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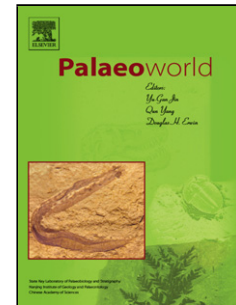Authors: Qi-Gao Jiangzuo, Jin-Yi Liu, Jan Wagner, Jin Chen

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Taxonomical revision of "*Arctonyx*" fossil remains from the Liucheng *Gigantopithecus* Cave (South China) by means of morphotype and morphometrics, and a review of Late Pliocene and Early Pleistocene *Meles* fossil records in China

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Abstract

"*Arctonyx*" fossil remains from the Liucheng *Gigantopithecus* Cave, Guangxi, are redescribed and analysed in details. Detailed tooth character differences between *Arctonyx* and *Meles* are analysed. It is shown that materials from the Liucheng *Gigantopithecus* Cave actually belong to two species of *Meles*: *Meles minor* and *Meles magnus* n. sp. At the same time, a review of Late Pliocene and Early Pleistocene *Meles* records in China is made. During Late Pliocene, *Meles* are only represented by *M. chiai* and one archaic form. During Early Pleistocene, *Meles* from northern and central part of China are represented by two nearly sympatric species *Meles chiai* and *Meles teihardi*. *Meles* from South China are represented by *M. minor* and *M. magnus* n. sp., though the distribution of the two species is still unclear. *M.*

magnus n. sp. is so far only known from the Liucheng *Gigantopithecus* Cave, whereas *M. minor* is probably also known from Longgupo, Chongqing in the central part of China besides Liucheng. Great diversity of *Meles* in Early Pleistocene in China indicates that the genus radiated earlier than previously thought. Phylogenetic analysis suggests *M. magnus* n. sp. is sister group to living *M. leucurus*, whereas *M. minor* and *M. chiai* are early branches in *Meles* evolution.

Keywords: Liucheng *Gigantopithecus* Cave; *Meles*; *Arctonyx*; Morphotype; Morphometrics; Phylogeny

1. Introduction

The classic early Early Pleistocene fossil site Liucheng *Gigantopithecus* Cave in Guangxi, southernmost China (24°40′N, 109°15′E, exact location see site 12 of Fig.12), produced numerous Carnivora fossils (Pei, 1987). The cave was found in 1957, when a team from IVPP (led by Professor Wen-Zhong Pei) surveyed the *Gigantopithecus* fossils in South China. The excavation lasted for seven years until 1963. Thirteen Carnivora species were described from in the Liucheng *Gigantopithecus* Cave, including *Cuon dubius*, *Arctonyx minor* n. sp., *Arctonyx collaris*, *Ursus* aff. *thibetanus*, *Ailuropoda microta* n. sp., *Pachycrocuta licenti* (in the original book as *Hyaena licenti*), *Panthera pardus*, *Felis* sp. 1 (large sized with possible *Panthera* or *Puma* affinity), *Felis teihardi*, *Felis* sp. 2 (small sized), *Acinonyx pleistocaenicus*, *Viverra* sp., and *Paguma larvata*. The major research work was done by Pei in 1965 but it was not published until 1987. The exact age of the Liucheng *Gigantopithecus* Cave site remains uncertain, but based on fauna analysis it is believed to be the second oldest locality in Quaternary South China, which is slightly younger than Longgupo with an age of 2.48 Ma (Han et al., 2015); therefore, the age of the Liucheng *Gigantopithecus* Cave probably lies between 2.0 and 2.48 Ma. Pei left many questions in his book about fossil carnivores due to inaccessibility of specimens for comparison at that time. The knowledge about Pleistocene carnivores has greatly enriched during last decades. However, as one of most important fossil

sites of Early Pleistocene in South China, the taxonomic status of the Liucheng *Gigantopithecus* Cave carnivores has never been reviewed. Some taxa need further study (for example, *Ursus* aff. *thibetanus*, *Panthera pardus*, *Paguma larvata*, and *Arctonyx* in this study). Therefore, a revision of Carnivora remains from the Liucheng *Gigantopithecus* Cave is very important to understand the Early Pleistocene Carnivora evolution in East Asia and Southeast Asia.

Melinae are omnivorous Carnivora with enlarged upper and lower molars, consisting of at least six genera since Late Miocene: *Arctonyx* Cuvier, *Meles* Brisson, *Arctomeles* Stach, *Ferinestrix* Bjork, *Parataxidea* Zdansky, and *Melodon* Zdansky (Wallace and Wang, 2004; Wolsan and Sotnikova, 2013). Some other taxa such as *Promeles* are variously viewed as early representatives of Melinae (Petter, 1971; Ginsburg and Morales, 2000) or non-meline mustelids (Roussiakis, 2002), since some lineages such as Galictini also show a developed hypocone of P4 and an enlarged inner lobe of M1 (Ogino and Otsuka, 2008). *Arctonyx* and *Meles* are common members in Quaternary Chinese fossil sites. *Arctonyx* is mainly recorded in South China, though it is also distributed in North China (Gao, 1987), at least since Late Pleistocene (Tong et al., 2004). *Meles*, on the contrary, has a northern distribution, but fossils are also recorded in Central China during Early Pleistocene, for example, fossils from Longgupo, Wushan, Chongqing (Huang and Zhong, 1991) and the Renzi Cave, Fanchang, Anhui (Liu and Qiu, 2009).

There are two types of badger from the Liucheng *Gigantopithecus* Cave. The smaller one was erected as a new species of *Arctonyx* by Pei (1987), *A. minor*, based mainly on extraordinarily small size of the specimen (V5026.12). A Middle or Late Pleistocene specimen (V5026.13, single M1) was also tentatively assigned to this species by Pei. The other specimens from the Liucheng *Gigantopithecus* Cave were assigned to *A. collaris* by Pei. He noticed some differences between Liucheng badgers with typical *Arctonyx* from Middle and Late Pleistocene of Guangxi (though he didn't point out what were these differences), but he thought these differences were more probably intraspecific variation. In fact, though living *Arctonyx* differs greatly from *Meles* in skull and mandible morphology (Liu, 2002; Helgen et al., 2008; Liu and Qiu,

2009), single tooth of the two genera is hard to distinguish due to the great variation of the two genera (Pocock, 1941). Some specimens are easily distinguished (e.g., strong anterior protruding of antero-lingual corner of M1 in *Meles* and strong posterior retruding of antero-lingual corner of M1 in *Arctonyx*), but there is an overlap in morphology (e.g., position of antero-lingual corner between anterior tip of tooth and apex of paracone of M1 is present in both taxa), so it is often hard to tell the genus with single tooth. So far, no study has investigated to what extent the teeth of the two genera are overlapped. The situation will evidently become much more complicated if fossil species are taken into consideration. Therefore a comprehensive study of living species is needed to help better distinguish the fossil specimens.

On the other hand, Early Pleistocene *Meles* fossils were reported from several localities. Most specimens have been assigned to *Meles chiai*. However, as pointed by Qiu et al. (2004), Teilhard de Chardin and Leroy (1945) had already noticed the most common species in Early Pleistocene in China was not *M. chiai*, but another species. However, some later authors ignored this point and assigned badgers of Early Pleistocene into *M. chiai* without discussion. Qiu et al. (2004) erected *Meles teihardi* based on several skulls and mandibles from Longdan, and they thought this species was the one that mentioned by Teilhard de Chardin and Leroy (1945). Qiu et al. (2004) didn't review all the fossil records of *Meles* from old publications. So a critical review of Early Pleistocene *Meles* fossil records is very important to understand the early evolution of *Meles* in Asia.

In this study, starting from living species, a series of morphotypes of P4, M1 and m1 are described. Redescription of Liucheng badgers is also offered with emphasis on these morphotypes. At the same time, a review of Late Pliocene and Early Pleistocene *Meles* fossil records is made. Finally, a phylogenetic analysis based on morphometric and morphotypes is done to investigate the evolution of *Meles*.

2. Material and methods

2.1. Institutional abbreviations

IVPP: Institute of Vertebrate Palaeontology and Palaeoanthropology, Chinese Academy of Sciences, Beijing, China. Specimen number with capital V, RV and M are from IVPP. Catalogues started with V or RV are fossil materials from IVPP, whereas OV are specimens of living species.

THP: Tianjin Natural History Museum, Tianjin, China.

IOZ: Institute of Zoology, Chinese Academy of Sciences, Beijing, China.

2.2. Specimens examined

IVPP: "*Arctonyx*" *minor*: V5026.12, V5026.13; "*Arctonyx collaris*" from Liucheng *Gigantopithecus* Cave, Guangxi, V5023.1-2, V5024.1-5, V5026.1-12; *Arctonyx collaris* from late Middle Pleistocene and Late Pleistocene cave sites of Guangxi, RV87005, RV87006, RV87010; *Arctonyx collaris* from Chongzuo area of Guangxi, V22675.1-3, uncataloged specimens; *Arctonyx* sp. from Longgu Cave, Jianshi, Hubei, V13412.1-2; *Meles chiai* from Locality 18 of Zhoukoudian (this place is in fact in Huiyu of Mentougou in Beijing and far from Zhoukoudian area), RV40008; *Meles chiai* from Yushe Basin, Shanxi, uncataloged specimens (Schmidt-Kittler and Qiu, in preparation); "*Meles chiai*" from Danangou, Yuxian of Hebei, V7254; *M. teihardi* from Longdan of Gansu, V13534; *Meles* cf. *leucurus* from Gongwangling of Shanxi and Locality 1 and 13 of Zhoukoudian, V5411, c/c672, c/c673A, c/c674A, c/c675A, c/c676A, c/c2176, c/c2178; *Meles* sp. from Ningyang of Shandong, V12369.1-3; *Arctomeles suillus* from Yushe Basin of Shanxi, RV45005; recent *Arctonyx albogularis* and *Meles leucurus*, OV56, OV64, OV66, OVc030, OV469, OV470, OV625, OV634, OV764, OV1254.

THP: *Meles* cf. *teihardi* from Xiashagou of Nihewan, Hebei, TNP15153.

IOZ: Recent *Arctonyx albogularis* and *Meles leucurus*.

2.3. Measurement

For each premolar, length, width and height of the tooth are measured. For the first upper molar M1, four measurements are taken: total length (maximum length taken along the axis of paracone-metacone ridge. When position of antero-lingual

corner of inner cingulum protrude anterior to or at the anterior tip of paracone, the total length would equal internal length), external length, internal length (taken from the anterior corner of inner cingulum to the posterior tip of the tooth) and width (taken from labial rim of paracone to lingual rim of antero-lingual corner of inner cingulum). For the lower first molar m1, five measurements are taken: total length, external trigonid length (taken from anterior tip to posterior edge of protoconid), internal trigonid length (taken from anterior tip to posterior edge of metaconid), trigonid width (taken from width across protoconid) and talonid width (taken from widest part of talonid). See Fig. 1 for details. Measurements of specimens are given in Appendix (Tables A1-A3). Statistical analysis of measurements is performed in SPSS 20.0 and R (R Development Core Team, 2016).

