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LATE MIOCENE *PROMEPHITIS* (CARNIVORA, MEPHITIDAE) FROM CHINA

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ABSTRACT—*Promephitis* is a widespread late Tertiary Eurasian skunk in the family Mephitidae (Carnivora, Musteloidae), but many of the currently-recognized nine species were established on isolated dental material. Recent discoveries of *Promephitis* comprised of numerous nearly perfectly preserved skulls and jaws from Gansu Province, China, together with material from other Chinese localities plus unpublished material in the Frick Collection, make the Chinese record of *Promephitis* unrivaled in terms of quality, quantity, and species diversity.

Four species of *Promephitis* are present in the Baodean land mammal age of East Asia: *Promephitis parvus*, sp. nov., from Hezheng region of Gansu Province; *Promephitis qinensis*, sp. nov., from Fugu area of Shaanxi Province; *Promephitis hootoni*, the most common Chinese species; and *Promephitis alexejewi* from the terminal Miocene locality of Ertemte, which is still poorly known. *Promephitis parvus* represents the smallest known species of the genus and is also the most primitive in cranial and dental morphologies. *Promephitis qinensis* is a transitional form that may have given rise to *P. hootoni*. If so, the Turkish occurrence of *P. hootoni* must be the result of westward expansion of its range.

INTRODUCTION

Promephitis is a musteloid carnivoran widespread in the late Tertiary of Eurasia. It is a member of the skunk family Mephitidae, which includes three living genera in North and South America, *Mephitis* (striped and hooded skunks), *Spilogale* (spotted skunks), and *Conepatus* (hog-nosed skunks), and one genus in Southeast Asia, *Mydaus* (stink badger). Long known to be associated with *Hipparion* faunas, *Promephitis* ranges from the late Miocene to the Pliocene of Eurasia. Up to 10 species have been named, including two based on Chinese material, but fragmentary jaws and teeth represent most of the known forms scattered in more than a dozen localities.

In recent years, field projects in late Tertiary basins of North China resulted in an explosive growth of new knowledge of Chinese *Hipparion* faunas of the Baodean age. Accumulation of new Chinese *Promephitis* material has reached the point where a nearly continuous series of species emerges, and new and more complete specimens make it possible to resolve some long standing questions regarding the systematic status of taxa from such classic basins as Yushe, Baode, and Fugu. Furthermore, a new collection of *Promephitis* from the Hezheng region in Gansu Province yielded the largest and best-preserved sample of this genus, including two contemporaneous species, each represented by more than a dozen skulls. Such a wealth of new information prompts us to re-evaluate Chinese *Promephitis* taxonomy and zoogeography in the late Miocene (Pliocene forms and overall phylogenetic relationships will be treated separately).

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; F:AM, Frick Collection, AMNH; HM, Hezheng Museum, Gansu Province; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; THP, Tianjin Museum of Natural History, Tianjin; UADP, Division of Paleoanthropology, University of Ankara, Turkey; and XM, Xuzhou Museum, Jiangsu Province.

SYSTEMATIC PALEONTOLOGY

Class CARNIVORA Bowdich, 1821
Superfamily MUSTELOIDEA Swainson, 1835
Family MEPHITIDAE Bonaparte, 1845
Genus *PROMEPHITIS*, Gaudry, 1861

Type Species—*Promephitis larteti* Gaudry, 1861.

Included Species—*P. larteti* Gaudry, 1861; *Promephitis maeotica* Alexejew, 1916; *Promephitis alexejewi* Schlosser, 1924; *Promephitis malustenensis* (= *Promephitis rumanus*) Simionescu, 1930; *Promephitis majori* Pilgrim, 1933a; *Promephitis hootoni* Şenyürek, 1954; *P. pristinidens* Petter, 1963; *Promephitis brevisrostris* Meladze, 1967; *Promephitis maxima* He and Huang, 1991; *Promephitis parvus*, sp. nov.; and *Promephitis qinensis*, sp. nov.

Distribution—Vallesian to Ruscian (?) (MN 9–MN 15), late Miocene to early Pliocene of Europe and western Asia; Baodean to Yushean, late Miocene to Pliocene of China.

Emended Diagnosis—*Promephitis* is characterized by a modest to extensive hypertympanic sinus, postsylvian and sylvian sulci absent, extremely reduced P2, shelf-like P4 protocone (in contrast to a conical P4 protocone in North America taxa), and an extra labial root on m1. It further differs from the New World taxa in its lack of a deep notch between metaconid and entoconid of m1.

Comments—All mephitids share an expansion of the epitympanic recess into the mastoid and squamosal areas (Schmidt-Kittler, 1981; 1984; Bryant et al., 1993; Wolsan, 1999). Such a middle ear space expansion can easily be detected as an inflated bulge on the lateral wall of the braincase just above the mastoid process. Mephitids are also unique in their possession of extra roots on the labial and lingual sides of m1 between the main anterior and posterior roots. The M1s of all mephitids are rather primitive with subequal paracone and metacone, and a protocone with a distinct postprotocrista, in contrast to most mustelids that have an extremely reduced or lost metacone and a lack of postprotocrista. *Promephitis* possesses all of the above characters and assignments of Eurasian specimens from the late Miocene to Pliocene to this genus are generally without controversy.

Furthermore, *Promephitis* is unique among the Mephitidae in having a crest-like protocone on P4, in contrast to conical protocones in New World forms.

Promephitis was first established with *P. larteti* from Pikermi, Greece (Gaudry, 1861; 1862). Since then, seven additional species were named from Europe and western Asia: *P. gaudryi* (Schlosser, 1902) from Melchingen, Germany (MN 9); *P. maeotica* (Alexejew, 1916) from Novo-Elisavetovka, Odessa, Ukraine (MN 12); *P. malustenensis* (= *P. rumanus*) (Simionescu, 1930) from Mălușteni, Rumania (MN 15); *P. majori* (Pilgrim, 1933a) from Quarry 1 of Samos (Main Bone Bed, Bernor et al., 1996:table 10.2), Greece (MN 12); *P. hootoni* (Şenyürek, 1954) from Küçükoyzgat, Anatolia, Turkey (MN 11?); *P. pristinidens* (Petter, 1963) from Viladecabals, Vallès-Penedès, northern Spain (MN 10); and *P. brevisrostris* (Meladze, 1967) from Bazalethi (MN 13), eastern Georgia. Additional eastern European specimens have been referred to *Promephitis* from various localities north of Black Sea (Korotkevich and Topachevskii, 1986).

Of the above seven named species, the generic status of two has been questioned. *Promephitis gaudryi*, based on a single m1, was referred to *Trocharion albanense*, a leptarctine mustelid (Major, 1903; Pilgrim, 1933b:859). *Promephitis malustenensis*, the only Pliocene form in Europe, was questioned by Pilgrim (1933a: 14), who considered its ramus too long and its premolars too large to belong to *Promephitis*. Generic membership of the remaining five species from Europe and western Asia seems not in question, although no modern systematic revision has been attempted. Werdelin (1996) listed four species from the late Miocene of Europe, *P. pristinidens*, *P. maeotica*, *P. larteti*, and *P. brevisrostris*. Ginsburg (1999:table 1), on the other hand, recognized only three: *P. gaudryi*, *P. pristinidens*, and *P. larteti* (which probably includes *P. majori* and *P. maeotica* in his concept).

In contrast to the multiple species spanning the late Miocene of Europe, only two endemic species of *Promephitis* were previously recognized in China, *P. alexejewi* from the latest Miocene locality of Ertemte in Inner Mongolia (Schlosser, 1924) and *P. maxima* from a late Pliocene (?) cave in Jiangsu Province along the east coast of China (He and Huang, 1991). Zdansky (1937) and Teilhard de Chardin (1945) referred a few fragmentary specimens from Baode and Yushe to the European *P. maeotica*.

PROMEPHITIS PARVUS, sp. nov.

Holotype—IVPP V13306, complete skull with complete upper dentition.

Type Locality—IVPP locality LX200033, Jinchanggou (Village), Guantangou, Hezheng County, Gansu Province; in brown mudstone, Dongxiang Formation (Baodean, late Miocene), Linxia Basin (see Li, 1995 for a recent summary of local stratigraphy).

Referred Specimens—see Appendix.

Distribution—Late Miocene of Linxia Basin, Gansu Province and late Miocene of Baode and Wuxiang regions, Shanxi Province.

