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NEW EARLY EOCENE CAMBAYTHERE (PERISSODACTYLA, MAMMALIA) FROM THE VASTAN LIGNITE MINE (GUJARAT, INDIA) AND AN EVALUATION OF CAMBAYTHERE RELATIONSHIPS

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ABSTRACT

A new collection of cambaytheres (Perissodactyla: Mammalia) from the early Eocene (Ypresian, ca. 52 Ma) deposits at the Vastan Lignite Mine, Gujarat, is described. The collection comprises both lower and upper dentitions, postcranials, and the rostrum of a new taxon (*Kalitherium marinus* n. gen. and n. sp.) from a higher stratigraphic level in the Vastan Lignite Mine. These specimens expand our knowledge of the cambaythere anatomy and also help to confirm their perissodactyl affinities.

Key words: Eocene, Perissodactyla, Mammals, India-Asia collision

INTRODUCTION

Cambaytheriidae is a family of early Eocene mammals discovered in 2005 by Bajpai *et al.* (2005a), and diagnosed on the basis of a single genus *Cambaytherium*, with three named species. The original collection from the Vastan Lignite Mine, District Surat (Gujarat, western India) included nearly 30 specimens of cambaytheres, but the continued field work over the past one year has augmented that collection approximately three-fold. Most of the material described by Bajpai *et al.* (2005a) consisted of lower dentitions, on which the original description focused. We here describe a number of additional specimens that significantly expand the anatomical coverage of the family. The new cambaythere specimens include the upper cheek teeth which we illustrate and describe in detail. The upper dentition of cambaytheres was described in some detail (but was not illustrated in the paper by Bajpai *et al.*, 2005a). We also describe a new cambaythere species from a higher level in the Vastan Lignite Mine, about 55m above the lower mammal horizon that has yielded a diverse land mammal fauna (Bajpai *et al.*, 2005a, b, c). In addition, we discuss the ordinal affinities of cambaytheres in this paper, based on dental as well as postcranial material.

Bajpai *et al.* (2005a) classified cambaytheres as perissodactyls, based on cusp patterns of upper and lower molars. Kumar (2006) questioned the classification of cambaytheres as perissodactyls, and observed that the cambaythere dentition 'looks closest' to anthracobunids, implying that cambaytheres may be tethytheres and not perissodactyls. Bajpai *et al.* (2005a) compared cambaytheres with phenacodontid and quettacyonid condylarths, but they did not compare cambaytheres with anthracobunids. Kumar (2006) did not discuss in which features cambaytheres resemble anthracobunids, although he did state that the 'P/4 of *Cambaytherium* is quite unlike that of perissodactyls'. We here discuss cambaythere affinities in detail, focusing on the question whether cambaytheres are perissodactyls or anthracobunids.

The collection described in this paper is housed in the Vertebrate Palaeontology Laboratory, Department of Earth Sciences, Indian Institute of Technology, Roorkee under the acronym IITR/SB/VLM.

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SYSTEMATIC PALEONTOLOGY

Order **Perissodactyla** Owen, 1848

Family **Cambaytheriidae** Bajpai *et al.*, 2005

Diagnosis: Bunodont perissodactyls, lacking lophs on their cheek teeth; paraconule and metaconule prominent.

Type genus and species: *Cambaytherium thewissi* Bajpai *et al.*, 2005.

Referred Genera: *Hallensia* Franzen and Haubold, 1986; *Kalitherium* n. gen.

Remarks: Franzen and Haubold (1986) described *Hallensia* from the middle Eocene of Europe as a phenacodontid condylarth. Later, Franzen (1990) described a complete skeleton for *Hallensia*, and showed that the taxon in fact pertained to perissodactyls, in spite of having teeth very much unlike those of other members of its order. Franzen (1990) refrained from assigning *Hallensia* to a known family of perissodactyls, although he suggested affinities to hyracotherines. We here refer *Hallensia* to Cambaytheriidae on the basis of the bunodont nature of its teeth. *Hallensia* is clearly different from *Cambaytherium* in having a mesostyle and in the shape of its p4, which bears a large metaconid, unlike in *Cambaytherium*.

Hyracotherium sandrae Gingerich (referred to as *Sifrhippus sandrae*, Froehlich, 2002) from the early Eocene of Wyoming, is at the base of the equid radiation and is more bunodont than other equids. However, it is clearly more lophodont than the cambaytheres. There are several other bunodont ungulates in the early Palaeogene of Asia, such as *Radinskya* from the late Palaeocene of China (McKenna *et al.*, 1989) and *Nakusia* from the early Eocene of Baluchistan, Pakistan (Ginsburg *et al.*, 1999). The former was described as perissodactyl-like and the latter was referred to anthracobunids. The relationships of these to cambaytheres are open to question.

Cambaytherium thewissi Bajpai *et al.*, 2005
(Pl. I, figs. 1, 3-14)

Holotype: IITR/SB/VLM 505 (left dentary with p4 – m3, right dentary with p4 – m3).

