

The first skull of the earliest giant panda

Changzhu Jin*, Russell L. Ciochon^{†‡}, Wei Dong*[§], Robert M. Hunt, Jr.[¶], Jinyi Liu*, Marc Jaeger^{||**}, and Qizhi Zhu^{††}

*Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China; [†]Department of Anthropology, University of Iowa, Iowa City, IA 52242-1322; [‡]State Key Laboratory of Pattern Recognition, Institute of Automation, Chinese Academy of Sciences, Beijing 100080, China; [§]Department of Geosciences and State Museum, University of Nebraska, Lincoln, NE 68588-0514; [¶]Joint Sino-French Laboratory in Informatics, Automation, and Applied Mathematics (LIAMA), Institute of Automation, Chinese Academy of Sciences, Beijing 100080, China; ^{**}Laboratory of Botany and Bioinformatics of Plant Architecture (AMAP), Agricultural Research Centre for International Development (CIRAD), TA40/PS2, 34398 Montpellier Cedex 05, France; and ^{††}Renmin Hospital, Peking University, Beijing 100044, China

Communicated by Richard G. Klein, Stanford University, Stanford, CA, May 8, 2007 (received for review January 10, 2007)

Fossils of the giant panda *Ailuropoda* (Order Carnivora, Family Ursidae) are largely isolated teeth, mandibles, and a few rare skulls, known from the late Pliocene to late Pleistocene in China and Southeast Asia. Much of this material represents a Pleistocene chronospecies, *Ailuropoda baconi*, an animal larger than the living giant panda, *Ailuropoda melanoleuca*. The earliest certain record of *Ailuropoda* is the late Pliocene chronospecies, *Ailuropoda microta*, smaller than either *A. baconi* or *A. melanoleuca*, and previously known only from teeth and a few mandibles from karst caves in south China. Here, we report the discovery of the first skull of *A. microta*, establishing its cranial anatomy and demonstrating that the specialized cranial and dental adaptations of *Ailuropoda* for durophagous feeding behavior centered on bamboo were already evident in this late Pliocene species. The skull from Jinyin cave (Guangxi) and dental remains from other karst localities in southeastern China show that *Ailuropoda microta* occupied south China from ≈ 2 to 2.4 Myr ago after a marked global climatic deterioration. Dental and basicranial anatomy indicate a less specialized morphology early in the history of the lineage and support derivation of the giant panda from the Miocene Asian ursid *Ailurarctos*.

Carnivora | *Ailuropoda microta* | China | karst caves | Southeast Asia

The limited fossil record of the giant panda *Ailuropoda* [Family Ursidae (1)] has, until recently, been primarily composed of teeth, mandibles, and a few skulls from the largest representative of the lineage, *Ailuropoda baconi*, found in Pleistocene cave fillings of Southeast Asia (2–5). The earliest record of *Ailuropoda* is a small late Pliocene chronospecies, *Ailuropoda microta*, until now known only from isolated teeth and a few mandibles from karst fissures in south China (4, 6, 7). Giant pandas are descended from a late Miocene ursid, *Ailurarctos* (8–10), with a poor fossil record. A few isolated teeth recovered from a site near the village of Lufeng, Yunnan, in south China, of late Miocene age (≈ 7 –8 Myr), mark the earliest record of the lineage in southeast Asia (no skull of the Lufeng panda is known), and demonstrate the first appearance of the crushing cheek teeth characteristic of the living species. The teeth of the Lufeng panda were initially mistaken for those of the small Holarctic ursine bear *Ursavus*. A marked similarity exists, in accord with the current view that *Ailurarctos* is derived from a Miocene species of *Ursavus* (8–10). In turn, the cusped teeth of *A. microta* suggest a dental stage intermediate between *Ailurarctos* and the complex occlusal pattern of the living giant panda. The new *A. microta* skull (Fig. 1) adds important data to that evolutionary hypothesis.

Results and Discussion

The new specimen establishes that the cranial anatomy of the giant panda (and probably the postcranial skeleton) remained essentially uniform, except for size and minor dental alterations, for more than 2 Myr during the late Pliocene and Pleistocene, a

