New Fossils of the Oldest North American Euprimate *Teilhardina brandti* (Omomyidae) from the Paleocene–Eocene Thermal Maximum

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ABSTRACT   More than 25 new specimens of *Teilhardina brandti*, one of the oldest known euprimates, are reported from earliest Eocene strata of the southern Bighorn Basin, Wyoming. The new fossils include the first upper dentitions, a dentary showing the lower dental formula for the first time, and the first postcrania ascribed to *T. brandti* (tarsals and terminal phalanges). The elongated navicular and long talar neck suggest that *T. brandti* was an active arboreal quadruped, and the terminal phalanges constitute the oldest evidence for nails in Euprimates. Phylogenetic analysis incorporating the new data indicates that *T. brandti* is more derived than *T. belgica* but less so than *T. americana*. The hypothesis that *Teilhardina* originated in Asia (*T. asiatica*) and dispersed westward to Europe (*T. belgica*) and then to North America (*T. brandti* and *T. magnoliana*) during the earliest Eocene Paleocene–Eocene Thermal Maximum is most consistent with available evidence, including the relative age of fossil samples and their stage of evolution. Am J Phys Anthropol 000:000–000, 2011.   ©2011 Wiley-Liss, Inc.

Except for the poorly known and enigmatic *Altiatlasius* from the late Paleocene of Morocco, euprimates are unknown in the fossil record until the beginning of the Eocene, when they abruptly appear, almost simultaneously, in Europe, Asia, and North America (Ni et al., 2004; Smith et al., 2006). In North America the omomyid *Teilhardina brandti* is arguably the oldest known euprimate, recorded from basal Eocene (earliest Wasatchian, Wa-0) sediments of northern Wyoming deposited during the Paleocene–Eocene Thermal Maximum or **PETM** (Gingerich, 1993; Smith et al., 2006). Carbon isotope stratigraphy indicates that *T. brandti* first appeared in the Bighorn Basin, Wyoming, ∼25 Kyr after the onset of the global carbon isotope excursion (**CIE**), which was coincident with the PETM. Based on dental differences among *T. asiatica*, *T. belgica*, and *T. brandti*, and their stratigraphic positions relative to the minimum value of the CIE, Smith et al. (2006) hypothesized that *Teilhardina* dispersed from eastern Asia to Europe and from there to North America during the first 25 Kyr of the PETM. In contrast, Beard (2008) argued that *Teilhardina magnoliana*, from the uppermost Tuscahoma Formation Red Hot local fauna of Mississippi, predated both *T. brandti* from the Bighorn Basin and *T. belgica* from the Tienen Formation at Dormaal, Belgium. He further hypothesized that *Teilhardina* first reached coastal areas of North America from Asia during the beginning of the PETM, later dispersing to Europe and the Bighorn Basin. Current evidence suggests that the adapoid primate *Cantius* did not appear in the southern Bighorn Basin until somewhat later in the PETM (Rose et al., in press), which makes *Teilhardina* the oldest North American euprimate. Dispersal of primates and other mammals was probably facilitated by the opening of high-latitude land connections between the northern continents associated with global warming during the PETM (McKenna, 1983; Krause and Maas, 1990; Clyde and Gingerich, 1998).

Teilhardina brandti was initially based on a single lower molar (Gingerich, 1993), and until now the species has been known only from a small number of fragmentary lower dentitions (Smith et al., 2006). Here we report 29 new specimens of *T. brandti*, including the first known upper dentitions, a lower jaw that shows for the first time the size and number of lower antemolar teeth, and the first postcrania attributed to this species, which include the oldest definitive evidence for the presence of nails in euprimates. In addition, a cladistic analysis of *Teilhardina* species, taking into account new anatomical information from these specimens, allows for re-evaluation of previously published, and highly debated, phylogenetic and biogeographic hypotheses of the first Euprimates to appear in North America, Europe, and Asia.

GEOLOGICAL SETTING AND AGE

Teilhardina brandti is restricted to the second earliest biozone of the early Eocene, Wa-0, which immediately follows the brief Wa-M biozone and coincides with most of the PETM. Besides including the oldest North American euprimates, the Wa-0 fauna is characterized by the first appearance of perissodactyls, artiodactyls, and hyaenodontid creodonts (Gingerich, 1989; Koch et al., 1992), and by small body size of some herbivorous and carnivorous mammals (Gingerich, 1989; Chester et al., 2010). The PETM was an episode of global warming, ~150 Kyr in duration (Aubry et al., 2007; Abdul Aziz et al., 2008), first detected from the CIE in marine sediments (e.g., Kennett and Stott, 1991; Zachos et al., 2001). Subsequently the PETM has also been recognized in continental sections on several continents based on carbon and oxygen isotope measurements from soil carbonates, hematite coatings on fossil bones, and fossil teeth (e.g., Koch et al., 1992, 2003; Fricke et al., 1998; Bao et al., 1999). The onset of the CIE is now used to mark the beginning of the Eocene, at ~55.8 Ma (Aubry et al., 2007).

The fossils reported here come from Wa-0 strata of the Willwood Formation, in the Sand Creek Divide and Cabin Fork sections of the southern Bighorn Basin, Wyoming. The primate fossils come chiefly from paleosols and small channel cuts into paleosols. Carbon isotope stratigraphy in the Sand Creek Divide and Cabin Fork sections places the lowest occurrence of *Teilhardina*

brandti between 8 and 10 m above the onset of the CIE (see Fig. 1) and ~5–10 m above the minimum δ^{13}C values (Rose et al., in press). This corresponds to the approximate date of the first appearance of *T. brandti* in the Polecat Bench section (northern Bighorn Basin), at ~25 Kyr after the start of the CIE and ~10 Kyr after the minimum δ^{13}C values (Bains et al., 2003; Magioncalda et al., 2004; Smith et al., 2006).

MATERIALS AND METHODS

We report here 23 new dental specimens (Tables 1 and 2) of *Teilhardina brandti* and attribute several isolated postcranial elements to this species. Specimens were recovered through both surface prospecting and screen-washing.

Morphology

Comparisons were made with other species of *Teilhardina* as well as a diversity of other primitive euprimates and plesiadapiforms. Lower tooth characters used in the phylogenetic analysis were primarily taken or modified from those of Smith et al. (2006) and Beard (2008). These are the most recent phylogenetic analyses focusing on *Teilhardina*, but both studies employed only lower tooth characters (upper teeth were previously unknown for *T. brandti*). Therefore, upper tooth characters were based mainly on those used by Seiffert et al. (2005), whose analysis encompassed a broad array of fossil primates including *Teilhardina* and a diversity of other omomyids. Some characters used in these previous analyses were omitted because they were deemed uninformative, ambiguous, or unrepeatable. Lengths and widths are maximum dimensions unless otherwise noted.

Particular attention was paid to characters of P_4 that have been considered to be informative for *Teilhardina* (see Fig. 2)—including tooth width, metaconid height (Bown and Rose, 1987; Smith et al., 2006; Beard, 2008), preprotocristid verticality (Beard, 2008), and abruptness of the transition from the postvallid to the buccal surface of the trigonid (Beard, 2008)—with the intention of quantifying previous qualitative observations. Trigonid length of P_4 was measured as the maximum distance from the mesial margin to the postvallid surface directly posterior to the protoconid, with the tooth viewed occlusally. To facilitate consistent measurements, we generated 3D digital models of 36 P_4s representing *Teilhardina* species, other early euprimates, and plesiadapiforms (see Appendix D). Models were generated by scanning casts of isolated teeth using a Scanco μCT 40, with settings of 70 kv, 114 μAmp, and voxel resolution of 8 μm. A LDI RPS-120 laser scanner was used to generate models of P_4 for the adapoids *Marcgodinotius* and *Asiadapis*. Resulting scans were processed and measured in Avizo 6.0 (see Boyer, 2008, for details on processing of microCT data). Digital photographs were measured for several comparative taxa (*Steinius, Tetonius, Cantius, Donrussellia, Altanius, Purgatorius*, and *Palaechthon*). The measurements and variables we present (see Appendix D and E) are those that best capture the originally described variation. Resulting values were incorporated into the phylogenetic analysis by assigning character states to different ranges of values (Appendix E).

In addition, we used principal coordinates analysis and the statistics software PAST.exe to analyze the significance of the various P_4 measurements noted above

| *Abbreviations*	
AMNH	Department of Vertebrate Paleontology, American Museum of Natural History, New York, New York
CM	Section of Vertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania
GU	Department of Geology, H.N.B. Garhwal University, Srinagar, Uttarakhand, India
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China
LACM	Los Angeles County Museum of Natural History, Los Angeles, California
MNHN	Muséum National d'Histoire Naturelle, Paris, France
PSS	Geological Institute Paleontology and Stratigraphy Section, Mongolian Academy of Sciences, Ulan Bator, Mongolian People's Republic
RS	Richard Smith collection, Wemmel, Belgium
UCMP	University of California Museum of Paleontology, Berkeley, California
UF	Vertebrate Paleontology Collection, Florida Museum of Natural History, University of Florida, Gainesville, Florida
UKMNH	University of Kansas Museum of Natural History, Lawrence, Kansas
UM	University of Michigan Museum of Paleontology, Ann Arbor, Michigan
USGS	US Geological Survey, Denver, Colorado; collection transferred to USNM
USNM	Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.
UW	Department of Geology and Geophysics, University of Wyoming, Laramie, Wyoming
YPM	Department of Vertebrate Paleontology, Peabody Museum of Natural History, Yale University, New Haven, Connecticut.
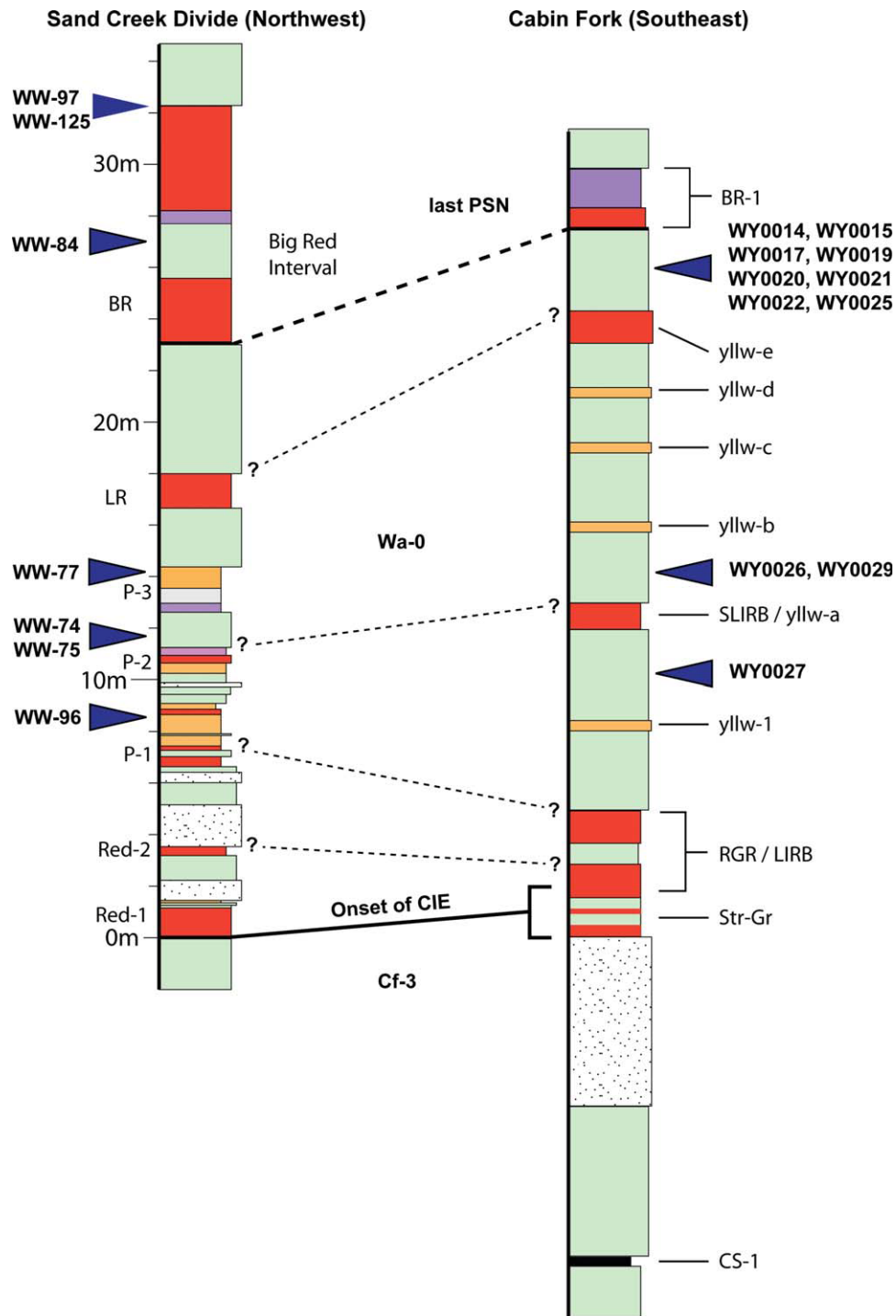
Fig. 1. Stratigraphic occurrences of *Teilhardina brandti* from the southern Bighorn Basin, Wyoming. Fossils are from two different stratigraphic sections, the bases of which are correlated via the onset of the Carbon Isotope Excursion (CIE), documented in dispersed organic carbon of the two sections (Wing et al., 2005; Rose et al., in press). The bold dashed line at the top is correlated at the base of a prominent red bed (Big Red) that contains the stratigraphically highest paleosol nodules (PSN). Close similarity in stratigraphic thickness (meters) suggests relative uniformity in depositional rates across the 10–20 miles separating the two regions. Possible correlative beds are shown by dotted lines. Blue arrows indicate localities that yielded *T. brandti*. Sand Creek Divide localities (with prefix WW) were established by Johns Hopkins University, Cabin Fork localities (with prefix WY) by the University of Florida. Sand Creek Divide section by Mary J. Kraus. Colors of beds roughly match appearance of paleosols in the field; yellow are immature, red and purple more mature. Sands are represented by speckled units. *T. brandti* first appears about 8–10 m after the onset of the CIE. Other abbreviations: BR-1, Big Red paleosol 1; CS-1, Carbonaceous Shale 1; LR, Little Red paleosol; (S)LIRB, (Second) Lowest Intermittent Red Bed; P-x, Purple-x; RGR - Red-Grey-Red; Str-Gr - strange gray.

TABLE 1. Measurements of upper teeth of Teilhardina brandti and T. americana[a]

	Locality	P^3L	P^3W	P^4L	P^4W	M^1L	M^1W	M^2L	M^2W	M^3L	M^3W
Teilhardina brandti											
USNM 540598	WW-74							1.80	3.10		
UF 244453	WY0017							1.70	2.90		
UF 244460	WY0014									1.15	2.20
UF 254927	WY0025					1.8*	2.80	1.65	3.20		
USNM 525543	WW-84	1.55	2.00								
USNM 533494	WW-74			1.60	2.40	1.75	2.70	1.70	2.90	1.10	2.05
USNM 539466	WW-74							1.70	2.85	1.15	2.10
USNM 539467	WW-74			1.60	2.35	1.75	2.70	1.80	3.00	1.20	2.00
N		1	1	2	2	3	3	6	6	4	4
Mean					2.38	1.77	2.73	1.73	2.99	1.15	2.09
Standard deviation					0.04	0.03	0.06	0.06	0.14	0.04	0.09
Standard error					0.03	0.02	0.03	0.03	0.06	0.02	0.04
Minimum					2.35	1.75	2.70	1.65	2.85	1.10	2.00
Maximum					2.40	1.80	2.80	1.80	3.20	1.20	2.20
Teilhardina americana											
UF 244459	WY0016	1.70	2.10	1.65	2.30	1.80	2.70	1.85	3.25	1.25	2.40

[a] L of upper molars = maximum L parallel to a line through paracone-metacone; W = maximum distance perpendicular to L.
*Denotes approximate. All specimens are new.

