Body mass evolution of the Quaternary giant panda coincides with climate change of southern China

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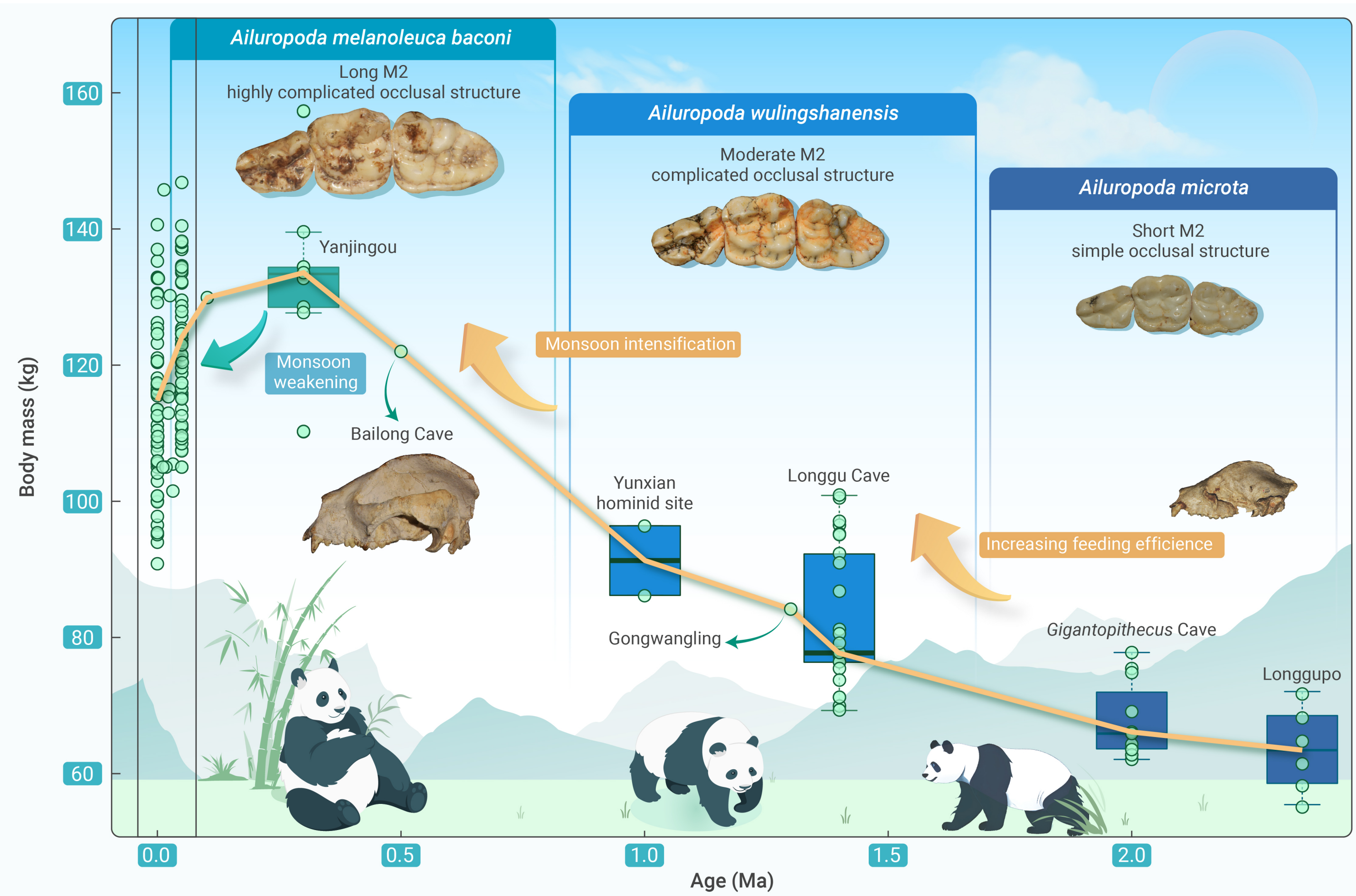
GRAPHICAL ABSTRACT



PUBLIC SUMMARY

- Comprehensive model comparisons confirm the m1 as a reliable body size indicator in Quaternary giant pandas.
- The body mass of Quaternary giant pandas first increased, then decreased, reaching its peak around 0.3 Ma.
- Quaternary giant panda body mass evolution was shaped by morphology and paleoclimate changes.

