Plioviverrops is short relative to the hindfoot.
Among these postcranials was a digitigrade
hindfoot and three forefeet, none of them
showing a first digit, hence Pilgrim (1931: 89)
presumed it was absent in both the fore- and
hindfeet of *Plioviverrops.*

Until 1969, the postcranials of *Protictithe-
rium* in association with teeth were poorly

known, however Crusafont-Pairo and Petter
(1969) reported upper jaws in association with
a partial postcranial skeleton of *P. crassum*
from Can Llobateres II (early late Miocene)
in Spain. These postcranials indicate that the
holotype species of *Protictitherium* was dig-
itigrade, having long, slender metapodials,
with five digits on the forefoot (digit 1 re-
duced), and only four on the hindfoot. Their
description makes clear that a digitigrade
stance was common to not only the late Mio-
cene lineages from Pikermi but also this *Pro-
tictitherium* from Spain.

Additional postcranial material of mid-
Miocene *Protictitherium* has been found in
Turkey (Schmidt-Kittler, 1976). The locality
of Candir (MN6) produced postcranials of
two sizes: the smaller bones were attributed
to *P. intermedium* (its distal humerus sug-
gests a small cursorial carnivoran); the larger
postcranials were assigned to *P.* aff. *gaillardi,*
including a partial left hindfoot. These post-
cranials are not directly associated with teeth:
they are referred to these species of *Protic-
titherium* on the basis of size correspondence.
Although not fully described, the bones that
are illustrated indicate small carnivorans with
a cursorial digitigrade stance as in *P. crassum.*

Thus mid- and late Miocene hyaenid post-
cranials belonging to four genera indicate that
digitigrady and a cursorial habitus were com-
mon attributes of hyaenids in the Miocene,
and therefore a digitigrade limb skeleton must
have been achieved early in the evolution of
the group. Whether this occurred once in a
common ancestor, or whether it was inde-
pendently attained in multiple lineages, re-
mains to be explored.

THE HINDFOOT OF
TUNGURICTIS SPOCKI

A nearly complete articulated left hindfoot
and a right metatarsus with two accompa-
nying digits (AMNH 99146) collected in 1930
from Wolf Camp Quarry can be assigned to
Tungurictis spocki on the basis of size and
anatomical structure (fig. 10, table 2). These
hindfeet indicate a digitigrade stance and very
likely belong to a single individual (they cor-
respond in size and structure), having been
found about 1 cm apart in the quarry.

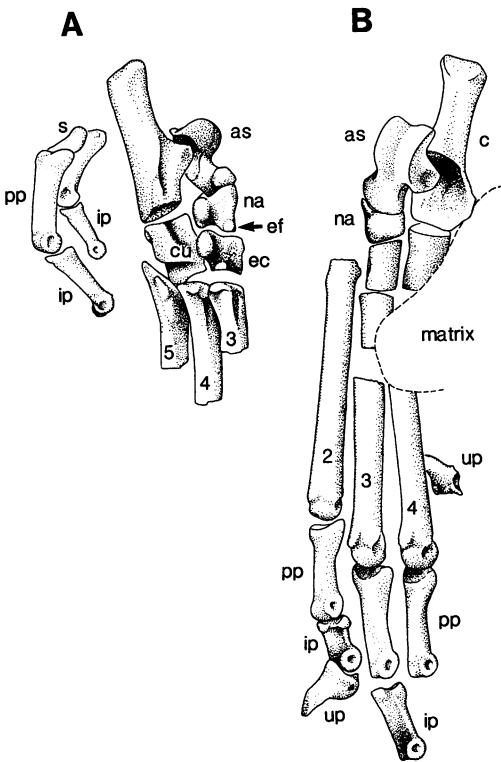|	
Length, calcaneum	25.0
Length, astragalus	13.7
Width, astragalar trochlea	10.1
Length, cuboid	9.8
Length, navicular, dorsal	4.4
Length, navicular, plantar	6.5
Width, navicular	6.1
Length, ectocuneiform	5.8
Length, metatarsal 2 (left)	(37.9)
Length, metatarsal 4 (left)	43.6
Length, proximal phalanx, digit 4	15.0
Length, proximal phalanx, digit 3	15.0
Length, intermediate phalanx, digit 3	11.4
Length, proximal phalanx, digit 2	12.9
Length, intermediate phalanx, digit 2	8.9
Length, ungual phalanx, digit 2	9.5
Length, isolated ungual phalanx	9.3
Length, metatarsal 2 (right)	37.0
Length, metatarsal 3 (right)	43.3
Length, metatarsal 4 (right)	44.2
Length, metatarsal 5 (right)	37.8

( ) = estimated.

