



## EARLY EOCENE PRIMATES FROM VASTAN LIGNITE MINE, GUJARAT, WESTERN INDIA

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### ABSTRACT

A new primate fauna of early Eocene (Ypresian, approximately 52 Ma) age is reported from the Vastan Lignite Mine, District Surat, Gujarat, western India. From the Indian subcontinent, this is the oldest known Cenozoic record as well as the largest single sample of Eocene primates, consisting of 3 fragmentary jaws and 4 isolated upper cheek teeth. The assemblage comprises at least three, but possibly 4 taxa, of which only two are being named here, an adapiform *Marcgodinotius indicus* n. gen. & n. sp., and an omomyid *Vastanomys gracilis* n. gen. & n. sp., distinguished mainly on the basis of their lower dental formula and lower molar characteristics. The fauna indicates considerable diversity of Eocene primates in Indo-Pakistan and is important in understanding early primate evolution in Asia and the mammalian dispersal into, or out of, from India in response to changing paleogeographic settings associated with the initiation of India-Asia collision.

**Key words:** Early Eocene, Primates, Vastan Lignite, Gujarat, India

### INTRODUCTION

The Palaeogene primate record from Indo-Pakistan is scanty, but the list was recently expanded by the recovery of several new Oligocene taxa from Pakistan (Marivaux *et al.*, 2001, 2005). From the Eocene of the Indian subcontinent, only ten primate specimens have been reported so far: nine specimens consisting mostly of single crowns from northern Pakistan (Russell and Gingerich, 1980, 1987; Thewissen *et al.*, 1997, 2001) and one isolated upper molar from northwestern India (Kumar *et al.*, 2002). Although this material is highly fragmentary, it shows a large diversity of primates during this period in Indo-Pakistan realm. There are at least three species of adapids and omomyids each. Additional Eocene primates occur in the Gandhera Quarry fauna from Pakistan, but these specimens have only been mentioned in a faunal list as '1-2 taxa' of 'Adapiformes' without any description (Gingerich *et al.*, 2001).

Here we report a new collection of primate fossils from the Vastan Lignite Mine, Taluka Mangrol, District Surat, Gujarat (see fig. 1 for locality and lithostratigraphic details). These primates are part of a rich fauna of land vertebrates, which includes many mammals (Bajpai *et al.*, 2005a, b; Rana *et al.*, 2005). As presently known, the Vastan mammal fauna comprises perissodactyls, artiodactyls, insectivores, proteutherians, apatotherians, marsupials, rodents (Bajpai *et al.*, 2005 a, b) as well as bats and two fragmentary premolars described as 'Primates?' (Rana *et al.*, 2005). Associated foraminifers, particularly *Nummulites burdigalensis*, indicate that the Vastan mammals are Ypresian (early Eocene) in age, corresponding to the shallow benthic foraminiferal zone SBZ 10, approximately 52 Ma (Serra-Kiel *et al.*, 1998; Govindan, 2003). Thus, the primates reported here are indeed the oldest Cenozoic record from India.

The material 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.

### SYSTEMATIC PALAEOLOGY

*Order* **Primates** Linnaeus, 1758

*Suborder* **Adapiformes** Hoffstetter, 1977

*Family* **Incertae sedis**

*Genus* ***Marcgodinotius*** n. gen.

*Type and only species:* *M. indicus* n. sp.

*Derivation of name:* Named for Dr. Marc Godinot in recognition of his contribution to the knowledge of Eocene primates.

*Diagnosis:* Adapiform with the following combination of characters: 4 premolars with a small, single rooted p1 and a double-rooted p2 (as based on alveoli); paraconid small; cristid obliqua relatively labial; relatively straight postcristid; m3 talonid elongate with transversely expanded hypoconulid; strong cingulid near the labial base of protoconid.

In contrast to *Marcgodinotius*, *Donrussellia* possesses a well-developed paraconid; longer as well as broader m3 talonid relative to trigonid; more labial and posteriorly extended hypoconulid, more posteriorly and labially positioned hypoconid (relative to protoconid) (Godinot 1992, 1994, 1998; Rose *et al.*, 1994). *Marcgodinotius* is also distinguishable from other adapiforms as follows: from *Mahgarita* by the presence of 4 premolars; from *Europolemur* by a weakly developed hypoconulid on m2; from *Protoadapis* and *Adapoides* by lacking a deep trigonid notch between protoconid and metaconid, and from *Agerinia* by the absence of a complete paralophid.

*M. indicus* is distinct from *Panobius afridi* (holotype)

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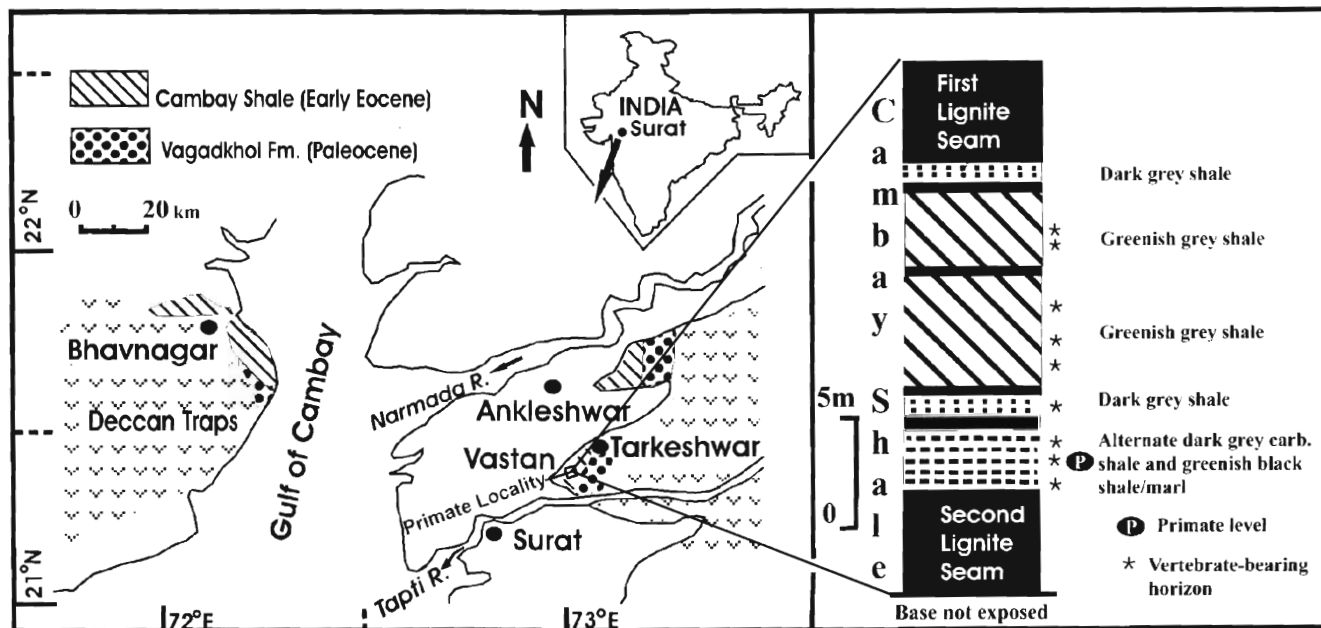