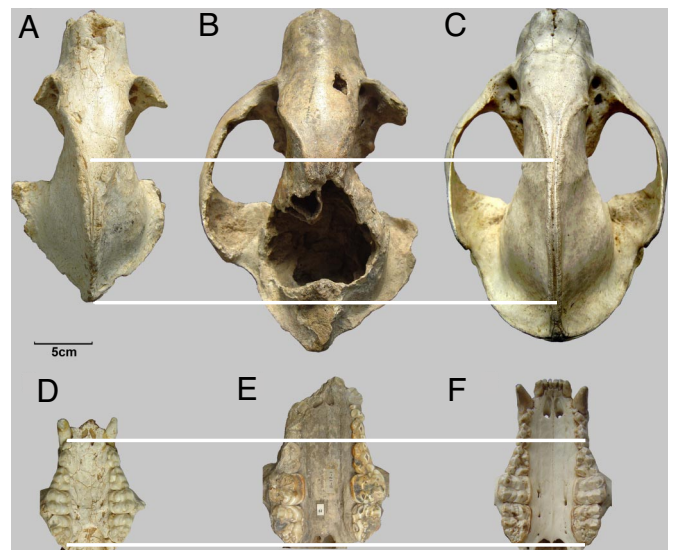


Fig. 1. Comparison of the skull and upper dentition of fossil and extant giant pandas. (A and D) *Ailuropoda microta* (IVPP V14564), late Pliocene, Jinyin cave, China. (B and E) *A. baconi*, Pleistocene, Liujiang, Guangxi, China. (C and F) Living *A. melanoleuca*, China.

period of pronounced global climatic instability. Because anatomical specializations of the teeth, skull, and jaws for crushing and grinding tough, fibrous food are evident in the *A. microta* skull, a preference for a diet of bamboo has probably characterized the lineage since the late Pliocene. These specializations include increased cusping of the cheek teeth for durophagy; the robust expansion of the posterior cranium for enhanced temporal musculature; and initiation of overgrowth of the auditory region by enlarging the jaw articulation of the skull. The limited geographic distribution of today's pandas, confined as isolated populations to rugged mountainous terrain in southeastern China (11, 12), indicates a profound loss of territory relative to the Plio-Pleistocene ranges of the earlier ailuropods (10, 13, 14).

Author contributions: C.J., R.L.C., W.D., and R.M.H. designed research; C.J., R.L.C., W.D., R.M.H., J.L., and M.J. performed research; M.J. and Q.Z. contributed new reagents/analytic tools; R.L.C., W.D., and R.M.H. analyzed data; and R.L.C., W.D., and R.M.H. wrote the paper.

The authors declare no conflict of interest.

Abbreviations: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; AMNH, American Museum of Natural History, New York, NY (Mammalogy).

[†]To whom correspondence should be addressed. E-mail: russell-ciochon@uiowa.edu.

This article contains supporting information online at www.pnas.org/cgi/content/full/0704198104/DC1.

