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First tillodont from India: Additional evidence for an early Eocene faunal connection between Europe and India?

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Vastan Lignite Mine in southeastern Gujarat, India, produces the oldest known Cenozoic land-mammals and the only early Eocene continental vertebrate fauna known from India (e.g., Bajpai et al. 2005; Rana et al. 2005, 2008; Rose et al. 2006, 2008, 2009; Smith et al. 2007; Rage et al. 2008). The fauna comes from the Cambay Shale Formation and has been dated as middle Ypresian (~52 Ma, early Cuisian) based on a common nummulitid foraminiferan from about 15 m above the vertebrate-producing layer (Sahni et al. 2006; Rana et al. 2008). However, a recent study of dinoflagellate cysts from the section suggests that the deposits may be as old as 54–55 Ma (Garg et al. 2008). Although some elements of the fauna, such as anthracobunids and lagomorphs, have Asian affinities, a surprising number of taxa among the snakes, bats, insectivores, primates, rodents, and artiodactyls appear to be most closely related to early Eocene European or North American taxa. This may simply reflect the poor state of knowledge of contemporary south Asian vertebrate faunas; alternatively, it might be evidence of previously unsuspected early Eocene faunal exchange between Europe and southwest Asia. We report here two teeth of a tillodont from Vastan Mine, which constitute the first record of the mammalian order Tillodontia known from India. Despite the much greater generic diversity of tillodonts in Asia than elsewhere, the Vastan tillodont shows clear affinities with Euramerican esthonychines.

Introduction

Tillodonts are a group of archaic Paleocene and Eocene Holarctic eutherian mammals characterized by enlarged, gliriform second incisors with restricted enamel, which became ever-growing in the most derived forms (Gazin 1953; Rose 2006). Where known, their skeletons were relatively robust and generalized and best adapted for terrestrial life, though at least some had a capacity for digging or climbing. They were herbivorous, and most were medium-sized to moderately large animals. Their precise relationships among eutherians are uncertain, but a close relationship to Pantodonta seems probable (e.g., Chow and Wang 1979; Lucas 1993). McKenna and Bell (1997) united Tillodontia with Pantodonta and other clades in the higher taxon Cimolesta.

The teeth reported here, believed to pertain to a single species, are a right I2 and a left M3 that show distinctive tillodont characteristics: the incisor is relatively large and rooted, with restricted enamel, and the molar has a broad stylar shelf with a hypertrophied parastylar lobe and well-developed anterior and posterior cingula. They are closely similar in size and morphology to their counterparts in North American *Esthonyx* and are comparable in size to basal Wasatchian *Esthonyx spatularius* and slightly smaller than early Wasatchian *E. bisulcatus*. In the

Table 1. Distribution of tillodont genera (modified from McKenna and Bell 1997, as noted). Ages of Asian records from McKenna and Bell (1997) and modified after Tong and Wang (2006). Abbreviations: e., early; l., late.

Genus	Age	NA	Europe	Asia
Anchilestes	early Paleocene			×
Plethorodon	early Paleocene			×
Lofochaius	early Paleocene			×
Meiostylodon	early Paleocene			×
Huananius[1]	early Paleocene			×
Deltatherium[2]	early Paleocene	×		
Benaius[3]	early Paleocene			×
Simplodon[4]	early Paleocene			×
Interogale	late Paleocene			×
Yuesthonyx[5]	l. Paleocene–e. Eocene			×
Azygonyx	l. Paleocene–e. Eocene	×		
Esthonyx	early Eocene	×	×[6]	
Franchaius	early Eocene		×	
Plesiesthonyx	early Eocene		×	
Paresthonyx[7]	early Eocene			×
Megalesthonyx	early Eocene	×		
Trogosus (= *Kuanchuanius*)	early–middle Eocene	×		×
Tillodon	middle Eocene	×		
Basalina	middle Eocene			×
Higotherium[8]	middle Eocene			×
Chungchienia	middle Eocene			×
Adapidium	middle Eocene			×

[1] Huang and Zheng (1999).