Fig. 1. Map and lithostratigraphic section of the primate-yielding locality.

from the Eocene of Pakistan (Russell and Gingerich, 1987; Thewissen *et al.*, 2001) in the size and shape of m1 trigonid. In the latter species, the trigonid is larger relative to the talonid and the posterior wall of the trigonid is oriented obliquely to long axis of the tooth. In addition, *Marcgodinotius* m3 lacks the well-developed paralophid seen in *P. afridi*. *M. indicus* is similar to *Panobius afridi* in molar size, as well as in the duplication of the entoconid.

Among the omomyids (Bown and Rose, 1987; Rose and Bown 1991; Rose, 1995; Ni *et al.*, 2004), *Marcgodinotius* differs from the three most primitive species of *Teilhardina* (*T. asiatica*, *T. belgica* and *T. americana*) primarily in having a double-rooted p2. *Marcgodinotius* is also distinct from the early Eocene Mongolian omomyid *Altanius* in that the latter has a double-rooted, unreduced p1, high paraconid and short talonid, and high lingual cusps (Dashzevez and McKenna, 1977; Rose *et al.*, 1994). *Marcgodinotius* differs from *Kohatius coppensi* from the Eocene of Pakistan (Russell and Gingerich, 1980; Thewissen *et al.*, 2001) in the smaller size of the paraconid and the size and shape of the entoconid. The latter is large and single in *Kohatius*, but small and duplicated in the new spe-

cies.

*Remarks:* Assignment of *Marcgodinotius* to Adapiformes is necessarily tentative and may have to be revised when more complete material becomes available. This uncertainty arises mainly because of the conservative molar morphology of early euprimates and the absence of premolars in the present collection. *Marcgodinotius* is here considered to be a primitive adapiform based mainly on the presence of a double-rooted p2 and four premolars (as based on the alveoli); relatively elongate m3 talonid with large hypoconulid; relatively straight posteristid and nearly centrally-positioned hypoconulid (Godinot, 1992; Rose *et al.*, 1994).

*Age and distribution:* early Eocene of India.

*Marcgodinotius indicus* n. sp.

(Pl. I, figs. a-g; Pl. II, figs. a-f; Pl. IV, figs. i-k)

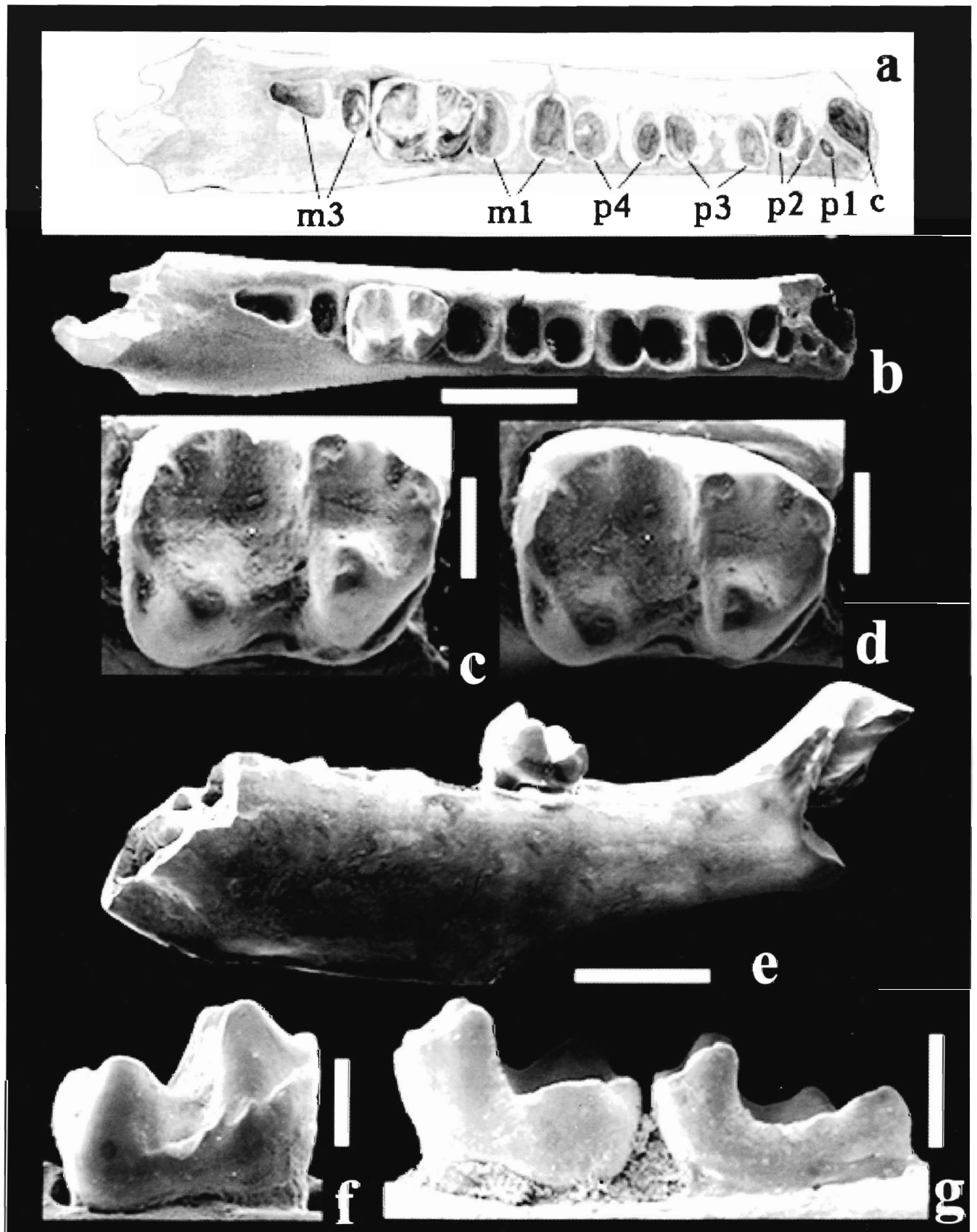
*Referred material:* IITR/SB/VLM 817 (right dentary with crowns for m2-3 and alveoli for m1-p1 and partial alveolus for canine); IITR/SB/VLM 642 (M2 or M3, lost during photography).