© 2007 by The National Academy of Sciences of the USA

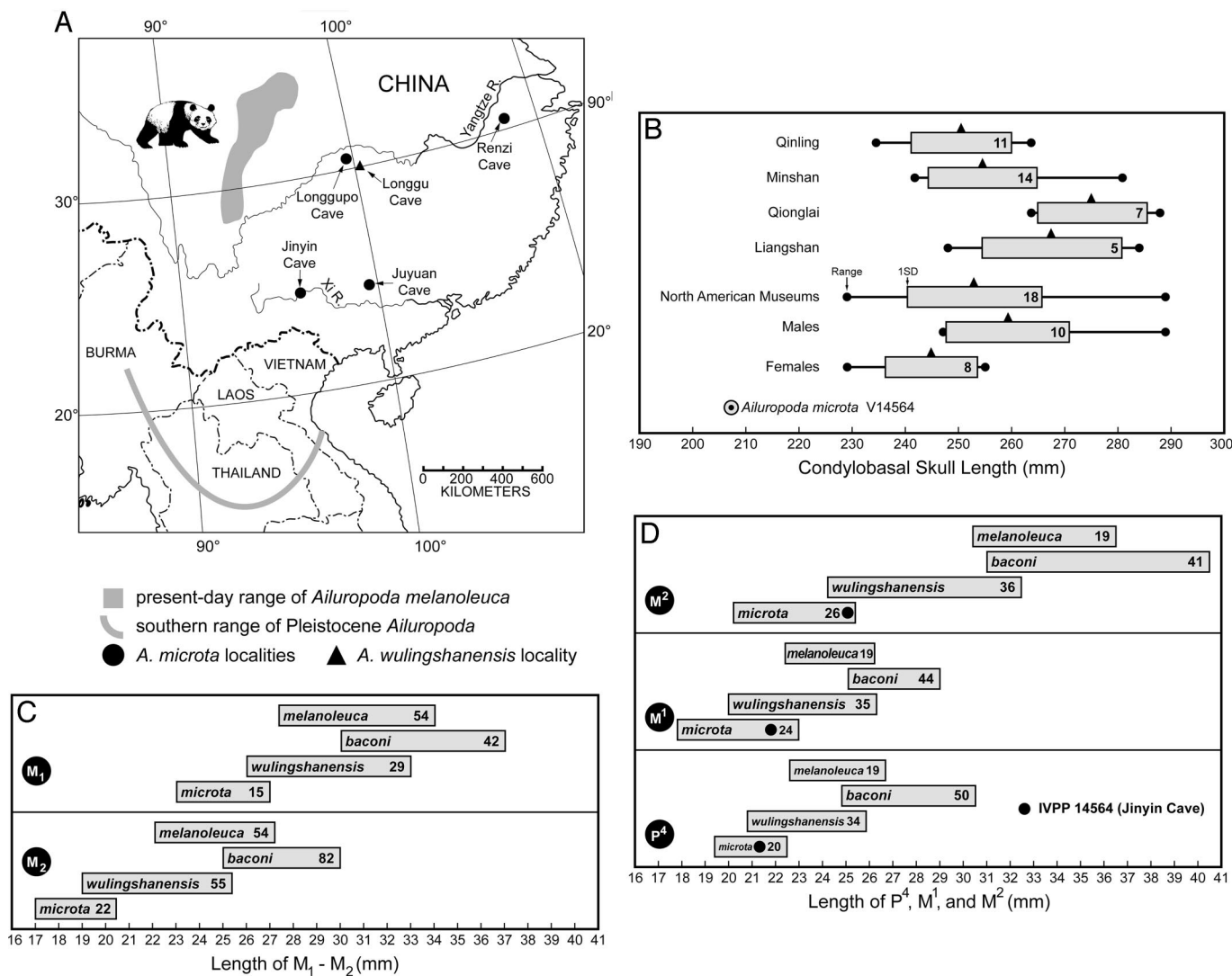


Fig. 2. Geographic distribution and craniodental dimensions of fossil and living giant pandas. (A) Localities yielding *A. microta* and *A. wulingshanensis* in southeastern China relative to the geographic range of the giant panda in the Pleistocene. Present-day range of the giant panda is from Loucks *et al.* (28). The southernmost range of the giant panda is defined by fossil discoveries at Mogok, Burma (5), Chaiphaphum, Thailand (14), and Lang Trang, Vietnam (29). (B) Condylobasal length of skull (in millimeters) for the living giant panda *A. melanoleuca* relative to the Jinyin cave *A. microta* skull (IVPP V14564). Range, 1 SD and the mean are indicated; sample size noted within each SD bar. The four upper samples represent subpopulations of the living giant panda (11); the lower three samples are 18 skulls of *A. melanoleuca* measured in North American museums (22). These 18 skulls are then separated by sex to demonstrate dimorphism. No skulls of *A. wulingshanensis* are known, and the few skulls of *A. baconi* fall in the upper part of the range of the living giant panda. (C and D) Distribution of dental measurements (in millimeters) for the four species of giant panda *Ailuropoda* (late Pliocene–Recent); M₁, M₂ lengths (C); P⁴, M¹, M² lengths (D). Sample size is indicated within each range bar.

Until 1985, only one site, at Juyuan cave, Liucheng (Guangxi) had yielded fossil evidence of the diminutive panda (15). The Juyuan cave fauna, with a typical Southeast Asian *Stegodon*–*Ailuropoda* component, is considered older than 1.2 Myr. However, discoveries from 1985 to 2002 brought to light new material from three additional sites (Fig. 2A), refining the age range for *A. microta*: (i) Longgupo cave, Wushan (Sichuan), where *A. microta* was paleomagnetically dated at ≈2 Myr ago (16, 17). Excavated in 1985–1988, the *A. microta* level (“middle fauna”) at Longgupo produced 92 mammal species, including *Gigantopithecus blacki*, *Sinomastodon*, the chalicothere *Nestoritherium*, *Equus yunnanensis*, and *Mimomys peii*: a late Pliocene fauna (16–19); (ii) Renzi cave, Fanchang (Anhui), biochronologically correlated to ≈2–2.4 Myr ago (17). Here, *A. microta* occurs with a late Pliocene fauna of 67 mammal species, evincing a Palaeartic bias. Renzi cave lacks

typical southern mammals (*Stegodon*, *Viverra*, *Gigantopithecus*) and is considered older than Juyuan cave (17); (iii) Jinyin cave, Leye (Guangxi), yielding the present skull (IVPP V14564), with an estimated age of >2 Myr. The skull, found by two of us (C.J. and J.L.) in 2001, was an isolated discovery with no associated fauna. It was recovered from a cemented calcic yellow clay at the cave wall. The scattered nature of the discontinuous cave deposits makes stratigraphic assessment difficult, and it has not been possible to date the skull directly. Although the sediments at Jinyin cave have not been dated, the biochron of *A. microta* established at Longgupo cave and Renzi cave supports a late Pliocene age.

