

Evolution of the tiger in mainland eastern Asia

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Abstract: This study presents the first comprehensive overview of tiger (*Panthera tigris*) evolution throughout its entire temporal range, from its Early Pleistocene origins (c. 2.5 Ma) to the present. By integrating morphological, functional and palaeobiogeographical data from across mainland Asia, we identify *Panthera palaeosinensis* as the most likely ancestral form of *P. tigris*. The earliest putative record of the latter dates to c. 1.3 Ma, followed by the appearance of archaic subspecies *P. t. lui* (c. 1 Ma) and the dwarf form *P. t. palaeobeijingensis* (c. 0.75 Ma). Morphological trends indicate progressive adaptations for predation on large prey and rapid killing of medium-sized prey, coupled with

reduced durophagy specializations paralleling those of saber-toothed cats. Body mass reconstructions indicate a general size increase through time, strongly influenced by climate oscillations after the Early–Middle Pleistocene Transition and by the extinction of major competitors. These results provide the first full evolutionary framework for the tiger lineage, highlighting the role of environmental instability in shaping its morphology, size and distribution.

Key words: *Panthera tigris*, *Panthera palaeosinensis*, functional evolution, palaeogeography.

THE tiger (*Panthera tigris*) is the current apex predator in Asian food webs in which they are extant (Tilson & Nyhus 2010) and an iconic symbol in many Asian cultures, exerting significant influence on both ecosystems and human societies. Historically, tigers ranged widely across Asia, from western regions through northeast and southern Asia to the islands of Southeast Asia (Kitchener & Yamaguchi 2010; Sanderson *et al.* 2025). However, due to human activity (primarily direct hunting and habitat destruction) their current distribution and population have drastically shrunk, and several subspecies have gone extinct, and there is an urgent need for protection (Luo *et al.* 2019). To better protect the tiger, we need to

understand their ecological adaptations and habitat requirements, past and present. The study of its evolutionary trajectory and anatomical change through time will greatly help to understand its adaptation to present ecosystems.

Pioneering morphological studies suggested that tigers represent a unique lineage within *Panthera* (Hemmer 1987), whereas molecular phylogeny works supports it as the sister group of the snow leopard *Panthera uncia* (Johnson *et al.* 2006; Li *et al.* 2016; Figueiro *et al.* 2017; Santos *et al.* 2025). Estimated divergence time (molecular clock) of the tiger and snow leopard dates back to the Late Pliocene, 3.47 Ma (Figueiro *et al.* 2017), but the diversification of the modern subspecies is much younger,

during the Late Pleistocene, *c.* 0.1 Ma (Luo *et al.* 2019; Sun *et al.* 2023). Additional DNA studies suggested that at least one ancient population (stem group outside the modern population) still existed in the Late Pleistocene (Hu *et al.* 2022; Sun *et al.* 2023), suggesting rapid dispersal ratio and population turnover in tiger evolutionary history. However, genetic data are limited with regard to the evolutionary history before the modern population diversified. The evolution of the tiger between 3.47 and 0.1 Ma, (i.e. since its divergence from the snow leopard to modern subspecies diversification) is unclear.

Fossil evidence provides pivotal information regarding this gap. Eastern Asia, especially China, has produced a rich fossil record of tigers (*P. tigris*) or tiger close relatives (e.g. *P. palaeosinensis*) from the earliest Pleistocene (Zdansky 1924; Pei 1934, 1940; Hemmer 1967; Qiu *et al.* 2004; Kitchener & Yamaguchi 2010; Mazák *et al.* 2011). However most previous in-depth analyses focused only on one or two well-preserved specimens (Hemmer 1967; Mazák 2010; Mazák *et al.* 2011), without evaluation of intraspecies variation, and the whole picture of tiger evolution is vague. In particular, the key morphological traits, adaptation of the tiger, and how these traits evolved during the whole evolutionary history, still remain to be elucidated. In recent decades, new material regarding tigers and their close relatives has continued to be unearthed in China, spanning from the earliest Pleistocene to the Late Pleistocene, including some very well-preserved ancient skulls. This material provides an opportunity to anatomically review tiger evolution.

In this study, we review and revise the fossil members of the tiger lineage, establish new taxa, explore the evolutionary adaption of the tiger lineage, their geographic expansion and its correlation with climate change.

MATERIAL & METHOD

We examined specimens of extant tigers and other pantherine cats in the natural history collections in Africa, Asia, Europe and North America (for the list of natural history collections see Appendix S1).

The tiger fossil material used in the present study is from the American Museum of Natural history (AMNH, New York, USA), Babiarsz Institute of Paleontological Studies (BIOPSI, Mesa, Arizona, USA), Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP, Beijing, China), Zhoukoudian Site Museum (Zd, Beijing, China), The Geological Museum of China (GMC, Beijing, China), Hezheng Paleozoological Museum (HMY, Linxia, China), Gansu Museum, (GSM, Lanzhou, China), Hubei Provincial Institute of Cultural Relics and Archeology (HPICRA, Wuhan, China), Yunxian Man Site Museum (YMSM, Yunyang, Shiyang, China), Yingliang

Stone Natural History Museum (YLSNHM, Nanan, China), Chongqing Key Laboratory of Paleontology and Paleoenvironment Co-evolution (Sichuan-Chongqing Joint Construction, Chongqing, China), No. 208 Hydrogeological and Engineering Geological Team, Chongqing Bureau of Geological and Mineral Resource Exploration and Development (CYM, Chongqing, China), Yunxian Man Locality Museum (YX, Shiyang, China), Cultural Relics Station of Yunxi County (YXM, Shiyang, China), Palaeontological Museum, University of Uppsala (PMU, Uppsala, Sweden), Kunming Institute of Zoology, Chinese Academy of Sciences (KIZ, Kunming, China), Institute of Zoology, Chinese Academy of Sciences (IOZ, Beijing, China), University of Lyon 1 (UCBL-FSL, Lyon, France), Mammalian collection of Museum für Naturkunde Berlin (ZMB, Berlin, Germany), University of Florida Museum of Natural History (UF, Gainesville, USA) and Museum of Comparative Zoology, Harvard University (MCZ, Boston, MA, USA). Fossil comparative material of *Panthera gombaszogensis* from the Naturhistorisches Museum Mainz/Landessammlung für Naturkunde Rheinland-Pfalz (MNHM, Mainz, Germany) and the collection from Jinyuan Cave, Luotuo Hill, Dalian, housed in the Administrative Committee of Dalian Jinpu New District (DJPJ, Dalian, China), and *Panthera spelaea* from Museum für Naturkunde Berlin (MNB, Berlin, Germany) were also checked.

The anatomical terms of the cranial specimens were taken from Jayne (1898) and Qiu *et al.* (2014). The elements of the craniodental measurements are shown in Figure 1, and listed in Tables S1 and S2. Statistical analyses were performed in R v4.0.1 (R Core Team 2024), while ggplot2 (Wickham 2016) was used to plot the results.

To better study the morphological evolution of dental structure at the population level, eight morphotypes are defined:

1. P3 anterior accessory cusp: 1, absent; 2, weak; 3, strong
2. P3 anterior cingulum: 1, absent; 2, weak; 3, strong
3. P4 buccal concavity: 1, absent; 2, weak; 3, strong
4. P4 preparastyle: 1, absent; 2, weak; 3, strong
5. p4 anterior accessory cuspid: 1, absent; 2, weak; 3, strong
6. p4 middle constriction: 1, absent; 2, weak; 3, strong
7. m1 paraconid robustness: 1, absent; 2, weak; 3, strong
8. m1 paraconid medial ridge: 1, absent; 2, weak; 3, strong.

The population mean score, used in the systematic comparison, is calculated for each morphotype in the studied populations/species/subspecies, as per (Jiangzuo *et al.* 2018).

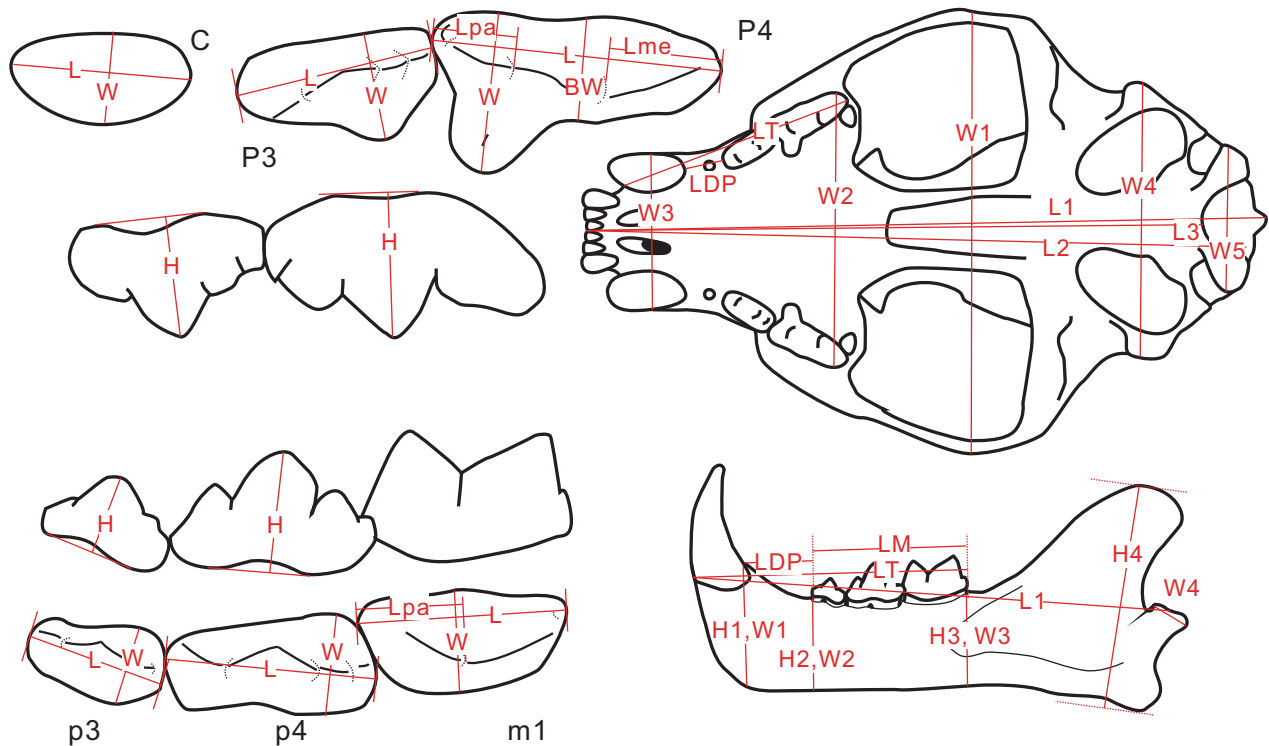


FIG. 1. Craniodental measurements of the tiger used in this study.

RESULTS

Key morphological traits & adaptations of the extant tiger

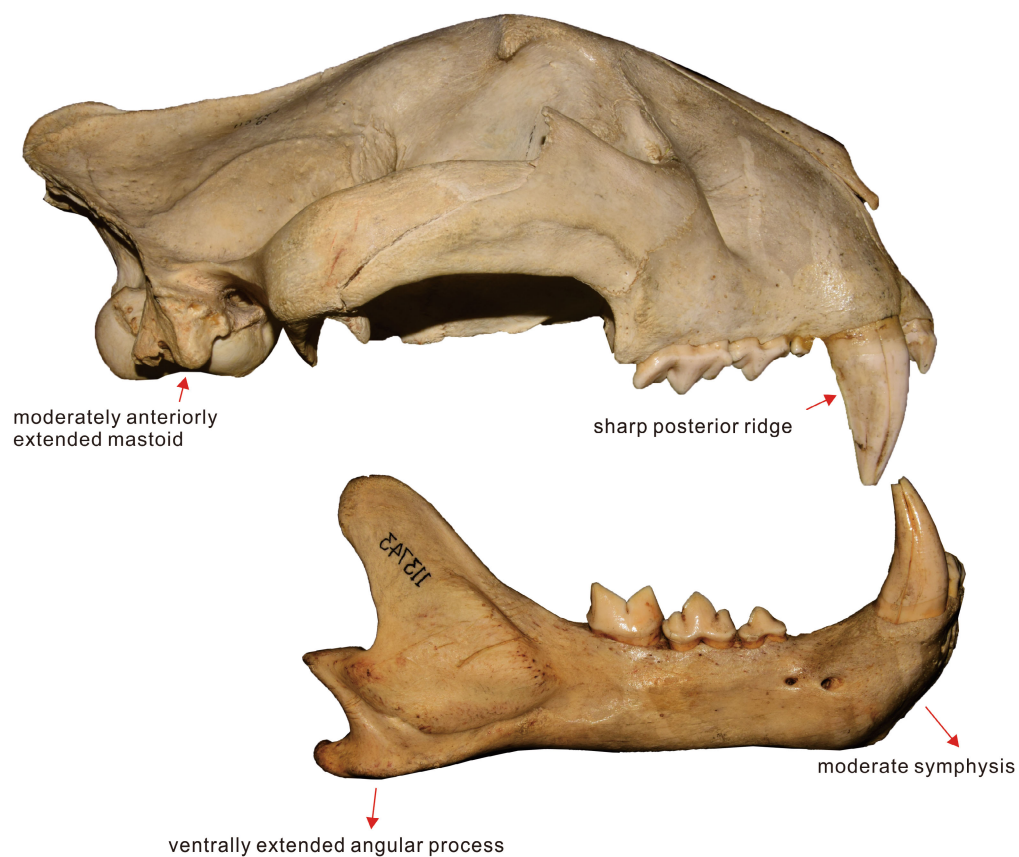
The anatomical cranial main characteristics of the tiger have been studied by many researchers (i.e. elongated nasal, straight mandible ventral profile, straight P4 buccal border; Boule 1906; Pocock 1930, 1939; Haltenorth 1936, 1937; Christiansen 2008; Jiangzuo & Liu 2020). Most of these characters are, however, not related to functional anatomy.