Fig. 10. Digitigrade paraxonic hindfoot (AMNH 99146) of *Tungurictis spocki,* Wolf Camp Quarry, Tung Gur Formation, Inner Mongolia. **A,** plantar view of left tarsus and proximal metatarsals 3, 4, and 5 in same block of matrix with proximal (pp) and intermediate (ip) phalanges of the right hindfoot (s, sesamoid); **B,** dorsal view of left tarsus, metatarsus, and digits 2, 3, and 4. Digit 2 includes proximal, asymmetric intermediate, and ungual phalanges (up). Note also asymmetric intermediate phalanx of digit 3. c, calcaneum; as, astragalus; na, navicular; cu, cuboid; ec, ectocuneiform; ef, facet on navicular for entocuneiform.

Nearly the entire left hindfoot is preserved in articulation, and includes the calcaneum, astragalus, navicular, cuboid, ectocuneiform, metatarsals 2, 3, 4, 5 (metatarsal 3 is missing a short section of its diaphysis, and the distal part of metatarsal 5 is lost), proximal phalanges of digits 2, 3, 4, intermediate phalanges of digits 2-3, and the ungual phalanx of digit 2. The left tarsus is lacking only the meso- and entocuneiform bones.

Reduction of digit 1 of the hindfoot was already initiated in *Tungurictis,* although it may not have progressed as far as in modern hyaenids. Despite the articulation of metatarsals 2–5 in both right and left hindfeet,

there are no first metatarsals preserved with this material, and the proximal metatarsal 2 presents a flattened surface for application of the entocuneiform and reduced first metatarsal. In the same block of matrix that contains the articulated left hindfoot is an isolated ungual phalanx, situated 6 mm from the diaphysis of metatarsal 4. This is certainly an ungual phalanx of this same individual, although it is not possible to decide to which foot it belongs. Also, two associated digits occur in this same block only 1 cm from the articulated left tarsus: each of these two digits is made up of the proximal and intermediate phalanges, but ungual phalanges are missing (a single sesamoid is in place at the proximal end of the longer digit). Because the intermediate phalanges are asymmetric, they demonstrate that these two digits belong to a right foot.

A right metatarsus occurs separately from the articulated left hindfoot but has been placed under the same catalog number (AMNH 99146). Metatarsals 2 through 5 are articulated as in life and must have been united by connective tissue at the time of burial. At the distal end of these metatarsals is a

jumble of sesamoids. Significantly, this metatarsus can be manually articulated with the proximal phalanges of the two digits lying in matrix next to the articulated left hindfoot. The best registration of these digits is with metatarsals 4 and 5. Thus the right and left hindfeet probably occurred in matrix within 1 cm of each other in Wolf Camp Quarry, and almost certainly belong to the same small carnivoran.

Tarsus: The tarsal bones are intermediate in size between those of the swift fox (*Vulpes velox*) and the North American red fox (*Vulpes vulpes*). The calcaneum has three features that indicate an early phase of cursorial adaptation: (1) in plantar view the bone is long and its distal portion remains as narrow as the proximal part; (2) the plantar surface of the sustentaculum is deeply grooved for the flexor hallucis longus tendon which ran parallel and close to the long axis of the bone; (3) the distal calcaneum below the sustentaculum is somewhat elongated. In living cursorial canids, these three features are pronounced, and the articulation between the calcaneum and cuboid is nearly a flat plane oriented at nearly a right angle to the long axis of the calcaneum. *Tungurictis* has not yet developed the degree of cursorial specialization in hindfoot structure seen in canine canids, and consequently retains a slightly tilted articular surface between calcaneum and cuboid as found in most aeluroid carnivorans.

