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Oldest South Asian tapiromorph (Perissodactyla, Mammalia) from the Cambay Shale Formation, western India, with comments on its phylogenetic position and biogeographic implications

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ABSTRACT

Kapur VV & Bajpai S 2015. Oldest South Asian tapiromorph (Perissodactyla, Mammalia) from the Cambay Shale Formation, western India, with comments on its phylogenetic position and biogeographic implications. The Palaeobotanist 64(1): 95–103.

A new tapiromorph perissodactyl (*Cambaylophus vastanensis* gen. et sp. nov.) from the basal Eocene (~54–55 Ma) Cambay Shale Formation, Vastan Lignite Mine, Gujarat, western India, is described for the first time. The new taxon, which represents the earliest known tapiromorph from South Asia and the second perissodactyl group in the Vastan mammal fauna after cambaytheres, is based on a partial maxilla with molars and deciduous premolars. *Cambaylophus* differs from Eocene tapiromorphs from the Indian Subcontinent mainly in having relatively narrow and less lophodont upper molars with a small, low and lingually shifted parastyle. Phylogenetic analysis suggests that *Cambaylophus* forms a clade with the early Eocene tapiromorph *Gandheralophus* from Pakistan, and that it is closely nested with the early Eocene (Bumbanian) tapiromorph *Orientolophus* from China. The study points out the importance of *Cambaylophus* in evaluating the evolutionary relationships of early radiation of tapiromorphs and ascertaining the degree of connectivity/isolation of the Indian Subcontinent around the Palaeocene–Eocene boundary, especially in the context of India–Asia collision.

Key–words—Perissodactyla, Tapiromorpha, Eocene, India,Vastan Lignite Mine.

जातिवृत्तीय स्थिति एवं जीवभौगोलिक निहितार्थों पर टिप्पणियों सहित वास्तान भूरा–कोयला खान, पश्चिमी भारत के कैंबे शेल शैलसमूह से प्राप्त प्राचीनतम दक्षिणी एशियाई टैपीरोमॉर्फ (पेरिसोडैक्टाइला, स्तनी वर्ग)

विवेश वीर कपूर एवं सुनील बाजपेई

सारांश

गुजरात, पश्चिमी भारत के वास्तान भूरा–कोयला खान के कैंबे शेल शैलसमूह से आधारी आदिनूतन (~ 5 करोड़ 40 लाख – 5 करोड़ 50 लाख) से प्राप्त एक अभिनव टैपीरोमॉर्फ पेरिसोडेक्टाइल (*कैंबेलोफ़स वास्तेन्सिस* वंश जाति नवम) पहली बार वर्णित की गई है। यह नूतन वर्गक, जो दक्षिण एशिया से प्रारंभिकतम ज्ञात टैपीरोमॉर्फ और कैंबेथेरीज के उपरांत वास्तन स्तनधारी प्राणिजात में द्वितीय पेरिसोडैक्टाइल समूह को निरूपित करता है दाढ़ व पर्णपाती दाढ़पूर्व पर आधारित है। लघु, अल्प एवं जिह्वा रूप से विस्थापित पराशूक सहित मुख्यतया बारीक व अल्प शिखरदंती ऊपरी दाढ़ संगतता रखने (संपदा, व्यवहार) में भारतीय उपमहाद्वीप से प्राप्त आदिनूतन टैपीरोमॉर्फ से *कैंबेलोफस* भिन्न है। जातिवृत्तीय विश्लेषण दर्शाता है कि *कैंबेलोफस* पाकिस्तान से प्राप्त प्रारंभिक आदिनूतन टैपीरोमॉर्फ *गाँधेरालोफस* से क्लेड गठित करता है और यह चीन से प्राप्त प्रारंभिक आदिनूतन (बुंबानियन) टैपीरोमॉर्फ *ओरिएंटोलोफस* दृढ़ता से जटिल है। यह अध्ययन टैपीरोमॉर्फ के प्रारंभिक विकिरण की विकासीय संबंधताएं मूल्यांकित करने और खासतौर पर भारत–एशिया संघट्ट के परिप्रेक्ष्य में पुरानूतन–आदिनूतन सीमा के इर्द–गिर्द भारतीय उपमहाद्वीप की सहयोजिता/विसंगता का अंश सिद्ध करने में *कैंबेलोफस* की महत्ता निर्दिष्ट करता है।

