Journal of Human Evolution xxx (2009) 1–39

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

# Early Eocene Primates from Gujarat, India

Kenneth D. Rose [a,*], Rajendra S. Rana [b], Ashok Sahni [c], Kishor Kumar [d], Pieter Missiaen [e], Lachham Singh [b], Thierry Smith [f]

[a] *Johns Hopkins University School of Medicine, Baltimore, Maryland 21205, USA*
[b] *H.N.B. Garhwal University, Srinagar 246175, Uttarakhand, India*
[c] *Panjab University, Chandigarh 160014, India*
[d] *Wadia Institute of Himalayan Geology, Dehradun 248001, Uttarakhand, India*
[e] *University of Ghent, B-9000 Ghent, Belgium*
[f] *Royal Belgian Institute of Natural Sciences, B-1000 Brussels, Belgium*

ARTICLE INFO

*Article history:*
Received 24 June 2008
Accepted 8 January 2009

*Keywords:*
Eocene
India
Notharctidae
Adapoidea
Omomyidae
Eosimiidae
Postcrania

ABSTRACT

The oldest euprimates known from India come from the Early Eocene Cambay Formation at Vastan Mine in Gujarat. An Ypresian (early Cuisian) age of ∼53 Ma (based on foraminifera) indicates that these primates were roughly contemporary with, or perhaps predated, the India-Asia collision. Here we present new euprimate fossils from Vastan Mine, including teeth, jaws, and referred postcrania of the adapoids *Marcgodinotius indicus* and *Asiadapis cambayensis*. They are placed in the new subfamily Asiadapinae (family Notharctidae), which is most similar to primitive European Cercamoniinae such as *Donrussellia* and *Protoadapis*. Asiadapines were small primates in the size range of extant smaller bushbabies. Despite their generally very plesiomorphic morphology, asiadapines also share a few derived dental traits with sivaladapids, suggesting a possible relationship to these endemic Asian adapoids. In addition to the adapoids, a new species of the omomyid *Vastanomys* is described. Euprimate postcrania described include humeri, radii, femora, calcanei, and tali, most of which show typical notharctid features and are probably attributable to asiadapines. Anatomical features of the limb elements indicate that they represent active arboreal quadrupedal primates. At least one calcaneus is proximally shorter and distally longer than the others, resembling eosimiids in this regard, a relationship that, if confirmed, would also suggest an Asian or southeast Asian faunal connection. Isolated teeth from Vastan Mine recently attributed to a new eosimiid, *Anthrasimias gujaratensis*, appear to provide that confirmation. However, their attribution to Eosimiidae is equivocal. They are similar to teeth here tentatively referred to *Marcgodinotius*, hence *A. gujaratensis* may be a junior synonym of *M. indicus*. Corroboration of eosimiids at Vastan requires more compelling evidence. Although definitive conclusions are premature, available evidence suggests that the Vastan adapoids, at least, were derived from western European stock that reached India near the Paleocene-Eocene boundary.

## Introduction

Early Eocene terrestrial mammals were unknown from India until very recently. In the last few years, exploration of lignite mines in the western states of Rajasthan and Gujarat produced the first early Eocene land mammals from India, discovered at the Vastan Mine east of Surat, Gujurat (Figs. 1, 2) (Rana et al., 2005; Rose et al., 2006). Further collecting at Vastan Mine has yielded at least 20 species of terrestrial mammals (Bajpai et al., 2005a,b, 2006; Rose et al., 2007a; Rana et al., 2008), including the most diverse early Eocene chiropteran assemblage known to date (Smith et al., 2007). Fishes, frogs, snakes, lizards, and birds have also been reported (Rana et al., 2004; Rose et al., 2006; Mayr et al., 2007; Folie et al., 2008; Rage et al., 2008).

The first early Eocene primates from India were recently reported from the Vastan Lignite Mine (Bajpai et al., 2005b; Rana et al., 2005). Both Adapoidea and Omomyidae have been described from jaw fragments and isolated teeth. Bajpai et al. (2005b) named a new adapiform, *Marcgodinotius indicus*, but did not assign it to family. They also described an omomyid, *Vastanomys gracilis*. The holotype specimens of both species are dentary fragments with a single molar, $M_2$. Rose et al. (2007a) recently named a third primate, the new adapoid *Asiadapis cambayensis*, based on a dentary with $P_3$-$M_2$. Bajpai et al. (2008) attributed several

---

* Corresponding author.
*E-mail address:* kdrose@jhmi.edu (K.D. Rose).

0047-2484/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jhevol.2009.01.008

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

**Figure 1.** Map of Indian subcontinent showing the location of the Vastan Lignite Mine (modified from Rose et al., 2006). Localities in bold have produced early or middle Eocene continental mammals.

isolated teeth to a new eosimiid, *Anthrasimias gujaratensis*, an assignment we consider questionable, as discussed below. We report here additional adapoid fossils from the Vastan Mine, as well as the first early Eocene primate postcrania from India. New jaws and teeth referred to *Marcgodinotius* and *Asiadapis* support their close relationship to each other and to primitive European cercamoniine notharctids. These primates contribute to mounting evidence for close ties between the early Eocene fauna of India and Europe.

The Vastan mammalian fauna also contains other taxa of European aspect, including the ailuravine rodent *Meldimys* (Rana et al., 2008) and the bat *Hassianycteris* (Smith et al., 2007), as well as more widespread Holarctic taxa such as *Diacodexis* and *Icaronycteris* (both also present in western Europe). In addition, there are Asian endemics such as anthracobunids (Rose et al., 2006) and a primitive lagomorph (Rose et al., 2008). Curiously, the endemic ctenodactyloid rodents (the oldest radiations of which were strictly Asian) and raoellid artiodactyls—both of which are characteristic of middle Eocene faunas of India—are absent so far at Vastan.

The Vastan land-mammal fauna is of particular importance for several reasons. Besides its intrinsic interest as the oldest Cenozoic mammal fauna from India, it dates from an interval that was probably contemporary with, or perhaps predated, India's collision with Asia (e.g., Rowley, 1996; Aitchison et al., 2007; Ali and Aitchison, 2008). Although the recent consensus has been that the collision was underway by the Paleocene-Eocene boundary (e.g., Beck et al., 1995, 1998; Briggs, 2003; Clyde et al., 2003), a new model proposed by Aitchison et al. (2007) suggests that it did not begin until about the Eocene-Oligocene boundary, as late as ~35 Ma. According to this model, which is supported by the paleoposition of India calculated by Schettino and Scotese (2005), the Vastan area would have been approximately at, or just south of, the equator—about 20° south of its present position—when the fossil primates reported here were alive (see also Clyde et al., 2003). Thus, the fauna in general, and the primates in particular, have significant paleobiogeographic implications.

## Methods

Morphological comparisons were made to fossil and extant primates, especially adapoids, omomyids, eosimiids, and extant strepsirrhines. Images of specimens in this paper include scanning electron micrographs and digital photographs in which specimens were whitened with ammonium chloride to bring out details, as specified in the captions.

Measurements of Vastan specimens were taken (to the nearest 0.05 mm) using a micrometer mounted in the lens of a Nikon binocular dissecting microscope or, for larger specimens, with digital calipers. Measurements and indices of comparative samples were taken from the literature, or were measured from original specimens or epoxy casts, as indicated in the tables. Principal components analyses of talar indices were conducted using SPSS 15.0. Further details of the PCA are presented in the discussion of the talus.

Phylogenetic analyses were run with PAUP version 4.0b10 (Swofford, 2002), adding *Marcgodinotius indicus* and *Asiadapis cambayensis* (including teeth, as well as femora, calcanei, and tali, here tentatively referred to those taxa, but excluding the forelimb elements, whose allocation is uncertain) to the character-taxon matrix used by Seiffert et al. (2005). Following Seiffert et al. (2005), we ordered and scaled some of the multistate characters and considered the loss of incisors and premolars in species or higher level clades to be irreversible. Heuristic analyses were run with 10,000 random addition replicates and a 30-second time limit on each replicate. A first analysis was based only on the morphological data matrix. A second cladistic analysis was performed where the relations of the extant crown strepsirrhines were constrained by a molecular scaffold, based on the molecular analysis of strepsirrhine Alu SINEs by Roos et al. (2004) and similar to the approach of Seiffert et al. (2005).

### *Abbreviations*

GU/RSR/VAS, Department of Geology, H.N.B. Garhwal University, Srinagar, Uttarakhand, India; IITR/SB/VLM, Vertebrate Paleontology Laboratory, Department of Earth Sciences, Indian Institute of Technology, Roorkee, India. For ease of reference, the shorter acronyms GU and IITR are used in this article. IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MNHN, Muséum National d'Histoire Naturelle, Paris, France; USGS, U.S. Geological Survey (Denver), collection now housed in the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; USTL, Laboratoire de Paléontologie, Université des Sciences et Techniques du Languedoc, Montpellier, France.

## Occurrence

Vastan Mine is developed in exposures of the lower Eocene Cambay Shale. Most of the sequence at the mine consists of

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

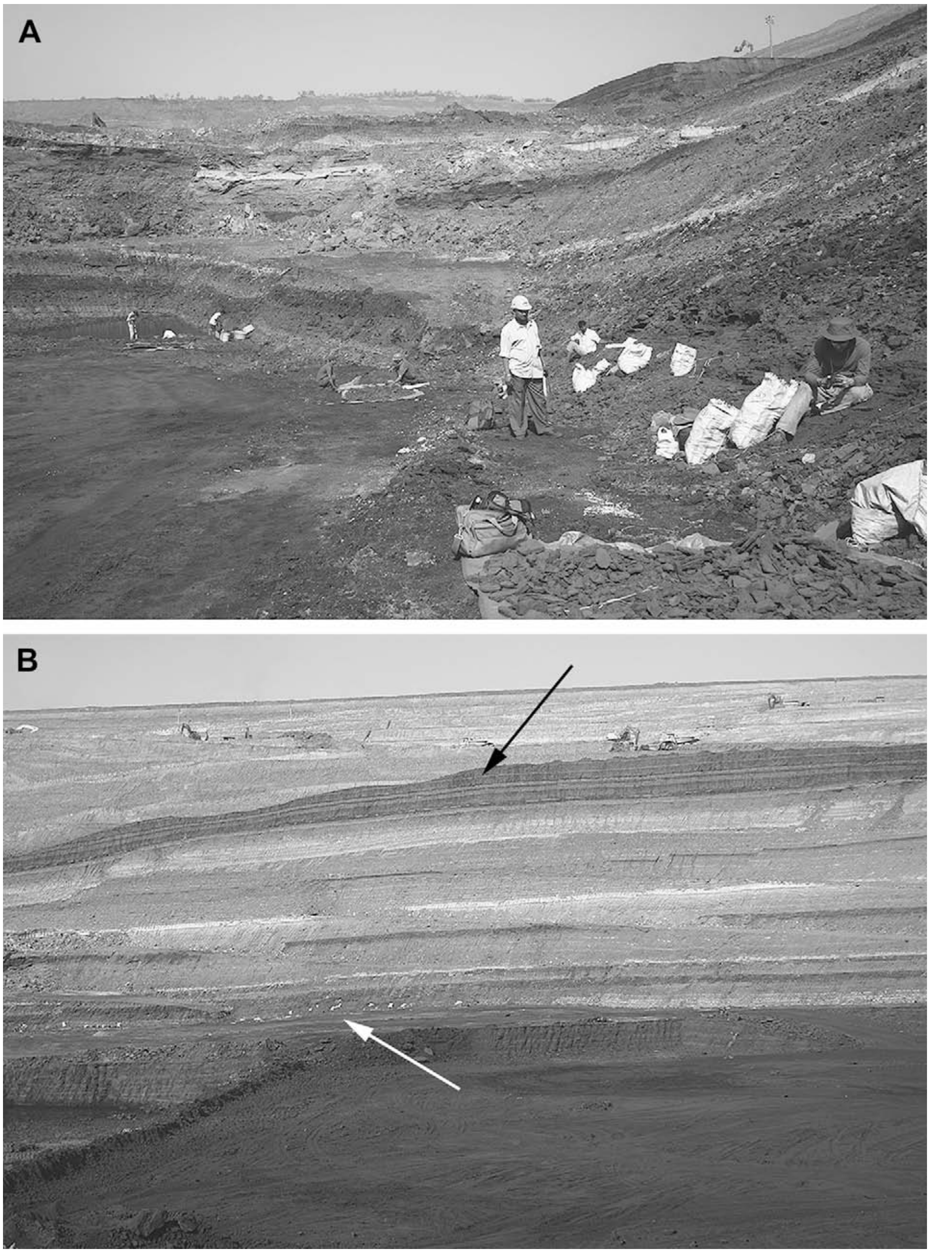

**Figure 2.** Vertebrate-bearing layer at Vastan Mine. (A) Excavation (just above lignite 2) and collection of matrix is shown in the foreground at right; drying of sediment and screen-washing operation can be seen in the background at left. (B) Location of the primate-producing layer (same as in A) is indicated by the white arrow; small white objects are sediment sacks situated on the pay layer. Top of lignite 2 is in the foreground. Black arrow at top indicates lignite 1.

near-shore intertidal, estuarine, and lagoonal strata, rich in organic remains including mollusks, foraminifera, and plants, as well as fossil vertebrates (Sahni et al., 2006). The fossil primates, like most of the smaller terrestrial vertebrates from Vastan Mine, come from a thin lens (<0.5 m thick) of dark, clayey silt and shale with abundant plant matter, about 1 m above the lower of two major lignites (Lignite 2) occurring in the mine (Fig. 2). Approximately 1–2 m higher is a dark clay zone that has produced larger terrestrial mammals (anthracobunids). Marine shell beds occur both below and above the mammal-bearing layers, indicating a near-shore environment. A stratigraphic section through this part of the mine (Fig. 3) contains the age-diagnostic foraminiferan *Nummulites burdigalensis burdigalensis* from about 14 m above the mammal layers. This foraminiferan is indicative of Shallow Benthic Zone (SBZ) 10 (Schaub, 1981; Serra-Kiel et al., 1998), which indicates an early Cuisian age (middle Ypresian), approximately 53 Ma (Berggren and Aubry, 1998; Luterbacher et al., 2004). However, dinoflagellate cysts recently reported from the section suggest that the deposits could be of early Ypresian age, ~54–55 Ma (Garg et al., 2008).

Outside of Vastan, the only previously reported primates of early Eocene age from the Indian subcontinent are adapoids from Gandhera Quarry in the upper Ghazij Formation of Baluchistan, Pakistan (Gingerich et al., 2001), which are soon to be described (Gunnell et al., 2008). Upper Ghazij sediments are believed to correlate with SBZ 10 or 11 (Gingerich, 2003), and paleomagnetic evidence indicates a maximum age of ~53.3 Ma (Clyde et al., 2003), suggesting that the upper Ghazij and Cambay Shale were

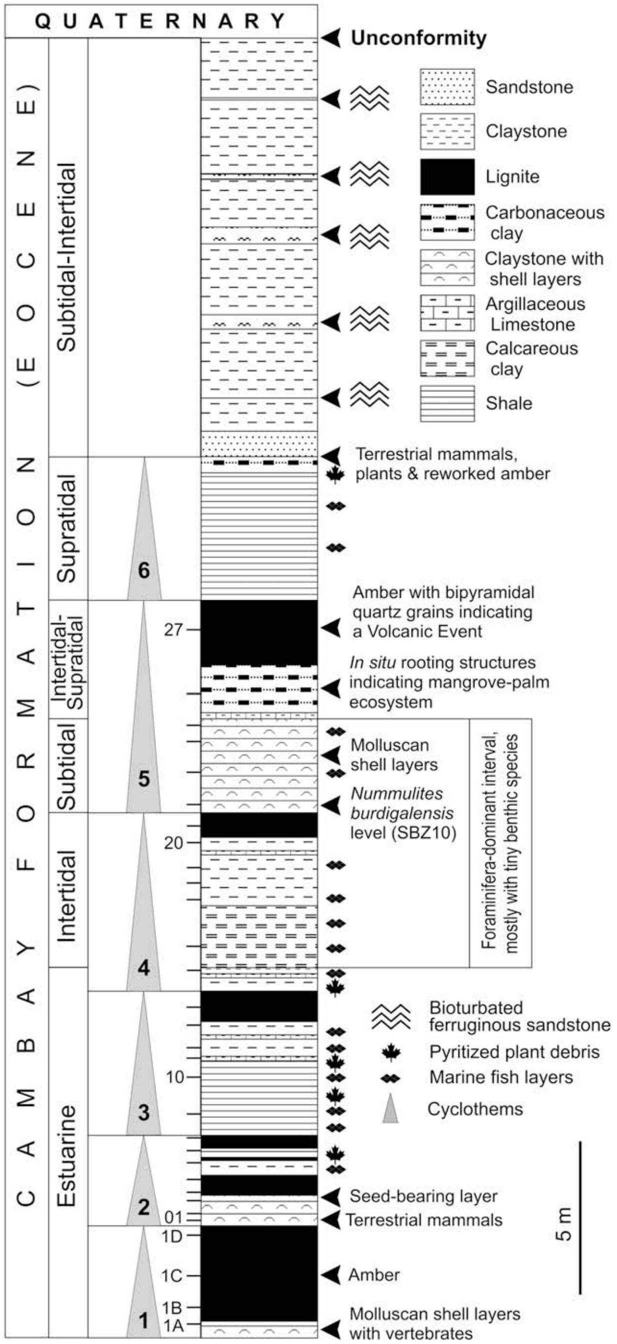

**Figure 3.** Stratigraphic section through the lower Eocene Cambay Formation in Vastan Mine. Section shows position of the vertebrate-producing layer in which the primates have been found relative to the two principal lignites in cycles 1 (lignite 2) and 5 (lignite 1). Note presence of foraminiferan *Nummulites burdigalensis* from about 14 m above the fossiliferous layer.

roughly coeval. Apart from these, the oldest primates from the region are adapoids and omomyids from the Kuldana Formation of Pakistan, including the "Mami Khel Formation" (Russell and Gingerich, 1980, 1987; Thewissen et al., 1997, 2001), which is now considered to be latest early Eocene or, more likely, early middle Eocene in age (Gingerich, 2003). This corresponds to SBZ 12 or 13. A middle Eocene adapoid is also known from the middle Eocene Subathu Formation of northwestern India (Kumar et al., 2002). All of these records consist of only isolated teeth or jaw fragments.

## Systematics

Order PRIMATES
Suborder EUPRIMATES
Infraorder STREPSIRRHINI
Superfamily Adapoidea Trouessart, 1879
Family Notharctidae Trouessart, 1879
Subfamily Asiadapinae, new
Included Genera– *Asiadapis* (type genus) and *Marcgodinotius.*

### *Diagnosis*

Small notharctids with relatively simple P$_{3\text{-}4}$ either lacking paraconid and metaconid, or P$_4$ variably with small, low metaconid and/or paraconid; P$_3$ unreduced and taller than P$_4$; lower molars with buccal cristid obliqua and more transverse (less oblique) protocristid and postvallid on M$_{2\text{-}3}$ than in other notharctids; M$_1$ postvallid even on both sides of cristid obliqua, in contrast to offset ("stepped") postvallid in other notharctids including *Donrussellia.* Molar trigonids with paraconids either small and buccally shifted, or sometimes absent on M$_{2\text{-}3}$; M$_{2\text{-}3}$ paracristids arcuate and joining protoconid to metaconid. Upper molars lacking *Nannopithex* fold; hypocone very small or absent; lingual cingulum weak or incomplete.

### *Remarks*

The Vastan adapoid genera have primitive molars that closely resemble those of cercamoniine notharctids such as *Donrussellia*, *Protoadapis*, and *Agerinia*, but they differ from cercamoniines and other notharctids in the features listed above. These differences indicate that they represent a separate clade from European cercamoniines, although the two subfamilies are probably closely related. Some of the diagnostic features of asiadapines could be as primitive as, or more so than, in *Donrussellia*: the unreduced P$_3$, the rather simple posterior premolars sometimes lacking a paraconid or metaconid on P$_4$, the smooth postvallid (= posterior wall of the trigonid) of M$_1$, and the weak hypocone and lack of a *Nannopithex* fold on the upper molars. Other features (e.g., buccal cristid obliqua, transverse protocristid, reduced or absent paraconids, and arcuate paracristids) are probable synapomorphies of the clade. Together this suite of dental characters suggests that asiadapines diverged from other notharctids very early in the evolution of the family, at a stage at least as primitive as *Donrussellia* or *Protoadapis*.

The early to middle Eocene adapoid *Panobius* from Pakistan (Russell and Gingerich, 1987; Gunnell et al., 2008) is similar in many respects to *Marcgodinotius* and might be referable to this subfamily, but available specimens are too incomplete to be certain of its affinities.

## Marcgodinotius indicus Bajpai et al., 2005b

### *Holotype*

IITR/SB/VLM 800, right dentary with M$_2$ and alveoli for most other teeth.

### *Referred specimens*

GU/RSR/VAS 7 (left dentary with M$_1$), GU 40 (right P$_4$), GU 41 (left dP$_4$), GU 44 (left M$_1$), GU 45 (left M$_2$), GU 46 (left M$_3$), GU 49 (right M$_1$), GU 50 (right dP$_4$), GU 51 (left M$_3$), GU 52 (right M$_3$), GU 54 (left M$_1$), GU 227 (right dentary with C, P$_{3\text{-}4}$, M$_{2\text{-}3}$, and roots of P$_{1\text{-}2}$), GU 552 (right P$_2$), GU 600 (right M$_1$), GU 611 (right M$_1$), GU

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

**Table 1**

Measurements (mm) of teeth and dentary depth of *Marcgodinotius indicus*. Lengths (L) are maximum mesiodistal dimensions; widths (W) of lower teeth are maximum mediolateral width of trigonid (Wtri) and talonid (Wtal). Dentary depth (JawD) was measured buccally below $P_2$ and $M_3$. Statistics for $dP_4$ do not include GU 601. Holotype dimensions from Bajpai et al. (2005b).

| Number | $P_3$L | $P_3$W | d$P_4$L | d$P_4$Wtri | d$P_4$Wtal | $P_4$L | $P_4$Wtri | $P_4$Wtal | $M_1$L | $M_1$Wtri | $M_1$Wtal | $M_2$L | $M_2$Wtri | $M_2$Wtal | $M_3$L | $M_3$Wtri | $M_3$Wtal | JawD $M_3$ | JawD $P_2$ | d$P^4$L | d$P^4$W | $M^1$L | $M^1$W | $M^2$L | $M^2$W | $M^3$L | $M^3$W |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| GU 7 | | | | | | | | | 2.40 | 1.50 | 1.65 | | | | | | | 3.70 | 3.90 | | | | | | | | |
| GU 40 | | | | | | 2.25 | 1.30 | 1.30 | | | | | | | | | | | | | | | | | | | |
| GU 41 | | | 2.30 | 1.00 | 1.10 | | | | | | | | | | | | | | | | | | | | | | |
| GU 44 | | | | | | | | | 2.20 | 1.30 | 1.40 | | | | | | | | | | | | | | | | |
| GU 45 | | | | | | | | | | | | 2.35 | 1.70 | 1.75 | | | | | | | | | | | | | |
| GU 46 | | | | | | | | | | | | | | | 2.30 | 1.50 | 1.35 | | | | | | | | | | |
| GU 49 | | | | | | | | | 2.40 | 1.30 | 1.55 | | | | | | | | | | | | | | | | |
| GU 50 | | | 2.25 | 1.05 | 1.20 | | | | | | | | | | | | | | | | | | | | | | |
| GU 51 | | | | | | | | | | | | | | | 2.25 | 1.50 | 1.30 | | | | | | | | | | |
| GU 52 | | | | | | | | | | | | | | | 2.40 | 1.40 | 1.30 | | | | | | | | | | |
| GU 54 | | | | | | | | | 2.30 | 1.50 | 1.55 | | | | | | | | | | | | | | | | |
| GU 227 | 1.90 | 1.25 | | | | 2.30 | 1.30 | 1.40 | | | | 2.30 | 1.60 | 1.75 | 2.40 | 1.60 | 1.40 | 3.60 | 3.70 | | | | | | | | |
| GU 600 | | | | | | | | | 2.30 | 1.40 | 1.55 | | | | | | | | | | | | | | | | |
| GU 601 | | | 2.15 | 1.00 | 1.20 | | | | | | | | | | | | | | | | | | | | | | |
| GU 611 | | | | | | | | | 2.20 | 1.25 | 1.40 | | | | | | | | | | | | | | | | |
| GU 643 | | | | | | | | | | | | 2.15 | 1.50 | 1.55 | | | | | | | | | | | | | |
| GU 644 | | | | | | | | | | | | 2.20 | 1.45 | 1.50 | | | | | | | | | | | | | |
| GU 645 | | | | | | | | | | | | 2.40 | 1.55 | 1.70 | | | | | | | | | | | | | |
| GU 646 | | | | | | | | | | | | 2.15 | 1.50 | 1.55 | | | | | | | | | | | | | |
| GU 703 | 1.90 | 1.15 | | | | | | | | | | | | | | | | | | | | | | | | | |
| GU 727 | | | | | | 2.00 | 1.35 | 1.30 | | | | 2.20 | 1.70 | 1.65 | | | | | | | | | | | | | |
| GU 743 | | | | | | | | | | | | 2.20 | 1.60 | 1.60 | | | | 3.55 | | | | | | | | | |
| GU 744 | | | | | | | | | | | | 2.30 | 1.55 | 1.60 | | | | 3.90 | 3.50 | | | | | | | | |
| GU 1534 | | | | | | | | | | | | | | | 2.30 | 1.40 | 1.20 | | | | | | | | | | |
| GU 1536 | | | | | | 2.30 | 1.25 | 1.25 | | | | | | | | | | | | | | | | | | | |
| GU 1538 | 2.00 | 1.10 | | | | | | | | | | | | | | | | | | | | | | | | | |
| GU 1544 | 2.00 | 1.25 | | | | | | | | | | | | | | | | | | | | | | | | | |
| GU 1554 | | | | | | 2.20 | 1.25 | 1.30 | | | | | | | | | | | | | | | | | | | |
| GU 1575 | | | | | | | | | | | | 2.30 | 1.60 | 1.60 | | | | | | | | | | | | | |
| GU 1591 | | | | | | | | | | | | | | | 2.35 | 1.35 | 1.30 | | | | | | | | | | |
| GU 1602 | | | | | | | | | | | | 2.30 | 1.60 | 1.60 | | | | | | | | | | | | | |
| IITR 800 holotype | | | | | | | | | | | | 2.23 | | 1.73 | | | | | | | | | | | | | |
| **MEAN** | 1.95 | 1.19 | 2.28 | 1.03 | 1.15 | 2.21 | 1.29 | 1.31 | 2.30 | 1.38 | 1.52 | 2.26 | 1.58 | 1.63 | 2.33 | 1.46 | 1.31 | 3.69 | 3.70 | | | | | | | | |
| **St Dev** | 0.06 | 0.07 | 0.04 | 0.04 | 0.07 | 0.12 | 0.04 | 0.05 | 0.09 | 0.11 | 0.10 | 0.08 | 0.08 | 0.08 | 0.06 | 0.09 | 0.07 | 0.15 | 0.20 | | | | | | | | |
| GU 42 | | | | | | | | | | | | | | | | | | | | 2.05 | 1.90 | | | | | | |
| GU 43 | | | | | | | | | | | | | | | | | | | | | | 2.20 | 2.50 | | | | |
| GU 47 | | | | | | | | | | | | | | | | | | | | | | | | | | 1.70 | 2.45 |
| GU 48 | | | | | | | | | | | | | | | | | | | | | | | | | | 1.50 | 2.15 |
| GU 243 | | | | | | | | | | | | | | | | | | | | 2.00 | 1.75 | | | | | | |
| GU 538 | | | | | | | | | | | | | | | | | | | | | | | | | | 1.80 | 2.40 |
| GU 705 | | | | | | | | | | | | | | | | | | | | 2.00 | 1.90 | | | | | | |
| GU 706 | | | | | | | | | | | | | | | | | | | | | | | | | | 1.55 | 2.30 |
| **MEAN** | | | | | | | | | | | | | | | | | | | | 2.02 | 1.85 | 2.20 | 2.50 | | | 1.64 | 2.33 |
| **St Dev** | | | | | | | | | | | | | | | | | | | | 0.03 | 0.09 | | | | | 0.14 | 0.13 |