Of the functional characteristics, some relate to the well-developed masticatory muscle system of the tiger. These include the wide zygomatic arch and prominent sagittal crest (Fig. 2A), which provide attachment areas for the extensive masticatory musculature. The angular process exhibits strong ventral extension. While a slight ventral extension of the angular process occurs occasionally in other *Panthera* species and in some *Neofelis* individuals (Fig. 2B–D), this feature is more pronounced in the tiger. The mastoid process is robust and moderately extended anteriorly, exceeding the development seen in lions and other *Panthera* species (Fig. 2A–D). In *Neofelis*, the mastoid is significantly less robust and proportionally smaller, although it is also moderately anteriorly extended. The mandibular symphysis is high in the tiger (large H1/H3 ratio), close to the level of *Neofelis*, and higher than other

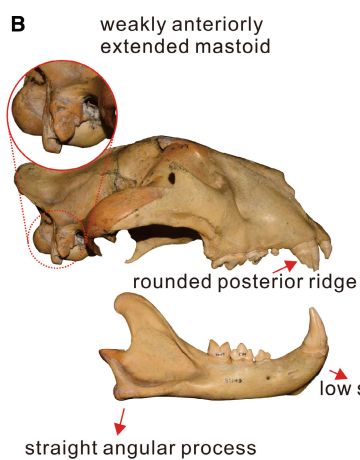
Panthera species. This is related to the large canine. The tiger's angular process and mastoid morphology converge with those of sabertoothed cats, which typically exhibit even greater development of these traits. Functionally, the angular process serves as the attachment site for m. masseter superficialis. Its ventral extension not only increases the muscle's attachment area but also orients the muscle fibres more vertically. This orientation enhances efficiency in generating the upward force component during jaw closure. The mastoid process provides attachment for neck and forelimb muscles, contributing to increased bite force. Consequently, the craniomandibular specialization of the tiger is designed to produce powerful bite forces, achieved through both greater muscle volume and improved bio-mechanical efficiency (Therrien 2006). Note that sabertoothed cats have been suggested to have a relatively weak bite force (Christiansen 2011; Wroe *et al.* 2013; Pollock *et al.* 2025). This is mainly due to the small area of the masticatory muscle in the sabertoothed cat (Christiansen 2007a), and the angular process probably developed to compensate for this.

The dentition of *Panthera* species is generally less differentiated, varying primarily in minor details (Jiangzuo & Liu 2020). Within the genus, tigers possess proportionally the largest canines in terms of anteroposterior diameter (Christiansen 2007b). Moreover, their canines typically have a sharper posterior ridge than those of

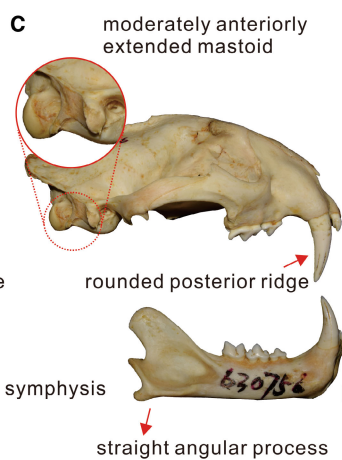
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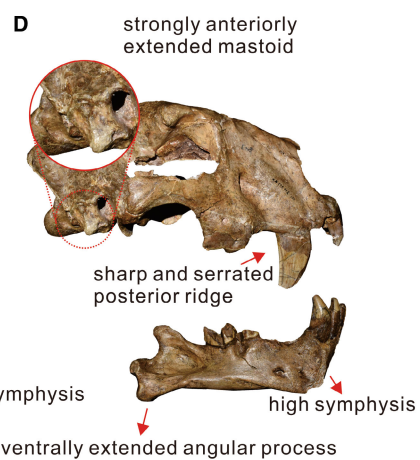
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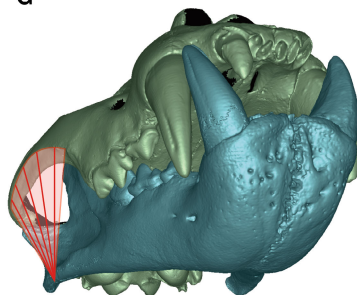
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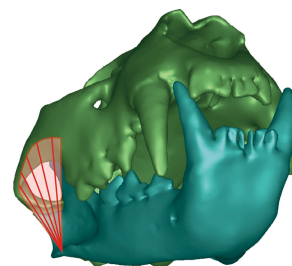


FIG. 2. Functions of the tiger skull. A–D, craniomandibular comparison with other big cats: A, *P. tigris*, AMNH M113743; B, *P. leo*, AMNH M85149; C, *Neofelis nebulosa*, KIZ003114; D, *Homotherium crenatidens*, UCBL-FSL 210986, Senèze. E–F, upper canine comparison in occlusal view, emphasis on the sharper ridge in the tiger: E, *P. tigris*, AMNH M113744; F, *P. leo*, AMNH M54996. G–H, skull comparison, showing the ventrally extended angular in tiger and the more vertical orientation of M. masseter superficialis: G, *P. tigris*, ZMB Mam 56 039; H, *P. pardus*, AMNH M113745. The model of *P. pardus* comes from Tseng (2016). Not to scale.

other extant felids (Fig. 2E, F). These large canines possess slight cutting capabilities, enabling them to cause severe injury and ensure rapid prey mortality. The tiger also retains more primitive cheek teeth, characterized by relatively small premolars with weak accessory cusps (Jiangzuo & Liu 2020). Correspondingly, the mandibular corpus of tigers is shallower, particularly compared with lions, suggesting less frequent consumption of hard tissue such as bone (Fig. 2A–D). The lions, being social hunters, benefit from rapid feeding due to communal consumption and competition with scavengers such as spotted hyenas (Sunquist & Sunquist 2002). Their larger premolars (better adapted for cutting) and deeper mandibles facilitate durophagous behaviour. In contrast, solitary tigers inhabit forests where prey is less accessible to competing carnivores (Kitchener & Yamaguchi 2010), reducing the need for bone-processing adaptations. In tigers, it is likely that the m1 paraconid compensates by becoming more robust and developing a medial ridge (Fig. 3). This trait, again convergent with derived Machairodontinae, enhances the paraconid's cutting ability. The medial ridge gives the paraconid greater resistance to pressure and helps it develop a small, sharp tip as the tooth wears

down moderately. This ultimately increases its effectiveness at cutting tough tissues such as the skin of large mammals (but not hard bone).

SYSTEMATIC PALAEOONTOLOGY

Order CARNIVORA Bowdich 1821

Family FELIDAE Batsch 1788

Subfamily FELINAE Batsch 1788

Genus *Panthera* Oken 1816

Panthera palaeosinensis (Zdansky 1924)

[= *Panthera zdanskyi* Mazák et al. 2011]

Figures 4I–K, 5

Holotype. PMU M3654, a complete skull (Fig. 4I–K).

Emended diagnosis. Medium-sized pantherine (jaguar size) with some tiger-like traits, such as relatively large upper canine, high and vertical mandibular symphysis; nasal extending slightly more distal than maxilla, mastoid moderately anteriorly extended but not robust, auditory bulla long, angular process weakly to

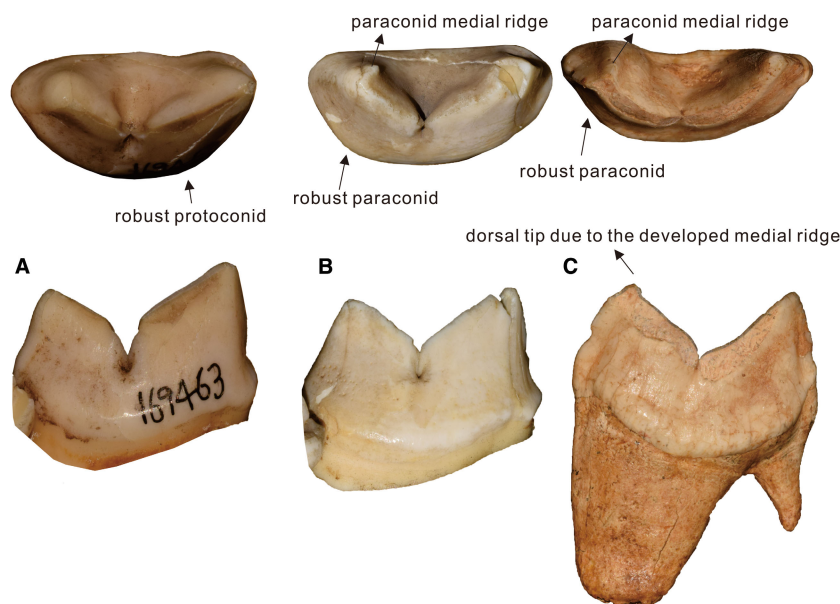


FIG. 3. Comparison of the m1 morphology (occlusal and lateral views), with emphasis on development of the m1 paraconid medial ridge. A, *P. leo*, AMNH M169463. B, *P. tigris*, IOZ 09417. C, *Homotherium serum*, UF22908, from Reddick 1A, Florida. Not to scale.

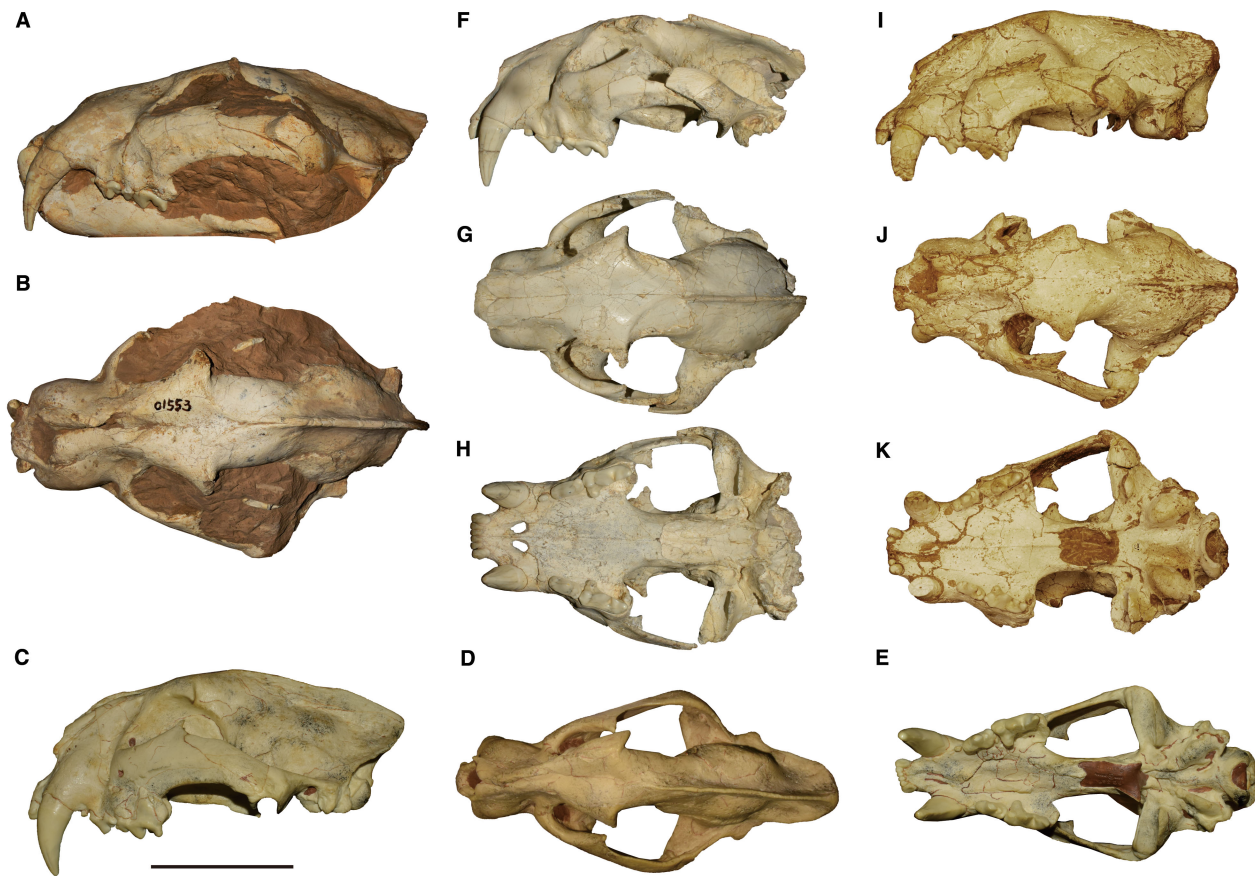


FIG. 4. Fossil crania of *Panthera palaeosinensis* from northern China early Early Pleistocene, in lateral, dorsal and ventral view. A–B, GSM 01553, male, Longdan. C–E, cast of the *P. zdanskyi* holotype (BIOPSI 00177), male, Longdan. F–H, YLSNHM03312, female, Longdan. I–K, *P. palaeosinensis* PMU M3654, holotype, female, Mianchi. Scale bar represents 10 cm.

moderately ventrally extended; P3 often with anterior cingulum, P4 often with small preparastyle; and mostly with buccal concavity between the parastyle and paracone, p4 with enlarged anterior accessory cuspid, m1 with buccolingually widest part at paraconid–protoconid notch, m1 with weak metaconid–taloid complex, m1 without paraconid medial ridge.

Differential diagnosis. Differs from *P. tigris* by having overall small size, shorter nasal, absence of dorsal profile concavity in the sagittal crest, longer rostrum, smaller mastoid process, more elongated auditory bulla, less ventrally extended angular process, more concave P4 buccal border, larger p4 anterior accessory cuspid, absence of m1 paraconid ridge, and less robust m1 paraconid; differs from *P. gombaszoegensis* by having longer nasal, more anteriorly extended mastoid, higher and more vertical mandibular symphysis, shallower mandibular corpus, generally straight mandibular ventral profile, more frequent presence of P3 anterior cingulum and P4 preparastyle.

Type locality. Mianchi, Henan, China c. 2 Ma (Zdansky 1924).

Other localities. Longdan, Dongxiang, Gansu Province, China (2.35 Ma); Longgupo, Wushan, Chongqing, China (2.35 Ma);

Gigantopithecus Cave, Liucheng, Chuifeng Cave, Baise, Guangxi Province, China (2–1.7 Ma); Longgudong, Jianshi, Hubei Province, China (1.4 Ma).

Newly assigned specimens: complete skull, GSM 01553, partial cranium YLSNHM03312 and mandibles HVM2028, HVM2029, HVM2030, HVM2031, HVM2073, and uncatalogued specimen at IVPP, all from Longdan.

Distribution & age. Southern part of northern China to southernmost China, 2.35–1.4 Ma.