सूचक शब्द—पेरिसोडैक्टाइला, टैपीरोमॉर्फ, आदिनूतन, भारत, वास्तान भूरा कोयला खान।

INTRODUCTION

IN recent years, concerted field work in the Early Eocene lignite–associated sedimentary deposits at Vastan Lignite Mine, District Surat, Gujarat, western India has yielded a diverse assemblage of modern orders of placental mammal fauna that includes artiodactyls, perissodactyls, primates, creodonts and several other groups (e.g. Bajpai *et al*., 2005a, b, 2006, 2008, 2009; Rana *et al.*, 2008; Rose *et al.*, 2013). This mammal fauna has attracted considerable attention because of its stratigraphic, tectonic and palaeogeographic context and is of great importance in tracing the biogeographic origins and early evolutionary history of several modern mammalian orders including perissodactyls and primates (Bajpai *et al.*, 2008; Bajpai, 2009; Clementz *et al.*, 2011). Most recently, Cambaytheriidae, a family of ungulate mammals from Vastan, first named and described as perissodactyls nearly a decade ago (Bajpai *et al.*, 2005a), has been conclusively established as a group of stem perissodactyls (Cooper *et al.*, 2014). Here, we describe a maxillary fragment of the first tapiromorph from Vastan that represents a new taxon and the second perissodactyl group after cambaytheres from the early Eocene of India. This discovery was recently (April, 2015) reported by the authors in a conference entitled "Palaeogene of the Indian Subcontinent" held at Birbal Sahni Institute of Palaeobotany (BSIP), Lucknow, India (Kapur & Bajpai, 2015).

The age of the Vastan mammals was initially considered to be late Early Eocene (middle Ypresian) based on the larger benthic foraminifera *Nummulites burdigalensis* that occurs well above the mammal–yielding level (Sahni *et al.*, 2006). However, the subsequent record of an age–diagnostic dinoflagellate assemblage from several levels at the Vastan lignite mine provided a more reliable basis for age determination, leading to the assignment of a basal Eocene age for the mammal–yielding horizon at Vastan (Garg *et al.*, 2008). Later, Clementz *et al.* (2011), based on the combined assessment of data on $\delta^{13}C$, $^{87}Sr/^{86}Sr$ and dinoflagellates from Vastan recognised a pronounced, negative carbon isotopic shift at a stratigraphic level over 20 m above the mammal horizon, which was correlated to the Second Eocene Thermal