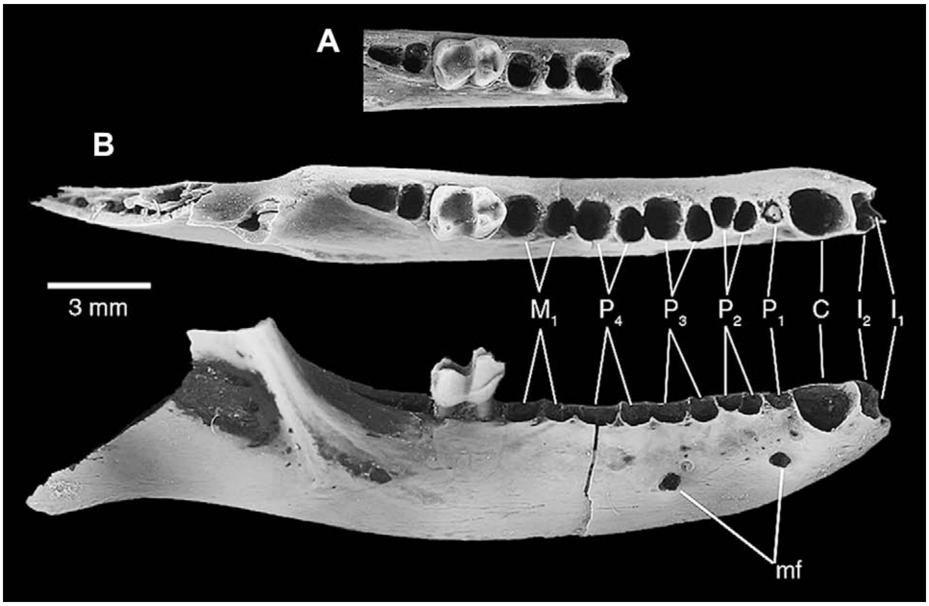

**Figure 4.** *Marcgodinotius indicus*. (A) GU 743, right dentary with $M_2$ in occlusal view. (B) GU 744, right dentary with $M_2$ and alveoli of all other teeth, in occlusal and lateral views. Alveoli and mental foramina (mf) are identified. Digital images; specimens coated with ammonium chloride.

643-GU 646 (left $M_2$s), GU 703 (right $P_3$), GU 727 (right dentary with $P_4$ and $M_2$), GU 743 (right dentary with $M_2$), GU 744 (right dentary with $M_2$ and alveoli of all other teeth), GU 1534 (left $M_3$), GU 1536 (right $P_4$), GU 1538 (left $P_3$), GU 1544 (left $P_3$), GU 1554 (right $P_4$), GU 1575 (left $M_2$), GU 1591 (left $M_3$), and GU 1602 (right $M_2$). Tentatively referred upper teeth: GU 21 (partial left $P^4$), GU 42 (left $dP^4$), GU 43 (right $M^1$), GU 47 (left $M^3$), GU 48 (left $M^3$), GU 243 (left $dP^4$), GU 538 (left $M^3$), GU 705 (right $dP^4$), and GU 706 (right $M^3$). Measurements are given in Table 1.

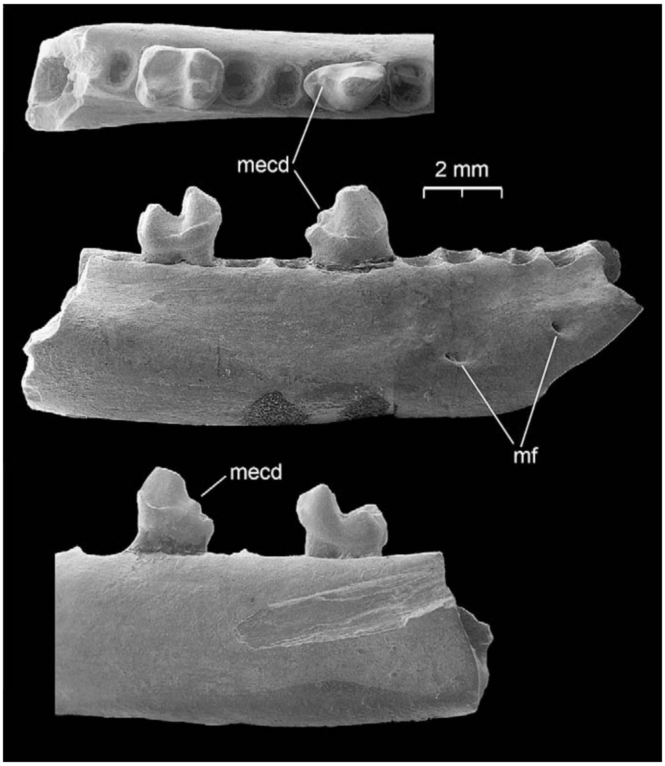

**Figure 5.** *Marcgodinotius indicus*, GU 727, right dentary with $P_4$, $M_2$, and alveoli of other postcanine teeth, in occlusal, lateral, and medial views. Lateral view shows front of dentary and mental foramina (mf). Note metaconid (mecd) on $P_4$. SEM images.

*Occurrence*

Known at present only from the early Eocene Cambay Shale Formation at Vastan Mine, Gujarat, India.

*Emended diagnosis*

Lower dental formula 2-1-4-3. $P_1$ small and single-rooted; $P_2$ two-rooted and obliquely oriented (anterior root buccal to distal root) as in *Donrussellia* and *Protoadapis*. $P_3$ smaller in length and width than $P_4$ but taller; $P_3$ and $P_4$ usually simple with tall protoconid, no paraconid or metaconid, and single talonid cusp; $P_4$ sometimes with small, low metaconid. Differs from all other notharctids except *Anchomomys*, *Periconodon*, and some individuals of *Asiadapis* in typically lacking a distinct metaconid on $P_4$. Molar paraconids small, low, and buccally shifted ($M_1$, some $M_2$s), or indistinct with arcuate paracristid extending to metaconid ($M_2$, $M_3$). $M_3$ with shorter, more constricted hypoconulid lobe than in *Donrussellia*, *Protoadapis*, *Cantius*, and many other adapoids.

*Description*

The original description of this species was based on only two dentary fragments and just two tooth loci, $M_{2\text{-}3}$. The larger sample now available expands our knowledge of this species considerably.

The dentaries described here show that the position of the mental foramina varies in this species, the new specimens having slightly different arrangements than in the holotype and referred jaw in the original description. All adequately preserved specimens have multiple foramina, one or two below anterior premolars and one or two below posterior premolars. In the small available sample of dentaries a single anterior mental foramen below $P_1$ is most frequent (in the holotype, IITR/SB/VLM 800, as well as IITR 817, GU 727, and GU 744 [Figs. 4 and 5]), but GU 227 (Fig. 6) has a pair of foramina inferior to $P_1$ and $P_2$. A single posterior foramen is

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

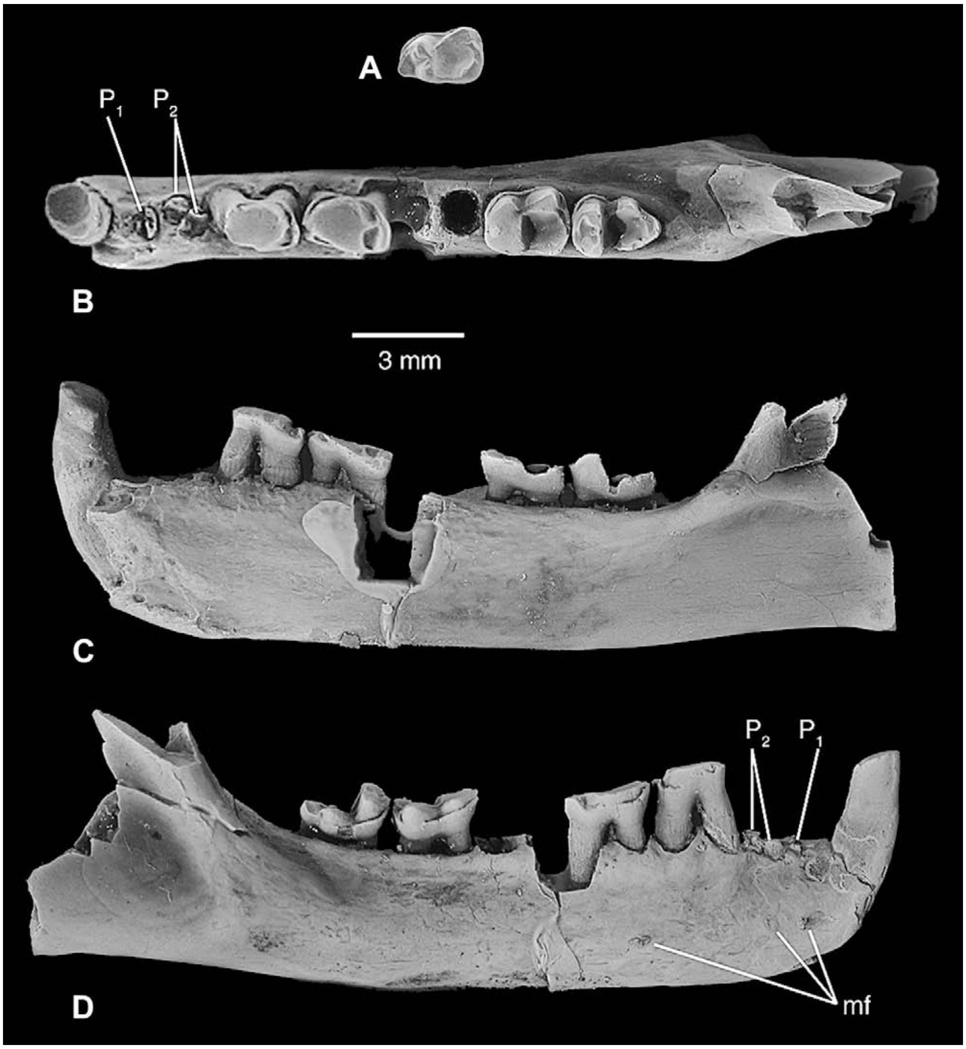

**Figure 6.** *Marcgodinotius indicus*. (A) GU 600, right $M_1$ in occlusal view. (B–D) GU 227, right dentary with $P_{3-4}$, $M_{2-3}$, in occlusal, medial, and lateral views, respectively. Roots of anterior premolars and mental foramina (mf) are indicated. Digital images; specimens coated with ammonium chloride.

also most common, though variable in position (below the middle of $P_3$ in GU 7 and GU 727, below the posterior root of $P_3$ in IITR 817 [Bajpai et al., 2005b] and GU 744, below the anterior root of $P_4$ in GU 227 and GU 743). The holotype has foramina below both $P_3$ and $P_4$. The dentary is relatively constant in depth, with slight variations (e.g., GU 227 is slightly deeper anteriorly, GU 744 is slightly deeper posteriorly despite having the largest canine alveolus). The unfused symphysis extends posteriorly to a point below the anterior root of $P_2$ (GU 744) or $P_3$ (GU 227).

Specimen GU 744 contains $M_2$ and preserves all of the other alveoli. It shows the lower dental formula and root configuration unambiguously; there are no diastemata. Although crowns are unknown for teeth anterior to $P_3$ except for the canine, some information can be deduced from the alveoli. The roots of the two incisors were slightly inclined, though not as much as in *Cantius abditus* (Rose et al., 1999). The alveolus of $I_2$ is slightly bigger than that of $I_1$ (the same size relationships as for the incisors of *Cantius* and *Notharctus*), and the long axis of both is almost transverse to the long axis of the tooth row (at an angle of 60–70° to the tooth row axis), which is much more oblique than in *Cantius*. The canine alveolus is almost round (slightly longer than wide), its longer dimension about the same as that of $P_3$ or $P_4$. The $P_1$ alveolus is small and round. $P_2$ was two-rooted and its alveoli are obliquely oriented. An oblique $P_2$ is characteristic of *Donrussellia* and *Protoadapis* but not *Europolemur*, *Cantius*, or *Notharctus*. The alveoli for $P_3$ and $P_4$ are almost identical in length.

Specimen GU 227 confirms the post-incisor dental formula observed in GU 744. Its canine, however, is smaller than in GU 744, the greatest diameter at the crown base being less than the length of any cheek tooth except $P_1$ or $P_2$. Although this might reflect sexual dimorphism, which has been documented in notharctids (Krishtalka et al., 1990; Alexander, 1994; Gingerich, 1995) but not in extant strepsirrhines, there is no appreciable difference in jaw depth. In fact, as noted above, the dentary with the smaller canine (GU 227) is slightly deeper than the one with a larger canine alveolus. Thus, additional evidence is required to confirm sexual dimorphism in *Marcgodinotius*. The canine in GU 227 is ovoid at the base, the long axis being oriented almost transversely. The crown is heavily worn.

An isolated $P_2$ (GU 552) is tentatively referred to *Marcgodinotius indicus*. The tooth is similar to $P_3$ (GU 703) but smaller, measuring 1.4 mm long and 0.95 mm wide, and has a less developed talonid. Like $P_3$, it has a tall protoconid, no paraconid or metaconid, and a prominent lingual cingulum.

Both $P_3$ and $P_4$ are simple, narrow teeth, each dominated by a tall trigonid, usually consisting of only the protoconid, followed by

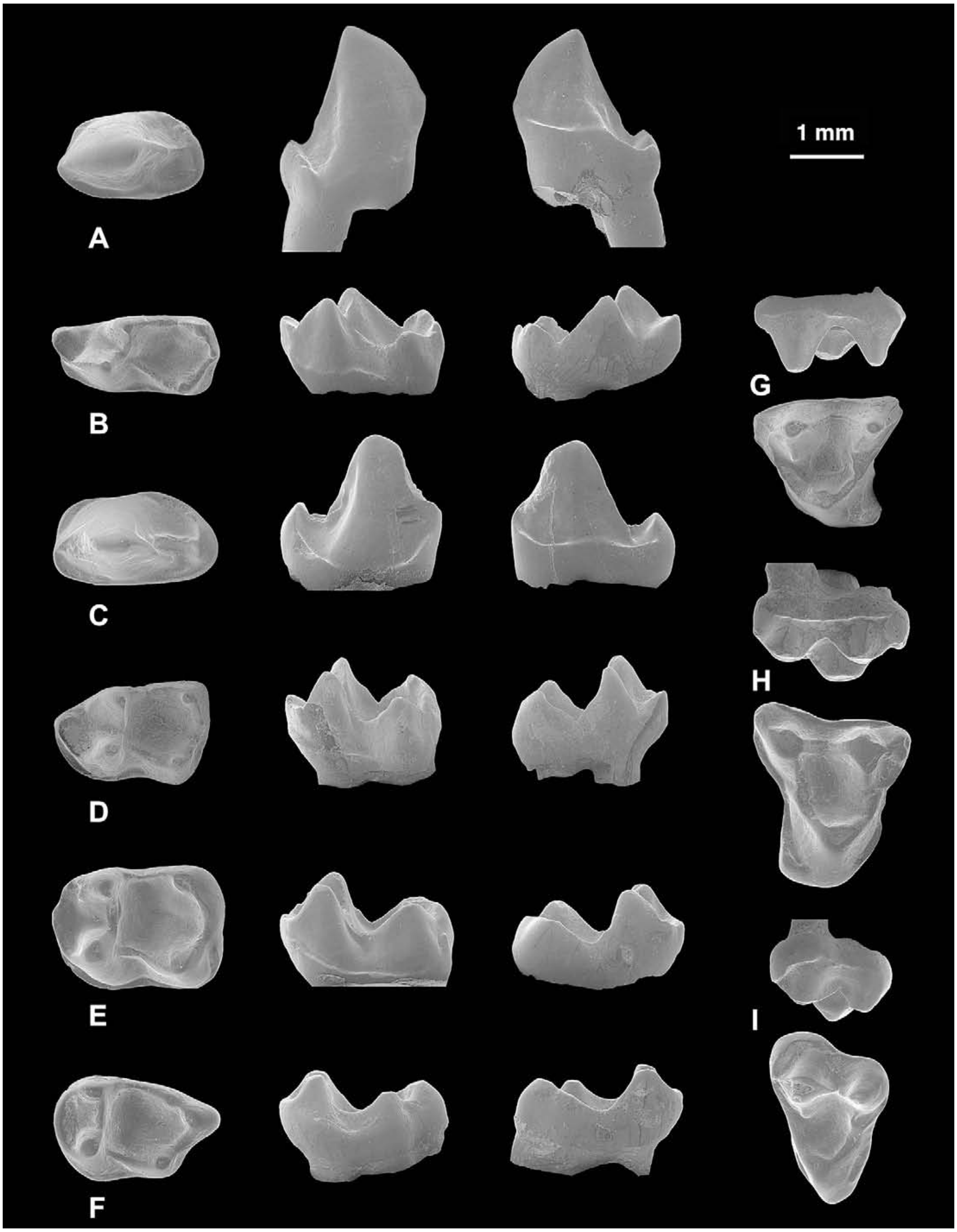

**Figure 7.** Isolated teeth allocated to *Marcgodinotius indicus*, all to the same scale. (A–F) Lower teeth in occlusal, buccal, and lingual views: (A) GU 703, right $P_3$; (B) GU 41, left $dP_4$; (C) GU 40, right $P_4$; (D) GU 44, left $M_1$; (E) GU 45, left $M_2$; (F) GU 46, left $M_3$. (G–I) Upper teeth in buccal and occlusal views: (G) GU 42, left $dP^4$; (H) GU 43, right $M^1$; (I) GU 47, left $M^3$. SEM images.

a small, single-cusped talonid. No known $P_3$ has a paraconid or metaconid, but a small metaconid is present on one $P_4$. $P_{3-4}$ are preserved in series only in GU 227 (Fig. 6). Although the alveoli for $P_3$ are slightly longer than those of $P_4$ in this specimen (because the roots diverge), the crown of $P_3$ is both narrower and shorter than that of $P_4$. The teeth are heavily worn in GU 227, obscuring much of the morphology, but details are better preserved in several other specimens, most of which are isolated teeth ($P_3$: GU 703, 1538, 1544; $P_4$: GU 40, 727, 1536, 1554; Figs. 5, 7). These teeth display the same size relationship as in GU 227 and show that, despite the size difference, $P_3$ has a taller crown than $P_4$. The best preserved $P_3$ (GU 703) has a narrow and continuous lingual cingulid and a weak ectocingulid distinct only anteriorly. A crest descends straight down from the protoconid to join a short crest extending forward from the centrally located hypoconid. Crests also run medially and laterally from the hypoconid, the medial crest joining the lingual cingulum to enclose a very small talonid basin. A groove separates the lateral crest from the trigonid on the buccal side. The best preserved $P_4$ (GU 40) is longer and wider than $P_3$, but its protoconid is not as tall. The tooth is otherwise similar to $P_3$ except for having better developed cingulids and a more complex talonid with a stronger hypoconid. A crest runs anteriorly from the hypoconid

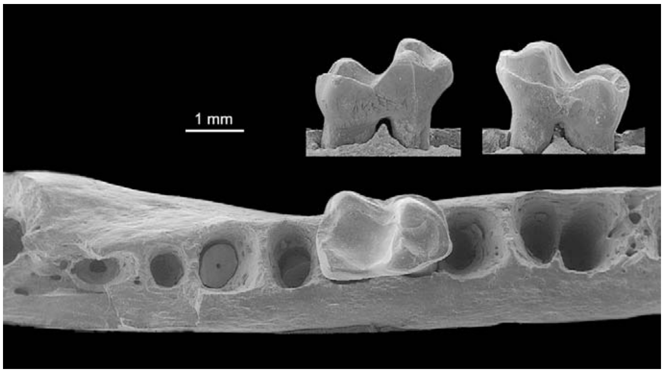

**Figure 8.** *Marcgodinotius indicus*, GU 7, left dentary with M$_1$, in occlusal view; M$_1$ shown in lingual and buccal views above. SEM images.

part way up the back of the protoconid, dividing the talonid in half. Just lingual to this crest, another crest descends from the protoconid into the middle of the small medially-situated talonid basin (between cristid obliqua and posterolingual cingulid). In *Donrussellia*, a crest in this position on P$_4$ terminates in a low metaconid, but GU 40 lacks both a paraconid and a metaconid, and the crest ends in the talonid basin. Consequently, its talonid basin is about the size of that of P$_3$ (GU 703). In the heavily worn specimen (GU 227), however, the talonid basin of P$_4$ is larger than that of P$_3$. Three other specimens (GU 727, 1536, 1554), though worn or eroded, show interesting variations in P$_4$. In GU 1536, the hypoconid is prominent and the talonid slightly longer than the others but not basined, whereas in the other two the hypoconid is small and the talonid is short and unbasined. GU 727 further differs in having a small, low metaconid well posterolingual to the protoconid (see Fig. 5), indicating lability of the P$_4$ metaconid in *Marcgodinotius*.

Deciduous P$_4$s include two isolated specimens (GU 41, 50; Fig. 7) referred to *Marcgodinotius indicus*. They resemble M$_1$ of this species except for being narrower and having a more open trigonid. They are molariform but narrow and elongate, with a wide open trigonid. In the unworn state (GU 41) the three trigonid cusps are strong but the paraconid is lower than the other two. The metaconid is almost as large as the protoconid and there is a well-defined trigonid notch. The cristid obliqua meets the postvallid just inferolateral to the trigonid notch. The talonid basin is longer than wide, and the hypoconulid is closer to the entoconid than to the hypoconid; a shallow notch separates the hypoconulid from the hypoconid. These two teeth closely resemble dP$_4$ of *Donrussellia provincialis* (Godinot, 1983: Plate 1) except that the cristid obliqua does not extend all the way to the metaconid. A third dP$_4$ of similar size (GU 601) differs from the other two in having a much weaker paraconid, lower metaconid, centrally positioned hypoconulid, and a talonid basin of nearly equal length and width which is wider than the trigonid. Its cristid obliqua extends diagonally across the back of the trigonid to the metaconid, resulting in a stepped postvallid. Although these differences might just reflect intraspecific variation, it is more likely that this tooth represents a different species—perhaps the similar-sized omomyid *Vastanomys gracilis*.

The lower molars of *Marcgodinotius* are distinctive in having the postcristid oriented less obliquely than in other notharctids; indeed, it is almost transverse on M$_{2-3}$. The cristid obliqua is relatively buccally oriented. As a result of these two features the entocristid and cristid obliqua may be nearly the same length, whereas in other notharctids the entocristid is decidedly shorter (especially on M$_2$). In unworn specimens the trigonid notch (between the protoconid and metaconid) is relatively deep. Well-developed ectocingulids are present on the trigonid and hypoflexid (buccal valley between the trigonid and talonid) of each molar but are weaker on the talonids, and a short postcingulid is present buccal to the hypoconulid.

