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# New skull of *Megantereon inexpectatus* (Carnivora: Machairodontinae) and its implications on evolution of *Megantereon* in North China

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## Abstract

*Megantereon* is an iconic sabertoothed cat known from the Quaternary deposits of the Old World, being its evolutionary scenario and phylogenetic relationships hotly debated the last decades. Several authors proposed that there is only one species, i.e. *M. cultridens*, or two species, plus *M. whitei* in Eurasia and Africa of Pleistocene, while some authors proposed multiple species present. Here we describe a mostly complete cranium and several fragmented mandibular fragments of a very large and robust form of *Megantereon* from Bajiazui, Qingyang, northwestern China, assigned to *M. inexpectatus*. Several new skulls/crania of *M. nihowanensis* from Longdan (Gansu, China) were analysed and they further provide a better basis for evaluating the intraspecific variability of this lineage. The analyses here reported, support the recognition of two species from a single lineage of *Megantereon* in northern China since the earliest Pleistocene to the middle Pleistocene, with smaller *M. nihowanensis* in the Gelasian, and slightly larger and more robust *M. inexpectatus* with more derived dentition during the Calabrian to the early Middle Pleistocene. This scenario is different from what is seen in Europe, where the primitive *M. cultridens* evolved to smaller and dentally specialized *M. adroveri*.

**Keywords** Bajiazui, Quaternary, *M. inexpectatus*, *M. nihowanensis*, *M. adroveri*

## Introduction

*Megantereon* is one of the most successful sabertoothed cats, spanning from the Pliocene to the middle Pleistocene, from Africa to eastern Asia, playing an important role in Quaternary taphocenoses (Lewis & Werdelin, 2010; Liu, 2005; Madurell Malapeira, 2025; Palmqvist et al., 2007; Zhu et al., 2020). Even though numerous fossil of this genus have been found around the world, the taxonomical diversity and evolutionary scenario of this sabertooth genus is still controversial (Liu, 2005; Martínez Navarro & Palmqvist, 1995; Palmqvist, 2015; Palmqvist et al., 2007; Qiu et al., 2004; Werdelin & Lewis, 2000, 2002; Zhu et al., 2020). Palmqvist et al. (2007) proposed a two-species system for *Megantereon*, with *M. cultridens* replaced by more derived *M. whitei* of African

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origin. While they provided evidence supporting this scenario in Europe (but see Lewis & Werdelin, 2010), their extension of this conclusion to the whole of Eurasia may be overly extensive.

In fact, Eastern Asia represents a different story for *Megantereon* evolution. Traditionally, four *Megantereon* species have been recognized in the region. The first erected species, *M. nihowanensis* by Teilhard de Chardin and Piveteau (1930), was described on the basis of several skulls from Xiashagou of Nihewan Basin (Nihewan classical sites). Among the material described by Teilhard de Chardin and Piveteau (1930) described, one specimen was later identified as belonging to *Homotherium*, while the others include two crania and one mandible of *Megantereon* (Schaub, 1934). Subsequently, much more abundant material of this species was recovered from Longdan, forming the largest known collection of *Megantereon* from a single site (Qiu et al., 2004). This species is generally similar to European *M. cultridens* in size, but it differs from the latter in having a smaller mandibular flange, more angled P3 and P4, more reduced P3 and p3 (fused root) (Qiu et al. (2004). However, further comparison based on new materials from Longdan reveals that these purported diagnostic characters in fact show considerable variation within *M. nihowanensis*. Not all *M. nihowanensis* specimens possess the aforementioned features, suggesting that these traits are more likely intraspecific variations. Therefore, *M. nihowanensis* may indeed be a synonym of *M. cultridens*.

A second species, *Megantereon inexpectatus*, was firstly described from Loc. 1 at Zhoukoudian (Teilhard de Chardin, 1939) and has recently been reported from the late Early Pleistocene of Linyi, Shanxi in Northern China (Li & Sun, 2021). It represents the youngest record of the genus globally. Teilhard de Chardin (1939) recognized the similarity of this species with *M. nihowanensis*, but they thought this species differed from the latter in having a larger body size, longer rostrum and more reduced P4 protocone. These differences were largely omitted when Palmqvist et al. (2007) analyzed the Eurasian population, and they directly assigned this species to *M. cultridens*, as their analysis mainly focuses on the P3/p3 size, which is indeed not different in *M. inexpectatus*, *M. cultridens* and *nihowanensis*. On the other hand, the evolutionary origin of this species remains debated. Li and Sun (2021) proposed an African ancestry, suggesting a close relationship with *M. whitei*, and regarded *M. inexpectatus* as a distinct immigrant lineage into northern China.

The third species, *Megantereon lantianensis*, was described based on material from the Gongwangling site in Lantian, Shaanxi, China (Hu & Qi, 1978). It is known only from an upper canine and a mandibular fragment, Hu and Qi (1978) observed that the specimens differed

from *M. inexpectatus* at Zhoukoudian Loc. 1 not only in the anteroposterior diameter of the upper canine, but also in carnassial length, indicating incompatible occlusal patterns between them. Based on these differences, they assigned the Gongwangling specimens to a new species, *M. lantianensis*. The mandible features a significantly large and wider mental lobe, a longer c-p3 diastema, and a relatively longer m1 compared to p3 and p4, all of which exceed the morphological variation observed in the Nihewan and Longdan specimens. This combination of characteristics most likely represents *M. inexpectatus*. (Li & Sun, 2021; Qiu et al., 2004).

The fourth species, *Megantereon microta*, is known from the Early Pleistocene of southern China and is significantly smaller in size than the northern China *M. nihowanensis* (Zhu et al., 2014, 2015). In a later revision, Zhu et al. (2020) further supported the validity of this primitive species, with short c-p3 and large, double-rooted p3, while also recognizing a derived condition in the small P4 protocone.

The validation of above-mentioned species, however, is not widely accepted. Especially whether the younger species of northern China, i.e. *M. inexpectatus* should be assigned to *M. cultridens* as proposed by Palmqvist et al. (2007). When this taxon was known only from a single skull, it was difficult to determine whether the observed differences from *M. nihowanensis* represented interspecific distinction or intraspecific variation, especially given the then poorly understood morphological range of *M. nihowanensis*. This taxonomic uncertainty has hindered a more systematic revision of *Megantereon* in northern China.

Here, we describe a nearly complete cranium and several isolated teeth of *M. inexpectatus* from Bajiazui, Qingyang, representing the second confirmed locality for this species. The cranium was briefly described and figured by Wang (2006), but the lower dentition and other materials have not been previously reported. In addition, several newly discovered skulls from Longdan are also figured and included in our analysis of craniodental morphology to assess intraspecific variation within *M. nihowanensis*.

### Geological background

Bajiazui fauna were found in the bottom of the Wucheng loess in Qingyang, Gansu province. A rich amount of fossil mammals, including *Talpinae* gen. et sp. indet., *Eospalax* sp., *Allosiphneus arvicolinus*, *Ochotona* sp.1, *Ochotona* sp.2, *Hystrix* sp., *Sinicuon chihliensis*, *Vulpes chikushanensis*, *Meles teilhardi*, *Pachycrocuta brevirostris*, *Megantereon inexpectatus*, *Homotherium* cf. *crenatidens*, *Coelodonta nihowanensis*, *Proboscidiapparion sinensis*, *Equus qingyangensis*, *Equus wangi*, *Equus*

*teihardi*, *Sus lydekkeri*, *Eucladoceros* sp, *Gazella sinensis*, *Bison palaeosinensis* and *Leptobos* cf. *amplifrontalis* were identified from this locality (Deng & Xue, 1999; Wang, 2006). The age of the Bajiazui fauna remains somewhat contentious. We concur with Xue et al. (2006) and Bartolini-Lucenti et al. (2023) that it dates to somewhere between 1.8–1.2 Ma, placing it slightly after the classical Nihewan fauna.