REPORT

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The trend of giant panda (*Ailuropoda*, Ursidae) body size evolution during the Quaternary has long been observed primarily through dental size analysis. However, exact body mass estimations have been lacking, whereas the dental size is generally viewed as a poor index for body mass estimation. In this study, we assess the accuracy of body mass prediction based on dentition using data from extensive cranial, dental, and postcranial fossil remains recovered in the Shuanghe Cave, Guizhou, southwestern China. Our results support a high degree of accuracy in body mass estimation based on m1 length, likely due to the relatively stable proportion of this tooth to the whole body in the Quaternary *Ailuropoda*. Our analyses of the body mass evolution of giant pandas since the earliest Pleistocene reveal rapid growth in body mass from *A. microta* to *A. melanoleuca* in the Early Pleistocene. This was followed by an initial increase and subsequent decrease in body mass, leading to the modern form since the Middle Pleistocene. The initial period of rapid growth is likely driven by the increasing feeding efficiency on bamboo, facilitating larger body sizes. In contrast, the later fluctuation in body mass coincides with climatic and monsoon change in the Middle and Late Pleistocene, directly impacting bamboo availability. The body mass evolution of the giant panda offers insights into its historical adaptation, highlighting the correlation of evolution and paleoclimatic change during the Quaternary.

INTRODUCTION

The giant panda (*Ailuropoda melanoleuca*) is now endemic to the mountainous region of central and southwestern China.[1,2] With its specialized appearance, unique diet and behavior, it becomes an iconic animal for both science and popularity.[3-5] As a vital member of Ursidae in order Carnivora, the giant panda is strictly herbivorous, primarily feeding on bamboo in the wild.[6,7] This is noteworthy since Carnivora with a body mass of more than 20 kg often switch to a hypercarnivorous diet due to energetic constraints,[8,9] as they (including the giant panda) lack a digestive tract, digestive enzymes, and a gut microbiota that are well-adapted to digesting plant material.[10] Understanding how and when the giant panda reaches its modern size, as well as factors influencing its body mass evolution, is essential for comprehending the unique morphological and physiological mechanism to maintain its large body size while subsisting on a bamboo diet.

The giant panda is an important component in the classical *Ailuropoda-Stegodon* fauna in southern China, with extensive dental remains in many southern China Pleistocene fossil localities.[11-16] Previous research has noted a general increase in the dental size of the giant panda from the Early to Middle Pleistocene, followed by a decrease from the Late Pleistocene to Holocene.[11,17] However, dental size is generally viewed as an inadequate proxy for body mass estimation compared with e.g., long bone, as it does not directly bear the body mass.[18,19] The majority of the giant panda fossil remains are, however, isolated teeth and the postcranial bones are virtually unknown, making accurate body mass estimation difficult.

An exception to this scarcity of postcranial remains is found in the Shuanghe Cave in Guizhou Province, southwestern China. In this region, several complete or partial skeletons and complete skulls of fossil *A. melanoleuca* baconi are preserved.[20] These remains provide an opportunity to estimate the body mass of the fossil giant panda using different skeletal components and cross-validate the accuracy of these various components.