*Derivation of name:* The species name is derived from the name of the country (India) where it is found.

## EXPLANATION OF PLATE I

(scale bar equals 3 mm for a, b, e; 700  $\mu$ m for c, d, f; 1 mm for g)

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|--|---|
| a. <i>Marcgodinotius indicus</i> n. gen. and n. sp., drawing of right dentary, holotype (IITR/SB/VLM 800), occlusal view.                        | e. <i>Marcgodinotius indicus</i> n. gen. and n. sp., holotype dentary (IITR/SB/VLM 800), lingual view.        |
| b. <i>Marcgodinotius indicus</i> n. gen. and n. sp., right dentary, holotype (IITR/SB/VLM 800), occlusal view.                                   | f. <i>Marcgodinotius indicus</i> n. gen. and n. sp., m2 from holotype dentary (IITR/SB/VLM 800), labial view. |
| c, d. <i>Marcgodinotius indicus</i> n. gen. and n. sp., magnified view of m2 from holotype dentary (IITR/SB/VLM 800), occlusal view, stereopair. | g. <i>Marcgodinotius indicus</i> n. gen. and n. sp., right m2-m3 (IITR/SB/VLM 817), lingual view.             |



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

*Holotype:* IITR/SB/VLM 800, a right dentary with m2 crown and alveoli for m3, m1-c.

*Description:* The holotype (IITR/SB/VLM 800) is a fragmentary right dentary that preserves the crown for m2, alveolus for m3 and ten complete alveoli anterior to the m2 crown. The six large alveoli anterior to m2 crown are interpreted to represent the double-rooted m1-p3. Farther anteriorly, the two smaller and slightly lingually displaced alveoli, of which the anterior is smaller than the posterior, are interpreted as being for a double-rooted p2. Anterior to p2 is an even smaller, single-rooted p1, and the canine is represented by the large, anteriormost alveolus in the specimen. A large mental foramen occurs lateral to the p1 alveolus, whereas a smaller foramen is present lateral to the anterior alveolus of p3. A third foramen, about as large as the first one, is seen ventral to the p4 alveolus. Only a part of the gradually ascending coronoid process is preserved.

The m2 is 2.23 mm long and 1.73 mm wide. The trigonid of m2 bears three cusps: protoconid, metaconid and the paraconid. The trigonid basin is shallow. The metaconid is slightly higher and larger in cross-section than the protoconid. These cusps are widely separated at their summits but are connected at their base by a very weak protocristid. The notch between the protoconid and metaconid is shallow. The paraconid is the smallest cusp, located slightly lingual to the tooth midline. The paracristid descends from the protoconid anterolingually, and then curves caudally to ascend the metaconid, becoming much weaker nearly half way up the latter. The talonid is deeply basined and slightly broader than the trigonid. The cristid obliqua extends from the labial side of the protoconid to the largest cusp on the talonid, the hypoconid. A weak and straight posthypocristid passes caudolingually to the middle of the posterior edge of the tooth. The entoconid is very small and relatively anteriorly positioned. The hypoconulid area is slightly damaged but, as seen in the cross section, the hypoconulid and the entoconid appear to be similar in size. There is a small cuspule approximately equidistant between hypoconulid and entoconid. A strong crest extends anteriorly from the entoconid

forming a lingual wall to the talonid basin. Cingulids are present on the lateral part of the anterior and posterior side of the tooth, as well as along the labial side of the trigonid and talonid. Cingulid is most prominent on the anterolabial side of the crown. There is no lingual cingulid.

