

# The oldest North American primate and mammalian biogeography during the Paleocene–Eocene Thermal Maximum

K. Christopher Beard<sup>†</sup>

Section of Vertebrate Paleontology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, PA 15213

Edited by Alan Walker, Pennsylvania State University, University Park, PA, and approved January 10, 2008 (received for review October 25, 2007)

Undoubted primates first appear almost synchronously in the fossil records of Asia, Europe, and North America. This temporal pattern has complicated efforts to reconstruct the early dispersal history of primates in relation to global climate change and eustatic fluctuations in sea level. Here, I describe fossils from the Tusahoma Formation on the Gulf Coastal Plain of Mississippi documenting an anatomically primitive species of *Teilhardina* that is older than other North American and European primates. Consistent with its antiquity, a phylogenetic analysis of dental characters recognizes *Teilhardina magnoliana*, sp. nov., as the most basal member of this genus currently known from either North America or Europe. Its stratigraphic provenance demonstrates that primates originally colonized North America near the base of the Paleocene–Eocene Thermal Maximum (PETM), but before an important fall in eustatic sea level. Correlation based on carbon isotope stratigraphy and sequence stratigraphy indicates that the earliest North American primates inhabited coastal regions of the continent for thousands of years before they were able to colonize the Rocky Mountain Interior. The transient provincialism displayed by early North American primates corresponds to similar biogeographic patterns noted among fossil plants. Decreased precipitation in the Rocky Mountain Interior during the early part of the PETM may have been an important factor in maintaining biotic provincialism within North America at this time. These results underscore the need to obtain multiple, geographically dispersed records bearing on significant macroevolutionary events such as the PETM.

*Teilhardina* | Wasatchian | dispersal | phylogeny | Omomyidae

Primates and several other modern mammalian groups (including artiodactyls and perissodactyls) first appear in the North American fossil record shortly after the Paleocene–Eocene (P/E) boundary (1–3), an interval marked by rapid and dramatic global warming known as the Paleocene–Eocene Thermal Maximum (PETM) (1, 4–6). Although it is generally accepted that the warmer climatic conditions during the PETM facilitated dispersal of primates and other mammals across two high latitude land bridges (Beringia and the North Atlantic land bridge then connecting Greenland and Scotland), identifying where these mammals originated and the pathway they took to achieve their widespread distribution remains contentious (1–3, 7, 8).

The most thoroughly studied North American terrestrial sequence spanning the PETM is in the Bighorn Basin of northwestern Wyoming (3, 4, 9, 10). There, the local first appearance of primates (including the omomyid *Teilhardina brandti*) occurs in biostratigraphic zone Wa-0, at a stratigraphic level estimated to be 19–25 Kyr above the P/E boundary (1). Correlation using the global carbon isotope excursion (CIE) at the P/E boundary suggests that *T. brandti* from the Bighorn Basin is slightly younger than the oldest primates currently known from Europe (*Teilhardina belgica*) and Asia (*Teilhardina asiatica*) (1, 7, 11). This agrees with phylogenetic analyses of *Teilhardina*, which recognize *T. asiatica* as the most basal species, followed by *T. belgica* and North American species of *Teilhardina*, respectively (1, 11). These geological and phylogenetic data have been

interpreted as evidence that primates dispersed from Asia to Europe to North America during the PETM, and that dispersal of *Teilhardina* from Europe to North America was made possible by an important drop in eustatic sea level during that interval (1).

Here, I describe an anatomically primitive species of *Teilhardina* from the Gulf Coastal Plain of Mississippi. This primate is one component of the earliest Eocene Red Hot local fauna, which also includes sharks and rays, bony fishes, snakes, lizards, crocodylians, birds, and a variety of other mammals (12–16). The Red Hot local fauna was recovered by screen-washing fine-grained glauconitic sands forming the uppermost part of the Tusahoma Formation at an outcrop south of Meridian, MS (15, 17). The distinctive geographic and stratigraphic setting of the Red Hot local fauna provides the basis for more detailed understanding of the initial dispersal of primates and other mammals into North America and the biogeographic response of North American mammals to global warming during the PETM.