Remarks. The nature of *P. palaeosinensis* as the ancestor of the modern tiger has been fully stressed by Hemmer (1967). Mazák (2010), using multivariate analyses of cranial measurements, suggested that it is in fact quite distinct from extant tigers, and instead associated this species with basal pantherines or as being close to living lions or leopards. Interestingly, the detailed anatomical traits proposed by Hemmer (1967) were not used by Mazák (2010). Later on, Mazák *et al.* (2011) erected a new species, *Panthera zdanskyi*, from Longdan, Gansu as the direct ancestor of the modern tiger, again based mainly on metric/ratio similarity. We concur with Mazák *et al.* (2011) that the type specimen of *P. zdanskyi* indeed shows greater similarity

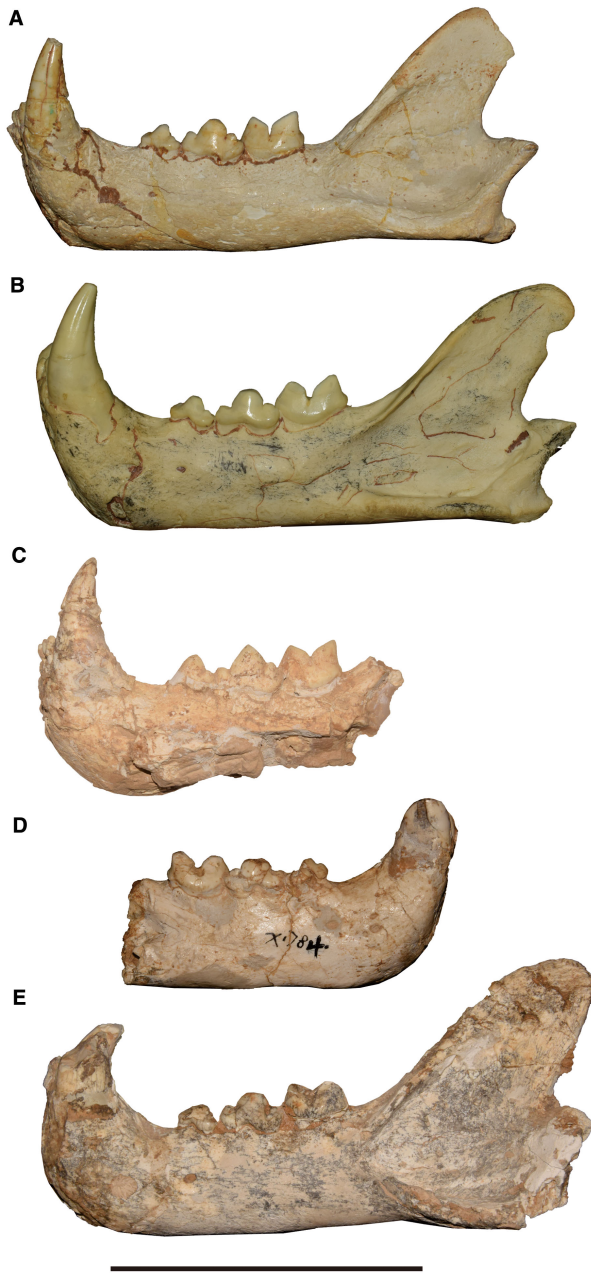


FIG. 5. Fossil mandibles of *Panthera palaeosinensis* from northern China early Early Pleistocene. A, PMU M3654, holotype, female, Mianchi. B–E, Longdan: B, cast of *P. zdanskyi* holotype (BIOPSI 00177); C, HMV2028; D, HMV2073; E, HMV2029. Scale bar represents 10 cm.

to that of *P. palaeosinensis*. However, the possibility that such differences represent intraspecies variation is not discussed due to the paucity of material at that time.

In recent years, several new specimens of large pantherines have been found in Longdan, which provide the opportunity to study intraspecies variability. The two most recently discovered crania possess interesting morphological traits. One large skull

(Fig. 4A, B) has a very similar morphology to the holotype of *P. zdanskyi* (Fig. 4C–E). Some of the key traits similar to those of the modern tiger include the very large canine, and the presence of postcanine constriction of the rostrum. Furthermore, the long postorbital constriction is similar to that of the holotype of *P. palaeosinensis* (Fig. 4A, B). Additionally, the second skull from Longdan (Fig. 4F–H) has smaller overall biometrical dimensions similar to the holotype of *P. palaeosinensis*. Regarding cranial morphology, in this second specimen the postcanine constriction of the rostrum is absent, and the postorbital constriction is shortened. Furthermore, it has a wide and blunt nasal distal process, and the middle spur in the bony choana is also absent (Fig. 4F–H).

Our observations of modern tiger specimens suggest that the male typically has a more pronounced postcanine constriction and a generally greater postcanine length. The differences reported in the Longdan sample, as detailed above, can therefore be attributed to sexual dimorphism. Consequently, the Longdan material encompasses the full range of morphological variability previously recorded in Chinese Early Pleistocene tigers (Hemmer 1967; Mazák *et al.* 2011). This supports the interpretation of *P. zdanskyi* as a junior subjective synonym of *P. palaeosinensis*, which has nomenclatural priority under the International Code of Zoological Nomenclature (ICZN 1999).

Among the dental traits, those of the holotype of *P. zdanskyi* are very similar to those of *P. palaeosinensis*. Both specimens have small P3 anterior accessory cusps, with a weak cingulum present at the anterior side, P4 with small preparastyle and large protocone, and similar-shaped lower cheek teeth (Fig. 6). As an example of the reported variability within *P. palaeosinensis*, another of the studied specimens, YLSNHM03312, from Longdan does not have a P3 anterior accessory cusp or P4 preparastyle. Notably, the P3 and p4 are proportionally larger than those in the modern tiger (Fig. 7).

Finally, in general terms, the p4/m1 length ratio in modern and Middle to Late Pleistocene tigers is consistently lower than 1, whereas in *P. palaeosinensis* it is typically close to 1 (Fig. 8). Earlier studies proposed that a relatively small p4 was characteristic of all Asian pantherines, noting that in both *P. tigris* and *P. uncia* the ratio is always below 1 (Jiangzuo & Liu 2020). In contrast, Jiangzuo & Liu (2020) reported that in the African pantherines *P. leo*, *P. pardus* and *P. onca*, the ratio is closer to 1. Given the overall similarity of *P. palaeosinensis* and *P. tigris*, we do not think that this trait supports *P. palaeosinensis* being close to the African pantherines; this trait may have limited phylogenetic value and could instead be functionally driven. Regarding the P3/P4 ratio, it is noteworthy that the two male individuals examined (BIOPSI 00177 and GSM 01553) have a significantly larger P3 (ratio > 0.7) than the two female individuals (PMU M3654 and YLSNHM03312, ratio < 0.65). Nevertheless, a larger sample is required to assess the statistical significance of this difference.

Panthera palaeosinensis is here proposed as the potential direct ancestor of *P. tigris* on the basis of: (1) morphological similarity, already discussed by Hemmer (1967) and supplemented in this study; (2) being found in the same (or close) geographical area and successive chronological range; and (3) classification as sister group in recent total-evidence phylogeny (Jiangzuo *et al.* 2025).

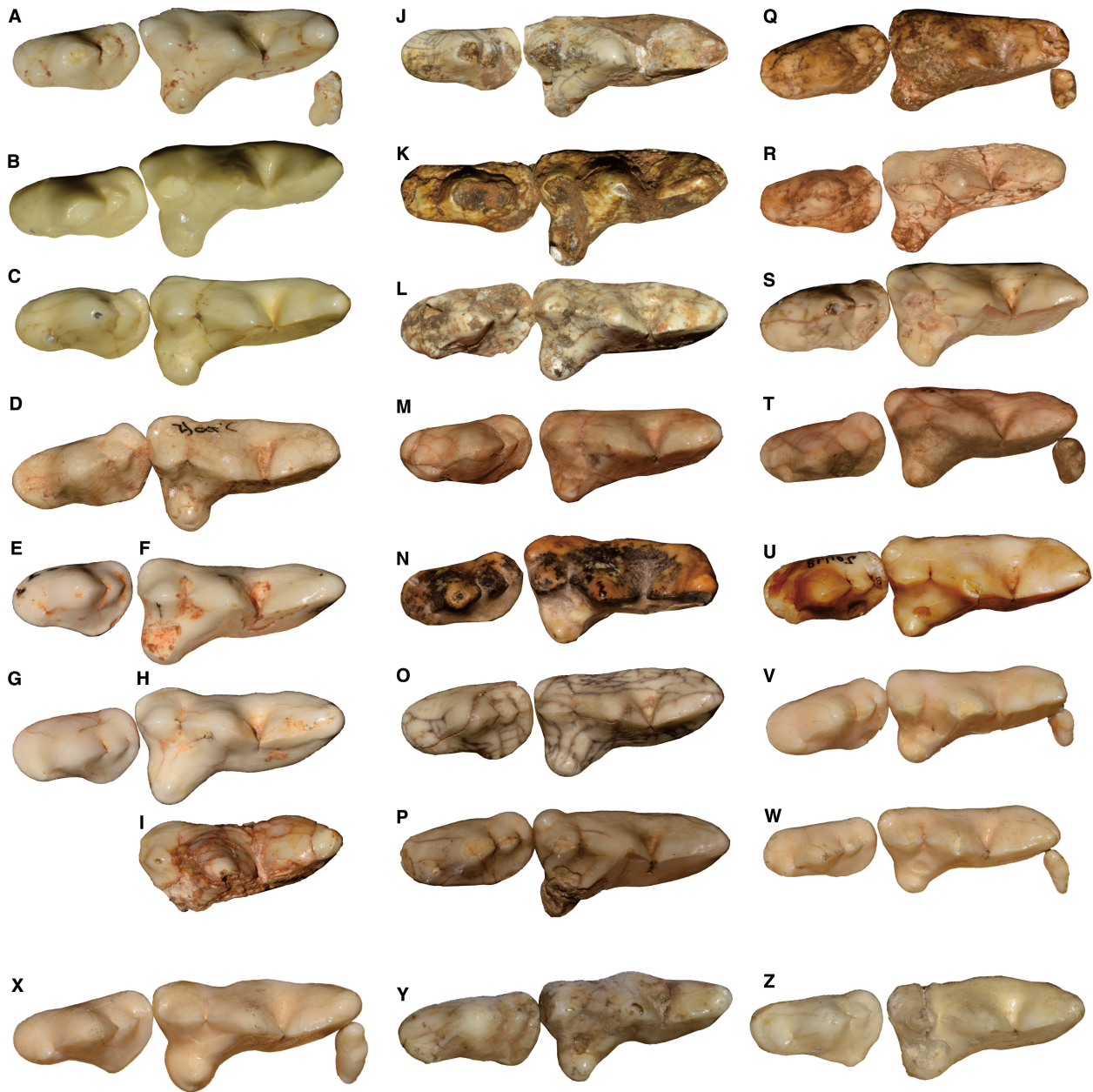


FIG. 6. Comparison of the occlusal views of the upper cheek teeth of *P. palaeosinensis*, *P. tigris*, and selected other species of *Panthera*. All mirrored to the left side for easier comparison. A–D, *P. palaeosinensis*: A, PMU M3654, holotype of *P. palaeosinensis*, Mianchi; B, cast of holotype (BIOPSI 00177) of *P. zdanskyi*, Longdan; C, YLSNHM03312, Longdan; D, IVPP RV87019, Liucheng *Gigantopithecus* Cave; E–H, Longgudong, Cave: E, IVPP V13448.1; F, IVPP V13446.2; G, IVPP V13444.1; H, IVPP V13450.1. I, *Panthera tigris* subsp., IVPP V5421, Gongwangling. J–L, *Panthera tigris lui* Xuetaolangzi; J, HPICRA 90YQT744-4-16; K, HPICRA 644-23; L, HPICRA 91YQT844. M, *Panthera tigris palaeobeijingensis*, Zd00215, Zhoukoudian Loc. 13. N–P, *Panthera tigris acutidens*, Zhoukoudian Loc. 1: N, IVPP C/C 1152; O, IVPP C/C 1152; P, IVPP C/C 700; Q, IVPP V2928.3, Chenjiawo; R, AMNH F:AM22334, Peiho. S–T, *Panthera tigris* subsp.: S, AMNH FM18741, Yanjinggou; T, GMC V171, Zhoukoudian Upper Cave. U–W, modern *Panthera tigris* subsp.: U, AMNH M201798; V, AMNH M45520; W, AMNH M113743. X, *Panthera pardus*, AMNH M19158, modern. Y, *Panthera gombaszoegensis*, MNHM Wo59, Mosbach. Z, *Panthera spelaea*, MNB MB.MA.50948, Zoolithen Cave. Not to scale.

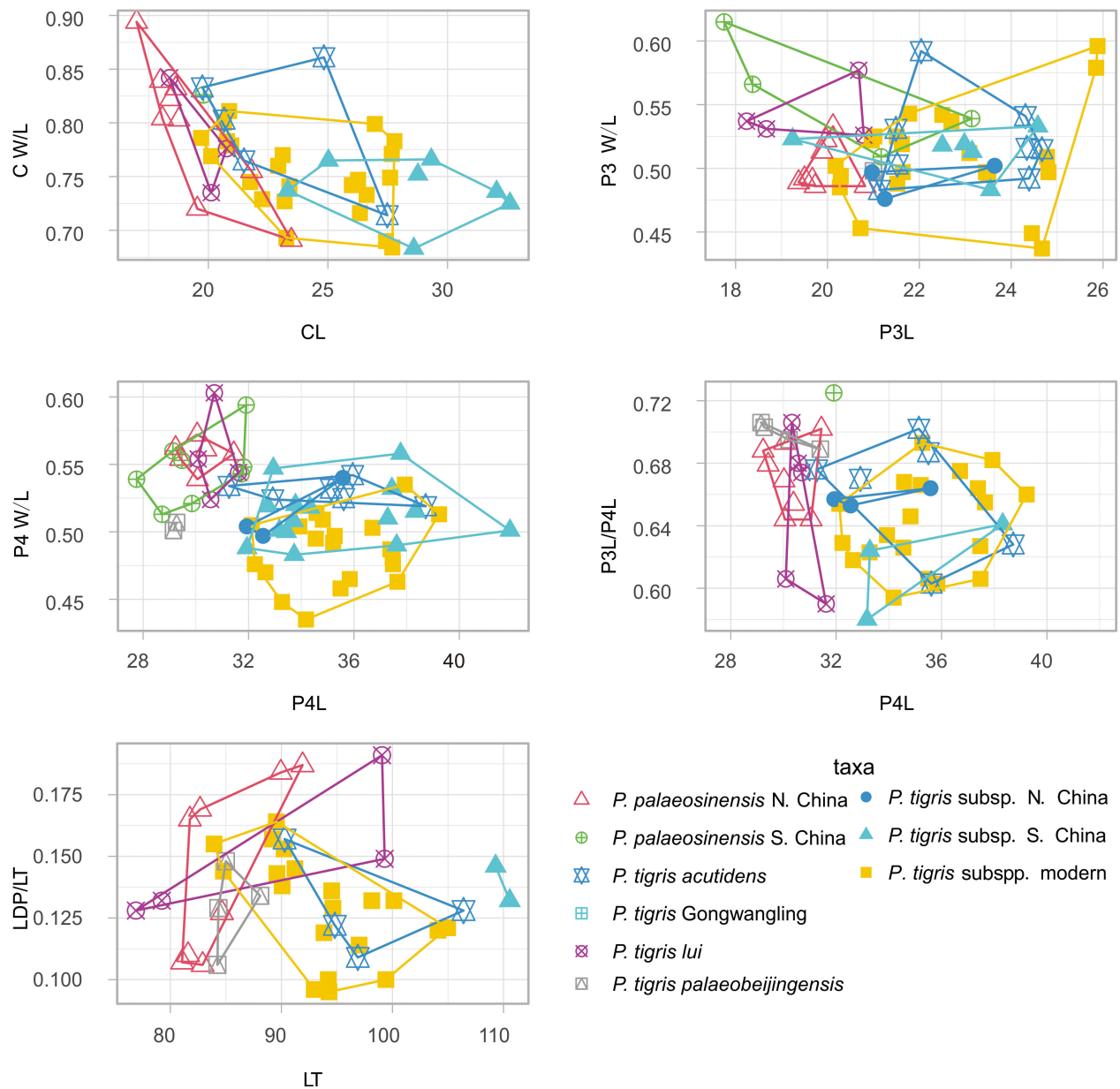


FIG. 7. Upper dental measurements (in mm) and ratios of the fossil and modern tiger. *Abbreviations:* C, canine; L, length; LDP, diastema length between C and P3; LT, tooth row length; P, premolar; W, width (see Fig. 1 for details).

