Rapid Asia–Europe–North America geographic dispersal of earliest Eocene primate *Teilhardina* during the Paleocene–Eocene Thermal Maximum

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True primates appeared suddenly on all three northern continents during the 100,000-yr-duration Paleocene–Eocene Thermal Maximum at the beginning of the Eocene, ≈55.5 mya. The simultaneous or nearly simultaneous appearance of euprimates on northern continents has been difficult to understand because the source area, immediate ancestors, and dispersal routes were all unknown. Now, omomyid haplorhine *Teilhardina* is known on all three continents in association with the carbon isotope excursion marking the Paleocene–Eocene Thermal Maximum. Relative position within the carbon isotope excursion indicates that Asian *Teilhardina asiatica* is oldest, European *Teilhardina belgica* is younger, and North American *Teilhardina brandti* and *Teilhardina americana* are, successively, youngest. Analysis of morphological characteristics of all four species supports an Asian origin and a westward Asia-to-Europe-to-North America dispersal for *Teilhardina*. High-resolution isotope stratigraphy indicates that this dispersal happened in an interval of ≈25,000 yr. Rapid geographic dispersal and morphological character evolution in *Teilhardina* reported here are consistent with rates observed in other contexts.

carbon isotope excursion | euprimates | omomyids

Primates of modern aspect (euprimates) make their first appearance in the fossil record during the Paleocene–Eocene Thermal Maximum (PETM) at the beginning of the Eocene epoch ≈55.5 mya. One genus, the omomyid *Teilhardina*, is the oldest primate known in both Asia (1, 2) and Europe (3). In North America, the first appearance of *Teilhardina*, also during the earliest Eocene, is contemporaneous with the appearance of another primate, the adapoid *Cantius* (4, 5). Four hypotheses have been proposed to explain this geographic distribution: (*i*) primates originated in Africa and dispersed through Europe and Greenland to reach North America (6); (*ii*) primates originated in North America and dispersed via the Bering route to reach Asia and via Greenland to reach Europe (7); (*iii*) primates originated in Africa or Asia and dispersed through North America to reach western Europe (4, 8); or (*iv*) primates originated in Asia and dispersed eastward to North America and westward to Europe (2, 9). One variation of hypothesis *iv* is that primates might have originated on India before it collided with the Asian plate near the Paleocene/Eocene (P/E) boundary, spreading into Asia after the collision (10). Here, we reevaluate these hypotheses using a combination of highly resolved ages for the earliest records of *Teilhardina* on each continent and new morphologic evidence from the *Teilhardina* species involved. We conclude that none of the existing hypotheses fits the pattern that has emerged.

Results

It has become possible to compare ages of first appearance of Asian, European, and North American earliest Eocene mammals only in the past 3 yr, with identification of the global PETM marked by the Paleocene–Eocene carbon isotope excursion (CIE) on all three northern continents (11–13). This CIE coincides with an episode of intense global warming lasting ≈100 thousand years (Kyr) (14, 15), and the starting point of the excursion defines the P/E boundary (16, 17). It was during the PETM that euprimates, perissodactyls, and artiodactyls first appeared across the Holarctic continents. Early in the CIE interval, δ^{13}C values decreased to a minimum and then gradually increased. The spike corresponding to the minimum value is situated 8.5–15 Kyr after the P/E boundary (14).

We correlated the CIE on the three northern continents and compared the stratigraphic positions and ages of the earliest records of *Teilhardina* on each continent (Fig. 1). The recently discovered *Teilhardina asiatica* from the Upper Lingcha Formation of China is from a level just above the P/E boundary, situated in the negative shift of the δ^{13}C excursion but before the minimum value of the excursion (1,12). The type species *Teilhardina belgica* is known from Dormaal, just above the base of the fluviolagoonal Tienen Formation of Belgium (11). This base also lies within the negative shift of the δ^{13}C excursion (18) and is estimated to be in an interval 4–10.5 Kyr after the P/E boundary (14). The early Eocene Willwood Formation of Wyoming has yielded five temporally successive *Teilhardina* species (*19*), of which *Teilhardina brandti* is the oldest. *T. brandti*, from the earliest Eocene (Wasatchian-0), was, until now, known from only one tooth (5), but several new specimens reported here reveal its phylogenetic importance. *T. brandti* and several other modern mammals (including artiodactyls and perissodactyls) first occur in a level that is situated above the minimum value of the δ^{13}C excursion and that has an estimated age of 19–25 Kyr above the P/E boundary (14, 20, 21).

