PALÆO VERTEBRATA

ARTICLE

First early Eocene tapiroid from India and its implication for the paleobiogeographic origin of perissodactyls

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Abstract: The presence of cambaytheres, the sister group of perissodactyls, in western India near or before the time of collision with Asia suggests that Perissodactyla may have originated on the Indian Plate during its final drift towards Asia. Herein we reinforce this hypothesis by reporting two teeth of the first early Eocene tapiromorph Perissodactyla from the Cambay Shale Formation of Vastan Lignite Mine (c. 54.5 Ma), Gujarat, western India, which we allocate to a new genus and species, *Vastanolophus holbrooki*. It presents plesiomorphic characters typical of the paraphyletic "Isectolophidae," such as small size and weak lophodonty. However, the weaker hypoconulid and low paralophid, higher cusps, lower cristid obliqua, and the lingual opening of the talonid are found in Helaletidae, the most primitive tapiroid family. *V. holbrooki*, gen. et sp. nov., may be the oldest and the most primitive tapiroid, suggesting that at least tapiroid perissodactyls originated on India.

Keywords: Paleogene, Vastan, Ceratomorpha, Tapiromorpha, Helaletidae

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INTRODUCTION

Perissodactyla is an order of ungulate mammals that includes the extant hippomorphs (equoids) and ceratomorphs (tapiroids and rhinocerotoids) and their extinct relatives, and other extinct groups (chalicotherioids, "isectolophids," and brontotherioids) (Hooker, 2005) (Fig. 1). It was during the Paleocene-Eocene Thermal Maximum, c. 56 Ma ago that perissodactyls (together with artiodactyls and primates) first appeared across the Holarctic continents (Gingerich, 2006; Smith *et al*., 2006), but their geographic origin is unclear (Krause & Maas, 1990). Recently, the presence of cambaytheriids, the sister group of perissodactyls, in the early Eocene Vastan Lignite Mine, western India near or before the time of collision with Asia, suggests that Perissodactyla may have originated on the Indian Plate during its final drift towards Asia (Rose *et al.*, 2014).

The Cambay Shale Formation, exposed at the Vastan open cast lignite mine near the Vastan village about 40 km northeast of Surat, Gujarat, western India (Sahni *et al*., 2006: fig. 1), is known for its well-preserved diverse fauna of terrestrial mammals as well as other vertebrates (Bajpai *et al*., 2005; Rose *et al*., 2006). The latter include marine and non-marine fishes (Rana, *et al*., 2004; Nolf *et al*., 2006), the earliest ranid and bombinatorid frogs (Bajpai & Kapur, 2008; Folie *et al*., 2013), agamid lizards (Prasad & Bajpai, 2008; Rana *et al*., 2013), terrestrial and aquatic snakes (Rage *et al*., 2008), and oldest birds of the Indian subcontinent (Mayr *et al*. 2007, 2010, 2013). The mammalian fauna of the Cambay Shale Formation is represented by the earliest modern mammals from the Indian subcontinent with the highest diversity of early bats (Rana *et al*., 2005; Smith *et al*., 2007), the earliest lagomorph (Rose *et al*., 2008), the first Asian ailuravine rodent (Rana *et al*., 2008), primitive adapoid and omomyid primates (Rose *et al*., 2009a), primitive artiodactyls (Kumar *et al*., 2010), the first Indian tillodonts (Rose *et al*. 2009b, 2013), the oldest hyaenodontid in South Asia (Bajpai *et al*., 2009; Rana *et al*., 2015), and perissodactyl-like cambaytheres (Bajpai *et al*., 2006; Rose *et al*., 2014).

We report here two teeth of the first early Eocene tapiromorph from India. It shares several characters with the family Helaletidae and has been discovered, like cambaytheriids, in the Cambay Shale Formation of Vastan Lignite Mine, Gujarat, western India (about 54.5 Ma, see discussion of the age of Vastan mammals in Rose *et al*., 2014). The age of the fossils here described and their geographic location suggest that at least tapiroids may have originated on India.

Abbreviations:

AMNH, American Museum of Natural History, New York, USA; GSP-UM, Geological Survey of Pakistan–University of Michigan collection, Quetta, Pakistan; GU/RSR/VAS, Garhwal University–Vastan collection, Srinagar, India; H-GSP, Howard University–Geological Survey of Pakistan, Quetta, Pakistan; IRSNB, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LMA, Land Mammal Age

(ALMA: Asian LMA; NALMA: North American LMA); LUVP Lucknow University (Vertebrate paleontology), Lucknow, India; ONG/K, Oil and Natural Gas Commission–Kalakot collection, Dehradun, India; UM, University of Michigan, Ann Arbor, Michigan, USA; USNM, United States National Museum, Washington, USA; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut, USA.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order PERISSODACTYLA Owen, 1848
Suborder TAPIROMORPHA Haeckel, 1866
Infraorder CERATOMORPHA Wood, 1937
Super-family TAPIROIDEA Gill, 1872
Family HELALETIDAE? Osborn, 1892
Vastanolophus gen. nov.

Type and only known species. *Vastanolophus holbrooki* sp. nov.