Diagnosis—Differs from *P. pristinidens* in a more lingually and anteriorly expanded internal cingulum in P4 that is elevated to form a protocone, a smaller P4 anterior cingulum, a more transversely widened M1, a better-developed M1 internal cingulum, a more prominent M1 parastyle, and a less posteriorly expanded M1 metacone. Differs from *P. majori* and more advanced species in its less expansion of mastoid process, shorter external auditory meatus, slightly more inflated bulla, double temporal crests, relatively long rostrum, and relatively long and narrow P3 and p4.

Etymology—*parvus*, Latin, little, small; in reference to its small size.

Description

Skull—Cranial proportions are best shown in IVPP V13306 and V13308, which are nearly free from distortion (Table 1). In dorsal view (Fig. 1F), sutures on the snout are still visible on IVPP V13306, but are all fused in other specimens. The posterior premaxillary process reaches back to the level of the tip of the canine. The nasal is short, its posterior margin stopping in front of the infraorbital canal. The frontal has an anterior process protruding forward between the posterior processes of the nasal. The postorbital process of the frontal is small but distinct. The postorbital constriction is near the postorbital process. In all of the specimens, regardless of ontogenetic age, the temporal crests always remain separate and do not form a single sagittal crest. The nuchal crest is low and indistinct.

In lateral view (Fig. 1E), the infraorbital canal is short and the orbit is large. The posterolateral aspect of the braincase in the holotype was peeled off during preparation, revealing a finely preserved endocast (Fig. 1F). There are two main sulci in the exposed neocortex. A lateral sulcus is gently arching backward, stopping shortly before the cerebellum. A suprasylvian sulcus is directed posterodorsally, ends at the level of the mastoid process, and has virtually no ventral expansion into a postsylvian sulcus as in *Melogale*, *Martes*, *Taxidea*, and other mustelids (Radinsky, 1973). There is no visible sylvian sulcus on the lateral part of the neocortex. This lack of postsylvian and sylvian sulci is closely comparable to the condition in *Mephitis* and *Mydaus*, seems slightly more primitive than that in *Spilogale*, and substantially different from that in *Conepatus*. *Promephitis* exhibits an overall similarity of endocast morphology among the mephitids, which represent primitive conditions for carnivorans (Radinsky, 1973).

In ventral view (Fig. 1G), the palate is short, and its posterior border is slightly rostral to the posterior margin of M1. There is no alisphenoid canal. The bulla is inflated compared to that of other species of *Promephitis*. The flask-shaped bulla has a very short external auditory meatal tube, in contrast to a more elongated tube in larger species of *Promephitis*. The mastoid process is slightly inflated, and in specimens with slight breakage in this area (IVPP V13307, 13308), the inflated area is occupied by hypertympanic sinuses, which become more expanded in *P. majori* and more advanced species. The paroccipital process is a thin, blade-like structure oriented in a posteroventral direction and extends laterally.

Dentary—Despite the wealth of well-preserved skulls, there are far fewer lower jaws in good condition. Our description is mainly based on two partial rami (IVPP V13307 and V13309). The partial ascending ramus on IVPP V13307 shows an erect anterior border (Fig. 2I). The horizontal ramus is generally slender with nearly uniform depth throughout. At the posterior end of the symphysis, there is a slight drop of a chin. There are two mental foramina, the anterior one between the p2 and p3 and the posterior one between the roots of the p4.

Upper Teeth—All upper incisors are single-cusped (Fig. 2G). The I3 has a slight internal cingulum. Upper canines are straight, without grooves but with an internal cingulum. P1 is absent. All specimens have a tiny P2 when this area is preserved and prepared (five from Hezheng). It is usually a simple peg sandwiched between C and P3 on the lingual side. The P3 is high-crowned with a single cusp and a weak posterior cingulum. The P4 has no carnassial notch and usually lacks an anterior cingulum. The protocone forms a large internal shelf and gives the impression of arising from the internal cingulum. This protocone shelf is nearly as wide as the main body of the paracone, and occludes with the paraconid of the lower carnassial. The apex of the protocone is slightly posterior to the apex of the paracone. Anterior to the protocone is a low shelf that expands slightly anteriorly to the anterior edge of the paracone. At the anterior end of this shelf, the cingulum is raised to form an indistinct cuspule in some

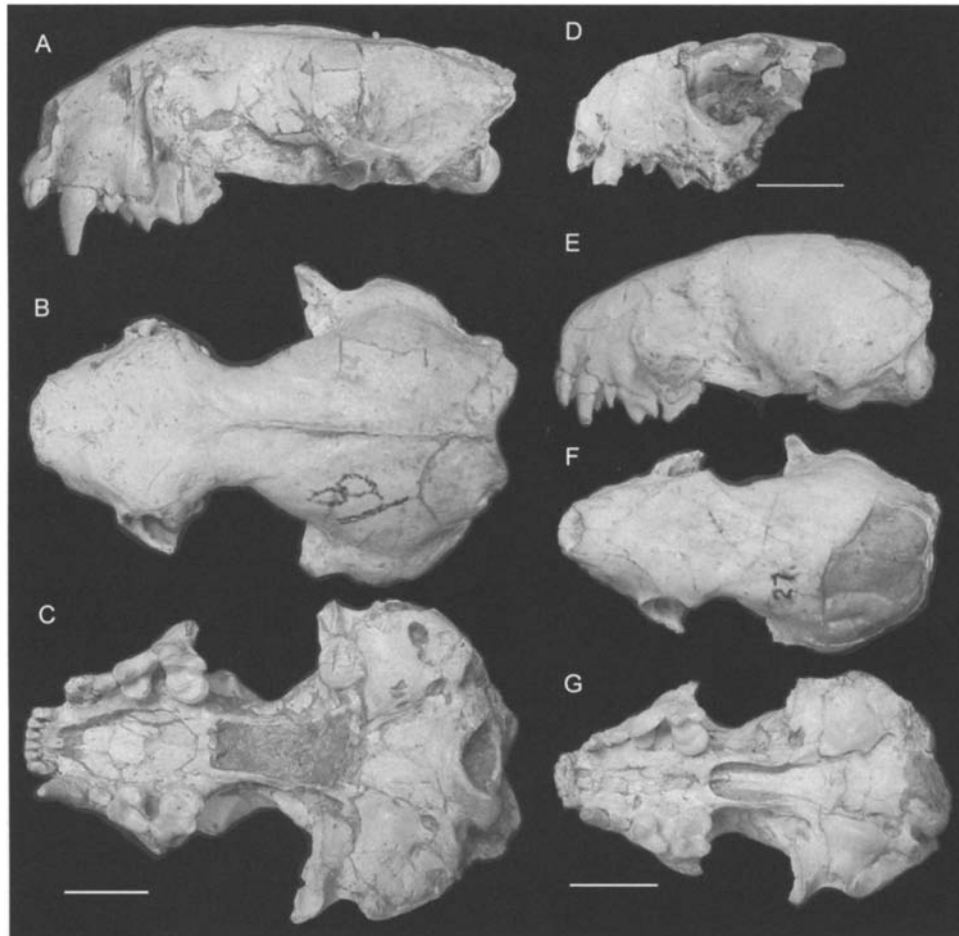


FIGURE 1. Skulls of *Promephitis* from China. **A**, lateral, **B**, dorsal, and **C**, ventral views of skull of *P. hootoni*, IVPP V13310. **D**, lateral view of skull, IVPP V13311, holotype of *P. qinensis*, sp. nov.; **E**, lateral, **F**, dorsal, and **G**, ventral views of skull, IVPP V13306, holotype of *P. parvus*, sp. nov.. Scale bars equal 10 mm.

individuals (e.g., IVPP V13306). Posterior to the protocone, the internal shelf abruptly narrows to become a narrow lingual cingulum. The M1 is rather primitive for a musteloid. The paracone is only slightly larger than the metacone. Nor is the parastyle greatly enlarged as it is in more derived *Promephitis*. Presence of a postprotocrista behind the protocone is another primitive feature that is lost in most mustelids. The postprotocrista ends at the posterior border of the tooth and shows no indication of a metaconule at its end. The internal cingulum completely surrounds the protocone, although the posterolingual part of the cingulum is much thicker than the anterior part, and there is no sign of developing into a conical hypocone. There is a rounded notch between the posterior end of the internal cingulum and the metacone.