Geological backgrounds

Shuanghe Cave is located in the mountainous region of Shuanghe Village, Suiyang, Guizhou Province of southwestern China. The vegetation in the area of Shuanghe Cave is characterized by subtropical evergreen and deciduous broad-leaved forests, with significant human influence leading to the preservation of original forests only in some high-altitude areas. The dominant tree species include *Fagus lucida*.[21] Bamboo resources are abundant, with *Chimonobambusa utilis* and *Yushania brevipaniculata* being the predominant species.[22] Common wild animals in the area include wild boars (*Sus scrofa*), muntjacs (*Muntiacus reevesi*), leopard cats (*Prionailurus bengalensis*), and porcupines (*Atherurus macrourus*). Additionally, within 5 kilometers of the Shuanghe Cave area, the wide-ranging Shiwandashan National Nature Reserve is home to a large population of François' langurs (*Trachypithecus francoisi*).

Shuanghe Cave is the longest cave system in Asia, primarily developed in a set of gypsum-bearing dolomite and bioclastic limestone of the Louguanshan Formation and Tongzi Formation, Upper Cambrian and lower Ordovician.[23] The surrounding area features typical karst peak-cluster and gorge landscapes, with minimal surface runoff and precipitation mainly infiltrating into underground rivers that eventually join low-altitude rivers. The so far measured length over 409.9 km, and a depth of 912 meters. The Shuanghe system has more than 300 cave openings, with 105 of them connected with each other. The altitude of the opens ranges from 600 to 1300 m. The cave system is mainly developed in the horizontal orientation, and with at most eight layers of cave channel in the deepest part. The fossil remains of the giant panda are abundant in the regions, with more than 30 individuals found so far, most of which were found in the surface, mostly with very little or no sedimentary burial.[20,24,25] The fossil remains of other large mammals are rare and not systematically collected yet. The so far recorded mammals include cf. *Cuon* sp., *Viverra* sp., *Ursus thibetanus*, Bovidae indet., Cervidae indet..

To survey the body mass evolution in the Quaternary, the materials from several other localities that produced rich fossil giant pandas were included in the study. These sites are Early Pleistocene Longgupo, Wushan, Chongqing,[26] *Gigantopithecus* cave, Liucheng, Guangxi,[11] Longgudong Cave, Jianshi, Hubei,[27] Xuetangliangzi, Yunxian, Hubei,[28,29] Middle Pleistocene Yanjinggou, Wanzhou, Chongqing,[30,31,32] and Late Pleistocene Yanjiawan Cave 2, Pingxiang, Jiangxi,[15,16] Xianren Cave, Xichou[33] and various late Middle and Late Pleistocene caves, Guangxi.[11] See Table 1 for details.

MATERIALS AND METHODS

The fossil material used to estimate and cross-validate the body mass of the giant panda comes from Shuanghe Cave, mostly housed in Guizhou