TABLE 2. Measurements of lower teeth of Teilhardina brandti

	Locality	P_4L	P_4W	M_1L	M_1Wtri	M_1Wtal	M_2L	M_2Wtri	M_2Wtal	M_3L	M_3Wtri	M_3Wtal	M_3W hyd
UF 244451	WY0015						2.05	1.75	1.75	2.10	1.40	1.15	0.55
UF 244454	WY0019	1.80	1.35										
UF 244455	WY0020			2.10		1.60	2.00	1.60	1.55				
UF 244456	WY0021						2.00	1.60	1.60	1.90	1.30	1.10	0.45
UF 244457	WY0022						1.85	1.50	1.40				
UF 254928	WY0020									1.95	1.40	1.10	0.60
UF 254929	WY0027			1.90	1.30	1.45	1.95	1.65	1.50				
UF 254931	WY0026			1.90	1.30	1.45							
UF 254935	WY0029									1.95	1.35	1.10	0.60
UM 99031 HT	SC-351						1.95	1.55	1.50				
UM 111434	SC-67		1.30	2.05	1.40	1.50	2.15	1.70	1.60	1.90	1.20	0.90	
USNM 493913	WW-108	1.60	1.20	1.95	1.40	1.60							
USNM 493914	WW-107						1.95	1.60	1.60	1.95	1.30	1.05	
USNM 521795	WW-75						2.00	1.55	1.60				
USNM 525543	WW-84	1.75	1.30	1.95	1.30	1.45	1.95	1.60	1.55				
USNM 525544	WW-84	1.75	1.20				2.00	1.55	1.55				
USNM 525545	WW-97						1.95	1.50	1.50				
USNM 525546	WW-96						1.90	1.50	1.50	1.90	1.35	1.15	
USNM 525621	WW-125			2.00	1.40	1.55	2.05	1.70	1.60	2.10	1.30	1.05	
USNM 525622	WW-96						1.95	1.45	1.45	1.80	1.25	1.05	
USNM 533505	WW-74						2.00	1.50	1.45				
USNM 533554	WW-77	1.80	1.20	2.05	1.40	1.50							
USNM 538082L	WW-84			2.00	1.25	1.35	2.00	1.55	1.50				
USNM 538082R	WW-84						1.95	1.60	1.50				
USNM 538084	WW-84						1.95	1.50	1.45				
N		5	6	9	8	9	19	19	19	9	9	9	4
Mean		1.74	1.26	1.99	1.34	1.49	1.98	1.58	1.53	1.95	1.32	1.07	0.55
Standard deviation		0.08	0.07	0.06	0.06	0.08	0.06	0.08	0.08	0.10	0.07	0.08	0.07
Standard error		0.04	0.03	0.02	0.02	0.03	0.01	0.02	0.02	0.03	0.02	0.03	0.04
Minimum		1.60	1.20	1.90	1.25	1.35	1.85	1.45	1.40	1.80	1.20	0.90	0.45
Maximum		1.80	1.35	2.10	1.40	1.60	2.15	1.75	1.75	2.10	1.40	1.15	0.60

Specimens in bold are new.
Abbreviations: L, length; W, width; W hyd, width of hypoconulid lobe; Wtal, width of talonid; Wtri, width of trigonid.

(buccolingual angle [character #26], preprotocristid verticality angle [#29], trigonid width index [#31], and mesial angle [#46]). Angles were analyzed in radians, thus having a magnitude and range of values similar to the P_4 trigonid width index. Metaconid height was excluded because this cusp is absent (*Purgatorius*) or variable (*Marcgodinotius* and *Asiadapis*) in some taxa in the analysis; however, results of an analysis including metaconid measurements on a reduced sample did not differ substantially from those excluding the measurements. The P_4 analysis included two euprimate outgroups (*Purgatorius, Palaechthon*), the probable basal euprimate *Altanius orlovi*, and several primitive euprimates (*Donrussellia gallica, Marcgodinotius indicus, Asiadapis cambayensis, Cantius ralstoni*) as well as six species of *Teilhardina* and two other omomyids (*Tetonius* and *Steinius*) (see Appendix D). A minimum spanning tree was imposed on the principal coordinate morphospace to
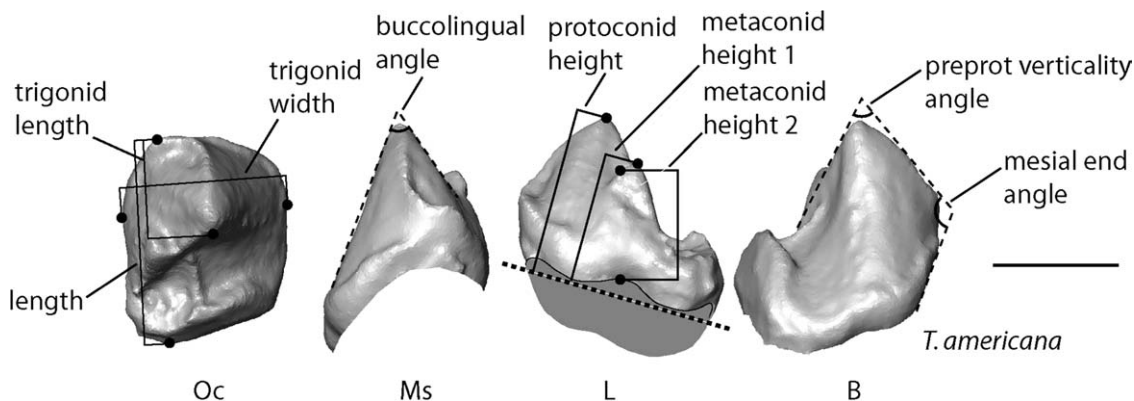
Fig. 2. Measurements of P_4. Abbreviations: B, buccal; L, lingual; Ms, mesial; Oc, occlusal; preprot, preprotocristid. Scale = 1 mm. See text and Appendix B for measurement definitions.

show nearest neighbors reflecting the four-dimensional distances between specimens.

Phylogenetic analysis

To assess relationships among *Teilhardina* species, a matrix including 13 taxa and 47 dental characters (see Appendices A, B) was assembled in MacClade 4.06 (Maddison and Maddison, 2003). All characters and taxa were reevaluated for this study. Our analysis included six species of *Teilhardina*: *T. asiatica*, *T. belgica*, *T. brandti*, *T. magnoliana*, *T. americana*, and *T. crassidens*. Other basal euprimates included in the analysis were the omomyids *Tetonius matthewi* and *Steinius vespertinus*, and the primitive adapoids *Donrussellia provincialis* and *D. gallica*. The probable basal euprimate *Altanius orlovi*, and the basal plesiadapiforms *Purgatorius janisae* and *Palaechthon nacimienti*, were also included. A branch and bound search was conducted in PAUP* 4.0b10 for Macintosh PPC (Swofford, 2003). *Purgatorius janisae* was set as the outgroup. All characters were treated as unordered and were weighted equally. Multistate characters were interpreted as polymorphic.

Descriptive paleontology

Family OMOMYIDAE Trouessart, 1879
Teilhardina Simpson, 1940
Teilhardina brandti Gingerich, 1993

New dental specimens—USNM 533494 (R maxilla, P^4-M^3), 533505 (R dentary, M_2), 533554 (L dentary, P_4-M_1), 538082 (isolated teeth: LM_1, LM_2, RM_2), 538084 (LM_2), 538361 (L dentary, M_2 talonid), 539466 (L maxilla, M^{2-3}), 539467 (L maxilla, P^4-M^3), 540598 (RM^2); UF 244451 (R dentary, M_{2-3}), 244453 (RM^2), 244454 (R dentary, P_4), 244455 (L dentary, M_{1-2}), 244456 (L dentary, M_{2-3}), 244457 (R dentary, M_2), 254927 (R maxilla, M^{1-2}), 254928 (L dentary, M_3), 254929 (R dentary, M_{1-2} and all anterior alveoli), 254931 (RM_1), 254935 (R dentary, M_3), and questionably 244460 (LM^{2-3}).

Maxilla and upper teeth. The maxilla is very shallow below the orbit, and the lingual root of M^2 protrudes into the orbital floor. The lower rim of the orbit is present in each of the more complete maxillae (see Fig. 3), but it appears to be too incomplete to provide a confident estimate of orbital diameter.

Alveoli in USNM 533494 (Fig. 3A,B) indicate that P^3 was a three-rooted triangular tooth, about as long mesio-

distally as P^4 but less transverse buccolingually, as in other species of *Teilhardina* and closely allied taxa. P^4 is markedly transverse, slightly waisted, and shorter mesiodistally than the molars. It is dominated by the large and high buccal cusp (paracone), the tallest cusp of the postcanine toothrow, which tilts distally. Although the base of the cusp is centrally positioned, the apex is distinctly distal to the buccolingual midline axis. A tiny parastyle is present but there is no discernible metastyle. The protocone is low and situated near the mesiolingual margin of the tooth. A weak postprotocrista descends distally to the postcingulum; a stronger preprotocrista runs buccally and becomes continuous with the precingulum, which extends to the parastyle.

The upper molars (Fig. 3A–C) are among the most primitive known for euprimates. The enamel is smooth, with little or no evidence of crenulation. The molar pattern is simple, with small conules, weak styles, no hypocone, and moderately developed cingula (buccally, mesially, and distally, but not lingually). A tiny parastyle is evident on all three molars, but the metastyle is indistinct. The postcingulum extends lingually slightly farther than the precingulum, but both end near the base of the protocone. At its lingual extent, the postcingulum is slightly broader than the precingulum, but there is no hypocone, and the cingulum is broadly discontinuous lingually. A faint swelling can be detected at the distolingual angle of the postcingulum, where a small hypocone may develop in later species. There is no trace of a nannopithex fold except in M^2 of USNM 539467, in which a faint elevation of the enamel in the appropriate location can be detected with reflected light; however, it is clearly not a typical nannopithex fold.

UF 244460 (Fig. 3F) differs from other upper molars of *T. brandti* in having weakly crenulated enamel, a nearly complete lingual cingulum, and a squared lingual margin of M^2 associated with a weak nannopithex fold. All of these features are known to vary in *Teilhardina americana* (which comes from the Wa-1/2 biozone) but are typically present in that species. Although this might suggest that UF 244460 actually comes from above Wa-0, local stratigraphy makes such contamination very unlikely. Thus it is probable that this specimen indicates intraspecific variation in *T. brandti* and provides evidence for a close (probably ancestor-descendant) relationship between *T. brandti* and *T. americana*.

Dentary and lower teeth. The dentary of *Teilhardina brandti* (UF 254929, Fig. 4) has an anterior mental foramen below P_1 and a posterior foramen below the anterior root of P_3. The symphysis extends back only to below P_2.
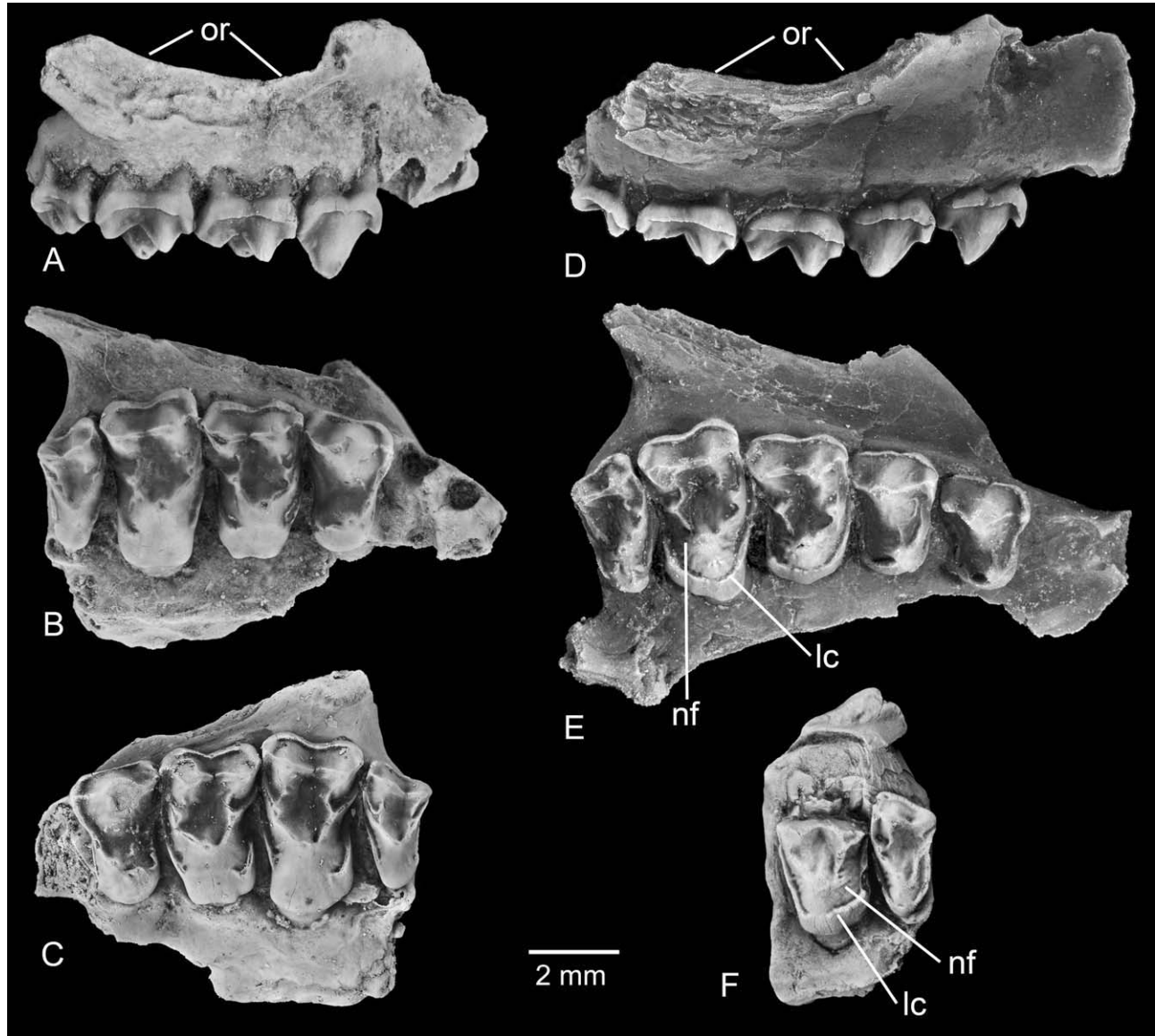
Fig. 3. Maxillary dentitions of *Teilhardina brandti* and *T. americana*. **A** and **B**, *T. brandti*, USNM 533494, right maxilla with P^4-M^3 in buccal (A) and occlusal (B) views. **C**, *T. brandti*, USNM 539467, left maxilla with P^4-M^3 in occlusal view. **D** and **E**, *T. americana*, UF 244459, right maxilla with P^3-M^3 in buccal (D) and occlusal (E) views. **F**, *T. brandti*, UF 244460, left maxilla with M^{2-3} in occlusal view. Note crenulation, lingual cingulum, and nannopithex fold in E, slightly less developed in F. lc, lingual cingulum; nf, nannopithex fold; or, orbital rim.

UF 254929 (see Fig. 4) is the first specimen of *T. brandti* to reveal the lower dental formula (2.1.4.3) and the size and position of anterior teeth. It clearly shows the presence of four premolars, including single-rooted P_2 and P_1, the latter diminutive and displaced laterally. Judging from its alveolus, the canine was comparatively smaller than in adapoids but relatively large for an omomyid. The incisor alveoli indicate that I_1 was slightly larger than I_2 and that both were very small, much smaller than the canine, and neither alveolus being larger than that of P_1. I_1 is situated medial to I_2, rather than largely anterior to it as is the case in the primitive adapoid *Cantius* (Rose et al., 1999). Because they are incomplete anteriorly, the orientation of the roots is difficult to determine with certainty, but they appear to have been essentially vertical and not nearly so anteriorly inclined as in *Cantius*.

P_4 has been considered the most important lower tooth for analyzing dental evolution in *Teilhardina* (Rose and Bown, 1984; Bown and Rose, 1987), so its morphology in *T. brandti* is of particular interest. USNM 533554 (Fig. 5A–C) contains the fifth known P_4 of *T. brandti* and only the second one preserved in sequence with M_1. All five P_4 specimens are relatively narrow and have a metaconid approximately two-thirds as high as the protoconid, which is essentially the same as in *T. belgica* and lower than in *T. americana* (Table 3 and Appendix D and E). The talonid is variable, ranging from very short and weakly developed (USNM 493913; Fig. 5D–F) to somewhat longer and basined (but open lingually) with a distinct cristid obliqua, hypoconid, and lower entoconid (USNM 533554).

The lower molars do not differ in any significant way from those described and illustrated by Smith et al.
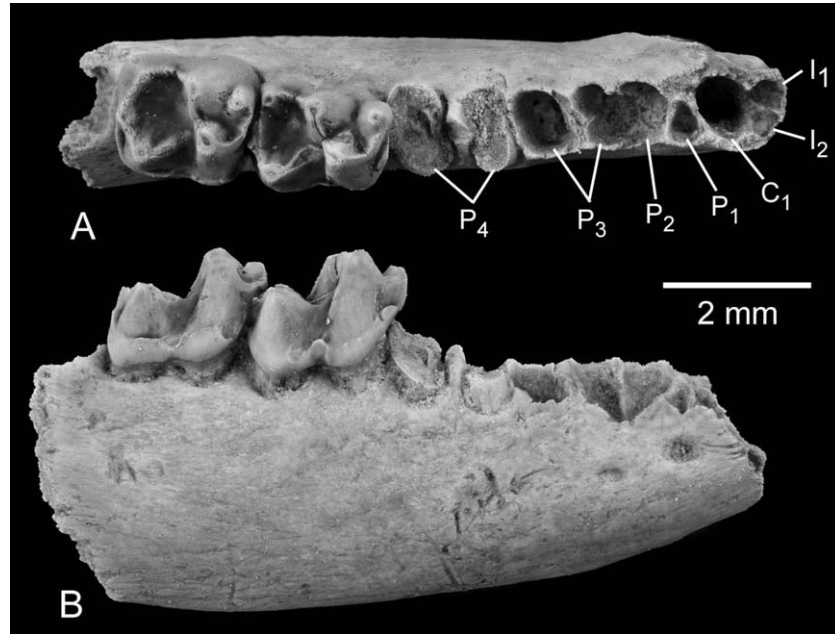
Fig. 4. Lower dentition of *Teilhardina brandti*, UF 254929, right dentary with M_{1-2} and alveoli or roots of I_1-P_4, in occlusal (**A**) and buccal (**B**) views. View in A is slightly oblique, with mesial end tilted upward to show incisor alveoli more clearly. Note presence of small, nearly vertical incisors, moderately large canine, and a small, buccally displaced P_1.