No fossils of the much larger Pleistocene panda, *A. baconi*, or an intermediate form, *Ailuropoda wulingshanensis*, occur at any of the four sites where *A. microta* is in some cases associated with the giant extinct primate *Gigantopithecus* (6, 7, 20). Based on

Table 1. Dimensions (in millimeters) of the upper teeth of species of the giant panda *Ailuropoda* and the Lufeng panda *Ailurarctos*

Tooth	Recent*	Pleistocene†	Late Pliocene–Early Pleistocene‡		Late Miocene§
	<i>Ailuropoda melanoleuca</i>	<i>Ailuropoda baconi</i>	<i>Ailuropoda wulingshanensis</i>	<i>Ailuropoda microta</i> ¶	<i>Ailurarctos lufengensis</i>
C ¹					
L	14.8–20.4	18.3–23.0 (3) ^{¶¶}			
W	10.3–13.9	14.4–16.0 (3)			
P ¹					
L	3.2–4.5	6.3			
W	2.5–4.6	5.2			
P ²					
L	12.1–14.2	12.3–15.0 (17)	8.6–12.3 (13)	9.0–11.0 (4)	8.6
W	6.1–7.4	6.9–8.5 (17)	4.9–7.0 (13)	4.8–6.4 (4)	5.2
P ³					
L	18.2–21.0	19.4–24.0 (42)	14.5–21.4 (23)	14.3–16.5 (6)	12.2
W	10.8–12.8	11.0–15.0 (42)	9.6–14.0 (23)	8.0–10.5 (6)	7.4
P ⁴					
L	22.6–26.7	24.8–30.5 (50)	20.8–25.9 (34)	19.4–22.5 (19)	15.5
W	16.8–20.1	16.5–21.8 (50)	14.1–18.6 (34)	12.0–16.0 (19)	11.3
M ¹					
L	22.4–26.2	25.1–29.0 (44)	20.0–26.3 (35)	17.7–23.0 (23)	17.3
W	25.1–29.6	26.0–31.5 (44)	21.8–27.5 (35)	16.5–23.2 (23)	≈15.3–15.6 (2)
M ²					
L	30.4–36.5	31.0–40.5 (41)	24.2–32.5 (36)	20.0–25.0 (25)	17.6–19.8 (2)
W	24.0–28.2	23.7–30.5 (41)	19.0–26.0 (36)	16.0–20.0 (25)	14.2–14.9 (2)
P ³ –M ²					
L	93.5–106.8	106.0–110.0	89.0–89.4	74.5	—

L, length; W, width.

*Data from Colbert and Hooijer (3), $n = 19$ for each dental measurement.

†Data from Pei (4): data column includes the large skull from Mogok, Burma, described by Woodward (5).

‡Data from Wei Dong, personal communication.

§Data from Qiu and Qi (8).

¶Numbers in parentheses represent sample size (n).

¶¶Does not include dental measurements from IVPP V14564 (Jinyin skull).

the chronological distribution of *A. microta* from ≈1.9–2.4 Myr ago, the skull, jaws, and teeth of the chronospecies comprise the oldest representative skeletal material of the giant panda lineage.

The Jinyin cave skull (IVPP V14564) is undistorted and nearly complete, lacking only the zygomatic arches (Fig. 1A). Its external form closely approaches that of the living giant panda (*Ailuropoda melanoleuca*) and the Pleistocene *A. baconi* but is smaller. Relative size of the skulls of *A. microta* and the living giant panda, indicated by condylobasal skull length (Fig. 2B), demonstrates that the Jinyin cave skull is ≈3 cm shorter than the smallest individual from a sample of 55 skulls of the living giant panda and significantly smaller than the known skulls of the large *A. baconi*.

Measurement of 32 upper and 35 lower cheek teeth, and four mandibles from the Juyuan cave first demonstrated the small size of *A. microta* relative to the large Pleistocene *A. baconi* (7). Dental dimensions of the upper carnassial (P⁴) and molars (M², M_{1–2}) of *A. microta* fall well below the range of measurements for both the living panda and Pleistocene *A. baconi* [Fig. 2 C and D, Table 1, and supporting information (SI) Tables 2 and 3], even when the smallest individuals of these sexually dimorphic taxa are included. However, dental measurements of *A. microta* grade into measurements of *A. baconi* through an intermediate form, *A. wulingshanensis*, which is best represented at Longgu cave, Jianshi, Hubei. *A. wulingshanensis* (known only from south China) is distinguished from *A. microta* by larger average size and more complex cuspsation of upper and lower premolars and from *A. baconi* by smaller size with less developed premolar