Lower Teeth—Lower incisors preserved on IVPP V13307 show progressively larger size from i1 to i3 (Fig. 2H). Wear on these incisors, however, does not permit recognition of detailed structure beyond a peg-like simple cylinder. Only the basal part of the lower canine is preserved. It is tightly packed next to the incisors. A p2 is indicated by a small root in IVPP V13309. The p3s in both IVPP V13307 and V13309 are damaged, and the remaining parts indicate a high-crowned, single-cusped tooth. The p4 is nearly as tall as the protocone of m1 (Fig. 2I). It has a small anterior accessory cusp and a posterior cingulum, which rises slightly to form a cuspule. The m1 is the longest tooth with a relatively long talonid. There is a weak carnassial notch. A tiny (third) root along the labial margin of the m1 is present below

the protoconid on IVPP V13309. The protoconid is the tallest cusp on the trigonid, almost twice as tall as the paraconid and metaconid. The paraconid bends slightly internally to occlude with the internal shelf of the upper carnassial. The metaconid is slightly behind the protoconid and has a sharp posterior edge to reach down to the entoconid crest. The talonid has a wide and tall hypoconid and a narrow and low entoconid. Both cusps are crest-like, although the hypoconid is thickened in the middle and rises slightly so that a distinct cusp can be recognized. The entoconid, on the other hand, is uniformly low and located along the lingual border of the talonid. Very weak notches along the entoconid crest divide it into two to three cuspules. Between the hypoconid and entoconid is a longitudinally oriented basin, which opens posteriorly. There is no cingulum on m1. The m2 is rounded in outline, often slightly wider than it is long. When unworn, it has a large protoconid on the middle part of the labial side. In front of the protoconid, there is no paraconid, simply a low shelf. Behind the protoconid is a small hypoconid. On the lingual side, the m2 is rimmed by a low crest divided by two small cuspules opposite the protoconid.

Discussion—Early records of *Promephitis* are very poor. Schlosser (1902) first named *P. gaudryi* from Melchingen, Germany (MN 9), which was later referred to *Trocharion* by Pilgrim (1933a; 1933b), although Ginsburg (1999:table 1) recently listed it as one of three valid species of *Promephitis* in Europe. Established on a single left m1, the true status of *P. gaudryi* remains uncertain until better material becomes available. Petter (1963)

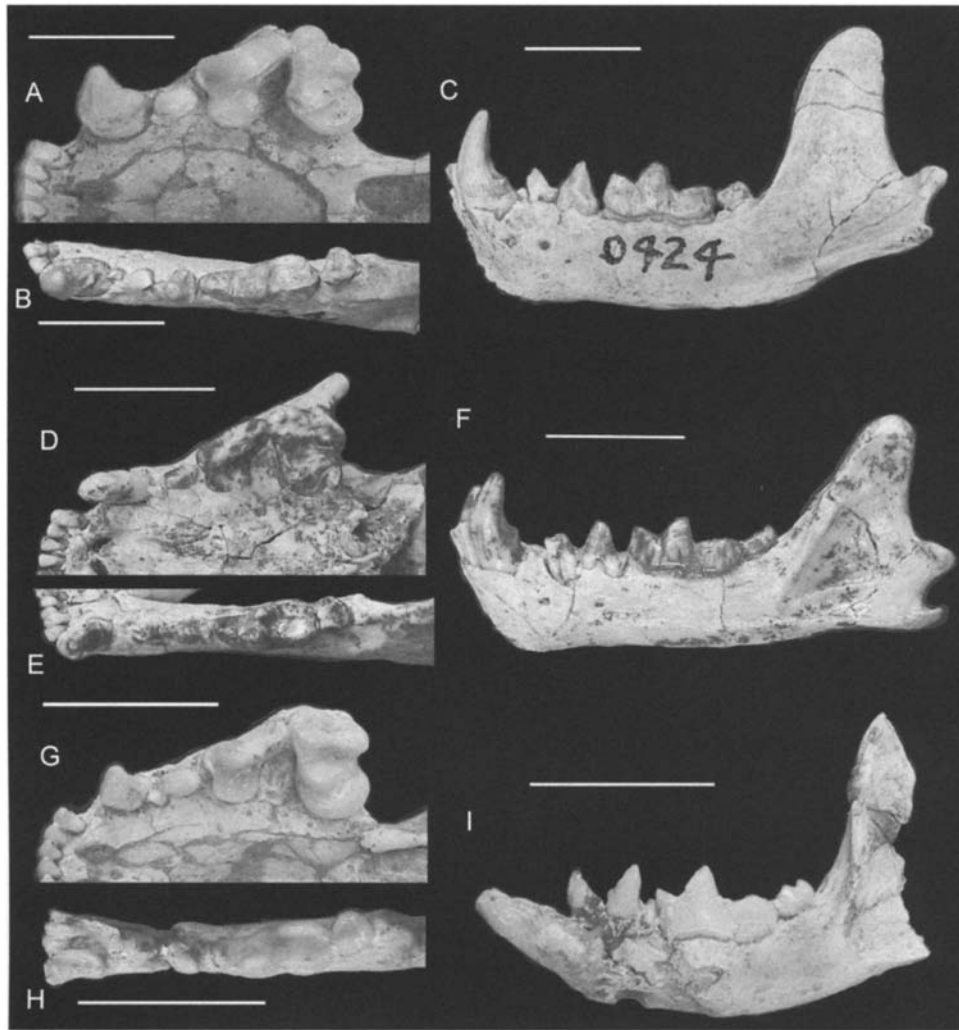


FIGURE 2. Lower jaws and teeth of *Promephitis* from China. **A**, occlusal view of upper teeth of IVPP V13310 (reversed from right side), **B**, occlusal view of lower teeth of HM V0424, and **C**, lateral view of ramus (HM V0424) of *P. hootoni*. **D**, occlusal view of upper teeth, **E**, occlusal view of lower teeth, and **F**, lateral view of ramus of IVPP V13311, holotype of *P. qinensis*, sp. nov. **G**, occlusal view of upper teeth (reversed from right side), **H**, occlusal view of lower teeth (reversed from right side), and **I**, lateral view of ramus (reversed from right side) of *P. parvus*, sp. nov., IVPP V13307. Scale bars equal 10 mm (specimens of the same species, e.g., A, B, and C, are all scaled to the same size).

recognized a late Vallesian species, *P. pristinidens*, based on a maxilla fragment with P4–M1 from Viladecabals (MN 10), Vallès-Penedès of Spain, and considered it the earliest and most primitive representative of the genus in Europe. More recently, Morales et al. (1999:table 6.1) extended the geologic range of this species further down to the older Can Llobateras locality (MN 9), also in the Vallès-Penedès Basin. However, they did not indicate the nature of their materials. Despite the meager material for the holotype of *P. pristinidens*, recent compilations of European Neogene carnivorans regarded it as a valid species (Werdelin, 1996; Ginsburg, 1999).

In dental measurements, *Promephitis pristinidens* is rather close to those of *P. parvus* (Table 2). The latter mainly differs from the former in a less prominent P4 anterior cingulum (parastyle), a higher-crowned P4 protocone arising from the internal cingulum, a more anteriorly protruded protocone crest of P4, and a less quadrate M1 with a more lingually expanded internal cingulum and a more reduced metacone. The M1 of *P. parvus* also differs from that of *P. pristinidens* in have a more inflated parastyle and better-developed postprotocrista.

The lack of a discrete protocone on the P4 of *P. pristinidens* is

in stark contrast to all later species of *Promephitis*, which have an elevated protocone. Although it is possible that the Spanish form may belong to a different lineage from *Promephitis*, its possession of a narrow internal cingulum, in place of a protocone, can also be viewed as a morphological precursor to later species of the genus (i.e., development of an elevated, crest-like protocone may be derived from a condition similar to that in *P. pristinidens*). New World mephitids all have a conical protocone and it is not clear whether it is developed from a cingular precursor or whether the conical protocone is simply a primitive condition for all mephitids.

In overall dental proportions and size, *Promephitis parvus* is also somewhat close to *P. majori*, the smallest *Promephitis* in the Turolian of Europe (Table 2). However, *P. majori* is more derived in several characters: single sagittal crest, lateral expansion of mastoid process, flattening of bulla, long external auditory meatus, shortened P3 and m2, and enlarged M1 parastyle. *P. parvus* is thus the most primitive *Promephitis* in China, only slightly more derived than *P. pristinidens*. Its small size and basal position thus indicate a form very close to the primitive morphotype of *Promephitis*.

TABLE 1. Measurements (in mm) of skull and lower jaws as defined by Pilgrim (1933a:10–11) as follows: **SL**, length of skull from occipital condyles to front edge of incisors; **FMI**, distance from lower edge of foramen magnum to front edge of incisors; **PI**, distance from hinder end of palate to hinder end of middle incisors; **BMP**, breadth of skull at mastoid processes; **BPC**, minimum breadth of skull behind postorbital processes; **BPP**, breadth of skull between postorbital processes; **BO**, minimum breadth of skull between orbits; **BC**, breadth of skull at canines; **BP**, breadth of palate between hinder ends of P4; **HS**, height of skull from occipital condyles to highest point of occiput; **CM2**, distance from front edge of canine to hinder end of m2; and **DR**, depth of mandibular ramus beneath middle of m1.