## Systematic Paleontology

**Primates Linnaeus, 1758.** Omomyidae Trouessart, 1879. *Teilhardina* Simpson, 1940. *Teilhardina magnoliana*, sp. nov.

**Holotype.** Carnegie Museum of Natural History (CM) 70435, an isolated left M<sub>2</sub> (Fig. 1).

**Hypodigm.** The holotype; CM 67854, isolated right P<sup>3</sup>; CM 67856, isolated left M<sub>1</sub>; CM 67858, isolated right M<sup>1</sup>; CM 67860, isolated left M<sub>1</sub>; CM 67861, isolated left P<sup>3</sup>; CM 70422, isolated left M<sup>2</sup> lacking the metacone; CM 70427, isolated right M<sub>3</sub>; CM 70430, isolated right M<sub>3</sub>; CM 70431, isolated right M<sup>1</sup>; CM 70433, isolated left P<sup>4</sup> lacking the buccal side of the paracone; CM 70434, isolated right P<sub>4</sub>; CM 70436, isolated left M<sup>2</sup>; CM 73229, isolated left P<sub>4</sub> trigonid; CM 77209, isolated right M<sub>3</sub> lacking part of the hypoconulid lobe; CM 77210, isolated right P<sup>4</sup>; CM 77211, isolated right M<sup>1</sup>; CM 77212, isolated right M<sup>2</sup> lacking the metacone [Fig. 1; see [supporting information \(SI\) Text](#) for detailed descriptions].

**Etymology.** For Mississippi, the Magnolia State.

**Type Locality.** CM locality 517, uppermost part of the Tusahoma Formation, Lauderdale County, MS.

**Diagnosis.** Trigonid of P<sub>4</sub> differs from that of all other species of *Teilhardina* except *T. asiatica* in being abbreviated mesiodistally, with relatively vertical preprotocristid and abrupt transition from buccal surface to postvallid. P<sub>4</sub> differs from that of *T. asiatica* in having metaconid more closely appressed to the base of the protoconid and weak mesial extension of cristid obliqua partially ascending postvallid. Lower molars differ from those of

Author contributions: K.C.B. designed research, performed research, analyzed data, and wrote the paper.

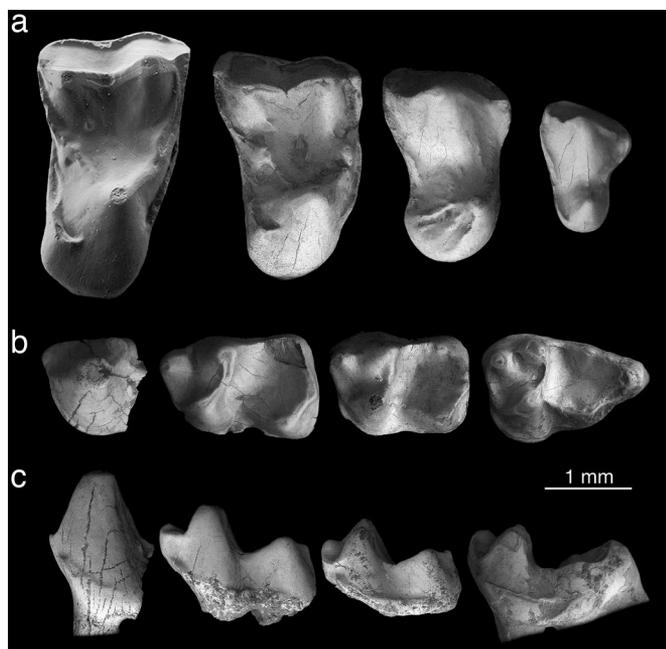
The author declares no conflict of interest.

This article is a PNAS Direct Submission.

<sup>†</sup>To whom correspondence should be addressed. E-mail: beard@carnegiemnh.org.

This article contains supporting information online at [www.pnas.org/cgi/content/full/0710180105/DC1](http://www.pnas.org/cgi/content/full/0710180105/DC1).

© 2008 by The National Academy of Sciences of the USA



**Fig. 1.** Composite partial dentition of *Teilhardina magnoliana* from the Tuscahoma Formation (earliest Eocene), Gulf Coastal Plain of Mississippi. (a) Composite right upper dentition ( $P^3$ – $M^2$ ) in occlusal view, based on CM 67854, CM 77210, CM 70431, and CM 70436 (reversed from left side). (b and c) Composite left lower dentition ( $P_4$ – $M_3$ ) in occlusal (b) and buccal (c) views, based on CM 73229, CM 67856, CM 70435 (holotype), and CM 70427 (reversed from right side).

all other species of *Teilhardina* except *T. asiatica* in being lower-crowned.  $M_{1-2}$  further differ from those of other North American species of *Teilhardina* in being relatively narrower, although not so narrow as in *T. asiatica*.