2.4. Terminology and morphotype of tooth

Terminology of tooth cusp is modified from Teilhard de Chardin and Leroy (1945) and Baryshnikov et al. (2003). See Fig. 2 for details. Given the great variation of P4, M1 and m1 of badgers, it is not easy to judge which species the specimen belongs to with only single isolated tooth. Baryshnikov et al. (2003) defined a series of morphotypes of *Meles*, but their work was concentrated on *Meles* only and is not sufficient to tell the differences between *Meles* and *Arctonyx*. Therefore, we define a new series of morphotypes of each tooth as follows and then make statistical analysis to get better knowledge of character differences between *Meles* and *Arctonyx* and different species within the two genera. Mean scores of each taxon is calculated as mean of the morphotype in each taxon. For example, there are 28 counted specimens of M1A of *Arctonyx albogularis*. 15 specimens show morphotype A1, 11 show A2 and 2 show A3, then mean score is calculated as $(15+11\times2+2\times3)/3 = 1.536$.

2.5. Morphotype description

P4 (Fig. 3.1-3.3)

A P4 Parastyle.

1. Small but distinct; 2. very weak, not distinct; 3. not developed.

B Position of middle point (note that middle point is used rather than anterior rim because in the morphotype in Fig. 3.1, it is impossible to find the accurate position of anterior rim. The same is true for antero-lingual corner of inner cingulum of M1, see below) of inner lobe (let the line of paracone-metacone in horizon).

1. Anterior to or approximately at the same position of the anterior tip of parastyle; 2. between the parastyle and apex of paracone but closer to parastyle; 3. between parastyle and apex of paracone but closer to paracone; 4. approximately at the same position of apex of paracone; 5. posterior to apex of paracone.

C Protoconule (Cusp c of Teilhard de Chardin and Leroy, 1945, fig. 18B).

1. Not developed; 2. developed.

D Protocone (Cusp b of Teilhard de Chardin and Leroy, 1945, fig. 18B).

1. Not developed; 2. developed but not subdivided; 3. developed and subdivided into two cusps.

E Hypocone (Cusp a of Teilhard de Chardin and Leroy, 1945, fig. 18B).

1. Not developed; 2. developed.

M1 (Fig. 3.4-3.6)

A Labial incision between paracone and metacone.

1. Not developed; 2. weakly developed; 3. well developed.

B Labial incision between metacone and metaconule.

1. Not developed; 2. weakly developed; 3. well developed.

C Labial incision posterior to metaconule.

1. Not developed; 2. weakly developed; 3. well developed.

D Metastyle (small cusp between metacone and metaconule).

1. Not developed; 2. developed.

E Position of antero-lingual corner of inner cingulum (let the line of paracone-metacone in horizon).

1. Anterior to anterior tip of paracone; 2. approximately at the same position of the anterior tip of paracone; 3. between anterior tip of paracone and apex of paracone; 4. approximately at the same position of apex of paracone; 5. between apex of paracone

and notch between paracone and metacone; 6. approximately at the same position or

posterior to notch between paracone and metacone.

F Accessory cusps at the margin distal to metaconule.

1. Not developed; 2. weakly developed (significantly smaller than half of metaconule);

3. well developed (about the half of metaconule).

G Ridge between distal cusp of protocone and metaconule.

1. Not developed; 2. weakly developed; 3. well developed.

H Ridge between distal cusp of protocone and hypocone.

1. Not developed; 2. weakly developed; 3. well developed.

m1 (Fig. 3.7-3.8)

A Position of anterior margin of hypoconid.

1. Anterior to apex of metaconid; 2. approximately at the same position of apex of

metaconid; 3. posterior to apex of metaconid.

B Small cusps distal to hypoconulid and entoconid 1.

1. Weakly developed; 2. well developed.

Common morphotypes of three teeth of badgers are calculated as means of value

of the type. The common morphotypes reflect the general tooth morphology of the

species. Phylogenetic analysis is performed based on the means of value of the type.

3. Systematic paleontology

Order Carnivora Bowdich, 1821

Family Mustelidae Fischer von Waldheim, 1817

Subfamily Melinae Bonaparte, 1838

Genus *Meles* Brisson, 1762

Type species: *Meles meles*, Linnaeus, 1758.

Skull and teeth diagnosis: Melinae with short snout. The posterior border of the

palate not extending to the postglenoid process. Osseous external auditory meatus not

greatly elongated. Mandible condyle approximately in the same line with lower teeth

row. Premolars higher and wider than other members of Melinae except *Parataxidea*. Parastyle of P4 present but small. M1 with distinct inner cingulum forming an antero-lingual corner. m1 metaconid not shift posteriorly. m2 generally wider than length.

Meles minor Pei, 1987

(Figs. 4A-C, 5C, 6D)

pars 1987   *Arctonyx minor* Pei – Pei, p. 16, pl. 1, fig. 3.

Holotype specimen: V5026.12 from Liucheng *Gigantopithecus* Cave is the only specimen when Pei erected the new species. See Fig. 4.

Emended diagnosis: *Meles* of small size (within the lower limit of living *Meles anakuma*). Infraorbital foreman large and located more posteriorly than other species of *Meles*. P2 is relatively reduced among Early Pleistocene *Meles* but P3 is relatively larger and narrower than other species of *Meles*. Inner lobe of the P4 not protrudes anteriorly. Protocone-hypocone complex weakly developed. Inner cingulum of M1 thin and not protrude anterior to paracone.

Stratigraphic and geographic range: early Early Pleistocene of Guangxi, and possible from Longgupo in Wushan, Chongqing (see Section 4.3. for detail).

Description:

V5026.12 is a fragment of upper jaw with P2-M1 (Fig. 4). The fragment is broken anterior to P2, so it is impossible to know whether P1 exists. The infraorbital foreman is very large. Its diameter (7.41 mm) is larger than the length of P4 (7.06 mm). The infraorbital foreman is subcircle in outline. Viewed from lateral side (Fig. 4A), the posterior tip of infraorbital foreman forms an indistinct angle and lies between the paracone and metacone of M1. The lacrimal fossa is relatively large, located dorsal to infraorbital foreman. Sphenopalatine foramen and posterior palatine foramen are located at the distal margin of M1 (Fig. 4C). Sphenopalatine foramen is slightly larger than posterior palatine foramen and located at a higher position.

No diastema exists between premolars. P2 and P3 are simply built and narrow. No cingulum cusp could be observed. P4 has an extremely weak parastyle. Inner cusps of protocone-hypocone complex are very weak without distinct cusp. The middle point of inner lobe is posterior to parastyle but anterior to apex of paracone (P4: B3, Figs. 4, 5C). In M1 the labial incision between paracone and metacone is not strong (M1: A2). No metastyle exists (M1: D1). There are no incisions between metacone and metaconule and posterior to metaconule (M1: B1C1). The inner cingulum is relatively thin. The position of anterior margin of inner cingulum is around at the apex of paracone (M1: E3). The protocone gives two distal ridges, one towards metaconule and one towards hypocone, both of which are not very strong (M1: G2H2, Figs. 4, 6D).

V5026.13 is an isolate M1 from Late Pleistocene, and it was also tentatively referred to *Arctonyx minor* by Pei. However it is evidently different from V5026.12. The overall size (total length 12.28 mm) is larger than that of V5026.12 (10.62 mm), but much smaller than other contemporary materials of *Arctonyx* in Guangxi (14.30-20.52 mm). Its morphology is typical of *Arctonyx* with posterior position of anterior margin of inner cingulum (M1: E5) and strong ridge connecting protocone and hypocone (M1: H3). This specimen is similar in size to living *Arctonyx albogularis* and probably belongs to this species, but with only one tooth, it is better to assign the specimen to *Arctonyx* sp. temporarily.

Meles magnus n. sp.
(Figs. 4D, 5A-B, 6A-C, 8A-C)

pars 1987   *Arctonyx collaris* Cuvier – Pei, p. 17, pl. 1, figs. 5, 8.

Etymology: Latin *magnus* for large, in allusion to the large tooth size (and presumed large body size) of the species.

Holotype: V5025.2, a maxilla fragment with P4 and M1 (Figs. 4D, 5B, 6A).

Paratype: V5023.1, mandible fragments with m1 (Fig. 8A).

Other included specimens: V5023.2, mandible fragment with m1; V5024.1-5, isolated m1; V5025.1, maxilla fragments with P4 and M1; V5026.1-11, isolated M1. All materials are from Liucheng *Gigantopithecus* Cave.

Diagnosis: Largest known species of *Meles*. Inner lobe of the P4 not protrudes anteriorly as in *M. chiai*. Protoconule of P4 not developed. M1 wider than living species of the genus but similar to other Early Pleistocene *Meles*. Inner cingulum of M1 not protrudes anteriorly as in *M. thorali* and *M. chiai*.

Stratigraphic and geographic range: So far only known from early Early Pleistocene of Guangxi.

Description:

The maxillae or mandibles are so fragmentary that they present nothing valuable for diagnosis, so only teeth are described here.

P4

There are only two P4 preserved in maxilla fragments. V5025.1 (Fig. 5A) is very large in size. The parastyle and protoconule are not developed, while protocone is well developed (P4: A1C1D2). Hypocone part is worn. The middle point of the inner lobe lies between the anterior rim of teeth and apex of paracone but closer to paracone (P4: B3). V5025.2 (Fig. 5B) is slightly smaller. The anterior tip of the cusp is broken. There is distinct incision at anterior rim of inner lobe, though not so distinct as in *M. chiai*. Protoconule is not developed, while protocone is well developed and is subdivided into two small cusps (P4: C1D3). Hypocone is well developed. The middle point of the inner lobe lies between the anterior rim of tooth and apex of paracone but closer to parastyle (P4: B2).