[2] Assigned to Tillodontia by McKenna and Bell (1997) and Lucas and Kondrashov (2004), but the latter authors list numerous differences from other tillodonts. *Deltatherium* has also been assigned to Arctocyonidae or Pantodonta; it is excluded from Tillodontia in this report.

[3] Wang and Jin (2004); age was unspecified Paleocene. Tong and Wang (2006) listed the age as early Paleocene (Shanghuan Land-Mammal Age).

[4] Huang and Zheng (2003). Original authors listed age as middle Paleocene, Tong and Wang (2006) placed it in late Paleocene.

[5] Tong et al. (2003).

[6] Nel et al. (1999).

[7] Tong and Wang (2006).

[8] Miyata and Tomida (1998).

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following section we describe the teeth and compare them, to the extent possible, with known tillodont genera from Asia, Europe, and North America (Table 1). Comparisons were based on published descriptions or, where available, specimens or casts.

Institutional abbreviations.—GU/RSR/VAS, H.N.B. Garhwal University, Srinagar, Uttarakhand, India; USGS, United States Geological Survey (Denver) collection, now housed at USNM; USNM, Department of Paleobiology, U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C.; UW, University of Wyoming Geological Museum, Laramie, Wyoming.

Description and comparisons

GU/RSR/VAS 1651 is an upper mesial incisor (Fig. 1A), measuring 23.2 mm long, 6.2 mm in labiolingual diameter, and 4.8 in mesiodistal diameter (diameters taken near the base of the crown). It is very similar in size and morphology to upper central incisors of *Esthonyx* from the early Eocene (Wasatchian Land-Mammal Age) lower Willwood Formation of the Bighorn Basin, Wyoming (e.g., USGS 10258, USNM 533591; Fig. 1B). These teeth are identified by convention as I2 following Gazin (1953) and Gingerich and Gunnell (1979), assuming that I1 was lost in esthonychines. As in esthonychines, but not trogosines, the tooth is rooted. The root and crown (as distinguished by absence of enamel on the root) in the Vastan tooth are of equal length. As in *Esthonyx*, the enamel completely covers the convex external curved surface (i.e., laterally and anteriorly), but only the labial half or less of the medial surface. The extension of enamel on the medial aspect is slightly greater than in the two *Esthonyx* I2s available for comparison (see Fig. 1). Unfortunately, few specimens of *Esthonyx* (or other tillodonts) include I2, and variations in its enamel have not been documented, so the significance of the difference observed is unknown. The enamel in the Vastan incisor is slightly rugose, with low and rounded, irregular longitudinal ribs, as in the I2 of *Esthonyx*. The lingual surface is devoid of enamel, most likely as a result of wear. This distribution of enamel results in a chisel-like cutting edge, similar to that of rodent incisors, consisting of a thin layer of enamel around the outer half of the crown surrounding softer dentine lingually. Unerupted or newly erupted upper incisors of *Esthonyx* retain very thin enamel on the lingual surface (e.g., USGS 10258) which is rapidly worn away (Gingerich and Gunnell 1979). The cross-section of GU/RSR/VAS 1651 is shaped like a slightly elliptical quadrant, which is also true of USNM 533591 and USGS 10258.

GU/RSR/VAS 1587 (Fig. 2A) is a left M3 also very similar to that of early Eocene *Esthonyx* from Wyoming (Fig. 2B, C). Its mesiodistal length is 5.75 mm, anterior width is 11.0 mm, and posterior width is 9.35 mm (near the metacone). It is tritubercular, with rounded paracone, metacone, and protocone. The protocone is the largest cusp, about the same height as the paracone; the metacone is lowest. The small paraconule is separated from the paracone by a distinct valley, whereas the larger and transversely longer metaconule is less clearly separated from the metacone.