Etymology. Vastan, referring to Vastan Mine, the locality from where this genus was first reported; and Greek *lophus*, crest, a common root in tapiromorph names.

Diagnosis. As for type species.

Vastanolophus holbrooki sp. nov.
Figs. 2-3

Holotype. GU/RSR/VAS 323, right m1.

Referred specimen. GU/RSR/VAS 1681, right fragmentary p4.

Etymology. The species name is in honor of Dr. Luke Holbrook, in recognition of his important contributions to the knowledge of tapiromorph perissodactyls.

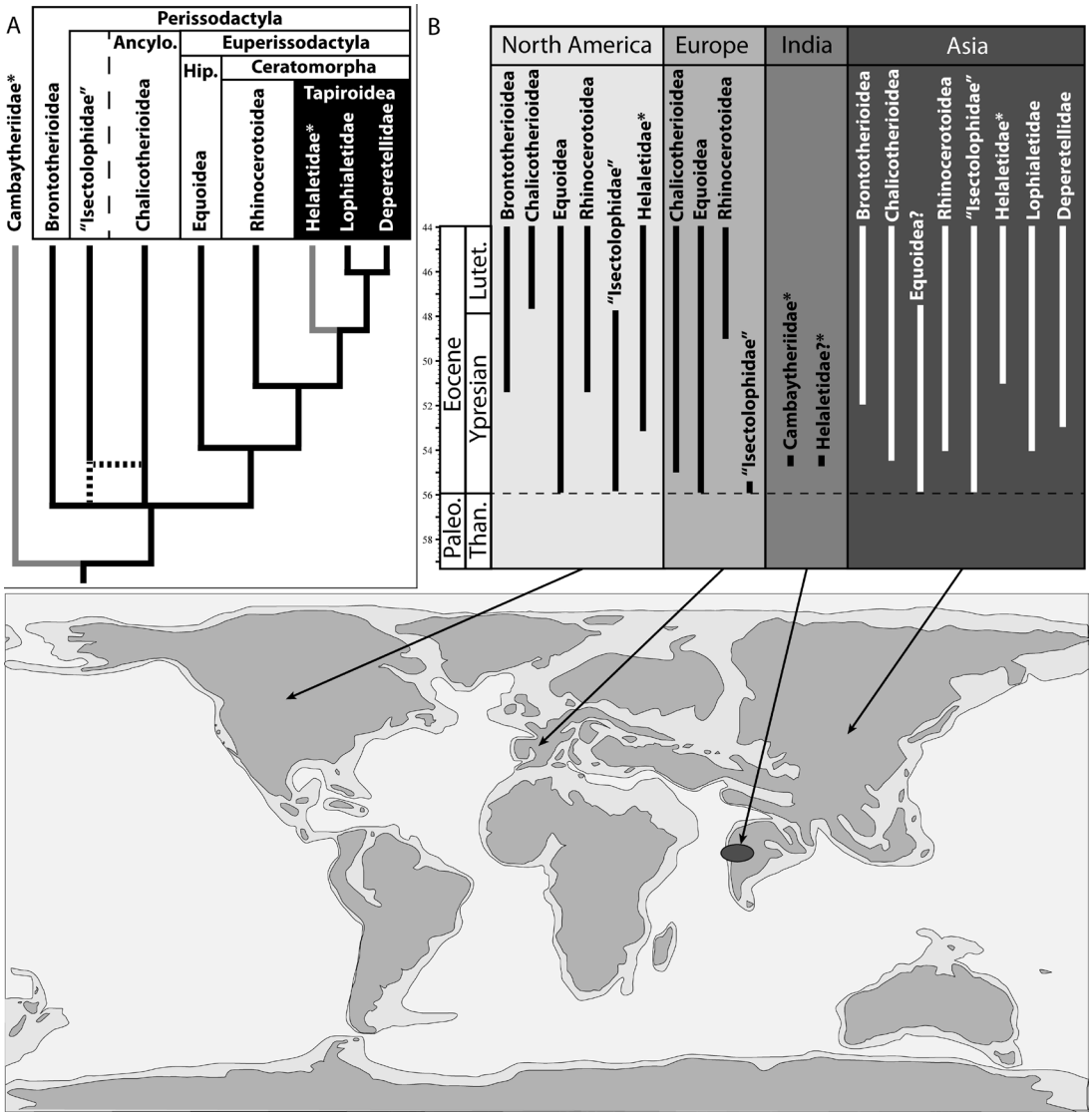

Figure 1. A, Simplified phylogeny of the perissodactyls with indication of the families recorded in Vastan (grey lines); modified from Holbrook (1999), Hooker & Dashzeveg (2004), Cooper *et al.* (2014) and Rose *et al.* (2014). **B**, Temporal range and geographic distribution of families and superfamilies of early perissodactyls in Laurasia. Chalicotherioidea include the Lophiodontidae, Chalicotheriidae and Eomoropidae; Equoidea include the Equidae and Palaeotheriidae; Rhinocerotoidea include the Hyracodontidae and Rhinocerotidae. Hooker & Dashzeveg (2004) considered that several "isectolophids" are closely related to Chalicotherioidea and should be included in Ancylopoda. *= families recorded in Vastan.