Referred Material: IITR/SB/VLM 548 (left m1 or m2); IITR/SB/VLM 551 (right m1 or m2); IITR/SB/VLM 726 (right dentary

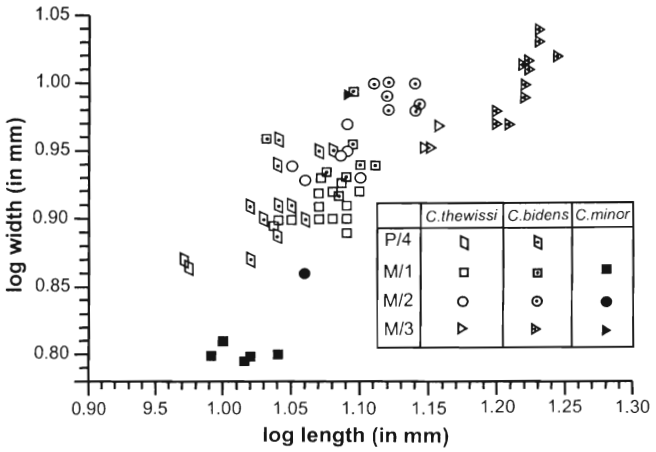


Fig. 1. Logarithmic comparison of the lower dentition of *Cambaytherium thewissi*, *C. bidens* and *C. minor*.

with, p3, m1-m3); IITR/SB/VLM 764 (right upper molar); IITR/SB/VLM 765 (left upper molar); IITR/SB/VLM 767 (right juvenile dentary, with m1 and unerupted p2): IITR/SB/VLM 830 right dentary with poorly preserved alveoli for p1-m3 and fragmentary crown of m1 or m2. IITR/SB/VLM 894 (incisor, P1?, right P2 or P3, right P4, and upper molar fragment).

Remarks: IITR/SB/VLM 894 includes a P2 or P3, and a P4, not previously known for *C. thewissi*. The former tooth is double-rooted, longer than wide (length: 12.0 mm; width: 7.6 mm), with a single large cusp (paracone) and a tiny metacone, the former of which bears a strong anterior and a weak posterior crest. P4 is three-rooted and transverse (length: 9.3 mm; width: 11.9 mm). It has three main cusps, the paracone being the highest, followed by the protocone and the metacone. The metacone is fused at its base with the paracone, but a transverse furrow extending apically shows the independence of these cusps. There is a weak parastyle, and a crest connects the parastyle to the paracone. A weak but distinct metastyle is also present. The preprotocrista extends from the protocone to the anterolingual base of the paracone, where it joins a small paraconule. The metaconule is somewhat smaller but distinct, and occurs at the base of the furrow separating the paracone and metacone. A weak postprotocrista extends from the apex of the protocone to the metaconule. Anterior and posterior cingula are strong and crenulated. The labial cingulum is interrupted and the lingual cingulum is lacking. The enamel surface shows concentric, wavy striations.