The Longdan fauna from Dongxiang, Gansu has been comprehensively studied in the monograph of Qiu et al. (2004) and several proceeding additions (Deng, 2012; Qiu et al., 2009; Wang, 2005). The fauna is dated to 2.2–2.5 Ma (Qiu et al., 2004) and has yielded the world's largest known sample of *Megantereon* remains. Except those described by Qiu et al. (2004), several new found or prepared skulls are also included in this study for the evaluation of intraspecific variation.

### Materials and methods

The *Megantereon* material described here is housed in the Northwest University (Xi'an, China). For comparison, *Megantereon* specimens from AMNH, ANSP, CECC,

HMV, IVPP, NMB, UCMP were checked for comparison. *Smilodon* spp. from AMNH, LACM, LACMHC and UF were also compared.

The location and chronology of fossil localities are illustrated in Fig. 1.

For the craniodental measurements see Jiangzuo and Liu (2020) and Fig. 2. The terminology of cranium follows Qiu et al. (2014) with modification.

### Anatomical abbreviations

H Height

L Mesiodistal length

M/m Upper/lower molar

P/p Upper/lower premolar

W Buccolingual width

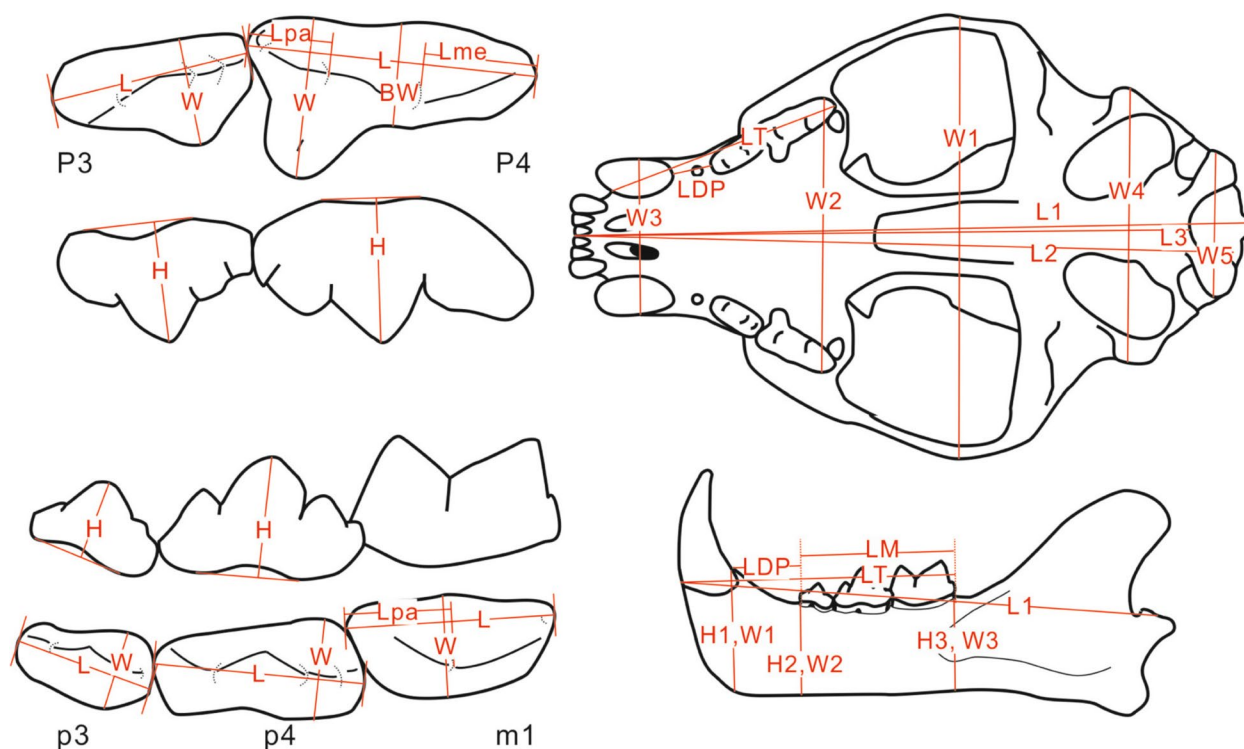
### Repositories and institutional abbreviations

AMNH FM Fossil mammal collection, American Museum of Natural History

AMNH F:AM Frick fossil mammal collection, American Museum of Natural History



**Fig. 1** Fossil localities of *Megantereon* in North China



**Fig. 2** Raniodontal measurements for felids. H1-3 and W1-3 in the mandible represent the mandibular height and width posterior to the canine, anterior to the p3, and posterior to the m1

**ANSP** Academy of Natural Sciences of Drexel University, Philadelphia, PA, USA

**CECC** Center for Conservation and Étude des Collections, Lyon, France

**HMV** Hezheng Paleozoological Museum

**IVPP** Collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences

**LACM** Natural History Museum of Los Angeles County, Los Angeles, USA

**LACMHC** Natural History Museum of Los Angeles County, Hancock Collection, Los Angeles, USA

**NMB** Naturhistorisches Museum Basel, Basel, Switzerland

**UCMP** University of California Museum of Paleontology, Berkeley, USA

**UF** University of Florida Museum of Natural History, Gainesville, USA

### Systematic palaeontology

Family Felidae Fisher [de Waldheim], 1817

Subfamily Machairodontinae Gill, 1872

Tribe Smilodontini Kretzoi, 1929

Genus *Megantereon* Croizet et Jobert, 1828

*Megantereon inexpectatus* (Teilhard de Chardin, 1939)

*Megantereon* cf. *inexpectatus*: Wang, 2006, p.32

**Holotype.** IVPP RV39094. A complete cranium lacking the zygomatic arch, from Loc.1 of Zhoukoudian.

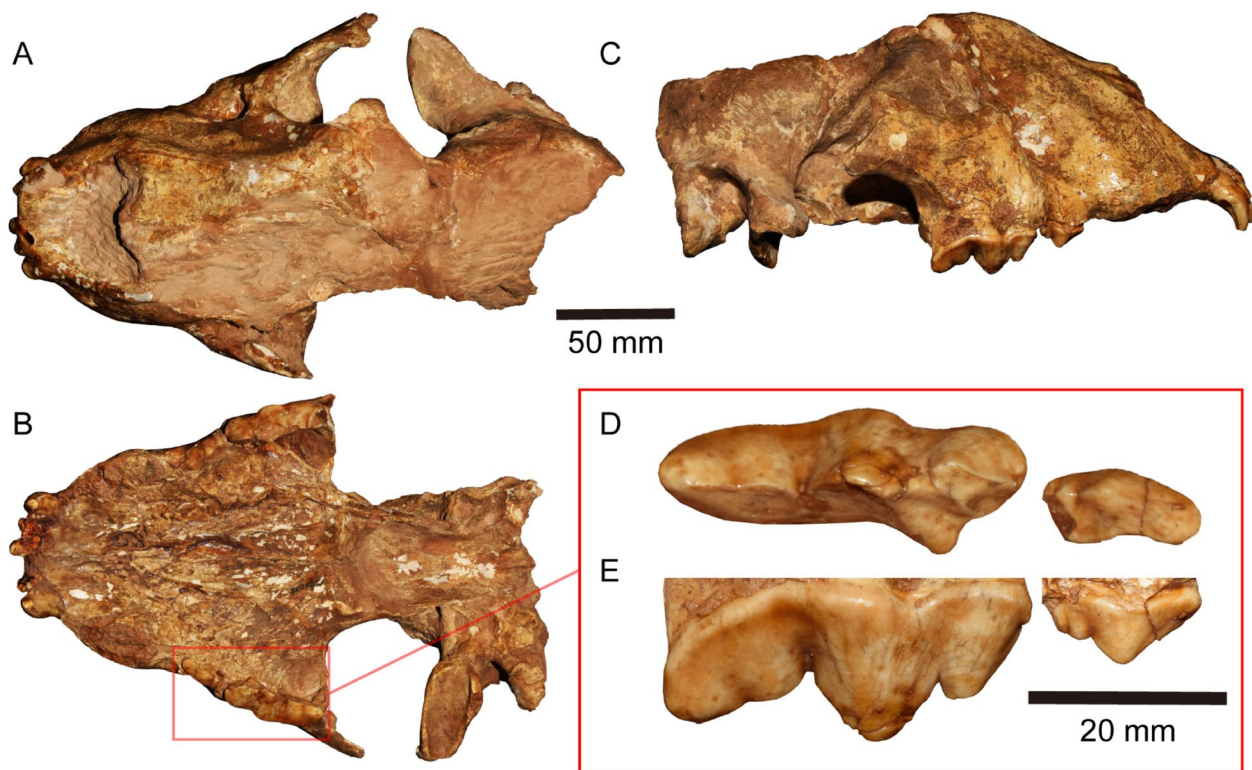
**Described material.** M63025, a mostly complete cranium, lacking the basicranial and occipital part; M63025.1, an isolated upper canine; M63027, a mandibular fragment with p4 and m1; M63032, an isolated m1; MLS006, isolated p3 and p4.