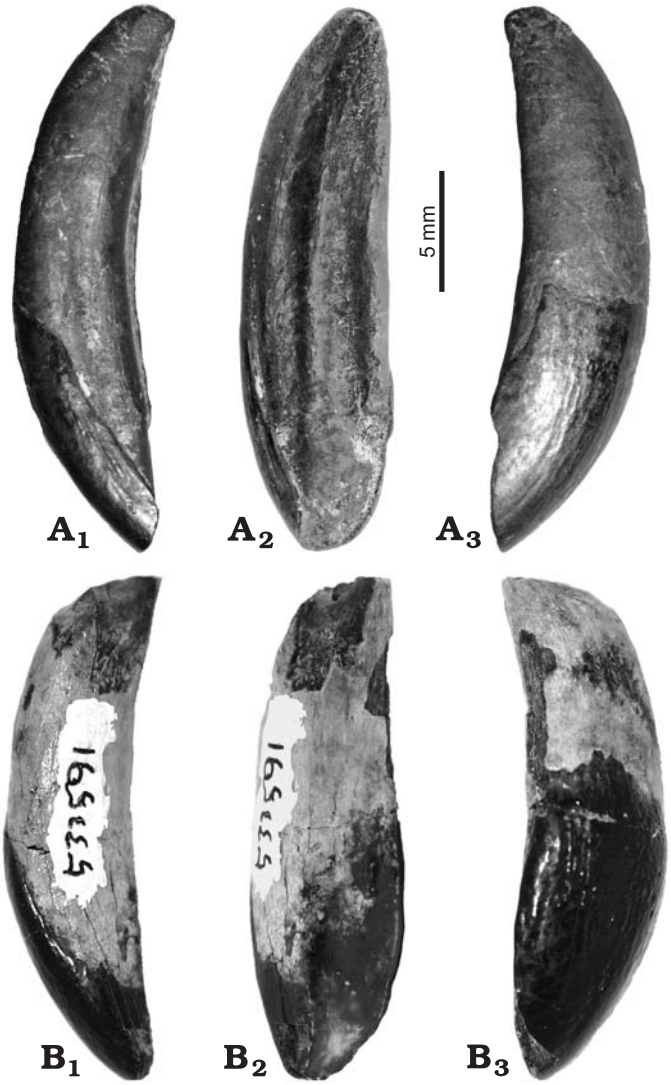

Fig. 1. Right I2 of esthonychine tillodonts. **A**. GU/RSR/VAS 1651, cf. *Esthonyx* sp., from Vastan Mine, in mesial (A_1), lingual (A_2), and distal (A_3) views. **B**. USNM 533591, *Esthonyx spatularius* Cope, 1880, early Eocene Willwood Formation (Wasatchian zone Wa-0), Bighorn Basin, Wyoming, in mesial (B_1), lingual (B_2), and distal (B_3) views.

There is a well developed anterolingual cingulum and a prominent, slightly broader posterolingual cingulum, but no trace of a hypocone. The anterolingual cingulum narrows toward the lingual end, unlike that in *Esthonyx* and *Azygonyx* M3s compared, which remain broad to the lingual base of the protocone. The ectocingulum is prominent and the stylar shelf is wide anteriorly, narrowing toward the metacone. The parastylar lobe is especially salient, bearing an acute parastyle (= stylocone according to Wang and Jin 2004) anterobuccal to the paracone. There are no other distinct stylar cusps. The ectocingulum is slightly thickened in the area where a mesostyle would develop, but there is no connection with the centrocrista. In most of these features GU/RSR/VAS 1587 corresponds closely to specimens of *Esthonyx* from the Willwood Formation (e.g., USGS 10258, USGS 25033, USNM 510865, UW 7433). M3 of *Esthonyx* is slightly more waisted (constricted) just lingual to the paracone and metacone, and it

tends to have slightly wider anterior and posterior cingula, a more swollen parastylar lobe, a less acute parastyle, and a deeper ectoflexus; but these differences appear to be minor, and exceptions to each were observed.

Latest Paleocene–earliest Eocene *Azygonyx* from North America is closely related to *Esthonyx* and differs from the latter principally in having an unfused mandibular symphysis. When Gingerich (1989) proposed the genus for a new species and several others formerly included in *Esthonyx*, no significant dental differences from *Esthonyx* were observed. To judge from published illustrations, the Vastan teeth closely resemble those of *Azygonyx*, except that the ectoflexus on M3 is shallower in *Azygonyx*. Consequently, a close relationship between the Vastan form and *Azygonyx* is also possible, although the known geographic distribution of *Azygonyx* makes this less likely than affinity with *Esthonyx*.

