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生物古地理、分子分异时间及化石纪录：古中华貂在内蒙古阿巴嘎旗晚中新世宝格达乌拉组的新材料[1)]

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摘要：北美现生的潘氏貂 *Martes pennanti*（荷兰殖民区俗名 fisher，北美印地安土著俗名 pekan）传统被归入貂属（*Martes*）。20世纪70年代初 Elaine Anderson 首先认识到北美 fisher 的祖先可以追溯到中国山西保德晚中新世的古中华貂 *M. palaeosinensis*。它们的共同特征是上裂齿唇侧具有一个孤立的小齿根。因此在众多的化石和现生貂中，这些具有多一个小齿根的种类可以归入它们自己的一个分支，并重新启用已建立的 *Pekania* 属来区别于其他种类。近年来新兴的分子系统研究也趋于把北美的 fisher 与中、南美的 *Eira* 及北半球的狼獾（*Gulo*）并列，甚至指示它可能是狼獾的姊妹群。因此把 fisher 独立归入 *Pekania* 属中可能是未来的方向。2009年我们在内蒙古阿巴嘎旗宝格达乌拉组的晚中新世地层中发现了一个古中华貂的上颌。这是该种在内蒙古的首次发现，借此机会对目前的分子系统关系、分异年代及化石记录进行综合探讨。虽然保德和宝格达乌拉的古中华貂在时代上与分子钟估算的5～8 Ma 比较一致，狼獾的化石记录却远比古中华貂的老（可以追到11 Ma 左右）。如果狼獾确实是 fisher 的姊妹群或与它并系的话，那么 fisher 的分异时间也可能更早。

关键词：内蒙古，中新世保德期，宝格达乌拉组，古中华貂，狼獾，动物地理，分子系统关系，分子钟，分异时间

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ZOOGEOGRAPHY, MOLECULAR DIVERGENCE, AND THE FOSSIL RECORD—THE CASE OF AN EXTINCT FISHER, *PEKANIA PALAEOSINENSIS* (MUSTELIDAE, MAMMALIA), FROM THE LATE MIOCENE BAOGEDA ULA FORMATION, NEI MONGOL

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Abstract Elaine Anderson first established in the early 1970s a close relationship between the Late Miocene Chinese *Martes palaeosinensis* and living North American fisher *M. pennanti*, based on their shared presence of an external rootlet on the upper carnassial. Such a recognition paved the way for their elevated status as a distinct genus of their own, *Pekania*, an implicit relationship increasingly corroborated by molecular phylogenetics, which tend to show that the living fisher is either a sister to the northern Holarctic wolverine (*Gulo*) or a stem group bracketed between Central and South American tayra (*Eira*) and a *Gulo-Martes* clade. We describe an upper jaw of *Pekania palaeosinensis* from the late Miocene (Baodean) Baogeda Ula Formation of Nei Mongol. We take this opportunity to review the molecular relationships, divergence time, and the fossil record of the *Pekania* clade. Although the Chinese records of the fishers are in close agreement with divergence time estimates of 5 – 8 Ma for the *Pekania* clade based on molecular clock estimates, a deep fossil record for the wolverines, on the other hand, suggests a much more ancient divergence time and by extension, for the fishers as well.

Key words Nei Mongol, China; Baodean, Miocene; Baogeda Ula Formation; *Pekania*, *Martes*, *Gulo*, zoogeography, molecular phylogeny, divergence time

1 Introduction

In his monographic treatment of Chinese late Tertiary carnivorans, Otto Zdansky (1924) described a fossil mustelid, *Mustela palaeosinensis*, based on abundant material from the "dragon bone" site in Baode County, Shanxi Province, then newly acquired by the Lagrelius Collections in the University of Uppsala, Sweden. Although complete skulls and lower jaws were available, making this species one of the best represented small carnivorans in his sample, Zdansky did not make comparisons with New World forms. Subsequently the generic taxonomy of this species has gradually settled to the wide-ranging genus *Martes*. Nearly half a century later, Elaine Anderson (1970) gained the key insight that *Martes palaeosinensis* was phylogenetically related to the living North American fisher *Martes pennanti*, based on her observation that, in addition to being of large size, they share an extra rootlet on the fourth upper premolar, a character that is absent in all other living species of *Martes* but which is present in the North American Pleistocene *M. diluviana*. Anderson thus placed all species sharing this extra P4 rootlet into the subgenus *Pekania*, and concluded that the ancestry of this lineage should be sought in the late Cenozoic of Asia.

In 2009, our excavations at a quarry in the Baogeda Ula Formation, a late Miocene site in Nei Mongol (Inner Mongolia) recovered a partial maxillary of *Pekania palaeosinensis*. This is the first time this species has been found in Nei Mongol. Although in itself this new record does not add much to the morphology of a relatively well known species, recent convergence of morphological studies, new fossil records, and molecular phylogeny is on the verge of shedding much light on the overall pattern of divergence time and zoogeography of *Pekania*. In particular, explosive developments in DNA sequencing in recent years have advanced to the point that the fisher is now recognized to fall outside of the main *Martes* clade, and is either related to the wolverine(*Gulo*) or being in a stem position paralleling modern tayra(*Eira barbara*) from Central and South America(Hosoda et al., 2000; Koepfli et al., 2008; Stone and Cook, 2002). Such new revelations not only help to resolve long-standing questions of species-level relationships, where living taxa are well represented, but are beginning to offer an independent check on the fossil record. This report thus presents an opportunity to review existing records of Asian fossil fishers and attempts to integrate fossil occurrences, molecular phylogeny, and zoogeography. Reciprocally, our new fossil specimen may also help to constraint new studies of molecular divergence time.