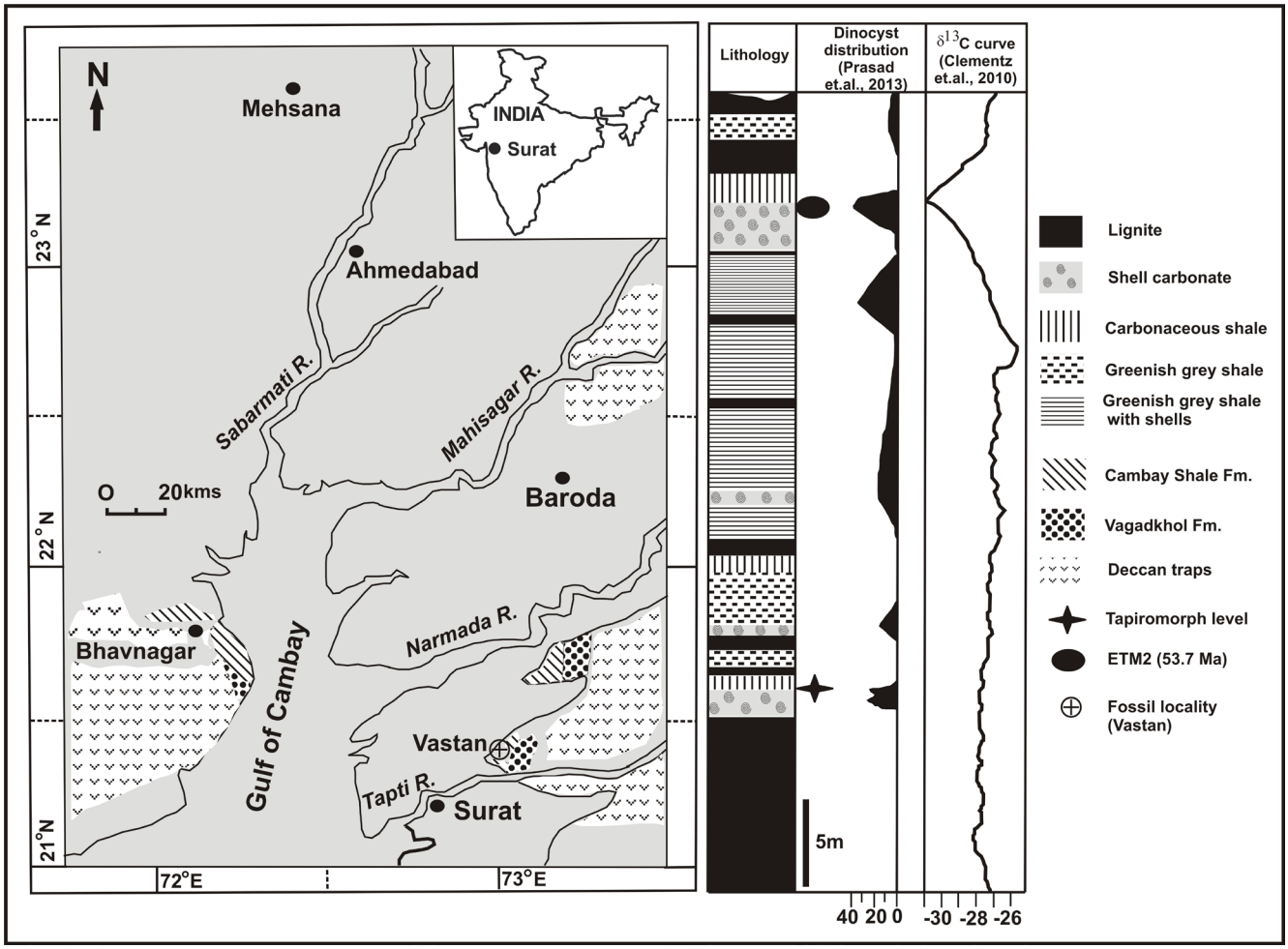

Fig. 1—Location map of the Vastan fossil locality with the lithostratigraphic section (after Prasad *et al.*, 2013).

Maximum (ETM2). Thus, as currently understood, the Vastan mammals, including the tapiroid described here, significantly predate the ETM2 datum (53.7 Ma) and are slightly younger than the Palaeocene–Eocene Thermal Maximum (PETM), which make them the oldest (~ 54.5 Ma) known Cenozoic mammals of South Asia. The details of the fossil locality and lithostratigraphic section are shown in Fig. 1. A detailed lithofacies and palaeoenvironmental analysis of the Vastan section can be found in Prasad *et al.* (2013).

SYSTEMATIC PALAEONTOLOGY

Class—MAMMALIA Linnaeus, 1758

Order—PERISSODACTYLA Owen, 1848

Suborder—TAPIROMORPHA Haeckel, 1866

Superfamily—TAPIROIDEA Gill 1872

Family—indet.

Genus—CAMBAYLOPHUS gen. nov.

(Fig. 2)

Type and only known species—Cambaylophus vastanensis gen. et sp. nov.

Etymology—The genus name is a combination of the name of the formation (Cambay Shale) in which the type species was found, with–*lophus* (masc.), in allusion to the lophodont dentition.

Age and distribution—Early Eocene (~ 54–55 Ma), India (Garg *et al.*, 2008; Clementz *et al.*, 2011).

Diagnosis—Small tapiromorph with squarish upper molars, no diastema between the upper deciduous premolars and molars; upper molars longer than wide, weakly lophodont and with prominent paracone, metacone, protocone and hypocone; posterior cusps closer to each other as compared to the anterior cusps; buccal cusps higher than the lingual cusps with the paracone highest and hypocone lowest; protocone and hypocone widely separated and not connected by any crest; protoloph joins the anterolingual base of the paracone while the metaloph joins the anterolingual base of the metacone; paraconule absent; metaconule weak; parastyle anteroposteriorly compressed, small, low, lingually shifted and located anterior to paracone; buccal cingulum continuous; lingual cingulum discontinuous.

Differential Diagnosis—Cambaylophus (not to be confused with *Cymbalophus*) differs from *Karagalax* by its 30% smaller molar size, weaker lophodonty, higher length/width ratio and an anteroposteriorly compressed, smaller, low, lingually shifted parastyle. Distinguished from *Gandheralophus* by less lophodont and squarish molars, higher length/width ratio, absence of a paraconule, presence of a metaconule, smaller and lingually shifted, low parastyle and by its protoloph joining the anterolingual base of the paracone. Differs from *Homogalax* by its smaller molar size (at least 25%), weaker lophodonty, higher length/width ratio and a smaller, low, lingually shifted parastyle and absence of a paraconule. Differs from *Cardiolophus* by its smaller size of the upper molars; smaller length/width ratio of upper molars; smaller and a low lingually shifted parastyle. Differs from *Isectolophus* by its smaller upper molars with higher length/width ratio; upper molars displaying relatively less lophodonty; presence of a metaconule and presence of a smaller and a low lingually shifted upper molar parastyle. Differs from *Cymbalophus* by the absence of a paraconule and a small, low and lingually shifted parastyle on upper molars. Differs from *Orientolophus* by a smaller, lower and lingually shifted upper molar parastyle, absence of a paraconule and continuous buccal cingulum.