**Emended diagnosis.** Large sized *Megantereon*, equal or slightly smaller than *Megantereon* from southern Asia. Dorsal contour with an angle anterior to orbit. Rostrum very wide. P3 not reduced in length and slender, with small angle with P4. P4 elongated, with very small protocone.

**Description.** The skull is undeformed, lacking the basicranial and dorsal part of the braincase.

**Dorsal view** (Fig. 3A): The skull M63025 is robust and broad. The nasal is wide, and slightly tapers backward. The posterior process of the premaxilla is greatly elongated, extending to 2/3 of the nasal length, with only a short distance (13.06 mm) with the anterior process of the frontal. The latter process is distinct but short. The postorbital process of the frontal is well developed, and a distinct postorbital constriction is present. The lateral wall of the braincase exhibits only a very weak concavity.

**Lateral view** (Fig. 3C): The anterior contour of the naris opening is nearly straight, while the dorsal contour



**Fig. 3** Cranium and upper cheek teeth of the *Megantereon inexpectatus* (M63025). **A** dorsal view of cranium; **B** ventral view of cranium; **C** lateral view of cranium; **D** occlusal view of upper cheek teeth; **E**, buccal view of upper cheek teeth. Scale bars represent: 50 mm (A–C); 20 mm (D–E)

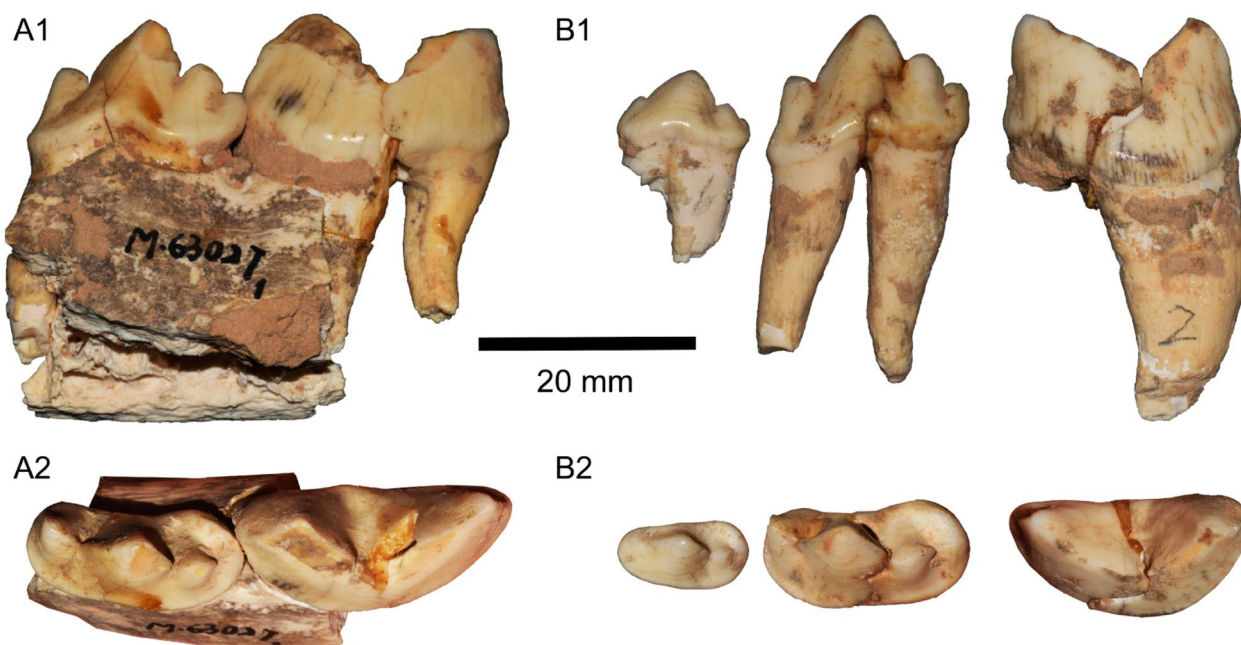
of the nasal is slightly concave. A distinct angular break is present on the dorsal border at the orbit. The infraorbital foramen is distinctly posteriorly inclined, located at the level between the P3/P4. The orbit is located significantly higher than the infraorbital foramen, and at the level of the P4 parastyle. The jugal extends anteriorly to the orbital margin, reaching the level of the lacrimal fossa, but does not project further anteriorly. The postorbital process of the jugal is well defined. The glenoid fossa is strongly extended ventrally.

**Ventral view** (Fig. 3B): The incisor row is straight, not procumbent. The rostrum is broad and widened backward. The diastema between the canine and the P3 is mesiodistally large. There are distinct ridges in the palate, starting from the anterior palatine foramen. These ridges converge anteriorly and fade near the ventral border of the medial pharyngeal fossa (bony choana). The area between the two ridges is concave, but with a central ridge. There is a distinct tubercle at the base of the bony choana. The glenoid fossa is antero-posteriorly wide. A large oval foramen is present medial to the fossa. The mastoid process is well developed. A central ridge is present in the basicranial region.

**Dentition** (Fig. 3D, E, Fig. 4): The left I1-3 and right I2-3 are preserved, but I2s from both sides are highly

broken and no morphology can be seen. The I1 is small, with two distantly located posterior accessory cusps. The orientation of the two accessory cusps forms a V shape. The I2 is slightly larger than the I1. The I3 is distinctly larger than the I1 and I2. There are two small accessory cusps in its mesial border, whereas no accessory cusp in the buccal border. The canine is mesiodistally large judging from the alveolus.

The P3 is mesiodistally elongated. The widest part of the tooth lies at the level between the main cusp and distal accessory cusp. The mesial accessory cusp is absent, a very slight contraction is present just before the main cusp, whereas the distal accessory cusp and distal cingulum cusp are both well developed. The P4 has a strongly undulated buccal contour, with a distinct buccal convexity at the paracone. There is no preparastyle. A small tubercle is present on the mesial cingulum of the right P4 parastyle, while it is indistinct on the left P4, likely a vestigial trace left by the reduction of the preparastyle; However, it might also represent merely a dental variation, as it is positioned only at the mesial end of the mesial cingulum, slightly offset toward the buccal side, and does not align linearly with the tip of the parastyle. The protocone is distinctly reduced in size. There is no cusp in the protocone.