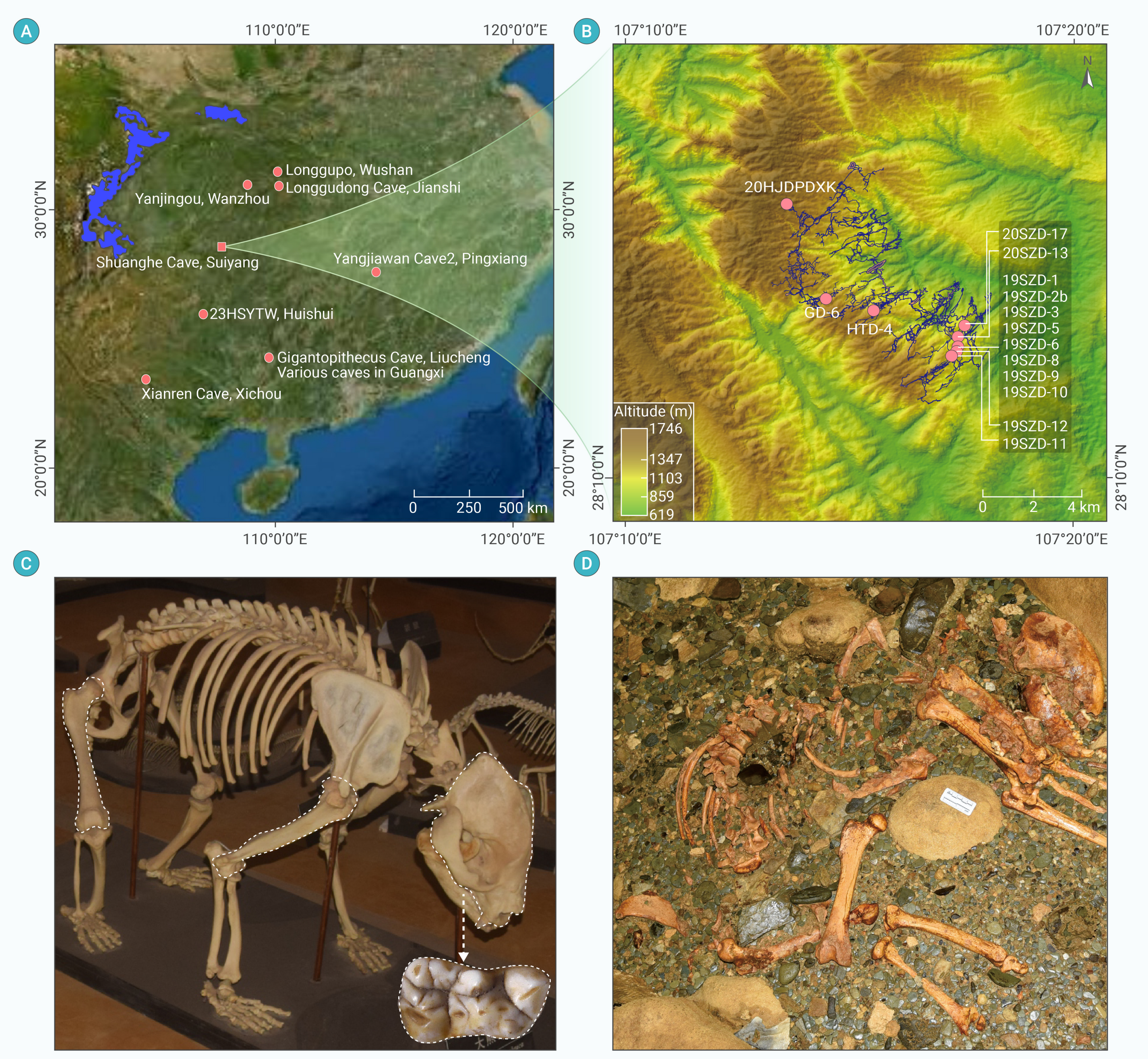

Figure 1. Overview of Giant Panda Fossil Sites and Skeletal Elements (A) Location of the fossil sites that produced the giant panda fossils used in this study; (B) Fossil localities in the Shuanghe Cave system; (C) Diagram of skeletal and dental elements (cranium, humerus, femur, and m1) used in body mass estimation. The skeleton is in exhibition at Kunming National History Museum of Zoology, and the tooth (m1 IOZ32752) is housed in the Institute of Zoology, CAS; (D) The partial skeleton of a fossil giant panda (19SZD-12) found in situ in the Shuanghe Cave system.

Institute of Mountain Resources, Guiyang, China (Figure 1). Modern skull and skeleton of the two subspecies of the giant panda, *A. m. melanoleuca* housed in IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China), IOZ (Institute of Zoology, Chinese Academy of Sciences, Beijing, China), KIZ (Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China), AMNH (American Museum of Natural History, NYC, USA), and *A. m. qinlingensis* house in SIZ (Shaanxi Institute of Zoology, Chinese Academy of Sciences), SFNR (Shaanxi Foping National Reserve). The giant panda fossil remains from other localities are mainly housed in IVPP, but also some from AMNH, a few from CYPL (Chongqing Key Laboratory of Paleontology and Paleoenvironment Co-evolution (Sichuan-Chongqing Joint Construction), No. 208 Hydrogeological and Engineering Geological Team, Chongqing Bureau of Geological and Mineral Resource Exploration and Development, Chongqing), and Wushan Museum, Chongqing, China.