	SL	FMP	PI	WMP	WPC	WPP	WO	WC	WP	HS	CM2	DR
<i>Promephitis maxima</i>												
XM 001	91.0	—	37.5	—	21.1	—	—	23.1	32.0	—	31.1	11.0
<i>Promephitis maeotica</i>	67.5	36.0	23.7	44.0	16.6	24.0	22.0	18.2	—	24.4	26.0	8.5
<i>Promephitis hootoni</i>												
HM V0417	61.7	32.8	22.5	41.2	16.1	21.1	19.7	16.9	24.1	22.2	—	—
HM V0424	64.5	34.7	22.8	—	17.0	21.5	21.1	16.8	24.3	—	24.9	7.5
HM V0425	60.8	31.5	24.3	35.0	14.6	18.3	17.2	14.5	—	20.4	23.5	6.8
HM V0429	61.9	32.7	22.2	42.1	15.4	21.1	20.0	16.2	23.6	23.8	—	—
HM V0428	64.1	33.3	23.3	41.0	15.3	22.4	20.8	17.2	25.0	23.0	—	—
HM V0411	62.3	32.4	22.5	41.9	16.8	22.8	21.3	17.5	23.1	—	—	—
IVPP V13310	60.2	32.0	22.1	41.0	14.3	22.6	21.5	16.2	22.6	19.5	—	—
<i>Promephitis qinensis</i> , sp. nov.												
IVPP V13311	—	—	20.4	—	—	—	—	13.5	19.4	—	22.4	6.4
<i>Promephitis majori</i>												
AMNH 20585	53.6	27.5	18.0	33.0	14.7	17.3	16.6	14.0	16.3	20.0	19.7	7.0
<i>Promephitis parvus</i> , sp. nov.												
IVPP V13306	45.0	23.7	21.2	25.6	12.7	16.0	14.1	10.7	16.7	—	—	—
IVPP V13307	45.1	25.0	16.3	26.0	12.5	14.9	13.9	11.0	16.5	14.7	—	4.5
IVPP V13308	43.7	22.8	15.5	26.8	13.6	15.5	14.6	11.5	17.7	15.6	—	—

Co-occurrence of two size-groups, *Promephitis parvus* and *P. hootoni*, in both Hezheng and Baode areas naturally raises the question of possible sexual dimorphism and/or stratigraphic succession. The possibility of these two size-groups belonging to different stratigraphic levels can quickly be ruled out because the two morphs co-occur in at least two localities in Hezheng area

(Shanjiawan, and Shuanggongbei) and two localities in Baode area (Du Kou and Chen Chia Mao Kou). Even after taking into account the imprecise nature of the stratigraphy of these two regions (both had been under extensive exploitation by “dragon bone” collectors), the numerous co-occurrences are difficult to explain away because most of these localities produce just a

TABLE 2. Dental measurements (in mm) of select species of *Promephitis*. All measurements are for maximum longitudinal length and transverse width, for example, P3L is length of P3 and P3W is width of P3. Measurements for European taxa are mostly from Pilgrim (1933a:10–11). Abbreviations after species: **HZ**, samples from Hezheng area only; **SX**, samples from Shanxi Province only.

	P3L	P3W	P4L	P4W	M1L	M1W	p3L	p3W	p4L	p4W	m1L	m1W	m2L	m2W
<i>Promephitis maxima</i>														
XM001	3.6	3.1	8.4	7.1	8.9	10.4	3.8	3.0	4.8	3.9	13.0	6.0	4.3	4.9
<i>Promephitis alexejewi</i>	—	—	8.0	5.0	5.8	7.6	—	—	3.8	2.0	10.6	4.8	—	—
<i>Promephitis larteti</i>	—	—	8.0	—	5.0	8.0	—	—	—	—	8.0	—	3.0	—
<i>Promephitis brevirostris</i>	—	—	—	—	—	—	—	—	—	—	9.0	4.0	—	—
<i>Promephitis maeotica</i>	2.5	2.0	7.1	5.3	5.7	9.1	—	—	—	—	10.2	4.7	—	—
<i>Promephitis hootoni</i> (type)														
UADP Ky. P. 1	2.8	1.9	6.1	5.1	5.7	7.6	2.5	1.8	3.7	2.8	8.8	4.3	—	—
<i>Promephitis hootoni</i> (HZ)														
Mean	2.60	2.00	6.70	5.20	5.78	7.77	2.67	1.90	3.40	2.65	8.87	3.85	2.70	2.95
SD	0.16	0.12	0.34	0.29	0.36	0.43	0.19	0.10	0.08	0.25	0.40	0.25	0.14	0.05
CV	6.28	5.77	5.01	5.54	6.17	5.53	7.07	5.26	2.40	9.43	4.54	6.49	5.24	1.69
Max	2.8	2.2	7.2	5.6	6.3	8.3	2.8	2.0	3.5	2.9	9.2	4.1	2.9	3.0
Min	2.3	1.8	6.0	4.8	5.0	7.1	2.4	1.8	3.3	2.4	8.3	3.6	2.6	2.9
Number	6	6	8	7	8	7	3	2	3	2	3	2	3	2
<i>Promephitis hootoni</i> (SX)														
Mean	2.76	1.89	6.78	5.23	6.01	8.16	2.65	1.87	3.65	2.70	9.11	4.05	2.89	2.86
SD	0.33	0.25	0.37	0.40	0.34	0.40	0.22	0.14	0.36	0.29	0.66	0.31	0.24	0.26
CV	12.01	13.03	5.50	7.65	5.67	4.84	8.40	7.58	9.79	10.59	7.24	7.61	8.23	9.23
Max	3.3	2.2	7.4	5.7	6.5	8.7	2.9	2.1	4.6	3.1	10.0	4.6	3.2	3.2
Min	2.0	1.3	6.2	4.5	5.6	7.4	2.3	1.6	3.2	2.3	7.8	3.6	2.5	2.5
Number	13	12	14	10	13	13	11	11	11	11	11	11	9	8
<i>Promephitis majori</i>														
AMNH 20585	2.5	1.8	5.7	4.0	5.9	7.3	2.0	1.4	3.0	2.0	7.9	3.5	2.4	2.4
<i>Promephitis qinensis</i> , sp. nov.														
IVPP V13311	2.6	1.7	6.3	4.2	6.0	7.3	2.6	2.1	3.4	2.5	8.1	3.7	2.9	2.7
<i>Promephitis parvus</i> , sp. nov. (HZ)														
Mean	2.28	1.57	5.40	3.70	4.78	6.15	1.95	1.50	3.25	1.90	6.95	3.05	2.50	2.30
SD	0.30	0.12	0.19	0.19	0.11	0.18	0.35	0.10	0.25	0.20	0.35	0.05	—	—
CV	13.32	7.96	3.46	5.06	2.28	2.93	17.95	6.67	7.69	10.53	5.04	1.64	—	—
Max	2.7	1.7	5.7	3.9	4.9	6.4	2.3	1.6	3.5	2.1	7.3	3.1	2.5	2.3
Min	1.9	1.4	5.2	3.4	4.6	5.9	1.6	1.4	3.0	1.7	6.6	3.0	2.5	2.3
Number	4	3	4	4	4	4	2	2	2	2	2	2	2	1
<i>Promephitis pristinidens</i>	—	—	6.1	4.0	5.5	6.4	—	—	—	—	—	—	—	—

single fossiliferous horizon. As for the possibility of sexual dimorphism, Van Gelder (1959; 1968) demonstrated that modern populations of skunks generally show modest dimorphism. In the hog-nosed skunks (*Conepatus*), adult males average 8.5% and 1.3% larger than adult females in condylobasal length of the skull and lower carnassial length, respectively. In the spotted skunks (*Spilogale*), adult males average 7% larger than adult females in most cranial measurements. In contrast, Chinese *P. hootoni* averages 39% larger than *P. parvus* among all cranial measurements (Table 1), far exceeding the magnitude of dimorphism seen in living skunks. Extant North American *Mephitis* and *Spilogale* have extensive overlap in their distributions, with the former almost twice as large as the latter, approximating the size differences seen in the fossil forms. The above evidence, plus the morphological differences listed in the diagnoses, leave little doubt of the co-existence of two species of *Promephitis* in China during part of the late Miocene.