**Fig. 4** Lower cheek teeth of the *Megantereon inexpectatus*. **A.** M63027 (p4 and m1); **B.** MLS006 (p3 and p4); **C.** M63032 (m1). 1. buccal view; 2. occlusal view. Scale bars represent: 20 mm

M63025.1 is nearly complete, but lacking the tip of the canine cusp. It is elongated without serration. The p3 of MLS006 is low-crowned and becomes buccolingually wide distally. Traces of the fusion of double roots can be seen in the middle of p3. The mesial accessory cuspid is very small, whereas the distal accessory cuspid is slightly larger. The distal cingulid is present but weakly developed. The p4 of M63027 is clearly distally tilted, especially its mesial accessory cuspid and the main cuspid. In occlusal view, the mesial accessory cuspid is distinctly medially turned. The distal accessory cuspid is similar to the mesial accessory cuspid in size. The distal cingulid is well developed and cusp-like in its distal end. The p4 of MLS006 has the same morphology. The m1s of M63027 and M63032 are both with only two cusps, and the paracoid is buccolingually wider and mesiodistally shorter.

Measurements are given in Tables 1 and 2.

## Comparison

### Comparison with holotype of *M. inexpectatus*

The cranium described in this study was very briefly described and assigned to *Megantereon cf. inexpectatus* by Wang (2006), based on morphometric analyses showing closest affinity to *M. inexpectatus* holotype specimens, however no detailed traits were analysed and no comprehensive comparison was made.

The holotype skull of *M. inexpectatus* (IVPP RV 39094, Fig. 5B, Fig. 6M) from Zhoukoudian Loc. 1 in Beijing, with the site dated to approximately 0.58–0.69 Ma (Chen

**Table 1** Cranial and upper dentition measurements of specimens from Bajiazui (mm)

	M63025 (left)	M63025 (right)
CL	~30	25.63
CW		12.82
P3L	17.32	16.52
P3W	8.42	8.22
P3W/L	0.49	0.50
P4L		37.32
P4W		14.72
P4W/L		0.39
P3L/P4L		0.443
LT	94.42	94.40
W1	158.6+	
W2	103.63	
W3	72.99	
LDP	8.92	9.34
LDP/LT	0.094	0.099

W1: maximum width across the zygomatic arches; W2: maximum transverse width across P4s; W3: maximum width across canine crowns; LDP: length of the diastema between the canine and P3

& Zhou, 2009; Shen et al., 2009) or around 0.5 Ma (Jiangzuo et al., 2018). It shares numerous cranial features with M63025, including a robust and broad skull, wide nasals and distinct angular dorsal contour anterior to the orbit (Fig. 5A, B). However, numerous differences exist between them. The posterior process of the premaxilla

**Table 2** Mandibular measurements of specimens from Bajiazui (mm)

	M63027	M63032	MLS006
p3L			11.70
p3W			6.25
p3W/L			0.53
p4L	21.02		18.62
p4W	9.88		8.31
p4W/L	0.47		0.45
m1L	25.5	21.86	
m1W		10.84	
m1W/L		0.50	
p4/m1	0.82		

in the Zhoukoudian specimen demonstrates greater posterior extension, reaching three-quarters of nasal length, and directly articulates with the anterior process of frontal without any gap, whereas the Bajiazui specimen shows shorter extension with a distinct gap. Regarding dental characteristics, both P3 and P4 of Zhoukoudian specimen and Bajiazui specimen are extremely buccolingually narrow and mesiodistally elongated, particularly in the P4, which is characterized by a blade-like crown structure. The protocone of the P4 is highly reduced. Additionally, the P3 of the Zhoukoudian specimen possesses both mesial additional cusp and mesial accessory cusp, with the widest portion of P3 located at the middle of the main cusp. A distinct preparastyle is also observable on P4.

We separately compared the Bajiazui specimens with both the Linyi specimen (Shanxi Province, China), the Gongwangling specimens (Lantian, Shaanxi Province, China) all previously referred to *M. inexpectatus* (Li & Sun, 2021).

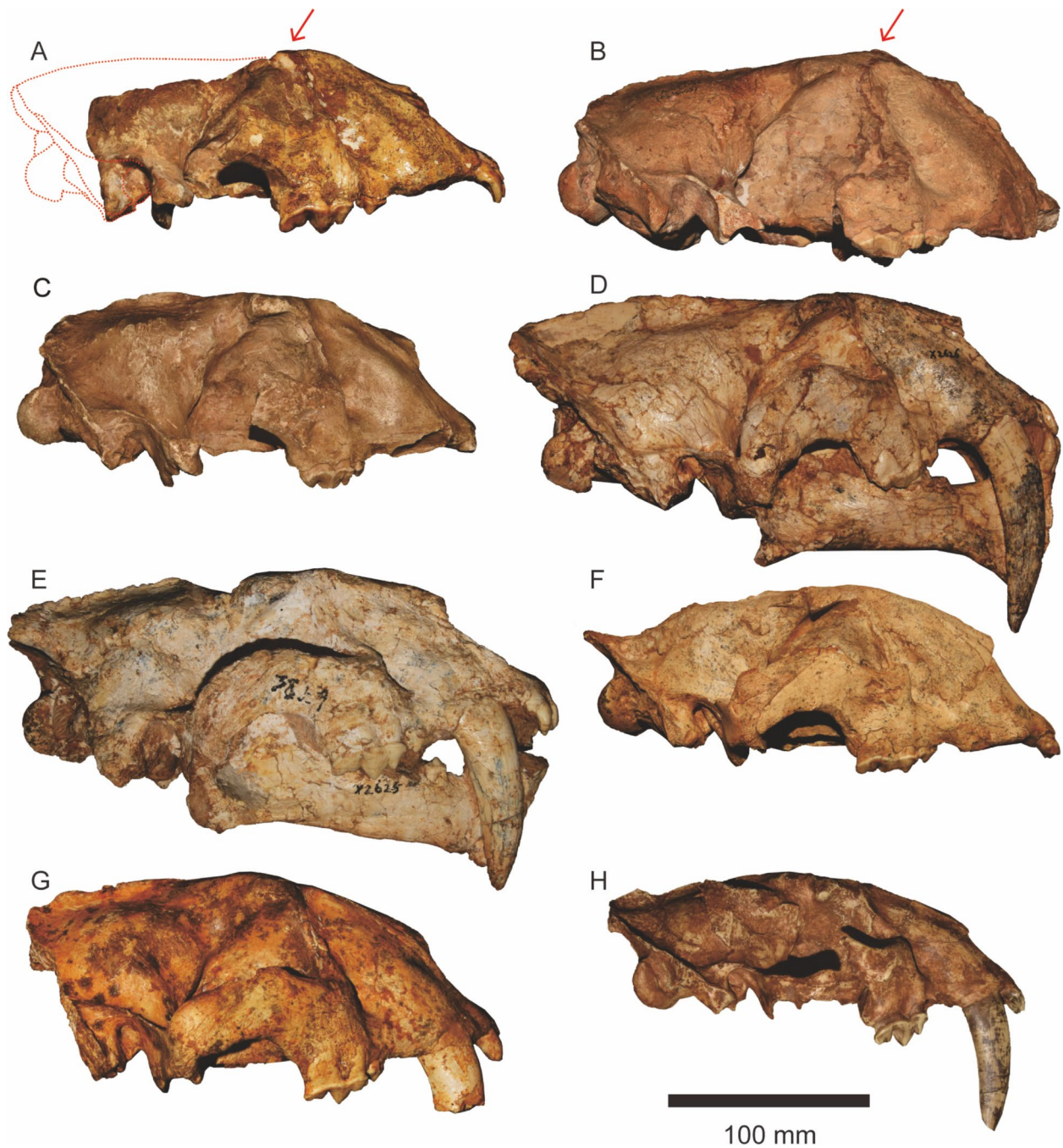
#### Compared with Linyi *Megantereon* specimen

Originally described by Chow (1965) as *M. nihowanensis*, the specimens (IVPP V3034, Fig. 6K) from Linyi, Shanxi (1.15–0.9 Ma) has a distinct P4 protocone and smaller size (Yue et al., 1994). However, our comparisons show that while the P4 protocone in Bajiazui specimen is less reduced than in the Zhoukoudian Loc. 1 specimens, this cusp already exhibits apparent reduction compared to that of *M. nihowanensis*. Li (2021) previously identified an increase in body size and reduction of the protocone as relatively stable evolutionary trends in *Megantereon*, assigning the Linyi specimen to an early evolutionary stage of *M. inexpectatus*. This trend of body size increase through time is further supported by recent research (Argant, 2025). We interpret increased body size as an evolutionary trend from *M. nihowanensis* to