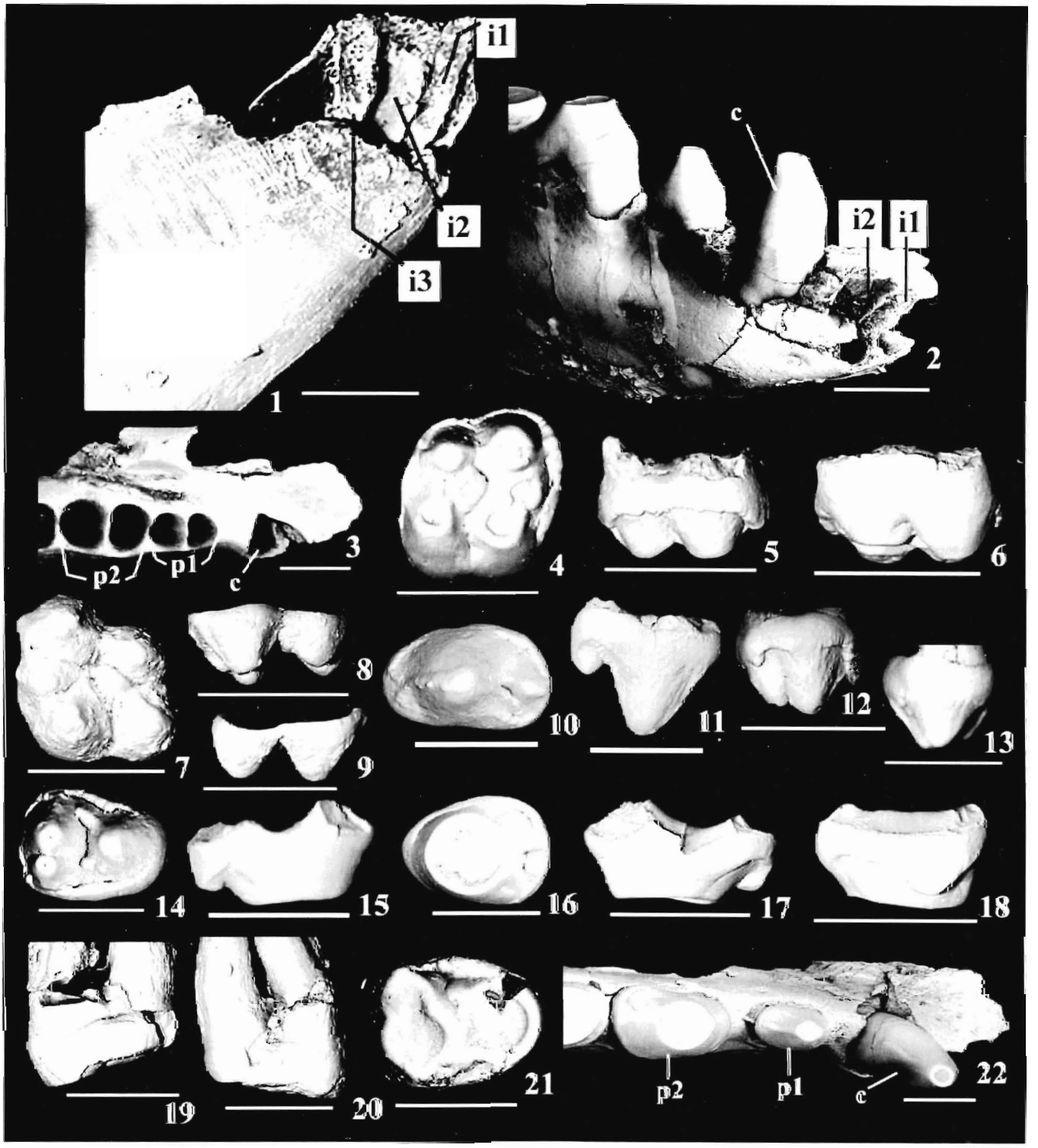
We refer IITR/SB/VLM 764 and IITR/SB/VLM 765, both isolated upper molars, to *C. thewissi*. Upper molars are bunodont and have six cusps. The paracone and the metacone are connected by a weak crest. The parastyle is connected to the anterior side of the paracone by a weak crest. A weak crest descends from the labial side of the hypocone. There are no crests connected to the protocone and the metaconule. The paraconule and metaconule are smaller than the remaining four cusps, and the paraconule is larger than the metaconule. The arrangement of cusps on the tooth is characteristic: protocone and hypocone are placed posterolingual to paracone and metacone, respectively. However, the paraconule and metaconule are placed anterolingual to paracone and metacone, respectively. Weak and incomplete cingula occur anteriorly, posteriorly, and labially in IITR/SB/VLM 765. This tooth is totally unworn and lacks roots, leading us to infer that it was unerupted and not fully mineralized. The dimensions of IITR/SB/VLM 765 are: length: 10.4 mm; width: 11.6mm. IITR/SB/VLM 764 is very similar to IITR/SB/VLM 765 in size and morphology. It shows two weak crests descending the labial face of the hypocone, the shorter of which extends anterolabially to join the metaconule and the longer one runs labially to join the base of the lingual face of metacone. The anterolingual face of the metacone is also connected to the metaconule. Anterior and posterior cingula are strong in this tooth, but the labial cingulum is weak. There is no lingual cingulum. Dimensions of this tooth are: length: 11.9 mm; width: 12.4 mm.

EXPLANATION OF PLATE I

(scale bar equals 1 cm in all cases)

1. ***Cambaytherium thewissi***, holotype right dentary showing alveoli for three incisors (IITR/SB/VLM 505), anterolabial view.
2. ***Cambaytherium bidens***, holotype right dentary showing alveoli for two incisors (IITR/SB/VLM 503), anterolabial view.
3. ***Cambaytherium thewissi***, holotype right dentary showing lack of diastema between p1 and p2 (IITR/SB/VLM 505), occlusal view.
4. ***Cambaytherium thewissi***, right M1 or M2 (IITR/SB/VLM 764), occlusal view.
5. ***Cambaytherium thewissi***, right M1 or M2 (IITR/SB/VLM 764), labial view.
6. ***Cambaytherium thewissi***, right M1 or M2 (IITR/SB/VLM 764), lingual view.
7. ***Cambaytherium thewissi***, left M1 or M2 (IITR/SB/VLM 765), occlusal view.
8. ***Cambaytherium thewissi***, left M1 or M2 (IITR/SB/VLM 765), labial view.
9. ***Cambaytherium thewissi***, left M1 or M2 (IITR/SB/VLM 765), lingual view.
10. ***Cambaytherium thewissi***, right P2 or P3 (IITR/SB/VLM 894), occlusal view.
11. ***Cambaytherium thewissi***, right P2 or P3 (IITR/SB/VLM 894), lingual view.
12. ***Cambaytherium thewissi***, right P4 (IITR/SB/VLM 894), labial view.
13. ***Cambaytherium thewissi***, right P4 (IITR/SB/VLM 894), lingual view.
14. ***Cambaytherium thewissi***, right P4 (IITR/SB/VLM 894), occlusal view.
15. ***Cambaytherium bidens***, right P2 (IITR/SB/VLM 502), labial view.
16. ***Cambaytherium bidens***, right P2 (IITR/SB/VLM 502), occlusal view.
17. ***Cambaytherium bidens***, right P2 (IITR/SB/VLM 502), lingual view.
18. ***Cambaytherium bidens***,, right P2 (IITR/SB/VLM 502), posterior view.
19. ***Cambaytherium bidens***, left P4 (IITR/SB/VLM 502), posterior view.
20. ***Cambaytherium bidens***, left P4 (IITR/SB/VLM 502), anterior view.
21. ***Cambaytherium bidens***, left P4 (IITR/SB/VLM 502), occlusal view.
22. ***Cambaytherium bidens***, holotype right dentary showing presence of diastema between p1 and p2 (IITR/SB/VLM 503), occlusal view.