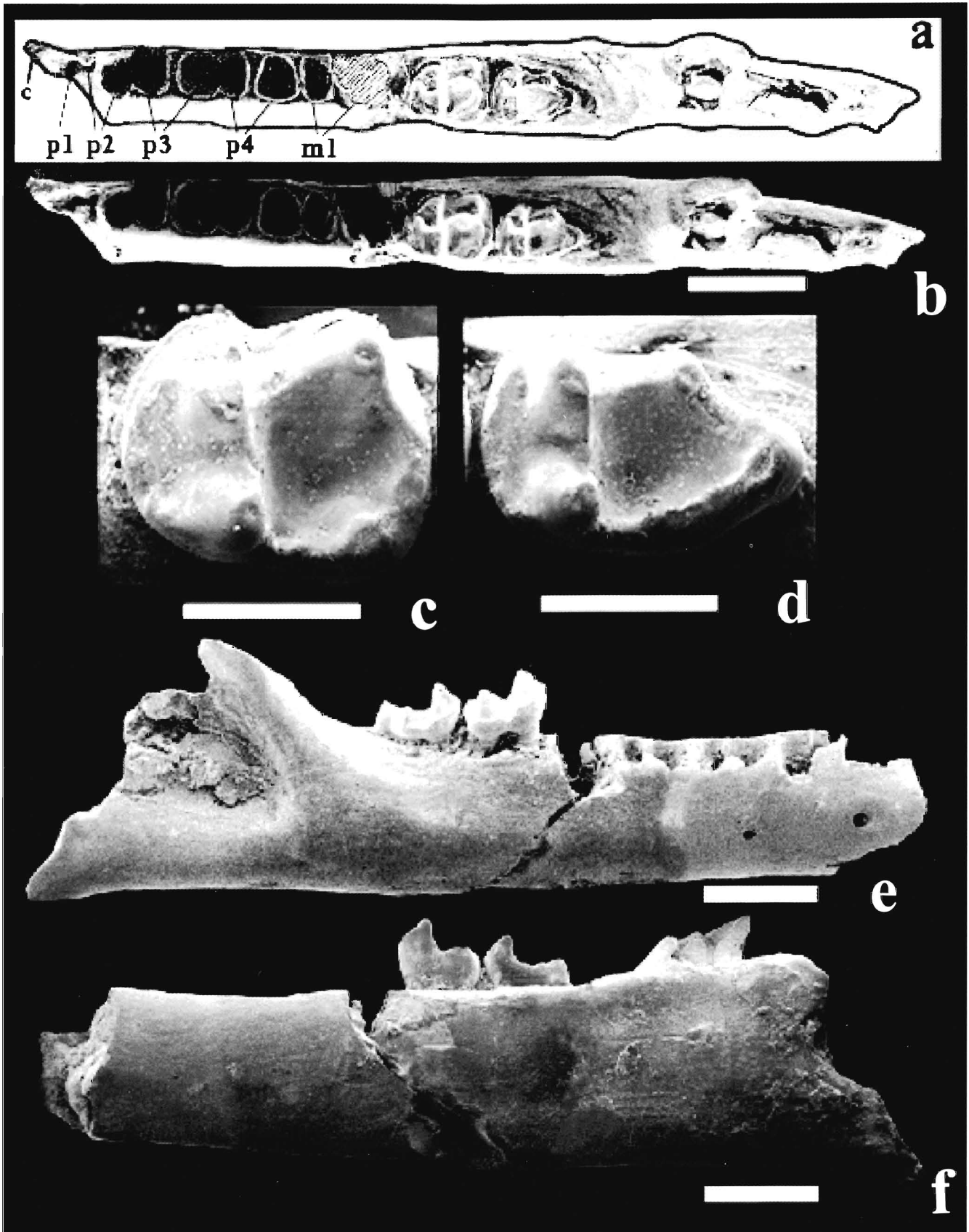
IITR/SB/VLM 817 is a right dentary referred to *Marcgodinotius indicus*. It preserves the crowns for m2-3 and one partial and nine complete alveoli for m1-p1. The anterior side of the mandible is broken, but much of this surface is slightly concave and smooth, suggesting that it is the posterior side of the alveolus a large single-rooted tooth, here interpreted as a canine. Posterior to this edge are two small, similar-sized alveoli, the anterior of which is here interpreted as a small p1, and the posterior one is considered as the anterior alveolus of a double-rooted p2. A small mental foramen occurs lateral to the p1 alveolus. The anterior alveolus of p2 is smaller and distinctly labially shifted relative to the posterior alveolus of p2. The p2 is followed posteriorly by five well defined alveoli that are interpreted as for the double-rooted p3 and p4, and the m1 trigonid. A second mental foramen occurs lateral to the posterior alveolus of p3. Posterior to the alveolus for m1 trigonid is the last alveolus in this row, which is irregularly-shaped and much larger than the alveoli anterior to it. It occurs in a crack in the jaw, and the jaw is slightly offset here. We interpret this alveolus as being the crushed posterior alveolus of m1. The ramus of the mandible is narrow, and the posterior part of the jaw preserves part of mandibular angle and coronoid process. The mandibular foramen is located far posterior to m3 and the masseteric fossa is deep.

In the molar morphology of m2 and the pattern of all of the preserved alveoli, IITR/SB/VLM 817 is more or less identical to the type dentary. Unlike the type dentary, however, the m2 in the referred dentary has a more or less semicircular anterior outline. Also, the protoconid is slightly larger in cross-section than the metaconid. The paraconid in IITR/SB/VLM 817 is not discernible since the anterior edge of the trigonid is slightly damaged. The most important difference between the two dentaries is that the depth of mandible in IITR/SB/VLM 817 is significantly less (about 70 % as deep as in the holotype). At the anterior margin of m1, for example, the mandibular depth in the type dentary is 5.5 mm and that in IITR/SB/VLM 817 is

## EXPLANATION OF PLATE II

(scale bar equals 3 mm for a, b, e, f; 1200 µm for c, d)

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| a. <i>Marcgodinotius indicus</i> n. gen. and n. sp., right dentary (IITR/SB/VLM 817), drawing in occlusal view.                | d. <i>Marcgodinotius indicus</i> n. gen. and n. sp., magnified view of m3 from right dentary (IITR/SB/VLM 817), occlusal view. |
| b. <i>Marcgodinotius indicus</i> n. gen. and n. sp., right dentary (IITR/SB/VLM 817), occlusal view.                           | e. <i>Marcgodinotius indicus</i> n. gen. and n. sp., right dentary (IITR/SB/VLM 817), labial view.                             |
| c. <i>Marcgodinotius indicus</i> n. gen. and n. sp., magnified view of m2 from right dentary (IITR/SB/VLM 817), occlusal view. | f. <i>Marcgodinotius indicus</i> n. gen. and n. sp., right dentary (IITR/SB/VLM 817), lingual view.                            |



4.0 mm. This difference is here attributed to sexual dimorphism of *M. indicus*. Similar differences in mandibular depths, attributed to sexual dimorphism, have been noticed previously in anthropoid primates and the adapid *Cantius torresi* (Fleagle *et al.*, 1980; Gingerich, 1995). At present, we consider it almost certain that the two dentaries (IITR/SB/VLM 800 and IITR/SB/VLM 817) are conspecific.

