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# Two new carnivores from an unusual late Tertiary forest biota in eastern North America

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Late Cenozoic terrestrial fossil records of North America are biased by a predominance of mid-latitude deposits, mostly in the western half of the continent. Consequently, the biological history of eastern North America, including the eastern deciduous forest, remains largely hidden. Unfortunately, vertebrate fossil sites from this vast region are rare<sup>1,2</sup>, and few pertain to the critically important late Tertiary period, during which intensified global climatic changes took place<sup>3,4</sup>. Moreover, strong phylogenetic affinities between the flora of eastern North America and eastern Asia clearly demonstrate formerly contiguous connections, but disparity among shared genera (eastern Asia–eastern North America disjunction) implies significant periods of separation since at least the Miocene epoch<sup>1,2</sup>. Lacustrine sediments deposited within a former sinkhole in the

southern Appalachian Mountains provide a rare example of a late Miocene to early Pliocene terrestrial biota from a forested ecosystem<sup>5</sup>. Here we show that the vertebrate remains contained within this deposit represent a unique combination of North American and Eurasian taxa. A new genus and species of the red (lesser) panda (*Pristinailurus bristoli*), the earliest and most primitive so far known, was recovered. Also among the fauna are a new species of Eurasian badger (*Arctomeles dimolodontus*) and the largest concentration of fossil tapirs ever recorded. Cladistical analyses of the two new carnivores strongly suggest immigration events that were earlier than and distinct from previous records<sup>6,7</sup>, and that the close faunal affinities between eastern North America and eastern Asia in the late Tertiary period are consistent with the contemporaneous botanical record<sup>8,9</sup>.

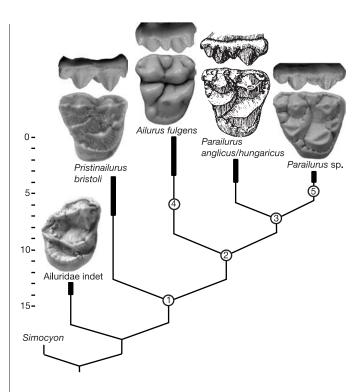
The Gray Fossil Site consists of a sequence of finely laminated clays, silts and fine sands intermixed with isolated gravel lenses that fill a former sinkhole within the Cambrian/Ordovician Knox Group near the small community of Gray in Washington Co., Tennessee. The deposit covers roughly 1.8–2.0 ha, is up to 39 m thick and is the result of a small lake or pond that formed within the sinkhole. Subsequent weathering and erosion of the enclosing bedrock has generated a reversed topography, leaving the site as a high point on the landscape

Vertebrate taxa such as *Tapiravus*, *Plionarctos*, *Pristinailurus* and *Arctomeles* (Table 1, left column) and abundant plant macrofossils (Table 1, right column) from *Quercus* (acorns) and *Carya* (hickory nuts) indicate that a dense forest surrounded the former 'pond'. *Quercus* and *Carya* constitute nearly 70% of initial pollen samples, and except for *Pinus* (which accounts for roughly 9% of the pollen count), the remaining taxa seem to be minor components of the flora. Both micro- and macrofossils reveal an arboreal flora, which was similar to that found in lower elevations of the southern Appalachians today.

The stratigraphic range of the rhino *Teleoceras*<sup>10,11</sup> and the short-faced bear *Plionarctos*<sup>12,13</sup> constrain the age of the assemblage to between 4.5 and 7 Myr (late Miocene to early Pliocene). This age is important because it occurs subsequent to the C<sub>3</sub>/C<sub>4</sub> plant transition<sup>4</sup>; that is, when grasses first become dominant in many ecosystems worldwide<sup>14</sup>, leading to the prevalence of many grassland-adapted taxa (horses, camels, antilocaprids and so on) within other Miocene/Pliocene faunas (particularly in North America). However, the absence of these grassland-adapted taxa and the predominance of forest-adapted taxa (Table 1) suggest that the Gray Fossil Site may have acted as a refugium from the changing