Aside from *Esthonyx* and *Azygonyx*, GU/RSR/VAS 1587 bears closest resemblance to the European early Eocene (Ypresian) tillodonts *Franchaius* and *Plesiesthonyx*. *Franchaius* (three species) is based on less than 20 isolated teeth, only one of which (the holotype of *F. luciae* Baudry, 1992, identified as a right M3 by Baudry 1992: fig. 8a, pl. 1.1) is potentially directly comparable with the Vastan molar (upper incisors have not been reported for European tillodonts). Judging from comparison with *Esthonyx*, however, the holotype of *F. luciae* appears more likely to be M2 based on its relatively unreduced metastylar lobe and wide postcingulum. Baudry's (1992) diagnosis and illustrations provide few features that distinguish *Franchaius* from *Esthonyx*; they are surely closely related if not synonymous. Nor do Baudry's (1992) brief generic diagnoses distinguish *Franchaius* from *Plesiesthonyx* (the diagnosis of *Franchaius* pertains only to upper teeth, that of *Plesiesthonyx* only to lowers), though her descriptions noted some minor differences between the uppers in cingulum development, position of stylar cusps, and relative smoothness of enamel. *Plesiesthonyx* (also known from only a small sample of isolated teeth) has generally been considered to be a synonym of *Esthonyx* (Gazin 1953; Gingerich and Gunnell 1979; Stucky and Krishtalka 1983; McKenna and Bell 1997), but Baudry (1992) and Lucas and Schoch (1998) retained it as a valid genus. Supposed features of distinction from *Esthonyx* include having more inflated molars with better developed cingula, closed molar trigonids with a high paracristid and reduced metastylid, and styles buccal (rather than anterobuccal) to the paracone and metacone. These features vary among North American specimens attributed to *Esthonyx*, hence it is questionable whether they merit generic distinction among the small sample of European tillodonts. Nevertheless, in those features that can be compared, the Vastan M3 is more like *Esthonyx* than like *Plesiesthonyx*. The recent identification of *Esthonyx* from the earliest Eocene (MP7) locality of Le Quesnoy, France (Nel et al. 1999), further suggests the close relationship, if not synonymy, of the European genera with *Esthonyx*. Larger samples and more complete specimens are required to resolve the relationships among European and North American esthonychines.

Although our comparisons suggest that the Vastan tillodont is most closely related to Euramerican esthonychines, it might be expected that the closest similarity would be to Asian tillodonts, particularly any from the Indian subcontinent. At present,

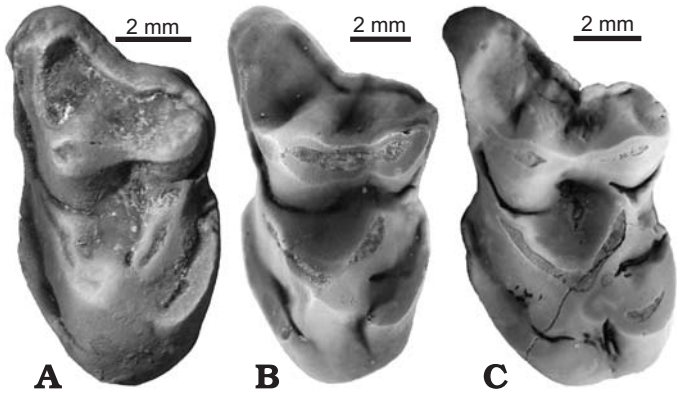

Fig. 2. Left M3 of esthonychine tillodonts. **A**. GU/RSR/VAS 1587, cf. *Esthonyx* sp., from Vastan Mine. **B**. USGS 25033, *Esthonyx bisulcatus* Cope, 1874, early Eocene Willwood Formation (Wasatchian zone Wa-6), Bighorn Basin, Wyoming. **C**. USNM 510865 (reversed), *Esthonyx bisulcatus*, early Eocene Willwood Formation (Wasatchian zone Wa-6), Bighorn Basin, Wyoming. Shown at same buccolingual width.