Thus *T. asiatica*, *T. belgica*, and *T. brandti* were almost contemporaneous, but the slight differences in their ages suggest that *Teilhardina* appeared first in Asia, dispersed from Asia to Europe at ≈5–12 Kyr after the P/E boundary, and reached North America no later than 25 Kyr after the P/E boundary. The entire dispersal of *Teilhardina* across the three northern continents, therefore, probably occurred within 15–25 Kyr. Such a high level of precision in correlating intercontinental biotic events is unprecedented for the Early Cenozoic and results from discovery of the global CIE. We cannot, as yet, constrain local first appearances statistically within the CIE interval, but the reported differences are corroborated by the character analyses

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Abbreviations: CIE, carbon isotope excursion; Kyr, thousand years; P/E, Paleocene/Eocene; PETM, Paleocene–Eocene Thermal Maximum.

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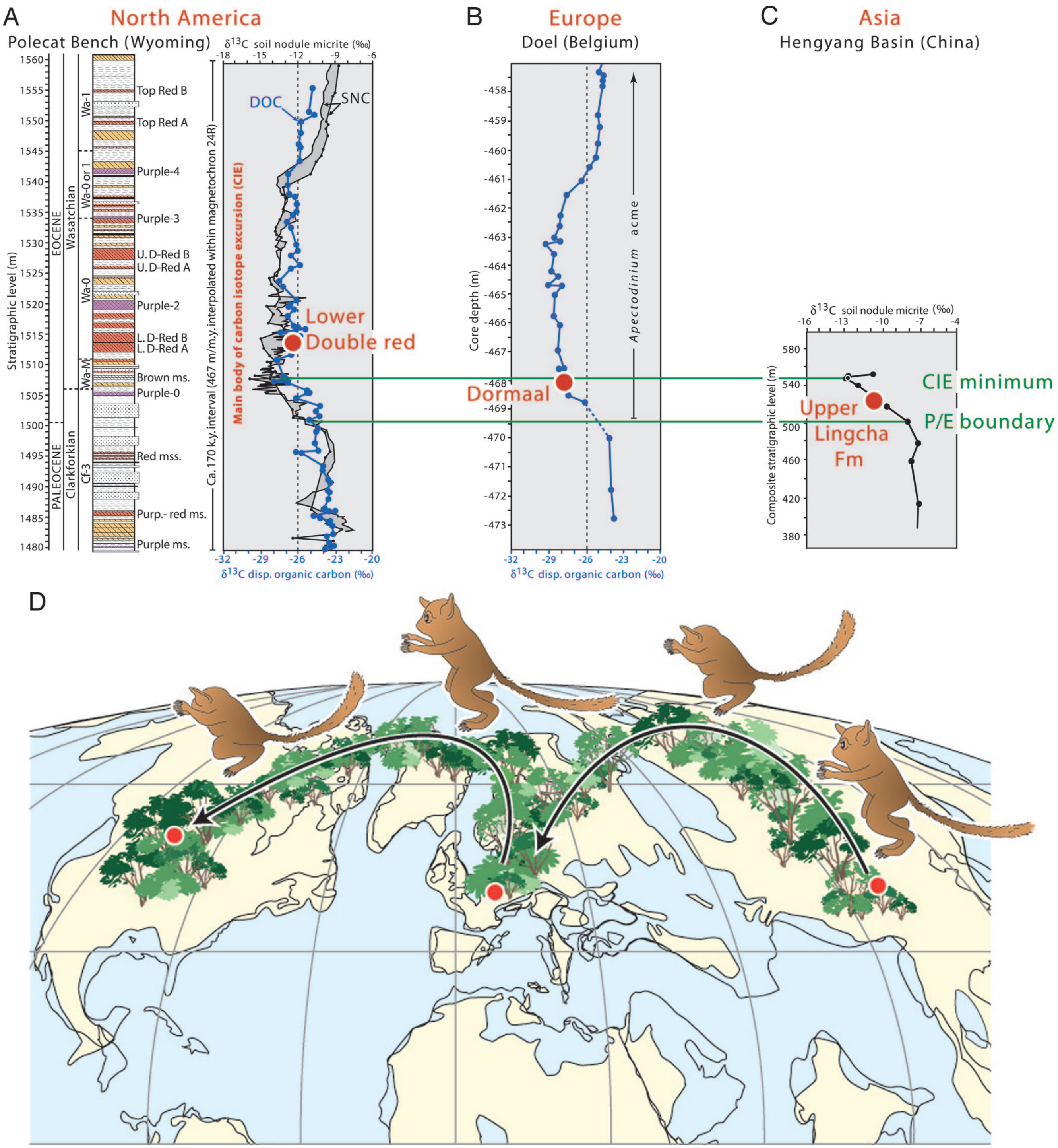