*M. inexpectatus*, though this character exhibits considerable plasticity and cannot serve as a primary diagnostic criterion. We found that they share common characters: the mesial accessory cusp of P3 is absent. There is a slight constriction on the anterior side of the main cusp. The distal accessory cusp of P3 is nearly the same size as the distal cingulum cusp. P4 lacks a preparastyle and shows a highly reduced protocone. The long axis of the P3 and P4 are nearly parallel. However, the Linyi specimen exhibits significantly smaller body size, and its P4 is generally less mesiodistally elongated and relatively wider compared to that of the Bajiazui specimens. Given that the Linyi specimen displays more derived features than *M. nihowanensis* while retaining a smaller body size, we tentatively assign it to *Megantereon* sp., distinguishing it from the larger-bodied *M. inexpectatus* represented by the Zhoukoudian specimens. The derived and small-body size of Linyi specimen is reminiscent of *M. adroveri* in Europe, but more material evidence is needed to further discuss its affinity.

#### Comparison with the Gongwangling *Megantereon* specimens

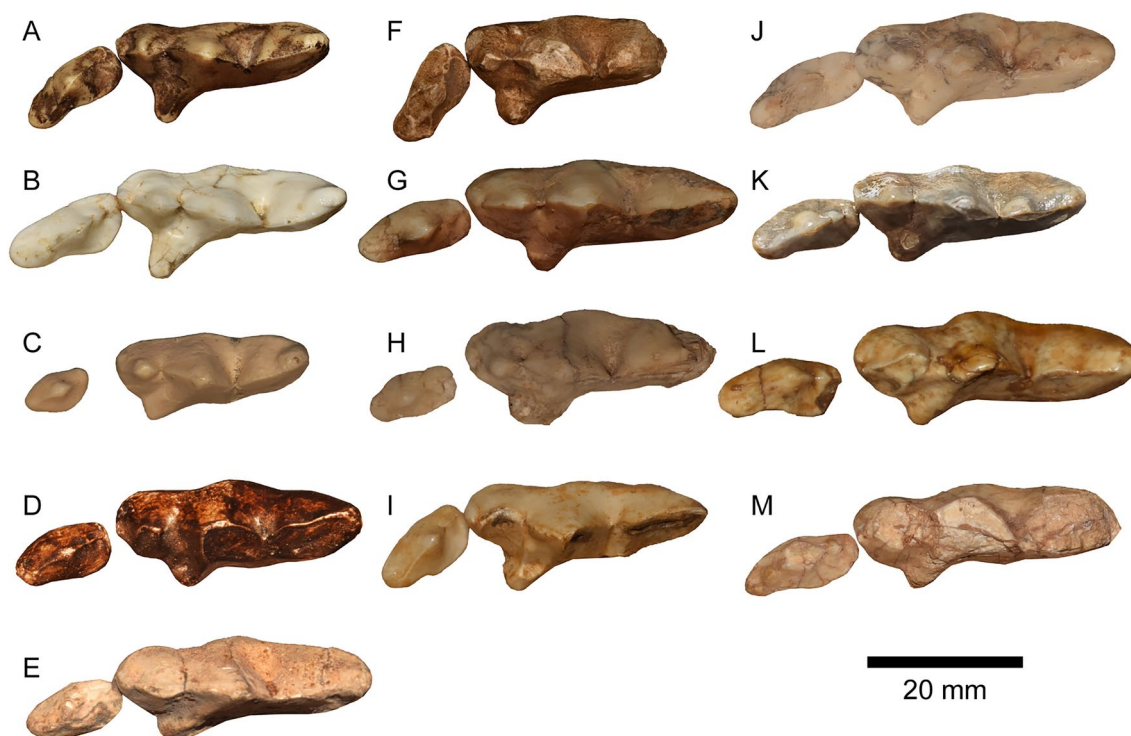
The Gongwangling site in Lantian County of Shaanxi Province was initially dated to approximately 1 Ma based on paleomagnetic studies of the fossil-bearing strata in the Gongwangling Fauna (Hu & Qi, 1978). Qiu (2006) proposed an age of ~1.3 Ma for the Gongwangling hominin based on paleoclimatic and paleontological evidence, while Zhu et al. (2015) determined a significantly older age of ~1.63 Ma through paleomagnetic analysis combined with climatic stratigraphic correlations of the loess-paleosol sequence. Li (2021) summarized previous studies and concluded that the Gongwangling and Linyi faunas are of correlative age. The specimens (IVPP V 2979.1-3) from Gongwangling were initially classified as a new species *M. lantianensis*. Subsequently, Qiu (2004) inferred the specimens as *M. inexpectatus* based on mandibular and dental characteristics combined with measurements. Li et al. (2021) also demonstrated that the anteroposterior diameter of upper canines exhibits intraspecific variation, and observed that the mean lengths of upper versus lower carnassials within the same species show significant disparities. These characteristics cannot therefore serve as reliable diagnostic features. The Bajiazui and Gongwangling specimens share several morphological characteristics: the mesial accessory cusp of p3 is markedly reduced, the P4/m1 length ratio is smaller than in *M. nihowanensis*. However, there are still some differences. The p3 of the Bajiazui specimens (MLS006) has not significantly reduced in size, the mesial accessory cuspid remains visible, and the distal cingulid is well developed. In contrast, the p3 of the Gongwangling



**Fig. 5** Comparison of cranium of *Megantereon*. **A–B:** *Megantereon inexpectatus*, **A.** M63025 (Bajiazui); **B.** IVPP RV 39094 (Zhoukoudian Loc. 1). **C–G:** *M. nihowanensis*, **C.** IVPP M0048 (Nihewan); **D.** HVM 2026 (Longdan); **E.** HVM 2025 (Longdan); **F.** HVM1215 (Longdan); **G.** IVPP V 26878 (Sabertooth Cave). **H:** *M. megantereon*, AMNH FM105446 (cast, Perrier). Red arrows indicate the position of the frontal convexity in *M. inexpectatus*. Scale bars represent: 100 mm

specimen has significantly reduced in size, the occlusal surface is shaped like a small oval, the mesial accessory cuspid is significantly reduced and scarcely discernible, while the distal cingulid is entirely absent. The p4 of the Gongwangling specimen has a larger proportion of the

main cuspid, and the distal cingulid is somewhat reduced compared to that of the Bajiazui specimens. Additionally, given similar size of Gongwangling specimen and Bajiazui specimens (MLS006, M63032), the Gongwangling specimen has a broader p4, along with a more elongated