Cambaylophus vastanensis sp. nov.

(Fig. 2)

Holotype—IITR/SB/VLM 760 (right maxillary fragment with alveoli for dP2 and crowns for well preserved dP3–dP4 and M1–M2 and an erupting M3; portion of anterior palate and part of right zygomatic arch are also preserved in this specimen).

Etymology—Species name is in reference to the locality *Vastan*.

Horizon and locality—Cambay Shale; Vastan Lignite Mine, District Surat, Gujarat, western India (Fig. 1).

Age and distribution—As for the genus.

Diagnosis—As for the genus.

Description—IITR/SB/VLM 760 is a right maxillary fragment that preserves damaged alveoli for dP2, well–preserved crowns for dP3–dP4 and M1–M2 and an erupting M3. There is no diastema between the teeth. It is important to note that the holotype exhibits the late retention of deciduous premolars even though M1 and M2 have erupted and the M3 is still erupting in the specimen. The alternative possibility that the teeth really represent dP2 to M2 (erupting) is unlikely since the M1 does not have enough wear as would be expected if it were dP4.

dP2 is double–rooted (inferred from alveoli). dP3 is longer than wide. Four prominent cusps are present on dP3 with the buccal cusps higher and closer to each other than the lingual cusps. The metacone is the highest cusp (slightly higher than paracone) while the protocone is the lowest. The hypocone is markedly higher than the protocone. The protocone and hypocone are widely separated and not connected by any crest. A weak, anteriorly projecting parastyle