M1

V5025.1 is heavily worn. Labial incision between paracone and metacone, between metacone and metaconule and posterior to metaconule are all weakly developed (M1: A1B1C1). The anterior margin of inner cingulum lies between anterior tip of paracone and apex of paracone (M1: E3). In V5025.2 (Fig. 6A), labial incision between paracone and metacone is deep (M1: A3), but incision between

metacone and metaconule and posterior to metaconule are not present (M1: B1C1). The inner cingulum is relatively thin. The anterior margin of inner cingulum also lies between anterior tip of paracone and apex of paracone (M1: E3). There is only one small cusp distal to metaconule (M1: F2). The protocone is subdivided into three cusps, the anterior one is smallest and inclines antero-labially, while the posterior two are in line and subequal in size. The protocone gives only one strong distal ridge towards hypocone (M1: G1H3). V5026.10 (Fig. 6C) is similar to V5025.2, but inner cingulum is stronger, the anterior margin of inner cingulum lies at anterior tip of paracone (M1: E2). A small ridge is present between metacone and metaconule. The protocone is subdivided into four cusps (a small cusp develops between two posterior cusps). The protocone gives two distal ridges, one towards metaconule and one toward hypocone, both of which are not very strong (M1: G2H2). V5026.5 (Fig. 6B) is relatively wide and short. Small cusps at the posterior margin are worn. The small ridge linking the metacone and metaconule is well developed. The other teeth are generally similar to these teeth.

m1

V5023.1 (Fig. 8A) is mandible fragment with m1 and posterior root of p4. Paraconid of m1 is slightly lower than metaconid. Notch between paraconid and protoconid is present but not distinct. The talonid is wide. The anterior margin of hypoconid lies approximately at the same position of apex of metaconid (m1: A2). There are two entoconids and hypoconids (including hypoconulid), in both cases the anterior one is larger than posterior one (general situation in *Meles*). The posterior margin of the tooth is subdivided into two cusps, one large cusp in the center and one smaller cusp distal to hypoconid (m1: B2). In V5024.2 (Fig. 8B) the anterior margin of hypoconid lies posterior to apex of metaconid. In the posterior margin of the tooth, only a very small cusp is developed in postero-lingual corner. In V5024.3 (Fig. 8C) the notch between paraconid and protoconid is distinct. The anterior margin of hypoconid also lies posterior to apex of metaconid (m1: A3). The posterior margin of the tooth is subdivided into three cusps, the central one is smallest and the other two

are subequal in size (m1: B2).

4. Comparisons and discussion

4.1. Morphotype and morphometric difference between *Arctonyx* and *Meles*

Means of score of different morphotypes are listed in Table 1 and metric values of teeth are given in Appendix (Tables A1-A3). *Arctonyx* differs greatly from *Meles* in following characters:

Premolars. The premolars are much lower than *Meles*. Most premolars are also distinctly narrower than *Meles*. Besides above morphotype differences, there is often larger diastema between anterior premolars.

P4. Parastyle is often absent. Middle point of inner lobe is located more posteriorly.

M1. Relatively narrow. Labial incision located between paracone and metacone is often weak or absent while labial incision located posterior to metaconule is often distinct; antero-lingual corner of inner cingulum located more posteriorly. Weak ridge between protocone and metaconule and strong ridge between protocone and hypocone are present.

m1. Relatively narrower. In addition, the notch between paraconid and protoconid in *Arctonyx* is often absent, while it is always present in *Meles* (Liu et al., 2006). We didn't count the development of notch because it is easily worn in *Arctonyx* and hard to tell the status in most cases.

4.2. *Meles* affinity of badgers from the Liucheng *Gigantopithecus* Cave

The two species of badgers from the Liucheng *Gigantopithecus* Cave should be assigned to *Meles*, not *Arctonyx*. First, the skull fragment of the small badger (V5026.12) preserves many important characters. The infraorbital foramen is very large with an oval outline, similar to *Arctonyx*, but the posterior tip of infraorbital foramen forms an angle from lateral view, which can be seen in living *Meles leucurus* in nearly half of specimens according to our observation, although morphotype where

infraorbital foramen without angle is also frequently seen in *M. leucurus* (Qiu et al., 2004) and *M. meles* (Miller, 1912). In *A. albogularis* we examined, the posterior tip of infraorbital foramen is always without any angle (see Fig. 10). Although the position of infraorbital foramen (posterior border) is rather variable, *Arctonyx* generally has more posterior located infraorbital foramen than *Meles*. In V5026.12 the position of infraorbital foramen lies between paracone and metacone of M1, which is in fact seen in both *Arctonyx* and *Meles*. Sphenopalatine foramen and posterior palatine foramen of V5026.12 are located at the distal margin of M1, which is also characteristic of *Meles*. In *Arctonyx*, these two foramina are always posterior to the distal margin of M1. So the maxilla fragment of small badger shows more similarity to *Meles* than to *Arctonyx*. Second, teeth of these two species from Liucheng *Gigantopithecus* Cave are also more similar to *Meles*. P2, P3 and P4 of small badger are distinctly higher than *Arctonyx* but similar to *Meles*. P4 and M1 of small badger are slightly worn, but middle point of inner lobe of P4 and antero-lingual corner of inner cingulum of M1 (P4B = 3.000, M1E = 3.000) are similar to living *M. leucurus* (P4B = 3.146, M1E = 2.319). In *Arctonyx*, these two points generally lie more posteriorly (P4B = 4.390, M1E = 4.786). The same differences can be seen between the large badger (mean P4B = 2.500, M1E = 2.692) and *Arctonyx*. In all m1, paraconid is not reduced, and the notch between paraconid and protoconid is well developed, similar to *Meles*. In *Arctonyx*, paraconid is often rather small, and the notch between paraconid and protoconid may be lost. It may be noted that the large badger does exhibit some intermedium characters, such as more posterior position of anterior margin of inner cingulum compared with other Early Pleistocene *Meles* and occasional developed of small cusp between metacone and metaconule. Since early records of *Arctonyx* are nearly unknown, it can't be ruled out that these characters represent the primitive states seen in living *Arctonyx*. However, *Arctomeles*, the possible ancestor *Arctonyx* (Stach, 1951; Petter, 1971; Wallace and Wang, 2004) is already specialised in tooth morphology with posterior position of anterior margin of inner cingulum of M1 and posterior shift of metaconid of m1 and low anterior premolars similar to *Arctonyx*. This indicates characters of the Liucheng *Gigantopithecus* Cave badgers are not

plesiomorphic characters for *Arctonyx* lineage but more probably belong to autapomorphies, so the intermedium characters could not be used as evidence supporting their affinity to *Arctonyx*. Third, the principle component analysis of M1 and m1 also shows that the Liucheng badgers are closer to other *Meles* rather than *Arctonyx* (Fig. 7; Appendix: Fig. A1 and Table A4). Cluster analyses of mean morphotype also group badgers from the Liucheng *Gigantopithecus* Cave with other *Meles* rather than with *Arctonyx* (see Fig. 9). Therefore, the two badgers are much more similar to *Meles* rather than *Arctonyx* and should be assigned to *Meles*.

4.3. Review of *Meles* fossils from China during Late Pliocene and Early Pleistocene and morphotype and morphometric analysis of *Meles*

Besides badgers from the Liucheng *Gigantopithecus* Cave, two badgers of Late Pliocene and Early Pleistocene have been named in China. *M. chiai* was erected by Teilhard de Chardin (1940) based on fossils from Locality 18 of Zhoukoudian and later was reported in the Yushe Basin (Teilhard de Chardin and Leroy, 1945). It was also reported from Danangou, Yuxian of Hebei (Li, 1984); Longgupo, Wushan of Chongqing (Huang and Zhong, 1991); Wangbuding, Dege of Sichuan (Zong et al., 1996) and the Renzi Cave, Fanchang of Anhui (Liu and Qiu, 2009). *M. teihardi* was erected by Qiu et al. (2004) based on materials from Longdan of Gansu. They thought this species had already been recognized by Teilhard de Chardin based on materials from Locality 12 of Zhoukoudian (Teilhard de Chardin and Leroy, 1945). *Meles* from Bajiazui, Qingyang of Gansu was also assigned to this species (Wang, 2006). A possible third species was recognized by Liu et al. (2007) based on fossils from Tuozi Cave, Nanjing of Jiangsu, but they didn't name the species due to scant materials (Liu et al., 2007; Dong et al., 2013).

M. chiai is most special for its P4 morphology (Teilhard de Chardin, 1940). Inner lobe of P4 extends anteriorly and the middle point of inner lobe often lies approximately at the same position of the anterior tip of parastyle (Fig. 5F). Protoconule, protocone and hypocone are all developed in the type specimen from

Locality 18 of Zhoukoudian (Teilhard de Chardin and Leroy, 1945), but these characters are extremely variable in living species. *M. teihardi* shows more similarities to living species in P4 morphology, but it retains primitive premolars morphology (P1 is present and P2 has two unfused roots) (Qiu et al., 2004). Besides differences mentioned above, some additional differences have been found by our observation. Lower premolars of *M. chiai* are often more elongated, whereas those of *M. teihardi* are wider (see Appendix: Table A3 for details). Premolar series of *M. teihardi* is also more crowded and lower anterior premolars are often imbricated. Our observation also confirms that P1 are often present and P2 have two unfused roots in both *M. chiai* and *M. teihardi*. P4 of *M. teihardi* is relatively large, while it is often smaller in *M. chiai* (see Appendix: Table A1). Based on differences of mentioned above, a brief review of Late Pliocene and Early Pleistocene *Meles* fossil records from China is given here.

Materials from Yushe are represented by maxilla fragment and several mandibles (Teilhard de Chardin and Leroy, 1945). The P4 is very similar to holotype of *M. chiai* from Locality 18 of Zhoukoudian (the inner lobe is even more anteriorly protruded than holotype) and premolars are also relatively thin. These characters evidently suggest this badger belong to *M. chiai*. Specimens from Xiashagou of Nihewan were originally assigned to *Meles* cf. *leucurus* based on single M1, a mandible with p2-m2 and a humerus. Only M1 and lower teeth are figured. Badgers from Xiashagou of Nihewan lack the characteristic P4, but the premolars of TNP15153 (mandible fragment with p2-p4) are relatively wide, which are similar to *M. teihardi*. Without additional specimens, badgers from this locality are assigned to *Meles* cf. *teihardi*. Specimens from Danangou were represented by a rostrum part of mandible and associated mandible (Fig. 11A and Fig. 11C) and were assigned to *M. chiai* without much discussion (Li, 1984). It has *M. teihardi*-like P4 morphotype (see Fig. 5E) and oval premolars, so badger from this locality probably also belongs to *M. teihardi* rather than *M. chiai*. Badger fossil from the Tuozi Cave is represented by single skull (Liu et al., 2007; Dong et al., 2013). The P4 has a small and posteriorly located inner