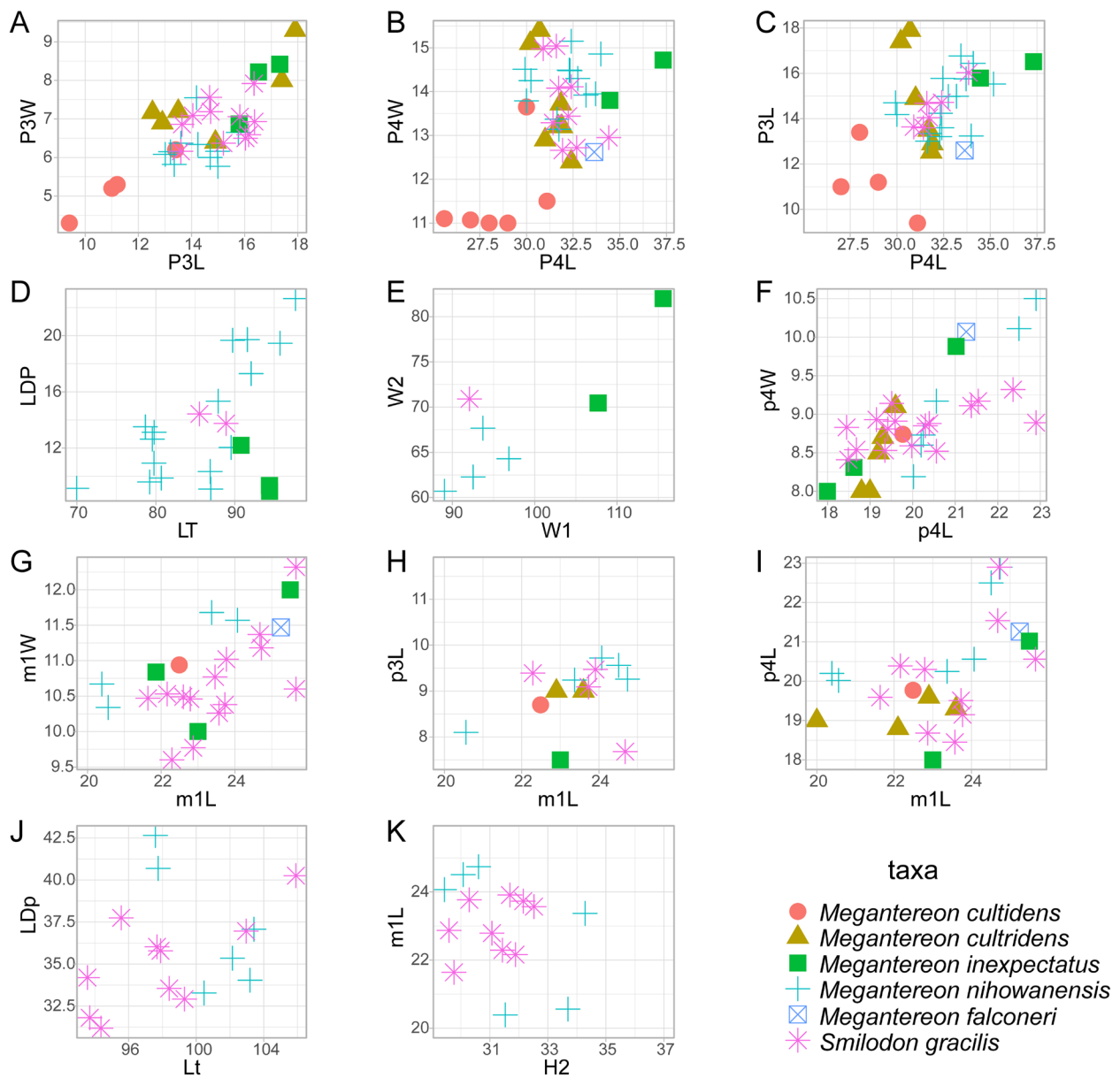
**Fig. 6** Comparison of upper cheek teeth of *Megantereon*. A-B: *Megantereon megantereon*, A. AMNH FM105446 (cast, Perrier); B. FSL20-16892 (Saint-Vallier). C: *M. whitei*, AMNH FM101471 (Koobi Fora). D: *M. cultridens*, AMNH FM113848 (Upper Valdarno). E: *M. falconeri*, ANSP10247 (cast, Pinjor). F-J: *M. nihowanensis*, F. IVPP M0048 (Nihewan); G. HMV 2025 (Longdan); H. HMV 2024 (Longdan); I. IVPP V 26878 (Sabertooth Cave); J. HMV 1696 (Longdan). K: *M. sp.*, IVPP V 3034 (Linyi). L-M: *M. inexpectatus*, L. M63025 (Bajiazui); M. IVPP RV 39094 (Zhoukoudian Loc. 1). Scale bars represent: 20 mm

m1 compared to that of the Bajiazui specimen. The proportional reduction of p3 and p4 relative to m1, coupled with m1 elongation, is generally considered more as advanced features appear in genus *Megantereon* (Li et al., 2021). Based on comparative analysis, the Gongwangling specimens belong to *M. inexpectatus* and represents a slightly more derived stage than the Bajiazui specimen.

#### Comparison with *M. nihowanensis*

The holotype specimen of *M. nihowanensis* is IVPP M0048 (Figs. 5C and 6F) from Nihewan, Hebei (Teilhard de Chardin & Piveteau, 1930). For comparative purposes, we primarily examined a large number of *M. nihowanensis* specimens from Longdan, Gansu (2.2–2.5 Ma) (Qiu et al., 2004). It has been argued that *M. nihowanensis* and *M. cultridens* share numerous similarities and should be considered conspecific (Ficcarelli, 1978; Li & Sun, 2021; Martínez Navarro & Palmqvist, 1995; Pons Moyà, 1987; Turner, 1987; Viret et al., 1954), although this view is not universally accepted (Berta & Galiano, 1983; Li et al., 2021; Qiu et al., 2004; Schaub, 1934; Sotnikova, 1989; Teilhard de Chardin, 1939; Teilhard de Chardin & Leroy, 1945).

While our interpretation leans toward their synonymy, a detailed treatment of this issue is beyond the scope of the present paper. Despite the overall cranial similarities between *M. inexpectatus* and the *M. nihowanensis*, many specific characteristics of *M. inexpectatus* fall outside the range of intraspecific variation. As shown in Fig. 7, our measurements provide clear evidence for these distinctions. Specifically, the maxillary length of *M. inexpectatus* falls within the range of *M. nihowanensis* (Fig. 7D), while its maxillary width significantly exceeds that of *M. nihowanensis* (Fig. 7E). The infraorbital foramen in *M. inexpectatus* is positioned more anteriorly and is larger than that of *M. nihowanensis*. The anterior palatal foramen of *M. nihowanensis* is located more anteriorly, is elongated, and its anterior margin lies in close proximity to the upper incisors. The key difference between the two is observed in P4: the P4 of *M. nihowanensis* is relatively mesiodistally short with a well-developed protocone, resulting in a triangular occlusal outline, whereas *M. inexpectatus* possesses an mesiodistally elongated (Fig. 7B, C), narrow P4 with reduced protocone, reflecting enhanced cutting adaptation (Teilhard de Chardin, 1939).



**Fig. 7** Bivariate plot to depict the size differences among the various species of the genus *Megantereon* (*M. cultridens*, *M. inexpectatus*, *M. nihowanensis* and *M. falconeri*) and *Smilodon gracilis*. L: length; W: width; LDP/LDp: length of the diastema between the canine and P3/p3; LT: length of the tooth row from the anterior edge of the canine to the posterior edge of the cheek teeth (C-P4 toothrow length); W1: maximum width across the zygomatic arches; W2: maximum transverse width across P4s; Lt: mesiodistal length from p3-m1; H2: vertical height at the posterior margin of m1

The new *M. nihowanensis* specimens from Longdan significantly enrich comparable materials for this species. Cranial shows that in some individuals of *M. nihowanensis*, the dorsal contour also possesses an angle anterior to the orbit (Fig. 5C, D, G), as previously noted by Qiu et al. (2004), and this angle appears even more prominent in *M. inexpectatus*. However, this characteristic is either absent or weakly developed in other *M. nihowanensis*

specimens (Fig. 5F). In *M. megantereon*, the dorsal contour anterior to the orbit is distinctly flat (Fig. 5H). Furthermore, in terms of the upper cheek teeth, the P3 of *M. nihowanensis* is generally mesiodistally shorter and buccolingually broader (Fig. 7A), with a particularly marked reduction in occlusal area in Fig. 6H, I. In contrast, the P3 in Fig. 6J is narrow and elongated in form. A reduced mesial accessory cusp characterizes all *M. nihowanensis*

specimens, reaching complete absence in Fig. 6H. The distal accessory cusp and posterior cingulum remain distinct in all specimens; the distal cingulum in Fig. 6G remains cusp-like. The P4 in Fig. 6J, G is characterized by relatively shorter and broader proportions, contrasting with the narrower and more elongated morphology of other specimens. The protocone is moderately developed, with notable reduction in Fig. 6J, H and G, and is already relatively weak, but it is still slightly more distinct than that of the *M. inexpectatus* representatives from Zhoukoudian Loc. 1 and Bajiazui. The preparastyle remains distinct in most specimens but shows considerable reduction in Fig. 6J, H, becoming virtually imperceptible in Fig. 6J. Thus, the narrow and elongated P3–P4 with reduced P4 protocone, distinctive features prominently developed in *M. inexpectatus*, are already incipiently observable in some *M. nihowanensis* individuals. Additionally, Morphological comparison with *M. nihowanensis* reveals a distinct trend of reduction in the lower dentition of *M. inexpectatus*. The p3 of *M. inexpectatus* is distinctly shorter, with its length falling completely outside the range of *M. nihowanensis* (Fig. 7H). A trend of reduction in p4 length is also evident in some specimens of *M. inexpectatus* (Fig. 7I).