(2006), and the new M_2s are essentially identical to the holotype. Lower molars of *Teilhardina brandti* are characterized by low entoconids, but are variable with regard to expression of buccal cingulids and hypoconulids. They are comparable in length to those of *T. americana* and are longer than molars of *T. belgica*. They are relatively narrower, on average, than molars of *T. americana*, and similar in relative width to those of *T. belgica* (Fig. 6; see also Fig. 14). Body mass estimates based on M_1 area (83.5 g using prosimian regression, 88 g using all primates) are comparable to those generated for *T. americana* (Conroy, 1987).

Dental comparisons

Based mainly on the new fossils, we compared *Teilhardina brandti* with the most primitive species of the genus (*T. asiatica*, *T. belgica*, *T. magnoliana*, and *T. americana*), as well as with *Baataromomys ulaanus* and the basal adapoids *Cantius* and *Donrussellia*. These comparisons are summarized here.

Teilhardina asiatica. The maxillary thickness between the alveolar border and the orbital rim is markedly shallower in *T. brandti* than in *T. asiatica*, which might suggest larger orbits in *T. brandti*. Nevertheless, orbital size in *T. brandti*, to the extent that it can be estimated from the short preserved portion of the orbital rim, appears to be comparable to that in *T. asiatica*.

Ni et al. (2004) considered the dental morphology of *T. asiatica* to be very similar to that of *T. belgica*, but they described M^1 of *T. asiatica* as having a more smoothly curved mesiolingual margin and a more "protuberant" distolingual aspect. These features could be interpreted as derived relative to *T. belgica* (when compared to other *Teilhardina*). In other respects, however, *T. asiatica* is plesiomorphic relative to most or all other species of *Teilhardina*. *T. asiatica* implicitly lacks a nannopithex fold (as *T. americana* was said to differ in having it) and has a weaker buccal cingulum than *T. americana* (Ni et al., 2004). The anterior lower dentition of *T. asiatica* is less compressed than in all other *Teilhardina*, with short diastemata separating the premolars, and a P_1 that is not laterally displaced. The metaconid of P_4 is very low relative to the protoconid. Compared to *T. brandti*, the lower molars of *T. asiatica* are relatively narrower (see Fig. 6) and lower crowned, and both the lower molars and P_4 have slightly more acute cusps. As in *T. brandti* and *T. belgica*, the lower molar entoconids are low, and as in some *T. brandti* the paraconid is distinctly lower than the metaconid.

Teilhardina magnoliana. This species was recently named based on a sample of isolated teeth from Mississippi (Beard, 2008; Beard and Dawson, 2009), which are roughly 10% smaller in linear dimensions than those of *T. brandti*. *T. magnoliana* is said to differ from other species of *Teilhardina* except *T. asiatica* in P_4 morphology and in having lower-crowned molars, and from *T. brandti* and *T. americana* in having relatively narrower molars (Beard, 2008). Only three P_4s are known for *T. magnoliana*, two of which are damaged and now lack the talonid (CM 70439 and 73229); the other one is more complete but abraded (CM 70434). Nevertheless, as the most important tooth for assessing evolutionary stage in *Teilhardina*, they merit attention. CM 73229 is slightly smaller than but otherwise very similar to P_4s of *T. brandti* and *T. belgica*, whereas CM 70434 differs in having a relatively wider trigonid, distinctly higher metaconid, and a more inclined (rather than nearly vertical) preprotocrista (Fig. 7, Table 3). These features contrast with those of P_4 in *T. asiatica* and compare more favorably with the more derived *T. americana* than with *T. brandti* or *T. belgica*. CM 70434 also has a basined talonid, as in one specimen of *T. brandti* (USNM 533554, Fig. 5). Beard (2008) and Beard and Dawson (2009) did not discuss these differences among the P_4s attributed to
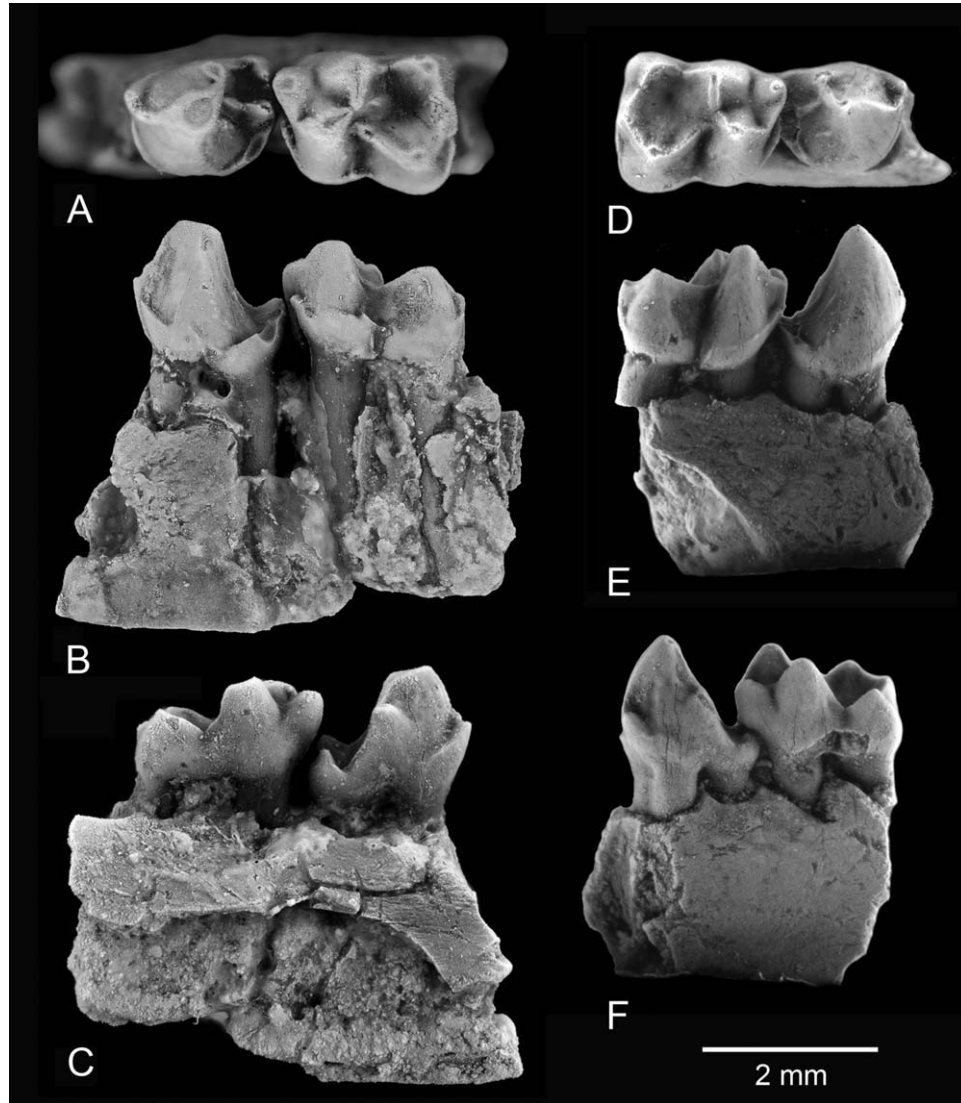
Fig. 5. Dentaries of *Teilhardina brandti* showing variation in P_4. **A–C**, USNM 533554, left dentary with P_4-M_1, in occlusal (A), buccal (B), and lingual (C) views. **D–F**, USNM 493913, right dentary with P_4-M_1, same views. Note larger talonid and metaconid on P_4 and stronger buccal cingulid on P_4-M_1 in USNM 533554.

T. magnoliana. If all three premolars represent *T. magnoliana*, it implies a substantial amount of morphological variation in this tooth in the Tuscahoma species.

T. magnoliana resembles *T. belgica* in its small size (although the holotype M_2 is smaller than in any other species), relatively weak buccal cingulids, and relatively narrow lower molars (Fig. 6; see also Fig. 14). However, their relative narrowness is proportionate to their smaller length, so the molars of *T. magnoliana* are on average only slightly narrower than those of *T. brandti* (M_1W/L = 0.70 in *T. magnoliana* compared to 0.75 in *T. brandti*; M_2W/L = 0.76 in *T. magnoliana* compared to 0.80 in *T. brandti*). Although the lower molars of *T. magnoliana* resemble those of *T. asiatica* in being lower crowned, on average, than both *T. belgica* and *T. brandti*, the latter two species are variable in this regard, with some specimens comparable in brachydonty to *T. magnoliana*.

The upper teeth of *T. magnoliana* are very similar to those of *T. brandti* except for being smaller. The few differences observed are quite subtle. P^4 (CM 77210) is virtually identical to that of *T. brandti* in expression of cingula, parastyle, and orientation and relative size of the two main cusps. However, the P^4 paracone of *T. magnoliana* appears to be taller, and the distal aspect of the protocone is slightly more complex than in *T. brandti*, with a weak postprotocrista and a more lingual crest descending nearly to the base of the protocone; the two crests frame a slightly concave surface on the distal face of the protocone. Both CM 77210 and CM 70433 (which is damaged buccally) have slightly lower pre- and postcingula, barely above the base of the crown. CM 70433 lacks evidence of a postprotocrista.

M^{1-2} of *Teilhardina magnoliana* are represented by nine isolated teeth (M^3 is not known). M^1 is about 10% narrower buccolingually than that of *T. brandti* but otherwise almost identical. It has small conules, a tiny parastyle, and an incipient metastyle. The cingula are similarly developed, but the postcingulum is slightly stronger and extends slightly farther lingually and mesially in *T. magnoliana*. The lingual cingulum is

variable but never strongly developed. Viewed from the lingual side, a nearly complete faint lingual cingulum is discernible in CM 67858 and especially CM 77211, but the cingulum is clearly discontinuous lingually in CM

TABLE 3. P$_4$ metaconid height index in Teilhardina

Species	Spec. no.	Metaconid height index[a]	Mean	Range
T. asiatica	IVPP 7165	0.63		
T. magnoliana	CM 70434	0.74	0.72	0.70–0.74
	CM 73229	0.70		
T. belgica	IRSNB CL192	0.65	0.67	0.62–0.73
	IRSNB CL246	0.66		
	IRSNB CL457	0.66		
	IRSNB M64	0.65		
	IRSNB M4090	0.68		
	IRSNB M4291	0.66		
	IRSNB M4292	0.64		
	IRSNB WL13	0.66		
	IRSNB WL159	0.62		
	IRSNB WL1052	0.69		
	IRSNB WL1062	0.73		
	IRSNB WL1180	0.71		
T. brandti	UF 244454	0.69	0.68	0.60–0.72
	USNM 493913	0.60		
	USNM 525543	0.72		
	USNM 525544	0.70		
	USNM 533554	0.72		
T. americana	UF 244452	0.75	0.75	0.71–0.81
	UM 65770	0.71		
	UM 75160	0.78		
	UM 76600	0.73		
	USGS 3849	0.81		
	USGS 15406	0.76		
	USGS 25324	0.72		
	USNM 539489	0.74		
	UW 7165	0.73		

[a] Metaconid height index = metaconid height 1/protoconid height (character 28).

70422 and CM 70431. Although a nannopithex fold is typically absent in both *T. magnoliana* and *T. brandti*, a weak, incipient fold is present in CM 70431 (M^1), as in M^2 of *T. brandti*, USNM 539467. Compared to *T. brandti*, M^2 of *T. magnoliana* is about 10% narrower and mesiodistally shorter lingually (the protocone is subtly less inflated) but similar in buccal length. It is otherwise identical to that of *T. brandti*. The three known M^{2}s lack both a nannopithex fold and a lingual cingulum.

These comparisons suggest that the upper teeth are virtually identical in the two species and differ in such subtle characters that they probably would not be distinguished if found together. The slightly smaller size of *T. magnoliana* might be related to its lower-latitude occurrence and possibly even warmer conditions along the Gulf Coast than in the continental interior during the early Eocene.

Teilhardina belgica. Smith et al. (2006) considered *Teilhardina brandti* to be very similar to *T. belgica* (Figs. 8A–C and 9A) and distinguished the two only by a few subtle features. *T. brandti* is slightly larger than *T. belgica* (<10%), the crowns of the cheek teeth are slightly more basally inflated (resulting in, on average, slightly greater relative width; see Figs. 6 and 7), and the buccal cingulids are variably stronger. All of these features are derived relative to *T. belgica*. Although *T. brandti* has cheek teeth of comparable length to those of the slightly younger *T. americana* (also from the Willwood Formation of the Bighorn Basin), but narrower, it is plesiomorphic and more like *T. belgica* in having a lower metaconid on P$_4$ (Table 3, Fig. 7), a narrower hypoconulid lobe on M$_3$, and a lower entoconid on M$_{1-2}$. For these reasons Smith et al. (2006) concluded that *T. brandti* is phylogenetically intermediate between *T. belgica* and *T. americana*. The larger sample now available for *T. brandti* shows variation in several traits
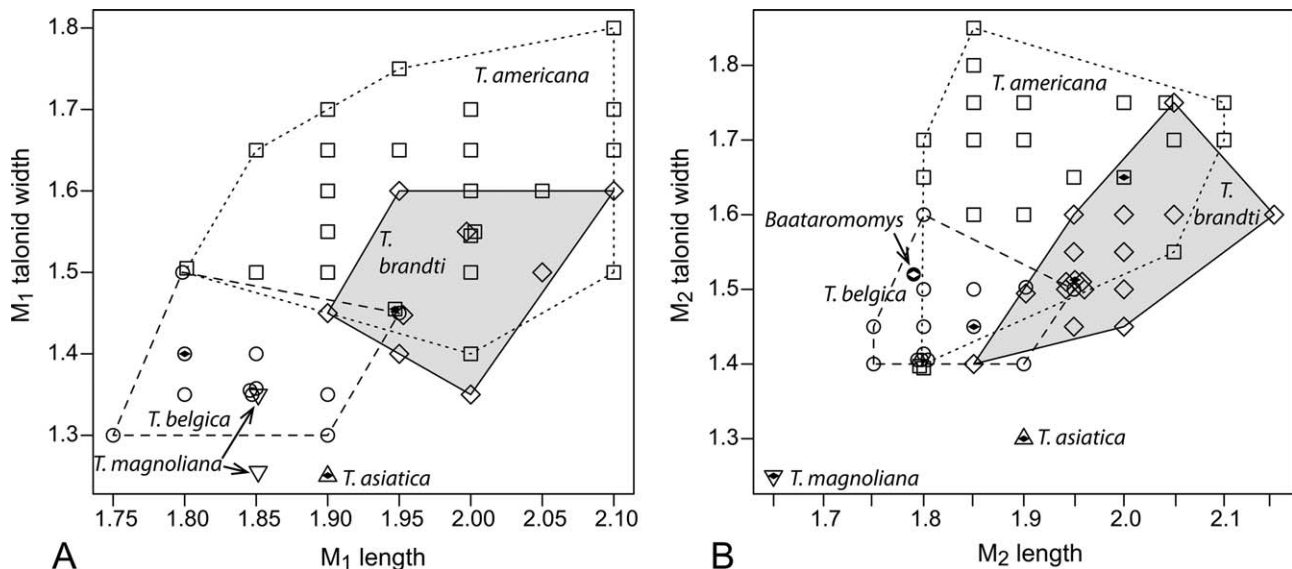
Fig. 6. Lower molar dimensions of *Teilhardina* species. Polygons delimit the observed range of each species (range of *T. brandti* is shaded). Where points appear clustered, all data points represent the same value but are spread apart to illustrate the number of points and species that overlap. Holotypes are indicated by a diamond within the point (lectotype for *T. belgica*). Specimens were measured to 0.05 mm except for *Baataromomys* (nearest 0.01 mm; from Ni et al., 2007). *T. brandti* is similar in molar length to *T. americana*, but its talonid width is intermediate between *T. belgica* and *T. americana*.
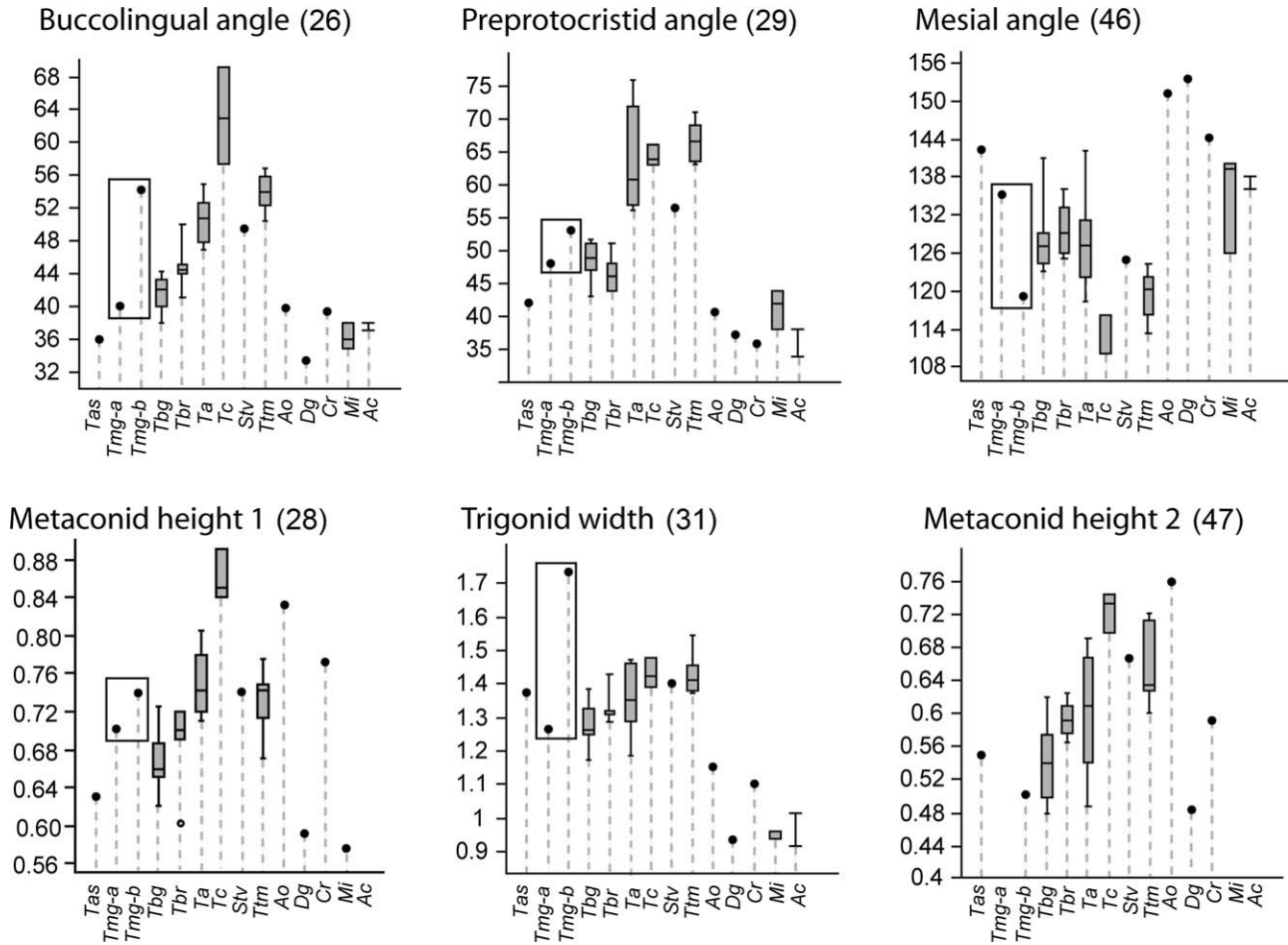
Fig. 7. Box plots for six shape variables of P_4 in *Teilhardina* and other primitive euprimates. Variable numbers correspond to character list in Appendix B. Single specimen positions are indicated by black circles. Two specimens for a taxon sample are indicated by two horizontal lines connected by a vertical line. For larger samples the observed range is shown by a solid line, while shaded boxes encompass 50% of the data points and a horizontal line indicates the median. Units for angles are degrees. Abbreviations: *Tas, Teilhardina asiatica; Tmg-a, T. magnoliana* CM 73229; *Tmg-b, T. magnoliana* CM 70434; *Tbg, T. belgica; Tbr, T. brandti; Ta, T. americana; Tc, T. crassidens; Stv, Steinius vespertinus; Ttm, Tetonius matthewi; Ao, Altanius orlovi; Dg, Donrussellia gallica; Cr, Cantius ralstoni; Mi, Marcgodinotius indicus; Ac, Asiadapis cambayensis*. See Methods for description of measurements, and Table 3 and Appendix D for variable values and specimen numbers.