Abbreviations AMNH, American Museum of Natural History, New York; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LACM(M), Department of Mammalogy, Natural History Museum of Los Angeles County, Los Angeles, California; PMU, University of Uppsala Museum of Evolution, Uppsala, Sweden.

2 Systematic paleontology

Class Mammalia Linnaeus, 1758
Order Carnivora Bowdich, 1821
Suborder Caniformia Kretzoi, 1943
Infraorder Arctoidea Flower, 1869
Superfamily Musteloidea Swainson, 1835
Family Mustelidae Fischer von Waldheim, 1817
Subfamily Martinae Burmeister, 1850
Genus *Pekania* Gray, 1865
***Pekania palaeosinensis*(Zdansky, 1924)**

Mustela palaeosinensis Zdansky, 1924:33, pl. VI, figs. 5-17, pl. VII, figs. 1-6; Teilhard de Chardin and Young, 1931:53
Martes palaeosinensis(Zdansky): Teilhard de Chardin and Leroy, 1945:5; Kurtén and Anderson, 1980:147; Powell, 1981:1
Martes(*Pekania*) *palaeosinensis*(Zdansky): Anderson, 1970:15; Anderson, 1994:14-15
Martes(*Pekania*) *anderssoni* Schlosser, 1924: Anderson, 1970:19(in part); Anderson, 1994:14-15

Lectotype PMU M3793, complete skull with entire upper dentition from Loc. 111. In possession of three complete skulls, four partial skulls, plus a number of jaws, Zdansky(1924) did not designate a holotype in his original description of *Mustela palaeosinensis*. Without any explanation, Anderson(1970:19), however, simply listed Zdansky's "Ex. 1" as the holotype: "PIU M3793 Loc. 111 Ex. 1. Skull w/R and L I1-3, C-M1." It is not clear if M3793 was subsequently designated as the holotype by Zdansky in PMU museum labels. In any case, Anderson's casual listing of M3793 as the "holotype" was mistaken and does not qualify as a lectotype because she failed to explicitly indicate that she "was selecting from the type series that particular specimen to serve as the name-bearing type"(article 74.5 of the International Commission on Zoological Nomenclature, 1999:83). We rectify this situation by formally designating PMU M3793 as the lectotype from Zdansky's syntype series from the Baode localities, and by fixing the name-bearing type based on this specimen(article 74.7).

Type locality and age Loc. 111, Nanlianggou, Jijiagou(Chi-Chia-Kou), Baode County, Shanxi Province(Zdansky, 1924), Baodean, late Miocene. The rest of the syntype series for this species include localities 30, 31, and 108 from Zdansky's Baode collections(see Anderson, 1970 for a list of specimens). Recent efforts in relocating and untangling the classic

Baode localities(English translation by Jokela et al., 2005; Zdansky, 1923)have succeeded in placing some of these localities within a modern stratigraphic context(Zhang et al., in press). Specifically, loc. 31 is among the oldest localities, loc. 108 is intermediate, and loc. 30 is the youngest in the Baode strata. Therefore the local stratigraphic range of *Pekania palaeosinensis* spans the entire series of fossiliferous horizons in the Baode Formation. Magnetic study of the Baode section by Zhu et al. (2008) suggests an age range of 7.23-2.72 Ma for the red clay accumulation(Baode and Jingle formations)and 7.0-5.7 Ma for the classic fossil localities.

Referred materials from Nei Mongol IVPP V 18408, partial right premaxillary and maxillary with I1-2 alveoli, I3, C root, P1-4, from IVPP locality IM0902, approximately 6 km northeast of the village of Baogeda Ula Sumu, 25 km northwest of the town Abag Qi, Nei Mongol. The specimen was collected by a team led by one of us(ZJT)in June 18-July 1, 2009 from the middle part of the Baogeda Ula Formation, within a light-gray blocky siltstone about 38 m stratigraphically below the lower basalt layer in the area(see below).

Age of Baogeda Ula Fauna IVPP locality IM0902 (Fig. 1) is within the type section (total thickness about 70 m) of the Baogeda Ula Formation, which can be seen to disconformably overlie the middle Miocene Tunggur Formation in an exposure(Loc. 482 = Ulan Hushuyin Nur)18 km southwest of Baogeda Ula Sumu(Wang et al., 2003). The main Baogeda Ula section is capped by two locally extensive basalt layers. Various basalts in the Abag region have been dated between 14.57 to 3.85 Ma(Luo and Chen, 1990). Published sample locations of these dates, however, are not specific enough to be sure of which basalt corresponds to those that cap the vertebrate fossil localities, although we singled out a date(7.11 ± 0.48 Ma)from sample B48 of Luo and Chen (1990: table 1) to be a possible candidate (Qiu et al., 2006: fig. 2).