Type locality and age. Vastan Lignite Mine (1-2 m above lower lignite: Lignite 2), about 40 km northeast of Surat, Gujarat, western India; Cambay Shale Formation, Ypresian, early Eocene.

Diagnosis. Small tapiroid with relatively narrow m1 (length:width ratio of about 1.57), low degree of lophodonty similar to isectolophids *Homogalax* and *Karagalax*, low hypoconulid weakly developed and completely isolated posterior to the hypolophid, and cristid obliqua more lingually directed than in helaletids *Heptodon* and *Helaletes*.

Measurements. p4 = 6.37 x 4.94 (trig.) mm; m1 = 8.51 x 5.27 (trig.) x 5.41 (tal.) mm.

Description

The p4 is broken and only the trigonid and a very small lingual part of the talonid are preserved. The trigonid cusps are close to each other and the greater constriction behind the trigonid suggests a p4 more than a molar. It presents a low paracristid that bears a small bulge (paraconid?). The protoconid and metaconid are low and have a similar height. A small cristid at the back of the metaconid descends posteriorly. No cristid obliqua is visible. A labial cingulum is present.

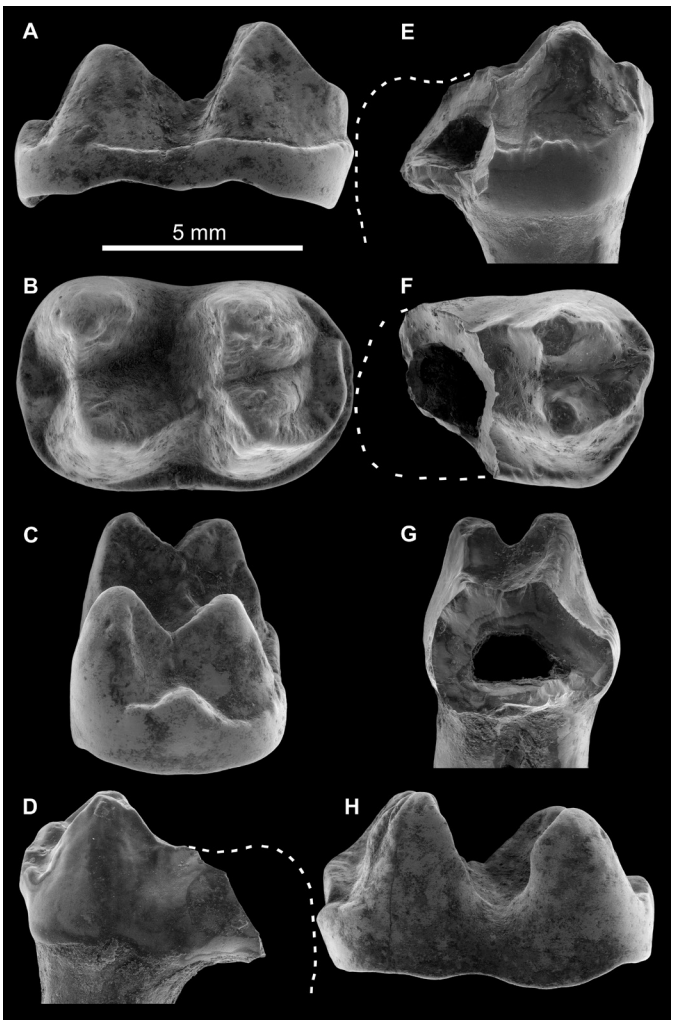

Figure 2. *Vastanolophus holbrooki* gen. et sp. nov. from the early Eocene of Vastan mine, India. A-C, H: GU/RSR/VAS 323, right m1 in labial (**A**), occlusal (**B**), distal (**C**), and lingual (**H**) views. D-G: GU/RSR/VAS 1681, right fragmentary p4, in labial (**E**), occlusal (**F**), distal (**G**), and lingual (**D**) views.

The m1 is very well preserved. No wear and no roots are present, suggesting a freshly erupted or possibly unerupted tooth. The trigonid width is slightly less than the talonid width, more like m1 than m2. The length of the tooth is 1.5 times its width, giving it a relatively elongate, rectangular shape in occlusal view. The paracristid is J-shaped with no paraconid, forming a low paralophid. The protolophid and hypolophid are transverse rather than oblique, and the ectocingulid, though weak on the hypoconid, appears to be complete.

The protoconid, metaconid, hypoconid, and entoconid are relatively high and the lophodonty is weakly developed because of relatively deep notches between metaconid-protoconid and entoconid-hypoconid. The cristid obliqua is relatively internally directed because of a deeper hypoflexid than in *Heptodon*, *Selenaletes*, and *Helaletes*. The low hypoconulid is weakly developed and completely isolated posterior to the hypolophid. The enamel is weakly crenulated on the paracristid, protolophid and hypolophid.