**Discussion.** *T. magnoliana* was a tiny primate. A regression equation predicting body mass from  $M_1$  area among living and fossil tarsioids (18) yields an estimated mean body mass of 28 g for *T. magnoliana*, placing this species at the lower limit of the range of adult body mass encompassed by living primates (19). Primates that are this small must adopt diets that are rich in calories, and small omomyids like *T. magnoliana* are thought to have eaten mainly fruits, gums, and insects (20). Our current knowledge of the anatomy of *T. magnoliana* limits the range of paleobiological inferences we can draw for this species. However, the closely related species *T. asiatica* possesses relatively small orbits that have been interpreted as evidence for a diurnal activity pattern (11). Tarsal bones of *T. belgica* suggest that it was an active arboreal quadruped that also engaged in powerful leaping (21).

## Results

Phylogenetic analyses indicate that *T. magnoliana* is a very basal member of the genus *Teilhardina* (Fig. 2a; for details see *SI Text* and *SI Fig. 3*), which is usually regarded as the most basal genus within Omomyidae and one of the most basal primate taxa currently known (1, 11, 22). Notably primitive characters that are retained in *T. magnoliana* (and *T. asiatica*) include its diminutive size, relatively low molar crown height, narrow  $M_2$ , and the distinctive structure of its  $P_4$  trigonid (including the relatively vertical orientation of the preprotocristid and the very abrupt transition from the buccal surface of the trigonid to the postval- lid). *T. magnoliana* more closely resembles European *T. belgica* than it does North American *T. brandti*. *T. brandti* is slightly larger than *T. magnoliana* and *T. belgica* and differs morpho-

logically from both species in having more nearly square occlusal outlines of  $M_{1-2}$  and stronger buccal cingulids on its lower molars.

All *T. magnoliana* fossils were recovered from the base of the T4 sand, a lenticular fine-grained sand body that locally forms the uppermost part of the Tuscahoma Formation (15, 17). The sediments comprising the T4 sand have been interpreted as estuarine tidal channels that were deposited very close to the ancient shoreline (17). Reflecting this depositional history, the T4 sand preserves a mixture of terrestrial and marine organisms. Dinoflagellate cysts from the T4 sand include abundant *Apectodinium augustum* and other *Apectodinium* species (15), indicating that the T4 sand correlates with the *Apectodinium* acme that coincides with the CIE at sites in Belgium, Austria, and New Zealand (23, 24). The *Apectodinium* acme is interpreted as an ecological response to the elevated sea surface temperatures that characterized the PETM (23). Accordingly, the cooccurrence of *T. magnoliana* and abundant *Apectodinium* in the T4 sand suggests that PETM warming began sometime before the deposition of this unit.

The unique stratigraphic context of *T. magnoliana* invites comparisons with penecontemporaneous strata in Europe that also yield *Teilhardina* and the *Apectodinium* acme. *T. belgica*, the oldest primate currently documented from Europe, occurs in the Dormaal mammal assemblage, derived from the basal part of the Tienen Formation in Belgium (1, 24, 25). The fluvial strata that yield the Dormaal mammal assemblage accumulated as incised valley-fill deposits, overlying an erosional surface that resulted from a major fall in eustatic sea level (24, 25). In contrast, the T4 sand that yields *T. magnoliana* was deposited under estuarine conditions, immediately before a major fall in eustatic sea level that caused a regional unconformity across the Gulf Coastal Plain of Mississippi and Alabama (15, 17). Only one significant drop in eustatic sea level is known to have occurred during the PETM, and the type 1 sequence boundary it produced provides an important datum for correlating strata on either side of the North Atlantic at this time (Fig. 2 d and e) (15, 24–26). Correlation on the basis of sequence stratigraphy indicates that *T. magnoliana* is older than *T. belgica*, although the precise duration of the temporal gap separating them remains unknown. The geographic and stratigraphic provenance of *T. magnoliana* demonstrates that *Teilhardina* inhabited coastal regions of North America before the fall in sea level during the PETM, thereby falsifying the hypothesis that this marine regression allowed *Teilhardina* to disperse from Europe to North America at this time (1). To the contrary, dispersal of *Teilhardina* from North America to Europe may have been facilitated by newly emergent land bridges resulting from lower sea level during the PETM regression (Fig. 2b).