The astragalus is more generalized in structure than the astragali of living canids and felids. In these latter two groups the distal neck of the bone is drawn underneath the proximal trochlear head, contributing to a more restricted fore-aft motion of the hindfoot. In canids the two trochlear ridges are nearly equally developed to produce a symmetrical pulley that constitutes a further specialization for such cursorial function. In living felids the two trochlear ridges are unequally developed as is the case in all aeluroids examined. *Tungurictis spocki* shows unequal development of the trochlear ridges, the medial ridge being only slightly elevated, and in addition the distal neck of the bone is not drawn in under the trochlea, and in this respect is developed exactly as in living hyaenids.

In cursorial canids the cuboid and navicular are somewhat distally elongated, and the

proximal surface of the cuboid that articulates with the calcaneum is nearly planar. *Tungurictis* lacks these cursorial specializations and has a more generalized cuboid and navicular, which are very similar in form to those of the domestic cat. In *Tungurictis* the proximal surface of the cuboid is flat on its lateral side, but mesially the surface is warped, with an elevated posterointernal corner. It is this elevated corner that produces a raised internal margin on the distal articular surface of the calcaneum, thus creating the inclined or tilted cuboid-calcaneal articular surface. The cuboid in living hyaenids is very similar to the cuboid in the domestic cat, except that in living hyaenids the groove for the tendon of the peroneus longus muscle (that runs transversely across the carnivoran tarsus to attach to the head of metatarsal 5) is not especially deeply incised in the plantar surface of the cuboid, whereas in most other carnivorans (including *Tungurictis*) this groove is pronounced. A weakly defined groove is characteristic of the living brown and spotted hyaenas.

The navicular of *Tungurictis* is similar to the navicular of *Hyaena brunnea,* yet differs in details of its shape. The proximal surface is typically concave to receive the neck of the astragalus, and the posterointernal process of the navicular that supports the most medial part of the astragalar neck is long and well developed as in the brown hyaena. Both the plantar process of the navicular and its small entocuneiform facet are positioned as in the brown hyaena, but in *Tungurictis* the facet is directed toward the plantar surface whereas in the brown hyaena it faces distad. This facet indicates that the entocuneiform and a probably reduced first metatarsal were present (neither are preserved).

The form of the ectocuneiform is also very similar to this bone in the brown hyaena. In carnivorans the navicular rests upon the ecto- and mesocuneiform bones, and the relative size of these two elements is registered on the underside of the navicular as two adjacent facets. In *Tungurictis* the mesocuneiform facet on the navicular is small in area (only the impression of the mesocuneiform is preserved in matrix), somewhat smaller than the same facet on the brown hyaena navicular, suggesting that the mesocuneiform of the Mongolian hyaenid is somewhat reduced, and

in fact more similar in relative size and proportion to the mesocuneiform of the domestic cat. On this basis, we infer some degree of proximal reduction in metatarsals 1–2 relative to metatarsals 3–4, presumably correlated with development of a paraxonic hindfoot.

Metatarsus: In shaft diameter and in the size of proximal and distal ends, metatarsals 2 through 5 are intermediate between the swift and red foxes but, in terms of length, the *T. spocki* metatarsals are somewhat shorter than the metatarsals of either of these species. In the swift and red foxes, length of metatarsals 3–4 relative to basilar skull length is 49.4% and 50.2%, respectively; assuming that AMNH 26600 (cranium) and AMNH 99146 (metatarsus) belong to the same individual, this same ratio is only 41.3% in *Tungurictis.*

In the foxes, the shafts of the four metatarsals are fitted tightly together—in fact the sides of the metatarsals are flattened to facilitate this registration. In *T. spocki* the metatarsals are appressed but the sides of the shafts do not show the extreme degree of flattening seen in the foxes.

The distal ends of the fox metatarsals display sharp keels for articulation with the proximal phalanges and sesamoids. In *Tungurictis* the metatarsal keels are present but not as well developed.

In the foxes the proximal ends of the metatarsals show very tight registration. We have chosen not to separate the articulated metatarsals of *Tungurictis,* hence some sediment intervenes between the proximal ends, however it appears that registration is not as tight as in the foxes, and is very similar to the registration found in the domestic cat. In structure and form of the proximal metatarsals, the small hyaenid is likewise similar to the pattern observed in the domestic cat.