The M$_1$ (Figs. 6A, 8) is narrow, with a relatively long trigonid (open lingually) that is distinctly narrower than the talonid. The paraconid is much lower than the subequal metaconid and protoconid, and is well anterior to the metaconid and more buccal, but still at the mesiolingual margin of the tooth. In unworn specimens (GU 44, 54) the metaconid is the largest trigonid cusp but the protoconid is slightly taller. The hypoconid is slightly larger, higher, and more anterior than the entoconid. The hypoconulid is small

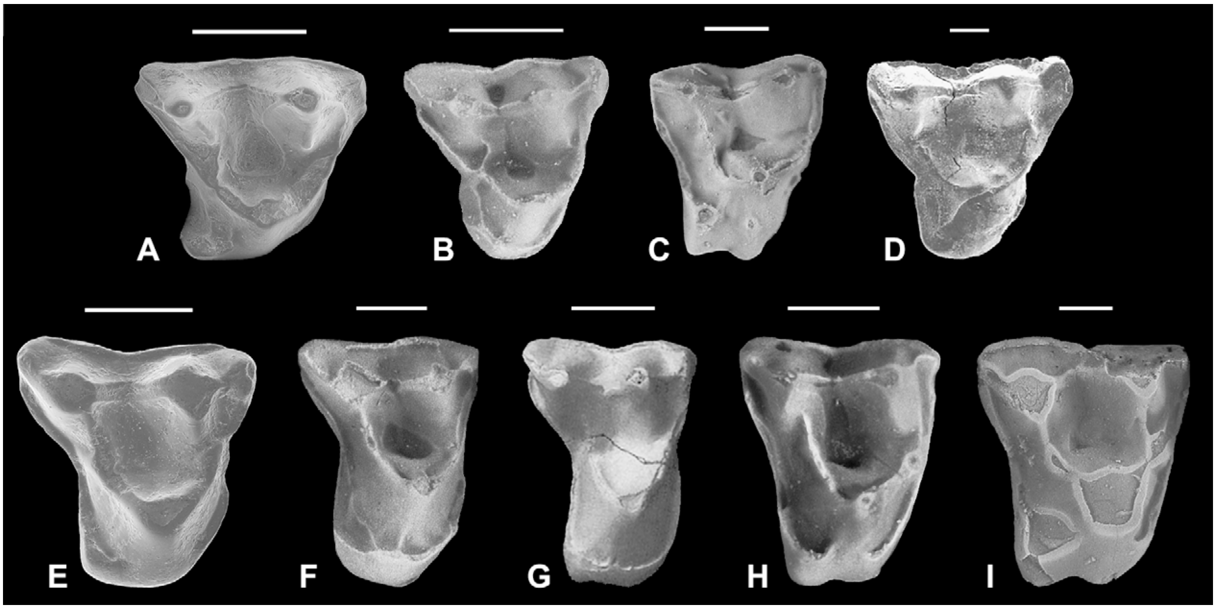

**Figure 9.** Upper teeth tentatively referred to *Marcgodinotius indicus* compared with those of some eosimiids and adapoids. (A–D) Right dP$^4$. (A) *M. indicus*, GU 42, left dP$^4$ (reversed); (B) *Eosimias centennicus*, IVPP V11996.2; (C) *Buxella prisca*, USTL BUX 66.133; (D) *Guangxilemur singsilai* (modified from Marivaux et al., 2002). (E–I) Right M$^1$. (E) *M. indicus*, GU 43; (F) eosimiid *Phenacopithecus krishtalkai*, holotype, IVPP V11997; (G) *Eosimias centennicus* (modified from Beard and Wang, 2004); (H) *Donrussellia gallica*, MNHN Av 4855; (I) *Pronycticebus gaudryi*, holotype, MNHN unnumbered. (A), (D), (E), and (G) are SEM images; others are digital images of casts coated with ammonium chloride. Scale bars = 1 mm.

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

and either central in position or slightly closer to the entoconid. The postcristid is not of even height; a shallow notch in the hypocristid, closer to the hypoconulid, separates the hypoconulid and hypoconid on both $M_1$ and $M_2$, as in $dP_4$. This notch is variable in expression; though obvious in most specimens, it is barely evident in some (e.g., GU 54). In most specimens the cristid obliqua is low and joins the back of the trigonid just buccal to the trigonid notch; it does not extend to the metaconid, and the postvallid is not "stepped" (with offset occlusal surfaces on the back of the metaconid and protoconid). In GU 600, however, the cristid obliqua ascends to the trigonid notch and the postvallid is weakly "stepped."

The trigonid of $M_2$ is almost as wide as the talonid, giving the tooth a more quadrate outline than $M_1$ (Figs. 4, 5, 7). The paraconid is small or indistinct. When present, it is very small and shifted buccally to a position equidistant from the protoconid and metaconid but well anterior to both (GU 643, 644, 744). In specimens with a less distinct or indistinct paraconid, the paracristid is arcuate, low, and continuous between the protoconid and metaconid (GU 45, 645, 743, 1575, 1602). In most other ways these teeth are virtually identical, hence we attribute the paraconid difference to intraspecific variation. GU 227 and 646 are too heavily worn to ascertain the paraconid condition. The cristid obliqua is low and markedly more buccal than on $M_1$, meeting the back of the trigonid at the base of the protoconid. The hypoconulid is low, poorly defined, and either centrally positioned on the postcristid or slightly closer to the entoconid (GU 45). Both the trigonid and talonid show noticeable variation in proportions. Extremes are seen in GU 643, which has a relatively long trigonid and a short, wide talonid basin, and GU 645 with a mesiodistally shorter trigonid and a longer talonid basin. However, this variation is not correlated (for example, distinct paraconid with short, wide basin); consequently, we interpret this also as intraspecific variability.

The $M_3$ (Figs. 6, 7F) is distinctive in apparently being relatively smaller than in other notharctids—about the same length as $M_2$ rather than distinctly longer as is typical in *Donrussellia*, *Protoadapis*, *Europolemur*, and *Cantius*. The paraconid is indistinct, and on relatively unworn teeth (GU 46, 52, 1534, 1591) the paracristid is arcuate, joining the protoconid to the metaconid. The trigonid is wider than the talonid, and the hypoconulid lobe is simple, relatively small, and neither transversely nor distally expanded. It is relatively shorter than in *Donrussellia*. Nevertheless, there is some variation in size of the third lobe. GU 46 and GU 51 have a very short third lobe with the hypoconulid and entoconid close together, whereas the entoconid is more anteriorly situated in GU 52 and IITR 817, resulting in a more distinct third lobe.

Several upper teeth that appear to pertain to small adapoids are tentatively referred to *Marcgodinotius indicus*. We have intentionally not included any of the features of the upper teeth in the emended diagnosis pending definitive association with lower teeth of this species. The teeth represented are $P^4$, $dP^4$, $M^1$, and $M^3$. They are of appropriate size and morphology to belong to the same species as the lower teeth described above, but all are isolated, and from the variation shown we cannot exclude the possibility that more than one taxon is represented. Hence, caution is warranted in their interpretation.

Only the buccal half of $P^4$ (GU 21) is preserved. It is dominated by a single tall buccal cusp (paracone) flanked by a tiny parastyle and metastyle. There are distinct pre-, post-, and ectocingula. A low crest running lingually from the paracone divides the buccal half of the tooth into anterior- and posterior-facing planes that are almost perpendicular to each other. This tooth fragment, recovered by screen-washing in 2003, was the first indication of primates in the Vastan fauna, and we previously compared it to omomyids (Rana et al., 2005). It remains possible that the tooth represents an omomyid (i.e., *Vastanomys*), but all the features described here are also seen in $P^4$ of the adapoid *Pronycticebus*.

The deciduous $P^4$ is a triangular tooth slightly longer than wide. GU 42 (Fig. 7G) is the best preserved of three specimens, the other two being abraded. The tall paracone and metacone and the much lower protocone are situated peripherally, so that the stylar shelf is very narrow. The conules are very small or indistinct and there are no distinct stylar cusps except for a hint of a very small parastyle. A short premetaconule crista and a longer postmetaconule crista converge where a metaconule would be, but the latter is poorly defined in the available specimens. The small but distinct hypocone is posterolingual to the protocone and joined to its base by a weak crest. A narrow anterior cingulum is present at the base of the protocone, and there is a weak, incomplete ectocingulum.

The $M^1$ (GU 43, Fig. 7H) is a generalized molar somewhat wider than long, with well-separated paracone and metacone; the paracone is somewhat larger, and there is a well-developed ectocingulum. The outline of the tooth is more triangular than quadrate, the buccal border being much longer mesiodistally than the lingual border. The perimeter is abruptly constricted at the conules. There is a distinct parastyle and a smaller, less distinct metastyle. The protocone is shifted anteriorly to a position almost directly lingual to the paracone. A small cingular hypocone is present posterolingual to the protocone, but there is no crest (*Nannopithex* fold) joining it to the protocone. The conules are small, with poorly defined crests. A faint crest or enamel fold descends posterior to the metaconule, but it does not extend either buccally or to the postcingulum, and therefore is not developed like a true postmetaconule crista, which is typically absent in adapoids. A similar weak postmetaconule fold is present in the holotype of *Pronycticebus gaudryi*, and a somewhat stronger fold is present extending posteriorly from the metaconule in *Cantius*. The overall shape of $M^1$ is quite similar to its counterpart in *P. gaudryi*, except for being smaller and having a smaller hypocone (see Tattersall and Schwartz, 1983: Fig. 9; see also Fig. 9 herein).

The $M^3$, represented by 4 specimens, is a generalized triangular tooth about 50% wider than it is long. The paracone is larger than the metacone and is preceded by a well-developed parastyle. A distinct, narrow ectocingulum extends posteriorly from the parastyle to the base of the metacone (GU 538, 706) or ends at the base of the paracone (GU 47, Fig. 7I). A continuous preprotocrista runs from the parastyle to the protocone, incorporating the small, low paraconule. Two specimens (GU 47, 538) have distinct pre- and postmetaconule cristae, but in GU 706 the postmetaconule crista appears to be lacking. There is no hypocone, nor any lingual expansion of the posterior cingulum. The pre- and postcingula are continuous and well-developed lingually in GU 48, continuous but weak lingually in GU 538, and discontinuous in the other two.

### *Discussion*

*Marcgodinotius indicus* is a very primitive adapoid, close in size and lower cheek tooth morphology to *Donrussellia gallica* and *D. provincialis* (for illustrations see Szalay, 1976; Godinot, 1998). The simple, unreduced premolars, oblique $P_2$, and uninflated molars with smooth enamel and simple cusps and crests are features shared with *Donrussellia* and, to a lesser extent, *Protoadapis*. Szalay and Delson (1979) regarded simple premolars and a taller $P_3$ than $P_4$ as particularly primitive adapoid characteristics, typifying the plesiomorphic tribe Protoadapini (= Cercamoniinae, following Godinot, 1998). If the upper teeth described above are correctly attributed, then *Marcgodinotius* may have been even more primitive than *Donrussellia*. Primitive upper molar traits include the wide buccal margin, waisted outline, a small or absent hypocone, absence of a *Nannopithex* fold, and the presence of a postmetaconule fold or crista. The lower molars of *Marcgodinotius* are also similar in size to those of the primitive omomyid *Steinius vespertinus* and slightly larger than those of *Teilhardina*, but the canine of *Marcgodinotius* is relatively larger and its premolars are more elongate than in these omomyids. The latter features are adapoid characteristics. Dental proportions of *Marcgodinotius* are closely comparable to those of *D. provincialis*: the dentition does not show any anterior compression as is typical of omomyids. Compared to *Donrussellia*, however, *Marcgodinotius* has a more buccal cristid obliqua on $M_1$, a less oblique (more transverse) protocristid on all molars, a smaller or indistinct paraconid on $M_{2-3}$, and a smaller hypoconulid lobe on $M_3$. As a result of its more transverse protocristid, the trigonid of $M_1$ of *Marcgodinotius* is typically less open than that of *Donrussellia*. These traits, except perhaps for the small hypoconulid lobe on $M_3$, are probably derived in *Marcgodinotius*. An arcuate paracristid on lower molars also occurs in some other cercamoniines (e.g., *Agerinia*, some *Protoadapis*). However, this is a derived trait that has arisen numerous times among fossil primates (e.g., some paromomyids, *Djebelemur*, the galagid *Wadilemur*), so its phylogenetic significance is limited.

Many other characteristics of *M. indicus* are probably plesiomorphic relative to most other adapoids, and a few features are possibly even more primitive than in *Donrussellia*: the simple $P_4$, unstepped $M_1$ postvallid, and small hypoconulid lobe on $M_3$. This can be inferred by comparison with other primitive euprimates. The most primitive species of *Teilhardina* (the oldest omomyid and one of the most primitive) have the smallest and lowest metaconids on $P_4$, an unstepped or weakly stepped $M_1$ postvallid, and a small hypoconulid lobe on $M_3$, suggesting that these are plesiomorphic states. Outgroup comparisons (e.g., to diverse plesiadapiforms and scandentians) are equivocal, but the most primitive members—*Purgatorius* and *Ptilocercus*, respectively—share those traits with primitive *Teilhardina* and *Marcgodinotius*. The $M_1$ postvallid is also unstepped in *Altiatlasius* (arguably the oldest and one of the most primitive euprimates); unfortunately, its $P_4$ and $M_3$ are unknown. Curiously, *Altiatlasius*, like *Marcgodinotius*, also has a transverse protocristid and a buccal cristid obliqua. On the other hand, Asian *Altanius*, another probable basal euprimate, shows different character states: it has a well-developed, high metaconid on $P_4$, a stepped postvallid on $M_1$, and a large hypoconulid lobe on $M_3$. Thus, the polarity of these characters is uncertain: absence of a metaconid on $P_4$, for example, could reflect the primitive state, or it could be a secondary loss (see discussion under *Asiadapis*).

Besides the resemblances already noted to *Donrussellia* and *Protoadapis*, *Marcgodinotius* shows additional similarities to these and various other primitive notharctids usually now classified as Cercamoniinae (Godinot, 1998). Molars of some species of these genera and *Agerinia* have a reduced paraconid, an arcuate paracristid, and a buccal cristid obliqua. The deciduous $P_4$ compares closely with that of *Donrussellia* (Godinot, 1983: Plate 1), and $dP^4$ resembles that of *Buxella* (which, however, lacks a postmetaconule crista and has a larger hypocone; see Fig. 9). Deciduous premolars of adapoids are not common, however, and in both cases the resemblance may not indicate any more specific affinity than to cercamoniines, notharctids, or adapoids (see below). The simple $P_4$ (lacking a metaconid) in *Anchomomys* and *Periconodon*, and the triangular $M^1$ with a small hypocone and small conules in *Anchomomys*, are reminiscent of conditions in *Marcgodinotius*, but other dental modifications (e.g., specialized molar trigonids in *Anchomomys*, large hypocones and pericones in *Periconodon*) suggest that the similarities are homoplastic.

Though as primitive as *Donrussellia* and *Protoadapis* in some respects, the notharctine *Cantius* is more derived than these cercamoniines and *Marcgodinotius* in having a $P_3$ that is reduced relative to $P_4$, a wider $P_4$ with a distinct metaconid, and inflated molars with moderately wrinkled enamel and often small accessory cuspules. Upper molars of *Cantius* also have a *Nannopithex* fold, which is absent in *Marcgodinotius*.

In the Vastan local fauna, *Marcgodinotius indicus* is also very close in size to the omomyid *Vastanomys gracilis*, which is based on a single jaw fragment with $M_2$ (Bajpai et al., 2005b). The $M_2$ of *Vastanomys* is basally more inflated, and its trigonid is anteroposteriorly shorter and has a more distinct paraconid, features consistent with omomyid affinity; otherwise, it is rather similar to $M_2$ of *Marcgodinotius*. Unfortunately, the structure of other molars and premolars is unknown. *Vastanomys* further differs from *Marcgodinotius* (and resembles omomyids) in having only 3 premolars, including a single-rooted $P_2$ (Bajpai et al., 2005b). To judge from their alveoli, the premolars were distinctly mesiodistally compressed relative to the situation in *Marcgodinotius*.

Except at Vastan Mine, only a few adapoid specimens are known from the Eocene of the Indian subcontinent. The only other early Eocene adapoids from the subcontinent come from the early Eocene Gandhera Quarry in the Ghazij Formation of Pakistan (Gingerich et al., 2001), but they have not yet been described. *Panobius afridi*, from the early middle Eocene Kuldana Formation of Pakistan (Russell and Gingerich, 1987), is slightly smaller than *Marcgodinotius* and generally similar. The $M_1$ of *P. afridi* resembles that of *Marcgodinotius* in having an unstepped postvallid. However, *Marcgodinotius* differs from *P. afridi* in having molar paraconids that are buccally shifted on $M_1$, and buccally shifted or absent on $M_{2-3}$. In *Panobius*, the paraconid is distinct and much more lingual on both $M_1$ (the holotype) and $M_3$; $M_2$ is unknown. In addition, *Marcgodinotius* has a longer talonid and entocristid on $M_1$ and a more transverse (less oblique) protocristid than *Panobius*, resulting in a more open, usually obtuse-angled talonid notch; in *Panobius* the notch is acute. Therefore, the two are clearly distinct taxa. Thewissen et al. (2001) assigned a specimen with $M_3$ and part of $M_2$ from the Kuldana ("Mami Khel") Formation of Pakistan (Gingerich, 2003) to *P. afridi*, but it is too fragmentary to be sure of its identity. It appears to be adapoid but is too large to be *P. afridi*, and its $M_3$

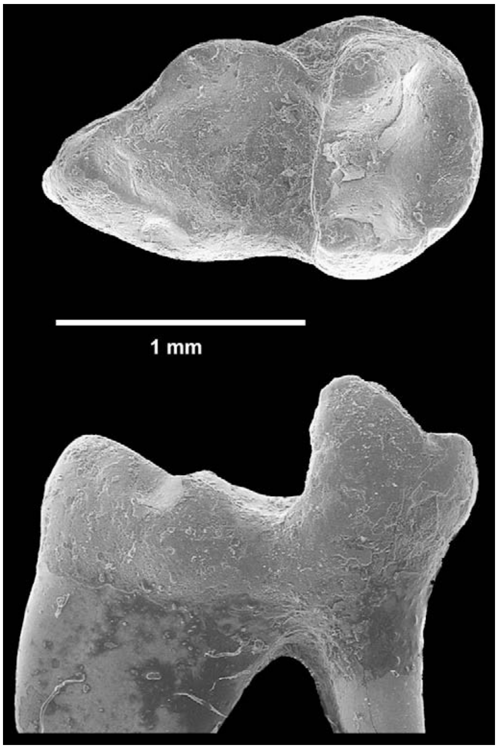

**Figure 10.** cf. *Marcgodinotius* sp., GU 1619, left $M_3$ in occlusal and lingual views. SEM images.

differs from that of *Marcgodinotius* in having a distinct paraconid and a much more oblique postvallid. Kumar et al. (2002) reported an isolated euprimate upper molar, which they questionably assigned to Adapiformes, from the middle Eocene Subathu Formation of northwestern India. This tooth is much larger than *Marcgodinotius* (and other Vastan primates) and further differs in having a much longer lingual protocone slope. Consequently it, too, must belong to a different taxon, but proper assignment will require more complete specimens.

Another primate from the Kuldana Formation that is of similar size to *Marcgodinotius* is *Kohatius coppensi*, a possible omomyid based on a single $M_1$ and a couple of tooth fragments (Russell and Gingerich, 1980). *Kohatius* differs from *Marcgodinotius* in having a distinctly cuspate trigonid, with a fully lingual paraconid. The talonid in *Kohatius* is relatively shorter and its talonid notch forms an acute angle, compared to the obtuse angle of the notch in *Marcgodinotius*. An isolated $P_4$ identified as *Kohatius* (Thewissen et al., 1997) is short and broad with a distinct metaconid, which is consistent with allocation to Omomyidae.

In addition to its resemblances to notharctids, *Marcgodinotius* shows potentially significant similarities to two other groups of Asian fossil primates: Sivaladapidae and Eosimiidae. The primitive sivaladapid *Paukkaungia parva* from the middle Eocene Pondaung Formation of Myanmar (Beard et al., 2007), while approximately 50% larger than *Marcgodinotius*, has generally similar lower molars and shares several dental features with the Vastan form, including a simple $P_4$ lacking a paraconid or metaconid, relatively transverse protocristids on the molars, a deep trigonid notch, and a shallow notch between the hypoconid and hypoconulid. The $dP^4$ of the Oligocene sivaladapid *Guangxilemur* from Pakistan (Marivaux et al., 2002: Fig. 2A) closely resembles that of *Marcgodinotius* as well (but is much larger), suggesting at least an adapoid affinity. Whether these resemblances imply a relationship or are merely convergent must await better samples of both taxa. Upper teeth of *Paukkaungia* are unknown, but upper molars of other sivaladapids, including *Guangxilemur*, are markedly derived compared to those here ascribed to *Marcgodinotius* in having crenulated enamel and a salient lingual cingulum with distinct pericone and hypocone cusps (Qi and Beard, 1998; Marivaux et al., 2002). This makes comparison difficult, but the upper molars provide little evidence to support a close relationship between *Marcgodinotius* and sivaladapids.

The upper teeth ($dP^4$ and $M^1$) tentatively referred to *Marcgodinotius indicus* also bear certain resemblances to those of the eosimiids *Eosimias* and *Phenacopithecus* (Beard and Wang, 2004: Figs. 7 and 22; see Fig. 9 herein). Furthermore, these Vastan teeth appear to be nearly identical to the recently described holotype $M^1$ and referred $dP^4$ of the supposed eosimiid *Anthrasimias gujaratensis* (Bajpai et al., 2008: Fig. 2) and almost certainly represent the same species. But is that species an eosimiid, or is it an adapoid? The $dP^4$ resembles that of *Eosimias centennicus* in its triangular shape and narrow stylar shelf, and the $M^1$ is similar to those of *Eosimias* and *Phenacopithecus* in having relatively unreduced parastylar and metastylar lobes, a waisted occlusal outline, and an expanded posterolingual cingulum. Bajpai et al. (2008) stated that both *Anthrasimias* and eosimiids are characterized by well-developed pre- and postprotocristae, small conules, and the absence of a *Nannopithex* fold (features also seen in the $M^1$ here referred to *Marcgodinotius*). However, all these traits also characterize primitive adapoids such as *Donrussellia gallica*, *Pronycticebus gaudryi*, and *Anchomomys gaillardi*. In addition, Bajpai et al. (2008) noted several differences between $M^1$ of *Anthrasimias* and that of eosimiids, including a more triangular and less transverse occlusal outline, a cuspate hypocone, larger conules, and an incomplete lingual cingulum in the Vastan form. The $dP^4$ of *Marcgodinotius* (and apparently that of *Anthrasimias*) differs from that of *Eosimias* in also lacking a lingual cingulum, and in having a smaller parastyle, a larger hypocone, more distinct conules, a crest (hypometacrista) joining the metaconule to the metacone, and a wider and deeper separation between the paracone and metacone. Nearly all these traits are shared with primitive cercamoniines (see Fig. 9). Eosimiids further differ from *Marcgodinotius* in having shorter and wider lower posterior premolars, more prominent molar paraconids, and shorter talonids—a combination of characters that does not strengthen any possible ties between these genera. These comparisons indicate that the case for adapoid affinity of these upper teeth, and their allocation to *M. indicus*, is at least as strong as that for eosimiid ties.

Bajpai et al. (2008) allocated two additional teeth to *Anthrasimias gujaratensis*, an $M^2$ and an $M_3$. The molar they identified as $M^2$ (IITR 1100; Bajpai et al., 2008: Fig. 2B) is very similar to the $M^3$s we tentatively allocate to *Marcgodinotius*. This tooth differs strikingly from the $M^2$ of eosimiids and many other euprimates in having a reduced metacone and posterobuccal lobe and a weak or narrow posterolingual cingulum—features that are usually typical of $M^3$ rather than $M^2$. In contrast, the metacone of $M^2$ in eosimiids is not reduced, and the posterolingual cingulum is well-developed (*Eosimias* and *Phileosimias*) or even expanded into a shelf (*Phenacopithecus* and *Bahinia*). Among eosimiids, $M^3$ has been reported only in Oligocene *Phileosimias*, in which it is dissimilar to IITR 1100 (rectangular, with well-developed cingula and a more reduced parastylar lobe; see Marivaux et al., 2005: Fig. 3). Thus, it is likely that IITR 1100 is an $M^3$ that belongs to the same taxon as the $M^3$s described above. An $M_3$ attributed to *A. gujaratensis* (IITR 1017; Bajpai et al., 2008: Fig. 2E) has a shorter and wider talonid than any here referred to *M. indicus*, and is said to resemble eosimiids in having a small, central paraconid, an open trigonid, a transverse protocristid, and a small hypoconulid not developed as a third lobe. In fact, the paraconid is reduced and buccally shifted, and the paracristid appears to be arcuate. Together with the transverse protocristid (a characteristic of asiadapines), these features make the trigonid closely comparable if not identical to that of *Marcgodinotius*. The paraconid of *Eosimias* and *Phenacopithecus* differs in being well-developed and almost fully lingual on $M_3$. Thus, the short talonid appears to be the only character more suggestive of eosimiid than adapoid affinity. However, the variability of $M_3$ in our small sample (including one, GU 46, that approaches the proportions of IITR 1017; see Fig. 7F) makes it quite possible that this tooth is merely a variant of *M. indicus*. Thus, definitive eosimiid teeth have yet to be confirmed at Vastan, and it is probable that *Anthrasimias gujaratensis* is a junior synonym of *Marcgodinotius indicus*.