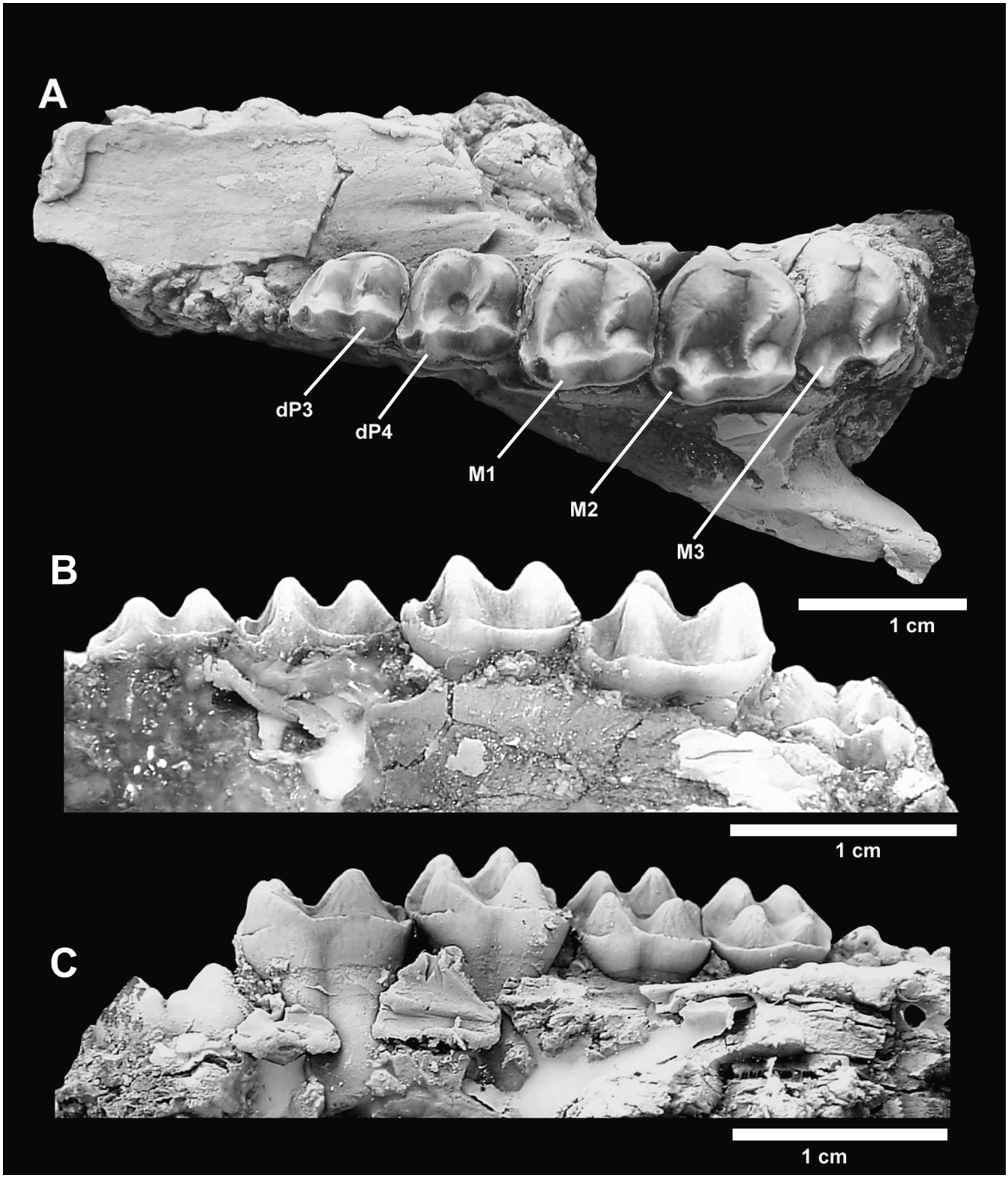

Fig. 2—*Cambaylophus vastanensis* gen. et sp. nov. IITR/SB/VLM 760, (holotype), right maxillary fragment with dP3–dP4 and M1–M3. A, occlusal view B, buccal view C, lingual view.

is present. There is no paraconule, whereas a metaconule is present. A low ridge connects the paracone and metacone. The buccal cingulum is discontinuous at the paracone while the lingual cingulum is complete. The posterior cingulum is broader than the anterior cingulum.

dP4 is squarish in occlusal outline. It is closely similar in morphology to dP3 but differs in being larger, with its buccal margin projecting more buccally than dP3. The paracone is the highest cusp (slightly higher than metacone). The buccal cingulum is continuous, lingual cingulum discontinuous and the anterior cingulum broader than the posterior cingulum.

M1 is bilophodont and high crowned, and has a squarish occlusal outline, only slightly longer than wide. The buccal cusps are higher than the lingual cusps, with the paracone being the highest. The posterior cusps are closely spaced relative to the anterior cusps. The protocone and hypocone are widely separated and are not connected by any crest. M1 preserves a very small, low anteroposteriorly compressed parastyle that is shifted lingually. The transverse lophs on M1 are more pronounced than those in the deciduous premolars. A low ridge connects the paracone with metacone. The protoloph and metaloph are present as low ridges with the metaloph shorter than the protoloph. The protoloph terminates at the anterolingual base of the paracone. A low crest joins the paracone and parastyle. The paraconule is absent. The M1 metaloph is anteriorly convex than the protoloph and joins the anterolingual base of the metacone. A very weak metaconule can be observed on the metaloph. The metacone joins the posterocingulum by a short crest. Crenulations are present on the protoloph and metaloph. The anterocingulum is much more developed than the posterocingulum.

M2 and M3 are closely similar in morphology to M1, but the molar size increases posteriorly (Table 1).

Repository—The specimen is housed in the Vertebrate Palaeontology Laboratory, Department of Earth Sciences, Indian Institute of Technology Roorkee, Uttarakhand under the acronym IITR/SB/VLM.

Comparisons—In general, the molars of *Cambaylophus* are relatively narrow and less lophodont than the other contemporaneous tapiromorphs. In the Indian Subcontinent, the known Eocene tapiromorphs include isectolophids from the Kuldana and Subathu formations (Kumar & Sahni, 1985; Sahni & Jolly, 1993; Maas *et al.*, 2001; Thewissen *et al.*, 2001) and from the upper part of the Upper Ghazij Formation of Pakistan (Missiaen & Gingerich, 2012). These isectolophids include the early middle Eocene *Karagalax mamikhelensis* and the late early Eocene *Gandheralophus minor* and *Gandheralophus robustus*. As shown above, *Cambaylophus* is distinguishable from these younger Indo–Pakistan isectolophids both in morphology and size (Fig. 3).

Outside the Indian Subcontinent, known isectolophids from Asia include *Orientolophus*, *Homogalax* and *Isectolophus* from the early Eocene of China and Mongolia. *Orientolophus* is considered to be the most primitive tapiromorph (Ting 1993, 1998). *Cambaylophus* is similar in size and degree of lophodonty to *Orientolophus* but the two differ in the position of parastyle and the presence/absence of conules on the upper molars. Comparison is not possible with *Meridiolophus expansus*, another early Eocene tapiromorph described recently from the Sansui Basin, South China (Bai *et al.*, 2014), since its upper dentition is not known.

Outside Asia, the best–studied isectolophids are those from North America, represented by *Cardiolophus*, *Homogalax* and *Isectolophus* (Gingerich, 1991; Froehlich, 2002). *Cambaylophus* clearly differs in morphology (see *Differential Diagnosis*) and size from the North American taxa (Fig. 4).