Panthera tigris (Linnaeus 1758)

Emended diagnosis (craniodental). Large pantherine. Nasal elongated, naris opening narrow, postcanine constriction present, distal part of sagittal crest upward extended, making the middle part of the dorsal profile concave (weak in *P. t. altaica* and *P. t. virgata*), mastoid robust and anteriorly extended, auditory bulla antero-posteriorly shortened, mandibular symphysis deep and vertical, mandible ventral profile straight, angular process ventrally expanded, canine large, with slightly sharp posterior ridge, P3/p3 with weak anterior accessory cusp, P4 often with

preparastyle, with straight buccal border, m1 with robust paraconid, often with medial crest, with metaconid.

Age & distribution. Middle Early Pleistocene to now (1.3–0 Ma), whole of Asia in general, except very high-altitude and high-latitude areas.

Remarks. The differentiated traits between the tiger and lion have been extensively studied (Boule 1906; Pocock 1930, 1939; Christiansen 2008; Jiangzuo & Liu 2020), and there are also detailed anatomical comparisons with other big cats

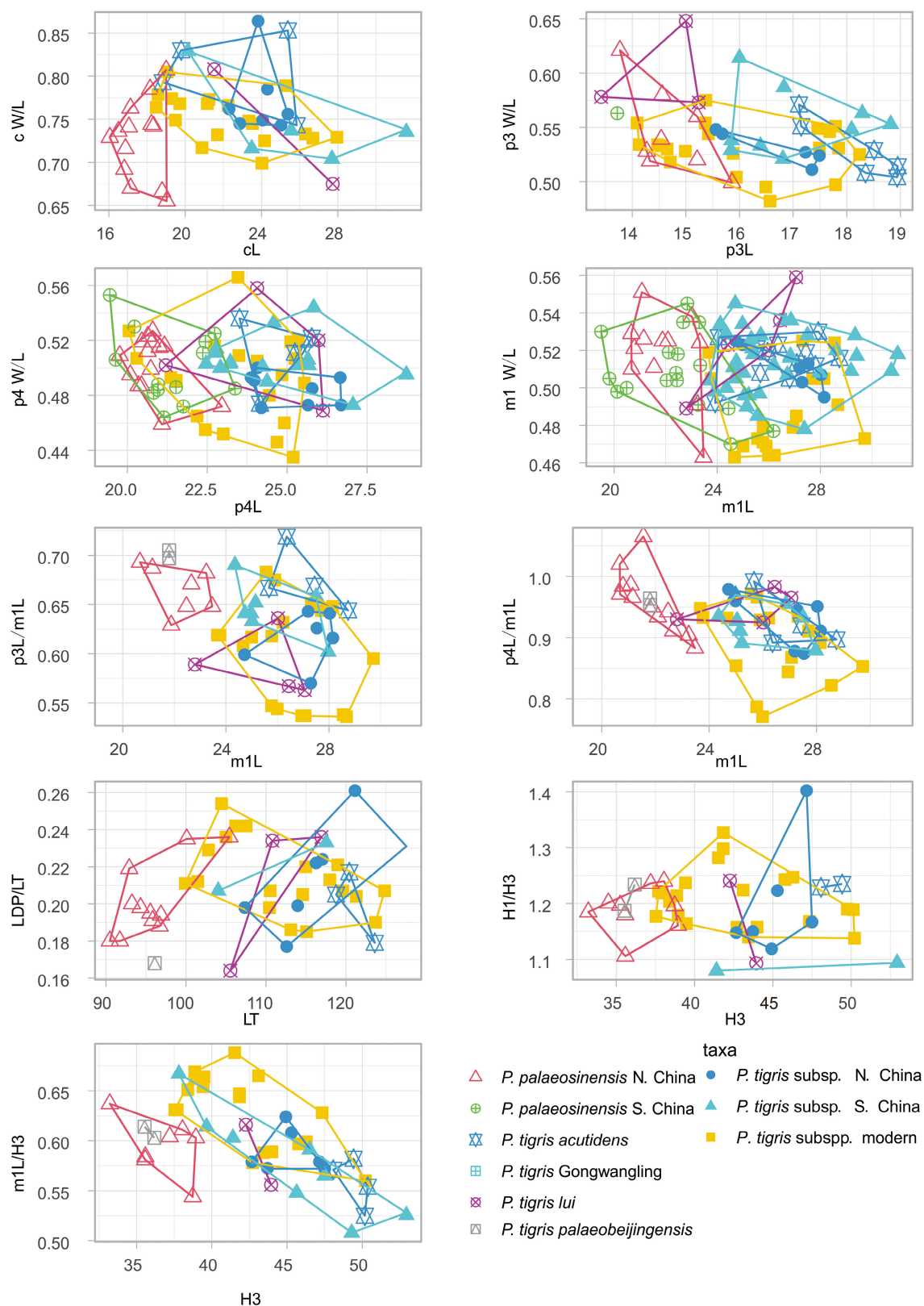


FIG. 8. Lower dental measurements (in mm) and ratios of the fossil and modern tiger. *Abbreviations:* c, canine; H1, mandibular depth behind the canine; H3, mandibular depth behind the m1; L, length; LDP, diastema length between c and p3; LT, tooth row length; m, molar; p, premolar; W, width (see Fig. 1 for details).

(Haltenorth 1936, 1937). Here we mainly want to stress the key differences between the tiger and its potential ancestor *P. palaeosinensis*: the general presence of dorsal profile concavity in the sagittal crest, due to the upward expansion of the sagittal crest at its distal side, and the antero-posteriorly shortened auditory bulla. The zygomatic arch in the modern *P. tigris* is generally wider than that of *P. palaeosinensis*. The dorsal profile concavity in the sagittal crest is present in most modern tiger subspecies, but is weak or absent in *P. t. altaica* and *P. t. virgata*, given that the latter two subspecies have further development of the sagittal crest in the middle part that fills the concavity (Cooper *et al.* 2022). Regarding the dentition, probably the most important new trait is the development of the m1 medial crest (Figs 9, 10). This structure is always absent in *P. palaeosinensis*, but is present in most individuals of modern *P. tigris*, although it is more variable in the early tiger population (*P. t. lui*, *P. t. palaeobeijingensis* and *P. t. acutidens*, see below). The other dental differences include the relatively small premolars, small p4 anterior accessory cusp and straighter buccal border with more frequent development of the P4 parastyle (Figs 6–10).

So far, the earliest record of *P. tigris* comes from Gongwangling, Lantian, Shaanxi Province (Hu & Qi 1978). The tiger from this locality is represented only by a P4, but this tooth is larger than any of those of *P. palaeosinensis*. Given that the material is poorly preserved, the nature of this population is unclear, and we tentatively regard it as the earliest record of *P. tigris*. The later tiger fossils are discussed in more detail below.

Panthera tigris lui subsp. nov.

Figure 11

LSID. <https://zoobank.org/NomenclaturalActs/8af492bc-c02a-4ada-b55e-e746ccc87b96>

Derivation of name. In honour of the team leader of the Yunxian excavation project, Chengqiu Lu, who has made a great contribution to archaeology and palaeontology in Hubei Province, and in Xuetangliangzi, Yunyang in particular.

Diagnosis. Relatively small- to medium-sized tiger. P3 and p3 overall slightly larger than modern subspecies, P4 with buccal concavity present, m1 with paraconid medial ridge occasionally present (in one in four specimens).

Holotype. HPICRA 90YQT744-4-16, a nearly complete skull (Fig. 11).

Paratype. YXSM 2024YX1.B-2-538, a nearly complete mandible (Fig. 11).

Type locality. Xuetangliangzi, Yunyang (old name Yunxian), Shichang, Hubei Province, China.

Other localities. Dayakou, Chongqing, China (Hu *et al.* 2025).

Assigned material. From Xuetangliangzi: maxilla, HPICRA 91YQT844, HPICRA 91YQT744:15, HPICRA 644–23; mandibular fragments or lower dentition, HPICRA 91YQT443-3-96, HPICRA 91YQT944-4-50, HPICRA 91YQT944-3:19. From Dayakou, m1, CYM0008.

Age. c. 1 Ma.

Remarks. The pantherine cats from Xuetangliangzi, Yunyang were first assigned to *P. gombaszogensis* without comparison, probably based mainly on size (Echassoux *et al.* 2008). However, cranial and dental traits support it as a member of the tiger lineage, and it differs from *P. gombaszogensis* by having a rostrum postcanine constriction, high mandibular symphysis, and shallow mandibular corpus (Fig. 11).

The tiger from Xuetangliangzi represents a transitional form between the typical *P. palaeosinensis* and *P. tigris*. The overall body size is larger than that of *P. palaeosinensis* and falls into the variation of body size of the modern tiger but is smaller than average (i.e. smaller than continental subspecies). The derived characters that distinguish it from *P. palaeosinensis* are the proportionally smaller P3 and p4, the p4 is always shorter than the m1, as in modern tigers; p4 anterior accessory cuspid not enlarged; and m1 paraconid medial ridge initially developed. These traits support the Xuetangliangzi tiger as a population within modern species *P. tigris*. In contrast, the Xuetangliangzi tiger also has several traits that are more primitive than modern and Middle–Late Pleistocene tigers. The P3 and p3, although smaller than those of *P. palaeosinensis*, are still proportionally larger than those of the modern subspecies; the P4 still has buccal concavity, and the p4 sometimes has a middle constriction (Fig. 9M); the m1 has a less robust paraconid, and the m1 paraconid medial ridge is only occasionally present. This combination of derived and primitive traits points to the translational nature of this population, and we name it as *P. t. lui* here. This represents so far the most primitive subspecies of *P. tigris*.

Panthera tigris palaeobeijingensis subsp. nov.

Figure 12

LSID. <https://zoobank.org/NomenclaturalActs/e5c445ef-78ee-4111-93aa-ff34073a14c0>

Derivation of name. The species name refers to the city of the fossil locality, Beijing.

Diagnosis. Small-sized tiger (size of Bali tiger). P3 and p4 proportionally larger than the modern subspecies, P4 with small protocone.

Type specimens. Holotype: Zd00215, a complete skull (Fig. 12); paratype: GMC Vm0207, a partial maxilla.

Type locality. Zhoukoudian Loc. 13, Beijing, China.

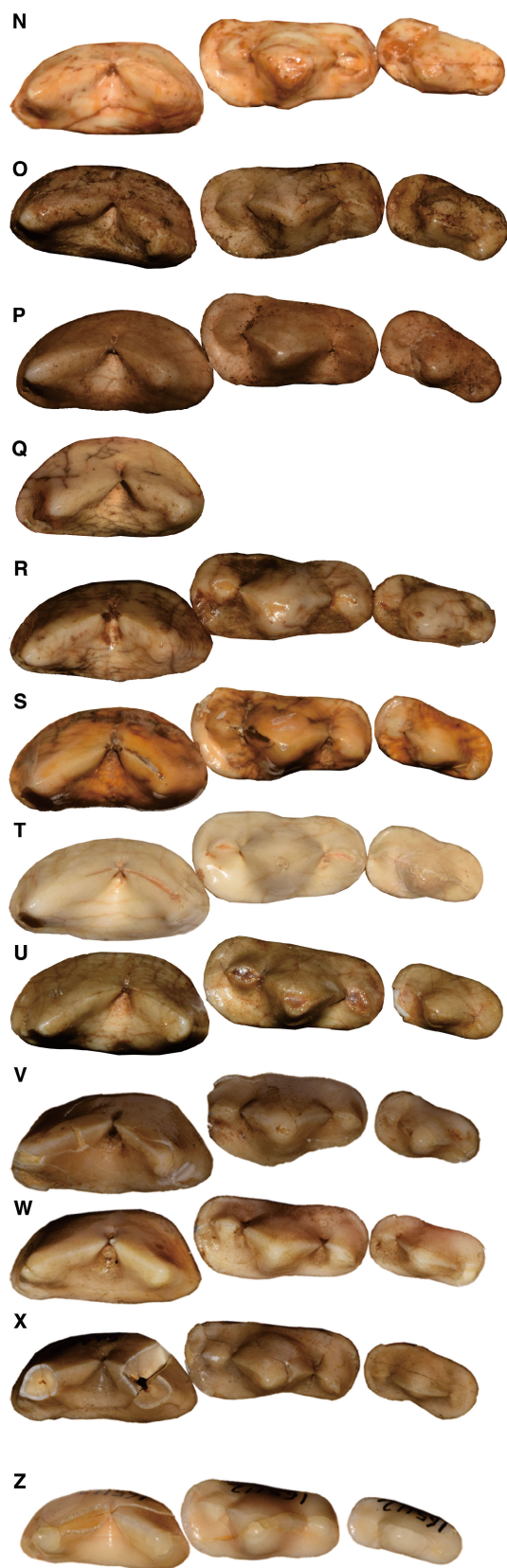
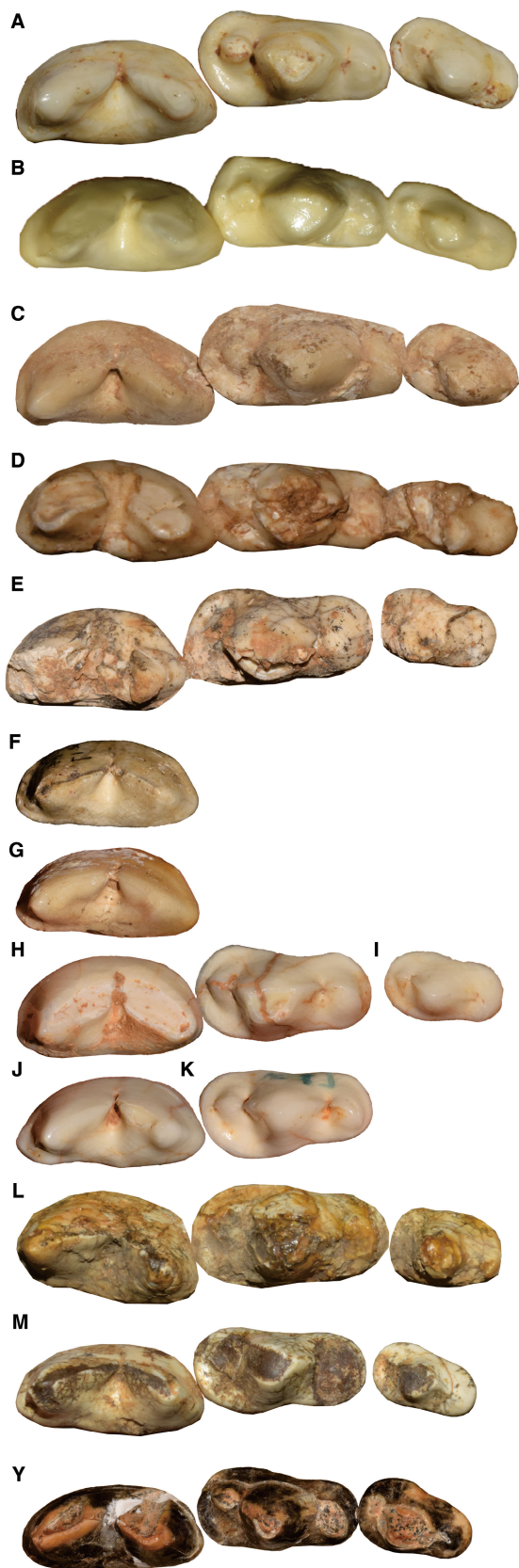