Twenty-six mammal taxa have been identified from the Baogeda Ula section, most of them being small mammals screen-washed from IVPP locality IM0702, about 16 m stratigraphically below IVPP locality IM0902. With the exception of a set of isolated teeth belonging to a single individual of *Hyaenictitherium hyaenoides*(Tseng and Wang, 2007), most of the mammals have not been formally described, although faunal lists from Baogeda Ula have been summarized previously (Qiu and Wang, 1999; Qiu et al., 2006). A recent update of the faunal list is presented by Qiu et al. (in press), including *Parasoriculus* sp., *Dipoides* sp., *Lophocricetus* cf. *L. gansus*, *Paralactaga* sp. A, *Paralactaga* sp. B, *Dipus* sp., *Kowalskia* sp., *Nannocricetus* sp., *Sinocricetus* sp., cf. *Sinocricetus* sp., *Microtoscoptes* sp., *Anatolomys* sp., *Rhinocerodon* sp., *Abudhabia* sp., *Hansdebruijnia perpusilla*, *Prosiphneus* sp., *Pararhizomys hipparionum*, *Alilepus* sp., *Ochotona* cf. *O. lagreli*, *Promephitis* sp., *Hyaenictitherium hyaenoides*, *Hipparion* sp., *Gazella* sp. 1, *Gazella* sp. 2, as well as several others that cannot be identified below the family level.

Constrained by contact relationships with the underlying Tunggur Formation and the overlying basalts, the mammal composition from the Baogeda Ula Fauna indicates an early Baodean age, i. e., 6-7 Ma in the late Miocene.

Description IVPP V 18408 was recovered from the southeast section(Quarry Area B4)of a 3.6 by 2.5 m quarry excavated during the 2009 field season. Bones were densely packed in a highly fossiliferous layer, which varied in thickness from 0.2 to 1.0 m in the excavated section. The fossiliferous stratum continues horizontally for tens of meters along strike, and it was estimated that the area sampled in 2009 was less than 25% of potentially fossiliferous horizon. Approximately 150 specimens were collected in 2009, including isolated jaws and semi-articulated postcranial elements of *Hipparion*, *Gazella*, other bovids and rhinos. In addition, a small pocket(under 50 cm) of fine-grained greenish mudstone within the quarry produced articulated postcranial remains of small mammals, isolated teeth, and a partial skull of *Hansdebruijnia*.

V 18408 (Fig. 2) consists of a partial right premaxillary and maxillary. Judging by the wear on the teeth, it belongs to an adult individual. At the site of a broken right canine, there