DISCUSSION

Relationships among the various basal groups of perissodactyls including tapiromorphs are not yet fully understood (e.g. Holbrook, 1999; Froelich 1999, 2002; Hooker & Dashzeveg, 2004; Holbrook & Lapergola, 2011; Bai *et al.*, 2014). Although the present material is fragmentary, a preliminary analysis was performed to assess the phylogenetic position of *Cambaylophus* by scoring its dental characters and adding these to the published matrix of Holbrook and Lapergola (2011) which includes a number of early perissodactyl groups including tapiromorphs from Europe, Asia and North America. Additionally, characters for *Karagalax*, *Gandheralophus* and *Meridiolophus* were also scored and were added into the matrix of Holbrook and Lapergola (2011). Also, the rescored character 83 was used for *Homogalax*, *Cardiolophus* and *Palaeosyops* and all characters were treated as unordered in the present analysis. The final matrix incorporates 44 taxa (excluding hyracoids and tethytheres) and 125 characters (character scores for *Cambaylophus* are provided in Table 2). The matrix was analysed using TBR method with 1000 replications (TNT version 1.1, Goloboff *et al.*, 2008). The software, Tree analysis using New Technology (TNT), found 40 Most Parsimonious

Table 1—Measurements (in mm) of the holotype (IITR/SB/VLM 760) of *Cambaylophus vastanensis* gen. et sp. nov.
* estimate.

	dP3	dP4	M1	M2	M3
Max. Length	6.1	6.4	6.9	7.6	6.0*
Max. Width	5.2	6.0	6.6	7.1	7.8

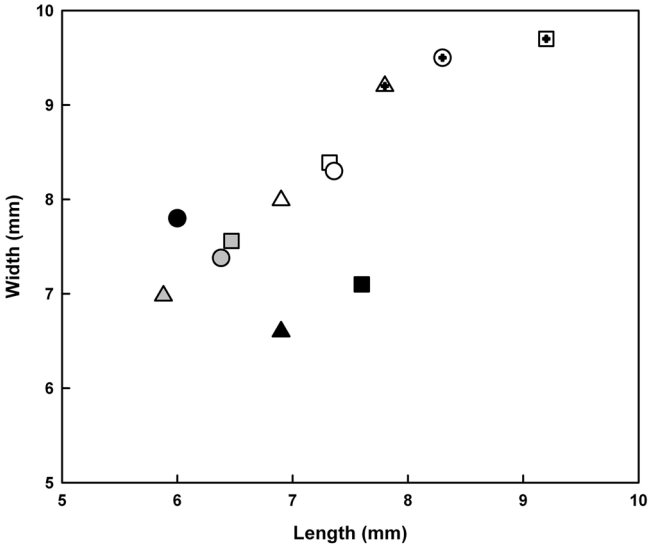

Fig. 3—Bivariate plot (length vs. width) of upper M1's (triangle), M2's (square) and M3's (circle) of *Cambaylophus vastanensis* (black colour); *Gandheralophus minor* (grey colour); *Gandheralophus robustus* (white colour) and *Karagalax mammikhelensis* (white colour with cross symbol). Measurements (mean values) for upper molars of *Gandheralophus minor* and *G. robustus* are from Missiaen and Gingerich (2012) and those for *Karagalax mammikhelensis* are from Mass *et al.* (2001).

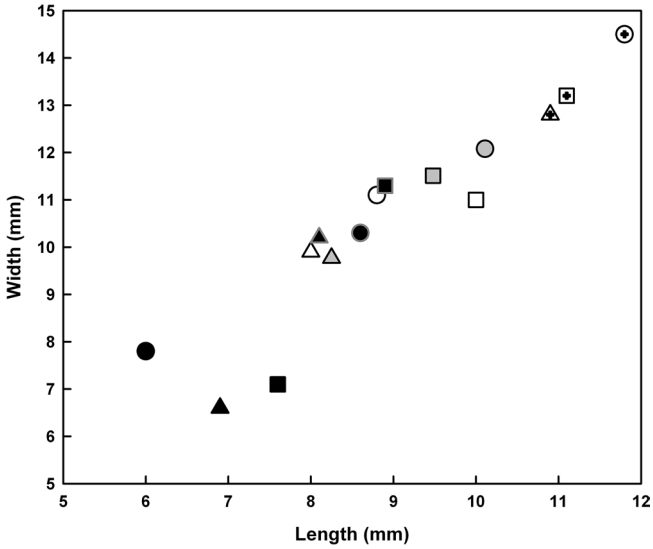

Fig. 4—Bivariate plot (length vs. width) of upper M1's (triangle), M2's (square) and M3's (circle) of *Cambaylophus vastanensis* (black colour); *Cardiolophus radinski* (white colour); *Cardiolophus semihians* (black colour with grey outline); *Homogalax namadicus* (grey colour) and *Isectolophus latidens* (white colour with a cross symbol). Measurements for upper molars of *Cardiolophus radinski* and *Cardiolophus semihians* are from Gingerich (1991), measurements for *Homogalax namadicus* are from Lucas and Kondrashov (2004) and measurements for *Isectolophus latidens* are from Lucas *et al.* (2003).