FIG. 9. Comparison of the occlusal views of the lower cheek teeth of *P. palaeosinensis* and *P. tigris*. All mirrored to the left side for easier comparison. A–K, *Panthera palaeosinensis*: A, PMU M3654, holotype of *P. palaeosinensis*, Mianchi; B–E, Longdan: B, cast of holotype (BIOPSI 00177) of *P. zdanskyi*; C, HVM2028; D, HVM2073; E, HVM2029; F–G, Liucheng *Gigantopithecus* Cave: F, IVPP RV87021; G, IVPP RV87021; H–K, Longgudong, Cave: H, IVPP V13450.7; I, V13445; J, IVPP V13448.3; K, IVPP V13448.2. L–M, *Panthera tigris lui* Xuetangliangzi; L, HPICRA 91YQT443-3-96; M, HPICRA 91YQT944-3-19. N–R, *Panthera tigris acutidens*: N, AMNH F:AM22334, Peiho; O, IVPP V2928.3, Chenjiawo; P–R, Zhoukoudian Loc. 1: P, GMC Vm0584; Q, IVPP V908; R, MCZ VPM6126. S–U, *Panthera tigris* subsp., Yanjinggou: S, AMNH FM21779; T, AMNH FM18740; U, Zd V358-11, Zhoukoudian Upper Cave. V–X, modern *Panthera tigris* subsp.: V, AMNH M201798; W, AMNH M54460; X, AMNH M113743. Y, *Panthera gombaszoensis* DJPJ191017, Jiyuan Cave, Dalian, China. Z, modern *Panthera pardus*, AMNH M165112. Not to scale.

Other localities. None.

Age. Earliest Middle Pleistocene, here an age of *c.* 0.75 Ma is adopted.

Remarks. The pantherine from Zhoukoudian Loc. 13 was initially assigned to *Panthera pardus* due to its small size (Teilhard de Chardin 1941). Only the maxilla and mandible (now with catalogue number GMC Vm0207) were mentioned at that time, and no complete skull was available. The skull Zd00215 provides much more information on its affinity. Although rather small in size, the craniodental traits clearly indicate its affinity with tigers. The distal part of the sagittal crest is slightly dorsally extended, as in the modern tiger. This trait is absent in all skulls of *P. palaeosinensis* (Fig. 3). The angular process, although partially broken, is clearly ventrally expanded. However, its P3 and p4 are still relatively large, as in *P. t. lui*. The auditory bulla is already anteroposteriorly shortened, as in the modern tiger, and differs from the antero-posteriorly elongated bulla seen in *P. palaeosinensis*. The mastoid process is also robust, clearly more so than in *P. palaeosinensis*, but similarly to that of the modern tiger subspecies. The P3 has an anterior cingulum, and the P4 has a straight buccal border, which are both common traits for tiger. A unique trait of the Zhoukoudian Loc. 13 tiger is the rather small P4 protocone, not seen in any other tiger. We therefore regard this population as a unique dwarf subspecies, *P. t. palaeobeijingensis*.

Panthera tigris palaeobeijingensis is more or less at the same evolutionary level as *P. t. lui* regarding the P3 and p4 size, although the several derived cranial traits, such as the dorsally extended sagittal crest and shortened auditory bulla, are unknown in *P. t. lui*. The reduced P4 protocone has convergently appeared in many felids, such as the sabretooth cat *Homotherium* (Jiangzuo et al. 2022a), *Megantereon* (Stimpson 2024; Madurell-Malapeira 2025) and feline *Acinonyx* (Jiangzuo et al. 2024a), and is often interpreted as increasing cutting efficiency. *Panthera tigris palaeobeijingensis* probably needed to increase the cutting efficiency for quickly consuming prey, given that its small size would have afforded it limited ability to defend the prey from *Pachycrocuta brevirostris sinensis* and *Ursus arctos* and even *Acinonyx pleistocaenicus*, all recorded in the same assemblages.

Panthera tigris palaeobeijingensis is the only mainland tiger in the Middle and Late Pleistocene with an average body mass lower than 100 kg (see body mass inference section). The reason

why such a small tiger evolved in northern China near the Early and Middle Pleistocene boundary is unclear. It was previously suggested that the harsh environment during the Early–Middle Pleistocene Transition, *c.* 1.2–0.7 Ma may have reduced the faunal diversity in eastern Asia (Zhou et al. 2018), and the small size of this subspecies could be related to the lack of prey during this time, but more evidence is needed to better explore the phenomenon.

Panthera tigris acutidens (Zdansky 1928)

Figures 13, 14

Emended diagnosis. Relatively large-sized tiger. Mainly modern tiger in morphology, but mandible with thick ventral border of the masseteric fossa, P3 has smaller anterior accessory cusp, P4 still more frequently has buccal concavity, m1 with less frequently developed paraconid medial ridge.

Type locality. Zhoukoudian Loc. 1, Beijing, China

Lectotype. GMC Vm0584, a partial mandible with c–m1.

Other localities. Chenjiawo, Lantian, China; Peiho, Shouyang, Shanxi Province, China.

Assigned material from: Zhoukoudian Loc. 1, Table S2; Chenjiawo, maxilla and mandible of a single individual, IVPP V2928.1; Peiho, nearly complete skull, AMNH F:AM22334.

Age. Early Middle Pleistocene, *c.* 0.65–0.5 Ma.

Remarks. Zdansky (1928) assigned several isolated teeth and mandible fragments (Fig. 13A, B) to a species he erected as *Felis acutidens*. Of these teeth, the dp4 was in fact not a felid, but belongs to *Pachycrocuta brevirostris sinensis*. Given that the differential of the species by Zdansky was largely based on this tooth, the original definition of the species is thus invalid. Fortunately, much more material was later found and described by Pei (1934). After evaluation of this material, we found that it is largely already a modern tiger, but still differs from the modern population in having a thicker ventral border of the masseteric fossa, and the same dental morphotype proportions. Specifically, it has a less well-developed P3 anterior accessory cusp, more frequent presence of the P4 buccal concavity, less

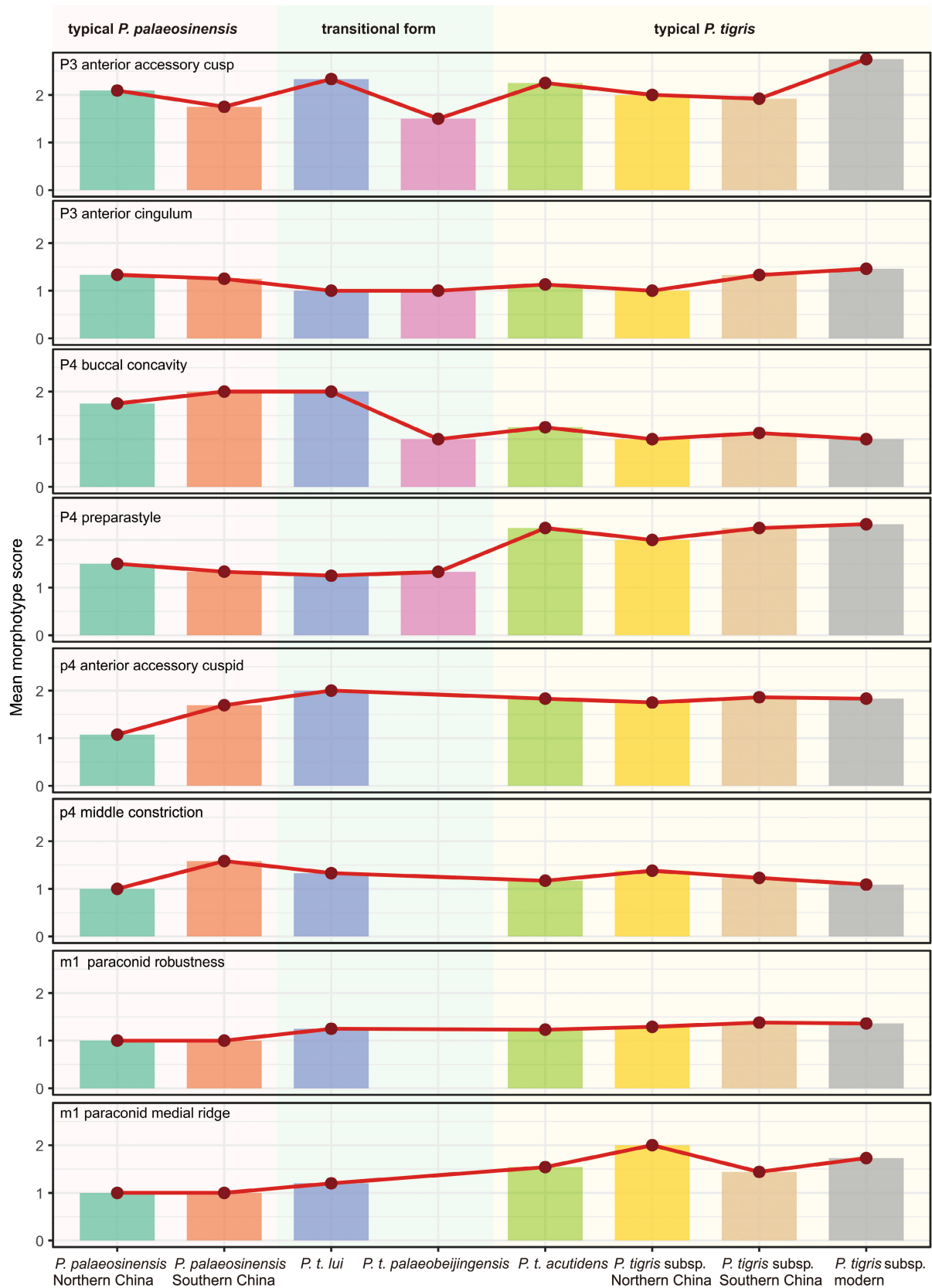


FIG. 10. Morphotype evolution of selected dental traits. For mean morphotype score see [Material & Method](#) for details.



FIG. 11. *Panthera tigris lui* subsp. nov. from Xuetaolangzi, Yunxian, latest Early Pleistocene. A–C, HPICRA 644–23: A, ventral; B, dorsal; C, lateral view. D–F, HPICRA 90YQT744–4–16: D, ventral; E, lateral; F, dorsal view. G–I, 2024YX1.B-2-538: G, lateral; H, dorsal; I, medial view. J–K, HPICRA 91YQT443–3–96: J, lateral; K, dorsal view. Scale bar represents 10 cm.

robust m1 paraconid and less development of the m1 paraconid medial ridge. The differences are not distinct, and we would not erect a new subspecies if it had not already been named. However, given its primitive nature and relatively old

age, we use the name *acutidens* as a Northern China early Middle Pleistocene subspecies.