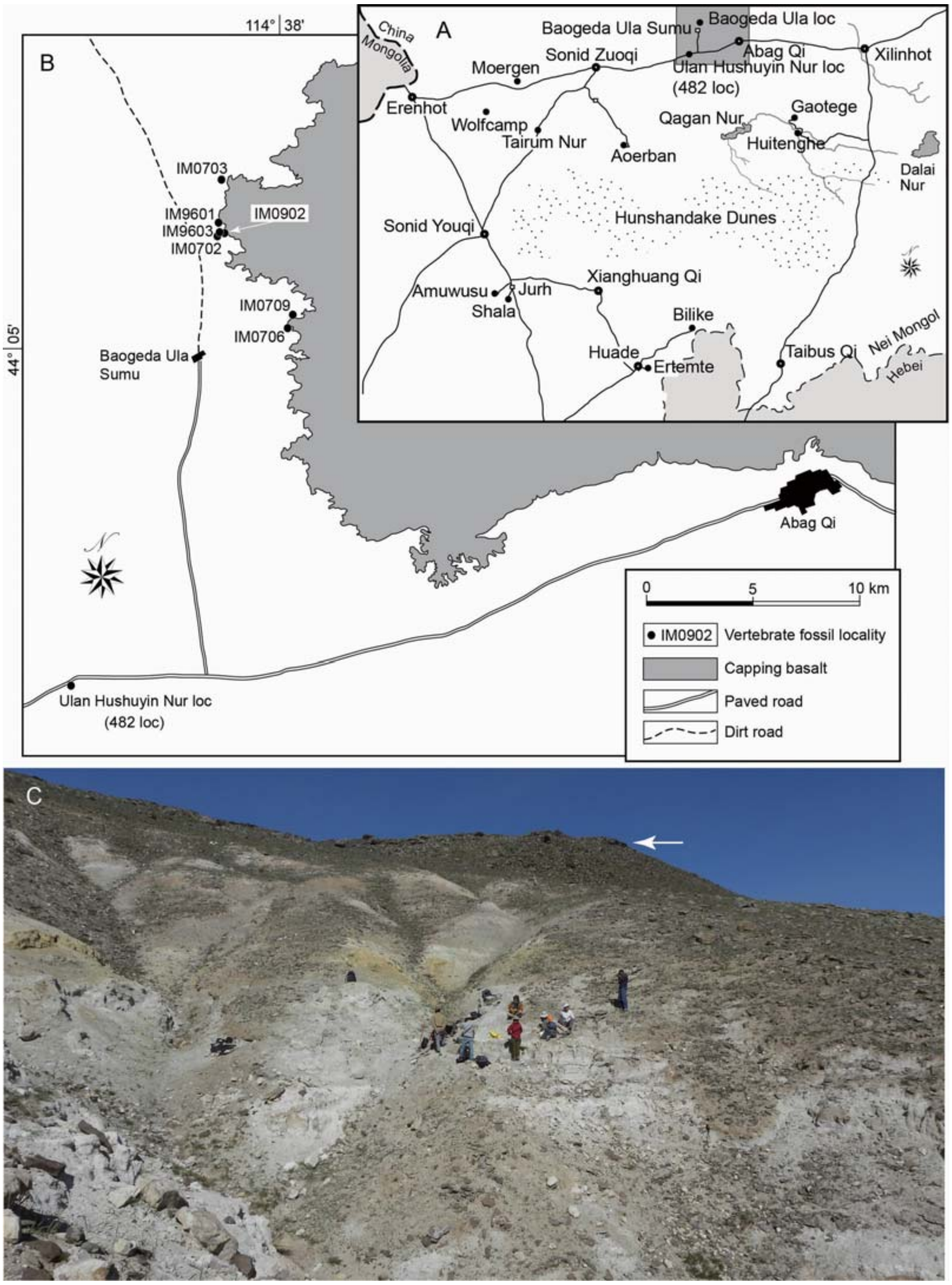

Fig. 1　Geology and location of IVPP locality IM0902

A. map of central Nei Mongol showing major vertebrate fossil localities (solid circles) to the east of the Zhangjiakou-Erenhot highway (formerly Kalgan-Eren Dabasu caravan trail); B. distribution of the Baogeda Ula Formation, as indicated by the capping basalt (shaded area) and location of IVPP locality IM0902; C. photograph of IM0902 fossil locality (looking toward the southeast; fossil quarry is surrounded by people and the capping basalt is visible as a dark rim on the top, shown by white arrow)

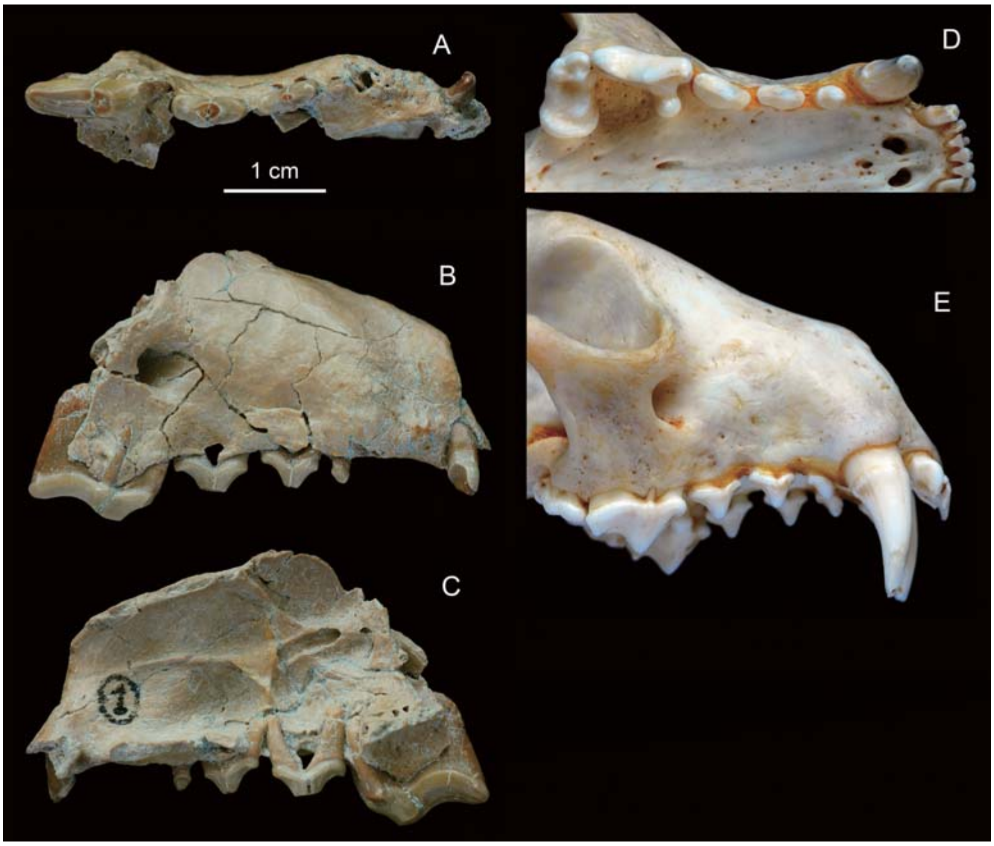

Fig. 2 *Pekania palaeosinensis*, IVPP V 18408(left), as compared to a living fisher, *Pekania pennanti*, LACM(M)92389(right, scaled to approximately the same size as the fossil specimen to the left
A. occlusal, B. lateral, and C. medial views of V 18408; D. occlusal, and E. lateral views of LACM(M)92389

are signs of injury and healing. Overgrowth of bone around the remnant of the canine suggests possible infection, probably caused by the breakage of the tooth and related trauma in the soft tissue(gum), and subsequent healing of the injury. Bone growth surrounding the canine root has practically sealed the fractured surface of the canine, leaving only an area of 1 mm ×3 mm near the posterior end of the canine still exposed. On the inner(nasal passage) side of the maxillary, there is no sign that the infection had invaded into the medial side of the upper canine root (Fig. 2C).

The maxillary is similar to that of a living fisher, and the infraorbital foramen is rounded and 3.5 mm in diameter. The top margin of the maxillary(maxillary/nasal suture) appears to be intact(it is relatively straight and bends medially in such a way that the margin should be in contact with the lateral edge of the nasal along the edge). If this is the case, V 18408 has a substantially narrower(dorsoventrally shallow) rostrum compared to the living fisher (Fig. 2E)—the rostrum in V 18408 is probably 3-4 mm shallower than its counterpart in an extant fisher specimen(LACM(M)92389).