(e.g., strength of hypoconulids and buccal cingulids, relative hypsodonty, crown width) that support this phylogenetic position. In certain other traits, variation has been observed in *T. belgica* (Gingerich, 1977) that overlaps the condition in *T. brandti*. For example, P_1 in *T. belgica* is small and laterally placed in the lectotype (IRSNB M64) and in IRSNB CL188, as in *T. brandti* (UF 254929), but it is somewhat larger and more centrally located in IRSNB M4296, and apparently absent in RS DIII467. The lower canine in *T. belgica* ranges from much larger than that of *T. brandti* (in the lectotype) to being comparable in size to that of *T. brandti* in IRSNB M4296 and RS DIII467. Judging from partial alveoli, the lectotype of *T. belgica* (like *T. brandti*) appears to have had small incisors (Gingerich, 1977), but their relative size and orientation are ambiguous.

Upper teeth of *T. brandti* (except for UF 244460) are virtually identical to those of *T. belgica*, except for being slightly larger. In the two available specimens of upper teeth of *T. belgica* (IRSNB WL 1299 and WL 1398) the precingulum extends slightly farther lingually than in *T. brandti*, but no other differences were observed.

Teilhardina americana. The lower canine in the holotype of *T. americana* (Fig. 8D–F) has a root of similar size to that of *T. brandti*; lower incisors of *T. americana* are unknown. P_1 is variably present in *T. americana* (see Bown and Rose, 1987); when present it is consistently very small and laterally displaced. The lower cheek teeth of *Teilhardina americana* are similar in length to those of *T. brandti* but are slightly wider (see Fig. 6). *T. americana* further differs from *T. brandti* in having a higher metaconid on P_4 (Table 3, Fig. 7), taller molar entoconids, and typically stronger cingulids and weaker hypoconulids. M_3 tends to be less reduced and to have a larger hypoconulid lobe. Upper molars of *T. americana* are derived relative to *T. brandti* in having a weak nannopithex fold and, often, a small hypocone (Figs. 3D,E, 9B). A lingual cingulum is present though variably developed, and the enamel tends to be weakly crenulated. These derived features relative to *T. brandti*, together with presence of *T. brandti* in immediately underlying strata, support direct descent of *T. americana* from *T. brandti*.

Teilhardina crassidens occurs in strata above those that yield *T. americana* and has been interpreted as a
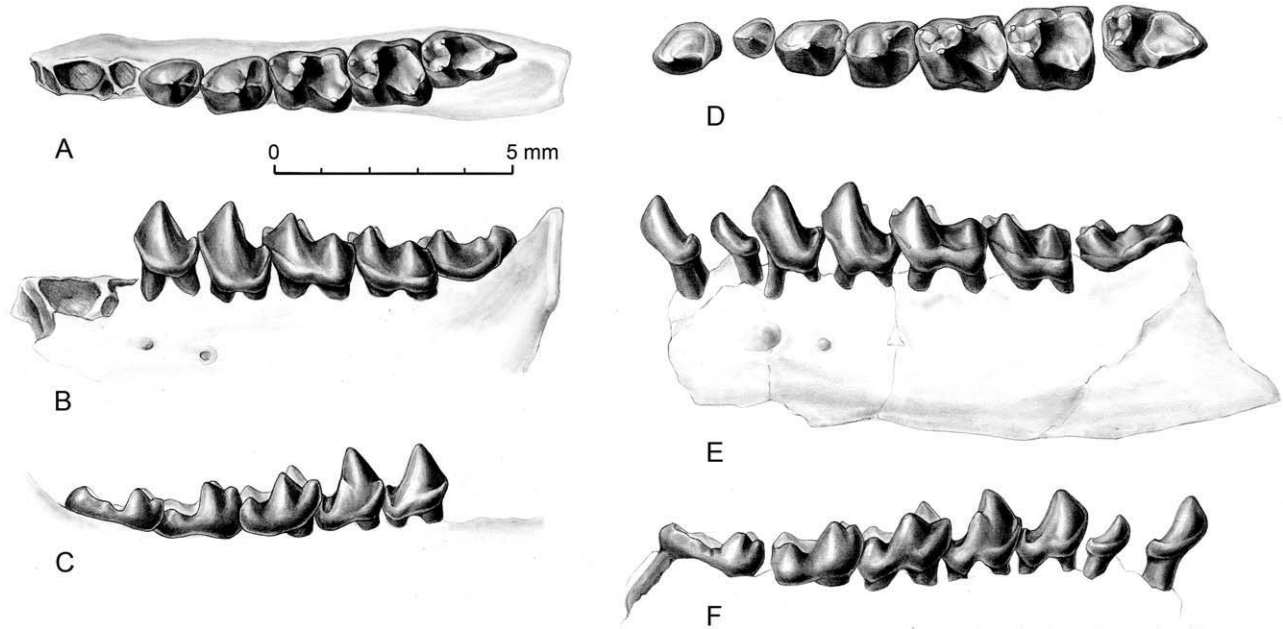
Fig. 8. Lower dentition of (**A–C**) *Teilhardina belgica*, lectotype, IRSNB M64, left P_3-M_3 and anterior alveoli, and (**D–F**) *T. americana*, holotype, UW 6896, left C_1-M_3. D–F from Bown and Rose (1987). Note that *T. americana* has relatively broader cheek teeth and a higher metaconid on P_4 compared to *T. belgica*.

direct descendant of *T. americana* (Bown and Rose, 1987). *T. crassidens* is more derived than *T. americana* in consistently lacking P_1 and having relatively wider and more inflated cheek teeth (see Fig. 14) and a more molarized P_4 with a higher metaconid, features contrasting with *T. brandti*. The younger species *T. tenuicula* and *T. demissa* remain rare and poorly understood. They differ from *T. brandti* in having relatively broad, low-crowned P_{3-4}, with mesiodistally extended trigonids and higher metaconids (Bown and Rose, 1987; Rose, 1995).

Baataromomys ulaanus. Ni et al. (2007) described this new omomyid based on an isolated M_2 from the Bumbanian (early Eocene) of Inner Mongolia, China. They showed that M_2s of *B. ulaanus* and *Teilhardina brandti* (which they assigned to *Baataromomys*) are intermediate in size and proportions between Old World *T. asiatica* and *T. belgica*, on the one hand, and other North American *Teilhardina* on the other (see Fig. 6 herein). *Baataromomys* was said to differ from *Teilhardina* (including North American species other than *T. brandti*) "in having a smaller paraconid that is more closely appressed to the metaconid, and a relatively lower hypoconid and cristid obliqua," and to differ further from North American *Teilhardina* "in having a lower entoconid, a much weaker crest connecting the entoconid with the metaconid, and a weaker buccal cingulid" (Ni et al., 2007: p 3).

Based on our analysis, when intraspecific variation is taken into account, none of these features seems to separate *Baataromomys* from *Teilhardina*, nor do they support a special relationship between *B. ulaanus* and *T. brandti*. Comparison of multiple specimens of *T. belgica*, *T. brandti*, *T. magnoliana*, and *T. americana* indicate that molar paraconid height and position relative to the metaconid are variable in *T. brandti*, with most specimens closely approximating *T. belgica* and *T. asiatica* in paraconid expression. Our comparisons revealed no significant differences in height of the hypoconid or cristid

obliqua, although *T. americana* and *T. crassidens* tend to be relatively slightly higher crowned. We agree that *B. ulaanus* and, to a greater extent, *T. brandti*, differ from *T. americana* and *T. crassidens* in having a lower entoconid, but this feature is shared with *T. belgica* and *T. asiatica* and may be plesiomorphic for *Teilhardina*. The metaconid and entoconid are not truly connected by a crest because the talonid notch intervenes; but to the extent that crests can be compared on the lingual side of M_2, again we found no significant differences between *T. brandti* and *T. belgica*. Development of the buccal cingulids is variable in *Teilhardina*, particularly so in *T. brandti*, with some specimens having weak or absent cingula as in *T. belgica* and others having moderate or strong cingula as in *T. americana* and *T. crassidens* (see Fig. 5). These comparisons support retention of *T. brandti* in *Teilhardina*, and call into question the generic distinction of *Baataromomys*.

Primitive adapoids. Compared to Wasatchian *Cantius*, the oldest and most primitive North American adapoid, *Teilhardina brandti* already exhibits the omomyid hallmark of mesiodistal compression of the dentition. Although its primitive euprimate dental formula is the same as that of *Cantius* (2.1.4.3), the antemolar dentition is conspicuously compacted relative to that of *Cantius*. The small incisors of *T. brandti* appear to have been more vertically implanted, with I_1 slightly larger than and medial to I_2. The lower canine is relatively smaller than that of *Cantius*. The premolars of *T. brandti* are especially crowded together, with both P_1 and P_2 single-rooted, P_1 reduced and displaced laterally, and no diastemata between any adjacent antemolar teeth. In contrast, *Cantius* typically has mesiodistally extended premolars, short diastemata between anterior premolars, P_1 not laterally displaced, and a two-rooted P_2 (except in Wa-0 *C. torresi*, in which the root is bilobed). In *Cantius abditus* I_1 is smaller than I_2 and the
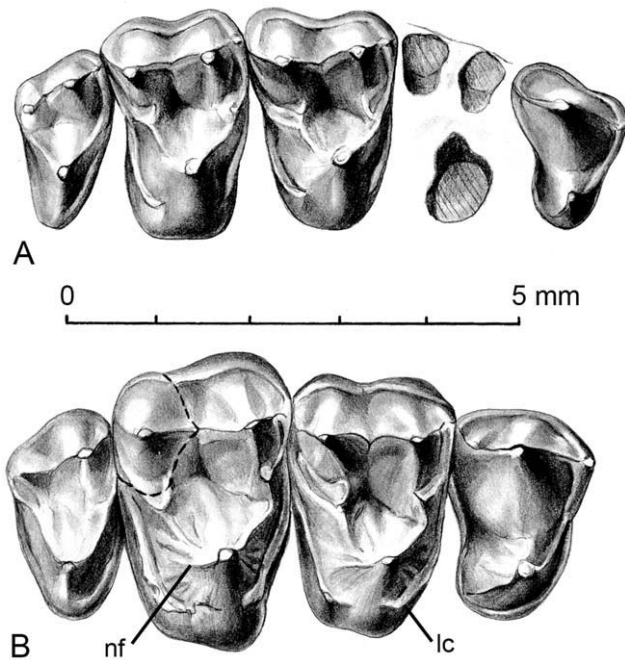
Fig. 9. Upper dentition of (**A**) *Teilhardina belgica*, IRSNB WL 1398, right P^3, M^{1-3}, and (**B**) *T. americana*, UW 8871, right P^4-M^3 (M^3 restored from UW 8961). B from Bown and Rose (1987). lc, lingual cingulum; nf, nannopithex fold. *T. americana* is larger than *T. belgica* and further differs in having crenulated enamel, a nannopithex fold, and a variably developed lingual cingulum.

incisors are anteriorly inclined at about 45° (Rose et al., 1999).

European *Donrussellia*, usually considered the most primitive adapoid, had a two-rooted, unreduced P_2 (Godinot, 1978). P_2 was also two-rooted in the asiadapine *Marcgodinotius*, the most primitive Asian adapoid (Rose et al., 2009). Both *Donrussellia* and *Marcgodinotius* have uncompressed antemolar dentitions and relatively larger lower canines than in *T. brandti*. These observations suggest that an uncompressed antemolar dentition with a relatively large canine and unreduced, two-rooted P_2 is primitive for adapoids. The metaconid on P_4 is very low in *Donrussellia* and asiadapines (when present), but relatively high in *Cantius*. The low paraconid in the most primitive *Teilhardina* species suggests that the plesiomorphic euprimate condition was a low paraconid on P_4.

Postcrania

Talus. The talus of *Teilhardina brandti* is represented by two incomplete specimens (USNM 539577 and USNM 504329; Fig. 10A–E). USNM 539577 consists of a complete but damaged body and the lateral border of the head and neck, whereas USNM 504329 is a well-preserved astragalar body. As in other omomyids and *T. belgica*, the trochlear rims are parallel and sharp and the trochlea is shallowly grooved (Simpson, 1940; Godinot and Dagosto, 1983; Dagosto, 1988, 1993; Gebo, 1988; Covert and Hamrick, 1993; Anemone and Covert, 2000; Dunn et al., 2006). The medial malleolar surface is vertical. The lateral malleolar surface (fibular facet) is vertical superiorly and flares laterally plantarly, identical to the condition in *T. belgica* and similar to that in other omomyids. Specifically, the angle between the fibular

facet and the trochlea (= lateral tibial facet) measures 108 degrees (see measurement methods in Boyer et al., 2010). This is similar to values measured by Boyer et al. for *Hemiacodon gracilis* (107) and *Tarsius syrichta* (106). Anthropoids measured by Boyer et al. exhibit a more strongly vertical facet (96–102), while strepsirrhines and adapoids have more sloping facets (109–121). There is a large, deep fossa just dorsal to the ectal facet and posterior to the fibular facet, probably for attachment of the posterior talo-fibular ligament. The posterior shelf of the trochlea is moderately developed, similar to the condition in *T. belgica* (Szalay, 1976; Gebo, 1988). The ectal facet is tightly curved. The fragmentary talar neck and head of USNM 539577 indicate that the neck was long. The proximal aspect of the neck preserves a bony ridge delimiting the distal margin of a squatting facet for articulation with the distal tibia. This feature is common in omomyids (e.g., Simpson, 1940; Covert and Hamrick, 1993; Dunn, 2010).