In most aspects of morphology, m3 trigonid is very similar to that of m2 and differs mainly in being slightly shorter in length and in having its anterior margin less broadly rounded. The anterior edge is damaged, but the paraconid was evidently quite small. Like in m2, the protoconid and metaconid are similar in height but the former is slightly larger in cross-section. The talonid of m3 is elongate but narrower than the trigonid, and the hypoconulid is the largest cusp on the talonid, located more or less at the anteroposterior midline. The entoconid is similar in size to the cusp between it and the hypoconulid. The lingual talonid wall is more distinct in m3 as compared to m2. The m3 is 2.22 mm long and 1.5 mm wide.

IITR/SB/VLM 642 (Pl. IV, figs. i-k) is a right upper molar, possibly M2 or M3, tentatively referred to *M. indicus*. The tooth is triangular in shape, conspicuously narrow lingually. The length is 1.46 mm and the width 2.56 mm. The paracone, metacone and protocone are well-developed with pointed apices, but the hypocone is absent. The paracone is higher than the metacone and protocone. The paraconule is absent whereas the metaconule is very weakly developed. The protocone is bent labially and has an extended lingual slope. The postparacrista and premetacrista are strong and join together to form a well-defined shearing edge. The preparacrista is pronounced and descends to join the well-developed, labially protruding parastylar region. The postmetacrista is absent. Both the preprotocrista and postprotocrista are strongly developed. The preprotocrista is arcuate and passes near the base of the paracone to meet the anterior cingulum. The postprotocrista passes over the diminutive metaconule and then blends with the hypometacrista to extend right up to the apex of the metacone. There is neither a postmetaconule crista nor a *Nannopithec* fold. The cingulum is strong but discontinuous on the lingual margin as well as on the anterior and posterior sides of the tooth.

*Remarks:* Although IITR/SB/VLM 800 preserves only one molar as opposed to two in the referred dentary (IITR/SB/VLM 817), we preferred to designate the former as the holotype because the alveoli in this specimen are better preserved and leave no doubt regarding the number and roots of premolars. However, most of the diagnostic features of this species rely on the identification of the jaw morphology and alveoli. The gracile mandible lacking any sign of the mandibular symphysis in the preserved fragment, and the number and large size of the premolar alveoli suggests to us that this jaw probably represents an adapiform and that the dental formula was ? . 1. 4. 3. The retention of four lower premolars is uncommon among Eocene primates. Four premolars are retained in the European genus *Donrussellia*, widely regarded as the most primitive known adapiform (Godinot *et al.*, 1998), and in some species of the omomyid *Teilhardina* (Rose and Bown, 1991). A double-rooted p2 is only present in *Donrussellia*. Godinot (1992) diagnosed *Donrussellia*, subgenus *Palettia*, from other adapids as having an m3 with its cristid obliqua joining the protoconid relatively lingually, and the entoconid reduced to two small cusps. These features also occur in *M. indicus*. Based on comparisons with published descriptions (Godinot, 1994, 1998), *M. indicus* is similar in size to *Donrussellia provincialis*, but differs in having a much smaller paraconid and in having a more labial cristid obliqua.

Referral of the upper molar (IITR/SB/VLM 642) to *M. indicus* is tentative and is based mainly on the presence of some of the important features that characterize primitive adapiforms, such as the loss of postmetaconule crista, a continuous crest from protocone to metacone and a relatively less pronounced lingual expansion of the protocone (Godinot, 1994, 1998; Rose *et al.*, 1994). Though similar in many features to the referred upper molar of *Vastanomys gracilis* (IITR/SB/VLM 617) described below, this tooth is easily distinguished by several characters: narrower lingual margin (i.e. more triangular tooth outline), more transverse shape, sharp crests, labial protrusion of the paracone, longer lingual slope of the protocone, a continuous crest between protocone and metacone and the absence of a paraconule.