The fossil material from Zhoukoudian Loc. 1, unfortunately is lacking a cranium. A maxilla and mandible from the same

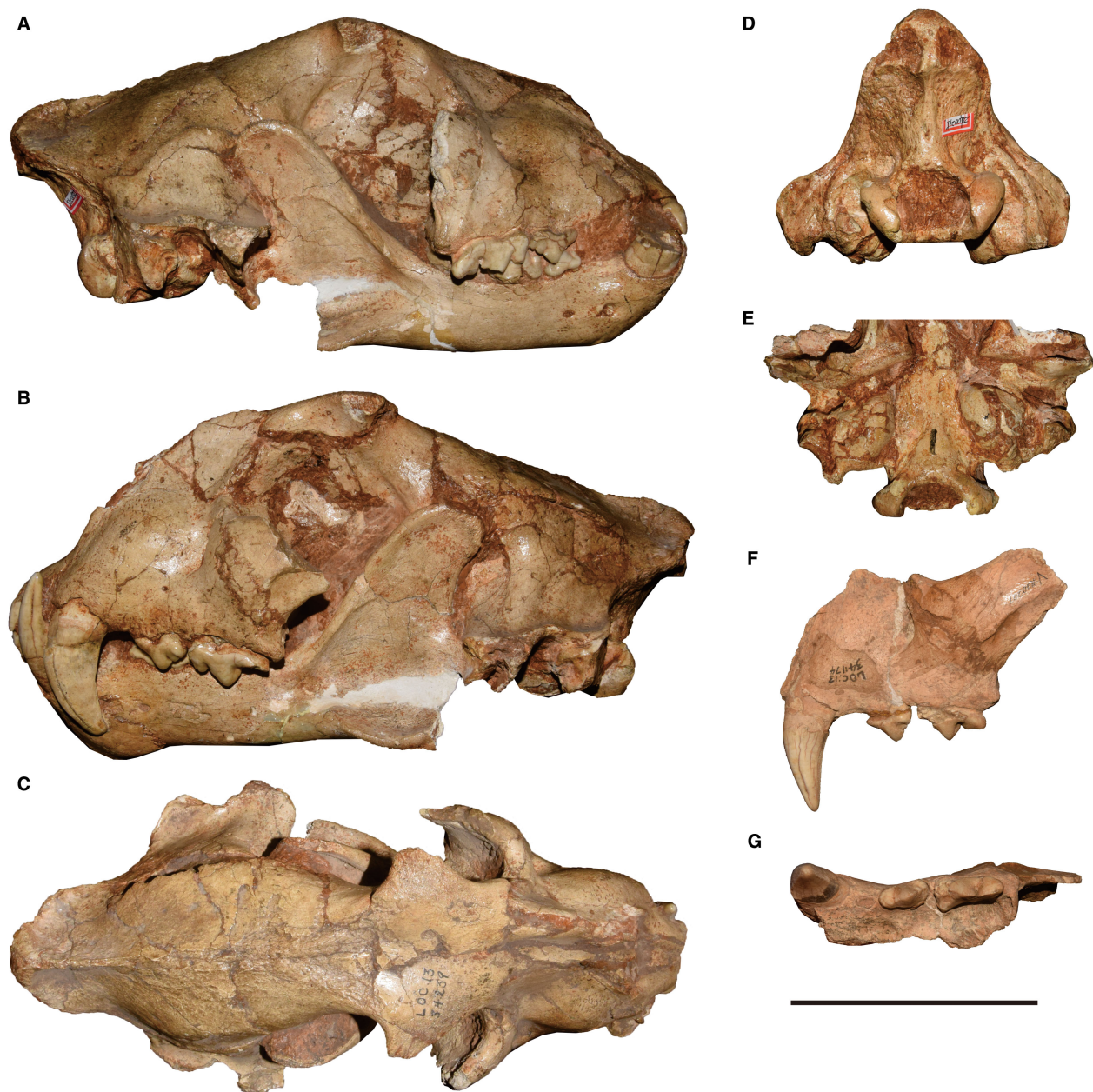


FIG. 12. *Panthera tigris palaeobeijingensis* subsp. nov. A–E, Zd00215 from Zhoukoudian Loc. 13, Beijing, earliest Middle Pleistocene: A, right lateral; B, left lateral; C, dorsal view; and D, occipital; E, ventral view of the basicranial region. F–G, GMC Vm0207: F, lateral; G, ventral view. Scale bar represents 10 cm.

individual from Chenjiawo, Lantian (Fig. 13F–J), dated 0.65 Ma, is generally similar to those from Zhoukoudian Loc. 1, and is here assigned to this subspecies. The rostrum has a postcanine constriction and the m1 has a distinct paracoid medial ridge, as in the modern tiger. In the Frick collection of the American Museum of Natural History, there is a nearly complete skull from Peiho, Shouyang, Shanxi province of northern China (Fig. 14). There are no other specimens from this site, and it is labelled as Biharian (Early Pleistocene).

However, the specimen is quite large, and the auditory bulla is antero-posteriorly shortened, and we think it is more likely to be Middle Pleistocene. In contrast, the distal part of the sagittal crest is not dorsally extended. We tentatively assign this specimen to *P. t. acutidens*. However, we must note that the ventral border of the masseteric fossa in this individual is not so thick as those from Zhoukoudian Loc. 1.

The contemporary tiger from southern China is mostly represented by very few teeth. The best material is a good



FIG. 13. *Panthera tigris acutidens*. A–E, Zhoukoudian Loc. 1: A–B, originally described material: A, PMU M3531; B, PMU M3532 (questionably *P. tigris*); C, GMC Vm0584; D, GMC Vm0591; E, MCZ 6126. F–J, Chenjiawo, IVPP V2928.3: F–H, rostrum: F, lateral; G, dorsal; H, ventral view; I–J, mandible: lateral; J, medial view. K, YXM-002, *Panthera tigris* subsp. from Bailongdong Cave; note the thick ventral border of the masseteric fossa. Scale bar represents 10 cm.

mandible from Bailongdong Cave, Yunxi, Hubei Province (Tong *et al.* 2019). Interestingly, this mandible (Fig. 13K) also has a thick ventral border of the masseteric fossa. This suggests that this trait is probably characteristic of the tiger subspecies of this geological age. However, given that the subspecies *P. t. acutidens* is mainly defined by dental morphotype, we do not assign subspecies to the southern Chinese population of this age.

Panthera tigris subsp. Figures 15, 16

Age & distribution. Late Middle to Late Pleistocene in general, far east of Russia, northern China, southern China, southeastern and southern Asia.

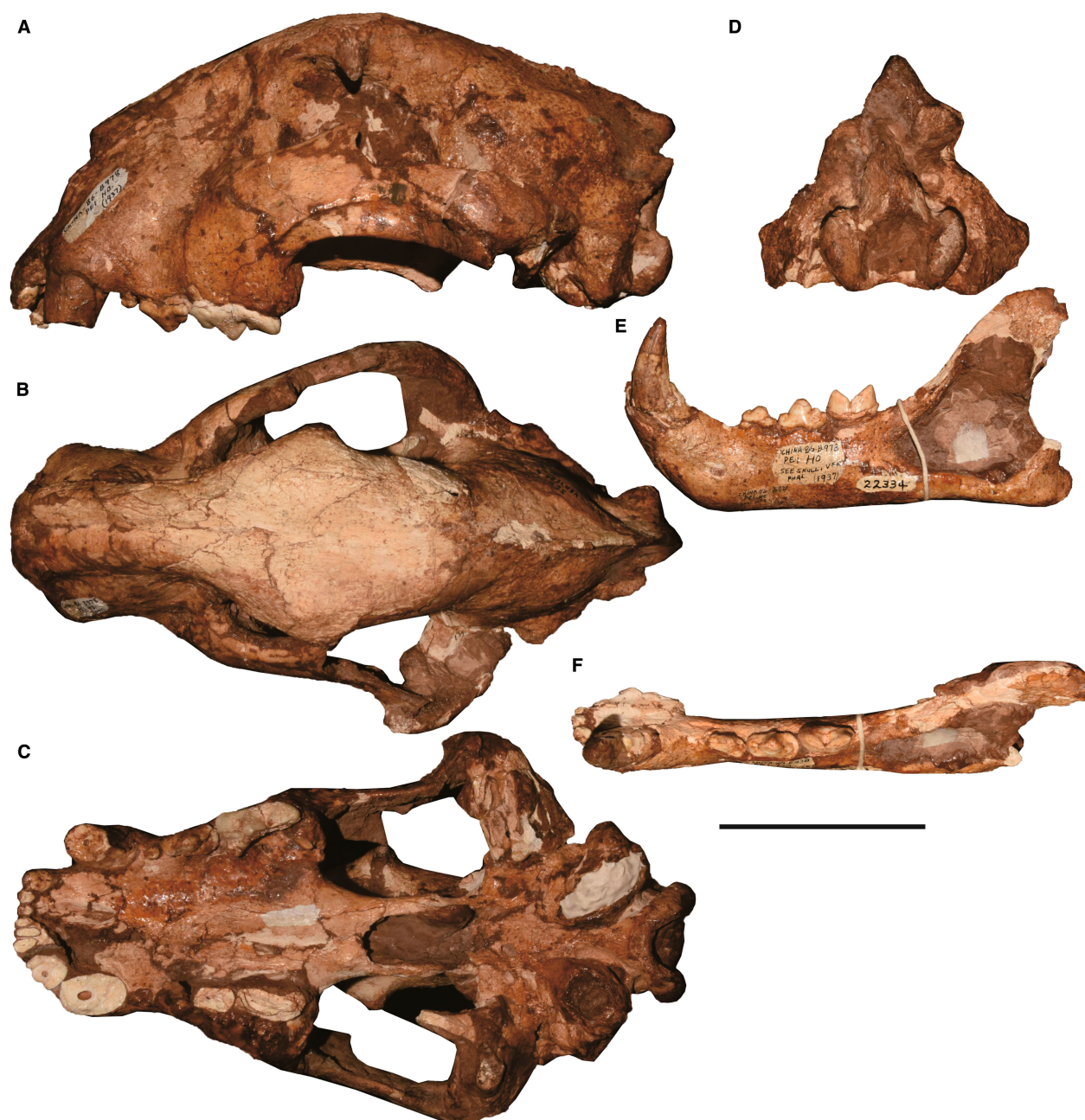


FIG. 14. *Panthera tigris acutidens* AMNH F: AM22334 from Pei Ho, Shouyang, probably Middle Pleistocene: A, lateral; B, dorsal; C, ventral view. D, occipital. E–F, mandible: E, lateral; F, dorsal view. Scale bar represents 10 cm.

Localities. The late Middle to Late Pleistocene tigers have been recorded in many sites in the distribution region. Some of the largest and best-preserved collections were discovered in Yanjinggou, Chongqing, southern China; Zhoukoudian Upper Cave, Beijing; Geological Society Cave, Russia.

Remarks. The late Middle to Late Pleistocene tigers are more widespread, and have been discovered in both northern and southern China, in the Russian far east, and the Indochinese

Peninsula. The best sample comes from Yanjinggou, Chongqing (formerly Sichuan Province), China (Fig. 15). Hooijer & Granger (1947) systematically studied this population, and suggested that it is larger than the extant form, with more robust metapodials. The fossils from Yanjinggou come from caves or fissure systems, dating from late Early Pleistocene to Late Pleistocene, and mainly Middle Pleistocene (Chen *et al.* 2013). Recent dating suggests an age of 0.3 Ma (Hu *et al.* 2023). This age probably could not apply to all fossil specimens, but given that there is no other



FIG. 15. Fossil *Panthera tigris* subsp. from Yanjinggou, Chongqing. A–B, AMNH FM18737: A, lateral; B, dorsal view. C, AMNH FM18740, lateral view. D–E, AMNH FM18624: D, lateral; E, dorsal view. Scale bar represents 15 cm.

evidence, this age is used for the whole sample in this discussion.

Among the craniodental traits, Hooijer & Granger (1947) noticed the mandible with convex ventral profile in the skull AMNH M18624 and interpreted it as deformation. However, we did not find clear evidence of such deformation in the mandible of this specimen. Moreover, several other specimens from Yanjinggou also have a convex ventral profile of the mandible (Fig. 15A, C, D). Hooijer & Granger (1947) regarded the Yanjinggou tiger as a unique subspecies, and assigned it to *P. t. acutidens* because of the similarly robust metapodials. According to our observations, the Yanjinggou tiger has typical tiger traits, such as the high mandibular symphysis, and rostrum postcanine constriction, and differs from the modern

tiger only by the presence of the convex ventral profile of the mandible. It is not necessary to erect a separate subspecies, and is best assigned to *P. tigris*. Given the age of *c.* 0.3 Ma, the Yanjinggou population probably pre-dates the modern tiger diversification (Luo *et al.* 2019), and belongs to an extinct early branch. This explains the frequently seen convex mandibular ventral profile, which is very rare in the modern tigers. The Yanjinggou tiger represents the largest sized mainland tiger discovered so far. This will be discussed further in the body mass evolution section.

Of the northern Chinese fossils, the tigers from the Upper Cave of Zhoukoudian represent the largest population of specimens (Pei 1940). According to the note in Pei (1940), several complete skeletons, many skulls and mandibles, and numerous

mandibles were discovered, but these specimens were lost prior to publication. Many young individuals were discovered, indicating that the Upper Cave was a tiger den. Now the available specimens are mainly housed at the Geological Museum, China and Zhoukoudian Site Museum (Fig. 16). Among these are some mandibles and a few maxillae. A mounted skeleton (possibly a composite from different individuals) is exhibited at the Zhoukoudian Site Museum. The skull in this skeleton is heavily restored and is not discussed here. Among the dental traits, the Upper Cave population has a weaker P3 anterior cingulum and accessory cusp, and a smaller P4 preparastyle, and otherwise is similar to the modern tiger. Of the mandibles, one (Fig. 16C) has a somewhat convex mandibular ventral profile. Given the relatively young age of the Upper Cave fauna at c. 0.05–0.03 Ma

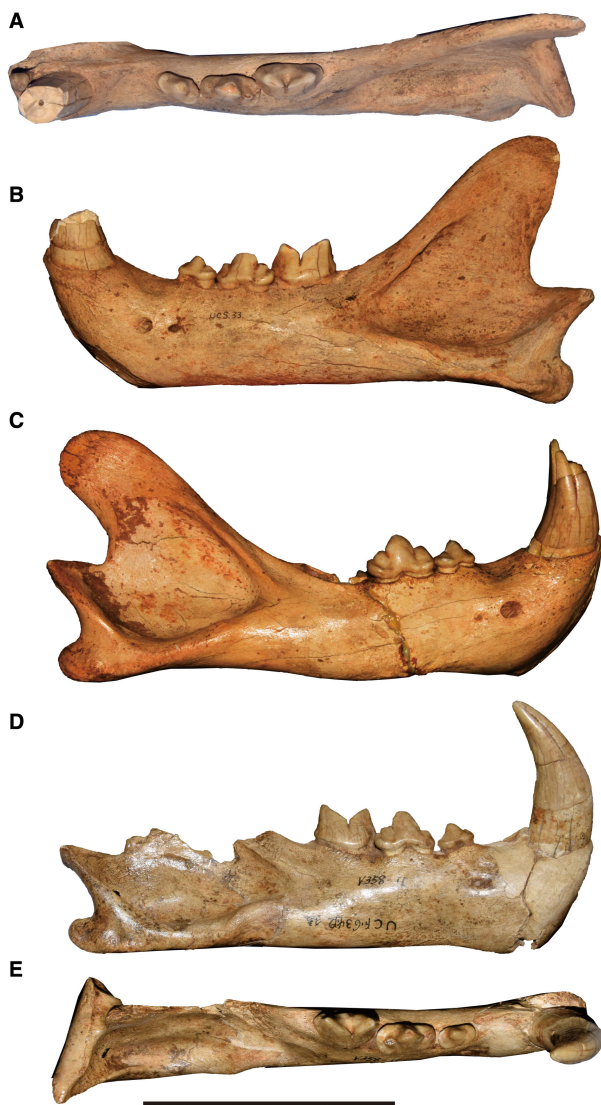


FIG. 16. *Panthera tigris* subsp. from Upper Cave, Zhoukoudian, Beijing, Late Pleistocene. A–B, GMC Vm0577: A, dorsal; B, lateral view. C, GMC Vm0578, lateral view. D–E, GMC V358-11: D, lateral; E, dorsal view. Scale bar represents 10 cm.

(Li *et al.* 2018), this population is probably already within the modern tiger diversification, but it is not possible to infer the subspecies without completely preserved material.