only a single tillodont has been described from the Indian subcontinent, *Basalina basalensis* Dehm and Oettingen-Spielberg, 1958, from the Kuldana Formation at Ganda Kas, northwestern Pakistan (see also Lucas and Schoch 1981). It is somewhat younger than the Vastan fossils, probably early middle Eocene or possibly late early Eocene (Gingerich 2003). *Basalina* is based on a poorly preserved jaw fragment with one incomplete cheek tooth (p4?) and roots of several other teeth. As a result of the poor condition of this specimen and the two other edentulous jaws referred to *Basalina*, little can be said about its relationships except that it is probably a tillodont (and even that has been questioned). Its size is not inconsistent with relationship to the Vastan form, but at present there is no other basis for comparison; better specimens of both are essential to evaluate a potential relationship. The only other tillodonts from the subcontinent are undescribed specimens from the early Eocene Ghazij Formation of Pakistan, which may represent two or three taxa in a new family (Gingerich et al. 2001). Even in the absence of their description, this assessment alone suggests that they are not particularly close to the Vastan tillodont teeth.

All other known Asian tillodonts (see Table 1) are from China or Japan and, with the possible exception of the recently described *Paresthonyx* (Tong and Wang 2006), none appears to be closely allied to the Vastan tillodont. Early Eocene *Paresthonyx* is roughly the same size as the Vastan form, but it cannot be directly compared because no teeth from the same loci as the Vastan specimens were illustrated, although an M3 was listed in the hypodigm. *Paresthonyx* is generally similar to *Esthonyx* but differs from the latter (and the Vastan M3) in having a deeper notch between paracone and metacone, a reduced anterolingual cingulum, a narrower stylar shelf, and a shallower ectoflexus.

Paleocene Asian tillodonts tend to be smaller and more primitive than the Vastan tillodont. Unfortunately, direct comparisons are impossible for many taxa for which I2 and M3 are unknown. Nevertheless, a few comments may be offered. *Anchilestes* is much smaller than *Esthonyx* or the Vastan tillodont, and its upper

molars are much more transverse and shorter anteroposteriorly. Its lower molars are poorly preserved but appear to have deeper hypoflexids than in *Esthonyx* and to lack metastylids as well as the columnar buccal aspect typical of more derived tillodonts. *Plethorodon* (not certainly a tillodont) has a more compact trigon and less developed stylar shelf and stylar cusps (especially the parastylar lobe of M3) than in *Esthonyx* or the Vastan M3; it further differs from *Esthonyx* in having a larger hypocone on M1–M2. The parastyle of M3 in *Plethorodon* extends more anteriorly than in the Vastan M3. No upper incisors are known. *Lofochaius* is much smaller than *Esthonyx* and the Vastan form and, like *Plethorodon*, has a more compact trigon and a narrower stylar shelf. Ting and Zheng (1989) and Huang and Zheng (1999) considered *Lofochaius* to be a pantodont. *Meiostylodon* is closer in size to the Vastan tillodont, but its upper molars (only M1–M2 are known) are shorter anteroposteriorly and have a narrower stylar shelf than in *Esthonyx* and the Vastan M3. *Huananius* was evidently only slightly smaller than the Vastan tillodont (no comparable teeth are preserved). However, it has a W-shaped ectoloph on M1-M2 (Huang and Zheng 1999), a derived feature shared with *Yuesthonyx* and *Adapidium* as well as North American *Megalesthonyx*, but unlike *Esthonyx* and the Vastan form. *Benaius* is known only from the lower dentition and at present cannot be directly compared with the Vastan tillodont. It seems to be somewhat smaller than the Vastan tillodont and, in contrast to *Esthonyx*, evidently lacks a metastylid and shows only incipient development of the columnar buccal aspect typical of tillodont lower molars. Notably, the incisors of *Benaius* are small, with i2 apparently not yet significantly enlarged (Wang and Jin 2004), which in turn suggests that I2 would not have been enlarged. *Simplodon* is known from a single maxillary dentition that includes M3. Its molars are primitive and tricusped, lacking conules (Huang and Zheng 2003). It further differs from *Esthonyx* and the Vastan M3 in having a narrower stylar shelf, more lingual protocone, and smaller parastylar lobe on M3. Relationship to Tillodontia is not certain, but the possibility of close relationship between *Simplodon* and *Benaius* should be considered. Late Paleocene *Interogale* is much smaller than the Vastan tillodont. Only lower teeth are known, making close comparison impossible. The cheek teeth are rather primitive and lack a metastylid, which has raised the question of whether it is a tillodont at all (e.g., Baudry 1992). This brief survey of Asian Paleocene tillodonts indicates that none of them is likely to have a closer relationship with the Vastan tillodont than does *Esthonyx*.