Vertebrates	Pollens
Reptilia	Conifers
Trachemys sp. <sup>20</sup>	Pinus (pine)
Chrysemys sp.	Tsuga (hemlock)
Alligator sp.	Deciduous
cf. Sistrurus sp.20	Quercus (oak)
cf. Regina sp. 20	Carya (hickory)
Aves	Ulmus (elm)
Passeriformes	Betula (birch)
Mammalia	Fraxinus (ash)
Soricidae	Celtis (hackberry)
Rodentia	Shrubs
Gomphotheridae	Alnus (alder)
Tapiravus polkensis	Salix (willow)
Teleoceras sp.	Herbs
Tayassuidae	Ambrosia-type ('ragweed')
cf. Megatylopus sp.	Cyperaceae (sedge)
cf. Machairodus sp.	Gramineae (grass)
Plionarctos sp.	Umbelliferae (parsely family)
Canidae	Caryophyllaceae (pink family
Pristinailurus bristoli gen. et sp. nov.	, , , ,
Arctomeles dimolodontus sp. nov.	

Excluding fishes and amphibians



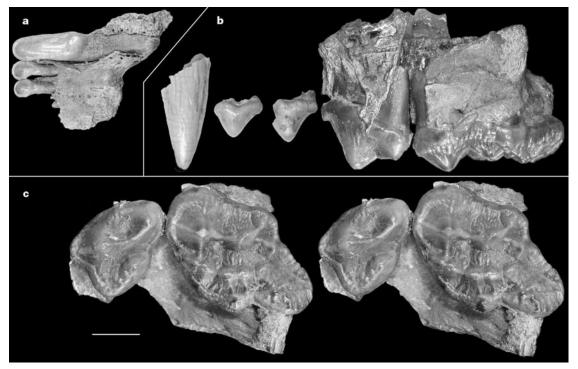
**Figure 1** Phylogenetic relationship and geological ages of red panda fossils. Taxa illustrated are: Ailuridae indet., FSL 66113, Four locality, France, middle Miocene<sup>21</sup>; *Pristinailurus bristoli* gen. et sp. nov., ETMNH-360, Gray Fossil Site, Tennessee, late Miocene/early Pliocene; *Ailurus fulgens*, LACM 62839, San Diego zoo, late Pliocene<sup>22</sup> to present; *Parailurus anglicus/hungaricus*, SMF 2000/235 (= Wö 21 in Tedford<sup>6</sup>), Wölfersheim, Germany, early Pliocene to late Pliocene<sup>6,23-26</sup>, and *Parailurus* sp., LACM 10808, White Bluffs, Washington, early Pliocene<sup>6</sup>. We use *Simocyon* as its nearest outgroup for the family<sup>27</sup>. M<sup>1</sup> s are scaled to be approximately equal in size. Scale represents age (Myr before present).

environment of the late Miocene, because of its isolation from the more 'open' ecosystems typical of similar-aged fossil deposits.

A unique combination of taxa makes the Gray Fossil Site very distinct from other late Miocene and early Pliocene faunas. Not only is there a strong southern influence (warm adapted) indicated by the occurrence of Alligator and Tapiravus, but also there is a strong northern component (cool adapted) represented by taxa such as Arctomeles and Pristinailurus. Just as important are the conspicuous absence of equids, which are typically abundant in Miocene and Pliocene faunas of central and western North America (often represented by multiple taxa)15, and the overabundance of tapirs, which are typically only minor components of faunas<sup>16</sup>. Although younger than the peak of equid diversity, between 15-8 Myr ago<sup>15</sup>, the lack of equids (or other such cursorial taxa) suggests little influence from the Great Plains or Gulf Coast grassland environments. Furthermore, the prolific number of individual tapirs at the site supports the dominance of an arboreal setting (at least in the immediate proximity of the sinkhole). Though Teleoceras has been considered a grazer<sup>17</sup>, recent isotopic analysis<sup>18</sup> has shown that at least some taxa were mixed feeders, which would not preclude its presence in a forested ecosystem.