Referred specimens from Shanxi Province (three from Baode County, F:AM 50630, 50631, and 50637, and one from Wuxiang County, F:AM 50636) are somewhat larger in size than the Hezheng samples, probably reflecting a younger age for these specimens from further east. Dentally, the Shanxi sample also displays slightly more derived features commonly seen in advanced species such as *P. hootoni*. These include a slight widening of the mastoid area, slightly inflated parastyle on M1, and reduced anterior segment of internal cingulum, although the stage of development of these features is far from the condition in *P. hootoni*. Therefore, the Shanxi sample must be a later extension of *P. parvus* from Hezheng and independently acquired these features within its own species lineage. Interestingly, the Baode sample of *P. hootoni* is also slightly larger in size than its counterpart from Hezheng and shows signs of slightly more derived states in dental morphology. It appears that the co-occurring *P. parvus* and *P. hootoni* species pair maintained their size differences while both increased their body size slightly.

Promephitis qinensis, sp. nov.

Holotype—IVPP V13311, rostral part of skull and partial mandible with right I1–P3 and left I1–M1, right i1–m1 (broken) and left i1–m2 (Figs. 1D, 2D–F).

Type Locality—Wangdaifuliang (MNU 9), Fugu County, Shaanxi Province.

Etymology—In allusion to the Qin region, which is centered around the present day Shaanxi Province north of the Qinling Mountain and gave rise to the ancient Qin Dynasty that unified China.

Diagnosis—*Promephitis qinensis* differs from *P. parvus* by its larger size, single sagittal crest, inflated M1 parastyle, reduced anterior segment of internal cingulum on M1, and broad p4. On the other hand, it differs from *P. hootoni* in its smaller size, lack of an inflated forehead, short incisive foramen, P4 protocone not lingually expanded, less inflated M1 parastyle, and less broadened p4. It differs from *P. majori* in its straight lower border of horizontal ramus, longer angular process, relatively longer P3 and p3, and broadened posterior half of p4; and differs from *P. pristinidens* in more prominent P4 protocone and transversely widened M1.

Description

Skull—*Promephitis qinensis* is larger than all specimens of *P. parvus*, but is either smaller or on the extreme lower limits of Chinese *P. hootoni* (Table 1). Only the anterior half of the cranium is preserved, which is crushed on the left side of the face. As in all species of *Promephitis*, the premaxilla and frontal are mostly fused together without clear trace of sutures. As in *P. majori*, the forehead area just above the orbit is rather flat without the prominent dome seen in *P. hootoni*. On the other hand,

the temporal crests converge just behind the postorbital constriction to form a single sagittal crest, in contrast to the double temporal crests in *P. parvus*. The postorbital processes on either side are broken. In palatal view, the incisive foramina are rather rounded, instead of the more elongated conditions in *P. hootoni*. The posterior margin of the palatine ends at the posterior border of the M1.

Dentary—The horizontal ramus is deepest at the mandibular symphysis, giving the impression of a slight chin (Fig. 2F). The ramus tapers slightly toward the posterior end. The lower border of the ramus below the masseteric fossa is straight without the step-like appearance in *P. majori*. The angular process stops at the posterior border of the mandibular condyle, and is longer than in *P. majori*. Its medial surface has two distinct fossae, a superior fossa for the insertion of the lateral pterygoid muscle and an inferior fossa for the medial pterygoid muscle. The anterior border of the ascending ramus reclines backward (approximately 45° from the horizontal ramus) whereas the posterior border is nearly vertical.

Upper Teeth—The entire upper incisor row is preserved and forms a nearly straight battery (Fig. 2D). The tips of the incisors are all worn and their cusp morphology is difficult to observe. I1 and I2 are nearly equal in size and they have an anteroposteriorly elongated cross-section. I3 is much larger than I1–I2 and has a lingual cingulum. The upper canine has a vague, cingulum-like swelling at the base, but is otherwise a simple cone. P1 is absent. A small peg-like P2 fits in the narrow area between the C and P3. The P3 has two roots and a single main cusp with an incipient posterior cingular cusp. The posterior half is substantially wider than the anterior half. The P4 has a slight swelling on the anterior cingulum in front of the paracone, but lacks a conical parastyle. The P4 has a distinct lingual cingulum but lacks a labial cingulum. Its protocone is elevated from the lingual cingulum, which continues forward in front of the protocone and forms a slight elevation near the anterior-most point of the cingulum. The protocone is not lingually expanded as much as in *P. hootoni* and *P. maeotica*, resulting in a relatively low width/length ratio of 0.68 as compared to an average of 0.76 for that of *P. hootoni* (N=7 from Hezheng area). The M1 has a slightly swollen parastyle compared to that in *P. parvus*. The paracone is worn but is probably substantially higher than the metacone. The postprotoconicrista is well developed and terminates at the posterior margin of the tooth. The internal cingulum still has an anterior segment that wraps around the protocone, but it is somewhat reduced and less distinct than in *P. parvus*.

Lower Teeth—Lower incisors form a transversely straight row (Fig. 2E). The occlusal surface of all incisors are worn. The i1 and i2 are equal in size, and i3 is larger than both. The lower canine follows immediately behind the i3. It hooks backward and has a distinct internal cingulum. There is no p1. Both left and right p2 are preserved only as tiny roots sandwiched between c and p3. The p3 main cusp is procumbent. A tiny anterior accessory cusp is also present. The p3 widens behind the main cusp and has an indistinct posterior cingulum. The p4 is taller than the m1 paraconid and is an enlarged version of the p3. The p4 widens posteriorly more strongly than the p3. The m1 metaconid is taller than the paraconid and located slightly behind the protoconid. The m1 talonid basin is flanked laterally by a slightly larger and taller hypoconid and medially by a smaller entoconid ridge. The entoconid is weakly marked by two shallow notches. The m2 is circular in outline, and has a low protoconid and a smaller metaconid. A small hypoconid is also present at the posterior rim.

Discussion—*Promephitis qinensis* is intermediate in size and morphology between *P. parvus* and *P. hootoni*, and is similar in its stage of evolution to *P. majori*. *Promephitis majori* from Quarry 1 (Main Bone Bed, MN 12) of Samos Island, Greece was described by Pilgrim (1933a). In recent studies, *P. majori* is generally regarded as a junior synonym of *P. larteti*, expressed ex-

licitly by Bernor et al. (1996:table 10.2) and Ginsburg (1999), or implicitly by Werdelin (1996). However, if Pilgrim's (1933a) measurements on the crushed skull of *P. larteti* are accurate, it is substantially larger than *P. majori*, clearly exceeding the range of variations of most skunks. While the taxonomic status of *P. larteti* needs to be re-examined, the much better-preserved and illustrated *P. majori* is better for comparative purposes.

Promephitis majori seems transitional in size and morphology between *P. parvus* and *P. hootoni* (Table 1). It possesses a combination of primitive and derived features that indicate its phylogenetic position between *P. parvus* and *P. hootoni*. Derived characters relative to *P. parvus* include larger size, single sagittal crest, expanded mastoid area due to enlargement of epitympanic space, elongated external auditory meatus, enlarged parastyle on M1, and reduced anterior segment of internal cingulum on M1. On the other hand, *P. majori* is primitive relative to *P. hootoni* in a number of features. These include flat forehead that is not expanded above the postorbital process, postorbital processes still present, mastoid area not extremely expanded, incisive foramen not elongated, P4 protocone not medially expanded, M1 parastyle not extremely enlarged, and p4 not broadened.

Promephitis qinensis is very close to *P. majori* both in size and morphology. Although lacking the posterior half of the skull, *P. qinensis* shares several characters with *P. majori*. These include a flat forehead, a single sagittal crest, a short incisive foramen, a narrow P4 protocone, a slightly enlarged parastyle of M1, a slightly reduced anterior segment of internal cingulum on M1. However, *P. qinensis* differs from *P. majori* in a straight lower border of the horizontal ramus, a longer angular process, a relatively longer P3 and p3, and a broadened posterior half of p4. In particular, *P. majori* appears to have a tendency towards reduced premolars (except P4). This is in contrast to an enlargement of premolars (particularly a broadened p4) in *P. qinensis*. Because the broadening of the p4 is a derived condition shared by all advanced species of *Promephitis*, *P. qinensis* is slightly closer to *P. hootoni* and all later *Promephitis*.

Promephitis hootoni Şenyürek, 1954

Promephitis cfr. *maeotica* Alexejew, 1916: Zdansky, 1937:325.