Important differences in the morphology of the proximal metatarsals occur among living hyaenids, *Tungurictis,* canids, and felids:

1. In living canids (subfamily Caninae) the proximal end of metatarsal 3 is compressed between the heads of metatarsals 2 and 4 when viewing the plantar surface of the hindfoot. This is not an effect of body size because this trait is found in both small (*Vulpes velox*) and large (*Canis lupus*) living canids. This metatarsal compression also appears in extinct early members of the family: an articulated hindfoot attributable to the *Mesocyon* lineage of early canids from late Oligocene rocks of western Nebraska shows a compressed metatarsal 3; the proximal end, however, is more robust and not as laterally compressed as in living Caninae.

2. Living felids show a degree of metatarsal 3 compression similar to but not as extreme as that of living canids.

3. The living hyaenids *Crocuta crocuta* and *Hyaena brunnea* do not show compression of the proximal metatarsal 3.

4. In *Tungurictis spocki* the proximal metatarsals are most similar to those of living felids such as the domestic cat. However, this is not necessarily a mark of close relationship but more likely indicates that both the domestic cat and the small Mongolian hyaenid share an aeluroid foot slightly specialized for a moderately cursorial digitigrade stance.

5. Living hyaenids show a very reduced peroneal process on the proximal end of metatarsal 5. However, a developed peroneal process is plesiomorphic for Carnivora, and *Tungurictis* still retains this process. Reduction of the process suggests a diminished attachment of the peroneus brevis muscle, and a lessened ability to evert the foot in living hyaenids.

6. In canids the plantar edges of the ectocuneiform and mesocuneiform bones that surmount metatarsals 2 and 3, respectively, are bladelike and compressed between the cuboid and entocuneiform. In living hyaenids the ecto- and mesocuneiform bones are more robust and their plantar margins are not as compressed as in canids. This tarsal-metatarsal compression is the morphological expression of the close apposition of the proximal metatarsals and distal tarsals in the living Canidae.

7. Living canids possess a well developed, blunt plantar process on metatarsal 2 that is absent in living hyaenids, felids, and in *Tungurictis.* It appears to be a specialization of the canine hindfoot.

8. In living canids the cuboid and navicular are slightly elongate tarsal elements. Their length is correlated with an elongate metatarsus. In a late Oligocene canid, however, the cuboid, navicular, and metatarsals are not elongated, nor are the proximal metatarsals closely appressed, as in the living canine canids. The hindfoot has not developed the de-

gree of elongation typical of the living species of the family. In living hyaenids the cuboid and navicular are not elongate, and *Tungurictis* has cuboid and navicular bones of this kind. Lack of tarsal elongation is clearly a plesiomorphic state for Carnivora. Thus the living canid hindfoot is specialized for cursorial gait in its elongate tarsal and metatarsal elements, the loss of digit 1, and the closely appressed and strongly keeled metatarsals.

Phalanges: The proximal phalanges of the hindfoot of *Tungurictis* reveal little worthy of comment, except that the phalanges of digits 3–4 are somewhat longer than the phalanges of digits 2 and 5. However, the intermediate phalanges are of much interest because of their evident asymmetry. The degree of asymmetry exceeds that seen in the same phalanges of the spotted and brown hyaenas, and is comparable to (but slightly less developed than) the asymmetry seen in the domestic cat. As in the domestic cat, the intermediate phalanges of digits 3 and 4 are longer than the same phalanges of digits 2 and 5, reflecting the paraxonic symmetry of the hindfoot.

Because the metatarsals, and proximal and intermediate phalanges of *Tungurictis* are similar to those of the domestic cat, one might expect to find comparable ungual phalanges as well. On the contrary, the ungual phalanges are about the same length, but lack the well-developed bony hood and large proximal plantar process for attachment of the flexor digitorum profundus tendon found in living felids with retractile claws (Gonyea and Ashworth, 1975). The ungual phalanges of *Tungurictis* are very similar to those of the living foxes, but are somewhat more laterally compressed. Furthermore, the degree of asymmetry of the intermediate phalanges of the North American red fox is comparable to the asymmetry observed in intermediate phalanges of *Tungurictis*. We infer no significant ability to retract the claws of the hindfeet of *Tungurictis* beyond that found in the North American red fox.