Training data

The giant panda has enlarged teeth compared to its overall body size, so the general equation for Ursidae or Carnivora will significantly overestimate its body mass. The best way is to do regression based on modern species body mass-bone/tooth measurements. Unfortunately, there is nearly no data on associated premortal body mass and bone measurements. Different literature gives slightly different but largely overlapped body masses for the giant panda, e.g., average male 118kg, and female 97 kg;[1] 80-110 kg;[2] 75-160 kg.[34] Recently, Zhang et al.[35] published a large dataset of more than 200 captive individuals kept at the China Conservation and Research Center for the Giant Panda (CCRCGP), Dujiangyan, Sichuan, China, and gave 108. 35 ± 11. 01 kg for adult (7-16 years old) female, 118. 85 ± 10. 79 for adult (7-16 years old)

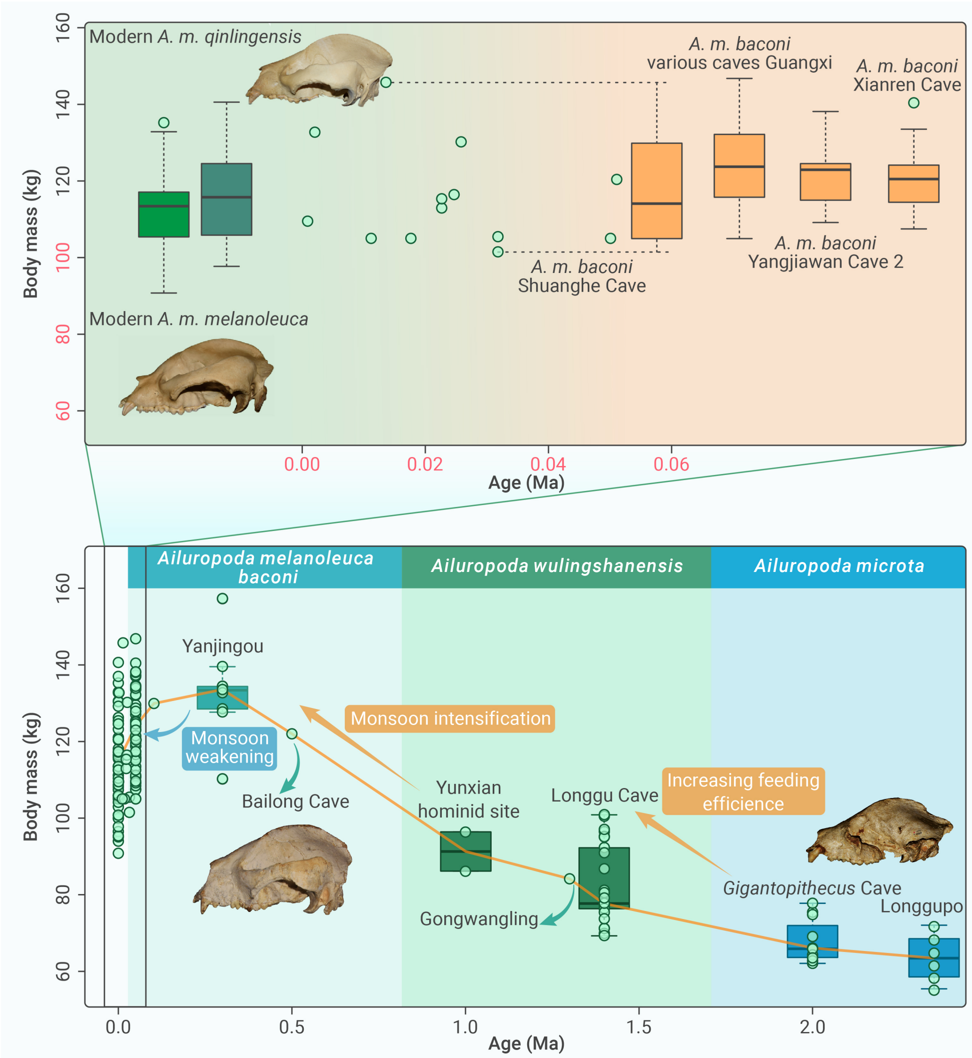

Figure 2. Body mass evolution of the Quaternary giant panda.