lobe similar to *M. teihardi*. Liu et al. (2007) believed the badger of Tuozi Cave was different from *M. teihardi* in relatively larger P4 to M1 external length, smaller size and different position of anterior rim of orbit. These characters are in fact very variable in living *M. leucurus*, and large P4 is actually well fitted to the characters of *M. teihardi*. Therefore the differences between the Tuozi Cave badger and Longdan *M. teihardi* mentioned by Liu et al. (2007) probably belong to geographic variation and badger from the Tuozi Cave is assigned to *M. teihardi*. Badgers from Renzi Cave are represented by some broken mandibles and several isolated teeth (Liu and Qiu, 2009). P4 from the Renzi Cave badger is very similar to holotype of *M. chiai*. Therefore, assignment of badger from this locality to *M. chiai* is supported. Badger from Bajiazui is only represented by broken maxilla with only P3 and P4 (Wang, 2006). P4 has similar inner lobe with Longdan badgers, so its assignment to *M. teihardi* is also supported. Three broken mandibles of *Meles* are reported from Ningyang as *Meles* sp. (Zhang, 2001). The premolars are relatively stout and imbricated. Therefore badgers from this locality probably belong to *M. teihardi*. Badgers from Longgupo were assigned to *Meles* cf. *chiai* and *Arctonyx* cf. *minor* (see discussion below) (Huang and Zhong, 1991). The P4 of badgers from Longgupo has anterior protruded inner lobe as in *M. chiai*, but the size (m1 length 18.42 mm) is much larger than *M. chiai* (m1 length 15.26-16.38 mm) and comparable to large badgers from the Liucheng *Gigantopithecus* cave (m1 length 17.20-21.06 mm). Therefore the status of this badger is not clear. Single M1 was reported from Jigushan of Zhoukoudian (Young, 1930). It has rather anteriorly protruded inner cingulum and short talon similar to European *M. thorali*. However this morphology is probably variable and it is not possible to give an exact assignment with only one M1. A skull fragment was assigned to *M. chiai* from Wangbuding, Dege of Sichuan (Zong et al., 1996). P4 of badger from Wangbuding has anteriorly protruded inner lobe similar to *M. chiai*, but it is distinct from the latter in enlarged parastyle and widened inner lobe with two large protocones. The premolars on the other hand are relatively wide which are similar to *M. teihardi*. Therefore *Meles* from this locality probably not belongs to *M. chiai* nor *M. teihardi*, but probably has closer affinity to *M. chiai*. According to

mammalian fossils, Wangbuding fauna probably belongs to Mazegouan LMS/A (Deng and Hou, 2011; Qiu et al., 2013), namely Late Pliocene. Therefore badger of Wangbuding probably belongs to early representative of *Meles*, but a more detailed observation (which is not available for authors now) is needed for better assignment of the specimen. A single mandible from Gongwangling, Lantian of Shaanxi (late Early Pleistocene) was assigned to *Meles* cf. *leucurus* (Hu and Qi, 1978). It is hard to distinguish the single mandible of different species of *Meles*, but badger from Gongwangling is distinctly larger than living species and has very elongated premolars similar to *M. chiai*. More materials are needed to clarify the status of the badgers from Gongwangling and it is assigned to *Meles* cf. *chiai*. Early Pleistocene *Meles* fossils were also reported from Tianzhen, Shanxi (Qiu et al., 2002) and the Yimu River Basin, Shandong (You and Xu, 1996), but the original papers give neither description nor figures of the materials and the specimens are not available to authors. So badgers from these localities are not discussed here. Therefore, there are two species known during Early Pleistocene in North China. These two species largely coexisted widely in North China. The distribution of above fossils sites and known distribution are given in Fig. 12.

M. minor is distinct from all above species by its smaller size and narrower P3 (Appendix: Table A1). Like *M. chiai*, *M. minor* has a narrower P2 compared with *M. leucurus*. This is partially due to unreduced P2 (compared to P3) in Early Pleistocene *Meles* (thus P2 is longer and relatively narrower). In fact, *M. minor* has the most reduced P2 among these Early Pleistocene *Meles*, within the upper limit of *M. leucurus* and lower limit of *M. teihardi*. P3 of *M. minor* is relatively larger than other *Meles* in length and height (compared to P4) but not in width, making it narrower than other *Meles* and fully within the range of *Arctonyx*. P4 of *M. minor* is relatively narrower but within the variation of other *Meles*. P4 of *M. magnus* n. sp. is distinctly larger and the parastyle seems to be reduced (it is not clear due to the abrasion), which also distinguish this species to other *Meles*. Like *M. teihardi*, the position of inner lobe lies more anteriorly than *M. minor* and *M. leucurus*, but not to the extent of *M. chiai* and *Meles* sp. Protoconule is not developed in both species as in most *Meles*,

while hypocone and protocone are variably developed. m1 of *M. magnus* n. sp. is similar to other *Meles*, but with a higher possibility to have well developed posterior cusps distal to hypoconid and entoconid. Two mandibles from Longgupo were assigned to by *Arctonyx* cf. *minor*. Premolars of figured specimen are distinctly higher and shorter than *Arctonyx* and can be confidently assigned to *Meles*. Though it is not possible to directly compare the specimen to *M. minor*, its size fits *M. minor* well. The p2 is more reduced relative to p3, while p4 is relatively large. This pattern (large posterior premolars) is similar to upper premolars of *M. minor*. It is highly probably that the specimen belongs to *M. minor*, but we treated it as *Meles* cf. *minor* before discovery of more materials that would enable a direct comparison.

See Table 3 for summary of summary of general morphology of badgers.

4.4. Comparison of Chinese *Meles* with European *Meles*

The fossil *Meles* in Europe have been assigned to different species or subspecies. *Meles atavus* was erected by Kormos (1914) based on remains from Püspökfürdö in Hungry due mainly to the accessory cusp between protoconid and hypoconid of m1 (Kormos, 1914). This cusp is also present in holotype of *M. chiai* (Fig. 8F) but it is absent in all other specimens of *Meles* in China. However, later most authors recognized this character as variable and regarded *M. atavus* as a subspecies of *M. meles* (Kretzoi, 1938; Argant and Mallye, 2005; Madurell-Malapeira et al., 2011a). *Meles thorali* was erected by Viret (1951) based on the remains from Saint-Vallier in France. The earliest record of *Meles* in Europe is an M1 from Almenara-Casablanca 4 of Late Pliocene (MN16), which was also assigned to *Meles* cf. *thorali* (Madurell-Malapeira et al., 2009). *Meles thorali spelaeus* was erected by Bonifay (1971) based on remains from Middle Pleistocene Lunel-Viel in France. Rabeder (1976) supported the specific assignation of this subspecies, but Argant and Mallye (2005) believed it was closer to *M. meles* and thus couldn't be regarded as a subspecies of *M. thorali*. *Meles hollitzeri* was erected by Rabeder (1976) based on badgers remains from Deutch-Altenburg 2. Badgers from Untermassfeld were also assigned to this species (Wolsan, 2001). This species was assigned to *M. meles* by

Madurell-Malapeira et al. (2011b). *Meles dimitrius* was erected by Koufos (1992) based on badger remains from Gerakarou and Apollonia in the Mygdonian basin (Greece) (Koufos, 1992). Later on more materials from Apollonia were described and assigned to this species (Koufos and Kostopoulos, 1997). This species was assigned to *M. thorali* by Argant and Mallye (2005). They believed the differences between Greece materials and *M. thorali* could only represent population variation (Argant and Mallye, 2005). This opinion was supported by Madurell-Malapeira et al. (2011a), though they thought only early-middle Early Pleistocene Gerakarou materials could be assigned to *M. thorali*, whereas late Early Pleistocene Apollonia materials represented *M. m. atavus* (Madurell-Malapeira et al., 2011a, 2011b). *Meles iberica* was erected by Arribas and Garrido (2007) based on remains from Fonelas P-1 in Spain, which is small but robust. Madurell-Malapeira et al. (2011a) assigned this species to *M. thorali*. Therefore, there is still much debate of taxa about European *Meles*. A taxonomical revision of European *Meles* is beyond the scope of this study. Considering the great variation of teeth proportion of modern species of *Meles*, we follow Madurell-Malapeira et al. (2011a) in regarding *M. dimitrius* and *M. hollitzeri* as primitive subspecies of *M. meles* while *M. iberica* as synonyms of *M. thorali*.

Among the Chinese *Meles*, *M. teihardi* is closest to *M. thorali* in morphology. The similarity between *M. teihardi* and *M. thorali* has been recognized by Qiu et al. (2004). Both taxa have similar premolars and P4 structures. Qiu et al. (2004) believed the major difference between them lied in the M1 morphology. They argued there was often distinct anterior protruding of inner cingulum and labial incision between metacone and metaconule in *Meles thorali*, whereas it was very weak or absent in *M. teihardi*. The *M. thorali* from Almenara-Casablanca 4 (Madurell-Malapeira et al., 2011a) and Saint-Vallier (Viret, 1951) do shows distinct labial incision, but if regarding *Meles* from Gerakarou (which is similar to *M. teihardi* in M1 morphology) as *M. thorali*, then these characters are also variable in *M. thorali*. Therefore, the above differences between *M. teihardi* and *M. thorali* are probably not so distinct and the two species are probably closely related to each other. *M. chiai* is evidently different from European *Meles* by its special P4 morphology. M1 of *Meles* is

extremely variable, but *M. minor* and *M. magnus* n. sp. are distinct from *M. thorali* by more posterior position of antero-lingual corner of inner cingulum. In summary, *Meles* has appeared in both sides of Eurasia during Late Pliocene. In Pliocene, the *Meles* from Europe (with affinity to *M. thorali*) and Asia is rather different (*M. chiai* or closely related species). During Early Pleistocene, *Meles* became more abundant in Europe, while in China *Meles* close to European ones (*M. teihardi*) appeared in North China, which possibly represents the European immigrant. New form of *Meles* that is different from *M. thorali* also appeared in South China, but its origin is still unclear due to lacking of fossil sites in Pliocene in South China and Southeast Asia.

4.5. Phylogeny of Early Pleistocene *Meles*

Traditional phylogenetic analysis based on character coding of each species is difficult to carry out due to the great variation of tooth morphology of *Meles*. To investigate the interrelationships of different *Meles*, means of score of morphotypes are used. Means of score of different morphotypes are transported to characters, representing the general type of population. Score 1-1.5 (not include 1.5) would be coded as 0, 1.5-2 (not include 2) as 1, 2-2.5 (not include 2.5) as 2 and the rest can be done in the same manner (see Appendix: Table A5). Space 0.5 is used as it properly distinguishes the different morphotypes and is not redundant. Besides above characters, five metric characters of premolar and molar are also added to character matric:

Relative width of premolars, using p4 as standard; 0.05 is chosen as discriminant (0.45-0.5 as 0, 0.5-0.55 as 1 and the rest can be done in the same manner);

Relative height of premolars, *Arctonyx* (0) has distinctly lower premolars than *Meles* (1) in this aspect;

Relative size of anterior premolars, using ratio of P3 length and P4 length. 0.1 is chosen as discriminant (0.5-0.6 as 0, 0.6-0.7 as 1 and 0.7-0.8 as 2);

Relative size of P4, using ratio of P4 length and M1 external length. Three types are set according to the mean of ratio: ratio < 0.9 as 0, 0.9 < ratio < 1.1 as 1 and ratio < 1.1 as 2;

Relative talon length of M1, using ratio of width and total length. 0.1 is chosen as discriminant (0.6-0.7 as 0, 0.7-0.8 as 1, 0.8-0.9 as 2 and ratio < 0.9 as 3).