Trees (MPTs) of Tree Length (TL) 580. The Consistency Index (CI) is 0.326 and the Retention Index (RI) is 0.707. The better resolved Majority Rule (50%) tree is shown as Fig. 5. The results are in general agreement with those of Holbrook and Lapergola (2011) with *Mesolambdolophus* occupying a sister taxon position to Tapiromorpha (clade highlighted in grey in Fig. 5). Isectolophids are a paraphyletic group, as also proposed by Hooker and Dashzeveg (2004) and Bai *et al.* (2014). *Cymbalophus* is a sister taxon to *Systemodon* and as a basal tapiromorph (as favoured by Froehlich 2002). Concerning *Cambaylophus*, two important results emerge from this study. First, *Cambaylophus* is nested within tapiromorphs in all of the 40 MPTs and forms a clade with the early Eocene *Gandheralophus* known from Pakistan. Second, *Cambaylophus* and *Gandheralophus* appear to be more closely related to *Orientolophus* than to the younger tapiromorphs *Karagalax* and *Isectolophus* from Indo–Pakistan. This suggests that both *Cambaylophus* and *Gandheralophus* may have been derived from an *Orientolophus*–like taxon that was possibly present in the Indian Subcontinent around the Palaeocene–Eocene boundary. However, it remains to be shown conclusively whether there were two different tapiromorph lineages in the Indian Subcontinent during the early Palaeogene, as pointed out by Missiaen and Gingerich (2012) in the context of *Gandheralophus* and *Karagalax*. A detailed phytogenetic analysis is beyond the scope of this paper and will be carried out once additional material becomes available.

In Asia, Eocene tapiromorphs are useful in mammalian biochronology and allow the division of the early Eocene Bumbanian ALMA into *Orientolophus*, *Homogalax* and *Heptodon* interval zones (Ting, 1998). Missiaen and Gingerich (2012) attempted a biochronological correlation between the Indo–Pakistan and Asian Eocene land mammals and correlated the Upper Ghazij Formation with middle to late Bumbanian ALMA. The early Bumbanian interval is marked by *Orientolophus* from the upper part of the Lingcha Formation, Hengyang Basin, China (Ting, 1993). Detailed magnetostratigraphic and chemostratigraphic studies show the upper Lingcha fauna containing *Orientolophus* to fall within the reversed polarity zone C24r (Bowen *et al.*, 2002; Ting *et al.*, 2011) and that this fauna occurs ~ 15 m above the Palaeocene–Eocene (P–E) boundary. This suggests that the early Bumbanian mammals (i.e. the *Orientolophus* interval)

Table 2—Character scores for *Cambaylophus vastanensis* gen. et sp. nov.