## cf. Marcgodinotius, unnamed new species

The specimen GU 1619 (Fig. 10) is a left $M_3$ of a distinctly smaller adapoid than those previously identified from Vastan. Its total length is 1.75 mm, the trigonid is 1.05 mm wide, and the talonid is 0.9 mm wide. It is thus 25–30% smaller in linear dimensions than $M_3$s assigned here to *Marcgodinotius indicus* but is similar to the latter morphologically. The protoconid and metaconid are prominent and conical, the metaconid somewhat higher. The paracristid is low and arcuate, as in *M. indicus*, with a very small paraconid toward its lingual end. The hypoconid and entoconid are situated more anteriorly than in GU 46 and GU 51 but are comparable to their positions in GU 52 and IITR 817, resulting in a relatively longer third lobe. As in GU 52 the entocristid is short and low, hence the talonid notch is deep. The postvallid is slightly more vertical and more oblique than in *M. indicus*. This tooth seems to represent a third adapoid in the Vastan local fauna, but more complete specimens are needed in order to characterize this species and to determine if it belongs in *Marcgodinotius* or another genus.

**Table 2**

Measurements (mm) of teeth and dentary depth of *Asiadapis cambayensis*. Dimensions same as in Table 1. Dentary depth was measured buccally below $M_1$. Measurements of IITR 928 from Bajpai et al. (2007). GU 33 ($dP_4$) and IITR 928 omitted from $P_4$ statistics.

| Number | $P_3$ L | $P_3$ W | $P_4$ L | $P_4$ Wtri | $P_4$ Wtal | $M_1$ L | $M_1$ Wtri | $M_1$ Wtal | $M_2$ L | $M_2$ Wtri | $M_2$ Wtal | $M_3$ L | $M_3$ Wtri | $M_3$ Wtal | JawD $M_1$ | $P^3$ L | $P^3$ W | $P^4$ L | $P^4$ W | $M^1$ L | $M^1$ W | $M^2$ L | $M^2$ W | $M^3$ L | $M^3$ W |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| GU 6, holotype | 2.60 | 1.70 | 2.60 | 1.60 | 1.70 | 2.85 | 1.80 | 2.00 | 2.90 | 2.15 | 2.15 | | | | 4.30 | | | | | | | | | | |
| GU 32 | | | | | | | | | | | | 2.80 | 1.75 | 1.70 | | | | | | | | | | | |
| GU 33 $dp_4$ | | | 2.80 | 1.25 | 1.50 | | | | | | | | | | | | | | | | | | | | |
| GU 35 | 2.70 | 1.50 | | | | | | | | | | | | | | | | | | | | | | | |
| GU 36 | | | | | | | | | 2.65 | 2.05 | 2.10 | | | | | | | | | | | | | | |
| GU 37 | | | | | | | | | 2.85 | 2.25 | 2.35 | | | | | | | | | | | | | | |
| GU 38 | | | 2.90 | 1.70 | 1.60 | | | | | | | | | | | | | | | | | | | | |
| GU 598 | | | | | | | | | | | | 3.40 | 2.05 | 2.00 | | | | | | | | | | | |
| GU 642 | | | | | | | | | 2.95 | 2.30 | 2.30 | | | | | | | | | | | | | | |
| GU 745 | 2.95 | 1.90 | 3.00 | 1.80 | 1.50 | 3.10 | 2.00 | 2.20 | 3.10 | 2.35 | 2.40 | | | | 4.10 | | | | | | | | | | |
| GU 1505 | | | | | | | | | | | | 3.25 | 1.90 | 1.80 | | | | | | | | | | | |
| GU 1537 | | | | | | 3.00 | 1.85 | 2.00 | | | | | | | | | | | | | | | | | |
| GU 1627 | | | 2.70 | 1.55 | 1.65 | | | | | | | | | | | | | | | | | | | | |
| GU 1649 | | | | | | | | | | | | 3.30 | 2.05 | 1.95 | | | | | | | | | | | |
| IITR 928, holotype of *Suratius robustus* | 2.68 | 1.54 | 2.54 | 1.92 | | | | | 2.70 | 2.40 | 2.40 | | | | | | | | | | | | | | |
| **MEAN** | 2.73 | 1.66 | 2.80 | 1.66 | 1.61 | 2.98 | 1.88 | 2.07 | 2.86 | 2.25 | 2.28 | 3.19 | 1.94 | 1.86 | 4.20 | | | | | | | | | | |
| **St Dev** | 0.15 | 0.18 | 0.18 | 0.11 | 0.09 | 0.13 | 0.10 | 0.12 | 0.17 | 0.13 | 0.13 | 0.27 | 0.14 | 0.14 | 0.14 | | | | | | | | | | |
| GU 34 | | | | | | | | | | | | | | | | | | 2.55 | 2.95 | | | | | | |
| GU 330 | | | | | | | | | | | | | | | | 2.30 | 2.75 | | | | | | | | |
| GU 609 | | | | | | | | | | | | | | | | | | | | | | 2.80 | 3.80 | | |
| GU 610 | | | | | | | | | | | | | | | | | | | | | | | | 2.20 | 3.35 |
| GU 656 | | | | | | | | | | | | | | | | | | | | 2.70 | 3.55 | 2.65 | 4.00 | 2.00 | 3.20 |
| GU 700 | | | | | | | | | | | | | | | | | | | | | | | | 2.30 | 3.30 |
| GU 701 | | | | | | | | | | | | | | | | | | | | | | 2.90 | 3.80 | | |
| GU 702 | | | | | | | | | | | | | | | | | | | | 2.60 | 3.20 | | | | |
| GU 1550 | | | | | | | | | | | | | | | | | | | | 2.55 | 3.30 | | | | |
| **MEAN** | | | | | | | | | | | | | | | | | | | | 2.62 | 3.35 | 2.78 | 3.87 | 2.17 | 3.28 |
| **St Dev** | | | | | | | | | | | | | | | | | | | | 0.08 | 0.18 | 0.13 | 0.12 | 0.15 | 0.08 |

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

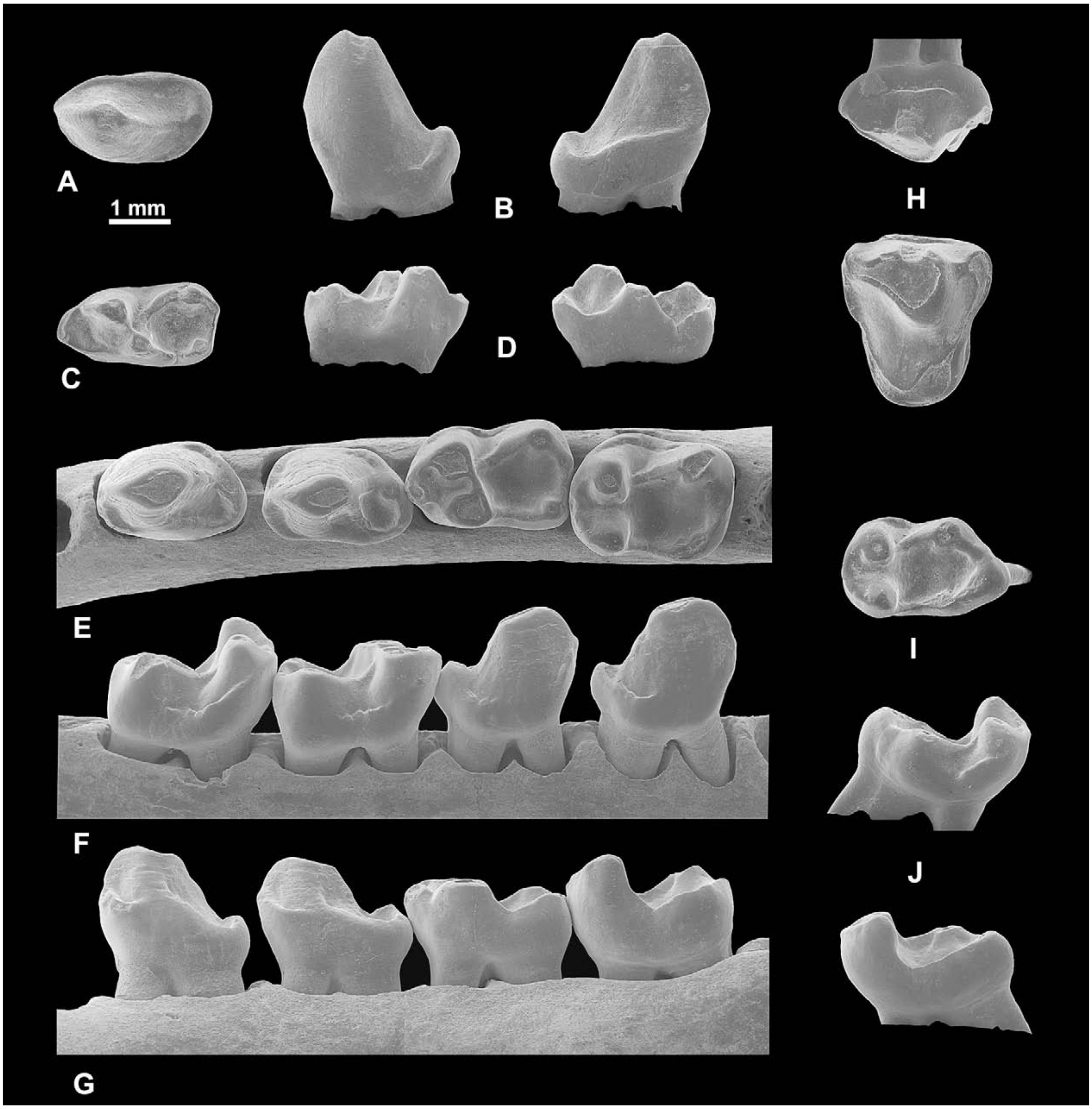

**Figure 11.** *Asiadapis cambayensis*. (A–B) GU 35, left $P_3$, in occlusal, buccal, and lingual views. (C–D) GU 33, right $dP_4$, in occlusal, buccal, and lingual views. (E–G), Holotype, GU 6, right dentary with $P_3$-$M_2$, in occlusal, buccal, and lingual views. (H) GU 34, right $P^4$, in buccal and occlusal views. (I–J) GU 32, right $M_3$, in occlusal, buccal, and lingual views. SEM images.

### Asiadapis cambayensis Rose et al., 2007a

*Holotype*

GU/RSR/VAS 6, right dentary with $P_3$-$M_2$ and alveoli for C, $P_2$, $M_3$.

*Synonym*

*Suratius robustus* (Bajpai et al., 2007).

*Hypodigm*

GU/RSR/VAS 32 (right $M_3$), GU 33 (right $dP_4$), GU 34 (right $P^4$), GU 35 (left $P_3$), GU 36 (right $M_2$), GU 37 (right $M_2$), GU 38 (right $P_4$), GU 330 (right $P^3$), GU 598 (left $M_3$), GU 609 (right $M^2$), GU 610 (right $M^3$), GU 642 (right $M_2$), GU 656 (left maxilla with $M^{1-3}$), GU 700 (right $M^3$), GU 701 (left $M^2$), GU 702 (right $M^1$), GU 745 (left dentary with $P_3$-$M_2$), GU 1505 (right dentary fragment with $M_3$), GU 1537 (right $M_1$), GU 1550 (left $M^1$), GU 1627 (left $P_4$), GU 1649 (right $M_3$), IITR/SB/VLM 928 (holotype of *Suratius robustus*). Measurements are given in Table 2.

*Occurrence*

Known at present only from the early Eocene Cambay Shale Formation at Vastan Mine, Gujarat, India.

*Emended diagnosis (modified from Rose et al., 2007a)*

Approximately 25–30% larger in linear dimensions than *Marcgodinotius indicus*, 50–60% larger than *Panobius afridi*, and 20%

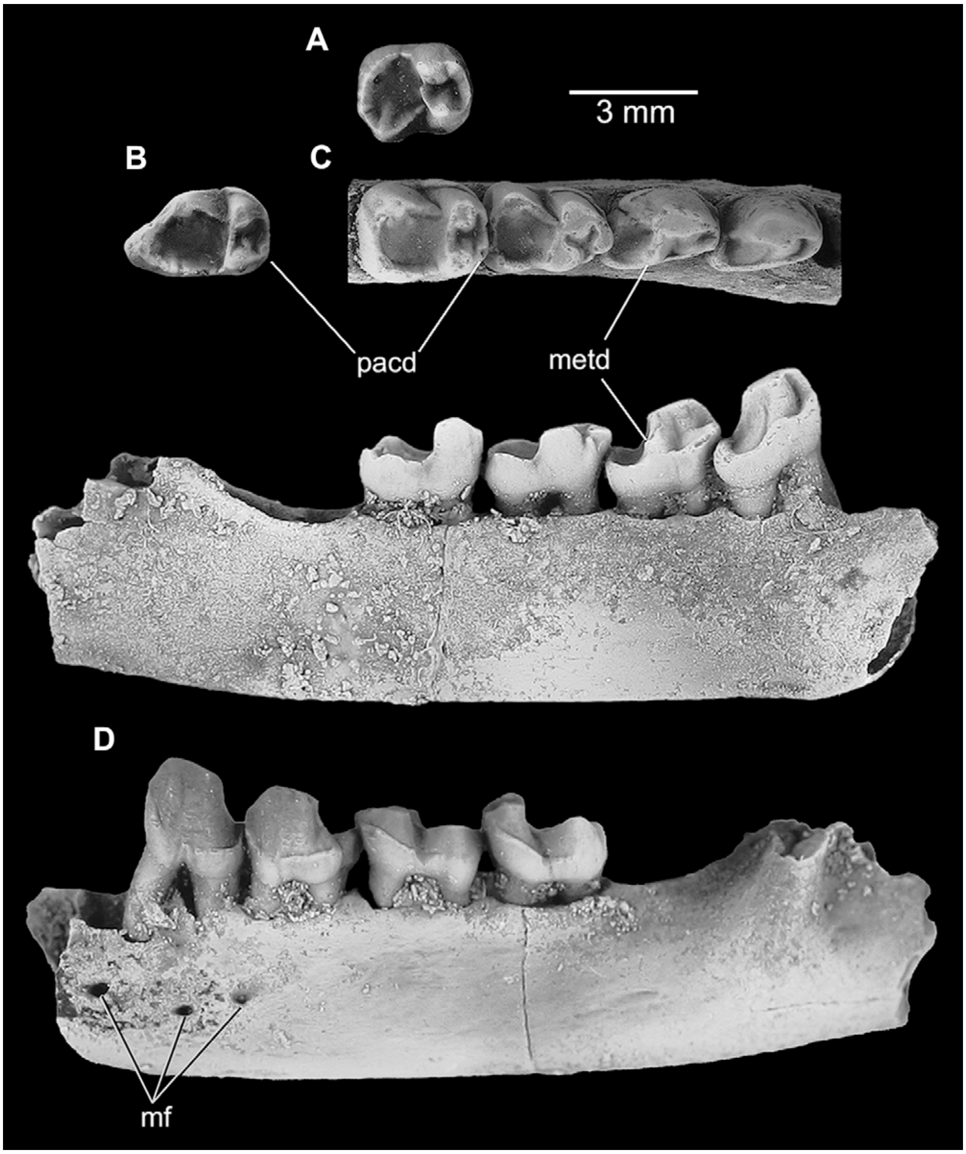

**Figure 12.** *Asiadapis cambayensis*. (A) GU 36, right $M_2$ in occlusal view. (B) GU 598, left $M_3$ in occlusal view. (C–D) GU 745, left dentary with $P_3$-$M_2$ in occlusal, lingual, and buccal views. Abbreviations: metd, metaconid; mf, mental foramina; pacd, paraconid. Digital images; specimens coated with ammonium chloride.

larger than *Donrussellia provincialis*. Lower dental formula 2?-1-3-3. $P_1$ absent and $P_2$ single-rooted, unlike *Marcgodinotius*. $P_3$ same size as $P_4$ but slightly taller, and simple with no paraconid or metaconid. $P_{3-4}$ with distinct hypoconid and small talonid basin. $P_4$ with variable paraconid and metaconid: either lacking paraconid and metaconid or with very small, low paraconid and/or small to moderate, low metaconid rising from lingual cingulid. Molars not basally inflated; molar cusps peripherally situated. $M_1$ with buccally shifted paraconid as in *Marcgodinotius*, but in contrast to *Panobius*; molars further differ from those of *Panobius* in having relatively longer and narrower talonid basins. $M_2$ trigonid anteroposteriorly shorter than in *Marcgodinotius*. Paraconid either very small or absent on $M_{2-3}$, and paracristids arcuate and continuous from protoconid to metaconid. $M_2$ protocristid almost transverse, not oblique. Cristid obliqua of $M_{1-2}$ meets trigonid buccally. Hypoconulid closer to hypoconid than to entoconid on $M_{1-2}$, but hypoconulid and entoconid barely distinct from postcristid of $M_2$. Upper molars similar to those of *Donrussellia gallica* in lacking *Nannopithex* fold but less tapered lingually; conules small; hypocone small or indistinct.

### *Description*

The following description, based on the larger sample now available, supplements those of Rose et al. (2007a) and Bajpai et al. (2007).

All three dentaries now known have a large canine alveolus anterior to the single alveolus for $P_2$. A very short diastema separates these two alveoli in IITR 928, but there is no diastema in the other two jaws. As in *Marcgodinotius*, the dentary is of essentially constant depth, and the mental foramina are variable in number, size, and position: a single anterior foramen below $P_2$ and one or two foramina more or less below the posterior root of $P_3$.

The $P_3$, known from four specimens, is a simple tooth, approximately the same size as $P_4$ but taller (Figs. 11, 12). Consequently, $P_3$ is larger relative to $P_4$ than in all or nearly all other adapoids. It is dominated by the tall protoconid, and there is no trace of either a paraconid or a metaconid. A crest descends anteriorly from the protoconid and is continuous with the lingual cingulid. In two specimens (GU 745 and IITR 928) this crest is separated from the columnar base of the protoconid by a vertical groove. The short, low

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

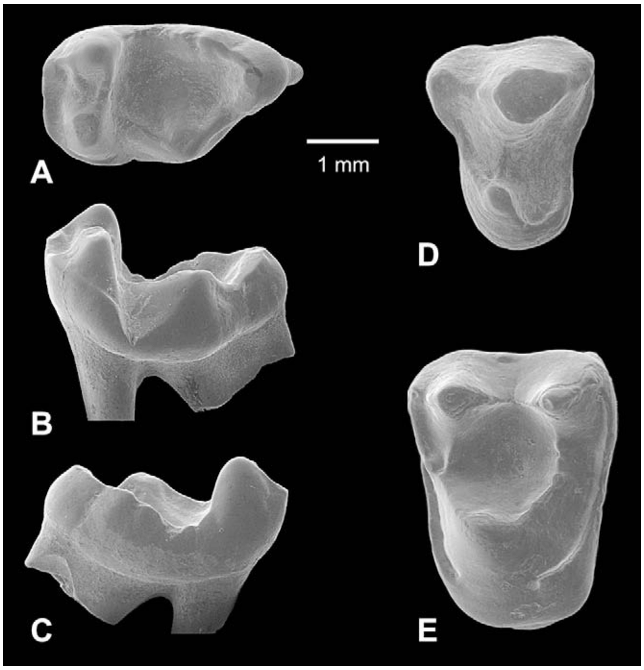

**Figure 13.** Isolated teeth of *Asiadapis cambayensis*. (A–C) GU 598, $M_3$ in occlusal, buccal, and lingual views. (D) GU 726, left $P^4$. (E) GU 701, left $M^2$. SEM images.

talonid bears a single poorly-defined cusp (hypoconid). Crests running medially and laterally from the hypoconid are continuous with the lingual and buccal cingulids. The lingual cingulid is much stronger than the buccal cingulid and is complete and sinuous in three of the four specimens. In two specimens (GU 6 and 35) the posterior end of the lingual cingulid encloses a small talonid basin, but in the other two the basin is indistinct. The buccal cingulid is weak or discontinuous, being well-developed only posteriorly.

The $P_4$ in the holotype resembles $P_3$ except for having a slightly lower protoconid, a more distinct hypoconid, and two crests (rather than one) descending posteriorly from the protoconid, which enclose a slightly larger talonid basin. Based on the holotype, $P_4$ was described as lacking the paraconid and metaconid, similar to $P_3$. Additional specimens now available show this to be variable, as in *Marcgodinotius indicus*. GU 38 and GU 1627, isolated $P_4$s, resemble the holotype in having a hint of a paraconid but no distinct metaconid. $P_4$ in GU 745 (Fig. 12) has a small, low paraconid and a slightly larger, low metaconid, both cusps arising from the lingual cingulid. Its talonid basin is larger than in the other specimens. IITR-928 lacks a paraconid but has a moderately developed, slightly higher metaconid. In all specimens, the more lateral of the two crests descending from the protoconid runs to the hypoconid and is thus continuous with the presumed homologue of the molar cristid obliqua; the other crest curves lingually and runs either down to the metaconid, or to (or just buccal to) the lingual cingulid in the absence of a metaconid. The buccal and lingual cingulids of $P_4$ are developed as on $P_3$, except for giving rise to a paraconid and/or a metaconid in some specimens. All specimens lack a distinct hypoconulid and entoconid.

A single $dP_4$ (GU 33; Fig. 11C–D) is referred to this species. It is similar to that of *Marcgodinotius* except that it is larger, the cristid obliqua clearly extends to the metaconid, and the hypoconulid is shifted buccally, very close to the hypoconid.

The $M_1$ is preserved in three specimens (the holotype, GU 745, and GU 1537) and is similar in all three. The trigonid is narrower than the talonid, and the paraconid is small and shifted buccally. The protocristid is slightly more oblique than in *Marcgodinotius*. The talonid is moderately elongate with a high hypoconid, lower entoconid (weaker than in *Marcgodinotius*), and weak hypoconulid. Unlike in *Marcgodinotius*, the hypoconulid is closer to the hypoconid and there is no notch between these two cusps. The cristid obliqua is perhaps slightly less buccal than in *Marcgodinotius* and extends more distinctly onto the postvallid but does not result in a stepped postvallid. In other respects the crown morphology is very similar to $M_1$ of *Marcgodinotius*.

A total of six specimens of $M_2$ are now known, three in dentaries and three isolated teeth. $M_3$ is known from one tooth in a dentary and three isolated teeth, which differ in size and some aspects of morphology. $M_2$ is quadrate; the trigonid and talonid are of more or less equal width. The paracristids of $M_2$ and $M_3$ are arcuate and extend from the protoconid to the metaconid, in some specimens without interruption; in others (GU 36, 598, 745) a small paraconid is present on the paracristid anterolingually (Fig. 12). The trigonids of $M_2$ and $M_3$ are typically divided in half by a deep longitudinal valley between the protoconid and metaconid that extends to the trigonid notch. The notch is deep enough in two specimens (the holotype and GU 32, an isolated $M_3$ that possibly pertains to the holotype) that the valley opens directly into the talonid basin; but in others, the notch is not quite deep enough to allow continuity into the talonid basin. On all molars the cristid obliqua is buccally situated, joining the back of the trigonid at the base of the protoconid (slightly more lingually on $M_1$). The hypoconid is the tallest talonid cusp. The talonid basins are broad and deep. The hypoconulid is shifted buccally on $M_{1\text{-}2}$, but both the hypoconulid and entoconid are weakly developed on $M_2$, and in less worn teeth (GU 36, 37) they can hardly be distinguished from other tiny cuspules developed on the postcristid. A weak notch is discernible between the hypoconulid and hypoconid of $M_2$, as in *Marcgodinotius*. On $M_3$ the hypoconulid is closer to the entoconid. A low entocristid leads into the relatively deep talonid notch, but the entocristid is high enough to prevent the basin from being open lingually. The protocristids of $M_{2\text{-}3}$ are nearly transverse to the long axis of the toothrow and the postvallids are vertically oriented, in contrast to the more oblique and inclined postvallid of $M_1$.

As noted above, the trigonid structure of GU 32 (Fig. 11I–J), an isolated $M_3$, is identical to that of $M_2$ in the holotype, hence we are confident that it represents the same species (perhaps even the same individual). GU 598 (Figs. 12B, 13A–C), another isolated $M_3$, is almost 20% larger than GU 32 and differs in having a straighter paracristid bearing a small, lingual paraconid, and in having a shallower trigonid notch, a low transverse ridge between the protoconid and metaconid that divides the trigonid basin into small anterior and posterior depressions, and a longer talonid basin. In all these traits, except the last one (which is unique to $M_3$), GU 598 is consistent with the morphology of $M_2$ in GU 745. GU 1505 and 1649 are $M_3$s that are slightly smaller than GU 598, with trigonid features more or less intermediate between those of the other two $M_3$s. $M_3$ is known to be more variable in length intraspecifically than other molars (Gingerich, 1974), hence the observed variation is not surprising. Consequently, as no other evidence of a larger adapoid has been found, it is probable that the three larger $M_3$s represent the same species as GU 32 rather than a different taxon.