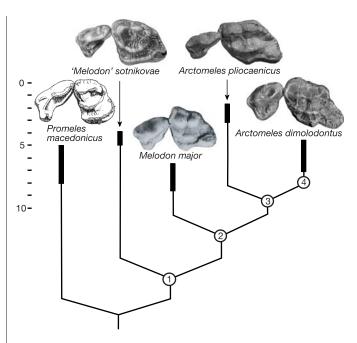
Terrestrial carnivorans are frequently long-distance dispersers because of their predatory behaviours. Consequently, their sudden appearance on different continents often serves as a useful marker for mammalian biochronology<sup>19</sup>. Therefore, in addition to revealing possible dispersal corridors previously hidden from our view because of the biased North American terrestrial fossil record, these new 'exotic' hypocarnivores (carnivorans that specialize in highly omnivorous diets) from the Gray Fossil Site will be ideal biostratigraphic markers where recovered.

Living red pandas are confined to the mountainous belt of the southern Himalayas, and like the giant panda, have a highly specialized diet of bamboo. This herbivorous diet is a rare occurrence among carnivorans. Although there is no evidence for the presence of bamboo in the Gray site (possibly owing to inherent difficulties in pollen identification in the Poaceae), it seems



**Figure 2** Arctomeles dimolodontus sp. nov., ETMNH-361, holotype. **a**, Occlusal view of left premaxillary fragment with I<sup>1-3</sup>. **b**, Lateral view of right C (reversed) and left P<sup>2</sup>–M<sup>1</sup>. **c**, Occlusal view of left maxillary with P<sup>4</sup> and M<sup>1</sup> (stereo pair). Scale bar, 5 mm.

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**Figure 3** Phylogenetic relationship and geological ages of the Gray–site badger. Taxa illustrated are: *Promeles macedonicus* (reversed from the right side), MA 406, Maramena, Greece, late Miocene<sup>28</sup>; "Melodon" *sotnikovae*, CMN 51770, Ellesmere Island, Canada, early Pliocene<sup>7</sup>; *Melodon majori*, locality 49, Yangmugou, Baode, Shanxi Province, China, late Miocene<sup>29</sup>; *Arctomeles pliocaenicus*, MF338, Weze 1 locality, Poland, early Pliocene<sup>30</sup>; and *Arctomeles dimolodontus* sp. nov., ETMNH-361, Gray Fossil Site, Tennessee, late Miocene/early Pliocene. We also include *Promeles*, a primitive meline, as an outgroup to establish character polarity<sup>28,29</sup>. Scale represents age (Myr before present).

probable that river cane (*Arundinaria gigantea*), a member of the bamboo clade that is native to Tennessee, or a similar form, may have been more widespread in the late Miocene. However, it is likely that the Gray—site panda was able to subsist on non-bamboo leaves while passing through an arctic arboreal corridor and ultimately found more habitable land in the eastern deciduous forest of the southern Appalachians.

Both new hypocarnivores (*Pristinailurus bristoli* and *Arctomeles dimolodontus*) show unique phylogenetic relationships with Eurasian taxa, indicating both the presence of a strong connection (physical and genetic) between the two regions until at least the late Miocene, and the likelihood of multiple immigration events into the New World from different Eurasian stock. The relationships and timing of these events are consistent with floral eastern Asia–eastern North America disjunction<sup>1,2</sup>.

#### Methods

Pristinailurus bristoli gen. et sp. nov.

**Etymology.** *Pristinus* (Latin), meaning former or previous, and *Ailurus* for the living genus. Species after Larry Bristol who found the holotype. Common name: Bristol's Appalachian panda.

**Holotype.** Right first upper molar ( $RM^1$ ) (East Tennessee Museum of Natural History = ETMNH-360); measurements (labial length  $\times$  transverse width): 11.4  $\times$  12.3. **Referred material.** Right first upper canine ( $RC^1$ ) (ETMNH-359) and  $RM^1$  (ETMNH-360) (Fig. 1).

**Diagnosis.** Pristinailurus differs from Parailurus and Ailurus in its retention of primitive characters on M¹: length less than width; metaconule enlarged, strongly crest-like and isolated from the protocone; metastylar and parastylar cusps poorly developed to lacking; absence of both a mesostylar cusp and a discrete accessory cusp on posterior cingulum between metastyle and metaconule; retention of a lingual cingulum that merges with the hypocone at its posterior end.