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2000?  ??00?  12???  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????
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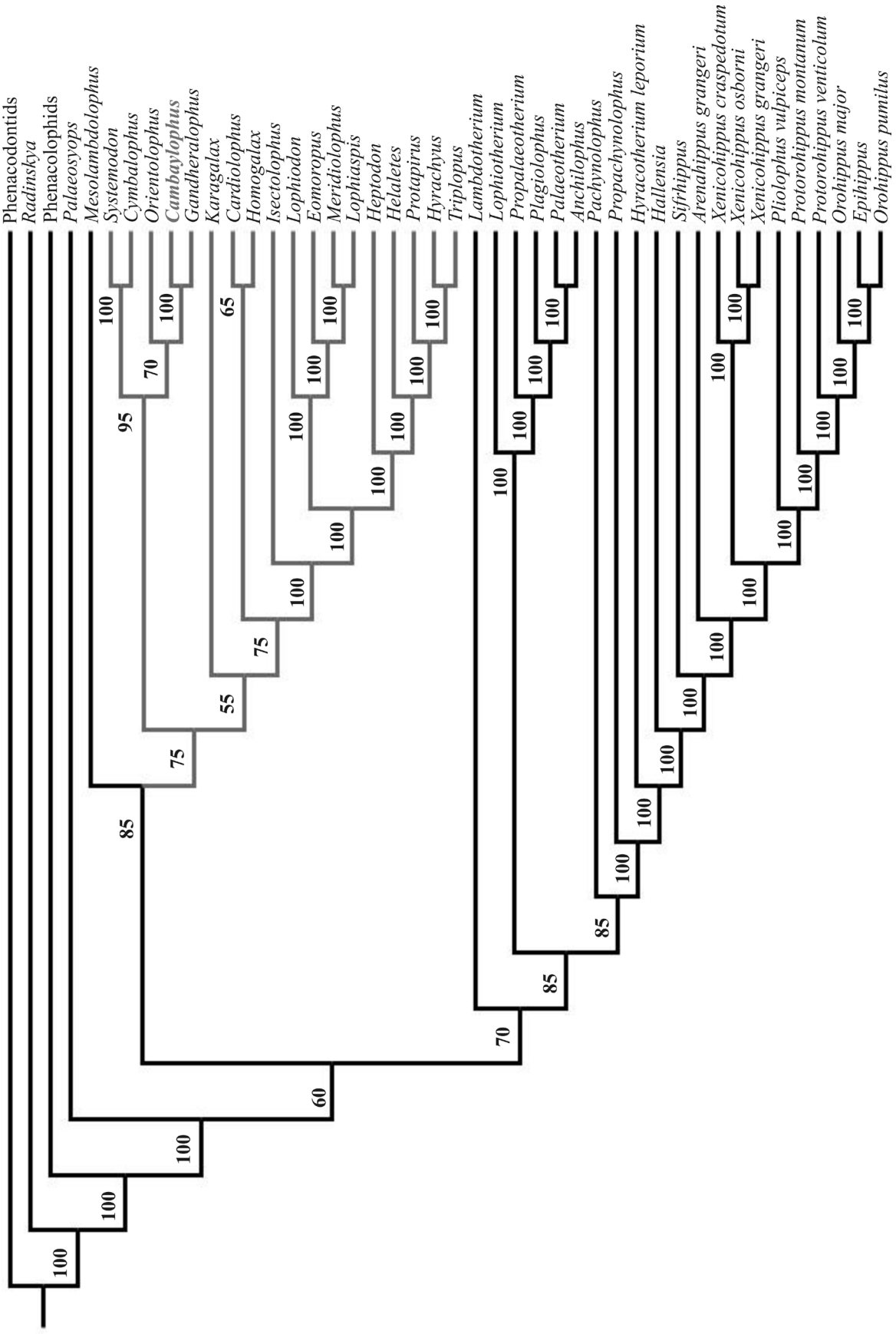

Fig. 5—50% Majority Rule consensus tree of 40 most parsimonious trees. Numbers along branches indicate frequency of clusters in the profile.

are younger than ~ 55.5 Ma. *Cambaylophus* from Vastan comes from a level about 20 m below the ETM2 (see Fig. 1) and its age is currently best estimated at between 54 Ma and 55 Ma. *Cambaylophus* is therefore, significantly older than the Upper Ghazij tapiromorphs and possibly corresponds to the early Bumbanian ALMA. However, with the resolution currently available, it is not possible to determine the precise age difference between *Cambaylophus* and *Orientolophus*.

The early Bumbanian ALMA interval is of great Palaeobiogeographic importance. By this time, the Indian Plate had either collided with Asia (DeCelles *et al.*, 2014) or was about to collide (Van Hinsbergen *et al.*, 2012) and this was also the time when most modern mammalian orders, including perissodactyls, originated and spread across the globe rapidly, possibly as a result of intense global warming that occurred around the Palaeocene–Eocene boundary (e.g. Bowen *et al.*, 2002; Gingerich, 2006; Clementz *et al.*, 2011). Most recently, Cooper *et al.* (2014) and Rose *et al.* (2014) supported the original classification of cambaytheres from Vastan as perissodactyls (Bajpai *et al.*, 2005a), and suggested that the origin of perissodactyls may have occurred on the Indian Subcontinent, as advocated previously (i.e. the *Out of India* hypothesis, Krause & Mass, 1990; see also Bajpai, 2009).

Biogeographically, the phylogenetic results presented here imply that terrestrial faunal exchanges involving medium–sized mammals such as tapiromorphs, occurred between India and Asia close to the Palaeocene–Eocene boundary. Exactly which terrestrial route facilitated such faunal exchanges remains to be established and must take into account the degree of connectivity/isolation of the Indian Subcontinent around the Palaeocene–Eocene boundary (e.g. Scotese, 2013), especially in the context of India–Asia collision.

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