Several isolated upper teeth and a maxilla with $M^{1\text{-}3}$ (Figs. 13, 14) are referred to *Asiadapis cambayensis* based on compatible size and crown morphology. Tooth positions represented are $P^3$-$M^3$. $P^3$ (GU 330) and $P^4$ (GU 34, 726) are morphologically similar to their counterparts in *Cantius* (e.g., *C. eppsi*, *C. ralstoni*, and *C. trigonodus*) and *Donrussellia gallica*, except that the single known $P^3$ of *Asiadapis* is less waisted and therefore less constricted (i.e., mesiodistally longer) lingually. As in *Cantius* and *Donrussellia*, both teeth are dominated by a large buccal cusp (the paracone); the protocone is much lower and smaller. A small parastyle is present mesiobuccally

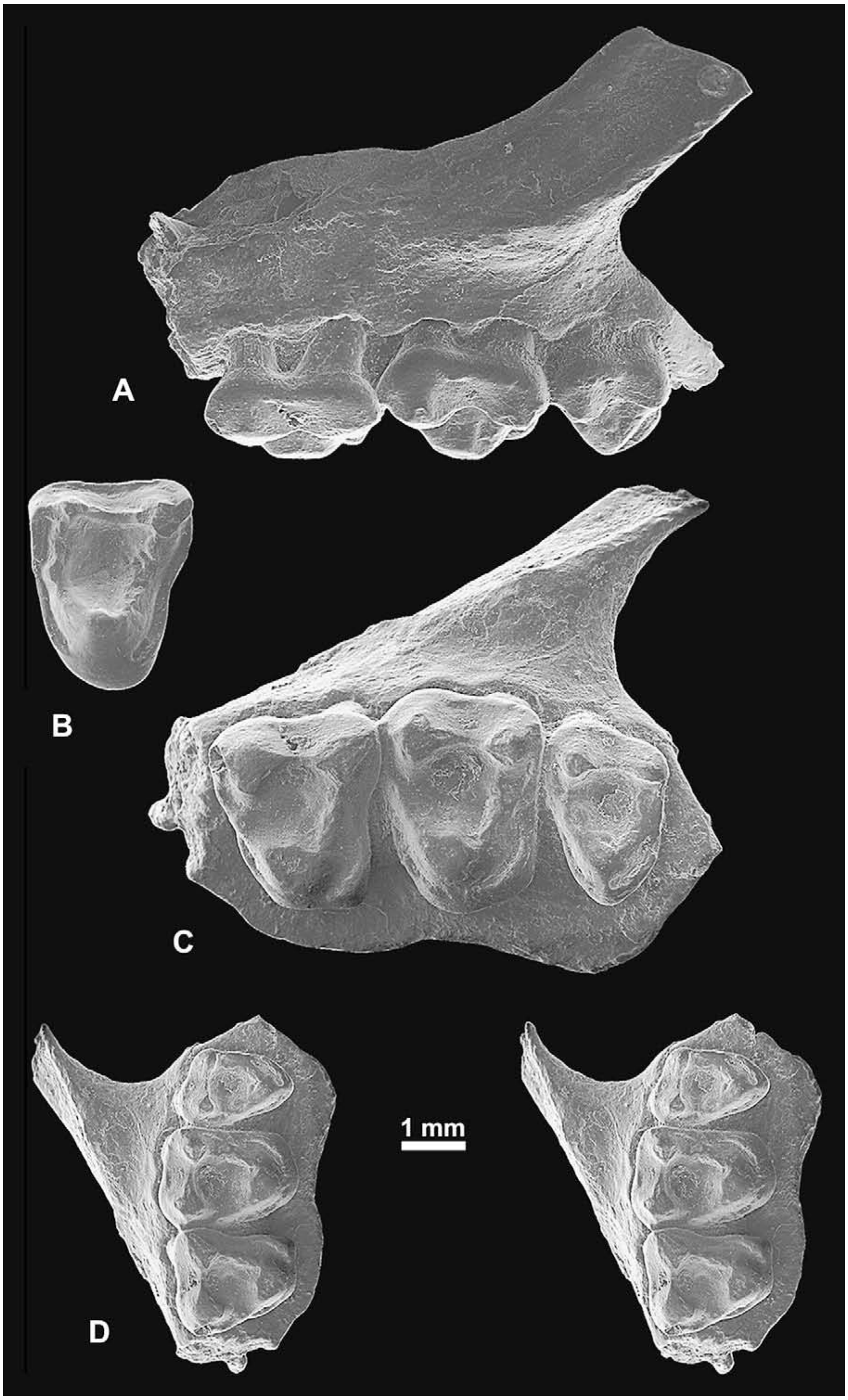

**Figure 14.** Upper molars of *Asiadapis cambayensis*. (A, C–D) GU 656, left maxilla with $M^{1\text{-}3}$, in buccal and occlusal views, including stereopair at bottom. (B) GU 1550, left $M^1$. SEM images.

at the buccal end of the precingulum and is connected to the weak ectocingulum. There is a low postcingulum but no metastyle, in contrast to *Donrussellia*. The protocone is lingual and slightly anterior to the paracone, and a small distal expansion extends behind the protocone. $P^4$ is similar to $P^3$ but more transverse, though relatively less transverse than in *Cantius*.

The molars are represented by the maxilla, GU 656, and at least one isolated tooth from each locus (GU 609, 610, 700–702, 1550). They have a very primitive aspect: there is no *Nannopithex* fold, the hypocone is small or absent, the pre- and postcingula are well-developed, and the buccal and lingual cingula are weak. In these regards they resemble *Protoadapis*. All except GU 656 lack a postmetaconule crista, loss of which characterizes adapoids (Godinot, 1992). A low and weak postmetaconule crista is present on $M^2$ in GU 656, but $M^1$ in this specimen clearly lacks this crest. The upper molars are somewhat triangular ($M^1$ and $M^3$) or subquadrate ($M^2$) in outline. The protocone is the largest cusp and is situated slightly anterior to a transverse midline. The paracone is similar in height to

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

the protocone and slightly taller than the metacone. A small cingular hypocone is barely discernible on $M^1$ (GU 656, 702). In the other $M^1$ (GU 1550), as in $M^2$, the postcingulum is slightly thicker and higher lingually but the hypocone is indistinct. The paraconule and metaconule are very small and weak, their positions indicated as much by the crests that converge on them as by a raised cusp. Very small parastyle and metastyle cusps are visible on the less worn teeth. The buccal cingulum is best developed in the shallow ectoflexus. Lingually, the cingulum is very weak (GU 656) or incomplete at the base of the protocone except in GU 609 ($M^2$), in which it is well-developed. GU 702 ($M^1$) has a smaller trigon basin than the other two $M^1$s, in which the cusps seem to be more peripheral; whether or not this difference is significant must await larger samples.

## *Discussion*

Bajpai et al. (2007) recently named *Suratius robustus* based on a single dentary fragment preserving $P_{3-4}$ and $M_2$, from the same stratigraphic level in Vastan Mine as *Asiadapis cambayensis*. Although named as an omomyid, *Suratius* is clearly an adapoid closely allied to *Marcgodinotius* and *Asiadapis*. Adapoid traits include the relatively large canine, uncompressed and relatively simple premolars, and $M_2$ with peripherally placed cusps. The only significant difference between *S. robustus* and the holotype of *A. cambayensis* is the presence of a low metaconid on $P_4$ of the former. Expression and elevation of the metaconid on $P_4$ have been considered to be important features of interspecific variability in some early euprimates, typically time-successive species (e.g., Bown and Rose, 1987; Smith et al., 2006). Variations in the five $P_4$s now known, however, indicate that paraconid and metaconid development is variable in *A. cambayensis*. It is important to emphasize that all these specimens come from the same horizon at Vastan mine and therefore are believed to have been essentially coeval. It has been shown that such variation in cusps—including the paraconid and metaconid of $P_4$—may occur intraspecifically in both extant and extinct primates (Cuozzo, 2008; Sauther and Cuozzo, 2008). Furthermore, it now appears that this kind of cusp variation can result from minor developmental changes (Jernvall, 2000; Kangas et al., 2004), a finding that led Jernvall (2000: 2644) to conclude that "small cusps may be unreliable as phylogenetic signals." For these reasons, *Suratius robustus* and *Asiadapis cambayensis* are here synonymized. Following article 21.3.1 of the International Code of Zoological Nomenclature (ICZN, 1999), *Asiadapis cambayensis* has priority and is the valid name. We further note that measurements of the holotype of *S. robustus* provided by Bajpai et al. (2007) are inaccurate. Width of $P_4$ is given as 25% greater than the width of $P_3$, but the two premolars are of essentially identical width.

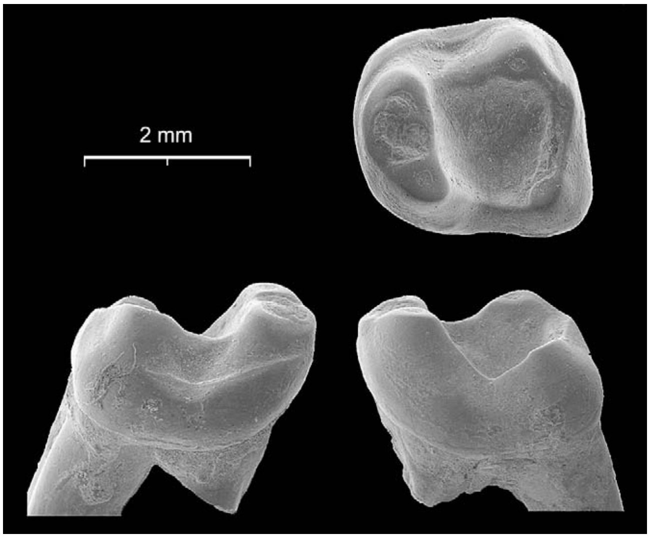

**Figure 15.** *Vastanomys major*, new species, GU 1541 (holotype), right $M_2$, in occlusal, buccal, and lingual views. SEM images.

Though more derived than *Marcgodinotius* in having only three lower premolars and a one-rooted $P_2$, *Asiadapis* is similar to the former in most other respects and appears to be closely related. *Asiadapis* shares several presumably plesiomorphic characters with *Marcgodinotius* (relatively simple and unreduced $P_{3-4}$, uninflated molars with peripheral cusps, upper molars with a small or indistinct hypocone, small conules, and no *Nannopithex* fold). These features also characterize *Donrussellia* and highlight the primitive nature of *Asiadapis*. They suggest an early divergence of asiadapines from the adapoid stem. Like *Marcgodinotius*, *Asiadapis* has relatively transverse protocristids and an unstepped postvallid on $M_1$ (polarity uncertain), as well as a buccally shifted paraconid on $M_1$ and arcuate paracristids on $M_{2-3}$ (probable asiadapine synapomorphies).

The $P_3$ and $P_4$ of *Asiadapis* are similar in their primitive structure to those of *Marcgodinotius*, but in *Asiadapis* these teeth are relatively slightly wider, with better defined cingulids, and the crests on the back of the protoconid of $P_4$ are wider apart, enclosing a wider talonid basin. The $P_3$ is relatively larger than in other adapoids (including *Donrussellia*, *Cantius*, *Protoadapis*, and even *Marcgodinotius*), suggesting that its particularly large size, rather than being plesiomorphic, could be an autapomorphy of *Asiadapis*. However, the tall crown of $P_3$, together with a large canine and small hypoconulids on the molars, have been considered primitive features of *Protoadapis* (Szalay and Delson, 1979). The $P_4$ of *Asiadapis*, like that of *Marcgodinotius*, is polymorphic, with a simple trigonid either consisting of only the protoconid, or bearing a small paraconid and/or metaconid as well. The $P_4$ is also very similar to those of *Donrussellia gallica* and *D. provincialis* except for being larger and having a slightly larger talonid basin. The range of variation among the six $P_4$ specimens here attributed to *Asiadapis cambayensis* is greater than typically seen in early euprimate species, but the consistency of size and morphology elsewhere in the dentition, together with the occurrence of all these specimens in the same horizon at Vastan, strongly suggests that they are conspecific.

Most cercamoniines have a distinct metaconid on $P_4$, but it is smaller and lower in *Donrussellia* (usually considered the most primitive adapoid) than in most other genera. Consequently, it is reasonable to infer that presence of a small metaconid on $P_4$ was the plesiomorphic condition for adapoids (and indeed for euprimates, as discussed above under *Marcgodinotius*). However, the variable absence of the paraconid and metaconid on $P_4$ of *Marcgodinotius* and *Asiadapis*, and their small size when present, suggest an alternative possibility: plesiomorphic absence of these cusps and their generation *de novo* in asiadapines, and perhaps in adapoids generally. It must be noted, however, that at least some specimens of *Anchomomys* and *Periconodon* lack a metaconid on $P_4$, in combination with more derived molar morphology, suggesting probable loss of the metaconid in those genera. Thus, the possibility that the $P_4$ metaconid was lost independently in asiadapines must also be considered.

The lower molars of *Asiadapis* differ from those of *Marcgodinotius* in having a mesiodistally shorter trigonid, and in having the hypoconulid closer to the hypoconid and lacking a notch between the two cusps. The entoconids are slightly weaker, and the paraconids (when distinct) are more lingual. The molars of early Eocene

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

*Agerinia* are particularly similar to *Asiadapis* in having an arcuate paracristid with the paraconid very small or indistinct, and a deep trigonid notch, but the protocristid is more oblique than in the Vastan form. *Asiadapis* is substantially larger than *Panobius* and differs from it in the same features as does *Marcgodinotius*.

The upper molars of *Asiadapis* closely resemble those of *Donrussellia*, differing principally in having slightly weaker conules (particularly the paraconule). Some, but not all, *Donrussellia* specimens compared differ further in having a deeper ectoflexus, a complete lingual cingulum, and in being wider transversely. The longer and less transverse shape of the upper molars of *Asiadapis* is probably derived relative to *Donrussellia gallica*, but in other ways these teeth differ little from those of *Donrussellia*. The cercamoniines *Protoadapis*, *Buxella*, and *Europolemur* are more derived than *Asiadapis* in generally having more inflated molars with larger hypocones, well-developed lingual cingula, and slightly wrinkled enamel.

There is a surprisingly close correspondence in size and general morphology between lower teeth of *Asiadapis* and those of the middle Eocene cercamoniine *Periconodon huerzeleri* from Bouxwiller, France (see Szalay and Delson, 1979: Figure 62C). $P_4$ in *Periconodon* is unusual among notharctids in having very small or indistinct paraconid and metaconid cusps. The overall shape and specific arrangement of crests running back from the protoconid in *P. huerzeleri* are very similar to the condition in the holotype of *A. cambayensis*. The molars have similar proportions and reduced paraconids. The closely related *Anchomomys*, especially *A. gaillardi*, also shows curious resemblances to *Asiadapis* in the simplicity of its $P_4$ and upper molars with small conules and hypocone. Closer examination, however, shows a much more oblique protocristid in *Periconodon* and *Anchomomys* and differences in paracristid and cristid obliqua construction. Moreover, as previously mentioned, the upper molars of *Periconodon* are mesiodistally longer and more derived in having large pericones and hypocones. Consequently, it is more likely that these resemblances support general asiadapine-cercamoniine ties rather than a specific relationship to *Periconodon* or *Anchomomys*.

Though generally similar to early Eocene *Cantius*, *Asiadapis* differs from *Cantius* in numerous details, most or all of which probably indicate a more primitive stage of evolution in the Vastan form. They include less inflated cheek teeth, smooth enamel, weakly developed molar conules and conule cristae, a small or absent hypocone, no *Nannopithex* fold, and a small hypoconulid lobe of $M_3$, as well as smaller size. In fact, most other adapoids differ from *Asiadapis* in having larger hypocones, and many also have upper molars with stronger cingula (especially lingual) and mesostyles.

The precise relationships of *Asiadapis* and *Marcgodinotius* relative to other adapoids are challenging to decipher in part because of our very incomplete knowledge of most Eurasian species, which often consists only of isolated teeth or jaw fragments. The paucity of fossils for many species has led to instability of the composition of Cercamoniinae and various other adapoid subfamilies. Until a better understanding of other Eurasian adapoids is achieved, however, the phylogenetic interrelationships among adapoids, particularly Cercamoniinae, are likely to remain controversial.

The molars of primitive adapoids, especially upper molars, are also quite similar to, and sometimes confused with, those of basal artiodactyls such as *Diacodexis*. This is important at Vastan because both groups are present in the local fauna. The resemblance to *Diacodexis* is accentuated in *Asiadapis* by the small or indistinct hypocone and the absence of a *Nannopithex* fold. However, *Asiadapis* differs from *Diacodexis* in having much smaller molar conules and conule cristae, as well as larger basins.

### Infraorder HAPLORHINI

### Parvorder TARSIIFORMES

### Family Omomyidae Trouessart, 1879

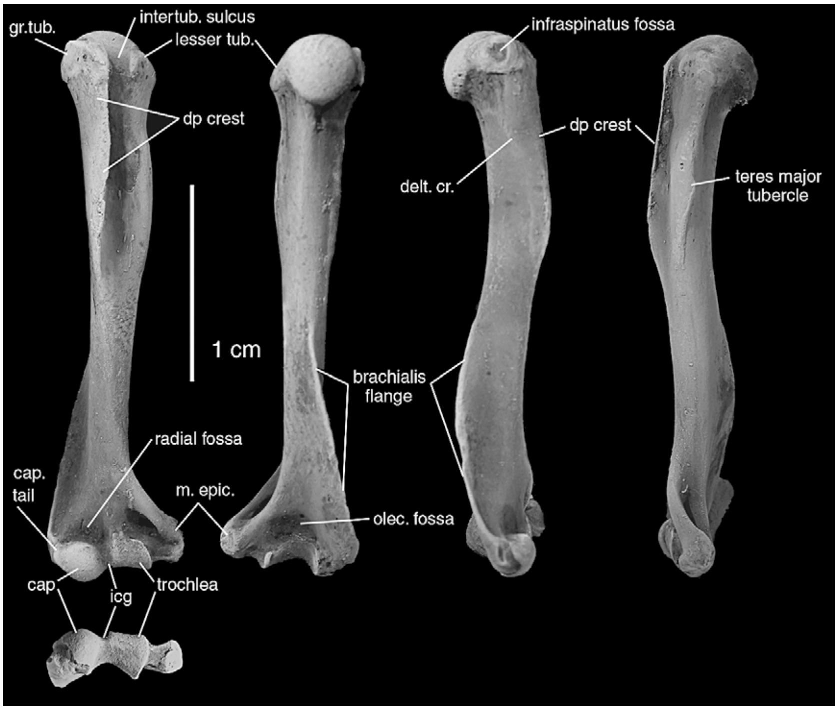

**Figure 16.** Right humerus of euprimate (GU 713) from Vastan Mine, in anterior, posterior, lateral, and medial views. Abbreviations: cap, capitulum; cap. tail, capitular tail; delt. cr., deltoid crest; dp crest, deltopectoral crest; gr. tub., greater tubercle; icg, intercondylar groove; intertub. sulcus, intertubercular sulcus; lesser tub., lesser tubercle; m. epic., medial epicondyle; olec. fossa, olecranon fossa. Digital images; specimens coated with ammonium chloride.

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

**Table 3**

Measurements (mm) and indices of Vastan euprimate humeri compared to those of various adapoids and omomyids. Comparative humeral head measurements after Schmitt (1996); trochlear diameters after Ford (1988); other distal measurements after Szalay and Dagosto (1980). *Absarokius* and *Microchoerus* measured from casts; *Cantius trigonodus* measured from original; other notharctid data from Gebo (1987); cf. *Tetonius*, *Hemiacodon*, *Necrolemur* from Dagosto (1993; note that these values differ markedly from those presented by Dagosto et al. [1999] which were presumably measured differently); other data from Szalay and Dagosto (1980). Capitular width of *Shoshonius* is anomalous and evidently was measured differently by Dagosto et al. (1999). Abbreviations: L, length; DPC L, deltopectoral crest length; BF L, brachialis flange length (measured as total length of supinator crest); Hd L, head proximodistal length (= PD median of Schmitt, 1996); Hd W, head width (= ML median of Schmitt, 1996); BC W, bicondylar width; AW, articular width; TW, trochlear width; TH, trochlear height; Cap W, capitular width; Tmin d and Tmax d, trochlea minimum and maximum anteroposterior diameter (= depth) measured from distal perspective.

| Name | Number | Family | Total L | DPC L | BF L | Hd L | Hd W | BC W | AW | TW | TH | Cap W | Tmin d | Tmax d | TW/AW | TH/TW | TW/Cap W | Tmin d/Tmax d | Hd L/Hd W |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Vastan humerus | GU 713 | Notharctidae? | 29.80 | 12.70 | 14.00 | 4.60 | 3.70 | 7.80 | 5.40 | 2.40 | 2.10 | 3.00 | 1.75 | 2.50 | 0.44 | 0.88 | 0.80 | 0.70 | 1.24 |
| *Cantius trigonodus* | USGS 5900 | Notharctidae |  |  |  |  |  |  |  | 7.60 |  |  | 4.60 | 6.00 |  |  |  | 0.77 |  |
| *Cantius mckennai* | USGS 6759 | Notharctidae |  |  |  |  |  | 17.80 | 11.50 | 5.10 | 3.70 | 6.40 |  |  | 0.44 | 0.73 | 0.80 |  |  |
| *Notharctus* sp. | AMNH 1727 | Notharctidae |  |  |  |  |  | 23.80 | 16.50 | 6.20 | 6.00 | 10.30 |  |  | 0.38 | 0.97 | 0.60 |  |  |
| *Smilodectes gracilis* | AMNH 11484 | Notharctidae |  |  |  |  |  | 20.15 | 13.80 | 4.90 | 5.20 | 8.90 |  |  | 0.36 | 1.06 | 0.55 |  |  |
| *Adapis parisiensis* | Basel QW 1481 | Adapidae |  |  |  |  |  | 20.35 | 14.15 | 5.65 | 4.25 | 8.55 |  |  | 0.40 | 0.75 | 0.66 |  |  |
| *Adapis parisiensis* | Basel QW 1482 | Adapidae |  |  |  |  |  | 17.45 | 12.75 | 4.80 | 3.80 | 7.75 |  |  | 0.38 | 0.79 | 0.62 |  |  |
| *Adapis parisiensis* | AMNH 81001 | Adapidae |  |  |  |  |  | 17.50 | 12.90 | 5.15 | 3.85 | 7.30 |  |  | 0.40 | 0.75 | 0.71 |  |  |
| *Leptadapis magnus* | Basel QD 663 | Adapidae | 111.35 |  |  |  |  | 38.40 | 25.10 | 10.10 | 7.90 | 15.15 |  |  | 0.40 | 0.78 | 0.67 |  |  |
| *Leptadapis magnus* | Basel QD 664 | Adapidae |  |  |  |  |  | 35.60 | 24.90 | 9.35 | 8.20 | 15.50 |  |  | 0.38 | 0.88 | 0.60 |  |  |
| *Leptadapis magnus* | Basel QD 681 | Adapidae |  |  |  |  |  | 40.10 | 26.80 | 10.60 | 6.80 | 16.10 |  |  | 0.40 | 0.64 | 0.66 |  |  |
| omomyid | AMNH 29126 | Omomyidae |  |  |  |  |  | 9.80 | 7.00 | 3.00 | 1.45 | 3.95 |  |  | 0.43 | 0.48 | 0.76 |  |  |
| omomyid | UCMP 113301 | Omomyidae |  |  |  |  |  | 5.15 | 2.73 | 1.21 | 0.75 | 1.50 |  |  | 0.44 | 0.62 | 0.81 |  |  |
| cf. *Tetonius* |  | Omomyidae |  |  |  |  |  |  |  |  |  |  |  |  | 0.44 | 0.62 |  |  |  |
| *Absarokius abbotti* | UCVM 62672 | Omomyidae |  |  |  |  |  | 6.15 | 4.10 | 1.90 | 1.50 | 2.20 | 1.40 | 2.00 | 0.46 | 0.79 | 0.86 | 0.70 |  |
| *Shoshonius cooperi* | CM 69755 | Omomyidae | 24.87 | 10.03 | 10.00 | 3.49 | 2.97 | 6.12 | 4.29 | 2.03 | 1.56 | 1.93 |  |  | 0.47 | 0.77 | 1.05 |  | 1.18 |
| *Hemiacodon* sp. |  | Omomyidae |  |  |  |  |  |  |  |  |  |  |  |  | 0.43 | 0.48 |  |  |  |
| *Necrolemur* sp. |  | Omomyidae |  |  |  |  |  |  |  |  |  |  |  |  | 0.49 | 0.76 |  |  |  |
| *Microchoerus* sp. | Basel QJ 620 | Omomyidae | 43.80 | 18.20 | 19.00 |  |  | 10.60 | 6.90 | 3.30 | 2.70 | 3.60 | 2.30 | 3.10 | 0.48 | 0.82 | 0.92 | 0.74 |  |
| microchoerine | Basel QD 328 | Omomyidae | 40.60 | 15.75 | 15.10 | 5.70 | 5.10 | 9.40 | 6.15 | 2.90 | 2.10 | 3.25 | 1.90 | 2.80 | 0.47 | 0.72 | 0.89 |  |  |
| microchoerine | Basel QV 18 | Omomyidae |  |  |  |  |  | 6.65 | 4.30 | 2.20 | 1.55 | 2.40 |  |  | 0.51 | 0.70 | 0.92 |  |  |
| microchoerine | Basel QK 989 | Omomyidae |  |  |  |  |  | 6.90 | 4.25 | 2.00 | 1.65 | 2.75 |  |  | 0.47 | 0.83 | 0.73 |  |  |

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

### Vastanomys major, new species

#### Holotype and only known specimen

GU/RSR/VAS 1541, right $M_2$.

#### Locality and horizon

Vastan Lignite Mine, Gujarat, India; early Eocene Cambay Shale Formation.

#### Diagnosis

$M_2$ basally inflated, about 35% larger in linear dimensions than *V. gracilis*. $M_2$ paraconid very small and shifted buccally to position almost midway between protoconid and metaconid.

#### Etymology

*major*, Latin, greater; larger than *V. gracilis*, the only other known species.

#### Description

The single known $M_2$ (Fig. 15) is conspicuously larger than that of *V. gracilis*, ruling out any reasonable likelihood that they represent the same species. As in the type species, the base of the crown is inflated, the trigonid is narrower than the talonid, and the breadth between the protoconid and the metaconid is much less than between the hypoconid and the entoconid. Also as in *V. gracilis*, the small paraconid, heavily worn in GU 1541, is centrally located at the front of the trigonid. It barely projects above the low, arcuate paracristid; however, the appearance of the paracristid as a low arc may be accentuated by abrasion. The cristid obliqua is very buccal in position, running almost directly anteriorly (rather than obliquely) from the hypoconid to meet the posterior trigonid wall on the buccal side of the base of the protoconid. Consequently, the talonid basin is very broad and much larger than the trigonid. The hypoconulid is indistinct as in *V. gracilis*, but its position can be inferred from an angle in the postcristid; it is situated much closer to the hypoconid than to the entoconid in both species. Although the talonid notch is moderately deep, the entocristid is high enough to close the talonid basin lingually. A moderately developed buccal cingulid extends mesially from the hypoflexid (just anterior to the hypoconid), rising steeply on the trigonid. The cingulid is similar in *V. gracilis* but does not appear to run as far distally.