DISCUSSION

Systematic affinities

The perissodactyls appeared abruptly across Laurasia shortly after the Paleocene-Eocene boundary (Gingerich, 1989; Ting, 1993; Ting *et al.*, 2003; Rose *et al.*, 2012; Missiaen *et al.*, 2013). Most of the major clades of perissodactyls seem to have originated during the early Eocene (Fig. 1A). Despite an excellent fossil record, it is hard to reconstruct the relationships within Perissodactyla and understand their early radiation. Consequently, establishing the phylogenetic position of *Vastanolophus*, based on only two teeth, is a complex task.

The cristid obliqua of the molar extends mesially and slightly lingually, a characteristic of tapiromorphs according to Hooker (1984). By contrast, this structure extends more lingually – to the middle of the metalophid or even close to the metaconid – in early equoids (e.g., *Hyracotherium* sensu lato). Moreover, the metaconid is not twinned in GU/RSR/VAS 323, whereas the metaconid of the molars is typically twinned in cambaytheriids (Rose *et al.*, 2014) and early perissodactyls such as early equoids and some isectolophids (Hooker, 1984, 2005). Consequently, the new taxon from Vastan should be compared with Tapiromorpha (*sensu* Holbrook, 1999).

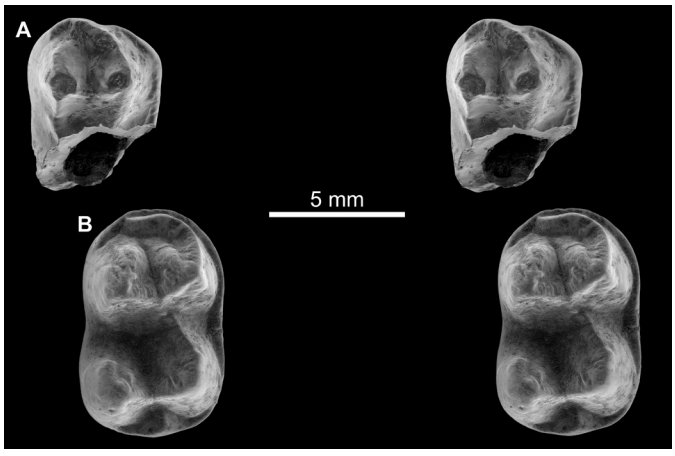

Figure 3. *Vastanolophus holbrooki* gen. et sp. nov. from the early Eocene of Vastan mine, India. Stereo pair in occlusal view of GU/RSR/VAS 1681, right fragmentary p4 (**A**) and GU/RSR/VAS 323, right m1 (**B**).

"Isectolophidae" is a paraphyletic assemblage that was regarded for a long time as the most primitive family of tapiromorphs (Radinsky, 1969). The following genera are generally referred to "Isectolophidae": *Isectolophus* and *Cardiolophus* from North America; *Homogalax* from North America and Asia; *Orientolophus*, *Chowliia*, *Karagalax*, *Kalakotia*, *Meridiolophus* and *Gandheralophus* from Asia; and *Cymbalophus* from Europe (Gingerich, 1991; Ting, 1993; Tong & Wang, 2006; Missiaen & Gingerich, 2012; Missiaen *et al*., 2013; Bai *et al*., 2014). The composition and validity of the family have recently been considered by several authors. Holbrook (1999) restricted the Isectolophidae to the genus *Isectolophus* and considered this family as the sister-group of Ceratomorpha. *Orientolophus* was excluded from the Isectolophidae by Hooker & Dashzeveg (2004) and considered as the most basal member of the Lophodontomorpha (= Ancylopoda + Euperissodactyla). Finally, other "isectolophids" (e.g., *Cardiolophus*, *Homogalax*, *Gandheralophus*) have been interpreted to have closest affinities with Chalicotherioidea and Lophiodontidae, and consequently are considered as stem members of Ancylopoda (Hooker & Dashzeveg, 2004; Bai *et al*., 2014). Whatever the exact relationships of "isectolophids" may be, a comparison with these taxa can enlighten the systematic position of *Vastanalophus*.

The small size of the Vastan tapiromorph is similar to the early-middle Eocene Asian "isectolophids" *Orientolophus hengdongensis* and *Meridiolophus expansus* from China (Ting, 1993; Bai *et al*., 2014), *Karagalax mammikhelensis* and *Gandheralophus robustus* from Pakistan (Maas *et al*., 2001; Missiaen & Gingerich, 2012), and *Kalakotia simplicidentata* from India (Ranga Rao, 1972) (Table 1).

Vastanolophus holbrooki shares with *Orientolophus* and the above mentioned "isectolophids" the weak development of lophodonty, which is characterized by the presence of notched protolophid and hypolophid, and a strong labial cingulid (Table 2). It is similar to *Orientolophus* and *Gandheralophus* in m1 length-width ratio (between 1.53 and 1.57; see Table 1). This ratio is only slightly lower for the large North American "isectolophids" *Homogalax protapirinus* and *Cardiolophus radinskyi*. This feature also clearly distinguishes *Vastanolophus* from *Meridiolophus*, which has a very low ratio close to 1.30, and from *Karagalax* and *Kalakotia* which have higher ratios (between 1.70 and 1.80). These two latter taxa have already been suggested to form a separate South Asian isectolophid lineage (Missiaen & Gingerich, 2012). However, examination of the specimen LUVP 15013 of *Kalokotia simplicidentata* Ranga Rao, 1972, from Kalakot, which was originally described as *Schlosseria radinskyi* by Sahni and Khare (1973) before its synonymy by Thewissen *et al.* (1987), shows that it is a little smaller than the holotype of *K. simplicidentata* (ONG/K/10), with different proportions, and with a m1 length-width ratio of 1.56 (Table 1). Despite that this ratio is similar to that of *Vastanolophus holbrooki*, the morphology of LUVP 15013 differs by the high paralophid and the low cusps that indeed characterize *K. simplicidentata*. However, some morphological differences with the holotype ONG/K/10, such as the reduced metaconid on p3 and narrower hypoconulid on m3, could suggest a different species of *Kalakotia*.