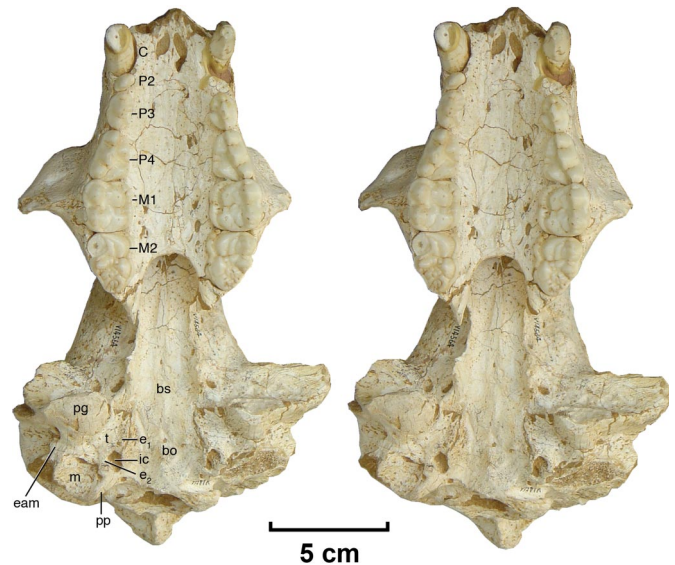


Fig. 3. Stereomages of the skull of *Ailuropoda microta*, Jinyin cave, China. Teeth, skull, and basicranial anatomy of IVPP V14564 show detail clearly comparable with these features in the living giant panda, indicating the appearance of these specialized traits in the lineage by the late Pliocene (≈2 to 2.4 Myr). bs, basisphenoid; bo, basioccipital; eam, osseous external auditory meatus; e1, anterior caudal entotympanic; e2, posterior caudal entotympanic; ic, entrance of internal carotid artery; m, mastoid; pg, postglenoid process of squamosal; pp, paroccipital process; t, ectotympanic; C, canine; P^{2–4}, premolars; M^{1–2}, molars.

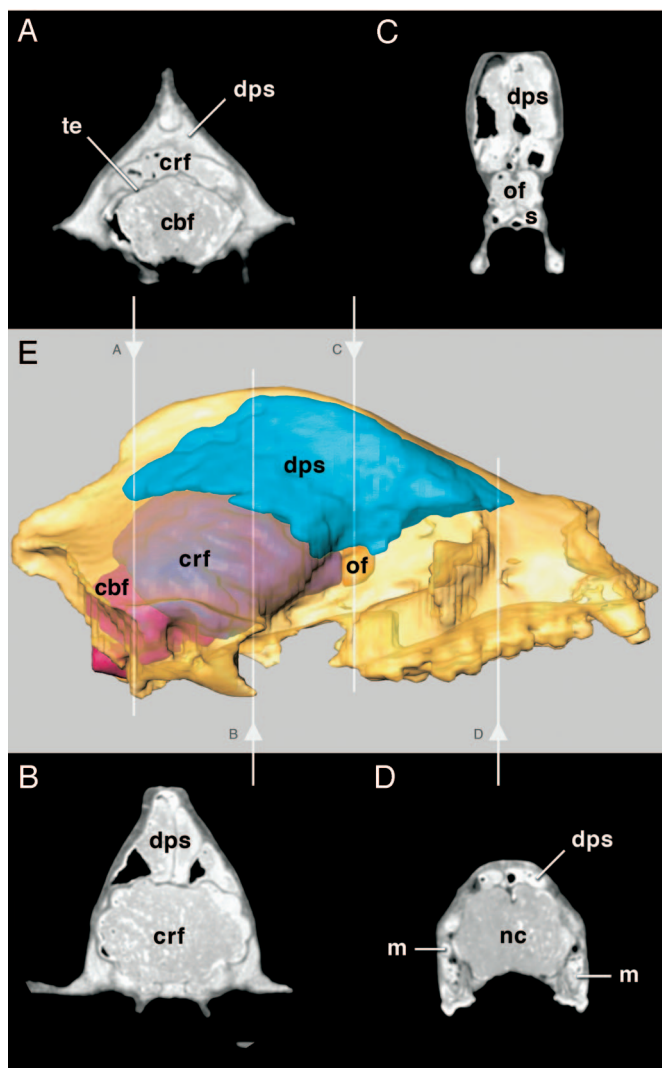


Fig. 4. CT scanned image and 3D reconstruction of *A. microta* skull, Jinyin cave, China. (A–D) Transverse CT sections through the dorsal paranasal sinuses (dps), cerebral fossa (crf), cerebellar fossa (cbf), and olfactory fossa (of). (E) Note greatly inflated dorsal paranasal sinus complex. m, maxillary sinus; nc, nasal cavity; s, sphenoid sinus; te, tentorium.

cusps and less elaboration of crenulated enamel on the molars (21). Because these three taxa do not occur together at any locality, the data (Fig. 2 C and D) could be interpreted as a succession of chronospecies belonging to a temporal continuum, increasing in size from *A. microta* through *A. wulingshanensis* to *A. baconi* and then declining to *A. melanoleuca* (9). Alternatively, the species *A. microta* and *A. wulingshanensis* may serve as nominal taxa that subsume the dental variation present in the giant panda lineage at various late Pliocene to earliest Pleistocene cave sites in southeastern China, where precise dates are elusive.