Fig. 1. Paleogeographic map showing hypothetical migration routes of *Teilhardina* during the earliest Eocene. (*A*–*C*) Timing of migration is obtained by correlations of the δ^{13}C excursion in North America (*A*), Europe (*B*), and Asia (*C*). *T. brandti* and other modern mammals first occur in the Lower Double Red (1,512 m) of Polecat Bench, Wyoming, which is situated above the minimum value of the δ^{13}C excursion (spike at 1,507 m). The Lower Double (L.D-) Red has an estimated age of 19–25 Kyr above the P/E boundary, based on soil carbonate nodules (SNC) and dispersed (disp.) organic carbon (DOC) (14, 20, 21). U.D-, Upper Double; Purp., purple; Fm, formation. (*D*) We hypothesize that *Teilhardina* dispersed through continuous forest from southern Asia to Europe and from nothern Europe to North America during the first 25 Kyr of the PETM.

below (Table 4, which is published as supporting information on the PNAS web site).

Dispersal rates of living mammals are in the range of 1–10 km/yr (22). The distance covered by *Teilhardina* would be ≈20,000 km. Thus, even if *Teilhardina* dispersed at the minimum rate documented in extant mammals, ≈1 km/yr, it could have covered this distance in 20 Kyr, which is consistent with the dispersal rate obtained by correlation of the CIE on the three northern continents.

We hypothesize that the primate *Teilhardina*, and probably basal genera of several other modern orders, dispersed east-to-west around the Northern Hemisphere at the beginning of the