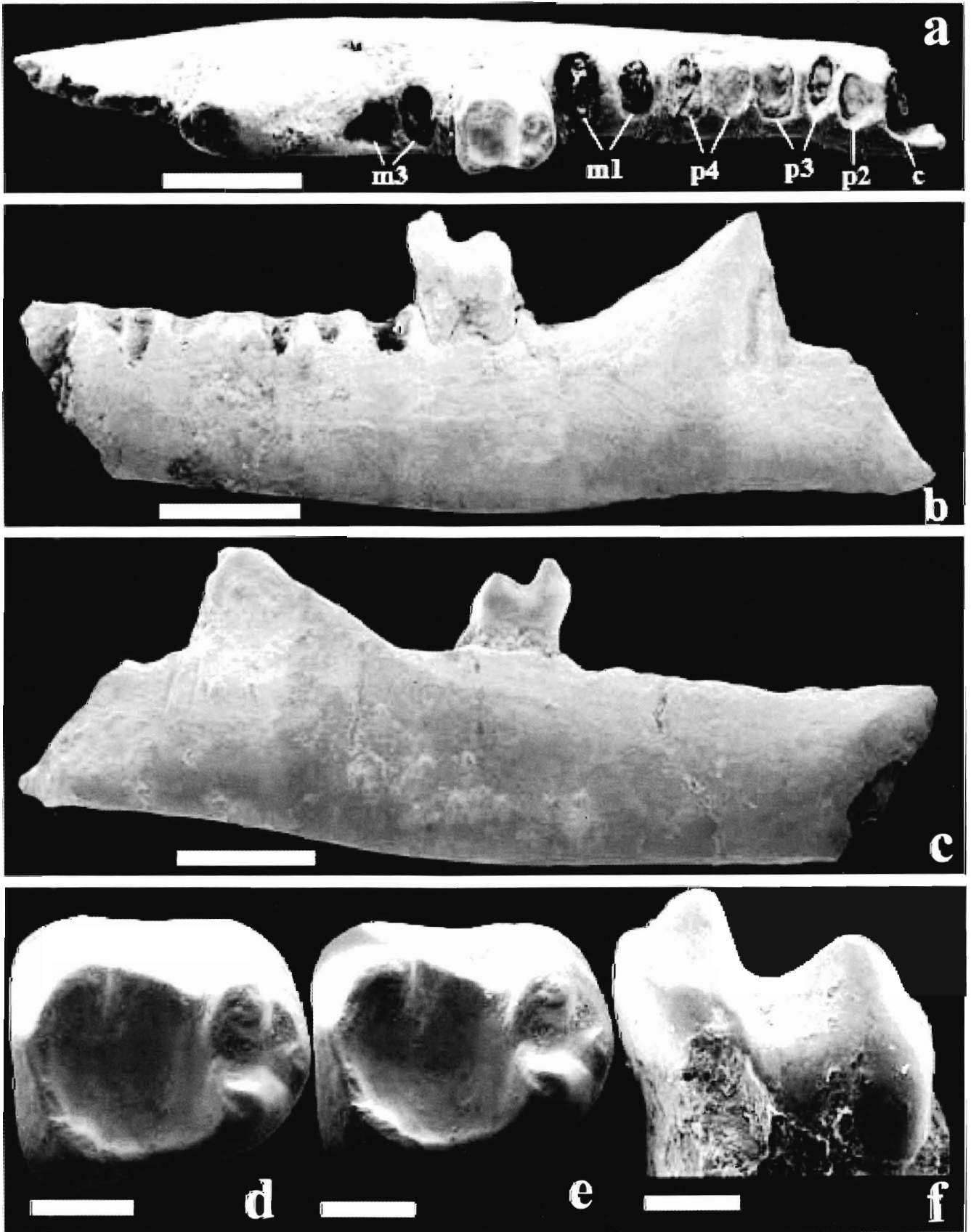
*Type Locality:* Vastan Lignite Mine, Taluka Mangrol, District Surat, Gujarat, India.

### EXPLANATION OF PLATE III

(scale bar equals 3 mm for a-c; 700  $\mu$ m for d, e; 600  $\mu$ m for f)

- a. *Vastanomys gracilis* n. gen. and n. sp., left dentary, holotype (IITR/SB/VLM 771), occlusal view.
- b. *Vastanomys gracilis* n. gen. and n. sp., left dentary, holotype (IITR/SB/VLM 771), labial view.
- c. *Vastanomys gracilis* n. gen. and n. sp., left dentary, holotype (IITR/SB/VLM 771), lingual view.
- d, e. *Vastanomys gracilis* n. gen. and n. sp., stereo pair of m2 from holotype dentary (IITR/SB/VLM 771), occlusal view.
- f. *Vastanomys gracilis* n. gen. and n. sp., m2 from holotype dentary (IITR/SB/VLM 771), labial view.





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

*Infraorder* Tarsiiformes Gregory, 1915

*Family* ?Omomyidae Trouessart, 1879

*Genus* *Vastanomys* n. gen.

*Type and only species:* *V. gracilis* n. sp.

*Derivation of name:* Combination of *Vastan*, the name of the lignite mine with *-omys*, a common suffix for omomyid primates.

*Diagnosis:* 3 lower premolars with a single-rooted p2; m2 trigonid markedly constricted relative to talonid; paraconid situated nearly halfway between protoconid and metaconid; strong paracristid; m2 hypoconulid indistinct.

*Remarks:* *Vastanomys* is tentatively interpreted here as an omomyid based on our interpretation of the alveoli, suggesting the presence of a large i1 and small c. This interpretation needs to be corroborated on when jaws with anterior teeth are discovered. *Vastanomys* differs from *Donrussellia* and other primitive adapiforms mainly in having three lower premolars, a single rooted p2 and a less elongate m3 talonid (as based on alveolus). A reduced lower dental formula with three premolars and a single-rooted p2 also distinguish *Vastanomys* from *Teilhardina belgica* and *T. americana*, the two long-known basal omomyids (e.g. Bown and Rose, 1987; Gunnell and Rose, 2002), as well as from the recently described Chinese early Eocene species *T. asiatica* (Ni *et al.*, 2004), possibly the most primitive species of this genus. The same character as well as the reduced size and relatively labial position of m2 paraconid differentiate *Vastanomys* from *Steinius vespertinus*, another very primitive early Eocene North American omomyid (Rose and Bown, 1991).

Among other Eocene anaptomorphine omomyids (Bown and Rose, 1987), *Tetonius* differs from *Vastanomys* mainly in having either two lower premolars or 3 premolars with a tiny p2, and its larger m2 width; *Pseudotetonius* is distinct in having

only two lower premolars. *Anaptomorphus* also differs in having two lower premolars (Gunnell and Rose, 2002) and *Altanius orlovi*, described from the early Eocene of Mongolia as the oldest known omomyid (Dashzeveg and McKenna, 1977), can be distinguished from *Vastanomys* primarily by the presence of a double-rooted p2.

*Age and distribution:* early Eocene of India.

*Vastanomys gracilis* n. sp.