Plate I


i1
i2
i3
1
c
i2
i1
2
p2
p1
c
3
4
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7
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10
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19
20
21
p2
p1
c
22

An important morphological difference between *C. thewissi* and *C. bidens* is the presence of three lower incisors in the former, whereas the latter has two incisors (Pl. I, figs. 1, 2). Also, there is no diastema between p1 and p2 in *C. thewissi*, unlike *C. bidens* (Pl. I, figs. 3, 20). A bivariate plot of the cambaythere lower dentition (p4-m3) further indicates that there is a consistent size difference between *C. bidens* and *C. thewissi*, and that both form distinctive clusters (Fig.1). Kumar (2006) doubted the distinctiveness of *C. thewissi* on the basis of size alone, although he concurred that the presence of three incisors in the species merits specific distinction.

Cambaytherium bidens Bajpai *et al.*, 2005
(Pl. I, figs. 2, 15-22; Pl. II, figs. 1-11)

Holotype: IITR/SB/VLM 503 (right dentary with c-m3, left dentary with p1-m3).

Referred Material: IITR/SB/VLM 502 (left dentary with p1 – p3, m1, m3, right dentary with p3 – m3, right premaxilla with C1 – P1, left C, right P2 and left P4, mandibular symphysis, maxilla fragment, nasals, atlas); IITR/SB/VLM 520 (highly worn m1 – m2); IITR/SB/VLM 521 (left mandibular fragment with m3 and associated M1 or M2); IITR/SB/VLM 532 (left c1, m1 – m3, mandibular fragments); IITR/SB/VLM 535 (right proximal astragalus) IITR/SB/VLM 541 (left C1); IITR/SB/VLM 542 (left c1); IITR/SB/VLM 543 (p1); IITR/SB/VLM 544 (unworn left p4); IITR/SB/VLM 545 (unworn left p4); IITR/SB/VLM 546 (left m1 or m2); IITR/SB/VLM 547 (unworn left mx); IITR/SB/VLM 558 (unworn left p2 –p3 and three unicuspid teeth); IITR/SB/VLM 764 (isolated left M1 or M2); IITR/SB/VLM 765 (isolated right M1 or M2); IITR/SB/VLM 786 (right dentary with p2-m3); IITR/SB/VLM 791 (right dentary with m1-m2); IITR/SB/VLM 792 (left dentary with p2-m3); IITR/SB/VLM 795 (left dentary with m1-m3); IITR/SB/VLM 811 (left dentary with p3-m3); IITR/SB/VLM 957 (left dentary with p4-m3 and alveoli for i1-p2).

Remarks: The new collection includes several dentaries of this species in which the molars are relatively unworn (IITR/SB/VLM 791). These confirm that the molar cusp morphology described for *Cambaytherium*, and based on a specimen of *C. thewissi*, also occurs in *C. bidens*. Upper premolars are preserved in IITR/SB/VLM 502, but all are worn, obscuring some aspects of morphology. A maxilla fragment of IITR/SB/VLM 502 includes the canine and P1. The latter tooth is two-rooted, with an expanded posterior basin and a weak but complete cingulum. Wear obscures the cusp morphology, but there was probably only a single cusp. Another upper premolar of IITR/SB/VLM 502 is probably P2 (length: 12.2mm; width: 8.9mm). It too, is heavily worn, but the circular outline of the abrasional wear facet suggests that only a single cusp was present. The cingulum is slightly interrupted lingually, absent labially and flares lingually posterior to the paracone. A larger style occurs on the posterior cingulum. The P4 of this specimen is heavily worn (length: 9.6 mm; width: 12.8 mm). It is three-rooted and resembles the P4 of IITR/SB/VLM 894 (described under *C. thewissi*) in all preserved features. An upper molar of *C. bidens* (part of IITR/SB/VLM 521), described (but not illustrated) by Bajpai *et al.* (2005a), is very similar to those of *C. thewissi* described above (see Plates I and II). This tooth is 11.4 mm long and 12.5 mm wide.

Cambaytherium minor Bajpai *et al.*, 2005
(Pl. III, figs. 1-3)

Holotype: IITR/SB/VLM 539 (right m1 with anterolabial part missing).

Referred Material: IITR/SB/VLM 540 (fragmentary left m1); IITR/SB/VLM 761 (right dentary with m1-m3); IITR/SB/VLM 830 (right dentary with fragmentary m1); IITR/SB/VLM 841(isolated left m1); IITR/SB/VLM 895 (fragmentary right m2).