male, 99.96 ± 17.26 for old (17-32 years old) female, and 102.15 ± 12.66 (17-32 years old) for old male. This dataset (only adult males and females) was used as basic body mass. The cranial, teeth and postcranial bones of modern two subspecies of giant panda were used as basic bone measurement data. The skeletons of the data measured are housed in AMNH, IOZ, IVPP, FP, and KIZ.

Linear models

As the body mass data and bone/teeth measurement data are not associated, we used an assumption that large body mass should correspond to large bone/teeth. This is natural but not necessarily correct in the real case, but this study only focuses on the population-level body mass evolution, not individual one, and there is no better way for inference. As the body mass data pool is larger than those of bone/teeth measurements, the same number of body mass values as the bone measurements were randomly selected for each analysis. To avoid the influence of random selection of body mass data, this process was performed 1000 times, and the mean value for prediction from each linear model was used as the final result.

RESULTS

For each skeletal and dental element, we conducted 1000 model iterations, from which the mean body mass predicted and mean R-squared values were derived. These results are presented in the in the Supplementary materials. The results indicate that the mean R squares for all elements are high, consistently exceeding or equaling 0.9. Notably, the model based on the m1 element has the highest mean adjusted R square (0.944). As the adjusted R square already removes the influence of the predictor number, this suggests that, at least in the modern giant panda, the m1 has a good performance in predicting the body mass.

We proceeded to compare the results of body mass estimation of different individuals of the same, including 17 modern skeletons and 7 partial fossil skeletons from the Shuanghe Cave. In both modern and fossil cases, the mean body mass differences (BM-skeleton/BM-m1) are very close to 1, so we combined them for analysis. We perform a linear model of the BM-skeleton and BM-m1 of these 24 samples, and the adjusted R square is relatively low (0.464). Two sample pared t test yields a very high p value of 0.89. These results combined suggest the skeletal elements and m1 do not give a uniformly higher or lower estimation compared with each other, but the differences between the two sides are still distinct. Further examination of a single case of the Early Pleistocene giant panda *A. microta* with cranial data revealed a body mass estimation of 70.7 kg. Remarkably, this aligns closely with the mean body mass of this species from the *Gigantopithecus* Cave, estimated from m1 length (68.0kg).

DISCUSSIONS AND CONCLUSIONS

Dental measurements as an attainable approach to estimating the body mass of Quaternary *Ailuropoda*

Our findings imply that, at least in the Quaternary *Ailuropoda*, m1 (lower first molar) length is a better reference for body mass, outperforming the skeletal elements in terms of the mean adjusted R square of the linear model. This advantage likely stems from the relatively stable proportion of the m1 length in relation to the whole body throughout the evolution of the Quaternary giant panda. Notably, the earliest known species of *Ailuropoda* in the Early Pleistocene, i.e., *A. microta*, exhibits virtually identical morphology and dental structure to the modern panda,[11,17] suggesting a similar feeding function since the Early Pleistocene. This stability implies that the dental proportions have not significantly changed throughout the Quaternary. Moreover, the m1 is one of the earliest specialized teeth, which evolves earlier than most other teeth.[36,37] Its form and function are thus remained relatively stable in the Early Pleistocene, making it a suitable candidate for body mass estimation. Consequently, we have based our discussion on body mass evolution primarily on estimates derived from m1 measurements, as it is more or less the only element preserved in earlier geological time among the four that we establish.