The Geological Society Cave and some nearby caves from the Russian far east also produced a large sample of fossil tigers (Baryshnikov 2016). This population also shows typical modern tiger traits, such as a high symphysis, and ventrally expanded mandibular angular process. Some morphotypes, such as the more frequent presence of the m1 metaconid, and longer m1 paraconid, suggest that this population is somewhat different from the modern Amur tiger, and may not be directly related to the modern subspecies (Baryshnikov 2016).

In southernmost China (Guangxi and Yunnan Provinces), many isolated teeth of the tiger have been discovered (Chen & Qi 1978; Pei 1987). These teeth are also from various caves with different ages, and could not be regarded as a single population (Pei 1987). They are generally united into a Yanjinggou fauna according to morphotype analysis in the present study. The Indochina Peninsula produced fewer teeth, which often were not figured and which were only listed in brief, and further analysis is not possible beyond species identification.

The date at which the tiger arrived in southern Asia remains unclear. The early Pleistocene pantherine from Pakistan has been assigned to *P. gombaszogensis* (Jiangzuo & Liu 2020). In the Late Pleistocene, the records of *P. tigris* have been documented in the Kurnool Caves complex in India (Lydekker 1886; Prasad 1996).

In general, the late Middle and Late Pleistocene forms are very difficult to distinguish from the modern subspecies. They may be different in dental details, but such differences are not stable and require large samples to be tested. We do not suggest assigning them to any subspecies.

DISCUSSION

Functional evolution

Tigers typically use two different ways to kill their prey: biting the throat of large prey, which leads to suffocation; or biting the back of the neck of small- and medium-sized prey, which directly destroys the spinal cord (Sunquist & Sunquist 2002). The craniodental adaptations of modern tigers shows great emphasis on producing a strong canine bite, with robust development of the sagittal crest and angular process, along with very wide zygomatic arches to accommodate large musculature, and enlarged canines. The enlarged and anteriorly extended mastoid suggests strongly developed neck musculature, which is especially useful to deliver greater force by shaking the head during bites to the back of the neck. The sharp canine ridge can produce severe injury during this behaviour.

In contrast, the here described craniodental traits of *P. palaeosinensis* show less adaptation for strong bites. While zygomatic width can seldom be measured due to fossil deformation, the distal part of the sagittal crest and

the angular process show less extension and expansion compared with that of extant tigers. Additionally, the mastoid process in *P. palaeosinensis* is also much less expanded than *P. tigris*. As analysed above, the enlargement of the mastoid process is probably related to the unique neck-biting hunting strategy, and this behaviour was probably not developed or was only in its initial stage for *P. palaeosinensis* (Fig. 17).

The P3, p4 and m1 morphology of extant tigers suggests that the function of the cheek teeth was concentrated in the carnassials and was an adaptation for cutting tough skin. The differences in P4 morphology are probably not functional but more investigation is needed. The dental differences between *P. palaeosinensis* and *P. tigris* indicate two key behaviours. First, the absence of the

derived m1 traits in *P. palaeosinensis* suggests that it had less ability to deal with the tough skin of large prey, and therefore was more likely to target medium–small prey. Medium-sized ungulates, such as *Metacervocerus* (Wang *et al.* 2026), *Antilospira* (Xu & Shi 2026) and *Proboscideiparion* (Deng 2012) were probably the primary prey of *P. palaeosinensis*. This is in accordance with the lesser developed masseteric muscle in *P. palaeosinensis*, which is necessary to handle large prey. Second, the anterior premolars in *P. palaeosinensis* are proportionally larger, unlike the modern tiger, but similar to the African pantherine. As we discussed above, a larger premolar is likely to be related to durophagous behaviour, and therefore to be related to high intra- and interspecies competition. Even though the palaeoenvironment of

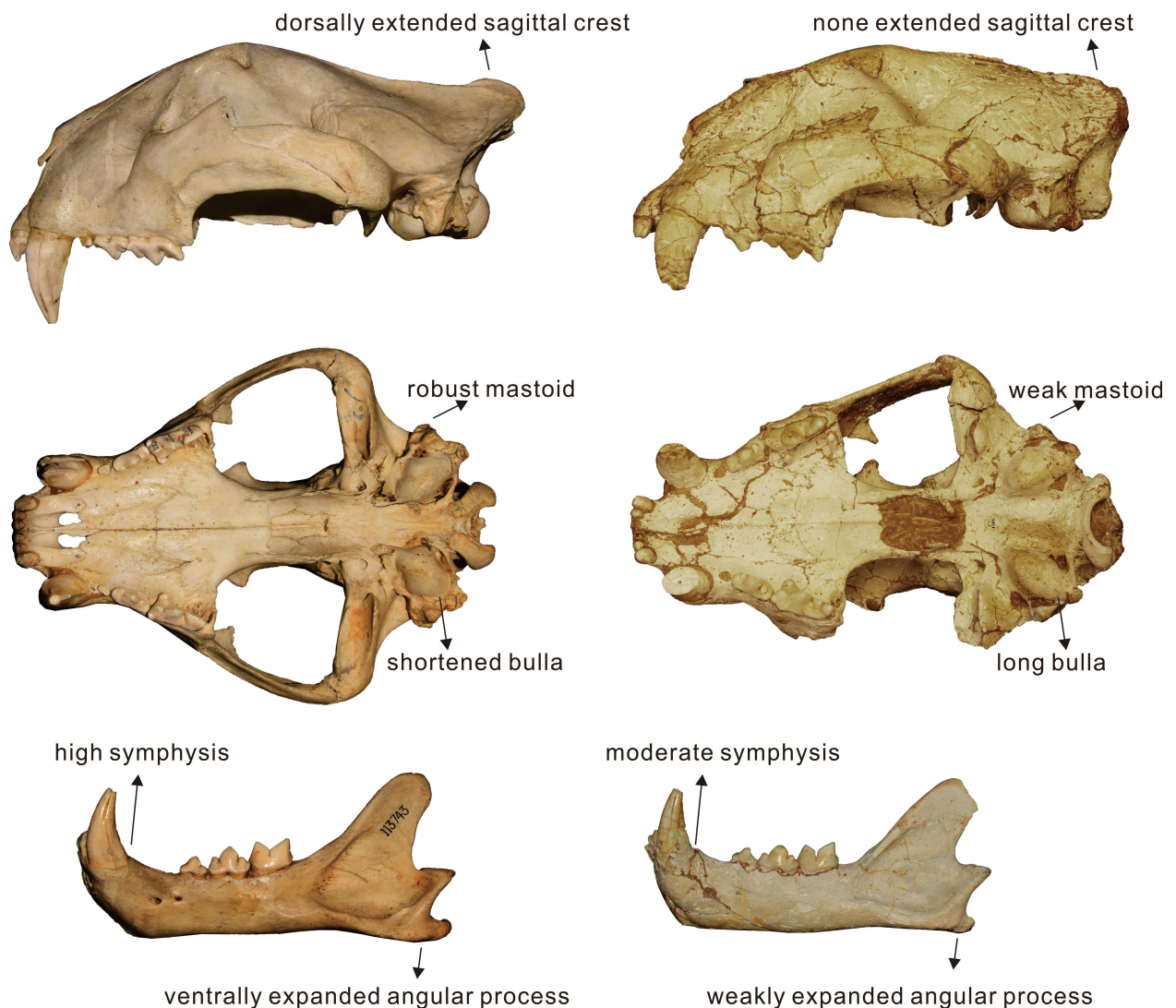


FIG. 17. Craniomandibular trait differences between *P. tigris* and *P. palaeosinensis*. With the exception of the shortening of the bulla (the function of which is unclear), the traits seen in *P. tigris* represent an increase in efficiency for hunting large prey and quickly killing medium–small-sized prey.

P. palaeosinensis seems to be similar to that of the modern tigers in general, given their largely overlapping distribution, the competitors are different. *Panthera palaeosinensis* is generally jaguar sized (see body mass below), and occurs in the same ecosystem as the modern tiger; for example, in Longdan, there are at least three felids of similar or even larger size, two sabertoothed cats *Homotherium crenatidens* and *Megantereon nihowanensis*, and the giant cheetah *Acinonyx pardinensis* (Qiu *et al.* 2004; Jiangzuo *et al.* 2024b). In addition, three large hyaenids are also present (i.e. *Pachycrocuta brevirostris licenti*, *Chasmaporthetes progressus* and *Crocota honanensis*; Qiu *et al.* 2004). In southern China, the competitors are rarer, but *Megantereon*, *Acinonyx* and *Pachycrocuta* coexisted with *P. palaeosinensis* (Pei 1987; Zhang & Feng 2004). In such an environment, *P. palaeosinensis* would need to quickly consume its prey before discovery by other large predators. When *P. tigris* appeared (1.3–1.0 Ma), the sabertoothed cats, although still present, had already become much less numerous, and several hyaenids had gone extinct (Qiu 2006). Moreover, *P. tigris* evolved a larger body size than most of these competitors, making it better able to defend the prey.

In summary, the functional evolution within the tiger lineage was mainly focused on the increased ability to hunt large prey and quickly kill medium–small prey, and with a reduced need for durophagy. These adaptations are related to the reduction of intraspecies competition within the carnivorous guild during the late Early Pleistocene.

Body mass evolution

One of the key changes in tiger evolution is the increase in body mass from the Early Pleistocene to modern times. The craniodental measurements of *P. palaeosinensis* are clearly overall smaller than those of the modern and late Middle to Late Pleistocene *P. tigris* (Figs 7, 8). However, the presence of the dwarf form *P. palaeobeijingensis* suggests that body mass did not always increase in the evolutionary history of the tiger. The postcranial material is often viewed as a better indicator of body mass (Van Valkenburgh 1990), but it is seldom preserved in the fossil record. To investigate the geographic and chronological pattern of body mass evolution in tiger, we inferred the body mass of the fossil tiger based on m1 length, using the Felidae equation from (Van Valkenburgh 1990). The m1 length is used because: (1) the m1 is one of the most frequently preserved elements in the fossil record; (2) Felidae generally have a stable dental structure (Werdelin *et al.* 2010); and (3) the m1 is a good indicator of body mass (Van Valkenburgh 1990, with the highest R^2 among the studied carnivore families).

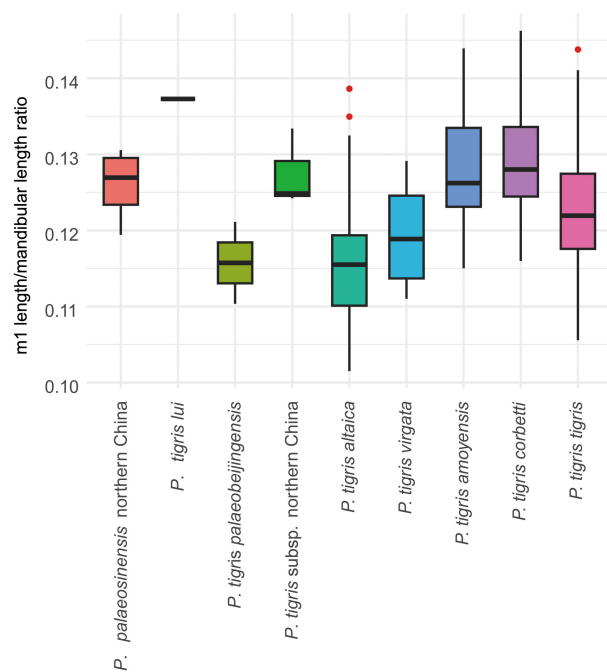


FIG. 18. Ratio of m1 length to mandibular length of different species/subspecies of the tiger lineage.

To test whether the tiger species/subspecies have different ratios of m1 relative to body size, we generated a box-plot of m1 length versus mandibular length in modern and fossil tigers (Fig. 18). In general, the variation in m1/mandible length ratio in fossil *P. palaeosinensis* and *P. tigris* falls within the range observed in modern tigers, although the mean values differ significantly. Among modern mainland subspecies, *P. t. altaica* has the proportionally smallest m1. Another subspecies with small m1 proportions is *P. t. virgata*, consistent with their close phylogenetic relationship (Driscoll *et al.* 2009; Luo *et al.* 2019). Among fossil species/subspecies, *P. t. palaeobeijingensis* has the same proportion as modern *P. t. altaica*, whereas *P. t. lui* has a high m1/mandible length ratio. Given that the sample size for *P. t. lui* is only 1, whether this subspecies has a relatively large m1/mandible length ratio remains unclear. To correct for body mass estimates, the m1/mandible length ratios for *P. t. altaica* and fossil *P. t. palaeobeijingensis* were increased by a factor of 1.069 (mean m1/mandible length ratio for other tiger subspecies = 0.124 (excluding *P. t. altaica* and *P. t. virgata*) vs mean for *P. t. altaica* = 0.116). Notably, in the *P. tigris* subsp. from northern China, primarily represented by the Zhoukoudian Upper Cave population (0.05–0.03 Ma), relative m1 size is distinctly greater than in *P. t. altaica*. This population is theoretically the most suitable ancestral population for modern *P. t. altaica*, but the significant m1 size difference suggests either: that the Upper Cave population is

not ancestral to modern populations; or that the reduced $m1$ evolved very late in the *P. t. altaica*–*P. t. virgata* lineage after it colonized northern Asia. Future genetic analyses are required to elucidate this evolutionary history.

We subdivided the distribution of fossil tigers into three natural bioprovinces: northern China – Russian far east; southern China; and southernmost China – Indochina Peninsula. The boundary between northern China and southern China is set at the classical Qinling Mountains–Huaihe River boundary (Pei 1957; Ji 1987; Xue & Zhang 1994). The boundary between southern China and southernmost China is set at the boundary of the Nanling Mountains and Yunnan–Guizhou Plateau, given that this is the natural distribution for many modern mammals (e.g. *Arctonyx ablogularis* and *A. collaris*).

The body mass of studied tigers in the three regions shows a general increase during the Early Pleistocene (Fig. 19). Southernmost China has the largest body mass during this period, but we note a significant age gap in

the body mass data. The body mass of tigers in southern and southernmost China shows minimal fluctuation during the Early Pleistocene, corresponding to the stable climate of southern China in this period (Li *et al.* 2020). Since *c.* 1 Ma, coinciding with the Early–Middle Pleistocene Transition and the local extinction of several large carnivores, the body mass of the tiger lineage in the three regions has shifted to a balanced but fluctuating pattern. Fluctuations in body size occur in all regions, but northern China to the Russian far east exhibits a greater amplitude of fluctuation. As aforementioned, this correlates with climate instability and glacial asymmetric cycles of the Early–Middle Pleistocene Transition (Ehlers *et al.* 2018). In southern and southernmost China, the environment is generally stable (Zhang *et al.* 2024), and during the last 1.8 Ma the climate has fluctuated on a 23 kyr cycle (Ao *et al.* 2012).