Extensive wear on the I3 has obliterated much of its cusp morphology. Such heavy wear appears to be due to occlusion with the lower canine. A prominent wear facet on the posterolateral aspect of the I3 suggests that the lower canine was a fully functioning tooth despite the loss of the upper canine(see above). The single-rooted P1 is tiny and is a simple peg with an indistinct posterolingual cingulum. The double-rooted P2 also has a single cusp but is much elongated. A weak cingulum is present in both its anterior and posterior margins. The double-rooted P3 is essentially an enlarged P2, except for a slightly more distinct anterior and posterior ridge along the main cusp. A distinct but slender rootlet can be seen on the lateral aspect of the P4 (Fig. 2B), straddled by two larger roots above the paracone and metastyle. To the labial side, the rootlet is unconstrained by the surrounding maxillary bone and is thus nearly fully exposed, and the exposed rootlet extends almost to the tip of the root. In occlusal view, this rootlet also causes a slight bulge on the labial border of the enamel crown, as is also the case in some individuals of living fishers. The P4 has a long, slender carnassial blade, which lacks a carnassial notch and is worn down considerably. The parastyle area is heavily worn but a distinct parastyle is probably present as it does in the samples from Baode (Fig. 3). It is likely that our measurement of the P4 length (Table 1) would have been somewhat longer if the tooth (especially the parastyle part) were unworn. The protocone is similarly worn but its root indicates a strongly lingually protruded position. The anterior edge of the protocone appears to be behind that of the parastyle. The M1 is not preserved.

Fig. 3 *Pekania palaeosinensis*, PMU M3793, lectotype from Loc. 111, Baode Formation, Shanxi Province, China, in lateral (A), ventral (B), and dorsal (C) views

Taxonomic remarks Martens (genus *Martes* Frisch, 1775) are widespread in much of Eurasia and North America both in the living and fossil record. Possibly because of its unspecialized dental and cranial morphology, indications of adaptation to a broad range of environments, early fossil records of *Martes*-grade are known in much of the Miocene in Europe (Ginsburg, 1961; Helbing, 1936; Koufos, 2011; Nagel et al., 2009; Viret, 1951) and in Asia (Colbert, 1935; Mein and Ginsburg, 1997; Orlov, 1941; Schlosser, 1924; Sotnikova et al., 1997; Vangengeim et al., 1993; Zdansky, 1924), as well as in the late Miocene of North America (Baskin, 1998; Merriam, 1919; Stevens and Stevens, 2003; Whistler et al., 2009). However, much of the literature on fossil *Martes* are descriptions of local forms, usually based on fragmentary jaws and teeth, and the genus *Martes* risks being in a waste basket status. It appears that throughout its history, *Martes* remained in some kind of an evolutionary stasis, their morphology remaining generalized despite being relatively species-rich for both living and extinct forms. Such status makes it particularly difficult to sort out their true relationships, and Anderson's (1970) attempt to bring order was only partially successful. Despite the above difficulties, however, Anderson was able to recognize a discrete clade for the American fisher, *Martes pennanti*, and its fossil relatives in Asia based on their common possession of an extra rootlet on P4 (see also Anderson, 1994).

V 18408 is nearly identical to the living fisher *Pekania pennanti* both in overall size and the dimensions of individual teeth. There are two noticeable differences. The premolars in V 18408 are more slender (about the same length but narrower) than their modern counterpart. This seems to be true for *P. palaeosinensis* from the Baode area as well (Fig. 3), especially for the pre-carnassial premolars (Table 1). Although such a subtle proportional difference may not be apparent in the upper carnassials (see Anderson, 1970: fig. 9) because of the medially expanded P4 protocone (which is the point of measurement for most authors), the slender dentition is readily discernible in Anderson's (1970: fig. 10) plots of lower carnassials. Another distinction is the different level in occlusal planes between P1-3 and P4 in V 18408. Such a difference results in a markedly dorsally receded P3 relative to P4 in *P. palaeosinensis* (Fig. 2C), as compared to the modern fisher (Fig. 2E).

Table 1 Measurements of upper teeth of *Pekania palaeosinensis* (mm)

	Baogeda Ula	Baode (Zdansky, 1924)								Fugu
	IVPP V 18408	M3793	Ex. 2	Ex. 3	Ex. 4	M3798	M7	Ex. 7	Baode	AMNH
	Loc. IM0902	Loc. 111	Loc. 30	Loc. 30	Loc. 30	Loc. 31	Loc. 108	Loc. 30	Mean	50519
Length of C		5.4	6.4	6.2	5.3	4.8	3.9		5.33	5.4
Width of C		4.1	4.5	4.5	3.9	3.7	3.1		3.97	4.3
Length of P1	1.87	2.1	2.0	2.2	2.2	1.8	2.1		2.07	2.0
Width of P1	1.75	2.2	2.3	1.6	2.2	1.6	1.9		1.97	
Length of P2	5.80	5.7	5.5	5.7	5.1	4.2	4.5		5.12	
Width of P2	2.19	2.4	2.5	2.4	2.4	2.3	1.9		2.32	
Length of P3	7.25	7.2	7.3	7.0	6.8	6.0	5.6	7.7	6.80	
Width of P3	3.16	3.5	3.7	3.3	3.4	2.8	2.6	3.7	3.29	
Length of P4	12.38	11.3	11.4	11.0	10.3	9.3	9.0	11.5	10.54	11.0
Width of P4	6.29	6.7	6.5	6.4	5.9	5.7	4.6	6.7	6.07	6.0

Note: Those from Baode are from Zdansky (1924) and from Fugu from Anderson (1970). We used PMU catalogue numbers from the Baode collection by following those listed in Anderson (1970). However, four specimens from locality 30 are not listed in Anderson (1970) and they are listed in Zdansky's (1924) original labeling system (Ex. 1, 2, 3, etc.).