Measurements of the holotype: length = 2.80 mm, width of trigonid = 2.30 mm, width of talonid = 2.45 mm. Measurements of the holotype of *V. gracilis*: length = 2.05 mm, maximum width = 1.81 mm (Bajpai et al., 2005b).

#### Discussion

Though based on a single dentary fragment preserving only $M_2$ and alveoli of most other teeth (Bajpai et al., 2005b), *Vastanomys* appears to be distinct from other omomyids, and most of the diagnostic features in the original description (those pertaining to $M_2$) are confirmed in GU 1541. Although we would ordinarily consider a single molar to be an inadequate basis for a new species (especially in omomyids), in this case the molar represents the same locus as the only tooth present in the unique specimen of the type species. It is similar enough to be confidently allocated to the same genus, and is too large to belong to the type species.

*Vastanomys major* is very close in size to *Asiadapis* but differs in having a relatively shorter, wider, and more basally inflated $M_2$, with a distinctly narrower and more mesiodistally compressed trigonid. Thus, the trigonid is smaller relative to the talonid in *V. major*. The same features distinguish *V. gracilis* from *Marcgodinotius*.

*Vastanomys* is at least the fifth omomyid genus known from Asia, all but one of which (*Teilhardina*) are poorly known and extremely rare. The only other omomyid from the Indian subcontinent is *Kohatius*, from the Kuldana Formation of Pakistan (Russell and Gingerich, 1980). As noted above, only two teeth are known, $P_4$ and $M_1$, making its relationships especially obscure. Although not directly comparable with *Vastanomys*, $M_1$ of *Kohatius* has an open trigonid with more acute cusps and a distinct, lingual paraconid, features contrasting with the $M_2$ trigonid of *Vastanomys*. Three omomyids are known from China. *Teilhardina* (possibly including *Baataromomys*) also differs from *Vastanomys* in having a stronger, more lingual paraconid. *Teilhardina asiatica* (Ni et al., 2004) further differs in having a relatively longer and narrower $M_2$ with more acute cusps and a lower entoconid. Besides having a distinct and fully lingual paraconid, *Baataromomys ulaanus* has a more lingual hypoconulid and less buccal cristid obliqua than in *Vastanomys* (Ni et al., 2007). *Macrotarsius*, which is much better known from North America, is represented in Asia by only $P_4$ and $M_1$ from the middle Eocene Shanghuang fissures (Beard et al., 1994). It is much larger than *Vastanomys* and has peripherally placed cusps, a strong, lingual paraconid on $M_1$, and strongly crenulated enamel. Perhaps closest to *Vastanomys* among known Asian omomyids is *Asiomomys*, which is known from a single jaw fragment from the Eocene Huadian Formation of Jilin Province, China (Beard and Wang, 1991). The age of the Huadian Formation is unconstrained, but probably is no older than Uintan—considerably younger than Vastan. *Vastanomys major* is about the size of *Asiomomys changbaicus* and further resembles it in having a nearly centrally placed paraconid. However, $M_2$ of *V. major* differs from that of *A. changbaicus* in having less peripheral cusps (associated with basal inflation of the crown), a weaker paraconid, a relatively taller trigonid, shallower trigonid and talonid notches, and smooth enamel (slightly crenulated in *Asiomomys*). Although the limited material precludes firm conclusions, these brief comparisons suggest that *Vastanomys* is not particularly close to any of the omomyids known from Asia.

A centrally placed paraconid is relatively unusual among omomyids and does not appear to be primitive for the family. North American omomyines that have a buccally shifted paraconid include the relatively derived genera *Dyseolemur*, *Chumashius*, *Chipetaia*, and *Stockia*. Of these, the most similar to *Vastanomys* is *Chumashius*, which differs in having a less mesiodistally compressed trigonid. *Vastanomys* also approaches *Anaptomorphus* in morphology and inflation of $M_2$, although *Anaptomorphus* has a more lingual paraconid, and its trigonid and talonid are less disproportionate in width.

Bajpai et al. (2008) placed *Vastanomys* close to the base of Omomyoidea, citing as primitive traits its large canine and large but single-rooted $P_2$ (both judged from alveoli). They further suggested that it is more primitive than *Steinius*, which has less inflated cheek teeth and is one of only two omomyid genera that retain $P_1$ (the other being primitive species of *Teilhardina*). Their analysis placed *Vastanomys* outside of *Altanius*, *Teilhardina*, and most other omomyids, but, curiously, not *Steinius*. Considerable evidence suggests that basal inflation of cheek teeth and a centrally positioned paraconid are derived traits in omomyids. Moreover, the canine in *Vastanomys* (inferred from a partial alveolus) seems to have been relatively larger than in *Altanius*, *Teilhardina*, and *Steinius*, suggesting that it may have been secondarily enlarged. Accurate assessment of the phylogenetic position of *Vastanomys* must await more complete specimens, but existing evidence does not support such a basal position among omomyids.

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

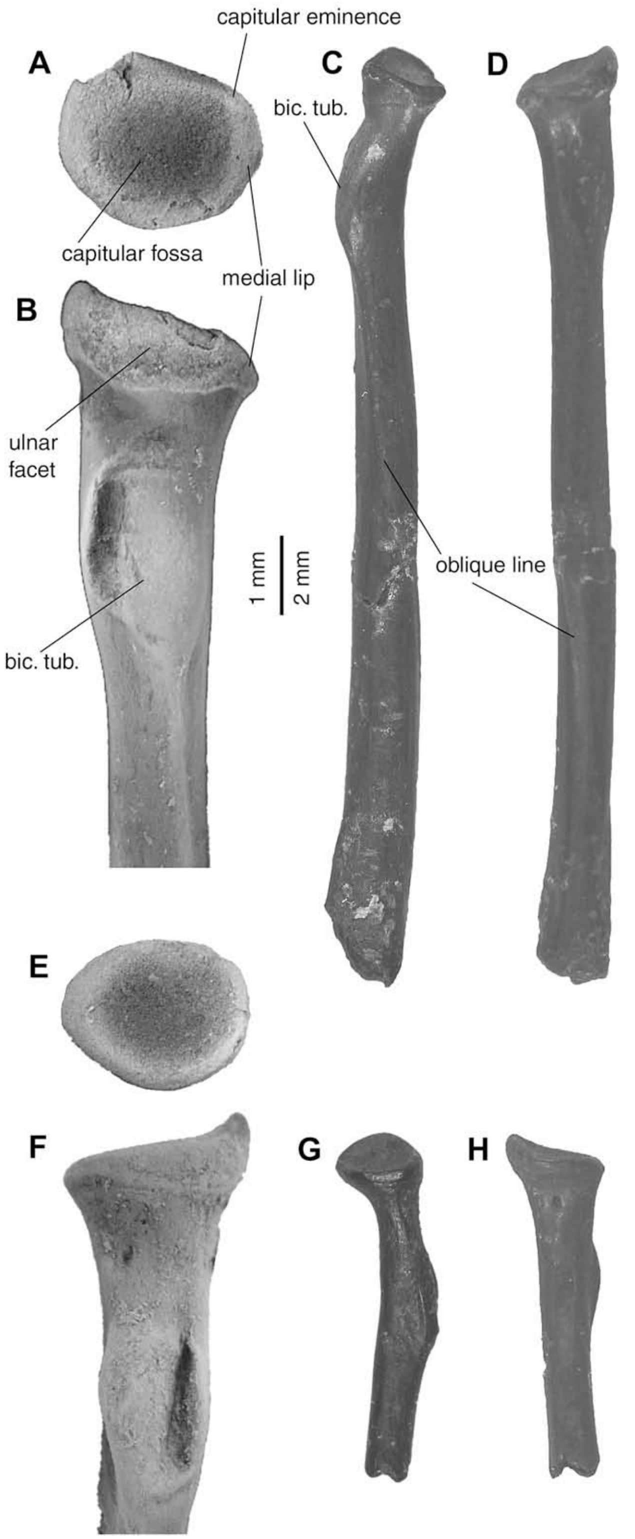

**Figure 17.** Euprimate radii from Vastan Mine. (A–D) GU 714, left radius, in proximal, posterior, medial, and anterior views (when pronated). (E–H) GU 759, proximal right radius, same views as A–D. A–B and E–F are enlarged to twice the size of C–D and G–H. Abbreviation: bic. tub., bicipital tuberosity. Digital images; specimens coated with ammonium chloride.

## Postcrania of Vastan primates

A number of postcrania found by excavation or screen-washing are here allocated to primates; they include humeri, radii, femora, calcanei, and tali.

### *Humerus*

A total of two euprimate humeri have been identified, a complete right humerus (GU 713) and a proximal right humerus (GU 746). They appear to represent the same species, as the latter specimen is almost identical in size and all features; hence, the description here is based on the well-preserved complete specimen (Fig. 16). It is moderately robust: more so than *Eulemur* but less so than *Notharctus* (e.g., Gregory, 1920: Figs. 6, 7) or *Protoadapis* (Godinot, 1994: Fig. 14). Humeral features correspond closely to those in extant lemurs, and muscle attachments can be reconstructed accordingly, following Jouffroy (1962).

The humeral head faces somewhat more superiorly (proximally) than in omomyids, *Notharctus*, or *Eulemur*. It is almost hemispherical, just slightly longer proximodistally than wide when viewed from behind (as in Fig. 16, posterior view). This is similar to other early Eocene primates such as *Cantius* and *Shoshonius* (Gebo, 1987; Dagosto et al., 1999) and therefore does not clearly differentiate between adapoids and omomyids; however, it does suggest locomotor behavior. Among extant prosimians a less elongate humeral head characterizes arboreal quadrupeds rather than vertical clingers and leapers (Schmitt, 1996). When proximodistal head length is measured diagonal to the shaft, following Schmitt (1996), the length/width ratio of GU 713 is 1.24 (Table 3), close to the mean for active arboreal quadrupedal strepsirrhines (1.22; Schmitt, 1996: Table 2) and well below the mean for vertical leapers (1.33; Schmitt, 1996: Table 2). This agrees with Schmitt's interpretation of *Cantius* as an arboreal quadruped.

The greater tubercle is prominent but low, its proximal margin well below the top of the head. Insertions of the rotator cuff muscles are well-marked. On the lateral side of the greater tubercle is a conspicuous fossa for the infraspinatus tendon. The superior margin of the tubercle is thickened for attachment of the supraspinatus muscle, while an eminence just posterior to the fossa marks insertion of teres minor. The lesser tubercle is much smaller and lower than the greater tubercle. A scar along its superior margin was the site of insertion of subscapularis. The intertubercular sulcus (for the tendon of biceps brachii) is relatively narrow and shallow and is evident only proximally. Below the lesser tubercle, ending a little more than a third of the way down the medial aspect of the shaft, is a swelling for the teres major insertion. Expression of these features is similar to that in *Eulemur*, except that the tubercles are slightly smaller and lower in the Vastan humeri. Their relative size, and the orientation of the humeral head, are consistent with the interpretation that these humeri represent a generalized arboreal quadruped (e.g., Kay et al., 2004).

The elevated deltopectoral crest (relatively more prominent than in *Eulemur*) extends less than half the length of the shaft (about 43%). Its medial edge is sharp and directed medially, slightly overhanging the bicipital groove. Laterally, a low, arcuate deltoid crest (perhaps marking the boundary between different heads of the deltoid) is barely evident. Pectoralis major tends to insert proximomedially along the deltopectoral crest, whereas deltoid attaches more distally and laterally. In the few omomyids for which a humerus is available, the deltopectoral crest is somewhat shorter (about 40% the length of the shaft), whereas from published illustrations of adapoids it appears to be almost half the length of the shaft. The Vastan humerus is more like that of omomyids in this regard.

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

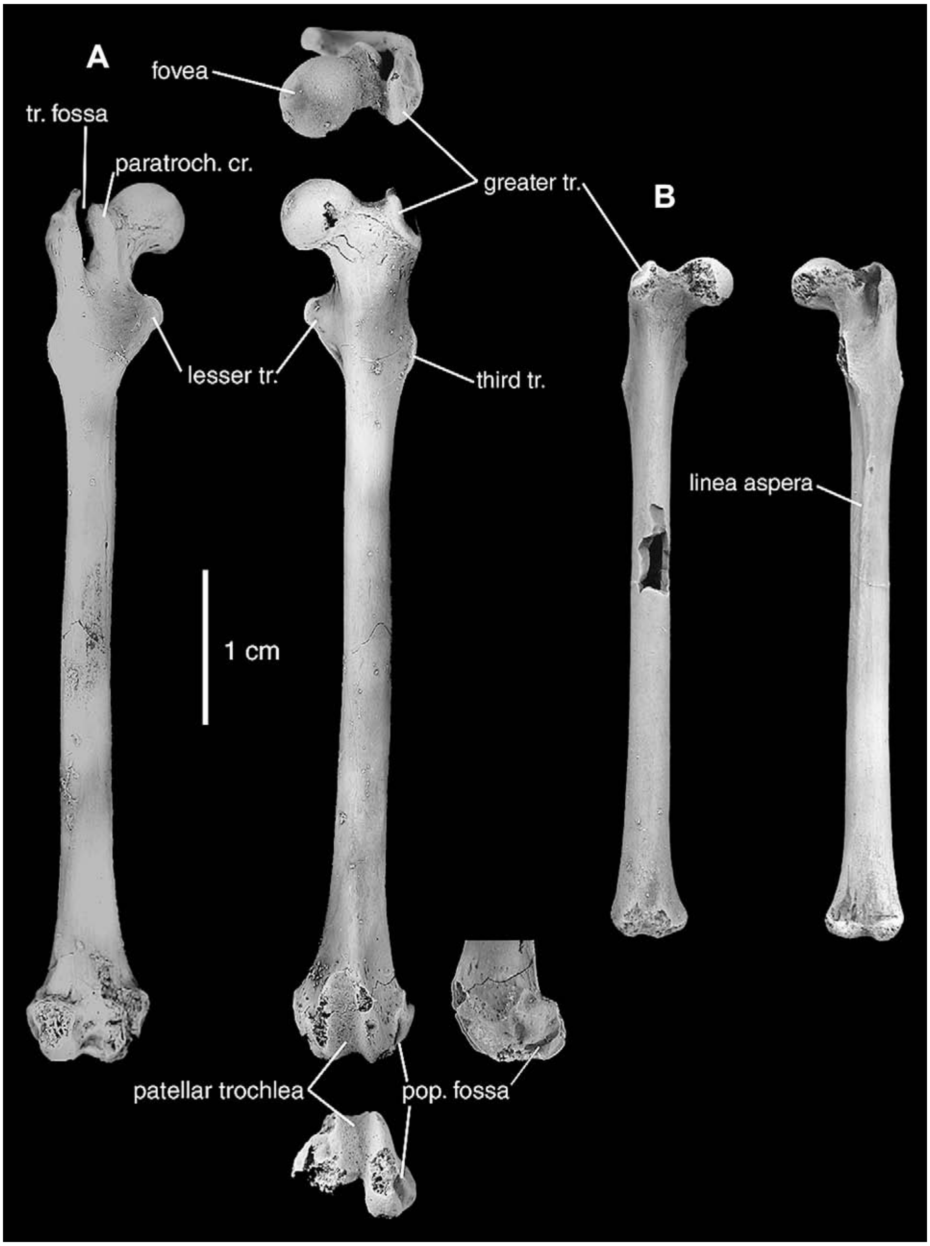

**Figure 18.** Probable asiadapine femora from Vastan Mine. (A) GU 756, left femur in posterior and anterior views; proximal end in superior view shown above, and distal view in lateral and inferior views shown below. (B) GU 715, right femur in anterior and posterior views. Abbreviations: greater tr., greater trochanter; lesser tr., lesser trochanter; paratroch. cr., paratrochanteric crest; pop. fossa, popliteal fossa; third tr., third trochanter; tr. fossa, trochanteric fossa. Digital images; specimens coated with ammonium chloride.

Distally, the brachialis flange (supinator crest) extends proximally almost half the length of the shaft. This implies either a well-developed brachialis muscle or a more proximally originating brachioradialis, or both. The common tendon for carpal and digital extensors originates just distal to the brachioradialis tendon. The medial epicondyle (from which the common flexor tendon originates) is robust, comparable in relative size to that of *Notharctus*, and projects directly medially and farther so than in lemurs. The olecranon fossa is comparatively shallow. These features indicate an ability for powerful flexion at forearm joints (and de-emphasis on extension), as would be expected in an arboreal primate. A proximally extensive brachialis flange is more typical of adapoids (Gregory, 1920; Dagosto, 1983) than of omomyids (see Table 3).

The distal humeral articulation shows typical primate features. The capitulum is spherical and projects distally slightly beyond the trochlea. The capitular tail is small, much narrower than in *Cantius* or the amphipithecid illustrated by Kay et al. (2004: Fig. 12) and apparently closer to the condition in omomyids. A shallow intercondylar groove (= zona conoidea [Rose, 1988]) separates the capitulum from the trochlea, as in other primitive euprimates (except *Adapis*) and many other primates. The capitulum and the trochlea are roughly equal in breadth. The trochlea is slightly narrower mediolaterally and more angled than in *Cantius* or *Notharctus*, so that the medial trochlear ridge projects more distally than in those genera. It is, however, less downturned than in *Microchoerus* or *Shoshonius*, although the difference is subtle, and closer to *Absarokius* in this respect. It is conical rather than cylindrical (minimum anteroposterior diameter of trochlea × 100/maximum diameter = 70; see Ford, 1988) and is bounded laterally by a distinct trochleocapitular ridge, which forms the medial margin of the

**Table 4**

Measurements (mm) and indices of Vastan euprimate femora, probably representing asiadapines, compared with those of various adapoids, omomyids, and extant strepsirrhines. Comparative data from Dagosto and Schmid (1996: Table 1) and Dagosto et al. (1999); additional values measured from original specimens or casts. Values for extant taxa are observed ranges given by Dagosto and Schmid (1996). Abbreviations: e, estimated measurement; L, length; LTB, lesser trochanter breadth; LT angle, lesser trochanter angle; BSDLT, breadth of shaft immediately distal to trochanters; 3rd Tr B, third trochanter breadth; Tr. fossa L, trochanteric fossa length; Neck 1 L and Neck 2 L, neck length including and excluding head, respectively; Patellar W and Ht, patellar groove width and height. See Dagosto and Schmid (1996: Figure 1) for precise method of measurement. Indices also follow Dagosto and Schmid (1996) and were calculated as (dimension shown/BSDLT) × 100.

| Taxon | Number | Family | Total L | LTB | LT angle | BSDLT | 3rd Tr B | Tr. fossa L | Neck 1L | Neck 2L | Neck angle | Patellar W | Patellar Ht | LTB index | 3rd Tr B index | Neck 1 index | Neck 2 index | Tr. fossa L index | Pat Gr W/H index |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Vastan femur | GU 715 | Notharctidae? | | | | 2.6 | 0.5 | 4.2 | 4.5 | ~2.3 | 58° | | | | 19.2 | 173.0 | 88.5 | 161.5 | |
| Vastan femur | GU 756 | Notharctidae? | 22.05 | 2.2 | 28° | 3.3 | 0.9 | 5.0 | 7.0 | 3.0 | 57° | 4.0 | 7.1 | 66.7 | 27.3 | 212.0 | 90.9 | 151.5 | 56 |
| *Cantius trigonodus* | USGS 5900 | Notharctidae | | | 17° | | | | | | 60° | 8.5 | 14.0 | 57.0 | 34.9 | 150.4 | 94.5 | 130.1 | 61 |
| *Notharctus* sp. | | Notharctidae | | | 11° | | | | | | 60.5° | | | 94.4 | 41.3 | 181.0 | 101.6 | 161.3 | |
| *Smilodectes gracilis* | | Notharctidae | | | 9° | | | | | | 58° | | | 75.0 | 23.6 | 140.3 | 80.4 | 100.3 | |
| *Adapis parisiensis* | | Adapidae | | | 11° | | | | | | 55° | 8.8 | 10.9 | 60.7 | 20.3 | 152.7 | 76.0 | 112.3 | 81 |
| *Shoshonius cooperi* | | Omomyidae | | | 30° | | | | | | 67° | | | 77.2 | | 162.0 | | 112.7 | |
| *Hemiacodon gracilis* | | Omomyidae | | | 23° | | | | | | 73.5° | | | 42.8 | 28.3 | 129.1 | 63.2 | 115.0 | |
| omomyid | USNM 336187 | Omomyidae | | | 20° | | | | | | 74° | | | 69.7 | | 137.6 | 63.2 | 113.3 | |
| ?*Omomys* | YPM 44515 | Omomyidae | | | 12° | | | | | | 71° | | | 38.9 | 19.1 | 129.3 | 71.2 | 101.7 | |
| *Microchoerus* sp. | | Omomyidae | | | | | | | | | | 5.6 | 10.7 | 72.7 | 76.1 | | | 107.8 | 52 |
| *Necrolemur* sp. | | Omomyidae | | | 47° | | | | | | 65° | | | | | 179.2 | 126.3 | 152.2 | |
| | | Cheirogaleidae | | | 9–23° | | | | | | 59–75° | | | 38.3–88.9 | 30.7–60.8 | 142.3–193.5 | 90.6–140.5 | 106.9–148 | |
| | | Lemuridae | | | 12–37° | | | | | | 57–75° | | | 45.0–77.1 | 28.0–64.8 | 168.4–206.4 | 96.3–134.2 | 110.2–170.2 | |
| *Lepilemur mustelinus* | | Lepilemuridae | | | 16–26° | | | | | | 69–79° | | | 38.2–75.3 | | 154.4–171.2 | 76.6–103.1 | 98.0–120.9 | |
| | | Indriidae | | | 10–22° | | | | | | 61–79° | | | 45.3–83.8 | 9.9–47.9 | 177.0–210.1 | 86.3–136.2 | 108.3–152.1 | |
| | | Galagidae | | | 7–16° | | | | | | 65–83° | | | 46.0–93.1 | 29.0–58.0 | 120.1–154.2 | 25.9–74.2 | 77.0–113.2 | |
| | | Lorisidae | | | 5–14° | | | | | | 51–69° | | | 65.3–98.8 | | 130.4–176.3 | 36.7–92.2 | 43.6–105.4 | |
| | | Tarsiidae | | | 6–13° | | | | | | 67–88° | | | 42.6–90.9 | 31.2–53.7 | 140.7–161.6 | 51.9–76.4 | 84.4–108.7 | |

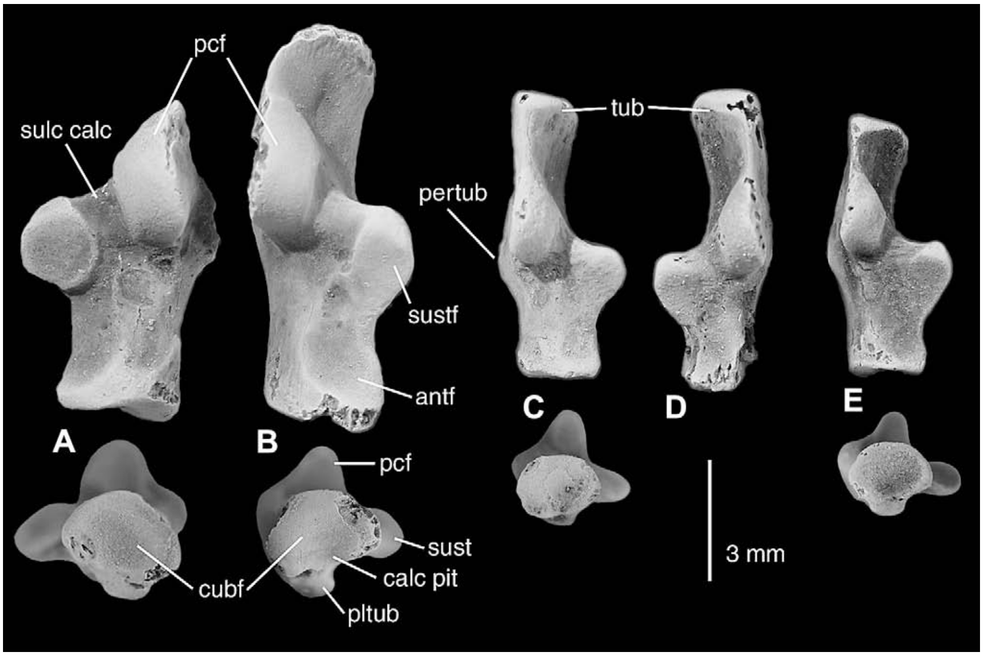

**Figure 19.** Calcanei of euprimates from Vastan Mine. (A-D) probable asiadapines: (A) GU 707, distal left calcaneus tentatively referred to *Asiadapis cambayensis*, in dorsal and distal views; (B) GU 716, right calcaneus tentatively referred to *Asiadapis cambayensis*, in dorsal and distal views; (C) GU 709, right calcaneus tentatively referred to *Marcgodinotius indicus*, in dorsal and distal views; (D), GU 708, left calcaneus tentatively referred to *Marcgodinotius indicus*, in dorsal view. (E) GU 710, right calcaneus, possibly of an eosimiid, in dorsal and distal views. Abbreviations: antf, anterior calcaneal facet; calc pit, calcaneal pit; cubf, cuboid facet; pcf, posterior calcaneal (= ectal) facet; pertub, peroneal tubercle; pltub, anterior plantar tubercle; sulc calc, sulcus calcanei; sust, sustentaculum tali; sustf, sustentacular facet; tub, tuber calcanei. Digital images; specimens coated with ammonium chloride.

intercondylar groove. The trochlear shape and proportions compare most closely with those of omomyids, particularly *Absarokius* (Szalay and Dagosto, 1980; Covert and Hamrick, 1993), but are also close to the notharctid *Cantius* (Table 3) and the amphipithecid. However, omomyids have a distinct dorsoepitrochlear fossa on the posterior surface between the trochlea and medial epicondyle, associated with the ulnar collateral ligament (Dagosto et al., 1999), whereas the fossa in the Vastan humerus is shallow and poorly defined. A large, relatively distal entepicondylar foramen is present at about the same level as the radial fossa; this is more distal than in most other primates compared, including *Cantius*, *Notharctus*, *Adapis*, some extant lemurs, *Absarokius*, *Shoshonius*, and microchoerids. There is no evident coronoid fossa.