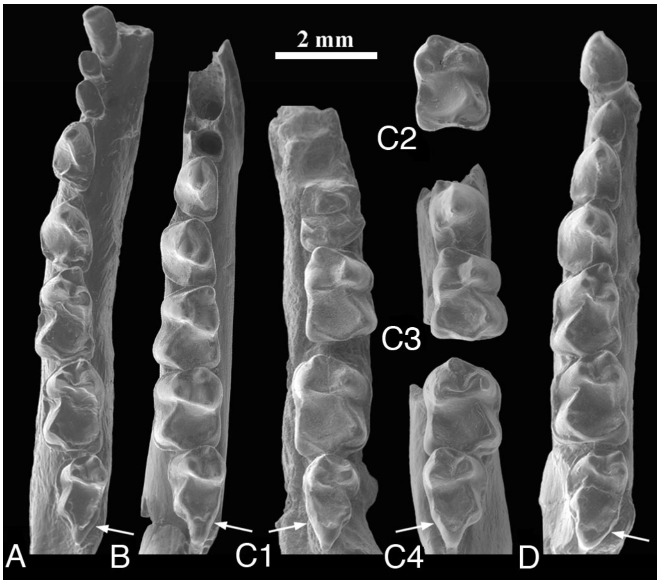

Fig. 2. Earliest Eocene *Teilhardina* species: *T. asiatica* (*A*), *T. belgica* (*B*), *T. brandti* (*C*), and *T. americana* (*D*): lower teeth in occlusal view. Shown are IVPP V12357 (*A*), IRSNB M64 (*B*), UM 111434 (*C1*) (reversed in Fig. 3), UM 99031 (*C2*), USNM 493913 (*C3*) (reversed in Figs. 3 and 4), USNM 493914 (*C4*), and UW 6896 (*D*). Arrows indicate increasing breadth of hypoconulid lobe of M_3.

PETM. They migrated from South Asia to Europe, crossing the Turgai Straits (23–25), and then dispersed to North America via Greenland (26). Recent description of *T. asiatica* (*1*), together with new specimens of *T. belgica* (3) and *T. brandti*, reported here, make it possible to evaluate dental morphology of *Teilhardina* on all three continents in detail (Figs. 2–4) to determine whether their anatomical differences are consistent with this dispersal hypothesis. Our comparisons indicate that morphological evidence mirrors the stratigraphic sequence of species just described.

T. asiatica is morphologically most similar to *T. belgica* (1). These species share the following primitive characters: presence of P_1, large canine, narrow cheek teeth, and weak labial cingulids, which, in combination, make them more primitive than any other omomyid. Neither species has any obvious autapomorphic features. But *T. belgica* is more derived and closer to American *Teilhardina* species in having stronger reduction of the first three premolars, a lower protoconid on P_{3-4}–M_1, a wider P_4, and a squarer M_2.

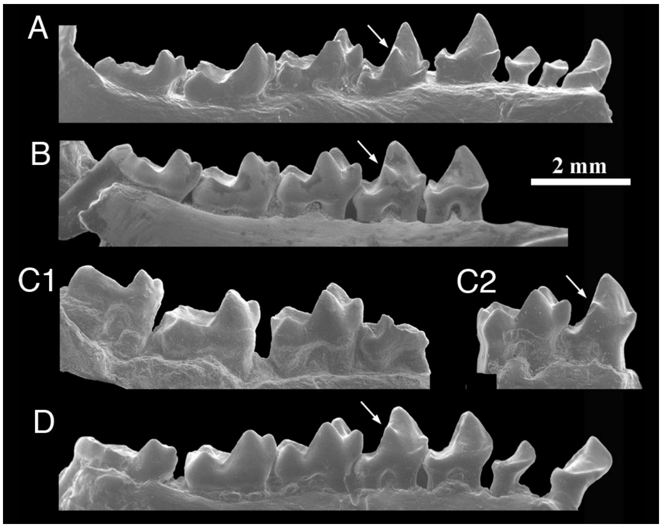

Fig. 3. Earliest Eocene *Teilhardina* species, *T. asiatica* (*A*), *T. belgica* (*B*), *T. brandti* (*C*), and *T. americana* (*D*): lower teeth in lingual view. Arrows indicate progressive elevation of metaconid on P_4. *T. brandti* shown are UM 111434 (reversed, C1) and USNM 493913 (reversed, C2).

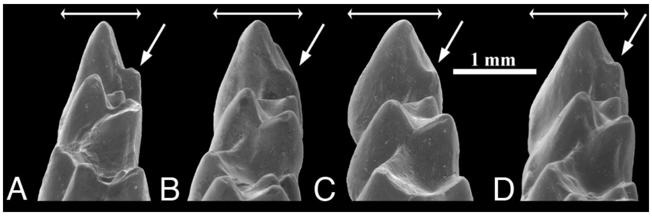

Fig. 4. Earliest Eocene *Teilhardina* species, *T. asiatica* (*A*), *T. belgica* (*B*), *T. brandti* (*C*), and *T. americana* (*D*): last lower premolar (P_4) in posterior view. Arrows indicate metaconid of P_4, bars show increasing width of P_4.