(Pl. III, figs. a-f; Pl. IV, figs. a-e)

*Referred material:* IITR/SB/VLM 617 (isolated right upper M1 or M2)

*Derivation of name:* The species name reflects the gracile morphology of the lower jaw of this species.

*Diagnosis:* specific and generic diagnosis cannot be distinguished at present.

*Holotype:* IITR/SB/VLM 771, a left dentary with crown for m2 and alveoli for c-m1 and m3.

*Description:* The holotype dentary preserves the crown for m2, two complete alveoli for m3 and seven complete alveoli between the m2 crown and a partial alveolus interpreted as for canine. The six alveoli anterior to m2 represent double-rooted m1, p4, and p3. The alveolus anterior to p3 is small and probably housed a single-rooted p2, immediately behind the much larger alveolus for canine.

The trigonid of m2 is markedly constricted relative to talonid. It bears three cusps of which the metaconid is the highest and protoconid is the largest in cross-section. The paraconid is small but distinct and is situated nearly halfway between protoconid and metaconid. The base of the protoconid is connected to the base of the metaconid by a weak protocristid. The paracristid is stronger than the protocristid. There is no crest between the paraconid and metaconid. The talonid is deep-basined and is both wider and longer than trigonid. The hypoconid and entoconid are similar in height but the hypoconid is larger in cross-section. The

#### EXPLANATION OF PLATE IV

(scale bar equals 600  $\mu$ m for a-c, e, g, i, j, l, m; 200  $\mu$ m for d; 700  $\mu$ m for k, n, o; 800  $\mu$ m for h; 900  $\mu$ m for f)

- |   |  |
|---|--|
| a, b. <i>Vastanomys gracilis</i> n. gen. and n. sp., right upper molar (IITR/SB/VLM 617), occlusal view, stereo pair. | i, j. <i>Marcgodinotius indicus</i> n. gen. and n. sp., right upper molar (IITR/SB/VLM 642), occlusal view, stereo pair. |
| c. <i>Vastanomys gracilis</i> n. gen. and n. sp., right upper molar (IITR/SB/VLM 617), drawing in occlusal view.      | k. <i>Marcgodinotius indicus</i> n. gen. and n. sp., right upper molar (IITR/SB/VLM 642), anterior view.                 |
| d. <i>Vastanomys gracilis</i> n. gen. and n. sp., right upper molar (IITR/SB/VLM 617), posterior view.                | l. <b>Primates indet.</b> 2, left deciduous P4 (?) (IITR/SB/VLM 659), occlusal view.                                     |
| e. <i>Vastanomys gracilis</i> n. gen. and n. sp., right upper molar (IITR/SB/VLM 617), anterior view.                 | m. <b>Primates indet.</b> 2, left deciduous P4 (?) (IITR/SB/VLM 659), drawing in occlusal view.                          |
| f. <b>Primates indet.</b> 1, right M3 ((IITR/SB/VLM 710), occlusal view.  | n. <b>Primates indet.</b> 2, left deciduous P4 (?) (IITR/SB/VLM 659), posterior view.                                    |
| g. <b>Primates indet.</b> 1, right M3 ((IITR/SB/VLM 710), posterior view.   | o. <b>Primates indet.</b> 2, left deciduous P4 (?) (IITR/SB/VLM 659), anterior view.                                     |
| h. <b>Primates indet.</b> 1, right M3 (IITR/SB/VLM 710), anterior view.   |  |





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hypoconulid is barely discernible. The cristid obliqua touches the labial side of the protoconid, and another crest extends between the entoconid and the lingual side of the trigonid. This tooth is 2.05 mm long and 1.81 mm wide. A cingulid is present on the anterolabial part of m2. The alveolus for m3 clearly shows that the talonid was less elongate than in the m3 of *M. indicus* described above. The cingulid is present only on the anterolabial part of the crown.

IITR/SB/VLM 617 (Pl. IV, figs. a-e) is an isolated right upper molar (M1 or M2) tentatively referred to *V. gracilis*. The tooth is transverse (l = 1.81 mm; w = 2.58 mm), triangular in shape, with the paracone, metacone and protocone well-developed and hypocone absent. The protocone is robust, larger than both paracone and metacone, and is bent slightly labially with a lingual slope. The metacone and paracone are similar-sized, with the latter only slightly larger. The parastyle is small. The paracone and metacone have the same labial extent. The paraconule is very small and the metaconule is absent. The postparacrista is longer than premetacrista, enclosing a well-defined narrow valley. The preparacrista blends with the parastyle, while the postmetacrista descends posteriorly and then curves to join the posterolabial cingulum. The preparaconule crista is short and extends labially to join the cingulum at the anterior base of paracone. The postparaconule crista is more sharply defined and ascends the paracone. The preprotocrista descends anterolabially to meet the small paraconule and the postprotocrista arcuates posterolabially and then bifurcates, with one of the branches extending anterolabially towards the base of the metacone and the other running posterolabially to meet the posterior cingulum. The trigon basin is deep. The lingual cingulum is discontinuous with posterolingual part thicker than the anterolingual cingulum. There is no *Nannopithecus* fold. The labial cingulum is weak.

**Remarks:** The holotype dentary is tentatively assigned to Omomyidae based mainly on the following characters: three premolars with a single-rooted p2; relatively anteroposteriorly compressed premolars; small m2 trigonid and reduced third molar talonid (based on alveolus). A reduced dental formula with three premolars represented by a double-rooted p4 and p3, and a one-rooted p2, is observed in several Eocene omomyids, particularly in *Tetonius* and in some advanced species of *Teilhardina* (Bown and Rose, 1987). The alternative interpretation that the alveoli in IITR/SB/VLM 771 represent 4 premolars with a single-rooted p1-p3 and a double-rooted p4, seems unlikely at present. In any case, in the absence of anterior teeth, the present familial assignment is tentative and needs confirmation.