Specimen GU 713 is the best preserved early Eocene euprimate humerus reported to date, yet we cannot be confident about its attribution. Comparatively few Eocene euprimates are known from postcrania (Dagosto, 1993; Dagosto et al., 1999), and the majority of those for which postcrania have been identified are represented by only a few elements, often fragmentary or badly damaged. Complete humeri have been reported for at least six adapoid taxa and two omomyids, but condition and descriptions vary considerably, making thorough comparison difficult. Furthermore, only one of them (the damaged humerus of the omomyid *Shoshonius*) is of early Eocene age; humeri of early adapoid genera are either very poorly known or completely unknown (Gebo, 1987; Godinot, 1994). Consequently, we understand very little about humeral differences between omomyids and adapoids, especially early in their evolution. Based on the much greater frequency of adapoids than omomyids at Vastan, it is reasonable to conclude that GU 713 represents an asiadapine. Comparisons with extant primates including various galagids suggest that GU 713 is more likely to belong to *Marcgodinotius* than to *Asiadapis*. (Molars of *Marcgodinotius* are intermediate in size between those of *Galagoides demidoff* and *Galago moholi*, whereas molars of *Asiadapis* are close in size to those of the larger *Galagoides alleni*. GU 713 is much smaller than the humeri of both *G. alleni* and the smaller *Galago senegalensis*, and slightly larger than that of *Galagoides demidoff*.) However, most of its distinctive features are euprimate traits shared with both adapoids and omomyids.

### *Radius*

Euprimate radii include three specimens (GU 714, 750, 759; Fig. 17) of similar size and most likely belonging to *Marcgodinotius*. Their size (slightly smaller than the radius of *Galago senegalensis*) appears to be compatible with the humeri described above. The first two are essentially identical; GU 759 is slightly different and possibly represents a different taxon. They closely resemble the radii of *Cantius*, *Notharctus*, and extant lemurs in overall morphology but are much smaller and slightly less bowed. The most nearly complete of the three, GU 714 (left radius, proximal two-thirds), is close in size and shaft diameter to the radius of *Galago senegalensis* but has a slightly more ovoid head (ratio of maximum to minimum diameters is 2.80/2.30 mm = 1.22), which also characterizes the other two specimens (ratio of 1.23 in both). This is slightly rounder than in *Cantius* (1.3; Rose and Walker, 1985) and indicates the capability for substantial supination, comparable to extant prosimians or nearly so. The proximal articular surface consists almost entirely of the nearly round capitular fossa surrounded by a smooth, even peripheral rim. It is wider and higher laterally and tapers very slightly medially, where the rim is thickened and beveled, forming a narrow lip that articulated with the intercondylar groove (zona conoidea) during pronation. GU 759 shows no indication of a capitular eminence, whereas a hint of the eminence is present at the anterior edge of the medial lip in the other two specimens; however, this remnant is too small to have had much of an effect in either limiting supination or stabilizing the radiohumeral joint. Maximum and minimum diameters of the shaft just distal to the bicipital tuberosity are 1.25 × 1.1 mm, expanding

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

**Table 5**

Measurements (mm) and indices of Vastan euprimate calcanei compared with those of various adapoids, omomyids, eosimiids, and extant euprimates. Comparative data from Gebo et al. (1991, 2001) and Dagosto et al. (1999). *Cantius trigonodus* 1 and *Cantius abditus* 1 refer to sample designations of Gebo et al. (1991). Measurements taken following Gebo et al. (1991): C1 = calcaneal length; C2 = calcaneal maximum width at sustentaculum; C3 = ectal facet length; C4 = ectal facet width; C5 = greatest diameter of cuboid facet; C6 = width of cuboid facet perpendicular to C5; C7 = length of posterior arm proximal to ectal facet; C8 = length of anterior arm distal to ectal facet. Indices are ratio shown × 100. Angles of posterior facet and cuboid facet were deemed too difficult to measure consistently.

| Name | Number | Family | C1 calc L | C2 width | C3 ectal L | C4 ectal W | C5 W cub fac | C6 H cub fac | C7 post L | C8 ant L | C7/C1 | C8/C1 | C2/C1 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Marcgodinotius indicus* L | GU 708 | Notharctidae | >8.00 | >3.2 | 2.40 | 1.20 | | | 2.20 | >3.20 | <28 | >40 | >40 |
| *Marcgodinotius indicus* R | GU 709 | Notharctidae | 7.60 | 3.45 | 2.60 | 1.25 | 2.35 | 1.75 | 2.05 | 3.00 | 27 | 39 | 45 |
| *Marcgodinotius indicus* L | GU 1642 | Notharctidae | | 3.20 | 2.40 | 1.20 | | | 2.20 | >2.50 | | | |
| *Marcgodinotius indicus* R | GU 1643 | Notharctidae | 7.70 | | 2.70 | 1.30 | 2.15 | 1.70 | 1.90 | 3.30 | 25 | 43 | |
| *Asiadapis cambayensis* | GU 716 | Notharctidae | | >4.8 | 3.50 | | 3.90 | 2.60 | | 3.10 | | | |
| *Asiadapis cambayensis* | GU 707 | Notharctidae | | >5.25 | >3.5 | 2.00 | 3.50 | 2.60 | | 4.40 | | | |
| *Asiadapis cambayensis* | GU 760 | Notharctidae | ~11.10 | 5.50 | 3.70 | 2.20 | 3.30 | 2.60 | 2.80 | 4.50 | 25 | 41 | 50 |
| eosimiid? | GU 710 | ? | 6.70 | 3.35 | 2.20 | 1.10 | 2.20 | 1.60 | 1.60 | 3.05 | 24 | 46 | 50 |
| euprimate | GU 751 | ? | 8.20 | 4.30 | 2.70 | 1.20 | 2.60 | 1.95 | 2.00 | 3.50 | 24 | 43 | 52 |
| euprimate | GU 761 | ? | | 3.90 | | | 2.30 | 1.60 | | 3.30 | | | |
| euprimate | GU 1644 | ? | 7.10 | 3.70 | 2.50 | 1.35 | 2.25 | 1.75 | 1.60 | 3.00 | 23 | 42 | 52 |
| *Cantius mckennai* | | Notharctidae | 19.00 | | | | | | | | 28 | 44 | 44 |
| *Cantius trigonodus* 1 | | Notharctidae | 22.10 | | | | | | | | 27 | 41 | 41 |
| *Cantius abditus* 1 | | Notharctidae | 23.80 | | | | | | | | 27 | 41 | 43 |
| *Copelemur feretutus* | | Notharctidae | 20.25 | | | | | | | | 28 | 41 | 43 |
| *Notharctus tenebrosus* | | Notharctidae | 25.35 | | | | | | | | 30 | 36 | 42 |
| *Notharctus pugnax* | | Notharctidae | 25.65 | | | | | | | | 28 | 39 | 44 |
| *Smilodectes gracilis* | | Notharctidae | 24.55 | | | | | | | | 31 | 38 | 42 |
| *Adapis parisiensis* | | Adapidae | 18.70 | | | | | | | | 36 | 32 | 38 |
| *Leptadapis magnus* | | Adapidae | 31.00 | | | | | | | | 36 | 31 | 36 |
| *Teilhardina belgica* | | Omomyidae | | | | | | | | | 26 | 51 | |
| *Tetonius* sp. | | Omomyidae | | | | | | | | | 28 | 49 | |
| *Hemiacodon gracilis* | | Omomyidae | | | | | | | | | 29 | 52 | |
| *Arapahovius gazini* | | Omomyidae | | | | | | | | | 21 | 54 | |
| *Washakius insignis* | | Omomyidae | | | | | | | | | 24 | 52 | |
| *Shoshonius cooperi* | | Omomyidae | 9.79 | 3.25 | 2.23 | 1.25 | 2.32 | 1.55 | 2.22 | 5.10 | 23 | 52 | 33 |
| *Microchoerus* sp. | | Omomyidae | | | | | | | | | 15 | 50 | |
| *Necrolemur* sp. | | Omomyidae | | | | | | | | | 16 | 65 | |
| *Microcebus murinus* | | Cheirogaleidae | | | | | | | | | 19 | 61 | |
| *Cheirogaleus medius* | | Cheirogaleidae | | | | | | | | | 23 | 50 | |
| *Cheirogaleus major* | | Cheirogaleidae | | | | | | | | | 26 | 48 | |
| *Otolemur crassicaudatus* | | Galagidae | | | | | | | | | 20 | 65 | |
| *Galagoides demidovii* | | Galagidae | | | | | | | | | 13 | 77 | |
| *Galago senegalensis* | | Galagidae | | | | | | | | | 17 | 72 | |
| *Tarsius bancanus* | | Tarsiidae | | | | | | | | | 12 | 76 | |
| *Cebuella pygmaeus* | | Cebidae | | | | | | | | | 22 | 41 | |
| *Callithrix jacchus* | | Cebidae | | | | | | | | | 28 | 41 | |
| *Callithrix argentata* | | Cebidae | | | | | | | | | 27 | 42 | |
| *Saguinus oedipus* | | Cebidae | | | | | | | | | 27 | 40 | |
| *Callimico goeldi* | | Cebidae | | | | | | | | | 23 | 41 | |
| *Saimiri sciureus* | | Cebidae | | | | | | | | | 21 | 46 | |
| *Cebus apella* | | Cebidae | | | | | | | | | 30 | 42 | |
| *Callicebus donaphilus* | | Pitheciidae | | | | | | | | | 24 | 42 | |
| IVPP V11848 | | Eosimiidae | 4.25 | 1.80 | 1.20 | 0.65 | 1.25 | 0.90 | 0.85 | 2.20 | 20 | 52 | 42 |
| IVPP V11851 | | Eosimiidae | 6.60 | 2.95 | 1.80 | 1.10 | 1.87 | 1.15 | 1.70 | 3.10 | 26 | 47 | 45 |
| IVPP V12280 | | Eosimiidae | 7.90 | 3.25 | 2.30 | 1.17 | 2.15 | 1.45 | 1.70 | 3.90 | 22 | 49 | 41 |
| IVPP V12281 | | Eosimiidae | 7.50 | 3.25 | 2.15 | 1.22 | 2.02 | 1.35 | 1.85 | 3.50 | 25 | 47 | 43 |
| IVPP V12283 | | Eosimiidae | 7.60 | | 2.25 | 1.25 | | | 1.70 | 3.40 | 22 | 45 | |
| IVPP V12284 | | Eosimiidae | 7.66 | 2.90 | 2.38 | 1.20 | 1.90 | 1.20 | 1.80 | 3.48 | 23 | 45 | 38 |
| IVPP V12286 | | Eosimiidae | 8.20 | 3.50 | 2.50 | 1.25 | 2.35 | 1.50 | 1.70 | 4.00 | 21 | 49 | 43 |
| IVPP V12313 | | Eosimiidae | 8.20 | 3.60 | 2.50 | 1.20 | 2.40 | 1.80 | 1.80 | 3.90 | 22 | 48 | 44 |

distally to 1.5 × 1.5 mm (GU 714); 1.3 × 1.2 mm (GU 750); and 1.1 × 1.1 mm (GU 759).

All three specimens have a prominent bicipital tuberosity of similar form, consisting of a salient, elongate eminence anteriorly and a thin ridge posteriorly, the two separated by a longitudinal depression. The morphology is similar to the bicipital tuberosity in *Cantius* (USGS 5900), but the anterior eminence is more swollen and elevated from the shaft in the Vastan radii, especially GU 714. Its expansion may be a modification to enhance the power of the biceps for supination when the elbow was flexed. In GU 759 the anterior eminence has a sharper anterior border. An oblique line can be seen in GU 714 on the anteromedial surface extending from the anterior eminence diagonally to the front of the shaft, where it thickens slightly at its distal end. In extant lemurs, this line marks the boundary of the insertion of the supinator muscle anteriorly and the origin of flexor digitorum profundus (including flexor pollicis longus) posteriorly and, more distally, the insertion of pronator teres (Jouffroy, 1962). The interosseous crest extends distally from the posterior ridge of the bicipital tuberosity. It is considerably less sharp than in *Cantius*, consequently the shaft is more nearly round in cross-section for most of its length.

### *Femur*

Femora include two specimens of slightly different sizes (GU 715, 756; Fig. 18), which appear to belong to euprimates, the larger one (GU 756) more surely so. As for the humerus, similarities to extant lemurs are close enough to allow inferences of muscle attachment based on living forms (Jouffroy, 1962).

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

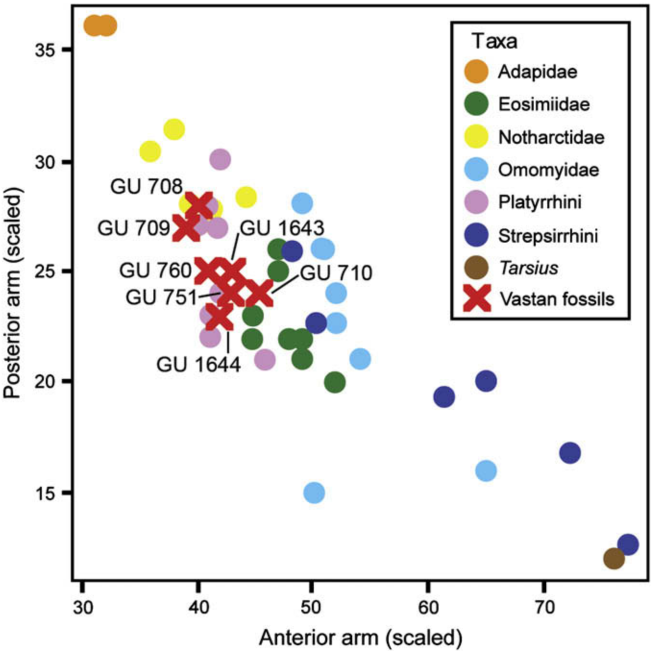

**Figure 20.** Proportions of Vastan euprimate calcanei (posterior or proximal arm vs. anterior or distal arm, scaled to calcaneal length) compared with those of selected fossil and extant primates. Among probable relatives, GU 708 and GU 709 compare closely with notharctids, whereas GU 710 plots at the edge of the eosimiid cluster. Other specimens (including GU 760, believed to represent *Asiadapis cambayensis*) fall between the notharctid and eosimiid clusters. Data for notharctids from Gebo et al. (1991), for *Shoshonius* and strepsirrhines from Dagosto et al. (1999), other comparative data from Gebo et al. (2001).

In both specimens the proximal end tilts slightly anteriorly relative to the shaft, though not as much as in *Shoshonius* (Dagosto et al., 1999). The articular surface extends posterodorsally onto the femoral neck, approximately as in *Cantius*. Posterodorsal extension of the articular surface of the femoral head is characteristic of active arboreal primates, especially vertical clingers and leapers, though its precise functional significance is controversial (Ford, 1988). The head is subspherical, with a slightly more extensive articular surface anteriorly than in *Cantius* (Rose and Walker, 1985); this is better preserved in GU 756. Adapoids and extant lemurs have a similar subspherical head. In contrast, the femoral head of galagos and tarsiers is cylindrical, and that of omomyids is semicylindrical (Dagosto and Schmid, 1996; Dagosto et al., 1999).

A narrow but deep trochanteric fossa (for insertion of obturator and gemelli muscles, which are principally lateral rotators of the thigh) is bounded medially by a salient paratrochanteric crest (Hershkovitz, 1988) that extends proximodistally along the full length of the trochanteric fossa. The fossa is relatively long as in *Notharctus* and *Necrolemur*, and relatively longer than in other adapoids (including *Cantius*) and omomyids (Table 4). The fossa thus compares well with that in some extant lemurs. GU 715 is less well-preserved but appears to be similar in all features except for having a shorter and less prominent paratrochanteric crest. Ford (1988) noted the presence of this crest in platyrrhines (except *Cebus*) and several other primates including *Daubentonia*, and suggested that it correlates with a well-developed ischiofemoral ligament; nevertheless, its precise functional significance remains unclear. Dagosto and Schmid (1996) reported that the paratrochanteric crest is widespread among primates (though missing in galagos and tarsiers) and could find no correlation with locomotor behavior. Even so, the prominence of the crest in GU 756 is notable because it appears to be larger than in omomyids or adapoids that can be compared, except perhaps for *Adapis* type 1 of Bacon and Godinot (1998: Fig. 1).

The shape and orientation of the greater trochanter corresponds closely to that of notharctids. It is relatively larger and reflected slightly laterally in GU 756, whereas in GU 715 it does not bend laterally. In contrast to many extant lemurs, it does not project proximally as high as the head. The prominent lesser trochanter projects mainly medially and somewhat posteriorly. The lesser trochanteric angle is about 28° in GU 756 (see Dagosto and Schmid, 1996); in GU 715 the trochanter is broken but appears to have had a similar orientation. A medially projecting lesser trochanter is typical of arboreal mammals, and this angle is within the range of extant prosimians. The angle is larger than in adapoids but comparable to many extant lemurs (including vertical clinging and leaping taxa); it is at the upper end of the values for many omomyids but smaller than in *Microchoerus* (Dagosto and Schmid, 1996;

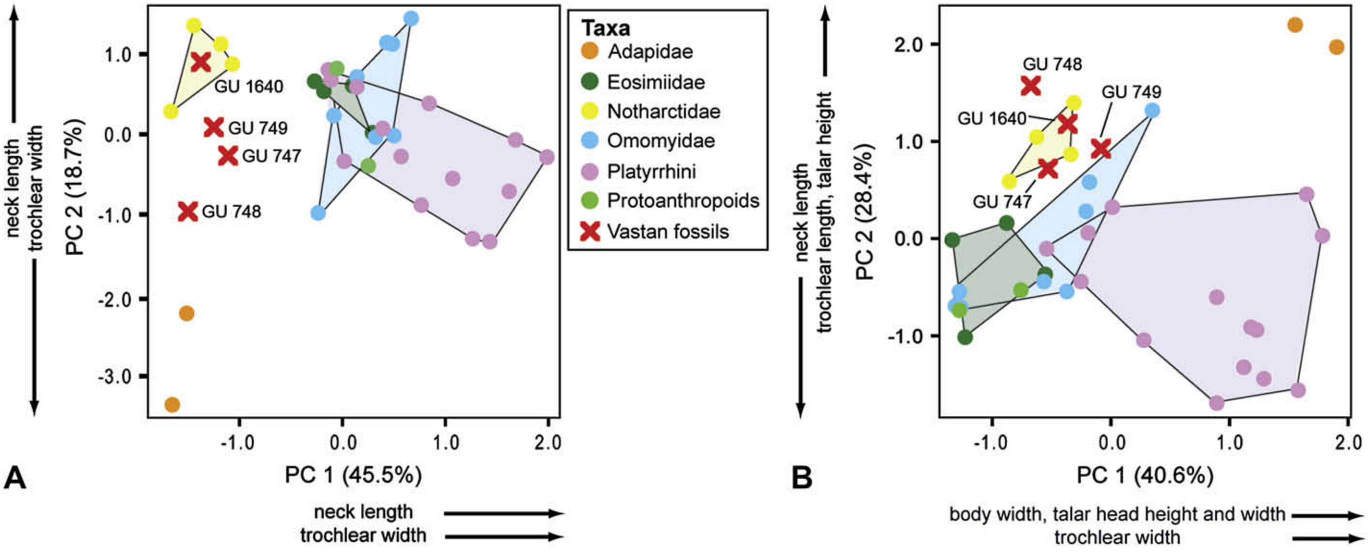

**Figure 21.** PCA of talar indices in selected fossil and extant primates (see Tables 6 and 7 for indices used; comparative data from Gebo et al., 2001). (A) Analysis of indices from Gebo et al. (2001) places GU 1640 within the notharctid polygon, and other Vastan tali closest to adapoids on PC 1 and between notharctids and adapids on PC 2. (B) Analysis of modified indices places Vastan tali closest to notharctids, although GU 749 also plots close to the polygon circumscribing the distribution of omomyids. See text for further discussion.

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

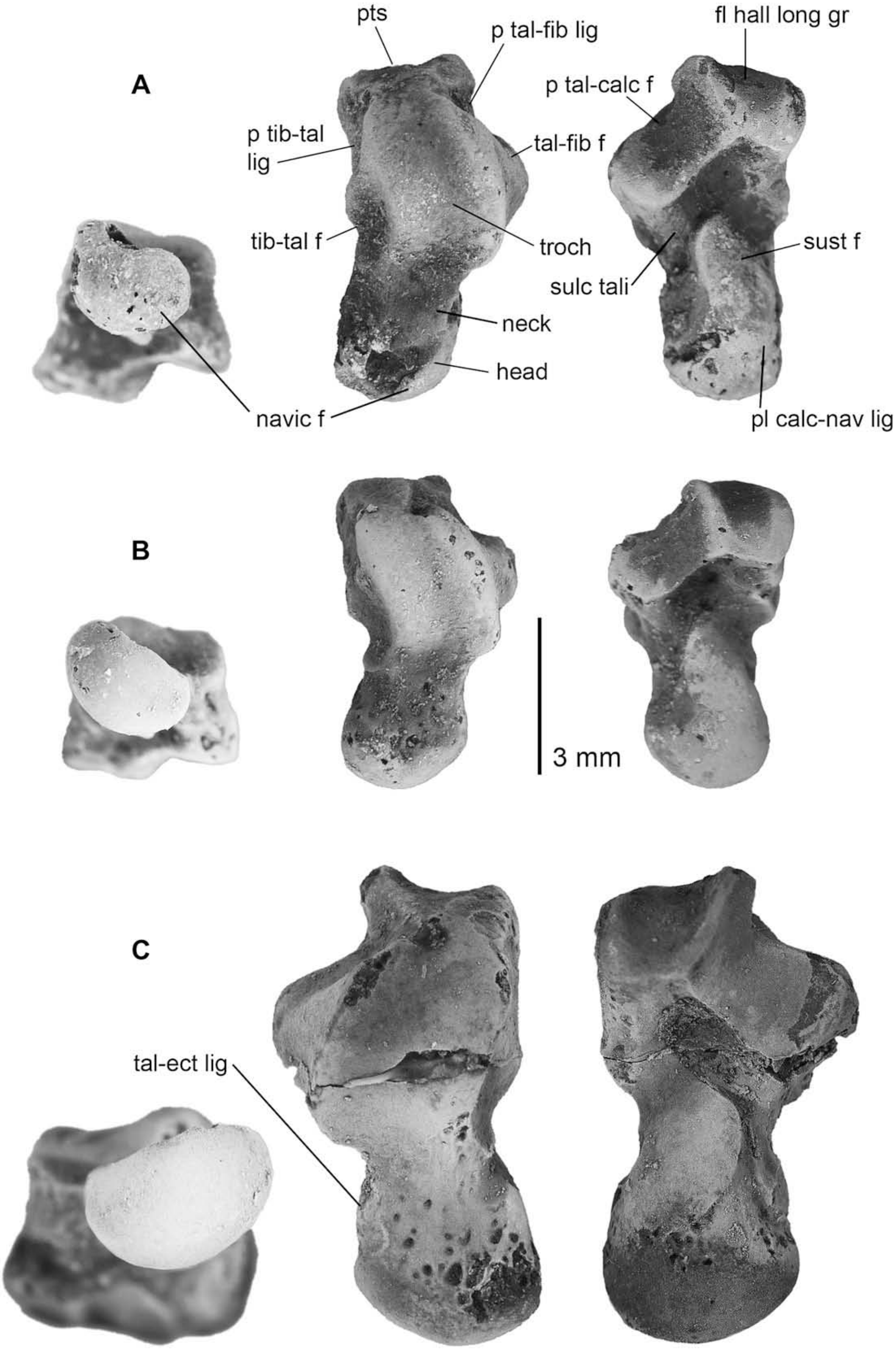

**Figure 22.** Tali of euprimates from Vastan Mine, in distal, dorsal, and plantar views. (A) GU 748, left talus tentatively referred to *Marcgodinotius indicus*. (B) GU 749, left talus tentatively referred to *Marcgodinotius indicus*. (C) GU 747, right talus tentatively referred to *Asiadapis cambayensis*. Abbreviations: fl hall long gr, flexor hallucis longus groove; navic f, navicular facet; p tal-calc f, posterior talocalcaneal (ectal) facet; p tal-fib lig, posterior talofibular ligament; p tib-tal lig, posterior tibiotalar ligament; pl calc-nav lig, plantar calcaneonavicular (spring) ligament; pts, posterior trochlear shelf; sulc tali, sulcus tali; sust f, sustentacular facet; tal-ect lig, tubercle for talo-ectocuneiform ligament; tal-fib f, talofibular facet; tib-tal f, tibiotalar facet; troch, trochlea. Digital images; specimens coated with ammonium chloride.