In general, *Arctonyx* is more specialised than *Meles* in tooth morphology, so choosing *Arctonyx* as outgroup would bias the polarity of characters. *Ferinestrix* is instead chosen as outgroup since it was regarded as early representative of Melinae and retains many plesiomorphic characters (Wolsan and Sotnikova, 2013). *M. thorali* is also added based on the figures and measurements from Viret (1951) and Madurell-Malapeira et al. (2011a). All characters are set as additive, since these characters reflect the means of the population morphotypes, which evidently evolve gradually.

Phylogenetic analysis was performed in the program TNT 1.1 (Goloboff et al., 2008), and the size of the dataset allows exact searches under the implicit enumeration algorithm. All characters are treated as additive. The exact search find single most parsimonious tree with a length of 87 steps (CI = 0.632, RI = 0.418). The phylogenetic tree is shown in Fig. 13.

Phylogenetic tree supports both badgers from Liucheng *Gigantopithecus* Cave in *Meles* rather than *Arctonyx*. The monophyly of *Meles* is supported by high premolar and three M1 characters: anterior position of inner cingulum and strong development of ridge between protocone and hypocone and weak development of ridge between protocone and hypocone. However, these characters are probably plesiomorphic characters since they are common in Mustelidae. A more comprehensive analysis of Melinae including *Arctomeles*, *Melodon*, *Parataxidea* is needed to answer the question, which is beyond the scope of present work. Among *Meles*, *M. minor* and *M. chiai* are early branches, and *M. teihardi* and *M. thorali* are closer to living species. *M. magnus* n. sp. is grouped with *M. leucurus* by four characters: similar position of middle point of inner lobe of P4 and antero-lingual corner of inner cingulum of M1; relatively weak development of both ridges from distal cusp of protocone to metaconule and hypocone relative to other *Meles*. The phylogenetic tree suggests *Meles* probably originated in Asia, and later dispersed to Europe. Due to the lacking data of some species for analysis, the bootstrap value and bremer support of the tree is

not high. Note that for *M. minor*, there is only one specimen and statistics of morphotypes of *M. thorali* and *M. meles* are not available for authors, so their positions are still open to discussion.

5. Conclusion

Arctonyx is distinct from *Meles* in tooth morphology in statistics aspect. "*Arctonyx*" fossil remains from the Liucheng *Gigantopithecus* Cave are distinct from *Arctonyx* and can be assigned to *Meles*: *M. minor* and *M. magnus* n. sp. *M. minor* is distinctly smaller than other *Meles* with large infraorbital foreman and special teeth morphology. *M. magnus* n. sp. is distinctly larger than other *Meles* and shows a combination of characters not seen in other *Meles*. There are at least two species of *Meles* during Pliocene (*M. chiai* and *Meles* from Wangbuding) and four species during Early Pleistocene (*M. chiai*, *M. teihardi*, *M. minor* and *M. magnus* n. sp.) (see Table 3 for a summary). It is interesting to note that during early Early Pleistocene (2.6-1.8 Ma) four species of *Meles* coexisted in China. This may be explained by two fact: 1. The four species are different in size and are not all sympatric in distribution, with *M. chiai* and *M. teihardi* largely sympatric in North China and central part of China (but the two species have never been discovered at the same site) while *M. minor* and *M. magnus* n. sp. in southernmost China (*M. minor* may distributed to Chongqing); 2. There are no reliably *Arctonyx* records in China during early Early Pleistocene (2.6-1.8 Ma), and *M. minor* and *M. magnus* n. sp. might take the niche of *Arctonyx* at this time. *M. chiai* was general thought to be ancestor of *M. leucurus* due to absence of P1 (Baryshnikov et al., 2003; Madurell-Malapeira et al., 2011a), but as stated above, most specimens of *M. chiai* do have a P1. Our phylogenetic analysis suggests *M. chiai* as early branch of *Meles*, and supports *M. magnus* n. sp. as closer related species to *M. leucurus*. It is a pity that most species are represented by isolated teeth only, which are in turn with great variation, so the tentative phylogenetic analysis comprising 20 characters is only a preliminary work. More materials (e.g., skulls) are needed to better clarify the taxonomic position of *M. minor* and *M. magnus* n. sp.

Acknowledgements

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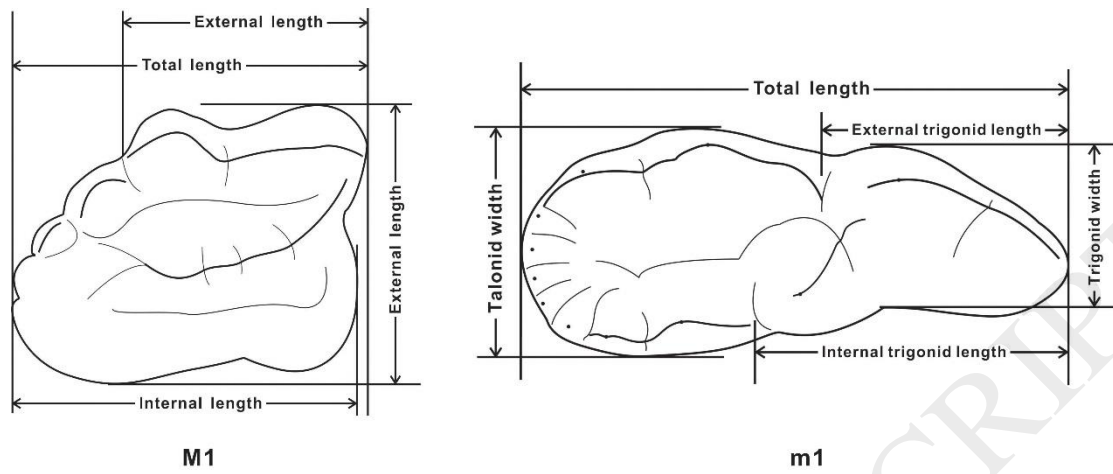
Fig. 1. Measurements of M1 and m1.

Fig. 2. Terminology of P4, M1 and m1 structure. Dash line indicates metastyle, which is generally absent in *Meles*, but more frequently present in *Arctonyx*. Note that protoconule and protocone of M1 together form a continuous ridge with several cusps, so this complex is just called protocone.
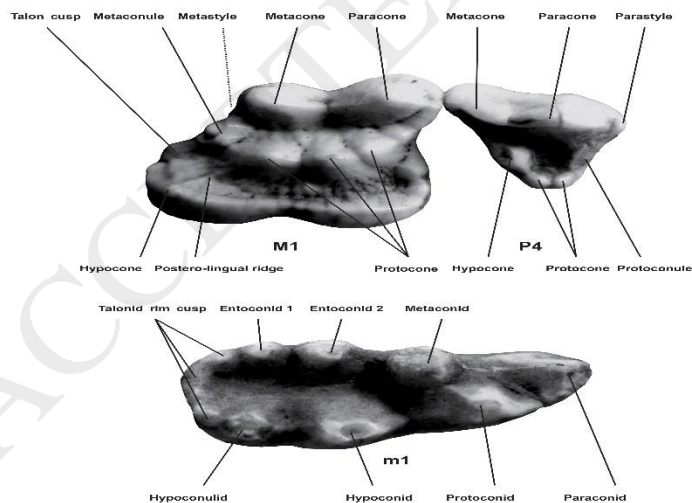
Fig. 3. Morphotypes of P4, M1 and m1.
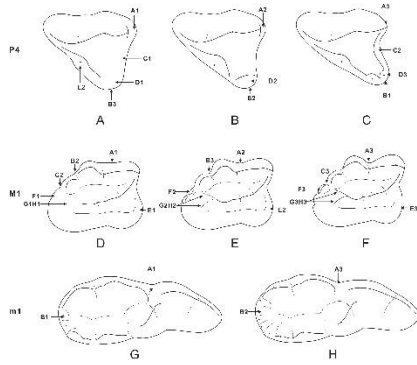
Fig. 4. (A-C) Holotype of *M. minor*, V5026.12; (A) lateral view; (B) distal view; (C) ventral view. (D) *M. magnus* n. sp., V5025.2, ventral view. Scale = 1 cm.
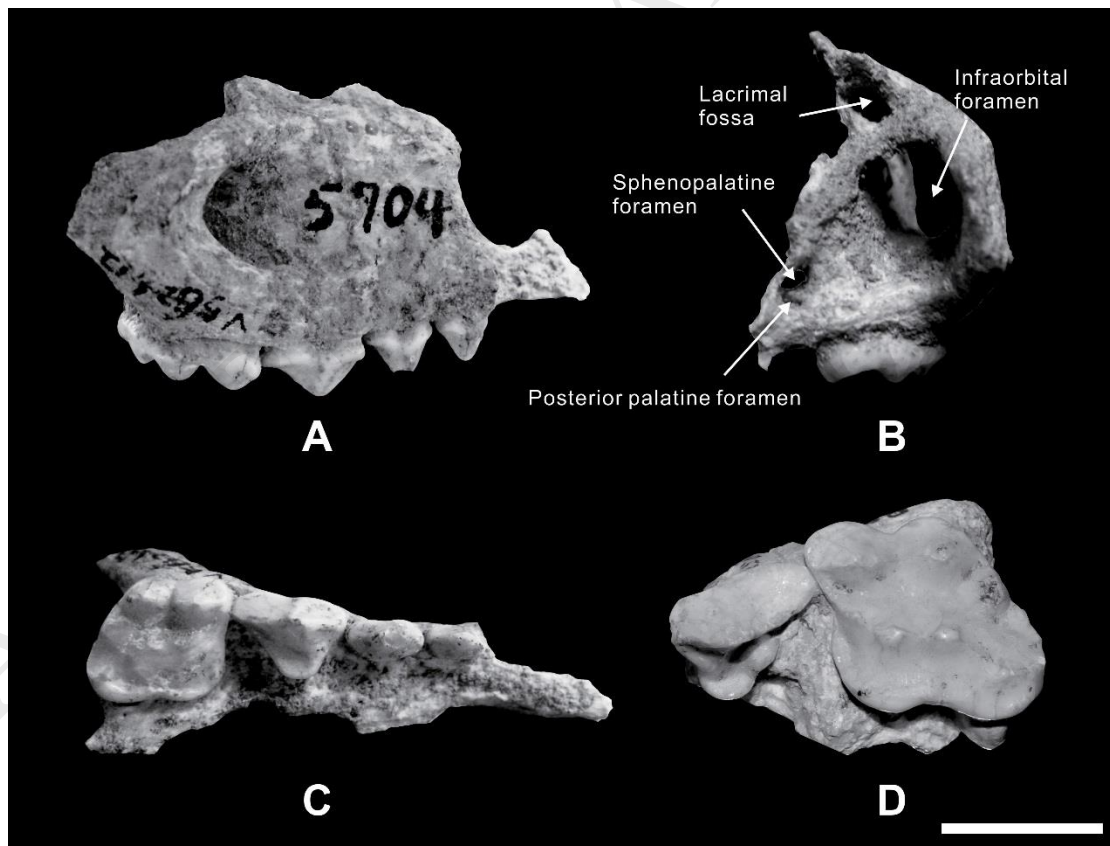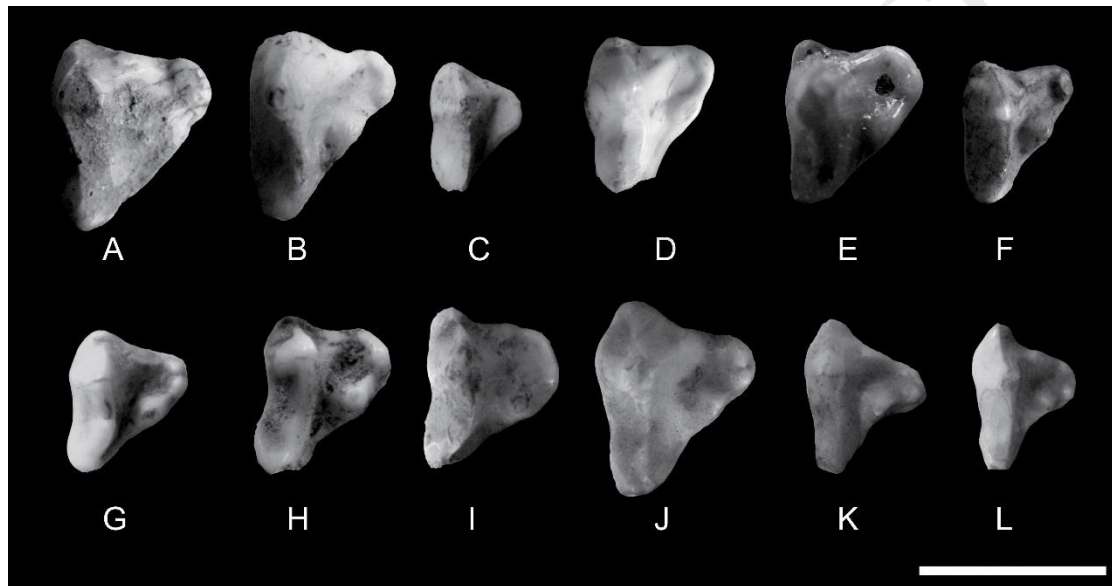
Fig. 5. P4 of *Meles* and *Arctonyx*. (A, B) *M. magnus* n. sp. from the Liucheng *Gigantopithecus* Cave; (A) V5025.1; (B) V5025.2. (C) *M. minor* from the Liucheng *Gigantopithecus* Cave, V5026.12. (D, E) *M. teihardi* from Longdan and Danangou; (D) V13534; (E) V7254. (F) *M. chiai* from Locality 18 of Zhoukoudian, RV40008. (G-I) *M. leucurus*; (G) IOZ 08129; (H) OV625; (I) IOZ H1452. (J-L) *A. albogularis*; (J) IOZ H1467; (K) IOZ uncataloged; (L) IOZ uncataloged. Scale = 1 cm. Note that (A, D, H, J, L) are mirror images for better comparison. See Appendix: Table A6 for details of morphotypes.