Measurements (mm)—USNM 539577, body length: 2.40; estimated total length: 4.50; trochlear width: 1.90; total width: 2.50; ectal facet length: 1.60. USNM 504329, body length: 2.50; trochlear width: 1.90; total width: 2.55; ectal facet length: 1.60.

Navicular. The navicular (USNM 542002, Fig. 10F–H) resembles those of cheirogaleids and omomyids in being longer than wide (Simpson, 1940; Gebo, 1988; Dagosto, 1993; Anemone and Covert, 2000; Dunn et al., 2006; Dunn, 2010). The navicular index (length/distal width × 100) is 165—slightly below the range of extant cheirogaleids (166–295), slightly above the range for larger-bodied Malagasy strepsirrhines (66–162), and well above the range seen in modern platyrrhines (61–95). The navicular is significantly longer than that of *Cantius* (129) and *Notharctus* (110) but slightly shorter than that of other known omomyids (*Hemiacodon* = 176–190; *Ourayia* = 181–189; *Chipetaia* = 226), and significantly less elongate than that of extant galagos (288–528) and tarsiers (434–626; ratios from Dunn, 2010). The proximal end is concave for articulation with the navicular facet of the talar head, with the medial side extending farther proximally than the lateral side. The distal end is relatively flat, lacking the expanded, bulbous articulations for the cuneiforms that are seen in galagos and tarsiers and more resembling the condition in other omomyids, adapids and strepsirrhines (Gebo, 1987; Dunn et al., 2006). The facet for the entocuneiform projects slightly more distally and is convex. A faint ridge is discernible separating the flat facet for the mesocuneiform from the slightly concave facet for the ectocuneiform.

Measurements (mm)—length: 3.80; distal width: 2.30.

Terminal phalanges. We attribute three isolated terminal phalanges (USNM 521825, 540587, and 542001; Fig. 11) to *Teilhardina brandti* based on their small size and distinctive euprimate morphology. The evolution of flat nails and expanded tactile pads (also called apical pads) on the tips of all digits is characteristic of euprimates and is widely considered a synapomorphy of the group (e.g., Clark, 1959; Cartmill, 1979, 1992; Dagosto, 1988, Hamrick, 1998; Soligo and Müller, 1999). This results in a unique morphology of the terminal phalanx in euprimates: the bone is flattened dorsoventrally and the tip is expanded mediolaterally. The expanded tip serves as the attachment for the flat nail dorsally and the tactile pad ventrally, and is often called the "apical tuft" (Hamrick, 1998, 2001; Mittra et al., 2007). The three
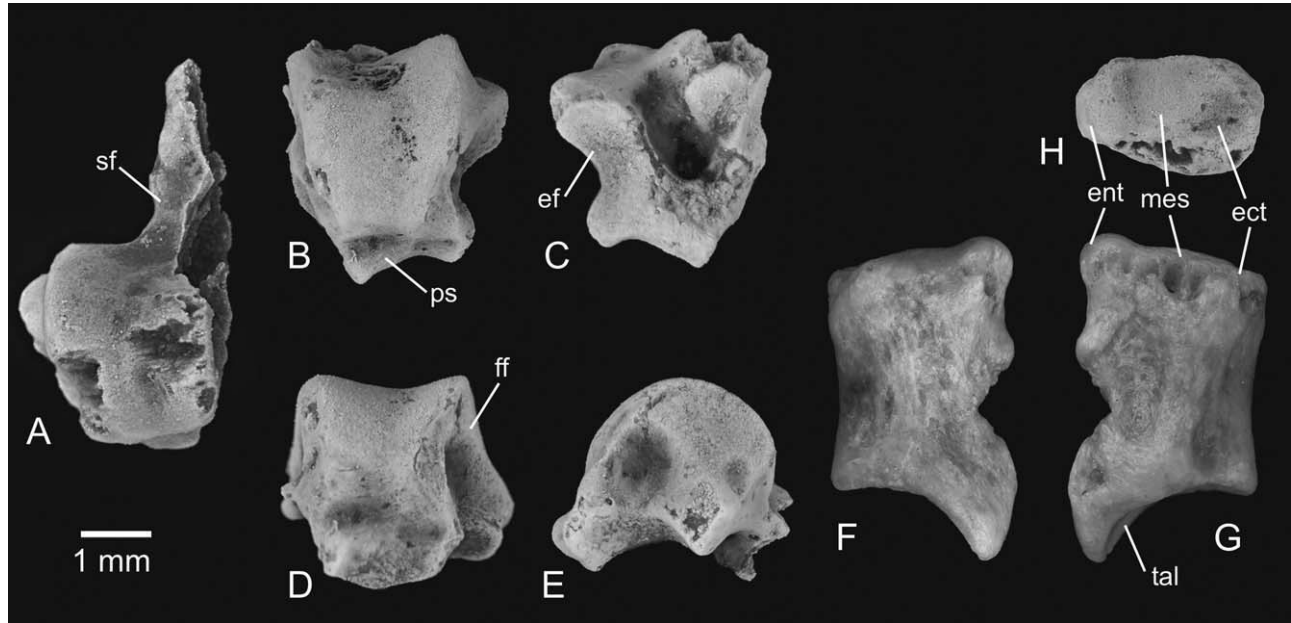
Fig. 10. Tarsal bones of *Teilhardina brandti*. **A**, USNM 539577, left talus in dorsal view (neck and head damaged). **B–E**, USNM 504329, right talar body in dorsal (B), plantar (C), posterior (D), and lateral (E) views. **F–H**, USNM 542002, left navicular in dorsal (F), plantar (G), and distal (H) views. Note relatively elongate navicular and talar neck. ect, facet for ectocuneiform; ef, ectal facet; ent, facet for entocuneiform; ff, fibular facet; mes, facet for mesocuneiform; ps, posterior shelf; ptfl, posterior talofibular ligament; sf, squatting facet; tal, facet for talar head.

terminal phalanges reported here, which are the first known for *Teilhardina*, clearly exhibit an expanded apical tuft, indicating the presence of flat nails rather than claws. Differences in length and morphology—one is noticeably larger than the other two—probably indicate either that they are from different appendages (manus and pes), from different digits (hallux/pollex and lateral digits), or both. All have small nutrient foramina on the dorsal surface but no evident foramina on the volar surface.

The larger phalanx (USNM 542001) is more robust, being wider in all dimensions than the smaller ones. The tip of the phalanx is "arrow-shaped" in dorsal view, pointed at the apex with relatively straight sides rather than having a more generally rounded outline. One of the sides projects farther proximally than the other, making the apex appear asymmetrical. There are several nutrient foramina present on the apex of the phalanx. In distal view, the dorsal and ventral surfaces of the apical tuft are separated by a groove that continues from the apex of the phalanx proximally up the shaft and terminates before contact with the base. The shaft increases in width proximally; the base is significantly wider than the tip despite one side being broken. On the unbroken side there is a disto-laterally projecting flange of bone, probably for the insertion of the interosseus ligament. The extensor tubercle is well-developed. The sulcus for insertion of the deep flexor tendon on the ventral surface of the base is large and well-defined.

The smaller phalanges (USNM 521825, 540587) are more slender and more symmetrical than the larger one, having a more rounded apical region, a shaft of more uniform width, and a less expanded base. The extensor tubercle on the dorsal surface of the base is well-developed, but there is not a clearly defined flexor sulcus on the ventral surface. Distally, there is a faint ridge on the

ventral surface of the outer edge of the expanded tip of the phalanx. In lateral view both phalanges are dorso-ventrally compressed, with a deeper base and tapering distally. This contrasts with the larger phalanx, which is more uniform in thickness.

The larger size, asymmetry, large flexor sulcus, and robust nature of the larger phalanx suggest that it may represent the terminal hallucal phalanx, as this is usually the largest and most robust ungual in extant primates and is often significantly larger in size than the others (Koenigswald, 1979; Godinot and Beard, 1991; Mittra et al., 2007). The smaller phalanges probably represent lateral digits either from the manus or pes. It has been suggested that terminal pedal phalanges have broader apical ends than those from the manus because feet have more morphological specializations for grasping (Godinot and Beard, 1991). However, a recent study indicated that there is no difference in shape between the terminal phalanges of the lateral digits in the manus and pes of extant prosimian primates (Mittra et al., 2007). In the Bridgerian adapoid *Notharctus*, the apical tufts of the terminal phalanges of manual digits III–V are slightly narrower than those of digits I and II (Hamrick and Alexander, 1996). The breadth of the apical tuft also varies by taxon, being more expanded in *Cantius* and *Europolemur* than in *Smilodectes* and *Adapis* (Covert, 1988; Godinot and Beard, 1991; Godinot, 1992). These observations further complicate the issue of allocating isolated phalanges to fore- or hind limbs. Compared to Bridgerian omomyid phalanges figured by Dagosto (1988), the small Wa-0 phalanges are narrower, with a less-expanded apical region, but this difference might be due to a more derived morphology in the Bridgerian taxa. The terminal phalanges of *Teilhardina brandti* differ from those of the adapoids for which lateral views of the unguals are known
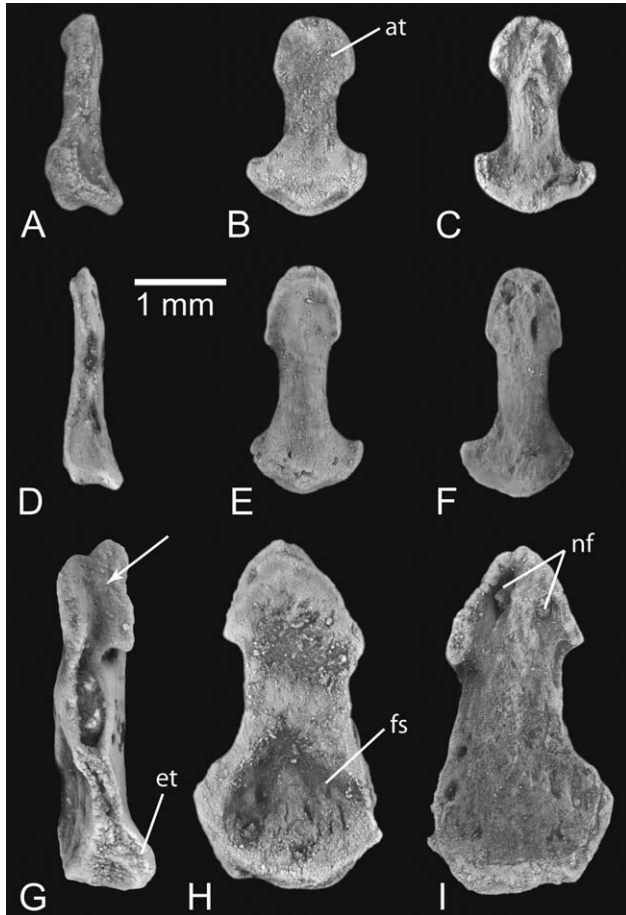
Fig. 11. Distal phalanges of cf. *Teilhardina brandti* in lateral (**A**, **D**, **G**), palmar (**B**, **E**, **H**), and dorsal (**C**, **F**, **I**) views. A-C, USNM 540587; D-F, USNM 521825; G-H, USNM 542001. at, apical tuft; et, extensor tubercle; fs, flexor sulcus; nf, nutrient foramina. Arrow indicates lateral groove.

(*Europolemur*, *Adapis*, *Smilodectes*, and possibly also *Darwinius*) in being flatter dorsoventrally (Koenigswald, 1979; Godinot and Beard, 1991; Godinot, 1992; Franzen et al., 2009). The groove on the tip of the larger phalanx has not been described in other fossil or extant primates, but is indicated in illustrations of adapid and omomyid phalanges (Koenigswald, 1979; Dagosto, 1988). Occurrence of the groove appears to be variable, and soft tissue correlates of this groove are unclear (Dagosto, personal communication).

Measurements (mm)—USNM 540587, $L = 1.60$, proximal $W = 1.10$, apical $W = 0.70$; USNM 521825, $L = 2.00$, proximal $W = 0.95$, apical $W = 0.70$; USNM 542001, $L = 3.10$; apical $W = 1.2$.

RESULTS

Principal coordinates analysis of P$_4$

Principal coordinates analysis of P$_4$ variables resulted in 88% of the sample variance being captured by the first two coordinates (see Fig. 12). Coordinate 1 accounts for 78% of the sample variance. Adapoids and omomyids form separate clusters distinguished by their coordinate

1 values. *Purgatorius*, *Palaechthon*, and *Altanius* are outside of the morphospace defined by omomyids and adapoids, with *Altanius* essentially morphologically intermediate between the latter two clusters. Primitive members of the *Teilhardina* clade (*T. asiatica* and *T. belgica*) are closer morphologically to the plesiadapiforms, adapoids, and *Altanius* than are other *Teilhardina* species. While *T. asiatica* is outside of the *T. belgica* cluster, its morphology is not obviously "more basal" according to this phenetic analysis, as some specimens of *T. belgica* are closer to the outgroup taxa than is *T. asiatica*. The two measurable specimens of *T. magnoliana* occupy very different regions of the morphospace. The fragmentary CM 73229 is within the cluster defined by *T. belgica*, consistent with the hypothesis that *T. magnoliana* is a relatively basal member of the clade (Beard, 2008). However, CM 70434 plots as an outlier to the *Teilhardina* cluster, which we find telling given its qualitatively unusual appearance.

Phylogenetic analysis

Two most parsimonious trees were recovered with a tree length of 169 steps, CI of 0.663, and RI of 0.558 (calculated in PAUP). Tree topology is identical for these trees except for the placement of *Teilhardina asiatica* and *T. magnoliana*. In the first most parsimonious tree, *Teilhardina asiatica* is the most basal species of *Teilhardina* (as in previous phylogenetic analyses: Ni et al., 2004; Smith et al., 2006; Beard, 2008) and is the sister taxon to a clade consisting of all other omomyids in the analysis; *T. magnoliana* + *T. belgica* are sister taxa and together form a clade that is sister to the other omomyids (Fig. 13A). *T. asiatica* and *T. magnoliana* switch positions in the other most parsimonious tree (Fig. 13B). In both trees *T. brandti* is more derived than *T. asiatica*, *T. belgica*, and *T. magnoliana*, and less derived than *T. americana*. A strict consensus (Fig. 13C) results in a polytomy at node 5, consisting of *T. asiatica*, *T. belgica*, *T. magnoliana*, and a clade consisting of remaining omomyids, in which *T. brandti* is most primitive. Character support for each node is listed in Figure 13C.

Our results, like other recent analyses of *Teilhardina* (Smith et al., 2006; Beard, 2008; Tornow, 2008), suggest that *Teilhardina* is paraphyletic (see also Rose and Bown, 1993) or possibly even polyphyletic. This is perhaps not surprising considering its basal position among omomyids. These possibilities should be further explored in future phylogenetic analyses of primitive euprimates.

DISCUSSION

Teilhardina brandti is the oldest and most primitive omomyid for which incisor alveoli are adequately preserved to enable a judgment of their relative size and orientation. The incisors were unequivocally small, with essentially vertical roots. Although I$_1$ was slightly larger than I$_2$, it was neither procumbent nor enlarged like I$_1$ in North American *Teilhardina crassidens, T. americana-T. crassidens* intermediates, *T. demissa*, *Anemorhysis*, *Tetonius*, *Pseudotetonius*, and *Steinius*. Early Eocene *Altanius orlovi* shows similar compression of antemolar teeth, but it has a two-rooted P$_2$ and apparently had small anteriorly inclined incisors whose alveoli are about equal in size. The incisors of *Donrussellia* are unknown, but the adapoid *Cantius* has uncompressed antemolar teeth and

Fig. 12. Plot of principal coordinates 1 and 2 resulting from principal coordinates analysis of four variables of P₄ morphology (buccolingual angle, mesial angle, preprotocristid verticality angle, trigonid width index). See Methods and Results for further explanation and Appendix D for values used. Numbered groups are: 1, omomyids; 2, notharctids; 3, asiadapines; 4, *Teilhardina belgica*; 5, *Teilhardina brandti*; 6, *Teilhardina americana*; 7, *Teilhardina crassidens*; 8, *Tetonius matthewi*. Note that *Teilhardina asiatica*, *T. belgica*, and one specimen of *T. magnoliana* plot closer to the region including plesiadapiforms and notharctids, consistent with cladistic results and previously described morphoclines indicating that these forms are more basal.

small, strongly inclined incisors, with I_2 larger than I_1. These observations provide evidence that the plesiomorphic condition in euprimates was to have small incisors, but their orientation is still uncertain. Hypertrophy of I_1 in various omomyids was, therefore, a derived condition.