Aside from *T. magnoliana*, the oldest North American primates come from zone Wa-0 in the Bighorn Basin of Wyoming (1). On the basis of their respective positions within the CIE, *T. brandti* from zone Wa-0 is younger than *T. belgica* (1). The temporal gap between *T. brandti* and *T. magnoliana* must be even greater, although it is probably <25 Kyr, the estimated duration of the interval between the P/E boundary and the first appearance of *T. brandti* (Fig. 2 c–e) (1). Although much of the mammalian fauna found associated with *T. magnoliana* in the T4 sand remains undescribed, certain taxa corroborate the correlation shown in Fig. 2. For example, the most common rodent in the T4 sand is the basal cylindrodontid *Tuscahomys* (16), which is also the most common rodent currently documented from zone Wa-M in the Bighorn Basin (although the specimens in question were identified as “*cf. Reithroparamys*, new species” in ref. 9). A second distinctive element of the Wa-M faunal zone in the Bighorn Basin is the hyopsodontid *Haplomylus zalmouti*, which is striking primarily for its diminutive size (9). A tiny species of *Haplomylus*, equivalent in size to *H. zalmouti*, is also



North American primates such as *T. magnoliana* that antedate the first record of this group in the Bighorn Basin is surprising and demands an explanation. Biotic provincialism is perhaps the most compelling potential reason for the apparent diachroneity in the local first appearances of primates along the Gulf Coast and the Bighorn Basin during the PETM. Small-bodied primates such as *Teilhardina* might be expected to be particularly prone to developing provincial distributions, especially during intervals of dynamic climate change such as the PETM. Tiny primates such as *T. magnoliana* are invariably arboreal, and primates are among the most thermophilic of all mammals. Additional factors, including specific food requirements or preferences, undoubtedly influenced their geographic distribution as well.

Fossil spores and pollen from the T4 sand indicate a humid, paratropical biome along the Gulf Coastal Plain during the PETM (28) and include distinctive plants that make a transient appearance during zone Wa-0 in the Bighorn Basin (4). Analysis of fossil floras and paleosols in the Bighorn Basin suggests significantly drier conditions during the earliest part of the PETM, followed by a return to higher levels of precipitation later in this interval (4, 5). Greenhouse warming at the onset of the PETM would have allowed *Teilhardina* to colonize coastal regions of North America, but primates and other Eocene mammalian immigrants apparently failed to extend their ranges into the Rocky Mountain Interior until regional patterns of

precipitation ameliorated, and local floral communities adapted to the new climatic regime. The development of significant biotic provincialism within North America during the PETM emphasizes how local records cannot adequately reflect the complexity of evolutionary and ecological changes on a continental scale, even when such local records are exceptionally dense and well documented.

## Materials and Methods

Specimens described in this report consist of isolated teeth collected by the author and his assistants during the course of multiple field seasons. For detailed anatomical descriptions of these specimens, see [SI Figs. 4–11](#). The phylogenetic analysis performed here is based on 11 taxa and 26 characters. The character–taxon matrix was assembled in MacClade 3.04 (29), and the data matrix and recovered trees were analyzed by using PAUP\* 4.0b10 for Macintosh PPC (30). The character list, the taxon–character matrix, and additional information regarding the phylogenetic analysis are provided in [SI Fig. 3](#).

**ACKNOWLEDGMENTS.** I thank D. T. Dockery III, S. L. Ingram, A. R. Tabrum, G. R. Case, and multiple volunteers from the Carnegie Museum of Natural History for their help in the field. Access to comparative specimens and/or casts was kindly granted by G. F. Gunnell, X. Ni, K. D. Rose, and T. Smith. L. E. Edwards provided information regarding the dinoflagellate record from the T4 sand. M. R. Dawson and Z.-X. Luo provided advice that significantly improved the manuscript. M. Klingler prepared the figures. Fieldwork and research were funded by National Geographic Society Grant 4299-90 and National Science Foundation Grants DEB 0073414 and BCS 0309800.