Fig. 6. M1 of *Meles* and *Arctonyx*. (A-C) *M. magnus* n. sp. from the Liucheng *Gigantopithecus* Cave; (A) V5025.2; (B) V5026.5; (C) V5026.10. (D) *M. minor* from the Liucheng *Gigantopithecus* Cave, V5026.12. (E-G) *M. teihardi* from Longdan, Danangou and the Tuozi Cave; (E) V13534; (F) V7254; (G) JNTZ1323. (H) *M. chiai* from Locality 18 of Zhoukoudian, RV40008. (I-L) *M. leucurus*; (I) IOZ H1461; (J) IOZ 08129; (K) IOZ H1452; (L) IOZ H1464. (M-P) *A. albogularis*; (M) IOZ H1467; (N) IOZ H1664; (O) IOZ uncataloged; (P) IOZ uncataloged. Scale = 1 cm. Note that (A, B, C, H, L, M, O, P) are mirror images for better comparison. See Appendix: Table A7 for details of morphotypes.
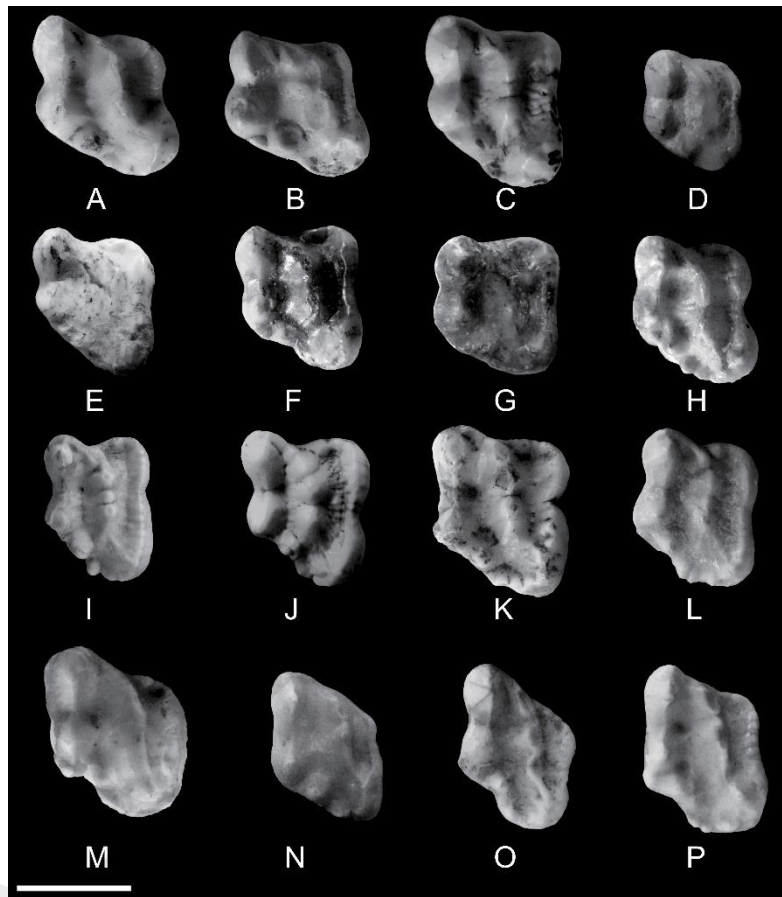
Fig. 7. Length and width plot of P4 and Principal component analysis of M1 and m1 of badgers. In both M1 and m1, PC1 (score of first principal component) is negative and have similar loadings to all original variables, so it is not shown here. See Appendix: Table A4 for details of PCA analyses. PC2 and PC3 are the scores of second and third principal component.
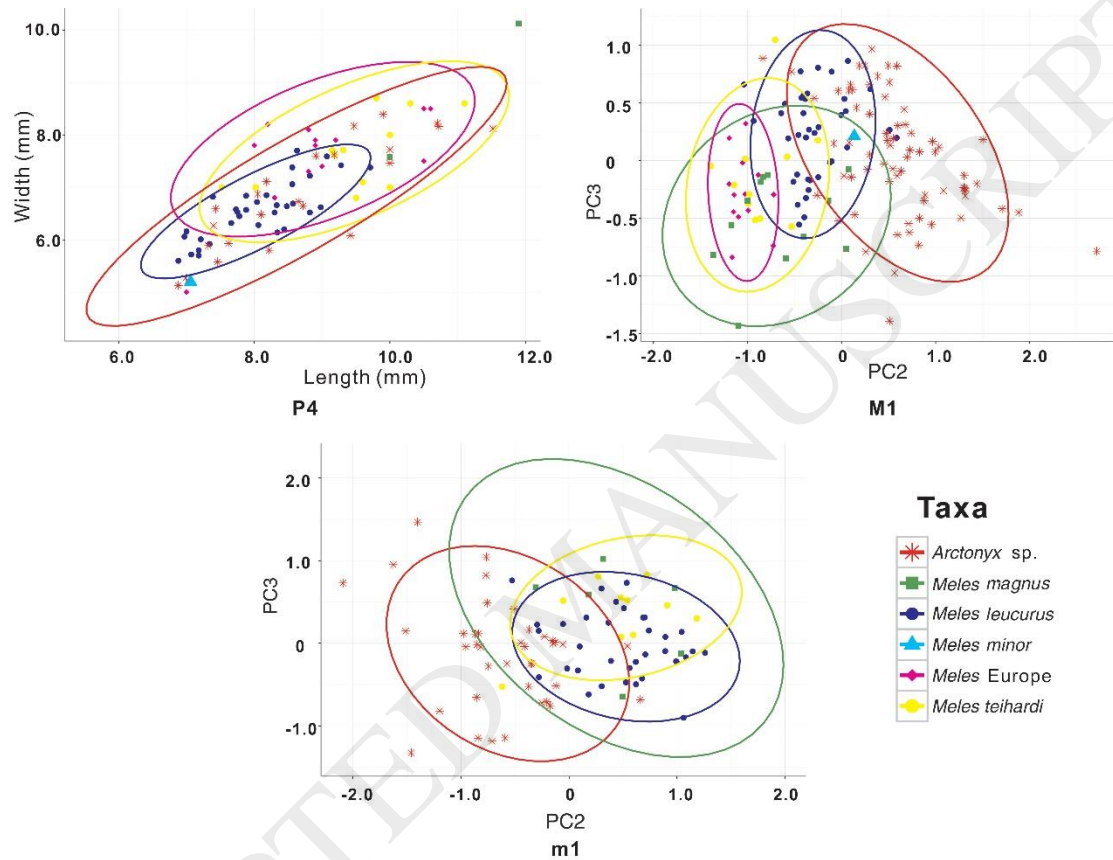
Fig. 8. m1 of *Meles* and *Arctonyx*. (A-C) *M. magnus* n. sp. from the Liucheng *Gigantopithecus* Cave; (A) V5023.1; (B) 5024.2; (C) V5024.3. (D, E) *M. teihardi* from Danangou and Ningyang; (D) V7254; (E) V12369.2. (F) *M. chiai* from Locality 18 of Zhoukoudian, RV40008. (G-I) *Meles leucurus*; (G) OV625; (H) IOZ H1461; (I) IOZ H1464. (J-L) *Arctonyx albogularis*; (J) IOZ H1469; (K) IOZ H1584; (L) IOZ uncatalogued. Scale = 1 cm. Note that (A, B, D, E, G, L) are mirror images for better comparison. See Appendix: Table A8 for details of morphotypes.
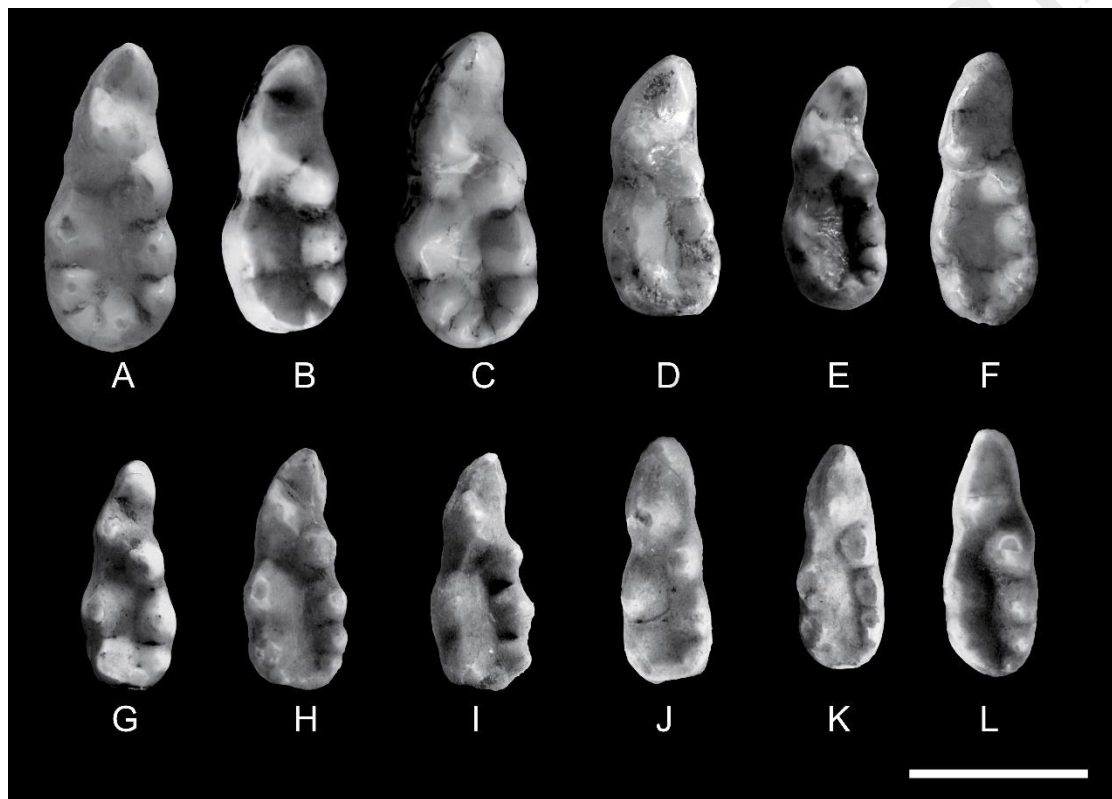
Fig. 9. Cluster analyses based purely on mean morphotype of each species. Since the lower tooth is absent for *M. minor*, both cluster analysis with *M. minor* based on upper teeth and cluster analysis without *M. minor* based on upper and lower teeth are done.