Promephitis alexejewi Schlosser, 1924: Teilhard de Chardin, 1945 (in part).

Holotype—UADP Ky P. 1, partial skull and mandible with I1-I2, C, P3-M1, and i1-m1.

Type Locality—From whitish calcareous marls of lacustrine origin at Küçükoyzgat, Anatolia, Turkey (Şenyürek, 1954).

Referred Specimens—see Appendix.

Distribution—Late Miocene of Turkey; late Miocene of Hezheng region, Gansu Province; Baode, Shou Yang and Wu Xiang regions, Shanxi Province; and Fugu region, Shaanxi Province.

Emended Diagnosis—Differs from *P. majori* and *P. qinensis* by having an inflated frontal creating a domed forehead, a long incisive foramen, a short and broad P4, an inflated M1 parastyle, a reduced anterior segment of M1 internal cingulum, and a broad and short p4. On the other hand, it differs from *P. maxima* and an undescribed form from Yushe in its lack of a reduced postorbital process of frontal, greater distance between postorbital process and postorbital constriction, tall and erect ascending ramus, loss of P2 and p2, and presence of a small entoconulid on m1.

Description

Skull—The large number of well-preserved skulls makes this species the best represented in *Promephitis*. To save space, the following descriptions only compare cranial and dental morphologies that are different from those in *P. parvus* and *P. majori* or to note intraspecific variation. Cranial proportions of *P. hoo-*

toni are different from those of *P. parvus*, *P. majori*, and *P. qinensis* in several ways. The rostrum is shortened relative to the temporal and parietal regions of the skull. The forehead above the orbit is more inflated, forming a prominent dome in certain individuals (e.g., IVPP V13310). The postorbital process of the frontal is also noticeably more enlarged, in contrast to a narrowed postorbital constriction. Most adult individuals have a single sagittal crest, instead of the double temporal crests in *P. parvus*. The nuchal crest is also more prominent than in *P. parvus*. The braincase of *P. hootoni* is dorsoventrally flattened and laterally expanded such that in dorsal view the braincase is substantially wider posteriorly. This lateral expansion is caused by enlarged air sinuses underneath the mastoid process and the full extent of the sinuses can often be delineated by a line of slight depression on the squamosal bone on the lateral wall of the braincase. This lateral expansion of the mastoid area also causes a considerable elongation of the external auditory meatus, which forms a long tube oriented anterolaterally. In ventral view, the ventral segments of the lambdoidal crest are pushed backward due to the mastoid expansion. The bullae are more flat than in *P. parvus*.

Upper Teeth—Upper incisors are simple, wedge-shaped, and without accessory cusps. Canines are more robust than in *P. parvus* and *P. qinensis*. A P2 is still present in specimens in which this part is well preserved (four from Baode, and three from Hezheng) although it is always a tiny, slender peg closely appressed to the anterolingual root of the P3 and much smaller than in *P. parvus* and *P. qinensis*. P3 is little different from that in *P. parvus* in morphology. P4 mainly differs from that of *P. parvus* and *P. qinensis* in a slightly longer protocone crest and broader lingual cingulum. The M1 has an enlarged parastyle that also inflates the labial cingulum around the paracone, so that instead of a distinctly lower cingulum surrounding the paracone (as in *P. parvus*), the cingulum is elevated to nearly the level of the paracone tip. The M1 generally has a more posteriorly expanded internal cingulum, leaving a more distinct notch between the cingulum and metacone than is shown in *P. parvus*. The anterior segment of the internal cingulum is either reduced or lost.

Lower Teeth—Lower incisors are formed by simple, peg-like teeth. The lower canine is recurved and has a lingual cingulum at its base. A p2 is present, but clearly nonfunctional, forming a tiny peg in front of p3. Both p3 and p4 have incipient anterior accessory cusps and a broad posterior shelf behind the main cusps. The posterior halves of the premolars are much broader than the anterior halves, especially in the p4. There is a small root below the protoconid of m1. The m1 differs very little, in morphology, from those in *P. parvus* and *P. qinensis*, and has a large, basined talonid. Both hypoconid and entoconid are ridge-like structures, the latter are further divided into smaller cusplets. The talonid basin is generally shallow compared to *P. parvus* and *P. qinensis*. The m2, on the other hand, is markedly wider than that in *P. parvus*, but is similar in width to *P. qinensis*.

Some specimens from Baode area (e.g., F:AM 50651, 50652, 50658) have substantially larger and broader cheek teeth than those from elsewhere. These large individuals are still smaller than those from Yushe (Teilhard de Chardin, 1945:fig. 19). Although closer in size to *P. alexejewi*, the large Baode individuals do not have the disproportionately longer upper and lower carnassials of the Inner Mongolian species. These individuals are here treated as large males within the range of variation of the species, if one considers the fact that *P. hootoni* has a larger sample size represented from a wide geographic distribution and long stratigraphic range.

Discussion—Two species of *Promephitis* from early Turolian localities of Europe and western Asia fall within the size and morphological range of the Chinese form: *P. maeotica* (Alexejew, 1916) and *P. hootoni* (Şenyürek, 1954). No systematic re-

view has been performed on these two species, although Şenyürek (1954) offered an extensive comparison.

The type specimen of *Promephitis maeotica* has not been re-examined since its original description. Some confusion exists in even what Alexejew (1916) wrote (the original was published in Russian). For example, Pilgrim (1933a:2) remarked on the presence of an "external cingulum" on m1 of *P. maeotica*, which was disputed by Zdansky (1937). Our own examination of the Alexejew paper reveals no mention of such a cingulum. Zdansky (1937) was the first to refer some Chinese materials to *P. cfr. P. maeotica*, when he described a partial cranium and some lower jaws from Yang-Mu-Kou, Chi-Chia-Kou, Baode (locality 49 of University of Uppsala). However, the m1 of *P. maeotica* is longer than all individuals of Chinese Baodean form (Table 2) and instead is comparable in size to *P. alexejewi* (see further comments below). The m1 of *P. maeotica* is also disproportionally wide (4.7 mm). Its upper molar is also extremely wide transversely (9.1 mm; Alexejew, 1916 #1021:table X). The size and proportional differences make it unlikely that *P. maeotica* is conspecific with the Chinese form.

Although we did not personally examine the type material of *Promephitis hootoni*, Şenyürek's (1954) exhaustive descriptions provide adequate information and as far as we can tell, it is indistinguishable from the Chinese form. Most measurements of the type of *P. hootoni* fall in the ranges of morphological variations of the large Chinese samples (Table 2). Referral of the Chinese materials to *P. hootoni* implies a great geographic range for this species across much of Asia, but modern skunks often have wide distributions spanning much of the entire North American continent.

Promephitis alexejewi Schlosser, 1924

Trochictis minutus Schlosser, 1924.

Type Series—No holotype was designated by Schlosser or subsequent authors. The topotype series consist of a left dentary fragment with p4-m1 and m2 alveolus, two right M1s, a left P4, two isolated premolars, a canine, and a few isolated foot bones (Schlosser, 1924:11, pl. I, figs. 31-35, 37, 38) in the Uppsala University collection. Having not seen the topotype series, we refrain from naming a lectotype.

Type Locality—Ertemte, 4 km southeast of Huade, Inner Mongolia, China. Latest Baodean (Chinese MNU 11) in late Miocene.

Referred Specimens—From type locality: IVPP uncatalogued, an isolated m1. From Olan Chorea: a left dentary fragment with broken m1 and m2 alveolus (holotype of *Trochictis minutus* Schlosser).

Emended Diagnosis—Larger than *Promephitis hootoni* but much smaller than *P. maxima*, *P. alexejewi* has a relatively longer P4 and shorter M1 compared to other species of *Promephitis*.

Discussion—This species remains very poorly known. Teilhard de Chardin (1945) attempted to synonymize *Trochictis minutus* (Schlosser, 1924) with *Promephitis alexejewi*, apparently based on a much broader concept of the latter species (placing materials from Yushe within *P. alexejewi*). Schlosser's *T. minutus* was based on a partial left dentary with m1 talonid from Olan Chorea approximately 2 km southwest of Ertemte. It differs from *P. alexejewi* mainly in having a more conical entoconid and additional cuspules on the talonid. Recent screen washing yielded an additional m1, measuring 10.4 × 4.2 mm, from the type locality of *P. alexejewi*. As commented by one of us (Qiu) in Fahlbusch et al. (1983), the new m1 was comparable to *T. minutus* in its bicuspid entoconid on m1, but was referred to *Promephitis* following the decision by Teilhard de Chardin.