**Discussion.** Tedford and Gustafson<sup>6</sup> reported *Parailurus* from the early Blancan of Washington on the basis of a single RM<sup>1</sup>. Fortunately the same tooth was collected from the Gray site, allowing direct comparison (Fig. 1). Shared derived characters at numbered nodes in Fig. 1 are as follows: (1) enlarged M<sup>1</sup> metaconule that is strongly crest-like and isolated from the protocone, presence of a metastylar cusp; (2) presence of a distinct mesostylar cusp, reduced lingual cingulum, a discrete hypocone on posterior end of

lingual cingulum; (3)  $M^1$  length equal to or greater than width, presence of a discrete accessory cusp on posterior cingulum between metastyle and metaconule; (4) presence of a distinct and enlarged parastylar cusp, major cusps swollen at the bases to encroach valleys between cusps; and (5)  $M^1$  length greater than its width, enlargement of a discrete protoconule (see further explanation in Supplementary Information).

The substantially more primitive Gray panda, in contrast to a highly derived *Parailurus* from Washington, permits evaluation of character polarities that were previously obscure. Our new phylogeny (Fig. 1) shows that *Pristinailurus* is at least five steps (characters) removed from the Washington *Parailurus*, and that the two North American pandas are separated phylogenetically by two intermediate Eurasian forms. Such a topology strongly suggests a separate immigration event independent from that represented by the Washington *Parailurus*, a pattern also consistent with the age estimate for the Gray site, which is older than the Taunton site in Washington.

Arctomeles Stach, 1951

Arctomeles dimolodontus sp. nov.

**Etymology.** Based on the inferred occlusion of the talon-like basin on  $M^1$  with the second lower molar ( $M_2$ ) (see Fig. 2). di (Greek) meaning two; mola (Latin) for millstone (as in molar); odontos (Greek) denoting tooth. Literally meaning 'two millstone tooth' or 'two molar tooth'. Common name: woodland badger.

**Holotype.** ETMNH-361 left premaxillary fragment with incisors  $LI^{1-3}$ ; associated premolars  $LP^{2-4}$ , molar  $LM^1$ , incisors  $RI^{1-3}$  and canine  $RC^1$  (Fig. 2); measurements (labial length × transverse width):  $P^4$ , 11.8 × 8.6 mm;  $M^1$ , 12.2 (maximum anteroposterior length: 18.3 mm) × 12.2 mm.

**Diagnosis.** Similar in size to *Arctomeles pliocaenicus*.  $P^4$  has an expanded cingular shelf and is large relative to  $M^1$ ;  $P^4$  hypocone is larger, and more posterior than in *A. pliocaenicus*;  $M^1$  lingual cingulum expands more anterolingually than in *A. pliocaenicus* but not nearly as far as in "*Melodon*" *sotnikovae*; talon-like basin on  $M^1$  extends well posterior of metacone and hypocone; however, there is a distinct constriction between the basin and the remainder of the tooth; postprotocrista of  $M^1$  is divided into three discrete cuspules;  $M^1$  has a metastylar cusp and enlarged paracone; accessory cusps and crenulations within the basins on both the  $P^4$  and  $M^1$  are larger and more elaborate than in *A. pliocaenicus*.

Included species. Listed in Tedford and Harington<sup>7</sup> except "Melodon" sotnikovae.

Discussion. This new taxon is more derived than other members of the genus in the development of the talon-like basin on M¹, size and morphology of the P⁴, and complexity of accessory cusps and crenulations on all teeth (Fig. 3). Shared derived characters at numbered nodes in Fig. 3 are as follows: (1) expansion of posterior part of talon on M¹, M¹ postprotocrista oriented anteroposteriorly resulting in a posteriorly open talon to occlude with a long talonid basin of M₁, presence of multiple cuspules along posterior cingulum and trailing behind metacone, and presence of metastylid on M₁; (2) M¹ posterior talon curves dorsally to be in contact with an expanded M₂, and presence of a P⁴ hypocone; (3) P⁴ protocone reduced to a low crest, and reduction of anterior portion of M¹ lingual cingulum; and (4) postprotocrista divided into three discrete cuspules, presence of a M¹ metastylar cusp, and enlargement of P⁴ hypocone (see further explanation in Supplementary Information).