The occlusal pattern of the upper cheek teeth of the Jinyin cave skull, together with basicranial anatomy (Fig. 3), indicate phylogenetic affinity with the Ursidae (see SI Fig. 6), where *Ailuropoda* is placed in a tribe Ailuropodini of the subfamily Ursinae (10). Ursine bears include both living *Ursus* and the ancestral Miocene *Ursavus*. Skulls of *Ailuropoda* have been modified from the plesiomorphic form typical of species of *Ursavus* by selective forces favoring efficient mastication of tough, fibrous plant material (22, 23). Hence, the posterior

cranium and mandibles have been shaped by powerful muscles of mastication (e.g., *m. temporalis*, *m. masseter*, *m. zygomatico-mandibularis*, *m. digastricus*) resulting in broadening of the posterior cranium accompanied by enlargement of the cheek teeth (9, 22). Fused cranial sutures and thickened bone characterize adult panda skulls that are subject to strong masticatory forces during the processing of bamboo. The Jinyin cave skull, despite its small size, clearly displays these anatomical specializations.

Of particular significance is that the Jinyin basicranium foreshadows the derived auditory anatomy of the living giant panda. A broad basicranial axis, flanked by an arctoid auditory region (24) with evident ursid affinity is intact without post-mortem distortion (Fig. 3). The auditory bulla, obscured in the living giant panda by overgrowth of the hypertrophied post-glenoid process of the squamosal, is more visible in the Jinyin cave skull, indicating retention of a plesiomorphic arctoid bulla assembled from a dominant ectotympanic bone and subordinate entotympanic elements typical of *Ursus* (25). It is the combination of auditory anatomy and dentition that allies IVPP V14564 with ursine ursids (26) and documents the antiquity of the association of the basicranium and dental pattern in the *Ailuropoda* lineage.

The Jinyin cave cranium was scanned by using computerized tomography (CT) to produce a virtual 3D image of the skull (SI Movie 1). This noninvasive technique yielded the volumes of the neurocranial spaces and paranasal sinuses (Fig. 4). Whereas the neurocranial spaces for the brain and olfactory bulbs are proportionally similar to those of the living giant panda, the dorsal sinuses situated in the cranial roof display greater length and height than in the living species, having a volume in the Jinyin cave skull of ≈ 140 cc.

The paranasal sinuses in the living giant panda include an expanded dorsal cranial sinus complex, extending from the nasal bones nearly to the occiput. The dorsal paranasal sinuses of the giant panda have been considered more developed than in any other living species of the Order Carnivora (22); however, similar dorsal sinus expansion has been reported in living hyenas (27). Ontogenetic expansion of the dorsal sinuses is known to occur in *Ailuropoda melanoleuca* (22) and probably took place in *A. microta*, most likely as a pleiotropic effect of selection for the masticatory apparatus. The greater volume of the dorsal sinuses markedly increases the surface area of the skull for the attachment of temporal muscles, maximizing bite force during mastication.

Conclusion

Although smaller in all dimensions relative to the Pleistocene and living giant pandas, the maxillary teeth of IVPP V14564 show a marked resemblance to them in cusp pattern and occlusal proportions (Fig. 1 D–F). The premolars (P^{3-4}) and molars are robust, broad crushing platforms, much as in the living giant panda. These cheek teeth differ, however, in the lack of complexity of cusp pattern on the molars and subsidiary cusps of the premolars. Some females of the living giant panda (e.g., AMNH 110451, Sichuan, China) have a cusp pattern of upper molars and premolars similar to *A. microta*. Nonetheless, there is an obvious proportional increase in length of the crushing M^2 within the *Ailuropoda* lineage (Fig. 2D), indicating a progression from the abbreviate M^2 of *A. microta* through the intermediate *A. wulingshanensis* to the elongate M^2 s of *A. baconi* and *A. melanoleuca*. The existence of this trend confirms that IVPP V14564 is outside the range of variation of the living giant panda and cannot be a small individual of that species.