New specimens of *T. brandti* were collected in 2003 and 2004 from three separate areas of basal Eocene (Wasatchian-0) age in the Bighorn Basin, Wyoming (Figs. 2–4 and Table 1). The new specimens corroborate the validity of the species, and their broad geographic distribution across the basin shows that *T. brandti* is an index fossil of the Wasatchian-0 fauna (like the primitive artiodactyl *Diacodexis ilicis* and the perissodactyl *Hyracotherium*

Table 1. List of specimens of *T. brandti* from earliest Eocene [Wasatchian (Wa)-0] of the Bighorn Basin, Wyoming

ID number	Description	Location
UM 99031	Holotype, M_2	SC-351, northern Bighorn Basin (5)
UM 111434	Fragment of right dentary with P_4–M_3, the most complete specimen of *T. brandti.* The three molars are well preserved and not worn; only the trigonid of P_4 is missing. The M_2 is identical in size and morphology to the holotype	SC-67, northern Bighorn Basin
USNM 493913	Right dentary fragment with P_4–M_1	WW-108, southern Bighorn Basin
USNM 493914	Right dentary fragment with M_{2-3}	WW-107, southern Bighorn Basin
USNM 521795	Right dentary fragment with M_2	WW-75, southern Bighorn Basin
USNM 525543	Left isolated P_4, left isolated M_1, left isolated M_2	WW-96, southern Bighorn Basin
USNM 525544	Left isolated P_4 and left isolated M_2	WW-84, southern Bighorn Basin
USNM 525545	Left isolated M_2	WW-97, southern Bighorn Basin
USNM 525546	Right dentary fragment with M_{2-3}	WW-96, southern Bighorn Basin
USNM 525621	Right dentary fragment with M_{1-3}	WW-125, southern Bighorn Basin
USNM 525622	Left dentary fragment with M_{2-3}	WW-96, southern Bighorn Basin

All specimens listed are new except the holotype, and all have been found in association with Wa-0 mammalian markers such as *D. ilicis*, *H. sandrae*, and *A. junnei*. SC, Sand Coulee fossil locality, UM; UM, University of Michigan Museum of Paleontology; USNM, Department of Paleobiology, U.S. National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC; WW, Willwood fossil locality, USNM.

Table 2. Characters used in phylogenetic analysis

Character no.	Character	Description
1	Canine alveolus	(0) Large; (1) small; (2) smallest
2	P_1	(0) Present; (1) reduced; (2) absent
3	P_3 shape	(0) Straight; (1) slightly procumbent; (2) procumbent
4	Length of $P_{3–4}$ compared with $M_{1–2}$	(0) $P_{3–4}$ not compressed; (1) $P_{3–4}$ anteroposteriorly compressed
5	P_3 paraconid	(0) Distinct cusp; (1) crestiform to absent
6	Protoconid on P_3 to M_1	(0) High; (1) low
7	P_4 shape	(0) Very narrow; (1) narrow; (2) wide; (3) very wide
8	P_4 paraconid	(0) Well developed and distinct; (1) small; (2) very small to absent
9	P_4 metaconid	(0) Low; (1) intermediate; (2) high
10	Postprotoconid crest on P_4 and M_1	(0) Absent; (1) present
11	Anterior portion of the oblique crest on P_4	(0) Reaching the base of the trigonid wall; (1) running part way up the trigonid wall; (2) rising on the trigonid wall, higher than the top of the metaconid
12	Anterior portion of oblique crest on M_1	(0) Reaching the base of the trigonid wall; (1) running part way up the trigonid wall; (2) reaching the top of the metaconid
13	Labial cingulids on lower molars	(0) Weak or absent; (1) moderate; (2) strong
14	Hypoconulids on M_1 and M_2	(0) Well defined; (1) weak
15	M_2 shape	(0) Narrow; (1) somewhat square; (2) clearly square; (3) square and inflated
16	M_2 entoconid	(0) Low; (1) high
17	Hypoconulid lobe on M_3	(0) Narrow; (1) intermediate; (2) wide