The *Teilhardina brandti* sample described here, in comparison with other primitive euprimates, provides further evidence that the following character states are plesiomorphic for Omomyidae and probably euprimates as well: four premolars including P_1 that is not laterally displaced; P_4 with small and low paraconid and metaconid; simple upper molars in which the hypocone and nannopithex fold are absent and the lingual cingulum is incomplete, and smooth enamel. Uncompressed antemolar dentition including an unreduced canine and a two-rooted P_2 are probably also primitive for euprimates.

Comparison of the postcanine teeth among species of *Teilhardina* indicates that *T. brandti* is morphologically intermediate between *T. belgica* and *T. americana*, and belongs in the genus *Teilhardina*. While its molar size more closely approximates that of *T. americana*, many features of the lower cheek teeth, including metaconid height of P_4 and proportions of M_1, are more similar to *T. belgica* than to *T. americana* or are intermediate between the two species (Figs. 6 and 14, Table 3). The upper teeth are also more similar morphologically to those of *T. belgica* than to those of *T. americana*, although one specimen (UF 244460) shows features more typical of *T. americana* (crenulation, a lingual cingulum,

and a weak nannopithex fold), suggesting a transitional stage. An alternative interpretation of this specimen is that it indicates the presence of *T. americana* in addition to *T. brandti* during the PETM; however, it is very improbable that two so similar species coexisted at that time, when all other evidence suggests they are segments of the same anagenetic lineage.

The isolated foot bones we attribute to *Teilhardina brandti* are among the oldest known for Euprimates. The terminal phalanges, which are also the smallest known for Euprimates, attest to the presence of nails rather than claws and support the hypothesis that nails were present in the last common ancestor of living euprimates (Soligo and Müller, 1999). However, the diminutive size of *T. brandti* and other basal euprimates is inconsistent with Soligo and Müller's contention that nails arose in association with an increase in body size early in the evolution of Euprimates (see also Gebo, 2004, who argued that the ancestral euprimate must have been very small, and Bloch et al., 2007, and Sargis et al., 2007, who argued that nails evolved in the common ancestor of plesiadapoids and Euprimates). The relative elongation of the navicular compared to that of notharctids, and the long, straight talar neck, are evidence that very early in their history omomyids were already more specialized for active arboreal locomotion than were notharctids.

The cladistic analysis presented here is the most comprehensive attempt to resolve interrelationships among
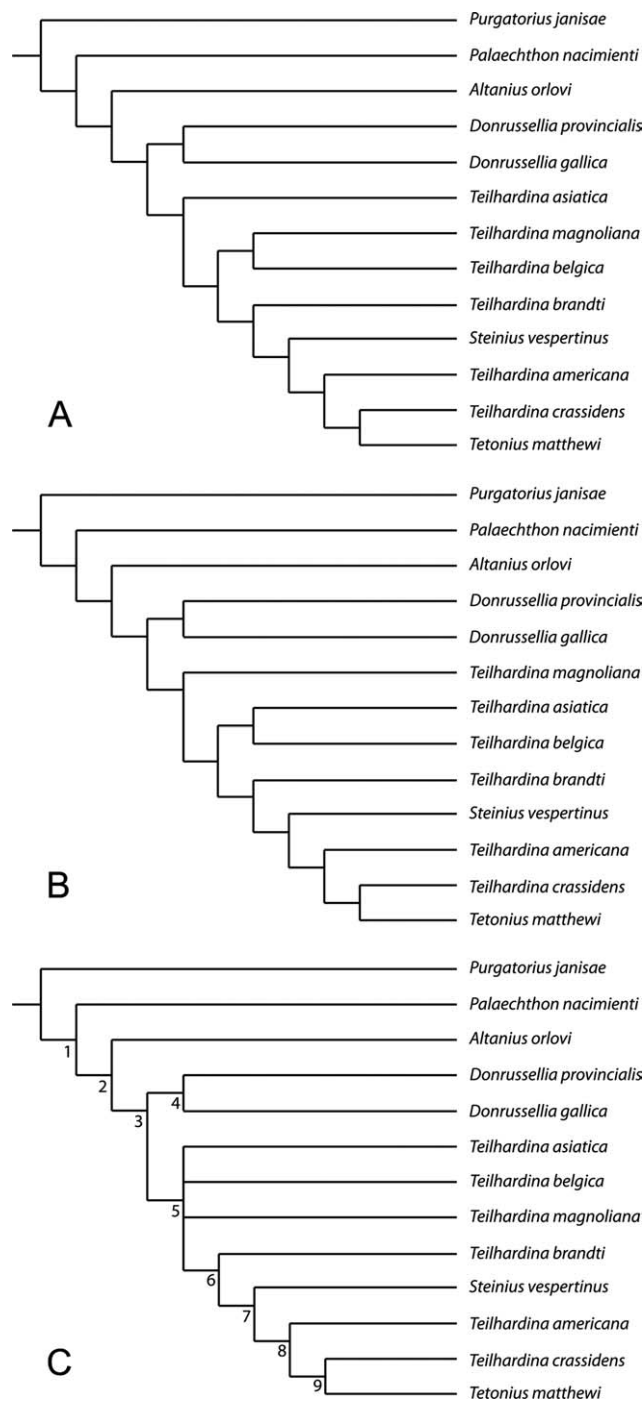
Fig. 13. Results from cladistic analysis of 47 characters and 13 taxa (see Appendix). **A**, One of two most parsimonious trees resulting from branch and bound search using unordered characters; tree length: 169. **B**, Second of two most parsimonious trees. **C**, Strict consensus of the two most parsimonious trees. Unambiguous synapomorphies, with superscript R indicating instances of reversal: Node 1, 3(1), 8(1), 15(1), 17(1), 33(1), 38(3), 42(1); Node 2, 4(1), 5(1), 16(1), 45(1); Node 3, 10(1), 28(2), 37(2), 38(2); Node 4, 12(2), 30(2), 43(1); Node 5, 31(1), 42(0)[R]; Node 6, 11(1), 28(1); Node 7, 3(0) [R], 18(0) [R], 29(2), 37(1), 45(0) [R]; Node 8, 1(1), 20(1), 21(1); Node 9, 22(2), 26(2), 29(3), 46(2).

species of *Teilhardina* to date. It incorporates upper tooth characters for the first time, as well as additional characters of the lower dentition, some of which quantify previous qualitative observations. Postcranial traits were excluded because they are still much too poorly known to be informative within *Teilhardina*. Strict consensus of the two most parsimonious trees results in a polytomy among the most basal species of *Teilhardina*, whereas the two most parsimonious trees recover either *T. asiatica* or *T. magnoliana* as the most basally divergent species of *Teilhardina*. Previous cladistic analyses have also resulted in *T. asiatica* as the most basally divergent species of *Teilhardina* (e.g., Ni et al., 2004; Smith et al., 2006; Beard, 2008). Morphological features of *T. asiatica*, such as the less-reduced P_1 relative to other species of *Teilhardina*, suggest that this is the most primitive species known (e.g., Ni et al., 2004). Although features of the anterior dentition cannot be assessed for *T. magnoliana*, the only other cladistic analysis that incorporated *T. magnoliana* and *T. asiatica* supported *T. asiatica* as more basally divergent (Beard, 2008). Consequently, we regard the topology of the first most parsimonious tree (Fig. 13A), with *T. asiatica* basal, as the most likely arrangement based on present evidence.

Carbon isotope stratigraphy suggests that the relative ages of *T. asiatica*, *T. belgica*, and *T. brandti* are sequential and that all were restricted to the PETM. Based on this evidence and stage of evolution, Smith et al. (2006) hypothesized that *Teilhardina* originated in Asia and dispersed westward, successively to Europe and then to North America. Beard (2008), however, used sequence stratigraphy to argue that *Teilhardina magnoliana*, from the uppermost Tuscahoma Formation Red Hot local fauna of Mississippi, predated both *T. brandti* from the Bighorn Basin and *T. belgica* from the Tienen Formation at Dormaal, Belgium. On the basis of this inference, he postulated that dispersal was in the opposite direction—from Asia to North America (Gulf Coast) at the beginning of the PETM, and from there northward to Wyoming and eastward to Europe. He bolstered his proposal by citing various mammalian species in the Red Hot fauna that resemble species from the very short Wa-M biozone that immediately underlies Wa-0 in the Bighorn Basin. However, most of the taxa in the Red Hot fauna that are comparable to Bighorn Basin taxa, including the rodent *Tuscahomys* (one of the two taxa Beard mentioned), are similar to species known from throughout the Wa-0 interval. One Tuscahoma species considered particularly suggestive of a close correspondence with the Wa-M biozone is the tiny condylarth *Haplomylus meridionalis* (Beard and Dawson, 2009), which was compared to a species (*H. zalmouti*) known only from Wa-M in the Bighorn Basin. However, Gingerich (2010) showed that *H. meridionalis* is much closer in size to early Wasatchian *H. speirianus*, suggesting on this basis that *H. meridionalis* is more comparable to Wa-1 species.

The Red Hot local fauna comes from a vertebrate lag at the top of the Tuscahoma Formation immediately below the Wasatchian Bashi Formation, and recent studies of pollen and foraminifera suggest that the vertebrate lag dates from later rather than earlier in the PETM (Harrington, 2003; Fluegeman, 2009). The conclusion that the Red Hot local fauna dates from well after the beginning of the PETM also appears to be supported by sedimentary evidence from a recent core taken near the site, which found the Paleocene–Eocene boundary to be 30 feet below the vertebrate lag (Dockery and
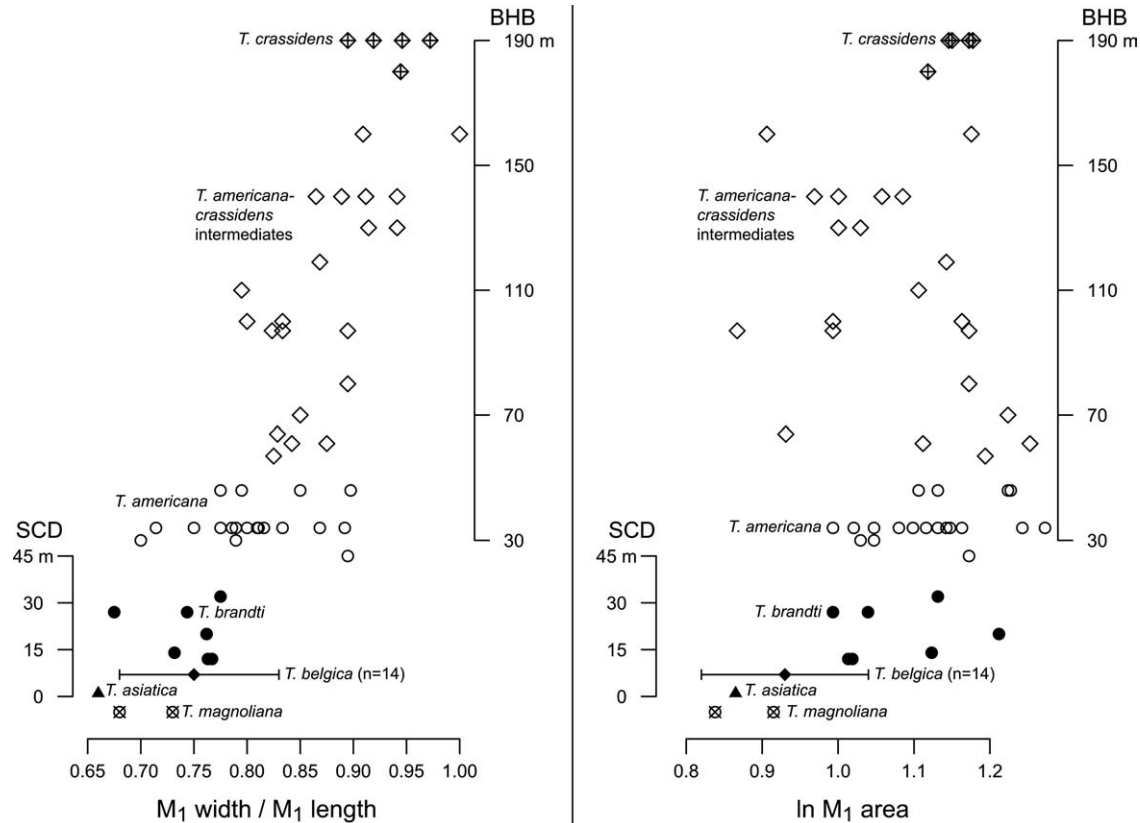
Fig. 14. Proportions and size (ln area) of M_1 in *Teilhardina* in the lower Willwood Formation of the Bighorn Basin, Wyoming. Stratigraphic levels (m) of *T. brandti* from the Sand Creek Divide section (SCD) are indicated at the lower left of each plot; three specimens from the Cabin Fork section have been interpolated based on Figure 1. Levels in other sections in the southern Bighorn Basin (BHB; see Bown et al., 1994) are shown at right of each plot. The 30-m level in the latter sections appears to correlate closely with ~45 m in the SCD section. *T. belgica* and *T. asiatica* are plotted stratigraphically below *T. brandti*, following Smith et al. (2006). *T. magnoliana* is shown below the section, as its stratigraphic position is ambiguous. Note that M_1 increases in relative width through the section, but M_1 area shows no obvious trend, though *T. asiatica*, *T. belgica*, and *T. magnoliana* average smaller than the Bighorn Basin species. Data from Bown and Rose (1987), Smith et al. (2006), Beard and Dawson (2009), and this paper. Data for *T. belgica* based on original measurements of epoxy casts of specimens listed in Appendix C.

Thompson, 2009). In the absence of detailed chemostratigraphy of the Tuscahoma Formation, the age of *T. magnoliana* relative to other early species of *Teilhardina* is difficult to establish; but existing evidence casts doubt on the hypothesis that the Red Hot fauna and *T. magnoliana* predate the first occurrence of *Teilhardina* in the Bighorn Basin. It may not be possible to determine the relative age of the Red Hot local fauna compared to the Bighorn Basin Wa-0 faunas without knowing its precise position relative to the CIE, and specifically, to the minimum value of $\delta^{13}C$. A detailed carbon isotope section through the Tuscahoma Formation, which could resolve the controversy, has not yet been published.

    T. magnoliana appears to be as primitive as *T. brandti* or more so in most features, but possibly more derived in others (e.g., P_4 metaconid height and talonid structure). Judging from dental morphology, it is more likely that *T. magnoliana* evolved independently from *T. belgica* than directly from either *T. asiatica* or *T. brandti*, but a larger sample and more complete specimens are needed in order to determine its phylogenetic position with confidence. Consequently, available evidence favors the westward dispersal hypothesis of Smith et al. (see also Gingerich et al., 2008).

CONCLUSIONS

1. The first known upper teeth of *Teilhardina brandti* have primitive molars with no hypocone or nannopithex fold, an incomplete lingual cingulum, and smooth enamel. They are essentially identical to upper teeth of *T. belgica* but slightly larger.
2. A new dentary reveals the lower dental formula (2.1.4.3), including alveoli of small, apparently vertical incisors (I_1 slightly larger than I_2), a moderate-sized canine, a reduced and laterally displaced P_1, and a single-rooted P_2. Other new specimens show talonid variation in P_4.
3. Analysis of P_4 characters confirms the low metaconid on P_4 of *Teilhardina brandti* (similar in height to that of *T. belgica*). Molar lengths are comparable to those of *T. americana*, whereas relative molar width is comparable to that of *T. belgica*.
4. The first known postcrania for *Teilhardina brandti* include tarsals (elongate talus and navicular, indicative of active arboreal locomotion) and terminal phalanges (the oldest evidence for nails in euprimates).
5. Phylogenetic analysis places *Teilhardina brandti* essentially intermediate between *T. belgica* and

T. americana. Two most parsimonious trees were recovered. As in previous analyses, the first result supports *T. asiatica* as the most basal species of *Teilhardina*. The second result supports *T. magnoliana* as the most basal species, but we consider this scenario less likely in light of the available geological and morphological evidence.

6. *T. magnoliana* is probably not older (and quite possibly is younger) than *T. brandti* from the Bighorn Basin. Together with the morphologic evidence, this suggests that the hypothesis that *Teilhardina* dispersed from Asia westward to Europe and then to North America during the PETM remains most probable.