Yuesthonyx, from the late Paleocene and early Eocene of China, is similar in size to *Esthonyx* and the Vastan tillodont, but its upper molars (including M3) are markedly different in having a strong W-shaped ectoloph and mesostyle (Tong et al. 2003). Its anterior and posterior cingula are less well developed and the buccal part of tooth is less asymmetrical than in *Esthonyx* or the Vastan M3. Tong et al. (2003) proposed a new family, Yuesthonychidae, for tillodonts with mesostyles, including the three Asian genera (*Yuesthonyx*, *Adapidium*, and *Huananius*) and North American *Megalesthonyx*. Differences among these four genera, however, suggest the possibility that appearance of a mesostyle and a W-shaped ectoloph may have occurred more than once in tillodonts. In any case, this derived condition diminishes the probability that any of these genera has a close relationship to the Vastan tillodont.

The remaining genera are usually grouped in the subfamily Trogosinae, characterized by their large size and hypertrophied, ever-growing I2/i2. *Trogosus* itself is known from both North America and Asia. The other genera (*Tillodon*, *Higotherium*, and *Chungchienia*) are more derived than *Trogosus* in dental formula or hypsodonty. *Chungchienia* even achieved ever-growing cheek teeth with enamel limited to the buccal surface (Chow et al. 1996). The relatively small size and rooted I2 of the Vastan tillodont clearly exclude it from close affinity with trogosines.

Discussion

Our comparisons of the Vastan teeth to the 20 or so genera of tillodonts currently recognized indicate that the closest similarity and probable affinity are to the esthonychine *Esthonyx*, although close relationship to North American *Azygonyx* or European *Plesiesthonyx* or *Franchaius* cannot be ruled out. The Vastan teeth lack the derived traits of Trogosinae and clearly are closer in size and morphology to the paraphyletic Esthonychinae. It is significant that the Vastan form shows no particular resemblance or likely close relationship with any of the 14 tillodont genera known from Asia, with the possible exception of *Paresthonyx* and *Basalina* (though resemblances are not as close as to *Esthonyx*). The likelihood that the Vastan tillodont is closely allied to a western European or Euramerican taxon adds to mounting evidence of faunal interchange between the Indian subcontinent and Europe during the early Eocene (e.g., Gunnell et al. 2008; Rage et al. 2008; Rana et al. 2008; Rose et al. 2009; Smith et al. 2007).

The diversity of early Paleocene tillodonts in Asia strongly implies that Tillodontia originated and underwent its initial radiation in Asia. Dispersal of tillodonts from Asia to North America was one of the faunal events that marked the beginning of the Clarkforkian Land-Mammal Age (Rose 1981). The evidence at present suggests that esthonychines dispersed to Europe from North America at the beginning of the Eocene, and probably from Europe to India very soon thereafter.

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References

Bajpai, S., Kapur, V.V., Das, D.P., Tiwari, B.N., Saravanan, N., and Sharma, R. 2005. Early Eocene land mammals from Vastan Lignite Mine, District Surat (Gujarat), western India. *Journal of the Palaeontological Society of India* 50: 101–113.

Baudry, M. 1992. Les tillodontes (Mammalia) de l'Éocène inférieur de France. *Bulletin du Muséum National d'Histoire Naturelle, Paris, 4e sér.* 14: 205–243.

Chow, M. and Wang, B. 1979. Relationship between the pantodonts and tillodonts and classification of the order Pantodonta. *Vertebrata PalAsiatica* 17: 37–48.

Chow, M., Wang, J.-W., and Meng, J. 1996. A new species of *Chungchienia* (Tillodontia, Mammalia) from the Eocene of Lushi, China. *American Museum Novitates* 3171: 1–10.