Outgroup taxon was *Donrussellia provincialis*. All characters were ordered.

sandrae). *T. brandti* is morphologically intermediate between European *T. belgica* and North American *T. americana*. *T. brandti* is slightly larger than *T. belgica* and about the same size as *T. americana* (Table 5, which is published as supporting information on the PNAS web site). In several characters, *T. brandti* more closely resembles *T. belgica*: the lower metaconid on P_4, the smaller and narrower hypoconulid lobe on M_3, the tendency to have better defined hypoconulids on $M_{1–2}$, the lower entoconid on M_2, and the more open talonid notch between the entoconid and the trigonid (Fig. 3). At the same time, *T. brandti* resembles *T. americana* in having slightly wider cheek teeth because of basal inflation of the crown, a stronger ectocingulum, or both. In fact, labial cingulid development is intermediate between the two species: some specimens have little or no cingulum, as in *T. belgica*, whereas others have a moderately to well developed cingulum, as in *T. americana*.

Whereas *T. brandti* is intermediate between *T. belgica* and *T. americana*, *T. belgica* is intermediate between *T. asiatica* and *T. brandti* (Tables 2 and 3). This morphocline suggests a basal omomyid lineage *T. asiatica*–*T. belgica*–*T. brandti*–*T. americana*, with a clear evolutionary gradient in dental characters. The Holarctic *Teilhardina* lineage is characterized by progressive reduction of the first three premolars, increasing elevation of the metaconid relative to the protoconid on P_4, and widening of P_4 and the molars (Fig. 4). Concomitantly, the medial incisor enlarged while the primitive caniniform canine became premolariform. Such gradual evolution was documented in endemic American lineages of omomyids, including *Teilhardina* (19, 27). This kind of dental modification probably reflects a shift in diet to a regimen richer in fruit and gums (28). The *Teilhardina* lineage is supported by an equally weighted parsimony analysis of 17 dental characters (Fig. 5). Only the omomyid *Steinius vespertinus* could modify the morphocline because *S. vespertinus* is more primitive than *T. americana*. However, *Steinius* occurs >1 million years later than *T. americana* (29) and could derive directly from a different Eurasian euprimate stock.

Discussion

Fossil evidence suggests that North American omomyids came from Europe via the Greenland bridge rather than directly from Asia across the Bering land bridge. This hypothesis is in agreement with other Euroamerican mammal lineages studied from the earliest Eocene. The best species correlations are between representatives of modern orders from the Wasatchian-0 fauna

Table 3. Character matrix used for phylogenetic analysis

Genus and species	Position on matrix																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Donrussellia provincialis	0	0	0	0	0	0	0	0	1	0	2	2	1	0	1	0	1
Teilhardina asiatica	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Teilhardina belgica	0	1	1	0	1	1	1	1	0	0	1	1	0	0	1	0	1
Teilhardina brandti	?	?	?	?	1	1	1	1	0	0	1	1	0/1/2	0	2	0	1
Teilhardina americana	1	1/2	2	0	1	1	2	1	1	0	2	1	2	1	2	1	2
Steinius vespertinus	0	1	1	0	1	1	2	2	1	1	2	1	2	1	2	1	2
Teilhardina crassidens	1	2	2	1	1	1	3	1	2	1	-	2	2	1	3	1	2
Tetonius mckennai	2	2	2	1	?	1	3	1	1	0	2	1	2	1	2	1	2

Changes in omomyid species, together with increasing I_1 size, were probably related to increasing gum-feeding and frugivory (28). P_1 for *T. americana* (character 2) is either reduced (most specimens) or absent (at least one) (19). Low entoconid on M_2 (character 16) can be objectively assessed by measuring the angle made by the entocristid and post-entocristid (part of postcristid), i.e., the crests running anteriorly and posterolabially from the entoconid: When viewed from above or obliquely from the labial side, this angle is always obtuse in *T. belgica* and *T. brandti* (resulting in a low entoconid) and acute in *T. americana* and *T. crassidens* (high entoconid). Labial cingulids (character 13) are variable in *T. brandti*.