Remarks: The m1 of the new jaw (IITR/SB/VLM 761) is identical in size and morphology to that of the holotype. Apart from the smaller size of m1 (mainly in width), this specimen also shows that the m1 in *C. minor* is somewhat anteriorly narrower, unlike that in *C. bidens* and *C. thewissi*. Further, the m3 in this specimen lacks the prominent third lobe and the posteriorly tapering talonid, exhibiting a somewhat rectangular occlusal outline (Pl. III, fig. 1), unlike in the other *Cambaytherium* species. IITR/SB/VLM 761 also suggests that the premolars of this species may be shorter (based on alveoli) than those of *C. thewissi*. Although not well preserved, these alveoli suggest that *C. minor* had a shorter snout.

Genus ***Kalitherium*** n. gen.

Type and only species: *Kalitherium marinus* n. sp.

Derivation of name: *Kalitherium* combines *kali*, Hindi word for black as well as the name of the Goddess *Kali*, and *therium*, Latin for beast. The name refers to the black color of the holotype specimen (as well as all other mammals from the type locality).

Diagnosis: large cambaythere with P2 longer than other premolars; M1 much smaller than M2 and M3; M2 wider than M1; M3 with reduced and relatively anteriorly positioned metacone, enlarged metaconule and paraconule and distinct accessory cusps on the anterior and posterior aspects of hypocone. Differs from *Cambaytherium* and *Hallensia* in being larger. Also, *Kalitherium* lacks a mesostyle unlike *Hallensia* in which it is commonly present.

Remarks: *Kalitherium* is tentatively placed in the family Cambaytheriidae. At present, *Kalitherium* is known from a single partial rostrum with upper cheek teeth. This implies that no direct comparisons can be made with *Cambaytherium*,

EXPLANATION OF PLATE II

(scale bar equals 1 cm in all cases)

1. ***Cambaytherium bidens***, left m3 (IITR/SB/VLM 792), occlusal view.
2. ***Cambaytherium bidens***, left m3 (IITR/SB/VLM 792), labial view.
3. ***Cambaytherium bidens***, left m3 (IITR/SB/VLM 792), lingual view.
4. ***Cambaytherium bidens***, right m1-m2 (IITR/SB/VLM 791), lingual view.
5. ***Cambaytherium bidens***, right m1-m2 (IITR/SB/VLM 791), labial view.
6. ***Cambaytherium bidens***, right m1-m2 (IITR/SB/VLM 791), occlusal view.
7. ***Cambaytherium bidens***, left M1 or M2 (IITR/SB/VLM 521), occlusal view.
8. ***Cambaytherium bidens***, left M1 or M2 (IITR/SB/VLM 521), labial view.
9. ***Cambaytherium bidens***, left M1 or M2 (IITR/SB/VLM 521), lingual view.
10. ***Cambaytherium bidens***, left M1 or M2 (IITR/SB/VLM 521), anterior view.
11. ***Cambaytherium bidens***, left M1 or M2 (IITR/SB/VLM 521), posterior view.

Journal of The Palaeontological Society of India
Volume, 51(1), June 2006

Plate II

which is predominantly known from lower dentition and for which only a few upper teeth are available. However, in teeth which can be compared directly (e.g. P4, M1 or M2). *Kalitherium* is easily distinguishable from *Cambaytherium* (*C. bidens* and *C. thewissi*) by its much larger size (approximately 130% in P4 length; 150% in M1 length; 200% in M2 length).

Age and Distribution: early Eocene of India.

Kalitherium marinus n. sp.
(Pl. III, fig.4; Pl. IV, figs. 1-3)

Derivation of name: *marinus* refers to the ocean, since the specimen was recovered in sediments deposited in a tidal flat complex on the shore.

Diagnosis: generic and specific diagnoses cannot be differentiated at the present time.

Holotype and Only Specimen: IITR SB VLM 931, snout without premaxillae, but with orbits and right postorbital process, root of right canine, damaged crowns of right P1 and P2, worn crowns of right P3-M2, and well-preserved crown of right M3, damaged bases of left C-M3. The holotype specimen was provided to one of us (VVK) by a miner at the Vastan Lignite Mine.

Description: The P1 has two roots of similar size. The crown is not preserved. Length: 13.5 mm; width (maximum): 7.0 mm. The P2 has two roots, the posterior of which is expanded and projects lingually, giving rise to a protocone lobe on the tooth. No occlusal morphology is preserved, but the tooth has a strong caudal cingulum. Length: 20.0 mm; width (maximum): 14.0 mm.

The P3 has three roots. Much of the occlusal morphology is worn, but a tall shelf of enamel remains, surrounding the tooth, implying that it was relatively high-crowned. The anterobuccal corner of the tooth bulges, suggesting that a parastyle was present. Buccally, the enamel is grooved from base to occlusal surface, implying that the paracone and the metacone were present. A cingulum is preserved anteriorly and posteriorly. Length: 17.0 mm; width: 19.0 mm.