#### Comparison with *M. adroveri*

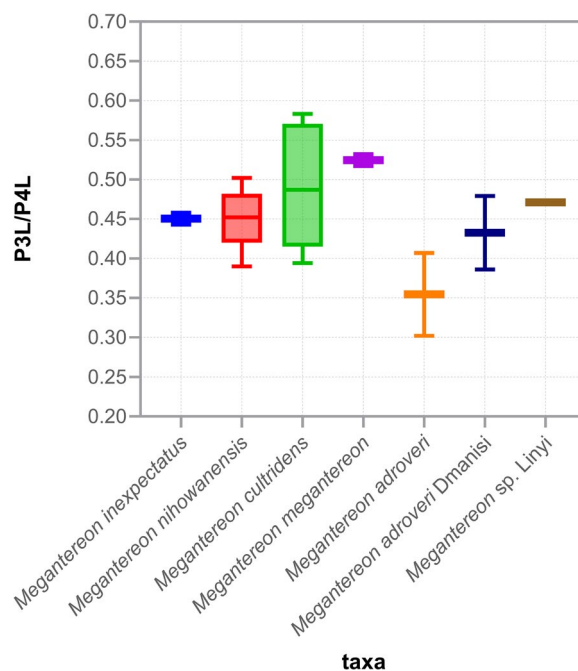
The most derived European species, *M. adroveri* was erected based on mandible from Venta Micena by Pons Moyà (1987). The age of the locality is thought to be approximately 1.6–1.5 Ma (Rodríguez-Gómez et al., 2017). Originally, *M. adroveri* was designated as a new subspecies (*Megantereon cultridens adroveri* n. ssp.) based on two key morphological characteristics: (1) the more reduced morphology of its p3 and p4 compared to that of *M. nihowanensis* and *M. cultridens*, and (2) morphometric analyses demonstrating its smaller size relative to specimens from Puebla de Valverde (Kurtén, 1977) and Vald'Arno (Ficcarelli, 1978) (Martínez-Navarro & Palmqvist, 1995; Pons Moyà, 1987). Martínez-Navarro & Palmqvist (1995) proposed that *M. adroveri* originated from the African *M. whitei* through a northward migration event that led to the replacement of European *M. cultridens*, based on their comparative analysis of dental morphology (particularly P4 and lower cheek teeth measurements) and body size estimations, it is untenable. The p3 of *M. whitei* is highly reduced, becoming very small or even absent, and their incisors and mandibular flange are also not well-developed (Lavrov et al., 2022). These characteristics show almost opposite trends in *M. adroveri*, making it impossible for them to belong to the same species.

In contrast to *M. adroveri*, *M. inexpectatus* represents a morphologically distinct form characterized by

significantly greater body size, an unreduced P3 in the upper cheek teeth, with these differences being numerically evident in its greater P3/P4 length ratios (Fig. 8). Material of *M. adroveri* from Untermassfeld (IQW 1992/24 037 [Mei. 23 560]) exhibits: smaller body size, reduced P3 with absent mesial accessory cusp, markedly reduced distal accessory cusp, and loss of the distal cingulum cusp (Hemmer, 2001). The similarly reduced P3 from Pirro Nord (G1) is confidently attributed to *M. adroveri* based on these morphological synapomorphies (Petrucci et al., 2013).

*Megantereon* from Dmanisi represents the oldest *M. adroveri*, have a smaller body size compared to *M. cultridens* and *M. nihowanensis*. These individuals show a moderately reduced P3 (though still larger in size than in the late-stage *M. adroveri*), while retaining most dental morphology, including a visible distal cingulum cusp and a reduced P4 protocone (Vekua, 1995). Significant variation in P3/P4 length ratio is observed among these specimens (Fig. 8), we interpret this as intraspecific variability. The Dmanisi material is further characterized by small and reduced p3 with an elongated p3–p4 diastema, consistent with diagnostic features of *M. adroveri*. Collectively, these morphological patterns suggest the Dmanisi materials represent an early form of *M. adroveri*.

The specimen (PIN No. 5644/95) from Taurida Cave in Crimea (Lavrov et al., 2022), Russia has a suite of derived characteristics, including a well-developed mandibular



**Fig. 8** Box plot comparing P3/P4 length ratios among *Megantereon* species

flange, prominent incisors and canines, and an elongated c1–p3 diastema, that closely parallel the morphological pattern seen in *M. adroveri* from Dmanisi, Argentina, and Apollonia-1 (Koufos, 2018; Lavrov et al., 2022; Sardella, 1998; Vekua, 1995). Critically, the ratio of m1 anteroposterior length to mandibular vertical height beneath m1 falls intermediate between typical *M. cultridens* and *M. adroveri* values, demonstrating transitional morphology that provides compelling evidence for the anagenetic evolution of European *Megantereon* from *M. cultridens* to *M. adroveri* during the Early Pleistocene (Lavrov et al., 2022).

#### Comparison with *M. falconeri*

*Megantereon falconeri*, originally described by Pomel (1853) and recently revised by Stimpson (2024), is a species recorded in the Upper Siwalik (Pinjor Zone). This species is characterised by an elongated and narrow P4, resembling that of *M. inexpectatus*, though with a less reduced protocone compared to the latter. Overall morphological similarities to *M. cultridens* are present, but significant diagnostic differences exist. Based on our observations of specimen ANSP10247 (Fig. 6E), we found that the P3 is more reduced than in *M. cultridens*, with a short, broad oval occlusal outline, whereas the P4 is narrow and elongated, bearing a small but distinct pre-parastyle. The protocone is reduced, though not to the degree seen in *M. inexpectatus*. Stimpson (2024) found that the P3 of *M. falconeri* falls near the smaller end of the size range for *M. nihowanensis* and overlaps with *M. adroveri*. Further comparative measurements of *M. falconeri* align closely with *M. cultridens* and *M. nihowanensis* in most features, but *M. falconeri*'s reduced P3 and P4 proportions sufficiently distinguish it from these taxa. Werdelin and Flink (2018) considered the only significant distinction between *M. falconeri* and *M. cultridens* to be the larger body size of the former, regarding them as synonymous. Previously, some researchers including Martínez-Navarro & Palmqvist (1995) had also supported the equivalence of *M. falconeri* with *M. cultridens*. Based on our comparative analysis above, distinct diagnostic characteristics clearly differentiate *M. falconeri* from *M. cultridens*. Stimpson (2024) suggested that *M. falconeri* might represent parallel evolution of advanced morphotypes within *M. cultridens*, or an early divergent lineage. We agree with this interpretation, proposing that *M. falconeri* likely originated from a southward dispersal of *M. cultridens* into the Siwalik region, where it developed more derived than *M. cultridens*.