ACKNOWLEDGMENTS

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APPENDIX A. CHARACTER-TAXON MATRIX[a]

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
D. provincialis	0	1	1	1	1	1	2	1	0,1	1	0	2	0	0	1	1	1	0,1	?	0	0	0	0	0
D. gallica	0	1	1	1	1	0	0	0	0	?	1	2	1	0	0	1	1	0,1	?	0	?	?	?	?
T. asiatica	0	?	1	1	1	1	?	1	0	?	?	?	?	1	1	1	1	1	1	0	0	0	1	0
T. belgica	?	0	1	1	1	1	0	1	0	?	0	1	1	1	1	1	1	1	1	0	0	1	1	1
T. brandti	0	0	1	1	1	1	1	1	0	?	1	0	1	1	1	1	1	1	1	0	0	1	1	?
T. magnoliana	0	1	1	1	1	1	0	1	0	?	0	0	0,1	1	1	1	1	1	?	0	?	?	?	?
T. americana	1	0	0	1	1	1,2	1,2	0,1	1	1	1	0	1	1	0,1	1	0	0	1	1	1	1	1	1
T. crassidens	1	0	0	1	1	2	2	1	1,2	1	1	0	0,1	1	1	1	0	0	1	1	1	2	1	1
T. matthewi	1	0	1	1	1	1,2	0	1	1	1	1	0	1	1	0,1	1	0	0	1	1	1	2	1	0
S. vespertinus	0	0	0	1	1	1	0,1	1	2	1	1	1	1	0	1	1	0,1	0	1	0	0	1	1	1
Purgatorius	0	0	0	0	0	1	0	0	0,1	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0
Palaechthon	0	1	1	0	0	1	0	1	2	0	0	1	0	0	1	0	1	0	0	0	0,1	2	1	1
Altanius	1	0	1	1	1	0	0	1	2	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1

	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
D. provincialis	1	?	1	?	?	2	?	1	1	0	1	1	2	2	2	0	1	1	1	?	?	?	?
D. gallica	?	0	1	0	0	2	0	1	1	1	0	0	1	2	2	0	0	0,1	1	?	?	1	2
T. asiatica	0	0	2	1	0	0	1	0	1	0	0,1	0	2	0	1	1	1	0	0	?	?	0	2
T. belgica	0	1	1,2	1	1	1	1	0	0	0	1	1	2	1	2	1	1	0	0	1	1	0	2
T. brandti	?	1	2	1,2	1	1	1	0	0,1	0,1	1	1	2	1	2	0,1	1,2	0	0	1	1	0	1
T. magnoliana	?	1	2	2	1	1	1	0	0	0	1	0	2	2	2	0	0	0	?	?	0	?	
T. americana	1	1	2	2	2	0,1	1	0	1	1	2	2	1	2	2	1	1	0	0	?	?	0	1,2
T. crassidens	1	2	1	3	3	0,1	1	0	1	1	3	3	0	2	2	2	2	0	1	1	0	2	0
T. matthewi	1	2	2	2	3	1,2	1	0	0,1	1	3	3	1	3	?	1,2	2	0	0	1	0	2	1
S. vespertinus	1	1	2	2	2	1	1	0	1	1	1	1	1	2,3	?	1	2	0,1	1	1	0	0	0
Purgatorius	0,1	0	0	?	0	1	0	0,1	0	0	2	0,2	0	0	0	0	0	0	0	0	0	0	?
Palaechthon	1	0	0	2	2	0,1	0	0	1	0	1	1	0	3	0	0	0	1	1	0,1	0	0	0
Altanius	1	1	0	3	0	1	0	1	1	0	2,3	1,2,3	0	3	1	0,1	2	1	0	1	1	1	0

[a]See Supplemental information for Nexus file.

APPENDIX B: CHARACTER DESCRIPTIONS

Description of dental characters used in the cladistic analysis, with comments on characters.[1] Upper molar characters mainly adapted from Seiffert et al. (2005). Lower tooth characters mainly adapted from Smith et al. (2006; indicated by S) or Beard (2008; indicated by B). N designates new characters, while (m) indicates that character descriptions or states have been modified to facilitate scoring and repeatability.

1. P^4 parastyle: (0) present; (1) very small to absent
2. P^4 metastyle: (0) absent; (1) present
3. P^{3-4} buccal cingulum: (0) strong; (1) absent or weak

---

[1]Characters have been modified after Seiffert et al. (2005), Smith et al. (2006), and Beard (2008) to reflect nuances in character states in the principal taxa and to clarify ambiguities or quantify characters deemed otherwise too subjective to be repeatable. All taxa were reexamined based on available material (original specimens or casts) or literature. These new observations resulted in revision of the scores for several characters. Nearly all such cases pertain to subjective characters which are closer to the boundary between character states than to the extremes. Even when characters were quantified, ambiguity remains because quantitative boundaries for individual character states are necessarily arbitrary. Character scores were based on means of the available specimens or measurements, but ranges for taxa may encompass more than one character state. When only two or three specimens were available, characters were scored as polymorphic if the specimens differed substantially. Moreover, it should be obvious that a slight shift in the arbitrary boundaries may alter the character scores, which could easily affect the outcome of the analysis. Wherever possible, boundaries were imposed in this analysis where natural gaps occur.

4. P^4 metacone: (0) present; (1) absent
5. P^4 protocone: (0) high relative to paracone; (1) low relative to paracone
6. P^4 occlusal outline: (0) protocone lobe mesiodistally compressed, about half L of buccal margin (buccal L/lingual L <0.60); (1) protocone lobe about 2/3 L of buccal margin (0.61–0.70); (2) > 3/4 L of buccal margin (>0.71)
7. N. M^2 parahypocrista: (0) absent; (1) incipient; (2) distinct
8. M^1 hypocone size: (0) present; (1) absent
9. M^{1-2} nannopithex fold: (0) absent; (1) weak; (2) strong
10. N. Position of nannopithex fold: (0) posterolingually directed, to postcingulum; (1) posteriorly or postero-buccally directed, does not join cingulum
11. M^{1-2} premetaconule crista: (0) absent or weak; (1) strong
12. M^{1-2} postmetaconule crista: (0) strong; (1) weak; (2) absent
13. M^{1-2} lateral posterior transverse crista: (0) indistinct; (1) distinct
14. M^2 shape (W/L): (0) wide (1.3–1.65); (1) very wide (>1.65)
15. M^2 hypocone: (0) present; (1) absent
16. M^2 postmetacrista: (0) longer, trenchant, and more buccally extended; (1) short, indistinct or absent
17. M^2 buccal extension of paracone: (0) slight expansion; (1) no expansion
18. M^{1-3} anterior cingulum: (0) strong, complete, long; (1) strong, short
19. M^3 paraconule: (0) distinct, somewhat large (1) absent or very small

20. N. Enamel texture: (0) smooth; (1) crenulated

21. S(m). Lower canine alveolus: (0) distinctly larger than adjacent teeth; (1) not distinctly larger than adjacent teeth

22. S. P_1: (0) present; (1) reduced and laterally shifted; (2) absent

23. B(m). P_2: (0) two-rooted, unreduced; (1) one-rooted and reduced, or absent

24. S(m). $P_{3-4}L:M_{1-2}L$: (0) P_{3-4} not compressed (P_{3-4} >0.85 × $M_{1-2}L$); (1) P_{3-4} anteroposteriorly compressed (P_{3-4} <0.85 × $M_{1-2}L$)

Compression of premolars is often said to characterize various lineages of omomyids, in contrast to adapoids. Although this character was used previously by Smith et al. (2006) and Beard (2008), it was not quantified. Here length of the teeth involved was compared (means were scored where sufficient specimens were available), with in some cases surprising results. Using this criterion, scores in many cases differ from previous assessments. Apparent compression of P_{3-4} may be due in part to relative widening of these teeth. In addition, the relative length is affected by mesiodistal compression of the molars, which may explain why *Tetonius* scores as having less compressed premolars than *Steinius*. Antemolar compression is more evident anterior to P_3.

25. B. P_3 protoconid: (0) mesial, preprotocristid relatively vertical (mesial to the midpoint of the trigonid); (1) approximately at midpoint or distal to midpoint, with more gently sloping preprotocristid.

This character (character 4 of Beard, 2008) replaces character 3 of (Smith et al. 2006: P_3 shape, described as relative procumbency), allowing it to be assessed more objectively. The trigonid was viewed lingually and protoconid position was observed along a line from the mesial end of the trigonid to the talonid notch.

26. N. P_4 buccolingual angle: (0)< 39; (1) 39–55; (2) >55

The tooth is oriented by using the lingual margin to define the mesiodistal axis. The occlusal surface is oriented so the lingual and buccal faces of the protoconid have equal slopes and so the postvallid surface and preprotocristid surface have roughly equal slopes. The tooth is then viewed from the mesial end. The buccal arm of the angle is defined by the buccal surface of the protoconid. The lingual arm is defined by the lingual surface, excluding any projection of the metaconid.

27. S(m). P_4 paraconid: (0) distinct and high; (1) distinct and low; (2) small and low, very small, or absent

28. N. P_4 metaconid height 1: metaconid height/protoconid height: (0) <0.60; (1) 0.60–0.68; (2) 0.69–0.78; (3) >0.78

P_4 metaconid height has long been recognized as a critical morphoclinal character in *Teilhardina* (Bown and Rose, 1987; Smith et al., 2006; Beard, 2008), yet it has previously been assessed only qualitatively. In an effort to characterize metaconid height more objectively, we have quantified it in two ways. For character 28, the tooth was viewed lingually and a base line was drawn joining the lowest extent of the enamel of the trigonid and talonid. Height of the metaconid was measured as a perpendicular from this base line to the tip of the metaconid. Character 28 is the index of this value compared to protoconid height (= crown height) measured from the same base line. See also character 47.

Specimens with obvious wear or damage to the protoconid were excluded.

29. N. P_4 preprotocristid verticality angle (0) <43; (1) 43–52; (2) 53–62; (3) >62

The tooth is oriented using the same procedure as for character 26. The tooth is then viewed from the buccal side. The mesial arm of the angle is defined by the greatest linear segment of the preprotocristid, which is usually the most mesial part that contacts the paraconid, when present. The distal arm of the angle is defined by the postvallid surface of the trigonid, excluding any topography due to the projection of the metaconid.

30. S. P_4 cristid obliqua: (0) extends to base of trigonid wall; (1) runs part way up trigonid wall; (2) extends up trigonid wall above metaconid

31. N. P_4 trigonid width index (0) <1.21; (1) 1.21 and greater

The index used is trigonid length/trigonid width. Trigonid length was used instead of total length so that CM 73229 (*Teil. magnoliana*) could be included.

32. S. M_1 cristid obliqua: (0) extends to base of trigonid wall or runs part way up trigonid wall; (1) extends to metaconid

33. S. Buccal cingulids on lower molars: (0) weak or absent; (1) moderate to strong

Buccal cingulids in some taxa (e.g., *Teilhardina asiatica*) are strong on parts of some molars but weak or absent elsewhere. Such taxa were scored as moderate.

34. S. Hypoconulids on M_{1-2}: (0) well defined; (1) weak

Hypoconulids were scored as well defined if either a distinct cusp is present or a distinct elevation occurs on the postcristid in the position of a cusp.

35. B(m). M_1 shape: (0) narrow (M_1L/W > 1.40); (1) somewhat square (M_1L/W = 1.30–1.40); (2) more nearly square (M_1L/W = 1.20–1.30); (3) square and inflated (M_1L/W < 1.20)

M_1 shape is included here, following Beard (2008), although in most cases it duplicates character 36 (M_2 shape).

36. S(m). M_2 shape: (0) narrow (M_2L/W > 1.30); (1) somewhat square (M_2L/W = 1.21–1.30); (2) more nearly square (M_2L/W = 1.11–1.20); (3) square and inflated (M_2L/W<1.10)

The single known complete M_2 of *T. magnoliana* (the holotype) is narrow (L/W = 1.32), whereas M_2s of *T. belgica* and *T. brandti* are, on average, wider (L/W index = 1.25 for both species). However, three specimens of *T. brandti* have indices of 1.30–1.34, comparable to *T. magnoliana*.

37. S(m). M_2 entoconid: (0) High (as high as or nearly as high as hypoconid); (1) intermediate; (2) Low (distinctly lower than hypoconid in lingual and posterior views)

As for many characters, while extremes are simple to code, many specimens fall into a more or less intermediate state that is difficult to code consistently.

38. S(m). M_3 hypoconulid lobe: (0) very narrow (<1/3 as wide as M_3 maximum width); (1) narrow (36–45% as wide as M_3 maximum width); (2) intermediate (46–55% as wide); (3) wide (>56% as wide)

Variations in shape of the M_3 hypoconulid lobe make it difficult to obtain consistent width measurements. As a measure of hypoconulid lobe size, maximum width of the hypoconulid lobe was compared with maximum M_3 width; higher values reflect relatively wider hypoconulid lobes. Values for *Teilhardina* species are: *T. asiatica* = 0.32; *T. brandti* = 0.39; *T. belgica* = 0.41; *T. magnoliana* = 0.47; *T. americana* = 0.51; *T. crassidens* = 0.54.

39. N. M_2 relief index: (0) >0.55; (1) 0.55–0.53; (2) <0.53
    The relief index was calculated as the [natural logarithm (square root of M_2 3-D surface area/square root of M_2 2-D surface area)]. See Boyer (2008) for measurement methods and descriptions.
40. B(m). M_2 paraconid position: (0) well separated from metaconid; (1) intermediate; (2) connate with metaconid or absent.
41. B(m). M_2 paraconid height: (0) situated low on trigonid, well below metaconid; (1) slightly below metaconid; (2) situated high on trigonid, at or near level of metaconid.
42. B(m). M_3 trigonid: (0) wider than talonid; (1) similar in width to talonid
    M_3 trigonid was scored as similar in width to the talonid if differences in width were ≤0.05 mm; if the difference was ≥0.10 mm the trigonid was scored as wider than the talonid. (Measurements were taken to the nearest 0.05 mm).
43. B(m). M_3 trigonid: (0) significant baso-buccal distension; (1) buccal surface nearly vertical
    This character (= character 24 of Beard, 2008) is considered to include Beard's character 25, relative inflation of M_3 trigonid cusps.
44. N. Lower incisors (number): (0) 3; (1) 2
    Silcox (2001) inferred the presence of I_3, and thus three lower incisors, in *Palaechthon nacimienti*, but only two in *P. alticuspis*.
45. N. Size of I_1: (0) >C (hypertrophied); (1) <C (comparable to other incisors)
46. N. P_4 mesial angle: (0) 125–145; (1) >145; (2) <125
    The tooth is oriented as for character 26 and is viewed buccally. The upper (more dorsal) arm of the angle is the same as the mesial arm of the verticality angle defined for character 29. The lower (more ventral) arm is defined by the longest linear segment of the anterior part of the trigonid's cervical margin. This segment usually extends from the mesial half of the mesial root to the end of the anteroexternal cingulid.
47. N. P_4 metaconid height 2: metaconid height/P_4 length: (0) >0.66; (1) 0.56–0.66; (2) <0.56
    Character 47 compares metaconid height to P_4 mesiodistal length. The tooth is oriented as for character 26 and is viewed lingually. Metaconid height is the dorsoventral distance (perpendicular to the occlusal plane) from the apex of the gap between the mesial and distal roots to the notch between the protoconid and metaconid.

APPENDIX C: TAXA AND SPECIMENS EXAMINED, WITH COMMENTS

Teilhardina asiatica—Cast of IVPP V-12357 (lower); other data from Ni et al. (2004).

Teilhardina belgica—Casts of IRSNB nos. M64 (lectotype), M65, M4290, M4291, M4292, M4296, CL 182, CL231, CL246, CL455, CL457, WL13, WL128, WL159, WL180, WL1052, WL1060, WL1062, WL1180, WL1299, WL1398; also casts of RS nos. DIII15S, DIII16S, DIII19S, DIII20S, DIII467, DIII844, DIII952, DIIC761. Other data from Smith et al. (2006).

Teilhardina brandti—UM 99031 (holotype, cast), USNM nos. 493913, 493914, 521795 525543—525546, 525621, 525622, 533494, 533505, 533554, 538082, 538084, 538361, 539466, 539467, 540598; UF nos. 244451, 244453—244458, 244460.

Teilhardina magnoliana—Casts of CM nos. 67854, 67856, 67858, 67860, 67861, 70422, 70427, 70430, 70431, 70433, 70434, 70435 (holotype), 70436, 73229, 77209–77212.

P_4 morphology, particularly changes in width and metaconid development, are of particular significance in the evolution of this genus (e.g., Rose and Bown, 1984; Bown and Rose, 1987). Unfortunately, only three specimens of P_4 are known for *T. magnoliana*, one badly eroded and the other two fragmentary trigonids. Consequently P_4 traits are difficult to assess with certainty and appear to differ significantly between the two specimens we examined (CM 70434 and 73229). This ambiguity may affect the outcome of the analysis.

Teilhardina americana—UF nos. 244452, 244459; UM nos. 65770, 75610, 76600 (casts); USGS nos. 3849, 3863, 8886, 9037, 12747, 15406, 15450, 23838, 23963, 25324 (cast); USNM nos. 539489, 539491; UW nos. 6896 (holotype, cast), 6907, 7098 (cast), 8871, 8961. Other data from Bown and Rose (1987).

Teilhardina crassidens—UM 71071 and 73908 (casts); USGS 7204, 15409; USNM 487869; UW 8959 (holotype, cast); YPM 24626 and 30721 (casts). Other data from Bown and Rose (1987).

Tetonius matthewi—USNM nos. 487864, 487865, 487870, 521477, 527712, 527713, 533455, 533620; USGS 3841; CM 12190 (holotype, cast); YPM 23031 and 25027 (casts); UM 76675 (cast). AMNH 4194, holotype of *T. homunculus*, was also compared and was found to score the same in nearly all features.