- Smith T, Rose KD, Gingerich PD (2006) Rapid Asia–Europe–North America geographic dispersal of earliest Eocene primate *Teilhardina* during the Paleocene–Eocene Thermal Maximum. *Proc Natl Acad Sci USA* 103:11223–11227.
- Beard KC, Dawson MR (1999) Intercontinental dispersal of Holarctic land mammals near the Paleocene/Eocene boundary: Paleogeographic, paleoclimatic and biostratigraphic implications. *Bull Soc Géol France* 170:697–706.
- Gingerich PD (1989) New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: Composition and diversity in a rarely sampled high-floodplain assemblage. *Univ Michigan Pap Paleontol* 28:1–97.
- Wing SL, Harrington GJ, Smith FA, Bloch JL, Boyer DM, Freeman KH (2005) Transient floral change and rapid global warming at the Paleocene–Eocene boundary. *Science* 310:993–996.
- Kraus MJ, Riggins S (2007) Transient drying during the Paleocene–Eocene Thermal Maximum (PETM): Analysis of paleosols in the Bighorn Basin, Wyoming. *Palaeogeogr Palaeoclimatol Palaeoecol* 245:444–461.
- Sluijs A, et al. (2006) Subtropical Arctic Ocean temperatures during the Palaeocene/Eocene thermal maximum. *Nature* 441:610–613.
- Bowen GJ, et al. (2002) Mammalian dispersal at the Paleocene/Eocene boundary. *Science* 295:2062–2065.
- Krause DW, Maas MC (1990) The biogeographic origins of late Paleocene–early Eocene mammalian immigrants to the Western Interior of North America. *Geol Soc Am Spec Pap* 243:71–105.
- Gingerich PD, Smith T (2006) Paleocene–Eocene land mammals from three new latest Clarkforkian and earliest Wasatchian wash sites at Polecat Bench in the northern Bighorn Basin, Wyoming. *Contrib Mus Paleontol Univ Michigan* 31:245–303.
- Yans J, et al. (2006) High-resolution carbon isotope stratigraphy and mammalian faunal change at the Paleocene–Eocene boundary in the Honeycombs area of the southern Bighorn Basin, Wyoming. *Am J Sci* 306:712–735.
- Ni XJ, Wang YQ, Hu YM, Li CK (2004) A euprimate skull from the early Eocene of China. *Nature* 427:65–68.
- Holman JA, Case GR (1992) A puzzling new snake (Reptilia: Serpentes) from the late Paleocene of Mississippi. *Ann Carnegie Mus* 61:197–205.
- Case GR (1994) Fossil fish remains from the late Paleocene Tuscahoma and early Eocene Bashi formations of Meridian, Lauderdale County, Mississippi. Part I. Selachians. *Palaeontographica* (Abt A) 230:97–138.
- Case GR (1994) Fossil fish remains from the late Paleocene Tuscahoma and early Eocene Bashi formations of Meridian, Lauderdale County, Mississippi. Part II. Teleosts. *Palaeontographica* (Abt A) 230:139–153.
- Beard KC, Dawson MR (2001) Early Wasatchian mammals from the Gulf Coastal Plain of Mississippi: Biostratigraphic and paleobiogeographic implications. In *Eocene Biodiversity: Unusual Occurrences and Rarely Sampled Habitats*, ed Gunnell GF (Kluwer/Plenum, New York), pp 75–94.
- Dawson MR, Beard KC (2007) Rodents of the family Cylindrodontidae (Mammalia) from the earliest Eocene of the Tuscahoma Formation, Mississippi. *Ann Carnegie Mus* 76:135–144.
- Ingram SL (1991) The Tuscahoma-Bashi section at Meridian, Mississippi: First notice of lowstand deposits above the Paleocene–Eocene TP2/TE1 sequence boundary. *Mississippi Geol* 11:9–14.
- Gingerich PD (1981) Early Cenozoic Omomyidae and the evolutionary history of tarsiform primates. *J Hum Evol* 10:345–374.
- Gebo DL, Dagosto M, Beard KC, Qi T (2000) The smallest primates. *J Hum Evol* 38:585–594.
- Strait SG (2001) Dietary reconstruction of small-bodied omomyoid primates. *J Vert Paleontol* 21:322–334.
- Gebo DL (1988) Foot morphology and locomotor adaptation in Eocene primates. *Folia Primatol* 50:3–41.
- Rose KD, Bown TM (1991) Additional fossil evidence on the differentiation of the earliest euprimates. *Proc Natl Acad Sci USA* 88:98–101.
- Crouch EM, et al. (2001) Global dinoflagellate event associated with the late Paleocene thermal maximum. *Geology* 29:315–318.
- Steurbaut E, et al. (2003) Palynology, paleoenvironments, and organic carbon isotope evolution in lagoonal Paleocene–Eocene boundary settings in North Belgium. *Geol Soc Am Spec Pap* 369:291–317.
- Steurbaut E (1998) High-resolution holostratigraphy of middle Paleocene to early Eocene strata in Belgium and adjacent areas. *Palaeontographica* (Abt A) 247:91–156.
- Rhodes GM, Ali JR, Hailwood EA, King C, Gibson TG (1999) Magnetostratigraphic correlation of Paleogene sequences from northwest Europe and North America. *Geology* 27:451–454.
- Marincovich L, Gladenkov AY (1999) Evidence for an early opening of the Bering Strait. *Nature* 397:149–151.
- Harrington GJ (2003) Wasatchian (early Eocene) pollen floras from the Red Hot Truck Stop, Mississippi, USA. *Palaeontology* 46:725–738.
- Maddison WP, Maddison DR (1992) *MacClade. Analysis of Phylogeny and Character Evolution* (Sinauer, Sunderland, MA).
- Swofford DL (2002) PAUP\*. *Phylogenetic Analysis Using Parsimony (\*and Other Methods)*. Version 4. (Sinauer, Sunderland, MA).