The only known primate upper molar from the Eocene of Indo-Pak is an unnamed M2 from the middle Eocene of Kalakot, NW Himalaya, India (Cat No. WIMF/A 1611, Kumar *et al.*, 2002). The Vastan molar (IITR/SB/VLM 617), tentatively referred to

*V. gracilis*, is similar to the Kalakot molar in many features: tooth shape, absence of a hypocone, discontinuous cingulum, strong labial inclination of protocone, U-shaped trigon basin, weak labial cingulum. However, the Kalakot molar is clearly different in its much larger size (l = 3.5 mm; width = 5.3 mm), labially protruded paracone, presence of a metaconule, much larger paraconule and presence of a postparaconule crista. Comparison of the Vastan molar cannot be made with any other previously described Eocene primates from the Indian subcontinent (*Kohatius*, *Panobius*, *Agerinia*) since no upper molars are known for those taxa.

Comparison with published illustrations (Godinot, 1994, 1998; Rose *et al.*, 1994) figures shows that the upper molar of *Vastanomys gracilis* (IITR/SB/VLM 617) is generally similar to the M2 of *Donrussellia provincialis*. However, *Donrussellia* molars can be distinguished by their larger size, more squared shape, slightly less bunodonty, presence of a metaconule, larger paraconule, less pronounced lingual expansion of the protocone, and the absence of a bifurcating postprotocrista.

Striking similarity of the upper molar (IITR/SB/VLM 617) is noticed with *Teilhardina*, one of the most primitive and widely distributed omomyids. The latter, however, differs in having a consistently longer lingual slope and, in some species such as *T. americana*, a more quadrate outline and a postprotocone fold.

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

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

#### *Primates indet. 1*

(Pl. IV, figs. f-h)

**Material:** IITR/SB/VLM 710 (isolated right M3)

**Description:** This tooth is markedly transverse (l = 1.85 mm, w = 3.46), relatively quadrate in shape, and is low crowned, with its posterolingual margin conspicuously bent. It has a small metacone and a much larger and higher paracone. The paracone extends labially relative to the metacone. Both the postparacrista and premetacrista are well-developed. The parastyle is indistinct. The protocone is large, bent anterolabially and has a strong preprotocrista that extends labially up to the base of the paracone where it joins the anterior cingulum. There is no crest running lingually from the paracone (hypoparacrista). The postprotocrista is slightly worn but it is arcuate in shape and extends to the base of the metacone where it is split into two short cristae, one running posterolabially and the other ascending a short distance on the metacone. A wide groove running more or less parallel to postprotocrista is probably the result of wearing. The labial and posterior cingulum is strong and the lingual cingulum is discontinuous.

**Remarks:** The M3s in early omomyids and adapiforms are much reduced in comparison to the anterior molars (e.g. Bown

and Rose, 1987; Godinot, 1998; Gebo 2002). Hence, the large size of IITR/SB/VLM 710 relative to the other isolated molars described above makes it unlikely that it is conspecific with any of them. Additional material is required to ascertain its affinities.

*Primates indet. 2*

(Pl. IV, figs. I-o)

*Material:* IITR/SB/VLM 659 (isolated left ?deciduous P4).

*Description:* The tooth is broadly triangular in shape but markedly less transverse as compared to the upper teeth described above. The length and width are 1.85 mm and 2.36 mm, respectively. The tooth is somewhat long for its width and it is possible that this specimen pertains to a deciduous P4. The labial margin of the tooth is almost straight. The lingual margin is broadly rounded and curved markedly posteriorly. The three main cusps- paracone, metacone and protocone- are well-developed, but the hypocone is absent. The paracone is slightly worn but evidently larger than the metacone. Their bases are separated. The parastylar region is reduced and more labially positioned than the paracone and metacone. The postparacrista and premetacrista are barely discernible. A weak crest (hypoparacrista) descends a short distance from the apex of the paracone. The protocone is bent slightly anterolabially and has an extended posterolingual slope. Both paraconule and metaconule are present, the latter being much larger. The paraconule is located anteriorly to the line joining paracone and protocone. The postprotocrista descends posterolabially from protocone to join the base of the metaconule. An anteroposteriorly directed groove separates the metacone from metaconule. The preprotocrista is weak. The preparaconule crista is short and extends anterolabially. The trigon basin is moderately deep. The labial cingulum is missing. A weak cingulum extends lingually from the anterolabial base of the paracone and is discontinuous near the posterior margin of the tooth. The posterolingual cingulum is pronounced.

*Remarks:* This tooth differs from IITR/SB/VLM 617 and IITR/SB/VLM 642 described above in being markedly less transverse (i.e. in being longer anteroposteriorly), in having a nearly straight labial margin and reduced parastylar region, in posteriorly protruding lingual margin and in the presence of a well-developed metaconule. At this stage, it is not possible to attempt a definite assignment.

## CONCLUDING REMARKS

The present collection, taken together with the previously described younger material from Pakistan, shows that the Eocene primate diversity in the subcontinent may be considerable. However, these taxa are still poorly known and their precise evolutionary relations are yet to be worked out. Godinot (1998) suggested that the known Pakistani primates, particularly *Kohatius* and *Panobius*, do not fit in the presently known subfamilies of adapiforms and omomyiforms and that

they may be part of a new group of Asian primates. Although known from fragmentary material, the early Eocene primates from Vastan and the middle Eocene Pakistani forms appear at present to be markedly different from contemporary taxa from North America and Europe, and may warrant erection of a new family. Ongoing work at the Vastan lignite mine has yielded additional and more nearly complete specimens that will clarify these relationships. Of particular importance is the relationship of the Indo-Pak primates with the early Eocene taxa from China and Mongolia, such as *Altanius* (Dashzeveg and McKenna, 1977; Gingerich *et al.*, 1991) and the recently described *Teilhardina* (Ni *et al.*, 2004). Once these relationships are established, it should also be possible to evaluate the hypothesis of primate origins in Indo-Pakistan and the question of their subsequent dispersal to the northern continents (Krause and Maas, 1990).

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