In addition to members of the *Pekania* clade, an extra rootlet on the carnassial is known in two other groups of musteloids. The European middle Miocene *Palaeomephitis steinheimensis*, if correctly synonymized with *Trochotherium cyamoides* by Wolsan (1999), possesses a highly peculiar upper and lower carnassial with a single domed cone and multiple rootlets along the entire rim (Fraas, 1870; Helbing, 1936; Wegner, 1913). Skunks (Mephitidae) are also known to possess an extra rootlet on the labial side of the lower carnassial, a stable character shared by all members of the mephitid clade (Harrison, 1978; Wang and Carranza-Castañeda, 2008; Wang et al., 2005). It thus appears that the P4 rootlet in *Pekania* is a highly conserved character permitting the easy recognition of the fisher clade, when this tooth is preserved.

Based on two jaw fragments and a few limb bones, Schlosser (1924) described *Martes anderssoni* from the latest Miocene Ertemte locality in Nei Mongol (see Qiu et al., in press for a summary of Nei Mongol faunas and strata). The type materials from Ertemte were originally discovered by Andersson (1923) and handed over to Schlosser for description, after which they were returned to the PMU collection. Anderson (1970), however, mistakenly listed the type of *M. anderssoni* as a complete skull and jaw (AMNH 50519) from Fugu County, Shaanxi Province, which is across the Yellow River on the north bank on the opposite side to Baode County, and has a similar depositional setting as the Baode strata (see "Type Locality and Age" above). This error was later repeated by Anderson (1994). She observed the presence of an external medial rootlet on the P4 in AMNH 50519, which is thus referable to *Pekania palaeosinensis*. Lacking an upper carnassial in the type series of *M. anderssoni* (Schlosser did, apparently reluctantly, refer one P4 to it) it remains unclear whether or not Schlosser's Inner Mongolian form is truly allied to *P. palaeosinensis*. The size of the Ertemte *Martes anderssoni* is small (m1 length = 9.5 mm) compared to the type series of *P. palaeosinensis* (11 – 13 mm), further casting doubt on their relationship (all known material of *Pekania* are consistently large in size).

In their monograph on Chinese mustelids, Teilhard de Chardin and Leroy (1945) referred two mandibles from Qingyang (K'ingyang), Gansu Province to *Martes palaeosinensis*. Although their illustrated left jaw (Teilhard de Chardin and Leroy, 1945: fig. 1) does seem to fall within the size range of *Pekania palaeosinensis*, confirmation of such assignment will have to wait when the upper carnassial becomes available, as in the case of *Martes anderssoni* above.

Teilhard de Chardin and Young (1931: 53) also mentioned a "perfectly preserved skull, with the complete lower jaw in connection" from "Locality 1 (N. of Chinglo)" (i. e., Jingle area in Shanxi Province), which they referred to *Mustela palaeosinensis*. Besides stating that the Jingle specimen is larger than the largest Baode specimens described by Zdansky, they did not provide additional details or an illustration. If this specimen turns out to really belong to *Pekania* (we did not examine this specimen), then it would probably represent the latest such record in Eurasia—the Hefeng Fauna in the Jingle Formation was magnetically dated to 2.5 – 3.0 Ma (Yue and Zhang, 1998).

Pekania (*Martes*) *palaeosinensis* have also been mentioned in the late Miocene Kalmakpay Fauna in Zaysan Basin, eastern Kazakhstan (Sotnikova et al., 1997), Pavlodar Fauna of Irtysh River, Kazakhstan (Vangengeim et al., 1993), and even as far south as the Shihuiba Fauna in Lufeng Basin, Yunnan Province, South China (Qi, 1985). Although these faunas are roughly contemporaneous with the Baode Fauna (Wang et al., in press), we have not examined these records of *P. palaeosinensis* and are unable to confirm their identity.

3 Molecular phylogeny and divergence time

Accumulation of records of *Martes* is slow, as is often the case for small mustelids, but does happen from time to time. In contrast, molecular phylogenetic studies have exploded with the increasing ease of sequencing techniques and decreasing costs. This is especially a blessing for Mustelidae, which is the most species-rich living carnivoran family, with 22 genera and 59 species, but is notorious for being a difficult group to work on with traditional morphological approaches due to convergent ecomorphologies.

With the exception of the highly hypercarnivorous *Gulo*, members of the martine clade (subfamily Martinae) are rather conservative in their morphology and with a moderately large number of living species (8 recognized in *Martes* by Wozencraft, 2005), they are difficult to sort out based on traditional morphologic characters (Anderson, 1970). Three recent molecular phylogenetic analyses sampled nearly all living species, and *Pekania* is either placed as a sister of *Gulo* (Hosoda et al., 2000; Marmi et al., 2004; Stone and Cook, 2002) or falling outside of a *Gulo-Martes* clade (Koepfli et al., 2008; Sato et al., 2012), with the Central and South American tayra (*Eira barbara*) being at the base of martine clade. Koepfli et al. have a much more extensive sampling of 22 gene segments with 12 000 bp, but bootstrap values for their proposed relationship of the fisher are still not high. Nonetheless, support for a *Gulo-Martes* clade is relatively stronger, which prevents the fisher from being moved into the *Martes* clade. Therefore, whereas molecular results may not be able to fully resolve the two likely scenarios of 1) the fisher standing alone outside a *Gulo-Martes* clade or 2) it being a sister to *Gulo*, it seems likely that the fisher clade is paraphyletic to the rest of the species of *Martes*. As a result, both molecular and morphological studies agree that a distinct generic designation for the fisher is warranted, for which *Pekania* Gray, 1865 is already in use.