Vastanolophus differs from the younger "isectolophids" *Gandheralophus* and *Kalakotia*, and the older "isectolophid" *Orientolophus*, by having more reduced hypoconulid and paralophid, a more lingually open talonid, a lower metalophid and higher cusps. It shares with *Karagalax* only the high cusps and lingual opening of the talonid. These derived features are found typically in tapiroid clades. The presence of these features together with an older age suggest that *Vastanolophus* belongs to a different lineage than these taxa and was separated early from them, possibly by the earliest Eocene.

The features that distinguish the Vastan species from "isectolophids" (weaker hypoconulid and paralophid, higher cusps, and lower cristid obliqua), as well as the separation of the metaconid and entoconid, are found in the tapiroid family Helaletidae, which are the most primitive tapiroids (Radinsky, 1969). They are, in general, also typical forms throughout the ensuing Bridgerian NALMA and Arshantan/Irdinmanhan ALMA. The genus *Heptodon* has been considered the most primitive helaletid, although Holbrook (1999) placed it in its own family, Heptodontidae. *Heptodon calciculus* marks the beginning of the late Wasatchian (Wa-6) in North America (Gingerich, 1991), and *Vastanolophus holbrooki* shares with it the strong reduction of the hypoconulid and paralophid, and the lingual opening of the talonid. A substantial difference from *Heptodon* is the much less pronounced lophodonty: *Heptodon* has very strong crosslophs of almost constant elevation and no notches. Other differences from *Heptodon* include the distinctly smaller size (Table 1), the transversely somewhat narrower shape, the slightly less reduced hypoconulid, and the stronger labial cingulid. As noted above, these differences are found in "isectolophids" and are generally considered primitive among perissodactyls. It is worth mentioning that *Karagalax*, which has several derived features in common with *Vastanolophus*, has been found to be closely related to *Heptodon* by Hooker & Dashzeveg (2004) and Bai *et al.* (2014). *Heptodon tianshanensis* is the oldest recorded Asian Helaletidae. It is based on a fragmentary maxillary bearing M1-3 from the Shisanjianfang Formation (Xinjiang Province, China) (Zhai, 1978), corresponding to the late early Eocene Bumbanian *Heptodon* interval (Missiaen, 2011). As *Vastanolophus* is known only from two lower teeth, it is impossible to compare the two species, but the Chinese species is distinctly larger than *Vastanolophus*. However, this is not surprising because the Chinese species is much younger than the Indian one.

Other small tapiromorphs such as *Selenaletes*, *Fouchia*, and *Dilophodon* have been related to helaletids. They are restricted to the latest early Eocene and middle Eocene of North America and distinguished from other helaletids including *Vastanolophus* by the absence of the hypoconulid on m1-3. They seem to form a separate group and their tapiroid affinities are still debated (Radinsky, 1966a; Emry, 1989; Colbert & Schoch, 1998; Zonneveld & Gunnell, 2003; Colbert, 2006).

Besides the Helaletidae that are the closest to *Vastanolophus*, early tapiroids are represented by two other families: Lophialetidae and Deperetellidae. However, they are more derived than helaletids. Lophialetidae such as *Lophialetes* and *Schlosseria* are small to medium size tapiroids that are distinguished by having oblique cross crests on molars and a rhinocerotoid-like cusp pattern, with relatively high paralophids and cristid obliqua (Radinsky, 1965). The oldest record and most plesiomorphic lophialetid is *Minchenoletes erlianensis* from the early Eocene of the Erlian Basin in Inner Mongolia, China (Wang *et al.*, 2011). It is smaller and more derived than *Vastanolophus holbrooki*, with a typical lophialetid morphology, but with a lesser degree than in *Lophialetes* and *Schlosseria* (Table 2). Deperetellidae such as *Deperetella* are medium to large size derived tapiroids that have lower molars with two parallel cross lophs, and paralophid and cristid obliqua extremely reduced (Radinsky, 1965).

In conclusion, the new Vastan species appears to be morpho-

logically intermediate between "isectolophids," notably Asian representatives, and the earliest helaletids (e.g., *Heptodon*). However, its derived morphology (lingual opening of the talonid and strong reduction of the hypoconulid) compared to both younger and older Asian "isectolophids" suggests that *Vastanolophus* is more closely related to helaletids than to "isectolophids." Thus we interpret *Vastanolophus* as a primitive tapiroid.