Schlosser's original dentary fragment of *Promephitis alexejewi* appears to have a crest-like entoconid on m1. However, this

tooth is heavily worn and does not permit a definite assessment of its morphology. The associated p4, on the other hand, was reported to be 3.8 mm long by 2.0 mm wide (Schlosser, 1924:12). This width is far too narrow for a late form of *Promephitis* and we suspect an error in Schlosser's measurements (his illustration of this tooth, pl. 1, fig. 32, also suggests a greater width than is indicated by his measurement).

Even allowing for error and imprecision, *P. alexejewi* still stands out among Chinese *Promephitis* in its relatively long P4 (Table 2), which is opposite to the general trend in the genus toward shortening of the upper carnassial. In addition, the m1 is substantially longer than those of *P. hootoni*. But the M1 is relatively small and falls within the range of *P. hootoni* (Table 2). Therefore, we cannot reject the possibility that isolated teeth from Ertemte may belong to more than one taxon or that *T. minutus*, despite our present synonym (following Teilhard de Chardin), may prove to be distinct from *P. alexejewi* after all. Given these peculiarities and uncertainties and also the fact that Ertemte is younger in age, we chose to leave *P. alexejewi* as a distinct species. If these unusual proportions reported by Schlosser (1924) prove to be true in the future, they are likely autapomorphies for the Ertemte form.

Promephitis brevisrostris from Bazaletli of the Dushetsk region of Georgia (Meladze, 1967) is the only late Turolian (MN 13) species of the genus, and approximately contemporaneous with *P. alexejewi*. However, both are based on fragmentary material and the m1 is the only tooth shared in common in their topotype series. The m1 of *P. brevisrostris* is 15% smaller than that of *P. alexejewi* (9 mm vs. 10.6 mm in length). Meladze (1967:23) noted the presence of three small tubercles on the entoconid in *P. brevisrostris*, a feature also seen in *P. alexejewi* (Fahlbusch et al., 1983) and in Pliocene species such as *P. maxima*. A shortened rostrum and loss of one lower incisor in *P. brevisrostris* are further indications of a more derived position compared to *P. maeotica* (Meladze, 1967). On the other hand, presence of a p2 and small size in *P. brevisrostris* seem to indicate a more primitive position compared to *P. maxima* and the other Chinese Pliocene species. *Promephitis brevisrostris* is thus in the same grade of evolution as *P. alexejewi*. Whether or not they are conspecific remains to be seen when better material becomes available for both species.

PHYLOGENETIC AND BIOGEOGRAPHIC COMMENTS

There is broad consensus from various molecular evidence that mephitids occupy a basal position in the arctoids but outside the Mustelidae (Vrana et al., 1994; Ledje and Arnason, 1996b, a; Drago and Honeycutt, 1997; Flynn et al., 2000), in contrast to its traditional placement within the Mustelidae, which is recently forcefully argued by Wolsan (1999) on morphological ground. Fossil records of primitive mephitids in Europe (e.g., Petter, 1967; Schmidt-Kittler, 1981; Schmidt-Kittler, 1984; Ginsburg, 1999) and North America (e.g., Hall, 1930; Dunkle, 1938; Hibbard, 1950; Hibbard, 1952; Bjork, 1970; Baskin, 1998) are often too late or too fragmentary to shed much light in the early history. It is beyond the scope of this paper to explore broader phylogenetic and geographic relationships. The following comments are restricted to the Chinese *Promephitis* from the late Miocene, and Pliocene taxa will be treated in a separate paper.

With the two new species and a large sample of a third described herein, it is clear that China has a similar species diversity of *Promephitis* to that of Europe in the late Miocene. Known species and undescribed forms from the Pliocene of China indicate a level of specialization not seen in Europe. These rich records in China permit a much better assessment of phylogenetic relationships within *Promephitis* than was possible with the European forms alone.

He and Huang (1991) described a large species, *P. maxima*, from a limestone fissure in Daheishan (Big Black Mountain) in

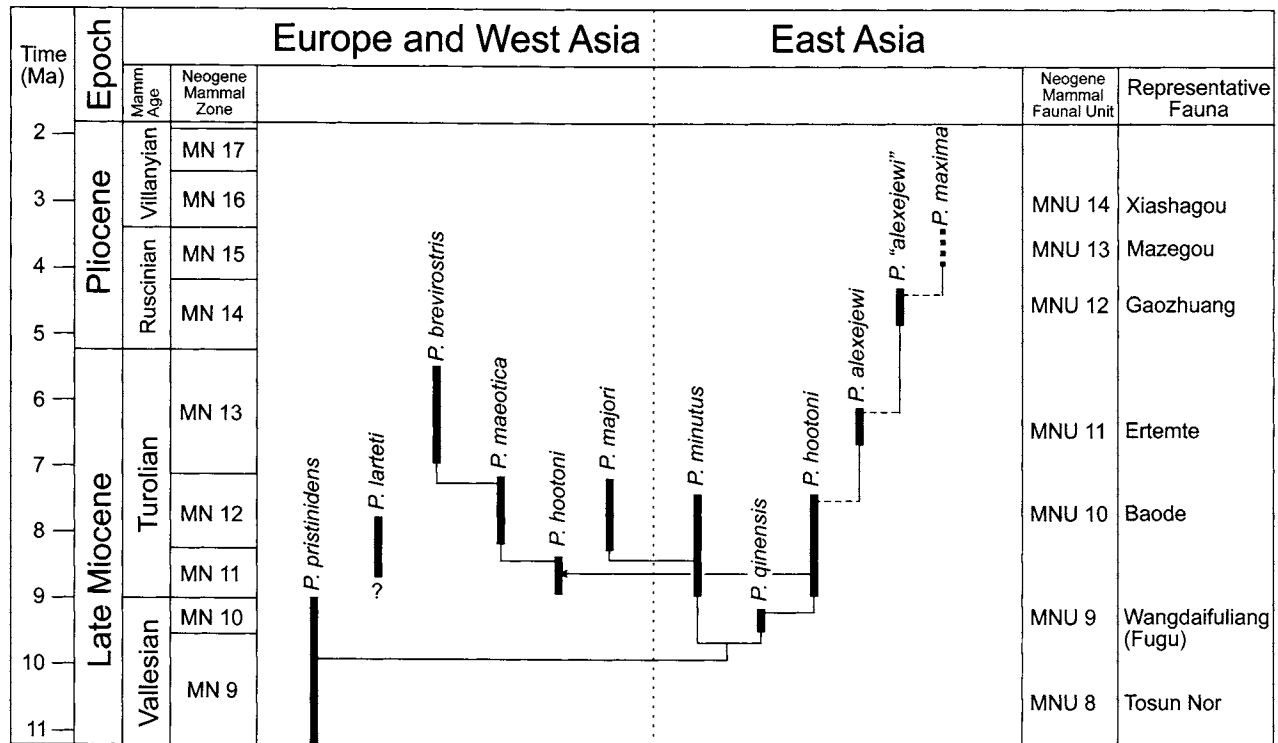


FIGURE 3. Chronological ranges of Chinese and European *Promephitis*. Correlation of the Chinese Neogene Mammal Faunal Units (MNU) with the European Neogene Mammal Zones is based on Qiu and Qiu (1995) and Qiu et al. (1999). *P. "alexejewi"* represents referred materials from the Yushe Basin in the Pliocene by Teilhard de Chardin (1945).

Tongshan County of Jiangsu Province (holotype XM 001, skull and lower jaw with I2-M1 and p3-m2). Despite its excellent preservation, the type and only specimen of *P. maxima* has no associated fauna to indicate its geologic age. However, its large size and advanced morphology suggest a younger age than other known species. Teilhard de Chardin (1945:figs. 19-20) also figured a maxillary fragment with P4-M1 (THP 25638) and a dentary fragment with p4-m1 from the Pliocene of the Yushe Basin. He referred them to "*P. cf. alexejewi*," even though the Yushe individuals are much larger than that from Inner Mongolia (additional unreported material from Yushe clearly indicates a distinct species).

As afforded by a spectrum of Chinese species in the late Miocene through Pliocene, from the small *P. parvus* to the large *P. maxima*, several cranial and dental trends are readily recognizable. From older to younger taxa, character transformations are mainly along the direction of progressive doming of the forehead, reduction or loss of the postorbital process, increasing epitympanic space by lateral expansion of mastoid area and flattening of the skull, elongation of the external auditory meatus, reduction or loss of anterior-most premolars, widening of posterior premolars, widening of upper carnassial, enlargement of M1 parastyle, and reduction of the anterior segment of internal cingulum.