#### Comparison with other *Megantereon* species

*Megantereon megantereon* (Figs. 5H and 6A,B), represented by specimens from the type locality Perrier, has

cranial condylobasal length not exceeding 20 cm, P4 length not exceeding 30 mm and is regarded as valid species as proposed by Qiu (2004) and Liu (2005). The P4 of *M. inexpectatus* is narrower and longer than that of *M. megantereon*, with a much more reduced P4 protocone, and the P3 is proportionally shorter. The features of *M. megantereon* suggest that it is a very primitive species.

*Megantereon ekidoit* is considered the earliest African species (Werdelin & Lewis, 2000), characterised most notably by the absence of p3. In contrast, Africa's Quaternary species, *M. whitei*, retains a highly reduced and small p3. The two species also exhibit differences in mandibular morphology, particularly in the masseteric fossa and coronoid process (Werdelin & Lewis, 2002). There is still some significant morphological difference persist between *M. whitei* and *M. inexpectatus* (Fig. 6C): The P3 of *M. whitei* is more reduced than that of *M. inexpectatus*, exhibiting a diminished mesial accessory cusp and distal accessory cusp, along with a complete loss of the distal cingulum. The P4 of *M. inexpectatus* is relatively narrower and more elongated compared to that of *M. whitei*.

#### Evolution scenario of *Megantereon* in northern China

The evolution of *Megantereon* has long been a widely and hotly debated topic in academia. Turner (1987) proposed that *Megantereon* comprised only a single species, *M. cultridens*, attributing observed size and morphological variations solely to sexual dimorphism, geographic distribution, and temporal differences. This hypothesis has gained widespread acceptance (Turner, 1987; Turner & Antón, 1997). However, Martínez-Navarro (1995) proposed an alternative interpretation, which Palmqvist et al., (2007) subsequently expanded through comprehensive comparative analyses of sexual dimorphism patterns in extant *Panthera pardus* and *Panthera leo* (Martínez Navarro & Palmqvist, 1995; Palmqvist et al., 2007). Their results demonstrated that the morphological disparity between *M. cultridens* and *M. whitei* exceeded the range expected from sexual dimorphism alone, leading them to propose that *Megantereon* consisted of at least two valid species: *M. cultridens* and *M. whitei*. As discussed earlier, other proposed species (e.g., *M. inexpectatus*, *M. adroveri*, *M. falconeri*) also exhibit diagnostic differences that exceed intraspecific variation. Many scholars have corroborated these findings, supporting a more speciose and morphologically diverse *Megantereon* lineage than previously recognised.

Liu (2005) proposed that carnassials (P4, m1) serve as the primary functional tools for feeding in carnivorans, with their morphology, size, and positional relationships holding significant taxonomic diagnostic value. Beyond carnassials, he argued that the other premolars (e.g., P3,

p4) also exhibit high functional importance. By focusing on length ratios of P3/P4 and p4/m1, Liu (2005) delineated three evolutionary lineages within *Megantereon*: One lineage is represented by the clade of *M. megantereon*, *M. inexpectatus*, and *M. hesperus*; ones represented by the clade of *M. cultridens*, *M. nihowanensis* and *M. lantianensis*; and the African lineage is represented by *M. whitei* and *M. eurynodon*. However, numerous diagnostic traits observed across the extensive *M. nihowanensis* specimens from Longdan exhibit intermediate morphological states between *M. nihowanensis* and *M. inexpectatus*. The gradational nature of these characteristics demonstrates an evolutionary relationship between the two taxa. Regarding the P3/P4 and p4/m1 length ratios, we argue that this feature does not represent a stable heritable trait in *M. nihowanensis*, as the ratios already exhibits substantial intrinsic variability within *M. cultridens* and *M. nihowanensis* (Fig. 7C, I; Fig. 8). During later evolution, this characteristic diverged into two distinct morphological trends: one is P3 reduction (exemplified by *M. falconeri*), where the tooth became more reduced; the other is P3 elongation (exemplified by *M. inexpectatus*), resulting in a narrower, more elongated morphology. Li and Sun (2021) inferred that *M. whitei* and *M. inexpectatus* might have originated from two branches of the same African lineage based on the following characteristics: vertical anterior margin of the outline of the mandibular symphysis (unlike *M. cultridens* and *M. nihowanensis*, where the anterior margin of the lateral outline of the mandibular symphysis is distinctly inclined to the horizontal plane) (Arribas & Garrido, 2008), reduced P4 protocones, and single-rooted p3. However, we have observed specimen (C0112) of *M. nihowanensis* with vertical anterior margin of the outline of the mandibular symphysis in our new materials from Longdan, indicating that this feature is also variable. A reduced protocone on P4 and a single-rooted p3 are present in some *M. nihowanensis* specimens from Longdan, with fused roots (from originally double roots) being recorded in *M. inexpectatus* specimens (MLS 006) from Bajiazui. On the other hands, *M. inexpectatus* and *M. whitei* are different in several aspects: *M. inexpectatus* is not only significantly larger in body size, with narrow and elongated upper cheek teeth, and its p3 lacks the pronounced reduction observed in *M. whitei*. While both taxa share certain derived features, we do not observe such a correlation between *M. whitei* and *M. inexpectatus*.

The examination of new *M. nihowanensis* specimens from Longdan reveals a considerable range of variation in several morphological characters, indicating their continuity within the population. These same characters are present in the stratigraphically younger *M. inexpectatus*, where they become more pronounced. Key changes

include a more sharply defined angle on the dorsal orbital border, elongation of the P3 and P4, a further reduced protocone on P4, and a more reduced p3. Given the stratigraphic integrity of the fossil sites, which confirms that *M. inexpectatus* postdates *M. nihowanensis*, the conjunction of morphological continuity and chronological succession strongly supports a mode of anagenesis. As established in prior work, such continuous character transformation is key evidence for recognizing ancestor-descendant relationships (ADR) (Dayrat, 2005; Gingerich, 1985). Consequently, we collectively argue that the morphological and stratigraphic evidence supports an ADR between *M. inexpectatus* and *M. nihowanensis*, and we propose that the evolution of *Megantereon* in northern China represents a single lineage exhibiting a single evolutionary progression.

The significant intraspecific variation within *M. cultridens* and *M. nihowanensis*, rather than merely representing polymorphism, can be viewed as providing the diverse morphological trajectories that facilitated subsequent evolution. The evolution of *M. cultridens* and *M. nihowanensis* gave rise to morphologically and size-divergent lineages across Eurasia, including the large-bodied *M. inexpectatus* and *M. falconeri*, as well as the small-bodied *M. adroveri*. Substantial intraspecific variation observed in *M. cultridens* and *M. nihowanensis* morphology indicates multiple potential directions for genetic divergence to occur. Within populations, the combination of traits with the greatest genetic variation ( $g_{\max}$ ) defines the “line of least resistance” to evolutionary change under natural selection, and evolution tends to follow the path of  $g_{\max}$  potential in recently diverged species (Schluter, 1996). However, shifts in selective pressures can override these internal constraints, driving evolution away from the path predicted by standing variation (Etterson & Shaw, 2001; Renaud et al., 2006). This may explain the divergent morphological adaptations present in the descendants of *M. cultridens* and *M. nihowanensis*.

## Conclusions

New specimens of *M. inexpectatus* from Qingyang and *M. nihowanensis* from Longdan provide direct evidence for the direct ancestor-descendent relationship for *M. nihowanensis* and *M. inexpectatus*. Our systematic review and comparative analysis of Eurasian *Megantereon* reveal that the northern Chinese lineage evolved primarily through anagenesis. However, the ecological and biogeographic drivers behind the divergence of Eurasian *Megantereon* populations require further investigation.

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#### Author contributions

DGG collected data, wrote the manuscript, and supervised the study. JMM collected data and supervised the study. KX, ZYL, CQ, and LL performed faunal dating analysis. QGJZ collected data, wrote the manuscript, and supervised the study. SQW supervised the study. All authors read and approved the final manuscript.

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#### Data availability

No datasets were generated or analysed during the current study.

#### Declarations

#### Competing interests

The authors declare no competing interests.

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