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# New evidence on the earliest human presence at high northern latitudes in northeast Asia

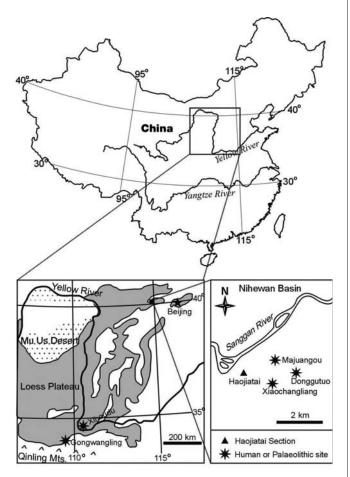
R. X. Zhu $^1$ , R. Potts $^2$ , F. Xie $^3$ , K. A. Hoffman $^4$ , C. L. Deng $^1$ , C. D. Shi $^1$ , Y. X. Pan $^1$ , H. Q. Wang $^1$ , R. P. Shi $^1$ , Y. C. Wang $^1$ , G. H. Shi $^1$  & N. Q. Wu $^1$ 

The timing of early human dispersal to Asia is a central issue in the study of human evolution. Excavations in predominantly lacustrine sediments at Majuangou, Nihewan basin, north China, uncovered four layers of indisputable hominin stone tools. Here we report magnetostratigraphic results that constrain the age of the four artefact layers to an interval of nearly 340,000 yr between the Olduvai subchron and the Cobb Mountain event. The lowest layer, about 1.66 million years old (Myr), provides the oldest record of stone-tool processing of animal tissues in east Asia. The highest layer, at about 1.32 Myr, correlates with the stone tool layer at Xiaochangliang¹, previously considered the oldest archaeological site in this region. The findings at Majuangou indicate that the oldest known human presence in northeast Asia

at 40° N is only slightly younger than that in western Asia<sup>2,3</sup>. This result implies that a long yet rapid migration from Africa, possibly initiated during a phase of warm climate, enabled early human populations to inhabit northern latitudes of east Asia over a prolonged period.

The Majuangou (MJG; 40° 13.517′ N, 114° 39.844′ E) section lies in the eastern margin of the Nihewan basin (Fig. 1). It is a lacustrine sequence with brief intervals of wetland and lake-margin sediments, and consists mainly of greyish-yellow and greyish-green clay, silty clay and silt. It is underlain by red Jurassic volcanic breccia. Loess sediments at the top of the section have been subjected to erosion. The four artefact layers found in the MJG section are, from top to bottom, Banshan<sup>4</sup> (44.3–45.0 m), MJG-I (ref. 5; 65.0–65.5 m), MJG-II (73.2–73.56 m) and MJG-III (75.0–75.5 m) (Fig. 2).

The Banshan artefact layer, discovered and excavated in 1990 (2 m² area, 70 cm thick), contained 95 stone artefacts in gravelly sandy silt⁴. Excavation of MJG-I in 1993 (20 m², 50 cm) yielded 111 stone tools in clayey silt⁵. Renewed excavation at Majuangou in 2001 and 2002 uncovered 226 artefacts in brown clayey silt of MJG-II (40 m², 36 cm) and 443 artefacts in greyish-black silty clay of MJG-III (85 m², 50 cm). The sediments, numerous molluscan shells (*Gyraulus chihliensis* and *Planorbis youngi*), and leaves and fruits of aquatic plants (for example *Trapa* sp.) in MJG-III indicate a lowenergy lakeshore or marsh environment rich in organic materials. The *in situ* artefact density in this layer was low overall (10.4 artefacts per m³), but artefacts and fauna in some 5-cm-thick



**Figure 1** Location of the Majuangou and Haojiatai sections in the Nihewan basin. Some sites mentioned in the text, Xiaochangliang, Donggutuo, Gongwangling and Xihoudu, are indicated. The Qinling Mountains (bottom left) are the traditional dividing line between north and south China. The Yellow River and Yangtze River are the major river systems in north and south China, respectively.

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