With the above phylogenetic comments, it is possible to make additional inferences on the biogeographic relationships of Eurasian *Promephitis* (Fig. 3). *Promephitis pristinidens* represents the earliest and most primitive species known so far and presumably gave rise to the rest of the species of the genus, although such a relationship is far from certain. *Promephitis parvus* is the first unambiguous *Promephitis* that is primitive enough to give rise to either *P. qinensis* or *P. majori*, or possibly both. An earlier age for the Wangdaifuliang fauna in Fugu implies that *P. parvus* must have had an origination at least as early as that of *P. qinensis*. *P. qinensis* possesses just the right combination of charac-

ters to be ancestral to *P. hootoni*. The age relationship between Fugu and Baode further indicates that *P. qinensis* and *P. hootoni* may have been a chronospecies pair. The Turkish occurrence of *P. hootoni* is likely the result of westward expansion of its range. The widespread occurrence of closely related species suggests that late Miocene *Promephitis* was adapted to an open environment in the middle latitudes of Eurasia (Schmidt-Kittler, 1984: 718).

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APPENDIX

Referred Specimens of *Promephitis parvus*, sp. nov.—From Hezheng area in Guanghe, Hezheng, and Dongxiang counties, Gansu Province: HM V0430, nearly complete skull with complete upper dentition, from loc. LX200029, Huaigou, Guanfang, Guanghe County; HM V0420, partial skull with left I3–M1 and right I2–P4 (broken) and articulated left ramus with left c–m2 and isolated right m1, from loc. LX200048, Shalugou, Maijiexiang, Guanghe County; HM V0412, nearly complete skull with left I2–3 (both broken), C–M1, right I2–M1 and articulated right ramus with left c–m2, from loc. LX200025, Shanjiawan, Sanhe, Hezheng County; IVPP V13307, complete skull with complete upper dentition, partial right ramus with complete lower dentition, from loc. LX200027, Shanzhuang, Maijiexiang, Guanghe County; IVPP V13308, complete skull with I1, I2–C alveoli, P2–M1, from loc. LX200030, Songshugou, Guanfang, Guanghe County; IVPP V13309, left ramus with c root, p2 alveolus, p3–m2, from loc. LX200047, Qiaojia, Maijiexiang, Guanghe County; HM V0415, partial skull with left C alveolus, P2, P3 alveolus, P4 (broken), M1, right C alveolus, P2–M1, from loc. LX200012, Zhonggou, Xinzhuang, Hezheng County; HM V0418, partial skull with left I1–3, C–P3 alveoli, P4–M1 (both broken), right I1–C, P3–4, from loc.

LX200007, Gucheng, Alimatu, Guanghe County; HM V0421, rostral part of skull with left I1–M1 and right C–M1, and articulated mandible with left c–m1 (all roots) and right i3–m2, from loc. LX200037, Panyang, Guantangou, Hezheng County; HM V0419, nearly complete skull and mandible with complete upper and lower dentition, from loc. LX200009, Shuanggongbei, Nalesi, Dongxiang County; HM V0422, rostral part of skull with left I1–P3, P4–M1 (both broken), right I1–M1, and articulated mandible (lower teeth not prepared), from loc. LX200009, Shuanggongbei, Nalesi, Dongxiang County; HM V0416, partial palate with left I1–3, M1 (broken), right I1–3, isolated P2, M1 fragment, and articulated nearly complete mandible with complete left and right lower dentition, from loc. LX200008, Houshan, Alimatu, Guanghe County; and HM V0431, partial skull with most teeth broken, from loc. LX200011, Dashengou, Xinzhuang, Hezheng County.

From Baode area, Baode County, Shanxi Province: F:AM 50630, partial skull with left P3–M1, Yang Mu Kou; F:AM 50631, crushed skull with left P3–M1 and right P4–M1, from Chen Chia Mao Kou; and F:AM 50637, rostral part of skull with right I1–P3 and left I1–M1, from Du Kou, Baode (?) County.

From Wuxiang area, Wuxiang County, Shanxi Province: F:AM 50636, nearly complete skull with left P4–M1 and right P3–M1, from Ching Kou.

Referred Specimens of *Promephitis hootoni*—From Hezheng area in Hezheng and Dongxiang counties, Gansu Province: HM V0429, complete skull with left I1–P3 alveoli, and right I1 broken, I2–3, C broken, P2–3 alveoli, P4–M1, from loc. LX200030, Songshugou, Guanfang, Guanghe County; HM V0411, complete skull with left I1–2, I3–C alveoli, P2–M1, and right I1, I2–C alveoli, P3–M1 (P4 and M1 both broken), from loc. LX200037, Panyang, Guantangou, Hezheng County; IVPP V13310, complete skull with complete upper dentition, from loc. LX200025, Shanjiawan, Sanhe, Hezheng County; HM V0417, complete skull with complete upper dentition (both canines are broken), from loc. LX200004, Yangjiashan, Sanhe, Hezheng County; HM V0428, almost complete skull with left I1–3 alveoli, C broken, P3–M1 and right I1–C alveoli, P3–M1, from loc. LX200034, Gaojiashan, Guantangou, Hezheng County; HM V0423, partial skull and articulated mandible with left cheek teeth all broken, right P4–M1, left p2–m2 and right p2–m2, from loc. LX200009, Shuanggongbei, Nalesi, Dongxiang County; HM V0413, nearly complete skull and articulated mandible with all upper teeth badly broken, broken right c–m2, associated partial vertebral column (thoracic and lumbar), from loc. LX200023, Hetuo, Diaotan, Hezheng County; HM V0424, complete skull and lower jaws with complete upper and lower dentitions, from loc. LX200047, Qiaojia, Maijiaxiang, Guanghe

County; HM V0425, complete skull and articulated mandible with complete upper and lower dentition, and articulated atlas and axis, from loc. LX200047, Qiaojia, Maijiaxiang, Guanghe County; HM V0426, nearly complete skull and articulated mandible with left C–M1, broken right C–M1, lower cheek teeth not fully exposed, from loc. LX200034, Gaojiashan, Guantangou, Hezheng County; and HM V0427, complete skull and articulated mandible with complete upper and lower dentition, from loc. LX200210/11, Citan, Guanfang, Guanghe County.

From Wuxiang area, Wuxiang County, Shanxi Province: F:AM 50642, partial skull with broken I1–M1, from Ching Kou.

From Fugu region, Fugu County, northern Shaanxi Province: F:AM 50640, nearly complete skull with all incisors, right P3–M1 and broken left P4–M1.

From Baode region, Baode County, northern Shanxi Province: F:AM 22329, partial skull with most upper teeth except canines, from Liao Wang Kou; F:AM 50634, partial skull and mandible with nearly complete dentitions (mostly broken), from Ma Chia Liang Kou; F:AM 50635, crushed skull and mandible with broken cheek teeth, from Ma Chia Liang Kou; F:AM 50644, partial skull and mandible with complete upper and lower dentitions, from Du Kou; F:AM 50645, skull and mandible with nearly complete upper and lower dentitions, from Ma Chi Liang Kou; F:AM 50650, broken skull and mandible with complete upper and lower dentitions, from Lao Yeh Miao Kou; F:AM 50651, complete skull and left horizontal ramal fragment with nearly complete upper dentition and c–m1 (broken), from Chen Chia Mao Kou; F:AM 50652, rostral part of skull with left P3–M1 and right C–M1, from Chou Feng Ta; F:AM 50653, rostral part of skull with left C–M1 and right I1–M1, from Liao Wang Kou; F:AM 50656, partial skull and mandible with nearly complete right upper and lower dentitions and broken left cheek teeth, from Ma Chia Liang Kou; F:AM 50658, crushed skull and mandible with nearly complete upper and lower dentitions, from Chen Chia Mao Kou; and F:AM 50659, partial skull and mandible with broken left cheek teeth and complete right cheek teeth, from Chi Chia Mao Kou.

From Shou Yang region, central Shanxi Province: F:AM 50641, partial skull with complete left and right dentition, from Nan Ho, 3 miles west of Pai Dao Tsun; F:AM 50648, partial skull and mandible with right I1–P3 and left I1–M1, left i1–m2 and right i1–p4, from 2 miles west of Chang Chia Chuang; F:AM 50649, left dentary with i3–m2, from Nan Ho, near Pai Tao Tsun; F:AM 50655, partial skull with right I1–P3 and left I1–M1, from Hsiao Kou Shan; and F:AM 50657, right dentary with i2–m2, from Hsiao Kou Shan.