We refrain from extending our estimation to deeper time, as there is a long gap in giant panda fossil records during the Pliocene. In the Late Miocene, several giant panda relatives are known, from both Europe and southern China.[38-42] These materials are very poorly preserved, limiting our ability to study the relationship between dental size and overall body size. Recent findings on an *Agriarctos* species from Bulgaria, reveal a P4 length similar to that of *A. microta*, but its canine is even larger than the modern *A. melanoleuca*,[42] suggests a very different proportion and bauplan from that of the Quaternary *Ailuropoda*.

The evolutionary tendency of body mass of the giant panda during the Quaternary

The body size increase of the giant panda in its early stage of evolution, from *A. microta* to *A. m. baconi*, followed by a decrease from *A. m. baconi* to modern form, has been noticed.[5,11,17,43-46] However, no exact body mass has been estimated, and there has been no clear chronological framework to constrain these evolutionary changes in body size. Utilizing our linear model based on the m1 and various isotopic dating methods applied to specimens from Shuanghe Cave and recent studies, we estimated the body mass of several different populations, covering the fossil species *A. microta*, *A. wulingshanensis*, *A. m. baconi*, and the modern subspecies *A. m. qinlingensis*.

Our results (Figure 2) support a continuous body size increase from the earliest Pleistocene to the late Middle Pleistocene. The earliest population is from Longgupo, Wushan, with an age of 2.2-2.5 Ma.[47] The giant pandas from this population is generally similar to those from *Gigantopithecus* Cave in Guangxi, which is slightly younger (2 Ma). Huang and Zhong[26] measured six m1s of this population, but they only gave ranges and mean values of the m1 length, but not individual data. To assess general variation in body mass, we interpolated six lengths at equidistant intervals (0.6 mm) within this range. The resulting body mass range and mean value is slightly smaller than that of *Gigantopithecus* Cave.[26] The next younger population is Longgu Cave, Jianshi. A high variation in body mass is observed in this population, which is not surprising given its large number of specimens. The sample from 1.0-1.3 Ma is rare but falls into the variation of the population of Longgu Cave, but their values are larger than the mean value observed in the Longgu Cave. A single case from the Bailong Cave, Yunxian, Hubei, ~0.5 Ma, falls into the variation of the younger *A. melanoleuca*. The peak of the giant panda body mass occurred in Yanjinggou, Wanzhou, Chongqing, with an age estimation of 0.35–0.26 Ma.[30] Both the crania and dentition from Yanjinggou have a large size and the mean and largest body masses of fossil giant panda are present here.

The three Late Pleistocene (in Guangxi there are some late Middle Pleistocene one mixed within the Late Pleistocene ones) giant panda populations (except Shuanghe Cave one) have similar mean body masses and ranges (p-value 0.28 for ANOVA of three populations), and they are significantly smaller than the population from Yanjinggou (with p value<0.01 for t-test, as a whole comparing the Yanjinggou population). Among the two modern populations, *A. m. qinlingensis* is slightly larger than *A. m. melanoleuca* in both range and mean value, but the differences are not insignificant (p-value 0.24 for t-test), but they are significantly smaller than those of the three Late Pleistocene populations (p value<0.01 for t-test).

Notably, the giant panda from the Shuanghe Cave System has a lower mean value compared to other Late Pleistocene populations, though the differences are not significant (p-value 0.09 for t-test). They are in fact more similar to the modern two subspecies in body mass (p-value 0.37 for t-test). This may be related to the generally young age of the Shuanghe Cave populations, with their age mostly within the past 50 kyr. But among the documented body mass and age in the Shuanghe Cave, we cannot discern a clear tendency for body size decrease in the past 50 kyr. Due to the lack of precise dating of other Late Pleistocene populations, we cannot draw definitive conclusions on the tendency of body mass evolution within the Late Pleistocene.