Garg, R., Khowaja-Ateequzzaman, Prasad, V., Tripathi, S.K.M., Singh, I.B., Jauhri, A.K., and Bajpai, S. 2008. Age-diagnostic dinoflagellate cysts from lignite-bearing sediments of the Vastan lignite mine, Surat District, Gujarat, western India. *Journal of the Palaeontological Society of India* 53: 99–105.

Gazin, C.L. 1953. The Tillodontia: an early Tertiary order of mammals. *Smithsonian Miscellaneous Collections* 121 (10): 1–110.

Gingerich, P.D. 1989. New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: composition and diversity in a rarely sampled high-floodplain assemblage. *University of Michigan Papers on Paleontology* 28: 1–97.

Gingerich, P.D. 2003. Stratigraphic and micropaleontological constraints on the middle Eocene age of the mammal-bearing Kuldana Formation of Pakistan. *Journal of Vertebrate Paleontology* 23: 643–651.

Gingerich, P.D. and Gunnell, G.F. 1979. Systematics and evolution of the genus *Esthonyx* (Mammalia, Tillodontia) in the early Eocene of North America. *Contributions from the Museum of Paleontology, The University of Michigan* 25: 125–153.

Gingerich, P.D., Arif, M., Khan, I.H., ul-Haq, M., Bloch, J.I., Clyde, W.C., and Gunnell, G.F. 2001. Gandhera Quarry, a unique mammalian faunal assemblage from the early Eocene of Baluchistan (Pakistan). *In*: G.F. Gunnell (ed.), *Eocene Vertebrates: Unusual Occurrences and Rarely Sampled Habitats*, 251–262. Plenum, New York.

Gunnell, G.F., Gingerich, P.D., ul-Haq, M., Bloch, J.I., Khan, I.H., and Clyde, W.C. 2008. New euprimates (Mammalia) from the early and middle Eocene of Pakistan. *Contributions from the Museum of Paleontology, The University of Michigan* 32: 1–14.

Huang, X.-S. and Zheng, J.-J. 1999. A new tillodont from the Paleocene of Nanxiong Basin, Guangdong. *Vertebrata PalAsiatica* 37 (2): 96–104.

Huang, X.-S. and Zheng, J.-J. 2003. A tillodont-like mammal from the middle Paleocene of Qianshan Basin, Anhui, China. *Vertebrata PalAsiatica* 41 (2): 131–136.

Lucas, S.G. 1993. Pantodonts, tillodonts, uintatheres, and pyrotheres are not ungulates. *In*: F.S. Szalay, M.J. Novacek, and M.C. McKenna (eds.), *Mammal Phylogeny—Placentals*, 182–194. Springer-Verlag, New York.

Lucas, S.G. and Kondrashov, P.E. 2004. A new species of *Deltatherium* (Mammalia, Tillodontia) from the Paleocene of New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 26: 45–53.

Lucas, S.G. and Schoch, R.M. 1981. *Basalina*, a tillodont from the Eocene of Pakistan. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie* 21: 89–95.

Lucas, S.G. and Schoch, R.M. 1998. Tillodontia. *In*: C.M. Janis, K.M. Scott, and L.L. Jacobs (eds.), *Evolution of Tertiary Mammals of North America. Volume 1: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals*, 268–273. Cambridge University Press, Cambridge.

McKenna, M.C. and Bell, S.K. 1997. *Classification of Mammals Above the Species Level*. 631 pp. Columbia University Press, New York.

Miyata, K. and Tomida, Y. 1998. A new tillodont from the early middle Eocene of Japan and its implication to the subfamily Trogosinae (Tillodontia: Mammalia). *Paleontological Research* 2: 53–66.

Nel, A., de Plöeg, G., Dejax, J., Dutheil, D., de Franceschi, D., Gheerbrant, E., Godinot, M., Hervet, S., Menier, J.-J., Augé, M., Bignot, G., Cavagnetto, C., Duffaud, S., Gaudant, J., Hua, S., Jossang, A., de Lapparent de Broin, F., Pozzi, J.-P., Paicheler, J.-C., Beuchet, F., and Rage, J.-C. 1999. Un gisement sparnacien exceptionnel à plantes, arthropodes et vertébrés (Éocène basal, MP7): Le Quesnoy (Oise, France). *Comptes Rendus de l'Académie des Sciences de Paris, Sciences de la Terre et des Planètes* 329: 65–72.