CONCLUSIONS

The small Mongolian aeluroid carnivoran *Tungurictis spocki* Colbert, from the mid-Miocene of Tung-Gur, long believed to be a viverrid, is in fact a true hyaenid, based upon the structure of its auditory bulla, dentition, and referred hindfeet. This small hyaenid was less than 5 kg in body weight, about the size of a swift fox (*Vulpes velox*), with hypercarnivorous dentition and digitigrade stance. It presumably paralleled the New World foxes in its ecological role.

The upper teeth of *T. spocki* are most similar to upper teeth of the small European hyaenid *Protictitherium gaillardi* (Forsyth-Major, 1903), from the mid-Miocene of La Grive, France. However, the species of *Protictitherium,* including the genoholotypic *P. crassum* (Deperet, 1892), are known only from dentitions and postcranials; no basicrania or complete skulls have been discovered. On the basis of the correspondence in their upper dentitions, *Tungurictis* Colbert 1939 is regarded as a junior synonym of *Protictitherium* Kretzoi 1938. The Mongolian cranium thus shows us for the first time the skull form and basicranial structure of the small hyaenid *Protictitherium.*

Protictitherium includes the oldest and most plesiomorphic species of hyaenids, hence *P. (Tungurictis)* provides insight into the cranial structure of the ancestral hyaenid stock. We separate *Protictitherium* into two subgenera: *P. (Protictitherium),* based upon *P. crassum* from La Grive, France, and *P. (Tungurictis),* from the Tung Gur Formation of Inner Mongolia.

Skulls of small hyaenids (less than 5 kg body weight) with intact well-preserved basicrania were previously known only from the late Miocene Turolian faunas of Pikermi and Samos (MN12, *Plioviverrops orbignyi*). *Plioviverrops orbignyi* appears to represent a relict late Miocene lineage of tiny hypocarnivorous protictitheres distinct from the more hypercarnivorous species that belong in *Protictitherium.* With the identification of *Tungurictis* as a hypercarnivorous protictithere, we now are able to recognize a second lineage of small Miocene carnivorans with a hyaenid auditory region. A third Miocene lineage of small hyaenids in which the basicranium and hyaenid bulla are preserved is represented by the recent discovery of a small cranium from zone MN6-equivalent rocks in China attributed to *Percrocuta primordialis.*

The conservative nature of the hyaenid basicranial pattern is indicated by the fact that a typical hyaenid auditory region occurs in

association with a different dental pattern in each of these mid- to late Miocene genera (*Plioviverrops, Percrocuta, Protictitherium* [*Tungurictis*]). Furthermore, this evidence in combination with the presence of hyaenid dentitions in European rocks as old as zone MN4b suggests that the hyaenid ancestor predates the mid-Miocene, and was probably an early Miocene or late Oligocene species of small body size and generalized aeluroid dentition, possessing the hallmark hyaenid bulla. We further conclude that the typical hyaenid auditory bulla evolved prior to the appearance of hyaenid dental specializations for durophagy (enormous carnassials and premolars, reduced tubercular molars, broad skull, wide palate), seen today in the living species (*Crocuta crocuta, Hyaena brunnea, H. hyaena*), and in several extinct mid- and late Cenozoic lineages.

The hindfoot of *Tungurictis* from Inner Mongolia appears to be very similar in anatomical detail to hindfeet of protictitheres found in Europe and in Turkey, suggesting that a paraxonic digitigrade stance was an early attribute of the family, evolving prior to the development of specialized durophagous dentitions, enlarged forequarters, and elongate forelimbs found in living hyaenid species. A small digitigrade paraxonic hindfoot may be an ancient acquisition of hyaenids, perhaps in response to expansion into more open environments during the Eurasian early and middle Miocene. The slight asymmetry of the median phalanges as seen in foxes and in *Tungurictis* may represent a plesiomorphic character state preceding the extreme phalangeal asymmetry and specialization of the ungual phalanges for claw retractility typical of living felids.

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