Cluster analysis with *M. minor* based on mean morphotype of upper teeth

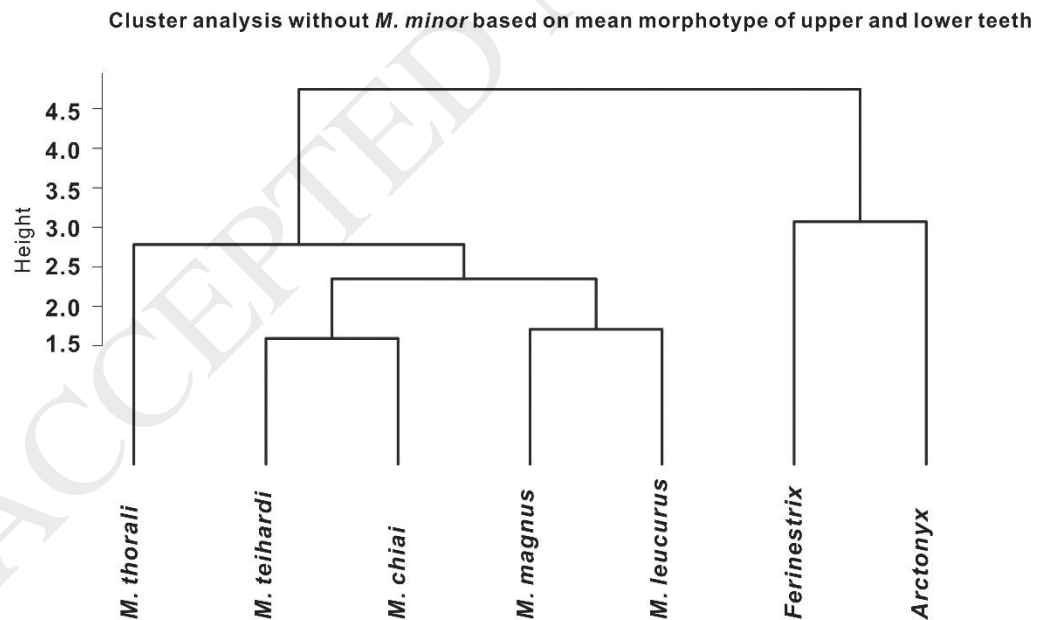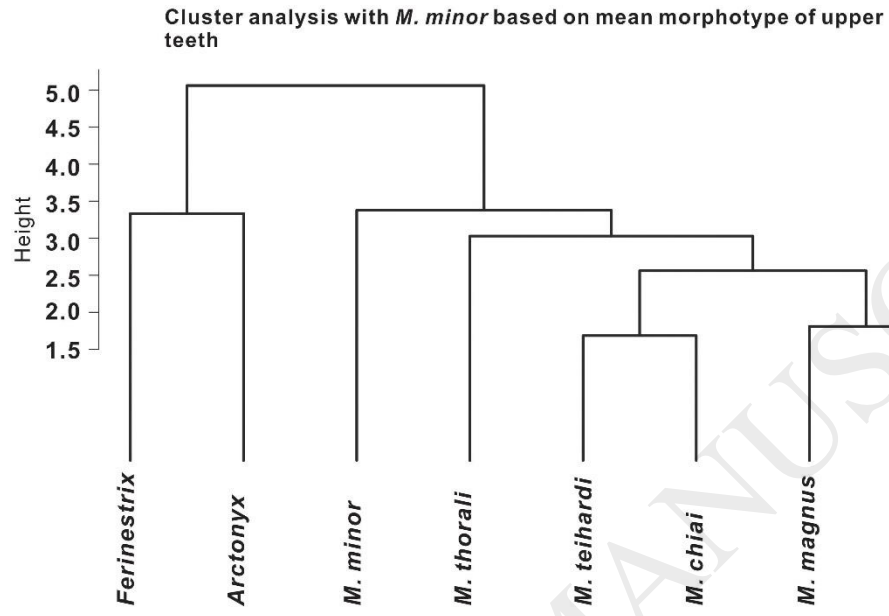Cluster analysis without *M. minor* based on mean morphotype of upper and lower teeth

Fig. 10. Comparison of infraorbital foreman of *Meles leucurus* (A) (IOZ uncatalogued) and *Arctonyx albogularis* (B) (IOZ H1662), lateral view. Scale = 2 cm.
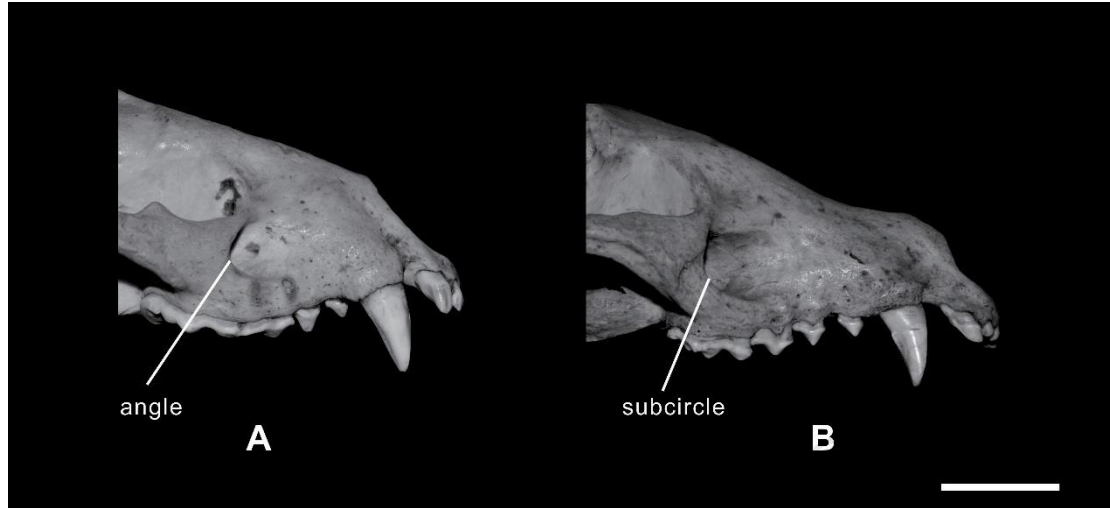