Implications for early perissodactyl paleobiogeography

Since perissodactyls appeared almost simultaneously in Europe, Asia and North America at the beginning of the Eocene, 56 Ma ago (Fig. 1B), the place of their origin has long been disputed and numerous authors have tentatively reconstructed the biogeographic history of the earliest perissodactyls from North America, Central America, Africa, India, or Asia (see Hooker, 2005, for a summary).

Until recently, two major areas were still envisaged as a potential geographic source for Perissodactyla: North America and Asia. The hypothesis of a North American origin is supported by possible relationships between perissodactyls and phenacodontid condylarths (Radinsky, 1966b), the North American continent being the main area of diversity for phenacodontid condylarths. However, the absence of morphological intermediates in the late Paleocene strata is a major weakness of this hypothesis. The hypothesis of an Asian origin (excluding India) was notably proposed by Beard (1998), who suggested it based on a study of the perissodactyl-like mammal *Radinskya* and on fragmentary teeth of a *Lambdotherium*-like mammal from the late Paleocene of China. This hypothesis has been more recently better supported by including the Asian phenacodontid *Lophocion* from the early Eocene of Wutu, China (Wang & Tong, 1997) in new phylogenetic studies

Family	Taxa	Locality and Age	Specimen	Size of m1	Ratio L/W	Reference
Helaletidae?	*Vastanolophus holbrooki*	Cambay Shale Fm., India; early Eocene	GU/RSR/ VAS 323	8.51 x 5.41	1.57	This paper
"Isectolophidae"	*Isectolophus latidens*	Bridger Fm., Wyoming; middle Eocene	*	10.88 x 7.10	1.53	Radinsky, 1963
"Isectolophidae"	*Orientolophus hengdongensis*	Lingcha Fm., China; earliest Eocene	IVPP V5789	7.02 x 4.60	1.53	Ting, 1993
"Isectolophidae"	*Cymbalophus cuniculus*	Tienen Fm., Belgium; earliest Eocene	IRSNB M167	6.79 x 4.95	1.37	Missiaen *et al*., 2013
"Isectolophidae"	*Karagalax mammikhelensis*	Mami Khel Fm., Pakistan; early middle Eocene	H-GSP 5139	7.58 x 4.45	1.70	Maas *et al.*, 2001
"Isectolophidae"	*Gandheralophus robustus*	Ghazij Fm., Pakistan; late early Eocene	GSP-UM6768	6.76 x 4.31	1.57	Missiaen & Gingerich, 2012
"Isectolophidae"	*Gandheralophus minor*	Ghazij Fm., Pakistan; late early Eocene	GSP-UM6770	5.16 x 3.35	1.54	Missiaen & Gingerich, 2012
"Isectolophidae"	*Kalakotia simplicidentata*	Subathu Fm., India; middle Eocene	ONG/K/10	8.48 x 4.71	1.80	Ranga Rao, 1972
"Isectolophidae"	*Kalakotia simplicidentata*	Subathu Fm., India; middle Eocene	LUVP 15013/1b	8.10 x 5.20	1.56	Sahni & Khare, 1973
"Isectolophidae"	*Meridiolophus expansus*	Huayong Fm., China; early Eocene	IVPP 20125	7.40 x 5.60	1.32	Bai *et al.*, 2014
"Isectolophidae"	*Homogalax protapirinus*	Willwood Fm., Wyoming; middle early Eocene (Wa-4)	UM 66650	9.98 x 6.77	1.47	Gingerich, 1991
"Isectolophidae"	*Cardiolophus radinskyi*	Willwood Fm., Wyoming; early early Eocene (Wa-1)	UM 64913	8.33 x 5.91	1.41	Gingerich, 1991
"Isectolophidae"	*Chowliia laoshanensis*	Wutu Fm., China: late early Eocene	IVPP V10740.7	10.20 x 7.20	1.42	Tong & Wang, 2006
Helaletidae	*Heptodon calciculus*	Wind River Fm., Wyoming; early Eocene	AMNH 4858	8.70 x 6.32	1.37	Cope, 1880
Helaletidae	*Helaletes nanus*	Bridger Fm., Wyoming; latest early Eocene	YPM 11080	9.92 x 6.75	1.46	Marsh, 1871
Helaletidae?	*Selenaletes scopaeus*	Wind River Fm., Wyoming; early Eocene	AMNH 8230	7.00 x 4.70	1.52	Radinsky, 1966a
Helaletidae?	*Fouchia elyensis*	Sheep Pass Fm., Nevada; middle Eocene	USNM 417339	5.50 x 4.10	1.34	Emry, 1989
Lophialetidae	*Lophialetes expeditus*	Indin Manha Fm., China; late early Eocene	AMNH 19162	11.00 x 8.20	1.34	Matthew & Granger, 1925
Lophialetidae	*Schlosseria magister*	Arshanto Fm., China; middle Eocene	AMNH 20243	10.60 x 7.60	1.39	Radinsky, 1965
Lophialetidae	*Minchenoletes erlianensis*	Nomogen Fm.,China; early Eocene	IVPP V 14694	6.75 x 4.32	1.56	Wang *et al.*, 2011
Deperetellidae	*Deperetella cristata*	Shara Murun Fm., China; late middle Eocene	AMNH 20291	20.00 x 16.70	1.20	Radinsky, 1965

Table 1. Diversity and measurements of m1 of early-middle Eocene "isectolophid" and tapiroid perissodactyls used in the present study. Fm.: Formation; Wa: Wasatchian. Size of m1 (LxW) in mm. * = mean of five specimens.