Furthermore, Koepfli et al. (2008) estimated that the *Pekania* clade has a divergence time of about 5 – 8 million years ago. If the molecular phylogeny and divergent time is correct, two corollaries must be true as well. The first is that Chinese fossil records of *Pekania* must be quite close to the origin of this small clade. The second is that much of the pre-late-Miocene Eurasian records of "*Martes*" probably belong to stem groups of the Martinae clade outside the crown clade of the modern species. Presumably all such forms fall below the divergent point for *Pekania* and *Gulo* (see more discussion below), and if so, cladistically they should not be called *Martes*. The cause of such taxonomic difficulty lies in the lack of morphological differentiation in the martine clade.

4 Zoogeography

Recently, another fossil fisher was found in the Rattlesnake Formation of central Oregon (J. Samuels, pers. comm.). The Rattlesnake Formation is capped by the Rattlesnake Ash Flow Tuff that was dated to 7.01 ±0.01 Ma (Streck and Grunder, 1995), and the type Rattlesnake Formation section was magnetically correlated to Chrons C3Bn to C3Br2n, about 6.9 – 7.3 Ma (Prothero et al., 2006). The new fisher fossil itself falls within the above bounds, i.e., 7.0 – 7.3 Ma (J. Samuels, pers. comm.; see also Samuels and Zancanella, 2011). The age of the Rattlesnake Fauna within is thus roughly the same as (or slightly older than) that of the Baode Fauna. Given that the fisher clade is largely bracketed by clades with an Old World origin, it is likely that the Rattlesnake record represents an immigrant event from Asia.

The living fisher, *Pekania pennanti*, is broadly distributed in high latitude forests in the northern Unites States and southern Canada, and has a strong preference to extensive, continuous canopy (Powell, 1981). Modern distribution of wolverines, on the other hand, covers much of the northern Holarctic, spanning from western Europe to eastern Canada (Pasitschniak-Arts and Larivière, 1995).

Based on molecular phylogeny, the Central and South American tayra, *Eira barbara*, is at the base of the Martinae clade and more basal to *Pekania* (Koepfli et al., 2008). The fossil record of the *Eira* lineage is quite poor. Ray et al. (1981) considered the North American Blan can *Trigonictis* to be the most basal galictine giving rise to the living tayra. However, molecular evidence strongly excludes tayra from the galictines (Koepfli et al., 2008), and the upper carnassial of *Trigonictis* and its related genera are quite distinct from those of *Eira*. Baskin (1998: 164) also pointed out that the "upper dentition of *Eira* indicates it is more closely related to the martens." More recently, Qiu et al. (2004) described a new genus and species, *Eirictis robusta*, from the early Pleistocene Longdan site in Linxia Basin, Dongxiang County, Gansu Province. As alluded to in their generic name, this large Chinese mustelid from the Pleistocene loess deposits bears a striking resemblance to the New World tayra, particularly in its dental morphology. They further pointed out that *Sminthosinis* from the mid-Pliocene Hagerman Local Fauna of Idaho in the United States also shows strong similarity to *Eirictis*, and echoing Baskin's conclusion, Qiu et al., too, considered *Eirictis* (by implication *Eira*) to belong to a different lineage from *Trigonictis* and *Pannonictis*. Qiu et al. further included in their newly erected *Eirictis* Plio-Pleistocene specimens from Yushe, Nihewan, and Shamar formally referred to *Martes pachygnatha* (Teilhard de Chardin and Piveteau, 1930). If Qiu et al.'s assessment is correct, then the *Eira* clade may be traced to the Pliocene of both the western United States and northern Asia. The Hagerman Local Fauna is constrained by volcanic ashes between 3.48 – 3.75 Ma (Bell et al., 2004), whereas the age of the Yushe *Eirictis pachygnatha* specimen (likely to be the oldest among Asian records) is probably in the Taoyang Member of the Gaozhuang Formation, about 4.5 – 5.3 Ma (Tedford et al., 1991). Thus, the Chinese record of the *Eira* lineage seems to predate the North American relatives. Still, the presence of a ghost lineage is implied if records of the *Plesiogulo*-*Gulo* clade are correctly identified (see below).

At the more derived side of the phylogenetic bracket, the *Gulo* clade also offers some constraints for the early divergence of *Pekania*. There seems to be a general agreement that the ancestry of living wolverines should be sought in the extinct late Miocene *Plesiogulo* of Eurasia, as the two genera share broad similarities (Harrison, 1981; Kurtén, 1970; Sotnikova, 1982, 1995). Sotnikova (1995) and Qiu (2003) considered records from Kalfa in Moldova as the earliest occurrence of *Plesiogulo*. Pevzner and Vangengeim (1993) placed the *Plesiogulo*-producing Buzhor-1 site in the upper part of a magnetically normal zone correlated to the long normal chron C5n.2n (9.9 – 11.0 Ma), i.e., early Vallesian, predating the Chinese Baodean records of *Plesiogulo*. Another early record of *Plesiogulo* is from the early Vallesian locality of Atzelsdorf in Austria (Nagel, 2009). The earliest appearance of *Plesiogulo* in the New World is in the latest Hemphillian about 5-6 Ma, again, suggesting a case of immigration from the Old World (Baskin, 1998). Records for the wolverine lineage are also consistent with a Eurasian late Miocene origin of the martines.