The P4 is three-rooted. It is oval in outline and the parastyle is absent. Judging from the sizes of the wear facets and the grooving of the labial enamel, the paracone and metacone were connate. A crest descended the metacone towards the posterior cingulum, giving rise to a weak metastyle. Anteriorly and posteriorly the cingulum is strong, and labially the cingulum is weak. There is no lingual cingulum. Length: 15.0 mm; width 20.2 mm.

The M1 is strongly worn and damaged, and is much smaller than the posterior molars. Lingually, its enamel bulges suggesting the presence of a protocone and hypocone of equal size. Wear has created two transverse troughs across the tooth, anteriorly across the protocone and paracone, and posteriorly across the metacone and hypocone. Length: 15.0 mm, width: 18.6 mm.

The M2 is also worn and is much larger than the M1. The occlusal outline is quadrate like in M1. Anteriorly, there is a broad wear facet across protocone, paraconule, and paracone. The paracone is expanded labially in the direction of the parastyle. The protocone is larger than the hypocone. Length: 20.5 mm, width: 24.0 mm.

The M3 is triangular in occlusal outline, and is much wider anteriorly than posteriorly. There are three main cusps: paracone, protocone and hypocone. The protocone and hypocone are subequal in size, but the paracone is slightly larger and higher. The metacone is much smaller than the paracone. The protocone lobe flares lingually much beyond the hypocone, unlike the condition in anterior molars in which the lingual margin runs parallel to the anteroposterior axis. The metacone lies markedly anteriorly and is similar in size to paraconule and metaconule. It is connected to the paracone at its base. There is a small cingular cusp posterolabial to the metacone. The paraconule is well developed. It occurs slightly anterior to the paracone-protocone line and is connected to both. The metaconule is also noticeably enlarged, and lies anterior to the line connecting the metacone and hypocone. It is situated nearly at the center of the trigon basin, immediately posterior to the paraconule. A crest extending posteriorly from the metaconule connects it to the labial side of the hypocone. The metaconule is also weakly connected to the anterolingual side of the metacone. A tiny cusp arises at the anterolingual face of the hypocone, and a somewhat larger cuspule was also present at the posterolabial corner of the hypocone. The cingulum is developed on the anterior and labial sides, it is particularly strong around the protocone and is discontinuous posterolingually. The enamel is finely crenulated. M3 length: 22.6 mm; width: 22.3 mm.

The rostrum is somewhat crushed, but preserves many morphological details. The nasals are narrow bones, extending caudally in the parasagittal plane. Dorsal to P3 the maxillonasal suture bends laterally, and over M1 it bends medially reaching the median plane. The nasals articulate with the maxillae anterior to the medial bent, whereas they articulate with the frontals caudal to this. The posterior extent of the nasals is over M2. The maxillae make up most of the lateral side of the face. They share a short suture with the frontals. The infraorbital foramen is over P3. The frontal is narrow over the orbit, and makes a clear postorbital process. The frontals are convex between the orbits, and the distance between the left and right orbit is approximately 10 cm. The lacrimal is a narrow bone, extending far forward on the face between frontal and maxilla.

Type Locality: Vastan Lignite Mine, Taluka Mangrol, District Surat, Gujarat, India.

Type Horizon: Cambay Shale, *N. burdigalensis* Zone (SBZ 10).