Rage, J.-C., Folie, A., Rana, R.S., Singh, H., Rose, K.D., and Smith, T. 2008. A diverse snake fauna from the early Eocene of Vastan Lignite Mine, Gujarat, India. *Acta Palaeontologica Polonica* 53: 391–403.

Rana, R.S., Kumar, K., Escarguel, G., Sahni, A., Rose, K.D., Smith, T., Singh, H., and Singh, L. 2008. An ailuravine rodent from the lower Eocene Cambay Formation at Vastan, western India, and its palaeobiogeographic implications. *Acta Palaeontologica Polonica* 53: 1–14.

Rana, R.S., Singh, H., Sahni, A., Rose, K.D., and Saraswati, P.K. 2005. Early Eocene chiropterans from a new mammalian assemblage (Vastan Lignite Mine, Gujarat, Western Peninsular Margin): oldest known bats from Asia. *Journal of the Palaeontological Society of India* 50: 93–100.

Rose, K.D. 1981. The Clarkforkian Land-Mammal Age and mammalian faunal composition across the Paleocene–Eocene boundary. *University of Michigan Papers on Paleontology* 26: 1–197.

Rose, K.D. 2006. *The Beginning of the Age of Mammals*. 428 pp. Johns Hopkins University Press, Baltimore.

Rose, K.D., DeLeon, V.B., Missiaen, P., Rana, R.S., Sahni, A., Singh, L., and Smith, T. 2008. Early Eocene lagomorph (Mammalia) from western India and the early diversification of Lagomorpha. *Proceedings of the Royal Society of London B* 275: 1203–1208.

Rose, K.D., Rana, R.S., Sahni, A., Kumar, K., Missiaen, P., Singh, L., and Smith, T. 2009. Early Eocene primates from Gujarat, India. *Journal of Human Evolution* 56: 366–404.

Rose, K.D., Smith, T., Rana, R.S., Sahni, A., Singh, H., Missiaen, P., and Folie, A. 2006. Early Eocene (Ypresian) continental vertebrate assemblage from India, with description of a new anthracobunid (Mammalia, Tethytheria). *Journal of Vertebrate Paleontology* 26: 219–225.

Sahni, A., Saraswati, P.K., Rana, R.S., Kumar, K., Singh, H., Alimohammadian, H., Sahni, N., Rose, K.D., Singh, L., and Smith, T. 2006. Temporal constraints and depositional palaeoenvironments of the Vastan Lignite Sequence, Gujarat: analogy for the Cambay Shale hydrocarbon source rock. *Indian Journal of Petroleum Geology* 15: 1–20.

Smith, T., Rana, R.S., Missiaen, P., Rose, K.D., Sahni, A., Singh, H., and Singh, L. 2007. Highest diversity of earliest bats in the Early Eocene of India. *Naturwissenschaften* 94: 1003–1009.

Stucky, R.K. and Krishtalka, L. 1983. Revision of the Wind River faunas, early Eocene of central Wyoming. Part 4. The Tillodontia. *Annals of Carnegie Museum* 52: 375–391.

Ting, S. and J. Zheng. 1989. The affinities of *Interogale* and *Anchilestes* and the origin of Tillodontia. *Vertebrata PalAsiatica* 27: 77–86.

Tong, Y.-S. and Wang, J.-W. 2006. Fossil mammals from the early Eocene Wutu Formation of Shandong Province. *Palaeontologia Sinica* 192, *new series C* (28): 1–195.

Tong, Y.-S., Wang, J.-W., and Fu, J.-F. 2003. *Yuesthonyx*, a new tillodont (Mammalia) from the Paleocene of Henan. *Vertebrata PalAsiatica* 41: 55–65.

Wang, Y.-Q. and Jin, X. 2004. A new Paleocene tillodont (Tillodontia, Mammalia) from Qianshan, Anhui, with a review of Paleocene tillodonts from China. *Vertebrata PalAsiatica* 42 (1): 13–26.

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