This species was used because it is much better known than the slightly more primitive *T. mckennai*.

Steinius vespertinus—USGS 502 (cast); USNM nos. 491935–491954, 527694.

Altanius orlovi—Casts of PSS nos. 7/20-8 (holotype), 20—58, 20—61, 20—85.

Donrussellia provincialis—Casts of MNHN RI-170 (holotype), RI-229. Other data from Godinot (1981, 1998).

Donrussellia gallica—Casts of MNHN Av nos. 4562, 4598, 4603, 4613, 4618, 4711, 4714, 4774, 4830, 4854–4856, 5015, 5017, 5022, 5654, 5721, 5755 (holotype), 5765, 5767, 5795, 5807, 5841, 5846, 5859, 5873, 6757, 6848, 7655.

Cantius ralstoni–USGS 13634; USNM nos. 522157–522159, 522168, 540506, 541830–541834; Casts of AMNH 16089 (holotype) and 16092; UW nos. 7063, 7066, 8842.

Cantius torresi—UM nos. 66143, 83470 [holotype], 83475, 87341, 87852, 101958.

Cantius mckennai—USNM 533559.

Marcgodotius indicus—GU nos. 7, 40, 44, 45, 46, 49, 51, 52, 54, 227, 600, 611, 703, 727, 743, 744, 1534, 1536, 1538, 1544, 1554, 1575, 1591, 1602 (Rose et al., 2009).

Asiadapis cambayensis–GU nos. 6, 32, 35–38, 598, 642, 745, 1505, 1537, 1627, 1649 (Rose et al., 2009).

Purgatorius janisae—Casts of UCMP 107406 (holotype), 107409; LACM 28128. Other data from Clemens (2004).

Palaechthon—Uppers are scored based on *P. nacimienti* (UKMNH 9557, cast); lower tooth characters partly from *P. nacimienti* (UKMNH 9559, holotype, cast). Some lower characters are scored based on *P. alticuspis* (casts of USNM 9532 [holotype] and AMNH nos. 35479 and 35488) due to availability and the fact that the holotype of *P. nacimienti* is heavily worn, obscuring some details and affecting some indices. Character 27 is scored as 0 because of elevation of the paraconid, though it may be distinct or less distinct. Characters 21 and 44 are scored as polymorphic to reflect more primitive conditions of *P. nacimienti* (Silcox, 2001).

APPENDIX D: RAW DATA FOR P$_4$ ANALYSES

Taxon	Spec. no.	L	Mtd h1	Prt h	Mtd h2	Tri W	Tri L	Pp Vt Ag	Bl Ag	Mes Ag	Tri W In	Mtd h1 In	Mtd h2 In
Teil. asiatica	IVPP 7165	1.43	0.84	1.35	0.79	1.20	0.87	42	36	142	1.37	0.63	0.548
Teil. magnoliana?	CM 70434	1.39	0.79	1.06	0.69	1.17	0.68	53	54	119	1.73	0.74	0.500
Teil. magnoliana	CM 73229	br	0.98	1.40	0.83	1.19	0.95	48	40	135	1.26	0.70	–
Teil. belgica	IRSNB CL 192	1.33	0.88	1.36	0.77	1.05	0.86	48	40	127	1.23	0.65	0.575
Teil. belgica	IRSNB CL 246	1.53	0.90	1.37	0.76	1.16	0.92	51	44	124	1.26	0.66	0.497
Teil. belgica	IRSNB CL 457	1.42	0.89	1.35	0.75	1.10	0.87	48	41	123	1.26	0.66	0.532
Teil. belgica	IRSNB M64	1.38	0.91	1.40	0.77	1.08	0.78	49	38	139	1.38	0.65	0.556
Teil. belgica	IRSNB M4090	1.48	0.95	1.39	0.79	1.21	0.89	50	42	129	1.36	0.68	0.531
Teil. belgica	IRSNB M4291	br	0.86	1.32	0.73	br	br	br	41	br	–	0.66	–
Teil. belgica	IRSNB M4292	1.44	0.85	1.33	0.69	1.07	0.85	51	43	123	1.25	0.64	0.479
Teil. belgica	IRSNB WL 13	1.41	0.83	1.26	0.76	1.09	0.93	51	40	128	1.17	0.66	0.539
Teil. belgica	IRSNB WL 159	1.35	0.78	1.26	0.66	1.11	0.87	43	40	141	1.27	0.62	0.491
Teil. belgica	IRSNB WL 1052	1.49	0.92	1.34	0.84	1.14	0.86	47	44	126	1.33	0.69	0.564
Teil. belgica	IRSNB WL 1062	1.31	0.87	1.20	0.81	0.99	0.77	52	42	125	1.29	0.73	0.618
Teil. belgica	IRSNB WL 1180	1.37	0.91	1.28	0.84	1.05	0.84	47	44	129	1.25	0.71	0.613
Teil. brandti	UF 244454	1.49	0.95	1.37	0.93	1.34	1.05	46	44	126	1.28	0.69	0.625
Teil. brandti	USNM 493913	1.48	0.87	1.44	0.88	1.22	0.93	44	45	129	1.31	0.60	0.591
Teil. brandti	USNM 525543	1.56	0.94	1.31	0.95	1.29	0.91	51	45	125	1.43	0.72	0.608
Teil. brandti	USNM 525544	1.57	1.02	1.46	0.90	1.28	0.97	44	50	133	1.32	0.70	0.577
Teil. brandti	USNM 533554	1.59	0.97	1.36	0.90	1.24	0.95	48	41	136	1.30	0.72	0.564
Teil. americana	UF 244452	1.36	0.94	1.26	0.87	1.19	0.88	59	55	124	1.35	0.75	0.638
Teil. americana	UM 65770	1.54	1.01	1.42	0.75	1.25	0.98	61	49	122	1.28	0.71	0.486
Teil. americana	UM 75160	1.37	1.05	1.35	0.94	1.36	0.97	61	50	131	1.41	0.78	0.690
Teil. americana	UM 76600	1.47	1.05	1.44	0.87	1.36	0.92	60	53	128	1.47	0.73	0.592
Teil. americana	USGS 3849	1.47	0.96	1.19	0.98	1.21	1.02	72	53	127	1.19	0.81	0.667
Teil. americana	USGS 15406	1.49	1.11	1.47	0.94	1.45	1.08	62	52	127	1.34	0.76	0.631
Teil. americana	USGS 25324	1.35	0.87	1.21	0.73	1.21	0.92	56	47	142	1.31	0.72	0.541
Teil. americana	USNM 539489	1.47	0.95	1.28	0.89	1.27	0.91	76	48	118	1.40	0.74	0.605
Teil. americana	UW 7165	1.39	1.00	1.38	0.85	1.38	0.95	57	51	127	1.46	0.73	0.608
Teil. crassidens	UM 71071	1.32	1.03	1.21	0.92	1.34	0.91	63	69	116	1.47	0.85	0.697
Teil. crassidens	UM 71126	1.37	1.09	1.30	1.02	1.32	0.95	66	63	110	1.39	0.84	0.745
Teil. crassidens	UM 71386	1.35	1.09	1.22	0.99	1.28	0.90	64	57	116	1.42	0.89	0.733
Marcgodinotius indicus	GU 40	na	nm	na	nm	1.31	1.40	42	38	139	0.94	–	–
Marcgodinotius indicus	GU 727	1.72	0.97	1.71	0.45	1.35	1.41	44	36	126	0.96	0.57	0.262
Marcgodinotius indicus	GU 1536	na	nm	na	nm	1.34	1.40	38	35	140	0.96	–	–
Asiadapis cambayensis	GU 38	na	nm	na	nm	1.69	1.85	38	37	138	0.91	–	–
Asiadapis cambayensis	GU 1627	na	nm	na	nm	1.59	1.57	34	38	136	1.01	–	–
Altanius orlovi	PSS 20-58	na	na	na	na	na	na	41	40	151	1.15	0.83	0.760
Tetonius homunculus	AMNH 4194-1	na	na	na	na	na	na	78	56	112	1.55	0.77	0.584
Tetonius matthewi	USGS 3841	2.07	1.35	1.73	1.11	1.97	1.37	71	56	118	1.44	0.78	0.536
Tetonius matthewi	USNM 487864	1.72	1.16	1.55	1.03	1.53	1.08	63	52	124	1.42	0.75	0.599
Tetonius matthewi	USNM 487865	1.94	1.25	1.62	1.15	1.72	1.23	69	57	113	1.40	0.77	0.593
Tetonius matthewi	USNM 487870	1.98	1.35	1.85	1.25	1.95	1.42	64	53	122	1.37	0.73	0.631
Tetonius matthewi	USNM 527713	1.90	1.32	1.97	1.17	1.92	1.32	63	51	121	1.45	0.67	0.616
Tetonius matthewi	USNM 533455	2.02	1.49	2.09	1.39	1.99	1.41	66	56	120	1.41	0.71	0.688
Tetonius matthewi	YPM 23031	1.82	1.30	1.75	1.19	1.79	1.30	65	54	116	1.38	0.74	0.654
Donrussellia gallica	composite	na	na	na	na	na	na	37	33	153	0.93	0.59	0.483
Steinius vespertinus	USGS 25027	na	na	na	na	na	na	56	49	125	1.40	0.74	0.668
Purgatorius janisae	UCMP 107406	na	na	na	nm	na	na	34	29	143	1.10	–	–
Palaechthon alticuspis	AMNH 35488	na	na	na	na	na	na	59	26	138	0.96	0.75	0.687
Cantius ralstoni	UW 8842	na	na	na	na	na	na	36	39	144	1.10	0.77	0.590

Abbreviations: Ag, angle; Bl, buccolingual; br, broken morphology; h, height; In, index; L, length; Mtd, metaconid; Mes, Mesial; na, measurement not available; nm, necessary morphology not present; Pp, preprotocristid; Prt, protoconid; Tri, trigonid; W, width; Vt, verticality. Angles measured in degrees; linear measurements in mm. Metaconid height 1 refers to character 28; metaconid height 2 is character 47.

APPENDIX E: P_4 AND M_2 CHARACTERS AND STATISTICS: (A) P_4 AND M_2 CHARACTERS, DESCRIPTIVE STATISTICS, AND CODINGS

	Pj	Pan	Ao	Cr	Dp	Dg	Mi	Asc	Tas	Tbg	Tbr	Tmg	Ta	Tc	Ttm	Stv
Character 26: P_4 buccolingual angle (0, <39; 1, 39-55; 2, >55)																
x, s.d.	29, na	26, na	40, na	39, na	?	33, na	36.33, 1.5	37.5, na	36, na	41.6, 2.0	44.9, 3.3	40, na	50.9, 2.6	63.1, 5.9	54, 2.3	49, na
range	na	na	na	na	?	na	35-38	37-38	na	38-44	41-50	na	47-55	57-69	51-57	Na
code	0	0	1	1	?	0	0	0	0	1	1	1	1	2	2	1
Character 28: P_4 metaconid height 1 (0, <0.60; 1, 0.60-0.68; 2, 0.69-0.78; 3, >0.78)																
x, s.d.	na, na	0.75, na	0.83, na	0.77, na	?	0.59, na	0.57, na	na, na	0.63, na	0.67, 0.03	0.68, 0.2	0.72, na	0.75, 0.03	0.86, 0.02	0.73, 0.03	0.74, na
range	na	na	na	na	?	na	na	na	na	0.62-0.73	0.60-0.72	0.70-0.74	0.71-0.81	0.84-0.89	0.67-0.77	na
code	?	2	3	2	?	0	0	na	1	1	1,2	2	2	3	2	2
Character 29: P_4 preprotocristid verticality angle (0, <43; 1, 43-52; 2, 53-62; 3, >63)																
x, s.d.	34, na	59, na	41, na	36, na	?	37, na	41.33, 3.0	36, na	42, na	48.8, 2.6	46.6, 3.0	48, na	63, 6.8	64.33, 1.53	66, 3.07	56, na
range	na	na	na	na	?	na	38-44	34-38	na	43-52	44-51	na	56-76	63-66	63-71	na
code	0	2	0	0	?	0	0,1	0	1	1	1	1	2	3	3	2
Character 31: P_4 trigonid width (0, <1.21; 1, 1.21 and greater)																
x, s.d.	1.1, na	0.96, na	1.15, na	1.1, na	?	0.93, na	0.95, 0.01	0.96, na	1.37, na	1.29, 0.06	1.28, 0.06	1.26, na	1.35, 0.09	1.43, 0.04	1.43, 0.03	1.4, na
range	na	na	na	na	?	na	0.94-0.96	0.91-1.01	na	1.23-1.38	1.17-1.38	na	1.19-1.47	1.39-1.47	1.37-1.55	na
code	0	0	0	0	?	0	0	0	1	1	1	1	1	1	1	1
Character 39: M_2 relief (0, >0.55; 1, 0.55-0.53; 2, <0.53)																
x, s.d.	0.63, na	0.56, na	0.55, na	0.49, 0.02	0.5	0.53, 0.02	0.55, na	0.52, na	0.55, na	0.50, 0.01	0.49, 0.02	0.51, na	0.51, 0.02	0.48, 0.01	?	?
range	na	na	na	0.47-0.53	na	0.50-0.56	na	na	na	0.48-0.52	0.47-0.51	na	0.48-0.52	0.48-0.49	?	?
code	0	0	1	2	2	2	1	2	1	2	2	2	2	2	?	?
Character 46: P_4 mesial angle (0, 125-145; 1, >145; 2, <125)																
x, s.d.	143, na	138, na	151, na	144, na	?	153, na	135, 7.8	137, na	142, na	128.5, 6.1	129.8, 4.7	135, na	127.3, 6.7	114, 3.5	119, 3.8	125, na
range	na	na	na	na	?	na	126-140	136-138	na	123-141	125-136	na	118-142	110-116	113-124	na
code	0	0	1	0	?	1	0	0	0	0	0	0	0	2	2	0
Character 47: P_4 metaconid height 2 (0, <0.56; 1, 0.56-0.66; 2, >0.66)																
x, s.d.	na, na	0.69, na	0.76, na	0.59, na	?	0.48, na	0.26, na	na	0.55, na	0.54, 0.05	0.59, 0.02	?	0.61, 0.06	0.72, 0.02	0.65, 0.05	0.67, na
range	na	na	na	na	?	na	na	na	na	0.48-0.62	0.56-0.62	?	0.49-0.69	0.70-0.73	0.60-0.72	na
code	na	2	2	1	?	0	0	na	0	0	1	?	0,1	2	1	2

x, mean; s.d., standard deviation; na, not applicable/available; Ao, *Altanius orlovi*; Asc, *Asiadapis cambayensis*; Cr, *Cantius ralstoni*; Dg, *Donrussellia gallica*; Dp, *D. provincialis*; Mi, *Marcgodinotius indicus*; Pan, *Palaechthon nacimiento*; Pj, *Purgatorius janisae*; Stv, *Steinius vespertinus*; Ta, *Teilhardina americana*; Tas, *T. asiatica*; Tbg, *T. belgica*; Tbr, *T. brandti*; Tc, *T. crassidens*; Tmg, *T. magnoliana*; Ttm, *Tetonius matthewi*.

APPENDIX E: P_4 AND M_2 CHARACTERS AND STATISTICS: (B) RESULTS OF KRUSKAL-WALLIS TEST OF P_4 AND M_2 CHARACTERS AMONG *TEILHARDINA* SPECIES IN WHICH n > 2

Characters	H	P	Tbg v. Tbr	Tbg v. Ta	Tbg v. Tc	Tbr v. Ta	Tbr v. Tc	Ta v. Tc
P_4 B-L angle	21.9	>0.0001	0.027/0.16	0.0001/0.001	0.013/0.08	0.016/0.1	0.037/0.22	0.016/0.1
P_4 metaconid height 1	20.2	0.0002	ns	0.0003/0.002	0.011/0.07	0.011/0.07	0.036/0.22	0.016/0.1
P_4 preprot verticality	21.0	>0.0001	ns	0.0002/0.001	0.013/0.08	0.003/0.02	0.036/0.22	ns
P_4 trigonid width	10.3	0.016	ns	0.03/0.2	0.013/0.08	ns	ns	ns
M_2 relief	6.1	0.106	ns	ns	ns	ns	ns	ns
P_4 mesial angle	8.5	0.038	ns	ns	0.012/0.07	ns	0.036/0.22	0.015/0.09
P_4 metaconid height 2	13.03	0.005	ns	0.03/0.2	0.013/0.08	ns	0.037/0.22	0.016/0.1

H, Kruskal-Wallis Chi-square statistic; P, probability of no differences; Ta, *Teilhardina americana*; Tbg, *T. belgica*; Tbr, *T. brandti*; Tc, *T. crassidens*. Pairwise comparisons are Mann-Whitney U tests. The value before the forward slash is the probability of no difference, uncorrected for multiple comparisons, while the second value is the probability Bonferroni-corrected. "ns" is used for comparisons that were non-significant prior to correcting for multiple comparisons.