In southern and southernmost China, the late Middle Pleistocene tigers had the highest body mass.

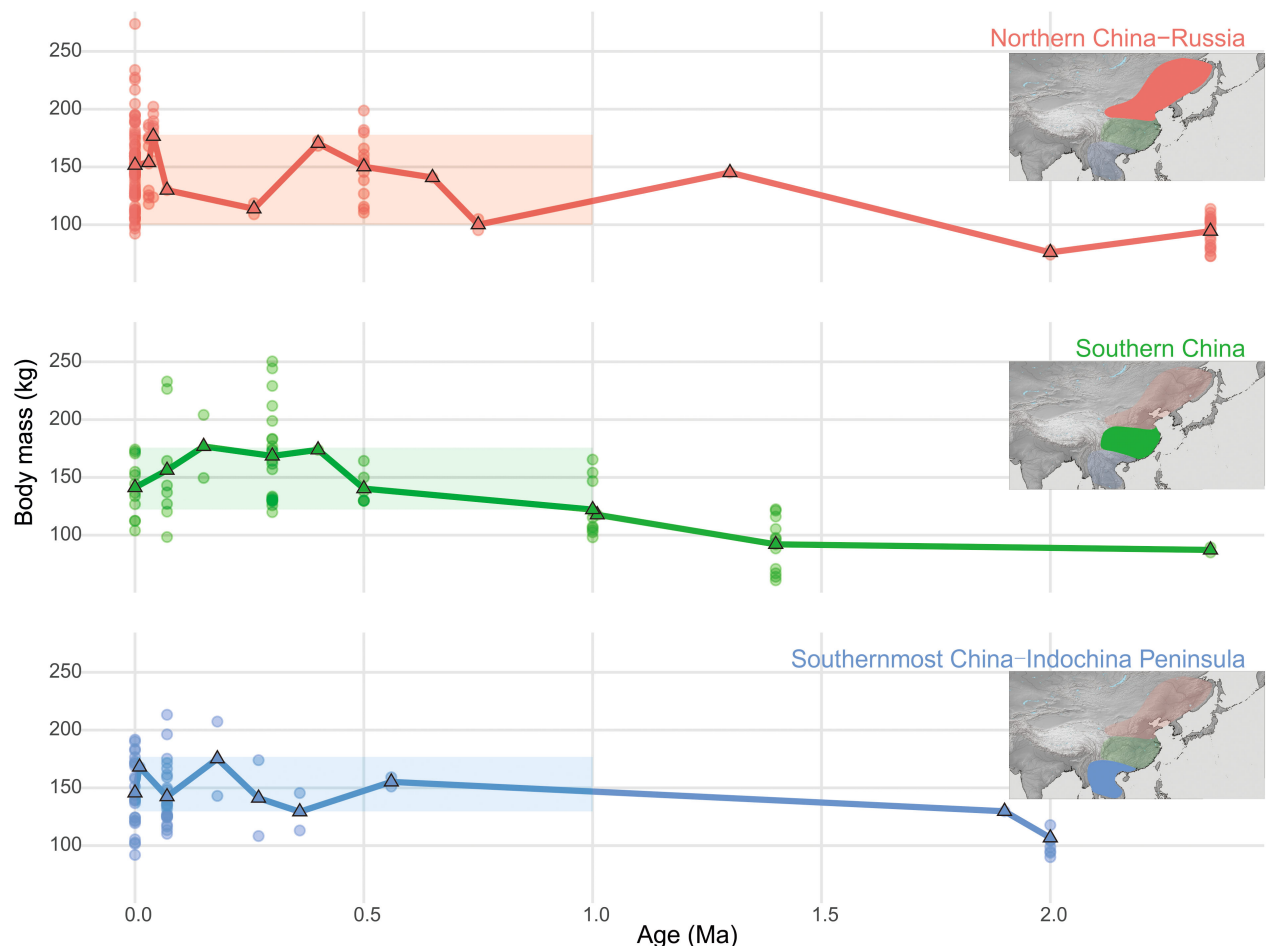


FIG. 19. Body mass evolution of the tiger lineage in the eastern part of Asia. Triangles represent the mean value of the population, and circles represent the individual data points. Maps from <https://www.simplemappr.net>

Interestingly, this coincides with the peak of body mass of the giant panda, which also reached the largest size during the late Middle Pleistocene (Jiangzuo *et al.* 2024b). Coinciding with the Brunhes event (EPICA Community Members 2004), in the Middle Pleistocene of southern China, intensification of monsoon produced abundant rainfall in southern China (Yin & Guo 2006; Hu *et al.* 2019), supporting a highly productive ecosystem, and, due to the abundant food, the tigers grew to a larger size, given that this favours intraspecies competition.

Although *P. palaeosinensis* is generally smaller than *P. tigris*, size cannot be used to differentiate the two species, given that some subspecies/populations have similarly small dimensions. The morphological characters proposed earlier should be prioritized as diagnostic criteria. However, we note that *P. palaeosinensis* and *P. tigris* represent chronospecies within a single lineage, making it difficult to definitively assign populations from transitional periods to either species.

Distribution & expansion of the tiger lineage

The geographical expansion of the tiger lineage can be subdivided into six chronological stages (Fig. 20). Since its first appearance (I), *P. palaeosinensis* has been recorded in northern and southern China, and southernmost China (Guangxi Province) (Qiu *et al.* 2004). However, it seems to be absent from the eastern part, not being recorded in the two main fossiliferous localities in the area: Renzidong and Tuozidong Caves, both dated between 2.5 and 2.0 Ma (Liu *et al.* 2007; Liu & Qiu 2009; Dong *et al.* 2013). In northern China, *P. palaeosinensis* is also present only in its southern and western part (Zdansky 1924; Qiu *et al.* 2004), and seems to be absent from the eastern and northern parts, given that it is absent from Zhoukoudian Loc. 18, Beijing (Teilhard de Chardin 1940), Nihewan, Yangyuan (Teilhard de Chardin & Piveteau 1930), Hebei Province, and Jinyuan Cave, Dalian, Liaoning Province (Jin *et al.* 2021 noted that *P. palaeosinensis* had been revised to the other species). After *P. tigris* appeared (II), its distribution seems to have remained unchanged, given that it is absent in the Jinyuan Cave, Luotuo Hill in northeastern China too. In this period, the fossil records are rare in China, and it is unclear whether it is present in the eastern part of southern China, because there are no fossil sites in these areas. At least since this time, the tiger has expanded its distribution into the Indochina Peninsula, given that it dispersed to Java, but we do not know whether it arrived there in period I.

In the earliest Middle Pleistocene (III), the tiger dispersed northwards, reaching the North China Plain, documented in Beijing. In the early Middle Pleistocene (IV), the tiger further slightly expanded its distribution

into the southern part of northeastern China and the eastern part of southern China. In the late Middle to Late Pleistocene (V), the tiger further expanded its distribution into the far east of Russia and southern Asia. The exact time when the tiger arrived there is, however, unclear, because there are no pre-Late Pleistocene localities in the Russian far east, and the ages of the Indian cave localities are mostly unclear (Prasad 1996). The last period is post-Last Glacial Period (VI), and the northern lineage of the tiger further dispersed in a western direction, reaching central to western Asia, in addition to some gene flow from southern Asia (Sun *et al.* 2023). Again, this pattern was determined using genetic studies only, given the lack of good fossil localities in central and western Asia.

In summary, during the first two-thirds of tiger evolution, the distribution of the tiger remained nearly unchanged, restricted to the southeastern part of Asia. Since the Middle Pleistocene, tigers have gradually expanded their range, especially into northeastern China and southern Asia. During the post-Last Glacial Period, tigers further colonized central and western Asia. The range expansion in the Middle Pleistocene was probably related to two factors. The exogenous factor involved longer and more extensive glacial–interglacial cycles (Ehlers *et al.* 2018), which provide more time windows for dispersal, as has been documented in many other taxa (Wagner *et al.* 2012; Jiangzuo *et al.* 2019, 2022b). The endogenous factor refers to further development of the ability to hunt large prey and quickly kill medium-to-small prey, which increases the adaptation advantage of tigers. The post-Last Glacial Period expansion into central and western Asia may be related to the demise of the cave lion (Stuart & Lister 2011), enabling tigers to occupy empty ecological niches.

CONCLUSION

This study represents the first comprehensive analysis of tiger evolution across its entire temporal range, integrating morphological, functional and palaeobiogeographic evidence from the Early Pleistocene to the present. By examining a broad fossil record, we trace the lineage back to *Panthera palaeosinensis*, widely distributed in both northern and southern China during the Early Pleistocene and here suggested to be the ancestral form of *P. tigris*. The earliest putative record of *P. tigris* (from Gongwangling, Lantian; c. 1.3–1.15 Ma) is based on a single tooth, but it signals the onset of a distinct evolutionary trajectory.

Our systematic review identifies and formally describes two archaic subspecies, *P. t. lui* (c. 1 Ma) from Xuetaugliangzi, Yunyang, southern China, the most primitive form in the modern species, and *P. t. palaeobeijingensis*

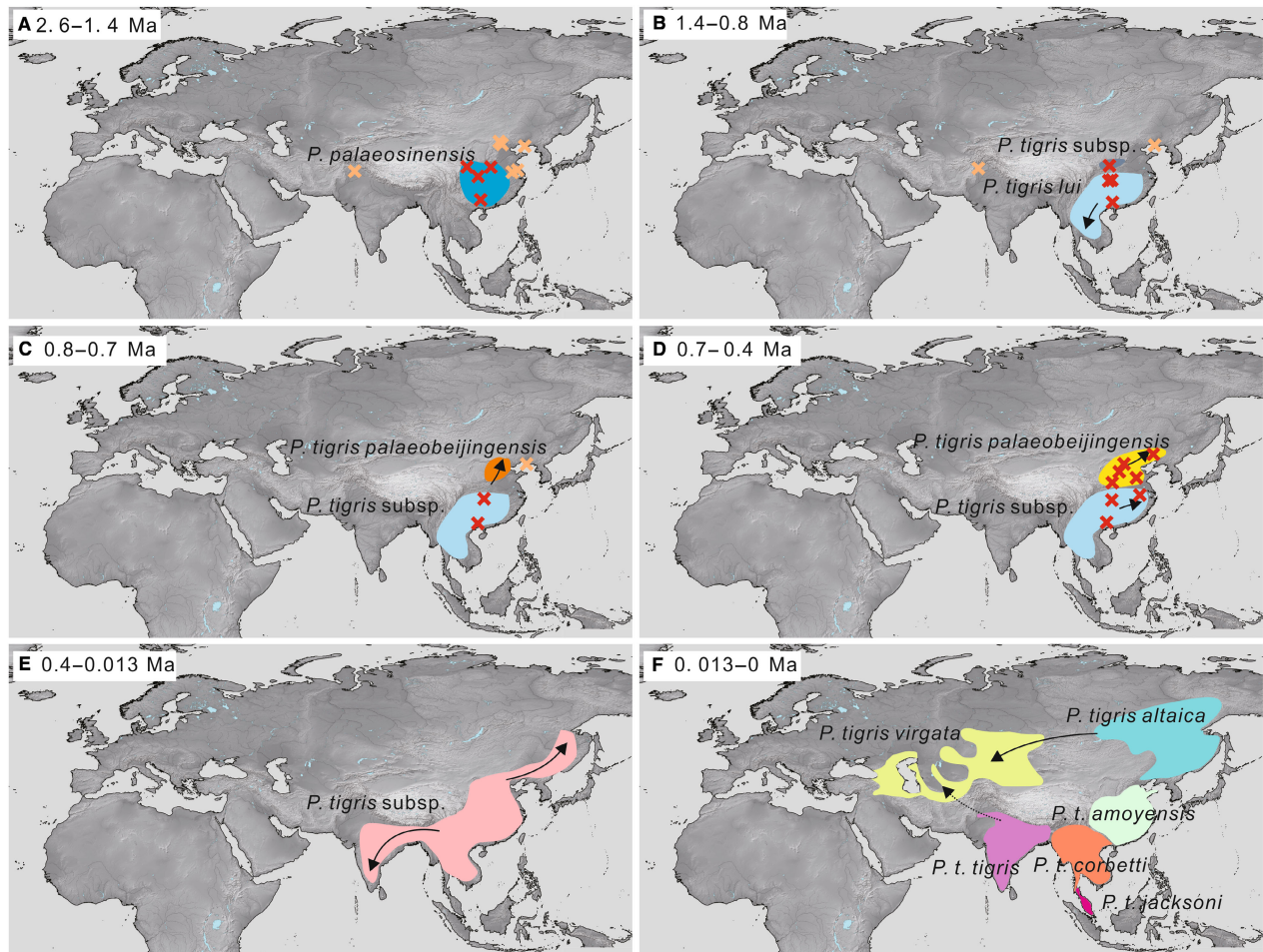


FIG. 20. Distribution of the tiger lineage through geological time (mainland only). Arrows indicate the direction of expansion relative to the last period. The red crosses represent important fossil localities of the tiger, whereas the orange crosses indicate evidence of absence. Maps from <https://www.simplereappr.net>

(c. 0.75 Ma) from Zhoukoudian Loc. 13, northern China, a dwarf subspecies averaging c. 100 kg in body mass. In addition, *P. t. acutidens* is revised to include early Middle Pleistocene tigers from northern China, morphologically close to the modern form but retaining primitive features. Later Middle Pleistocene and Late Pleistocene tigers are essentially indistinguishable from extant subspecies.

Morphological trends indicate progressive enhancement of adaptations for subduing large prey and delivering rapid, lethal bites to medium-sized prey, coupled with a reduction in durophagous traits; specializations that parallel those of sabertoothed cats. Body mass reconstructions indicate a general size increase through time, punctuated by regional fluctuations, with northern Chinese populations showing the greatest amplitude. These size dynamics appear strongly linked to environmental factors: intensified climate oscillations following the Early–Middle Pleistocene Transition, increased resource availability during humid

phases, and the extinction or decline of major competitors such as sabertoothed cats and large hyenas.

Together, these findings provide a complete evolutionary framework for the tiger lineage, highlighting the interplay between functional adaptation and environmental pressure in shaping its morphology, body size and geographical expansion over the last 2.5 myr.

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DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: <https://zoobank.org/References/40560d13-5b72-4aa0-8458-61b6c6b0a4a2>

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1002/spp2.70131>):

Appendix S1. Additional information about the modern tiger including a list of data sources for measurements.

Appendix S2. R code for biplot and body mass estimation.

Table S1. Cranial and upper dental measurements of the tiger lineage.

Table S2. Mandibular and lower dental measurements of the tiger lineage.

Table S3. Relationship of the P4 and m1 length, used for regression.

Table S4. Data for the m1 length used for body mass estimation.

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