DISCUSSION

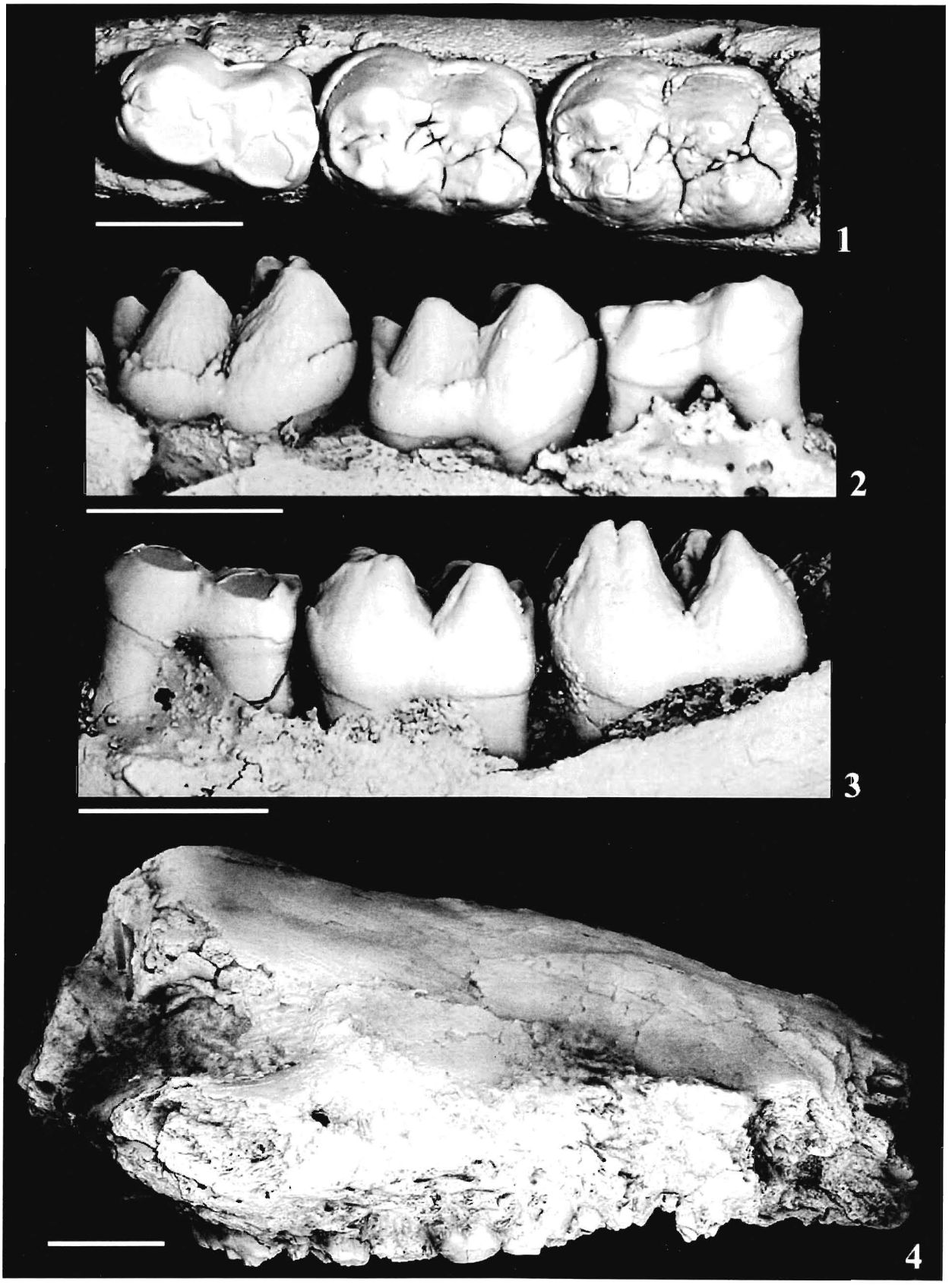
In the Eocene, the Indian subcontinent was home to a number of endemic bunodont ungulates, including quettacyonine arctocyonids (Gingerich, 1997), anthracobunid tethytheres (Dehm and Oettingen-Spielberg, 1958; West, 1980,

EXPLANATION OF PLATE III

(scale bar equals 1 cm for figs. 1-3 & 3cm for fig. 4)

1. ***Cambaytherium minor***, right m1-m3 (IITR/SB/VLM 761), occlusal view.
2. ***Cambaytherium minor***, right m1-m3 (IITR/SB/VLM 761), labial view.
3. ***Cambaytherium minor***, right m1-m3 (IITR/SB/VLM 761), lingual view.
4. ***Kalitherium marinus***, n. gen. & n. sp., rostrum, holotype (IITR/SB/VLM 931), right lateral view.

Plate III



BAJPAI, KAPUR, THEWISSEN, DAS AND TIWARI

1983; Wells and Gingerich, 1983; Kumar, 1991), and cambaythere perissodactyls (Bajpai *et al.*, 2005a). All of these taxa are only known from fragmentary material. This makes comparisons between them difficult, complicating assessment of ordinal relations. Here, we will focus on a comparison between cambaytheres and anthracobunids, in light of the suggestion by Kumar (2006) that cambaytheres are anthracobunids, not perissodactyls. We will discuss evidence from incisors, premolars, molars, tooth wear, scapula, astragalus, and mandible.

Incisors (Pl. IV, figs. 4-9): Kumar (1991) described the only known incisors for anthracobunids. Anthracobunid incisors are low teeth with one large bulbous cusp and several squat cuspules adjacent to it. Instead, Eocene perissodactyl incisors are usually spatulate or pointed (Hooker, 1989). Few incisors have been found associated with cambaythere jaws but many isolated incisors have been recovered. Given that cambaytheres are common and that there are no other common mammals of their size, it is likely that these isolated incisors represent cambaytheres. Isolated teeth whose roots fit cambaythere jaws include IITR/SBVLM 739, 772, 788, 806, 897. All of these are spatulate (e.g. IITR/SBVLM 739) or pointed (e.g. IITR/SBVLM 897), similar to perissodactyls and unlike anthracobunids.

Lower premolars: The p4 of cambaytheres is always shorter than m1, whereas the p4 of anthracobunids is longer than m1. Perissodactyls, such as *Hyracotherium*, *Karagalax*, and *Kalakotia*, retain a p4 which is longer than m1. A difference between cambaytheres on one hand and other perissodactyls and anthracobunids on the other is the lack of a paraconid in the p4 of the former. Thus, although the cambaythere p4 is unlike that of perissodactyls, it is equally unlike anthracobunids in this respect. In *Hallensia*, the paraconid is lacking (Franzen and Haubold, 1986).