Dental remains thus indicate that the giant panda lineage had evolved a precursor stage of its crushing dentition by ≈ 7 Myr ago as seen in *Ailurarctos*, initiating the trend toward a massive, robust skull and jaws for durophagous mastication. The Jinyin

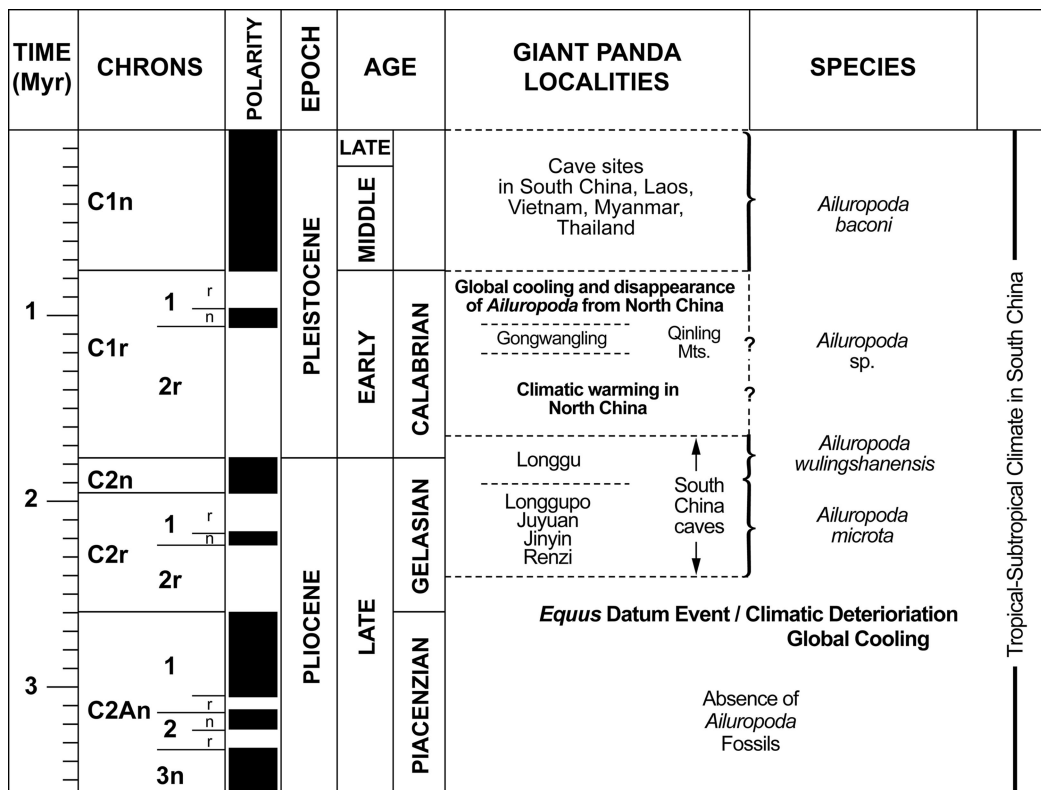


Fig. 5. Late Cenozoic temporal distribution of species of the giant panda *Ailuropoda* in southeastern Asia (9, 14, 16, 17, 21, 30–32); time scale (33).

cave skull of *A. microta* shows this adaptive cranial anatomy had been achieved by the late Pliocene (Fig. 5), implying that the giant panda could have developed dependence on bamboo by 2 Myr ago.

Materials and Methods

Computerized Tomography. The Jinyin skull (IVPP V14564) was scanned coronally every 2.5 mm by using computerized tomography (CT), yielding 100 slices with pixel size of 0.271484 mm × 0.271484 mm and image depth of 16 bits. This created a virtual image of the internal cranial spaces, including the cerebral cavities, and paranasal sinuses. The endoneurocranium comprises three principal cavities whose computed volumes are: olfactory fossa, 2.87 cc; cerebrum, 166.41 cc; cerebellum, 39.06 cc; and entire neurocranial space, 208.34 cc, approximately two-thirds the average neurocranial volume (≈313 cc, the mean of three individuals) of the living giant panda. The dorsal cranial sinus has a volume of 139.27 cc,

which is apparently more expanded than in the living species. The remaining paranasal sinuses are unclear from the available CT data. The 3D reconstruction (Fig. 4) was achieved by AMBIOS software with the funding support of LIAMA (Project 01–08).

We thank Prof. Shaohua Zheng for access to *A. wulingshanensis* material and Genjiao Chen, Guangxi Museum, for assisting in field work. This work was supported by Chinese National Natural Science Foundation Grant 40372016 (to C.J.). International travel for R.L.C. was provided by International Programs, University of Iowa (UI) and laboratory support from the Dean of the College of Liberal Arts and Sciences, UI, and the Human Evolution Research Fund, UI Foundation. A. Fox, University of Nebraska and J. Rogers, UI, created Fig. 2 and contributed to Figs. 1, 3, 4, and 5. R.M.H. was supported by the Meek Research Fund, University of Nebraska. K.L. Eaves-Johnson, UI, copy-edited the manuscript. Finally, we thank the late F. Clark Howell, who was keenly interested in carnivore evolution, for his comments on the manuscript. Clark Howell's many contributions to paleoanthropology, archaeology, and vertebrate paleontology will be missed.