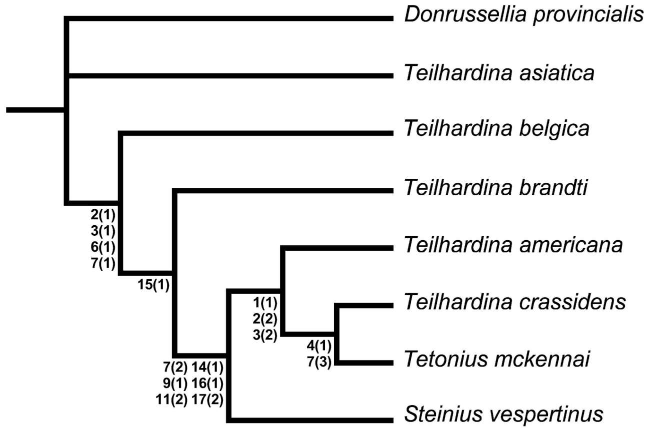

Fig. 5. Single most-parsimonious tree recovered in PAUP 4.0 b10 (34), derived from an equally weighted parsimony analysis of a matrix containing eight taxa and 17 dental characters (see Tables 3 and 5). Tree length = 36, consistency index excluding uninformative characters = 0.8286, retention index = 0.8286. Unequivocal character-state changes are indicated along each branch.

of the Willwood Formation of Wyoming and those from the Tienen Formation of Dormaal, Belgium. Indeed, the earliest North American artiodactyl *D. ilicis* is slightly larger and more derived than *Diacodexis gigasei* from Dormaal (8, 30). *D. ilicis* is considered to be at the base of the American dichobunoid radiation. In addition to the species *D. gigasei–D. ilicis*, other closely allied Euroamerican species pairs in which the European species is slightly more primitive include the proviverrine creodonts *Arfia gingerichi–Arfia junnei* and *Prototomus minimus–Prototomus deimos* (31) and several lipotyphlan species. These Euroamerican lineages do not exclude a migration route from Asia to North America via the Bering land bridge for other taxa. Because some typical Asian late Paleocene groups are present in the late Paleocene or early Eocene of North America and are unknown in Europe, they probably dispersed directly from Asia to North America, possibly during the late Paleocene. This scenario could be the case for representatives of some modern orders, such as rodents, some perissodactyls, and limnocyonine creodonts.

Dispersal of the earliest Eocene primate *Teilhardina* and other modern mammals took place during the onset of the PETM and near the beginning of a marine transgression. This transgression followed a major eustatic lowering of sea level (11), which we infer exposed land bridges between the northern continents. The exceptionally high temperature at the beginning of the Eocene, combined with the existence of temporary land bridges, evidently permitted small subtropical mammals to cross high-latitude land bridges such as Greenland and Beringia. Because omomyids were strictly arboreal mammals, their rapid dispersal argues for the existence of a continuous evergreen forest belt at high latitudes during the PETM (32). This hypothesis is reinforced by recent studies showing evidence for a shift in the state of the climate system during this time, characterized by large increases in tropospheric humidity and enhanced cycling of carbon through terrestrial ecosystems (33).

Materials and Methods

This study is based on anatomical comparisons of new specimens of North American *T. brandti* with specimens of other species of *Teilhardina* (see Tables 1 and 5). Relative age of fossils is based on recent high-resolution carbon isotope stratigraphy (11, 12, 14).

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