(Hooker & Dashzeveg, 2003, 2004). The latter authors hypothesized that the wide distribution of perissodactyls in the earliest Eocene could be explained by two opposite dispersals out of Asia (Fig. 4). First there was a colonization of Europe by Equidae and other perissodactyls such as the "isectolophid" *Cymbalophus* and hyracodontid rhinocerotoid *Hyrachyus*, across the Turgai Strait; the Equidae then dispersed into North America via the Greenland land bridge. North America was colonized via the Bering land bridge by Brontotheriidae, "Isectolophidae" and Ancylopoda, which then dispersed to Europe (except the Brontotheriidae) via the Greenland land bridge. Recently, Eberle (2005) even proposed a North American origin for tapiroids based on the discovery of the highly derived tapiromorph *Thuliadanta* from the late early Eocene (equivalent to the younger part of the Wasatchian NALMA) on Ellesmere Island, Arctic Canada.

The biogeography of tapiroids thus appears important for understanding their early dispersals as well as the first radiation of the Perissodactyla. Moreover, it is interesting to consider the geographic distribution of the earliest tapiroids because several mammal taxa found in Vastan (bats, rodents, primates, tillodonts) indicate faunal connections between Europe and India during the early Eocene (Smith *et al.*, 2007; Rana *et al.*, 2008; Rose *et al.*, 2009a, 2009b). By contrast, the Vastan fauna displays only a few specific similarities to Asian faunas (Rose *et al.*, 2008).

While the primitive "isectolophids" are recorded throughout Laurasia (Fig. 1B), the oldest and the most primitive tapiroid families (Helaletidae, Lophialetidae and Deperetellidae) are found only in Asia and North America (Radinsky, 1963, 1965; Colbert & Schoch, 1998; Missiaen & Gingerich, 2012, 2014). Astonishingly, no primitive tapiroid is known from Europe (Fig. 1B). This suggests that the new tapiroid from Vastan is part of an Asian-American history, in contrast to the majority of the Vastan mammals. The early age of *Vastanolophus* (54.5 Ma) and its primitive morphology compared to that of the

Family	Taxa	Paralophid	Cusps	Degree of lophodonty	Cristid obliqua	Separation entoconid-metaconid	Labial cingulid	Hypoconulid
Helaletidae?	*Vastanolophus holbrooki*	Low	High	Weak	Low	Well-developed	Present	Weakly developed
"Isectolophidae"	*Isectolophus latidens*	Low	High	Weak	High	Small	Reduced	Developed
"Isectolophidae"	*Orientolophus hengdongensis*	High	Low	Weak	High	Small	Present	Developed
"Isectolophidae"	*Cymbalophus cuniculus*	High	Low	Weak	High	Small	Present	Developed
"Isectolophidae"	*Karagalax mammikhelensis*	High	High	Weak	High	Well-developed	Present	Developed
"Isectolophidae"	*Gandheralophus robustus*	High	Low	Weak	High	Small	Present	Developed
"Isectolophidae"	*Gandheralophus minor*	High	Low	Weak	High	Small	Present	Developed
"Isectolophidae"	*Kalakotia simplicidentata*	High	Low	Weak	High	Small	Present	Developed
"Isectolophidae"	*Meridiolophus expansus*	High	Low	Weak	High	Small	Present	Developed
"Isectolophidae"	*Homogalax protapirinus*	Low	High	Weak	High	Small	Reduced	Developed
"Isectolophidae"	*Cardiolophus radinskyi*	Low	Low	Weak	High	Small	Reduced	Developed
"Isectolophidae"	*Chowliia laoshanensis*	Low	Low	Weak	High	Small	Present	Developed
Helaletidae	*Heptodon calciculus*	Low	High	Strong	Low	Well-developed	Reduced	Weakly developed
Helaletidae	*Helaletes nanus*	Low	High	Strong	Low	Well-developed	Reduced	Weakly developed
Helaletidae?	*Selenaletes scopaeus*	Low	High	Strong	Low	Well-developed	Reduced	Absent
Helaletidae?	*Fouchia elyensis*	Low	High	Strong	Low	Well-developed	Reduced	Absent
Lophialetidae	*Lophialetes expeditus*	High	High	Strong	High	Well-developed	Reduced	Absent
Lophialetidae	*Schlosseria magister*	High	High	Strong	High	Well-developed	Reduced	Absent
Lophialetidae	*Minchenoletes erlianensis*	High	High	Strong	High	Well-developed	Reduced	Weakly developed
Deperetellidae	*Deperetella cristata*	Low	High	Strong	Low	Well-developed	Reduced	Absent

Table 2. Synthetic table of the characters used for establishing the systematic affinities.