- McKenna MC, Bell SK (1997) *Classification of Mammals Above the Species Level* (Columbia Univ Press, New York).
- Matthew WD, Granger W (1923) *Bull Am Mus Nat Hist* 48:563–598.
- Colbert EH, Hooijer DA (1953) *Bull Am Mus Nat Hist* 102:1–134.
- Pei WZ (1987) *Mem Inst Vert Palaeontol Palaeanthropol Acad Sin* 18:104–106.
- Woodward AS (1915) *Proc Zool Soc London* 1915:425–428.
- Pei WZ (1963) *Scientia Sin* 12:222–229.
- Wang TK (1974) *Acta Zool Sin* 20:191–201.
- Qiu ZX, Qi G (1989) *Vert Palasiatica* 27:153–169.
- Huang WP (1993) *Vert Palasiatica* 31:191–207.
- Hunt RM, Jr (2004) in *Giant Pandas, Biology and Conservation*, eds Lindburg D, Baragona K (Univ of California Press, Berkeley, CA) pp 45–52.
- Wan QH, Wu H, Fang SG (2005) *Jour Mammal* 86:397–402.
- Schaller GB (1993) *The Last Panda* (Univ of Chicago Press, Chicago).
- Yong Y, Liu X, Wang T, Skidmore A, Prins H (2004) in *Giant Pandas, Biology and Conservation*, eds Lindburg D, Baragona K (Univ of California

- Press, Berkeley, CA) pp 159–169.
- Tougaard C, Chaimanee Y, Suteethorn V, Triamwichanon S, Jaeger J-J (1996) *C R Acad Sci Paris* 323:973–979.
- Pei WZ (1987) *Mem Inst Vert Palaeontol Palaeanthropol Acad Sin* 18:104–106.
- Huang WP, Ciochon R, Gu Y, Larick R, Qiren F, Schwarcz H, Yonge C, de Vos J, Rink W (1995) *Nature* 378:275–278.
- Jin C, Zheng L, Dong W, Liu J, Xu Q, Han L, Zheng J, Wei G, Wang F (2000) *Acta Anthropol Sin* 19(Suppl):235–245.
- Zheng SH, Li CK (1986) *Vert Palasiatica* 24:81–109.
- Qiu ZD, Li CK (2003) *Bull Am Mus Nat Hist* 279:586–602.
- Ciochon RL, Olsen J, James J (1990) *Other Origins: The Search for the Giant Ape in Human Prehistory* (Bantam Books, New York).
- Zheng SH (2004) *Jianshi Hominid Site* (Series Monograph I, State Key Project of the 9th Five Year Plan—Origin of Early Humans and Environmental Background) (Science, Beijing) 412 pp.
- Davis DD (1964) *Fieldiana Zool Mem* 3:1–339.
- Sicher H (1944) *Fieldiana Zool Ser* 29:61–73.

24. Hunt RM, Jr, Tedford RH (1993) in *Mammal Phylogeny (Placentals)*, eds Szalay FS, Novacek MJ, McKenna MC (Springer, New York), pp 53–73.
25. Hunt RM, Jr (1974) *J Morphol* 143:21–76, Pl 4.
26. Hunt RM, Jr (1998) in *Evolution of Tertiary Mammals of North America*, eds Janis C, Scott K, Jacobs L (Cambridge Univ Press, New York), pp 174–195.
27. Joeckel RM (1995) *J Vert Paleontol* 15(Suppl 3):38A.
28. Loucks CJ, Lü Z, Dinerstein E, Wang H, Olson DM, Zhu C, Wang D (2001) *Science* 294:1465.
29. Long VT, de Vos J, Ciochon RL (1996) *Indo-Pacific Prehist Assoc Bull* 14:38–56.
30. Tong YS, Zheng SH, Qiu ZD (1995) *Vert Palasiatica* 33:290–314.
31. Tong YS, Zheng SH, Qiu ZD (1996) *Vert Palasiatica* 34:215–227.
32. Tedford RH, Flynn LJ, Qiu ZX, Opdyke ND, Downs WR (1991) *J Vert Paleontol* 11:519–526.
33. Berggren WA, Kent DV, Swisher CC, Aubry MP (1995) *SEPM (Soc Sedimentary Geol) Spec Publ* 54:129–212.