Fig. 11. *Meles* fossils from North China. (A, B) *M. teihardi* from Danangou, V7254.1, lateral view and ventral view. (C, D) *M. chiai* from Locality 18 of Zhoukoudian, RV40008, lateral view and ventral view. (E, F) *M. teihardi* from Danangou, V7254.2, lateral view and dorsal view. (G, H) *M. chiai* from Locality 18 of Zhoukoudian, RV40008, lateral view and dorsal view. (I, J) *Meles* cf. *chiai* from Gongwangling, V5411, lateral view and dorsal view. Scale = 2 cm. Note (G, H, I and J) are mirror images for better comparison. Lower part of mandible of *Meles* cf. *chiai* from Gongwangling are reconstructed by plaster.
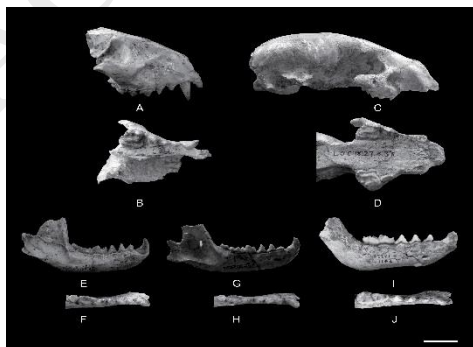
Fig. 12. Late Pliocene and Early Pleistocene *Meles* fossil records in China. 1. Wangbuding; 2. Yushe; 3. Locality 18 of Zhoukoudian; 4. Renzi Cave; 5. Longgupo; 6. Xiashagou of Nihewan; 7. Danangou; 8. Longdan; 9. Qingyang; 10. Ningyang; 11.Tuozi Cave; 12. The Liucheng *Gigantopithecus* Cave; 13. Gongwangling.
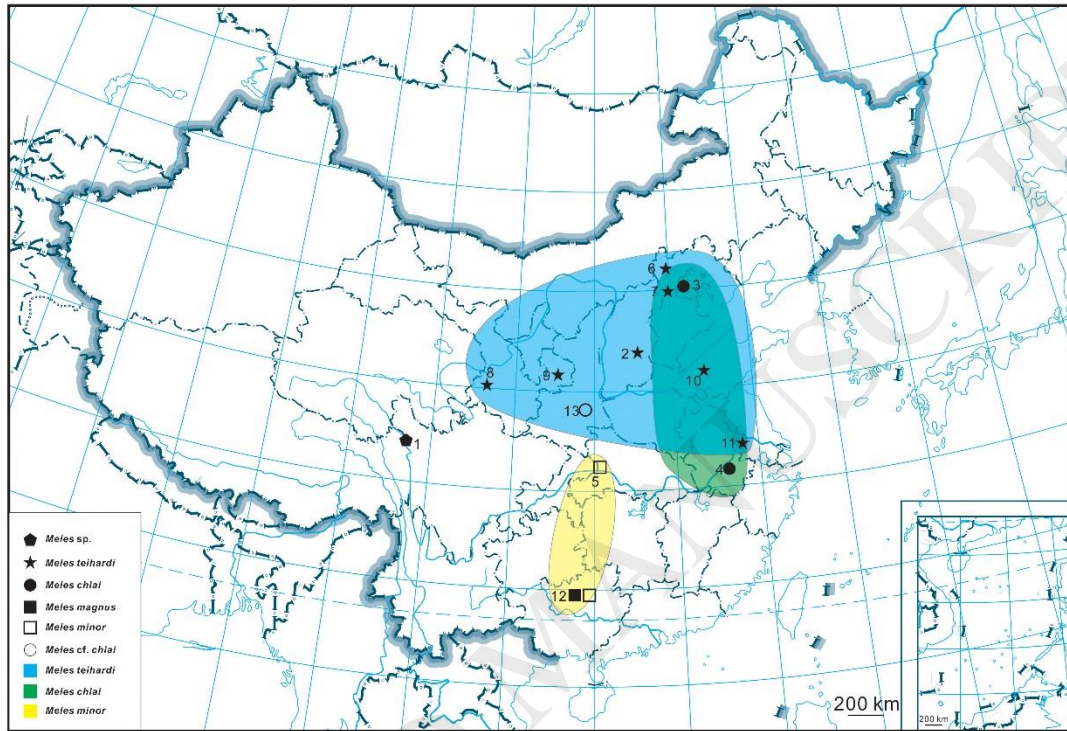

Fig. 13. Phylogenetic tree of *Meles*, value shown in the joint is the bootstrap value and bremer support (forms as bootstrap value / bremer support).
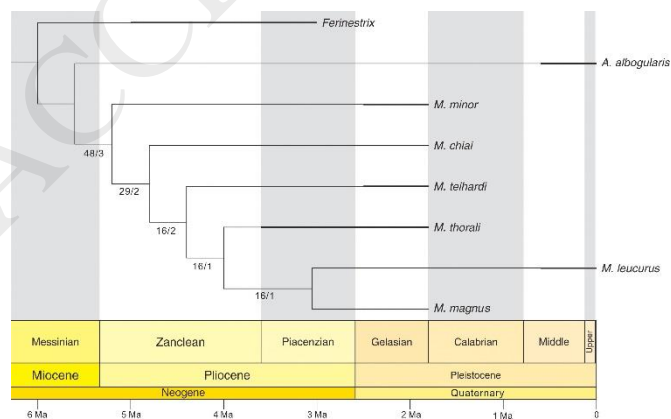
Table 1. Mean score of morphotype of studied badgers. Data of *Ferinestrix* are based in figures by Wolsan and Sotnikova (2013), and data of *M. thorali* are based on figures by Madurell-Malapeira et al. (2011a) and Viret (1951).

Taxa	P4					M1								m1	
	A	B	C	D	E	A	B	C	D	E	F	G	H	A	B
Ferinestrix	2.000	2.000	1.000	1.000	2.000	2.000	1.000	1.000	1.000	5.000	1.000	1.000	3.000	1.000	1.000
A. albogularis	2.930	4.390	1.500	1.860	2.000	1.536	1.000	2.460	1.500	4.786	2.185	1.136	2.818	1.800	1.350
M. magnus	1.500	2.500	1.000	2.500	2.000	2.615	1.231	1.231	1.167	2.692	2.000	1.444	1.889	2.333	1.710
M. teihardi	2.000	2.250	1.333	2.333	2.000	2.400	1.400	2.000	1.250	1.800	1.500	3.000	2.000	1.500	1.500
M. chiai	2.000	1.600	1.800	2.250	2.000	2.400	1.000	1.000	1.400	1.800	1.333	2.200	2.400	1.375	1.143
M. leucurus	2.051	3.146	1.143	1.714	1.952	2.574	1.702	1.532	1.064	2.319	2.167	1.878	1.791	1.256	1.263
M. minor	2.000	3.000	1.000	1.000	1.000	2.000	1.000	1.000	1.000	3.000	1.000	2.000	2.000	?	?
M. thorali	1.000	2.000	1.000	1.000	2.000	2.500	2.000	1.670	1.000	1.000	2.667	2.000	2.000	1.000	2.000

Table 2. Fossil sites with *Meles* during Late Pliocene to Early Pleistocene.

Fossil site	Age	Previous assignment	Present assignment
Yushe Basin, Shanxi	Late Pliocene (Qiu et al., 2013)	*M. chiai*	*M. chiai*
Wangbuding, Dege, Sichuan	Late Pliocene (Deng and Hou, 2011)	*M. chiai*	*Meles* sp.
Locality 18 of Zhoukoudian, Beijing	~2.0 Ma (Qiu, 2000, 2006)	*M. chiai*	*M. chiai*
Jigushan of Zhoukoudian, Beijing	Early Pleistocene (Young, 1930)	*Meles* cf. *leucurus*	*Meles* sp.
Xiashagou of Nihewan, Hebei	~1.9 Ma (Qiu, 2000, 2006)	*Meles* cf. *leucurus*	*Meles* cf. *teihardi*
Danangou of Yuxian, Hebei	early Early Pleistocene (Cai et al., 2013)	*M. chiai*	*M. teihardi*
Longdan, Gansu	2.58-2.25 Ma (Qiu et al., 2004; Qiu, 2006)	*M. teihardi*	*M. teihardi*
Bajiazui, Qingyang, Gansu	early Early Pleistocene (Wang, 2006)	*M. teihardi*	*M. teihardi*
Tianzhen, Shanxi	2.6-1.8 Ma (Qiu et al., 2002)	*Meles* sp.	Not examed
Tuozi Cave, Nanjing, Jiangsu	2.0 Ma (Dong et al., 2013)	*Meles* sp.	*M. teihardi*
Renzi Cave, Fanchang, Anhui	2.2-2.0 Ma (Liu and Qiu, 2009)	*M. chiai*	*M. chiai*
Ningyang, Shandong	early Early Pleistocene (Zhang, 2001)	*Meles* sp.	*M. teihardi*
Yimu River Basin, Shandong	Early Pleistocene (You and Xu, 1996)	*M. chiai*	Not examed
Gongwangling, Shaanxi	1.3 Ma (Hu and Qi, 1978)	*Meles* cf. *leucurus*	*Meles* cf. *chiai*
Longgupo, Wushan, Chongqing	2.48 Ma (Huang and Zhong, 1991; Han et al., 2015)	*M. chiai* *Arctonyx* cf. *minor*	*Meles* sp. *Meles* cf. *minor*
Liucheng *Gigantopithecus* Cave, Guangxi	2.48-2.0 Ma (Pei, 1987)	*A. collaris* *A. minor*	*M. magnus* *M. minor*

Table 3. Diagnosis of studied badgers based on morphotype analysis.

	M. minor	*M. magnus*	*M. chiai*	*M. teihardi*	*M. leucurus*	*Arctonyx*
P4	Parastyle weak, position of middle point of inner lobe often lies between parastyle and apex of paracone but mostly closer to paracone.		Parastyle usually weak, position of middle point of inner lobe often lies at parastyle or slightly posteriorly, protoconule often developed.	Parastyle usually weak; position of middle point of inner lobe often lies between parastyle and apex of paracone but mostly closer to parastyle.	Parastyle usually weak; position of middle point of inner lobe often lies between parastyle and apex of paracone but mostly closer to paracone.	Parastyle usually absent, position of middle point of inner lobe often lies around the apex of paracone.
M1	Metastyle absent.	Labial incision between paracone and metacone often weak or absent, labial incision posterior to metaconule often absent, metastyle seldom developed.	Labial incision between metacone and metaconule and incision posterior to metaconule distinct, position of antero-lingual corner of inner cingulum often lies at the anterior tip of paracone or slightly anterior to it, accessory cusps at the posterior	Metastyle seldom developed, position of antero-lingual corner of inner cingulum often lies at the anterior tip of paracone or slightly anterior to it; ridge linking distal cusp of protocone and metaconule strong while ridge linking distal cusp of protocone and hypocone are often present	Labial incision between metacone and metaconule often present, metastyle seldom developed; both ridges linking distal cusp of protocone and metaconule and hypocone are often present but weak.	Labial incision between paracone and metacone often weak or absent, labial incision between metacone and metaconule absent, labial incision posterior to metaconule often distinct, metastyle sometimes developed; position of antero-lingual corner of inner cingulum often lies between

			margin distal to metaconule often weak or absent, both ridges linking distal cusp of protocone and metaconule and hypocone are often present.	but weak.	anterior tip of apex of paracone and notch between paracone and metacone; ridge linking distal cusp of protocone and metaconule often absent while ridge linking distal cusp of protocone and hypocone often strong.
m1		Small cusps distal to hypoconid and entoconid often strong.				Position of anterior margin of hypoconid often lies at the approximately the same position of apex of metaconid.