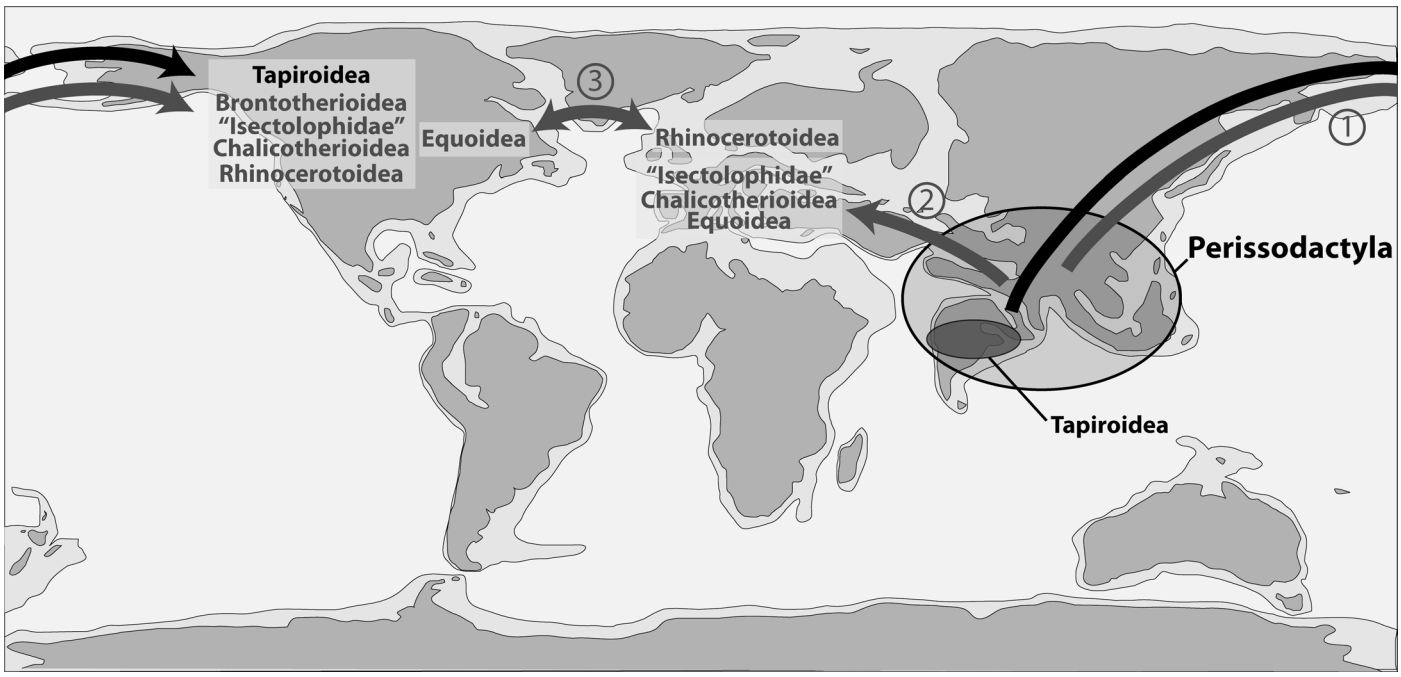

Figure 4. Schematic map showing the geographic dispersal of the early perissodactyls. 1: dispersal via the Bering land bridge; 2: dispersal via land connections across the Turgai Strait and/or along the Tethysian shore; 3: dispersal via the Greenland land bridge (adapted from Ron Blakey, Eocene, http://www2.nau.edu/rcb7/050Marect.jpg).

earliest American helaletids (Wa-6, ≈ 53 Ma; Woodburne *et al.*, 2009) allow the hypothesis that this group emerged in Asia *sensu lato*. Therefore, we propose that helaletids dispersed from Asia into North America during the Wasatchian via the Bering land bridge. Eberle & Eberth (2015) have interestingly demonstrated that some early tapiroids were adapted to Eocene Arctic environments, thus supporting the probability of Trans-Beringian dispersal.

The two rare ceratomorph taxa known from the Ghazij Formation also show affinities between Indo-Pakistan and Asia, but they belong to different families (Lophialetidae and Eomoropidae), and no Helaletidae have been identified (Missiaen & Gingerich, 2012). As noticed by Missiaen & Gingerich (2012, 2014), despite the proximity of Ghazij to Vastan, it is slightly younger (54-50 Ma), and the mammalian composition of the two faunas is not very similar. The discovery of *Vastanolophus* further underscores the difference between the Cambay Shale Formation and the Ghazij Formation. However, because helaletids are known in the middle Eocene of Asia, *Vastanolophus* would represents one of the few links suggesting a direct migration between India and Asia.

In conclusion, the discovery of *Vastanolophus* has important implications for reconstructing the place of origin of the Perissodactyla. As previously mentioned, Rose *et al.* (2014) recently proposed an Indian origin for this mammal group based on the basal position of the cambaytheres known from Vastan, reviving an hypothesis originally proposed by Krause & Maas (1990). The early tapiroid *Vastanolophus* indicates the presence in the Indian locality of definitive primitive Perissodactyla, and its age and plesiomorphic morphology suggests that Tapiroidea might have originated on India.

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