In summary, while the detailed trend within the Late Pleistocene remains unclear due to insufficient dating, a general increase in body size of *Ailuropoda* from the earliest Pleistocene to the late Middle Pleistocene, followed by a decreasing body size from the late Middle Pleistocene to modern time is supported. This contradicts with the previous classification on assigning all Middle and Late Pleistocene to *A. m. baconi*, which is mainly different from the modern subspecies by its larger size,[17] therefore implying that the body size decreases quickly at the Pleistocene-Holocene transition.

Body mass implication on the Quaternary climate change in southern China

The chronological framework and pattern of body mass evolution are important to understand the Quaternary environmental change in southern China. Several lineages, e.g., Asiatic black bear, tiger, and tapir, are known to have experienced a body size increase since the Early Pleistocene, followed by a size decrease to the modern species/subspecies level.[11,48,49] As in the case of the previous situation of the giant panda, no exact body mass or chronological constraint on the transition from increase to decrease of the body size has been surveyed. Our analysis of the giant panda, therefore, provides an opportunity to investigate whether such body mass changes are related to the Quaternary environmental change in southern China.

The giant panda is almost exclusively a bamboo feeder,[6,7,50,51] and its morphology reflects this specialized diet. Key adaptations include a heave and robust cranium, a thick zygomatic arch and mandible, enlarged premolars with cutting ability, enlarged molars with complicated surface morphology, enlarged radial sesamoid functioning as pseud-thumb.[2,4,36,39,50,52,53] The basic craniodental morphology has been developed since the Early Pleistocene, and the pseudo-thumb has its deep origination in the Late Miocene,[54,55] and developed at least to modern size since the Late Pleistocene.[20] Most stable isotopic studies also support an early specialization in the diet of the giant panda,[56,57] though some studies also suggested a wider range of diet in the Pleistocene panda.[58] The body mass evolution of the giant panda is therefore likely to be correlated with the development of bamboo in southern China.

The Early Pleistocene climate is largely stable in southern China.[59] An increase in masticatory apparatus and further enhanced surface complexity of the molars is seen in the evolution from *A. microta* and *A. m. baconi*,[11,17,30] and the body mass increase may be a result of increasing feeding efficiency of the giant panda, rather than a direct result of climate change. Since the Middle Pleistocene from *A. m. baconi* to modern subspecies, there has been very little change in morphology except for the body mass,[30] and the change in body mass in this stage is likely more influenced by climate change and bamboo biomass. Bamboo thrives in mild and humid climates.[60] During the Middle Pleistocene of southern China, the strong monsoon, and abundant rainfall in southern China[61,62] favored the development of bamboo forest, which provides abundant food sources for the giant panda. The transition from this condition occurs between 0.27-0.35 Myr, when the climate changes to a cold and dryer condition.[63-65] The decrease of the body mass of the giant panda exactly coincides with the beginning of such an environmental change. Notably, the falls and extinction of other large mammals with a preference for the bamboo diet, *Gigantopithecus*,[66,67] also coincides with this change.

In summary, the body mass increase observed from *A. microta* to the appearance of *A. melanoleuca* likely reflects the increasing adaption to the bamboo diet, and may not be directly influenced by climate change (but this needs more exploration). From the Middle Pleistocene onward, *A. melanoleuca* experienced an initial increase in body mass, peaking at ~0.3 Ma, followed by a decrease in body mass to modern size. During this period, the body mass shows a high congruence to climate change, particularly in relation to the development of bamboo forests.

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AUTHOR CONTRIBUTIONS

S. Li design the research; Q. Jiangzuo, D. Wang, C. Zhang, C. Zhang, J. Bottazzi, G. Kuang, S. Li, J. Fu, H. Hu, H. Tong, B. Zhang collect the data; perform the analysis; all authors write and review the paper. All authors contributed to and approved the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

DATA AND CODE AVAILABILITY

The data provided in the Supplementary materials.

SUPPLEMENTAL INFORMATION

It can be found online at https://doi.org/10.59717/j.xinn-geo.2024.100096.