Fig. 4 summarizes the known distribution of basal martines and estimated divergence time for four constituent clades. Fossil records indicate a northern Palearctic, or even Arctic, distribution of basal Martinae that expanded occasionally into the mid latitudes of North America. In rare occasions, such a pattern of distribution is also recorded in the Pliocene of the Canadian Arctic (Tedford and Harington, 2003). Estimates of divergence time based on molecular clock are consistent with the fossil record of *Pekania*. However, a much older record (early Vallesian, 10 – 11 Ma) of *Plesiogulo* demands that *Pekania* be equally early in divergence time. If *Plesiogulo* is truly a representative of the wolverine clade, then the assumptions of the molecular clocks need to be re-examined. Either the root/minimum age constraints (Koepfli et al., 2008) are not realistic or substantial intra-clade variations in the rate of molecular evolution exist that are not taken into consideration in the current estimates.

Even more troubling is the problem of early (pre-late-Miocene) records of *Martes*. If the molecular divergence time is a reasonable indication, then the early to middle Miocene forms referred to *Martes* probably belong to records in the stem position outside of the crown clade of Martinae. Sorting out those records will be an exclusive task of paleontology without the help of molecules.

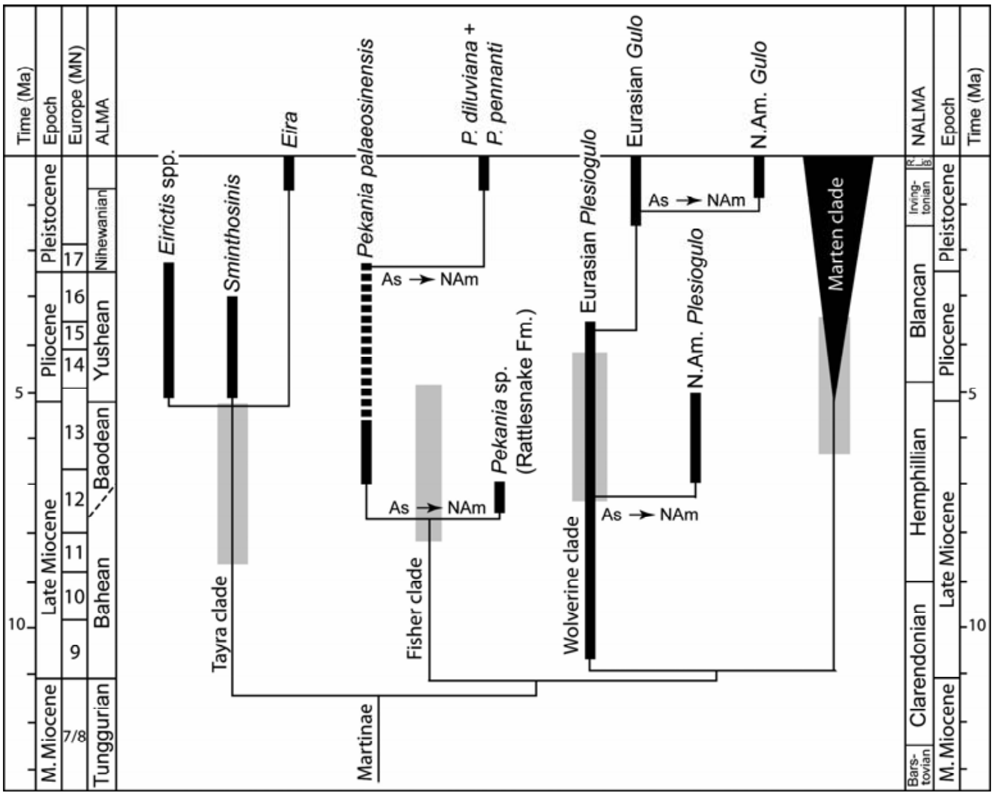

Fig. 4 Phylogeny, age range, divergence time, and zoogeography of basal Martinae
Phylogenetic relationship of basal martines is based on a Bayesian consensus tree derived from a data matrix of 22 gene segments(~12000 base pairs) by Koepfli et al. (2008: fig. 1). Approximate age ranges for relevant taxa are indicated by thick black lines and their main references are: *Eirictis*(Qiu et al., 2004), *Sminthosinis* (Baskin, 1998), *Eira*(Woodburne et al., 2006), *Pekania*(Anderson, 1970), *Plesiogulo* and *Gulo*(Harrison, 1981; Kolfschoten, 2001; Kurtén, 1970; Pasitschniak-Arts and Larivière, 1995; Sotnikova, 1982; Teilhard de Chardin and Leroy, 1945). Gray boxes are 95% brackets of highest posterior density estimates for divergence times derived from Bayesian relaxed molecular clock using a combination of 28.5 Ma root age prior and 24 Ma minimum crown age from Koepfli et al. (2008: table 2). Arrows indicate immigration events (As = Asia; NAm = North America)

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