Lower molars: The molars of anthracobunids are distinctive. They are bunodont, but the cusps are narrow and high, with pronounced valleys between them, making the teeth relatively hypsodont. This is very unlike cambaythere molars, and can be seen clearly in relatively unworn specimens, such as the type specimen of *Cambaytherium thewissi* (IITR/SB/VLM 505). Hypsodont molars occur in anthracobunids, such as *Anthracobune* (Kumar, 1991), *Pilgrimella* (West, 1980) and *Jozaria* (Wells and Gingerich, 1983). Cambaytheres, on the other hand have low, blunt cusps more similar to the cusps of the perissodactyl *Hallensia* (Franzen and Haubold, 1986; Franzen, 1990).

Tooth wear: Tooth wear in the lower cheek teeth of anthracobunids (*Anthracobune*, *Pilgrimella*, *Lammidhania* and *Jozaria*) is mostly transverse, producing clear facets along the posterior aspects of the protoconid/metaconid, and the hypoconid/entoconid. This points towards a distinctive tooth use pattern, involving predominantly medio-lateral chewing movements. This is unlike cambaytheres, where the cusps wear predominantly apically, producing circular or oval wear facets at their apices.

Scapula (Pl. IV, fig. 10): An isolated distal scapular fragment (IITR/SB/VLM 781) from Vastan is of a medium-sized mammal. At present, the Vastan collection only contains cambaytheres of this size. Our tentative identification is that this scapula represents a cambaythere. Proboscideans, including anthracobunids (Shoshani *et al.*, 1996) have a distinctively positioned glenoid, which makes a sharp, acute angle with the spine of the scapula, whereas glenoids are usually at right angles to the spine. If this scapular fragment indeed pertains to a cambaythere, then cambaytheres are not proboscideans.

Astragalus (Pl. IV, figs. 11-13): An isolated proximal astragalus of a medium-sized mammal (IITR/SB/VLM 535 mentioned by Bajpai *et al.*, 2005a; width of trochlea 17 mm) was found at the Vastan Lignite Mine. This astragalus has sharp trochlear ridges that are positioned at an angle to the astragalar neck. The proximal calcaneo-astragalar facet forms a deep, transverse trough, and the sustentacular facet is small. In all these features, this astragalus resembles perissodactyls such as *Hallensia* (Franzen, 1990). This astragalus is very much unlike the astragalus of anthracobunids (Gingerich, 1990), which has low and broad trochlear ridges that are parallel to the neck, and a shallow proximal calcaneo-astragalar facet. Moreover, one of the diagnostic features of proboscideans, including anthracobunids (Tassy, 1996), is the presence of a medial tubercle on the astragalar trochlea. No such tubercle is present on this specimen. Unlike anthracobunids and most perissodactyls, the astragalar canal is complete. This astragalus implies that a perissodactyl of medium-size occurred at the Vastan Locality. Aside from cambaytheres, the only perissodactyl evidence at Vastan discovered by the IIT Roorkee team is the jaw of a small tapiroid. However, this specimen is much too small to have an astragalus the size of IITR/SB/VLM 535. Although there is no direct evidence to refer this astragalus to cambaytheres, this is the most likely identification at this time, and supports our perissodactyl affinities for cambaytheres.

Mandible: The mandibular angle shows a large semicircular region for the insertion of masseter, and a very small coronoid process, for the attachment of the temporal

EXPLANATION OF PLATE IV

(scale bar equals 3 cm for figs. 1-2 & 1cm for figs. 3-13)

1. ***Kalitherium marinus*** n. gen. & n. sp., rostrum, holotype (IITR/SB/VLM 931), ventral view.
2. ***Kalitherium marinus*** n. gen. & n. sp., magnified occlusal view of right P1-M3 from holotype rostrum (IITR/SB/VLM 931).
3. ***Kalitherium marinus*** n. gen. & n. sp., magnified occlusal view of right M3 from holotype rostrum (IITR/SB/VLM 931).
4. ***Cambaytherium* sp. indet.**, incisor (IITR/SB/VLM 838), lateral view.
5. ***Cambaytherium* sp. indet.**, incisor (IITR/SB/VLM 821), lateral view.
6. ***Cambaytherium* sp. indet.**, incisor (IITR/SB/VLM 739), lateral view.
7. ***Cambaytherium* sp. indet.**, incisor (IITR/SB/VLM 963), lateral view.
8. ***Cambaytherium* sp. indet.**, incisor (IITR/SB/VLM 897), lateral view.
9. ***Cambaytherium* sp. indet.**, incisor (IITR/SB/VLM 806), lateral view.
10. ***Cambaytherium* sp. indet.**, distal scapula (IITR/SB/VLM 781), cranial view.
11. ***Cambaytherium* sp. indet.**, right proximal astragalus (IITR/SB/VLM 535), dorsal view.
12. ***Cambaytherium* sp. indet.**, right proximal astragalus (IITR/SB/VLM 535), plantar view.
13. ***Cambaytherium* sp. indet.**, right proximal astragalus (IITR/SB/VLM 535), lateral view.

Plate IV

muscle. This region of the mandible is very similar to that in perissodactyls, but it cannot be compared directly to anthracobunids, in which this part is not known. However, mandibles of other archaic proboscideans (e.g. *Numidotherium*, Mahboubi *et al.*, 1986) have mandibles in which the angle is not expanded.

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