The first skull of the earliest giant panda

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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 Jinjin 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 basi Cranial 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.

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 species, 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 chewing 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 Ailuropoda is derived from a Miocene species of Ursavus (8–10). In turn, the cuspat e 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 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 cuspation 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).


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).

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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 chalicotheres Nestoritherium, Eguus 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

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**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), Chaiyaphum, Thailand (14), and Lang Trang, Vietnam (29). (B) Condylar 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.

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the chronological distribution of *A. microta* from \( \approx 1.9-2.4 \) 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 \( \approx 3 \) 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 (M1–2) of *A. microta* fall well below the range of measurements for both the living panda and Pleistocene *A. baconi* [Fig. 2C 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 cuspation of upper and lower premolars and from *A. baconi* by smaller size with less developed premolar,

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

<table>
<thead>
<tr>
<th>Tooth</th>
<th>Recent*</th>
<th>Pleistocene†</th>
<th>Late Pliocene–Early Pleistocene‡</th>
<th>Late Miocene§</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ailuropoda melanoleuca</em></td>
<td><em>Ailuropoda baconi</em></td>
<td><em>Ailuropoda wulingshanensis</em></td>
<td><em>Ailuropoda microta</em></td>
<td><em>Ailurarctos lufengensis</em></td>
</tr>
<tr>
<td><strong>C</strong></td>
<td><strong>P1</strong></td>
<td><strong>P2</strong></td>
<td><strong>P3</strong></td>
<td><strong>P4</strong></td>
</tr>
<tr>
<td><strong>L</strong></td>
<td>14.8–20.4</td>
<td>18.3–23.0 (3)†</td>
<td>8.6–12.3 (13)</td>
<td>9.0–11.0 (4)</td>
</tr>
<tr>
<td><strong>W</strong></td>
<td>10.3–13.9</td>
<td>14.4–16.0 (3)</td>
<td>4.9–7.0 (13)</td>
<td>4.8–6.4 (4)</td>
</tr>
<tr>
<td><strong>P1</strong></td>
<td><strong>L</strong></td>
<td>3.2–4.5</td>
<td>12.3–15.0 (17)</td>
<td>14.5–21.4 (23)</td>
</tr>
<tr>
<td><strong>W</strong></td>
<td>2.5–4.6</td>
<td>6.9–8.5 (17)</td>
<td>4.9–7.0 (13)</td>
<td>8.0–10.5 (6)</td>
</tr>
<tr>
<td><strong>P2</strong></td>
<td><strong>L</strong></td>
<td>12.1–14.2</td>
<td>19.4–24.0 (42)</td>
<td>20.8–25.9 (34)</td>
</tr>
<tr>
<td><strong>W</strong></td>
<td>6.1–7.4</td>
<td>6.9–8.5 (17)</td>
<td>4.9–7.0 (13)</td>
<td>8.0–10.5 (6)</td>
</tr>
<tr>
<td><strong>P3</strong></td>
<td><strong>L</strong></td>
<td>18.2–21.0</td>
<td>11.0–15.0 (42)</td>
<td>14.1–18.6 (34)</td>
</tr>
<tr>
<td><strong>W</strong></td>
<td>10.8–12.8</td>
<td>11.0–15.0 (42)</td>
<td>14.1–18.6 (34)</td>
<td>12.0–16.0 (19)</td>
</tr>
<tr>
<td><strong>P4</strong></td>
<td><strong>L</strong></td>
<td>22.6–26.7</td>
<td>24.8–30.5 (50)</td>
<td>20.8–25.9 (34)</td>
</tr>
<tr>
<td><strong>W</strong></td>
<td>16.8–20.1</td>
<td>16.5–21.8 (50)</td>
<td>14.1–18.6 (34)</td>
<td>12.0–16.0 (19)</td>
</tr>
<tr>
<td><strong>M1</strong></td>
<td><strong>L</strong></td>
<td>22.4–26.2</td>
<td>25.1–29.0 (44)</td>
<td>20.0–26.3 (35)</td>
</tr>
<tr>
<td><strong>W</strong></td>
<td>25.1–29.6</td>
<td>26.0–31.5 (44)</td>
<td>21.8–27.5 (35)</td>
<td>16.5–23.2 (23)</td>
</tr>
<tr>
<td><strong>M2</strong></td>
<td><strong>L</strong></td>
<td>30.4–36.5</td>
<td>31.0–40.5 (41)</td>
<td>24.2–32.5 (36)</td>
</tr>
<tr>
<td><strong>W</strong></td>
<td>24.0–28.2</td>
<td>23.7–30.5 (41)</td>
<td>19.0–26.0 (36)</td>
<td>16.0–20.0 (25)</td>
</tr>
<tr>
<td><strong>P3–M2</strong></td>
<td><strong>L</strong></td>
<td>93.5–106.8</td>
<td>106.0–110.0</td>
<td>89.0–89.4</td>
</tr>
</tbody>
</table>

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).
道Does not include dental measurements from IVPP V14564 (Jinyin skull).
ancestral Miocene Ursavus tough, fibrous plant material (22, 23). Hence, the posterior Ursavus by selective forces favoring efficient mastication of modified from the plesiomorphic form typical of species of Ailuropoda phylogenetic affinity with the Ursidae (see SI Fig. 6), where cave skull, together with basicranial anatomy (Fig. 3), indicate elusive.ocene cave sites in southeastern China, where precise dates are giant panda lineage at various late Pliocene to earliest Pleistocene nominal taxa that subsume the dental variation present in the A. microta the species Ursinae (10). Ursine bears include both living A. microta – 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 (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 (P3–4) 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 M2 within the Ailuropoda lineage (Fig. 2D), indicating a progression from the abbreviate M3 of A. microta through the intermediate A. wulingshanensis to the elongate M3’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
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 $0.271484 \text{ mm} \times 0.271484 \text{ mm}$ 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 ($313 \text{ cc}$, 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).

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