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

**Table 6**

Measurements (mm) and indices of Vastan asiadapine tali compared with those of various adapoids, omomyids, eosimiids, and extant euprimates. Comparative data from Gebo et al. (2001). Measurements taken following Gebo et al. (1991) except that talar width (A2) was measured parallel to trochlear width (A4), as in Gebo et al. (2001). A1 = talar length; A2 = maximum talar width; A3 = trochlear length; A4 = trochlear width; A5 = neck length; A7 = talar height; A8 = head height; A9 = head width. (Note: Gebo et al. [1991] gave a value of 14° for the neck angle in *Cantius trigonodus*; the value given here is based on our measurement of USGS 5900. Our remeasurement of the neck angle in *C. mckennai* is also about 30°).

| Name | Number | Family | A1 talar L | A2 body W | A3 troch L | A4 troch W | A5 neck L | Neck angle | A7 talar ht | A8 head ht | A9 head W | A5/ A1 | A5/ A3 | A5/ A4 | A7/ A4 | A7/ A3 | A4/ A3 | A9/ A8 | A9/ A4 | A2/ A1 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Asiadapis cambayensis* | GU 747 | Notharctidae | 8.55 | 4.80 | 5.00 | 3.00 | 3.80 | 29° | 3.75 | 2.50 | 3.60 | 0.44 | 0.76 | 1.27 | 1.25 | 0.75 | 0.60 | 1.44 | 1.20 | 0.56 |
| *Marcgodinotius indicus* | GU 748 | Notharctidae | 6.30 | 3.50 | 4.00 | 2.10 | 2.50 | 26° | 2.85 | 2.10 | 2.30 | 0.40 | 0.63 | 1.19 | 1.36 | 0.71 | 0.53 | 1.10 | 1.10 | 0.56 |
| *Marcgodinotius indicus* | GU 749 | Notharctidae | 5.80 | 3.35 | 3.50 | 2.00 | 2.70 | 32° | 2.60 | 1.75 | 2.60 | 0.47 | 0.77 | 1.35 | 1.30 | 0.74 | 0.57 | 1.49 | 1.30 | 0.58 |
| *Marcgodinotius indicus* | GU 1640 | Notharctidae | 5.90 | 3.20 | 3.50 | 1.90 | 2.70 | 20° | 2.80 | 2.00 | 2.40 | 0.46 | 0.77 | 1.42 | 1.47 | 0.80 | 0.54 | 1.20 | 1.26 | 0.54 |
| *Marcgodinotius indicus* | GU 1641 | Notharctidae |  | 3.60 | 3.90 | 2.20 |  | 30° |  |  |  |  |  |  |  |  | 0.56 |  |  |  |
| *Cantius trigonodus* |  | Notharctidae |  |  |  |  |  | 30° |  |  |  | 0.46 | 0.81 | 1.38 | 1.30 | 0.82 | 0.58 | 1.29 | 1.23 | 0.50 |
| *Notharctus tenebrosus* |  | Notharctidae |  |  |  |  |  | 35° |  |  |  | 0.46 | 0.86 | 1.46 | 1.52 | 0.85 | 0.59 | 1.21 | 1.28 | 0.59 |
| *Notharctus pugnax* |  | Notharctidae |  |  |  |  |  | 29° |  |  |  | 0.43 | 0.82 | 1.39 | 1.58 | 0.93 | 0.58 | 1.23 | 1.28 | 0.57 |
| *Smilodectes gracilis* |  | Notharctidae |  |  |  |  |  | 30° |  |  |  | 0.43 | 0.72 | 1.36 | 1.49 | 0.78 | 0.53 | 1.30 | 1.30 | 0.59 |
| *Adapis parisiensis* |  | Adapidae |  |  |  |  |  | 38° |  |  |  | 0.33 | 0.50 | 0.80 | 1.17 | 0.73 | 0.62 | 1.27 | 1.16 | 0.67 |
| *Leptadapis magnus* |  | Adapidae |  |  |  |  |  | 37° |  |  |  | 0.37 | 0.60 | 0.91 | 1.24 | 0.80 | 0.66 | 1.32 | 1.28 | 0.65 |
| *Tetonius* sp. |  | Omomyidae |  |  |  |  |  | 30° |  |  |  | 0.55 | 1.06 | 1.44 | 1.16 | 0.99 | 0.79 | 1.40 | 0.90 | 0.57 |
| *Absarokius abbotti* |  | Omomyidae |  |  |  |  |  | 28° |  |  |  | 0.54 | 1.03 | 1.50 | 1.18 | 0.70 | 0.67 | 1.22 | 1.00 | 0.51 |
| *Shoshonius cooperi* |  | Omomyidae |  |  |  |  |  | 30° |  |  |  | 0.52 | 1.07 | 1.42 | 1.15 | 0.89 | 0.76 | 1.15 | 0.98 | 0.51 |
| ?*Omomys* |  | Omomyidae |  |  |  |  |  | 25° |  |  |  | 0.51 | 1.01 | 1.23 | 1.07 | 0.89 | 0.82 | 1.24 | 0.95 | 0.56 |
| ?*Hemiacodon gracilis* |  | Omomyidae |  |  |  |  |  | 25° |  |  |  | 0.51 | 0.99 | 1.26 | 1.10 | 0.86 | 0.75 | 1.26 | 0.94 | 0.57 |
| *Washakius insignis* |  | Omomyidae |  |  |  |  |  | 30° |  |  |  | 0.52 | 0.90 | 1.35 | 1.18 | 0.78 | 0.66 | 1.06 | 1.00 | 0.52 |
| *Arapahovius gazini* |  | Omomyidae |  |  |  |  |  | 26° |  |  |  | 0.58 | 0.98 | 1.35 | 1.26 | 0.88 | 0.78 | 1.12 | 0.87 | 0.47 |
| *Necrolemur zitteli* |  | Omomyidae |  |  |  |  |  | 30° |  |  |  | 0.52 | 0.72 | 1.24 | 1.13 | 0.70 | 0.62 | 1.03 | 0.89 | 0.54 |
| eosimiid | V11846 | Eosimiidae | 6.35 | 3.30 | 3.25 | 2.50 | 3.25 | 27° | 2.80 | 1.95 | 2.65 | 0.51 | 1.00 | 1.30 | 1.12 | 0.86 | 0.77 | 1.36 | 1.06 | 0.52 |
| eosimiid | V11849 | Eosimiidae | 5.95 | 2.87 | 3.03 | 2.30 | 3.05 | 30° | 2.20 | 1.78 | 2.38 | 0.51 | 1.01 | 1.33 | 0.96 | 0.73 | 0.76 | 1.34 | 1.03 | 0.48 |
| eosimiid | V11855 | Eosimiidae | 6.20 | 3.34 | 3.25 | 2.30 | 3.00 | 29° | 2.90 | 1.79 | 2.39 | 0.48 | 0.92 | 1.30 | 1.26 | 0.89 | 0.71 | 1.34 | 1.04 | 0.54 |
| eosimiid | V12303 | Eosimiidae | 5.70 | 2.95 | 3.00 | 2.25 | 2.75 | 30° | 2.65 | 1.35 | 2.15 | 0.48 | 0.92 | 1.22 | 1.18 | 0.88 | 0.75 | 1.59 | 0.96 | 0.52 |
| protoanthropoid | V12305 | ? | 5.08 | 2.85 | 2.44 | 1.75 | 2.50 | 35° | 2.05 | 1.41 | 1.95 | 0.49 | 1.02 | 1.43 | 1.17 | 0.84 | 0.72 | 1.38 | 1.11 | 0.56 |
| protoanthropoid | V12306 | ? | 4.95 | 2.65 | 2.59 | 2.04 | 2.45 | 33° | 2.10 | 1.44 | 1.95 | 0.49 | 0.95 | 1.20 | 1.03 | 0.81 | 0.79 | 1.35 | 0.96 | 0.54 |
| *Cebupithecia sarmientoi* |  | Platyrrhini |  |  |  |  |  | 35° |  |  |  | 0.54 | 1.05 | 1.36 | 1.05 | 0.81 | 0.77 | 1.10 | 1.15 | 0.59 |
| *Cebuella pygmaeus* |  | Platyrrhini |  |  |  |  |  | 42° |  |  |  | 0.63 | 1.14 | 1.25 | 0.87 | 0.79 | 0.91 | 1.21 | 0.86 | 0.61 |
| *Callithrix jacchus* |  | Platyrrhini |  |  |  |  |  | 40° |  |  |  | 0.66 | 1.25 | 1.29 | 0.89 | 0.86 | 0.97 | 1.24 | 0.88 | 0.65 |
| *Callithrix argentata* |  | Platyrrhini |  |  |  |  |  | 38° |  |  |  | 0.64 | 1.24 | 1.34 | 0.88 | 0.81 | 0.92 | 1.31 | 0.94 | 0.61 |
| *Saguinus leucopus* |  | Platyrrhini |  |  |  |  |  | 37° |  |  |  | 0.59 | 1.16 | 1.54 | 1.08 | 0.72 | 0.82 | 1.20 | 1.10 | 0.62 |
| *Saguinus midas* |  | Platyrrhini |  |  |  |  |  | 34° |  |  |  | 0.60 | 1.11 | 1.38 | 1.00 | 0.74 | 0.84 | 1.17 | 1.01 | 0.66 |
| *Saguinus oedipus* |  | Platyrrhini |  |  |  |  |  | 37° |  |  |  | 0.59 | 1.06 | 1.21 | 0.91 | 0.76 | 0.88 | 1.18 | 0.88 | 0.65 |
| *Callimico goeldi* |  | Platyrrhini |  |  |  |  |  | 38° |  |  |  | 0.60 | 1.11 | 1.25 | 0.85 | 0.76 | 0.89 | 1.25 | 0.92 | 0.69 |
| *Saimiri sciureus* |  | Platyrrhini |  |  |  |  |  | 30° |  |  |  | 0.54 | 0.99 | 1.33 | 1.08 | 0.76 | 0.85 | 1.30 | 0.98 | 0.58 |
| *Cebus apella* |  | Platyrrhini |  |  |  |  |  | 32° |  |  |  | 0.57 | 0.97 | 1.18 | 1.04 | 0.86 | 0.82 | 1.22 | 0.94 | 0.66 |
| *Cebus capucinus* |  | Platyrrhini |  |  |  |  |  | 33° |  |  |  | 0.56 | 1.01 | 1.46 | 1.34 | 0.90 | 0.67 | 1.27 | 1.23 | 0.70 |
| *Callicebus torquatus* |  | Platyrrhini |  |  |  |  |  | 34° |  |  |  | 0.52 | 0.91 | 1.44 | 1.18 | 0.82 | 0.77 | 1.31 | 1.18 | 0.56 |
| *Callicebus donaphilus* |  | Platyrrhini |  |  |  |  |  | 30° |  |  |  | 0.51 | 0.85 | 1.25 | 1.12 | 0.83 | 0.77 | 1.42 | 1.02 | 0.59 |
| *Aotus azarae* |  | Platyrrhini |  |  |  |  |  | 31° |  |  |  | 0.53 | 0.96 | 1.44 | 1.19 | 0.77 | 0.83 | 1.31 | 1.10 | 0.54 |

Dagosto et al., 1999). The shaft between the greater and lesser trochanters on the posterior aspect is slightly concave, and there is no evidence of an intertrochanteric line. A small third trochanter, for insertion of the superficial gluteal muscle, is present just opposite from the distal half of the lesser trochanter. The third trochanter in the Vastan femora is therefore more distal than in *Cantius*, *Notharctus*, *Adapis*, and omomyids, in which it is either directly opposite or proximal to the lesser trochanter (Gregory, 1920; Dagosto, 1983; Rose and Walker, 1985; Dagosto and Schmid, 1996; Bacon and Godinot, 1998; Anemone and Covert, 2000). The

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

two smaller trochanters have projection indices (Table 4) within the range of both notharctids and omomyids examined by Dagosto and Schmid (1996).

The femoral neck is oblique to the shaft at an angle of about 57° to the long axis of the shaft. The length of the neck is relatively long (Table 4; see Dagosto and Schmid, 1996). These features of the femoral neck are more comparable to those of adapoids than to omomyids. Adapoids and some extant lemurs tend to have a longer femoral neck that is obliquely oriented (smaller angle), whereas omomyids and active vertical clingers and leapers usually have shorter and nearly horizontal femoral necks.

The femoral shaft is elongate and slender, closely comparable to those in *Notharctus*, *Cantius*, and extant lemurs such as *Eulemur*. The shaft in both Vastan specimens is almost perfectly round in cross-section for most of its length, having a slightly greater anteroposterior diameter in GU 756. It is nearly smooth and featureless, except for the linea aspera (where adductor longus inserts), which descends posteromedially from below the lesser trochanter. The linea is more distinct, though still rather weak, in the smaller femur, GU 715.

The distal articulation of the femur is present only in GU 756, in which it is damaged. However, it is complete enough to suggest that it is not as deep anteroposteriorly as in *Cantius* or omomyids such as *Shoshonius* and *Microchoerus*, and the condyles do not project posteriorly to the extent that they do in *Cantius* and many lemurs. In addition, the patellar trochlea is less elevated than in *Shoshonius*, *Microchoerus*, or *Cantius*. The lateral trochlear ridge is similarly rounded but not as elevated, hence the patellar trochlea is less deeply grooved than in those forms. Otherwise, the trochlea is similar in proportions and shape to those of *Cantius* and *Microchoerus*. Compared to adapids (Dagosto, 1983; Bacon and Godinot, 1998), it is relatively narrower, higher (extends farther proximally), and deeper. Tardieu (1983) compared the index of trochlear width to height across primates, and found that the lowest values (i.e., relatively narrowest and longest grooves) occur in active arboreal primates, particularly vertical clingers and leapers, which typically have values of $\leq$70. GU 756 has a patellar trochlear width index of about 56 (lower than in most extant lemurs), compared to 61 in *Cantius* and 52 in *Microchoerus*; in *Adapis* the index is 81 (Table 4). Other details of the distal end of the femur, including muscle and ligament scars, compare closely with those in *Cantius*. In particular, the lateral epicondyle is well-developed, and distal and posterior to it is a well-marked fossa for origin of the popliteus muscle.

**Table 7**
Principal component loadings for (A) PCA of talar indices used by Gebo et al. (2001); (B) PCA of measurements scaled by talar length.

| Index | PC1 | PC2 | PC3 |
|---|---|---|---|
| A. | | | |
| A5/A1 | 0.934 | 0.192 | −0.141 |
| A5/A3 | 0.909 | 0.337 | 0.012 |
| A5/A4 | 0.190 | 0.867 | −0.294 |
| A7/A4 | 0.857 | 0.410 | −0.039 |
| A7/A3 | 0.101 | 0.520 | 0.615 |
| A4/A3 | 0.944 | −0.113 | 0.190 |
| A9/A8 | −0.137 | 0.099 | 0.827 |
| A9/A4 | −0.810 | 0.140 | 0.025 |
| A2/A1 | 0.214 | −0.552 | 0.162 |
| B. | | | |
| A2/A1 | 0.845 | −0.068 | −0.259 |
| A3/A1 | 0.337 | 0.734 | 0.322 |
| A4/A1 | 0.649 | −0.553 | 0.368 |
| A5/A1 | 0.272 | −0.841 | 0.366 |
| A7/A1 | 0.334 | 0.637 | 0.487 |
| A8/A1 | 0.838 | 0.105 | −0.059 |
| A9/A1 | 0.840 | 0.116 | −0.406 |

The two Vastan femora differ somewhat in size and in a few details of their anatomy, indicating that they represent two different species, most likely the two asiadapines whose teeth are described above. Although they show a mosaic of features found in adapoids and omomyids, more features seem to place them closer to notharctids than to other groups: head shape, morphology of the greater trochanter, angle and relative length of the neck, and anatomy of the distal end. The lesser trochanteric angle, however, is more like that of omomyids. The distal end appears to be slightly less specialized (at least in anteroposterior depth) than in omomyids or notharctids, but more so than in *Adapis*. In general, the features observed suggest that the Vastan femora belonged to arboreal primates that were active quadrupeds but not specialized leapers. Of the parameters analyzed by Dagosto and Schmid (1996), we found the indices of lesser trochanter projection and third trochanter projection (Table 4) to vary greatly among extant and fossil taxa (perhaps resulting from the difficulty of consistent measurement), and therefore to have little utility in separating either phylogenetic or locomotor groups.

### *Calcaneus*

A total of eleven primate calcanei have been identified (Fig. 19; Table 5). They sort into two distinct sizes, and thus represent at least two species. Slight differences among them, however, suggest that more than two taxa might be represented. At least seven of the Vastan specimens most closely resemble known adapoid calcanei, among living and fossil primates compared. As far as can be determined, their proportions are within or close to the observed range of variation of notharctines (*Cantius*, *Notharctus*, and *Smilodectes*) and extant lemurs (Gebo, 1988; Gebo et al., 1991), whereas they are proximally shorter and distally longer than calcanei of *Adapis* and *Leptadapis* (Table 5). These seven specimens are distally much shorter than calcanei of omomyids or eosimiids. Thus they almost certainly represent *Marcgodinotius indicus* and *Asiadapis cambayensis*. The other four calcanei, all approximately in the size range of those allocated to *Marcgodinotius*, differ somewhat in proportions, being relatively slightly wider, shorter proximally, and longer distally. These proportional differences suggest that they could belong to one or more other taxa. Other minor differences between them and the *Marcgodinotius* calcanei can probably be attributed to differential abrasion (e.g., water wear) and/or individual variation.

The three larger, incomplete calcanei (GU 707, 716, 760) resemble calcanei of *Cantius* except for being smaller. They are tentatively allocated to *Asiadapis cambayensis*. The entire posterior portion is missing from GU 707, whereas GU 716 and GU 760 preserve enough of the tuber calcanei to show a slight medial inflection. The calcaneal shaft of GU 760 is excavated posteromedially. The posterior calcaneal (ectal) facet in the Vastan calcanei appears to be relatively slightly shorter than in *Cantius*, but it is damaged in all three specimens, making comparison difficult. Its long axis is essentially parallel to the long axis of the bone. The sulcus calcanei, which separates the ectal and sustentacular facets, is wide and moderately deep. Together with the sulcus tali, it housed the strong interosseous talocalcaneal ligament. The flexor groove on the plantar surface of the sustentaculum is well-marked. The sustentacular (middle calcaneal) facet differs in shape in the three specimens, though the differences seem to be accentuated by abrasion in GU 716. In GU 716 and GU 760 the sustentacular facet is confluent with the anterior (distal) calcaneal facet, as is typical of notharctines (Gebo et al., 1991), forming an elongate, proximodistally concave articular surface that is constricted in the middle. The sustentacular facet itself is much longer than wide in GU 716 and is narrower than the anterior calcaneal facet, but in GU

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

760 it is only slightly longer than wide and about as wide as the anterior calcaneal facet. In contrast, the sustentacular facet in GU 707 is more nearly round and appears to have a distinct margin all around, isolating it from the anterior facet for the talus. Both conditions were observed in specimens referred to *Cantius trigonodus* from the Willwood Formation: USGS 6769 and 6783 closely approximate the condition in GU 760, whereas USGS 21829 resembles the condition in GU 707. The peroneal tubercle is damaged in GU 707 and GU 716, but its broken base shows that its distal limit was approximately even with the distal end of the ectal facet. The tubercle is complete in GU 760 and is slightly more proximal. The cuboid facet is ovoid (the ratio of maximum:minimum diameters ranging from 1.27 to 1.50) and faces almost exactly distally, its long axis oriented dorsomedially. The articular surface consists of a semilunar facet on the dorsal and lateral margins, surrounding a conical, central pit that is deepest at (GU 716, 760) or near (GU 707) the plantar margin. The pit is shallowest in GU 707 and deepest in GU 716. The articular surface extends to the anterior edge of the prominent anterior plantar tubercle, which is the site of attachment of the plantar calcaneocuboid ligaments. Whether the differences among these calcanei can be accommodated within a single species or signal taxonomic differences is uncertain. For comparison, however, we observed clear variation in these features among *Cantius* specimens, although variation of this kind has not been documented in early primates.

The eight smaller calcanei are similar in overall morphology, including details of the articular facets and position of the plantar and peroneal tubercles. The latter starts below the distal part of the ectal facet and extends beyond it distally, as in *Cantius*. The peroneal tubercle is thus more distal in the smaller calcanei than in the larger ones described above. In all eight, the proximal arm is about 50% deeper than wide, and its dorsal margin (between the ectal facet and the tuber calcanei) is sharp. The tuber is slightly expanded and medially inflected. All appear to have continuous sustentacular-anterior talar facets, comparable to GU 716. The calcaneal pit is moderately deep but variable, being shallowest in GU 709 and deepest in GU 751. In other anatomical aspects, except as specified below, these calcanei closely resemble the larger ones, hence it is reasonable to conclude that at least some of them represent the smaller adapoid *Marcgodinotius indicus.*

Closer examination reveals that the smaller calcanei vary in proportions, however. Four of them (GU 708, 709, 1642, and 1643) are similar enough to represent the same species, and we tentatively refer them to *Marcgodinotius indicus*. The other four (GU 710, 751, 761, and 1644) show proportional differences suggesting that they might lie outside the range of variation of *M. indicus* and could belong to one or more species not yet represented by teeth. The latter four differ slightly from the others in having a shorter proximal (posterior) region and longer distal region, though no two are exactly the same in this regard (Table 5). GU 710 further differs in having a shorter ectal facet and a slightly proximally projecting sustentaculum. The arc of the ectal facet thus has a smaller radius and a rounder profile in lateral view. The peroneal tubercles of GU 710 and GU 751 are slightly more proximal than in most of the other calcanei but still protrude beyond the distal end of the ectal facet, and a low ridge extends distally from the anterior end of the tubercle to halfway between the ectal and cuboid facets. The significance of this difference is unclear, as GU 1642 (referred to *M. indicus*) also has a relatively proximal peroneal tubercle. Relative calcaneal proportions in primates vary considerably with both function and taxonomic clade. As shown in Fig. 20, the proportions of several Vastan specimens, particularly GU 710, differ from typical notharctid proportions and approach those of *Eosimias* (Gebo et al., 2000, 2002). While it is possible that one or more of these calcanei belongs to an eosimiid, the nearly continuous distribution of Vastan specimens filling the gap between the notharctid cluster and the eosimiid cluster leaves open the alternative that most, if not all, of the smaller specimens could represent a single variable species, the notharctid *Marcgodinotius indicus*.

Several features of the Vastan calcanei have been considered to be general euprimate traits, including the medial curvature of the posterior calcaneus, an elongate proximodistally aligned ectal facet, distal elongation of the calcaneus, a prominent plantar tubercle, a relatively distal peroneal tubercle (compared to *Adapis* and *Leptadapis*, for example), a well-developed flexor groove under the sustentaculum tali, and a semilunar cuboid facet with a central pit (Gebo, 1988). While many of the traits of the Vastan calcanei characterize arboreal quadrupeds rather than specialized leapers, the unusual features of GU 710 (longer distal segment, shorter and more convex ectal facet) are more typical of leapers (Gebo, 1988), suggesting that this calcaneus might belong to an animal that was a more frequent leaper than the others.

### *Talus*

A total of five tali, a larger one (GU 747) and four smaller ones (GU 748, 749, 1640, 1641), belong to euprimates (Figs. 21, 22; Table 6). Several features, detailed below, indicate that they represent notharctids. They are appropriate in size to go with the two sizes of calcanei described above. The larger talus, about the size of that of *Hemiacodon*, is most likely attributable to *Asiadapis cambayensis* and the smaller ones, the size of the talus of *Absarokius*, to *Marcgodinotius indicus*. All five show typical euprimate traits including a long and narrow trochlea, high talar body, posterior trochlear shelf, shallow trochlear groove, long and medially angled neck, rounded talar head, confluent middle and anterior subtalar and navicular facets, and a well-defined tibial malleolar facet extending to the plantar margin of the body and onto the neck (e.g., Godinot and Dagosto, 1983; Gebo, 1988). The neck just anterior to the trochlea bears no evidence of the "squatting" facet characteristic of omomyids, *Tarsius*, adapines, and some lemurs (Decker and Szalay, 1974; Godinot and Dagosto, 1983).

In all five specimens the lateral side of the talar body, where the fibular malleolus articulates, is inclined rather than vertical and bears a prominent lateral projection. Posterior to the projection is a fossa of variable size for attachment of the posterior talofibular ligament. In GU 747 it is a moderate depression, whereas in the smaller tali it is deeper and better defined, but still not quite as deep as in notharctines. The posterolateral margin of the body in all five tali is a prominent projection formed by the lateral margin of the posterior talocalcaneal (ectal) facet, which is at the same time the lateral rim of the groove for flexor hallucis longus. This sulcus, on the posterior aspect of the talus, is oblique, its marginal rims raised and clearly directed lateral to the trochlear groove. The medial side of the body posteriorly is a relatively vertical, shallow fossa for attachment of the posterior tibiotalar ligament. Anterior to this is a smooth concavity whose anterior margin extends just onto the medial side of the neck; it articulates with the tibial malleolus. It is better defined and extends slightly farther distally than in notharctines, *Absarokius*, or *Shoshonius*.

The trochlear groove is very shallow in the smaller tali and slightly deeper in GU 747. The lateral rim is moderately sharp whereas the medial rim is more rounded, a subtle contrast, but one that is more apparent in the larger talus than in the smaller ones. The trochlear rims are of approximately equal height and are almost parallel but diverge slightly at the anterior (distal) end. As in *Cantius* (Rose and Walker, 1985), the trochlea is mediolaterally constricted posteriorly just above the attachments of the crurotalar ligaments. At this position on the lateral side of the trochlear

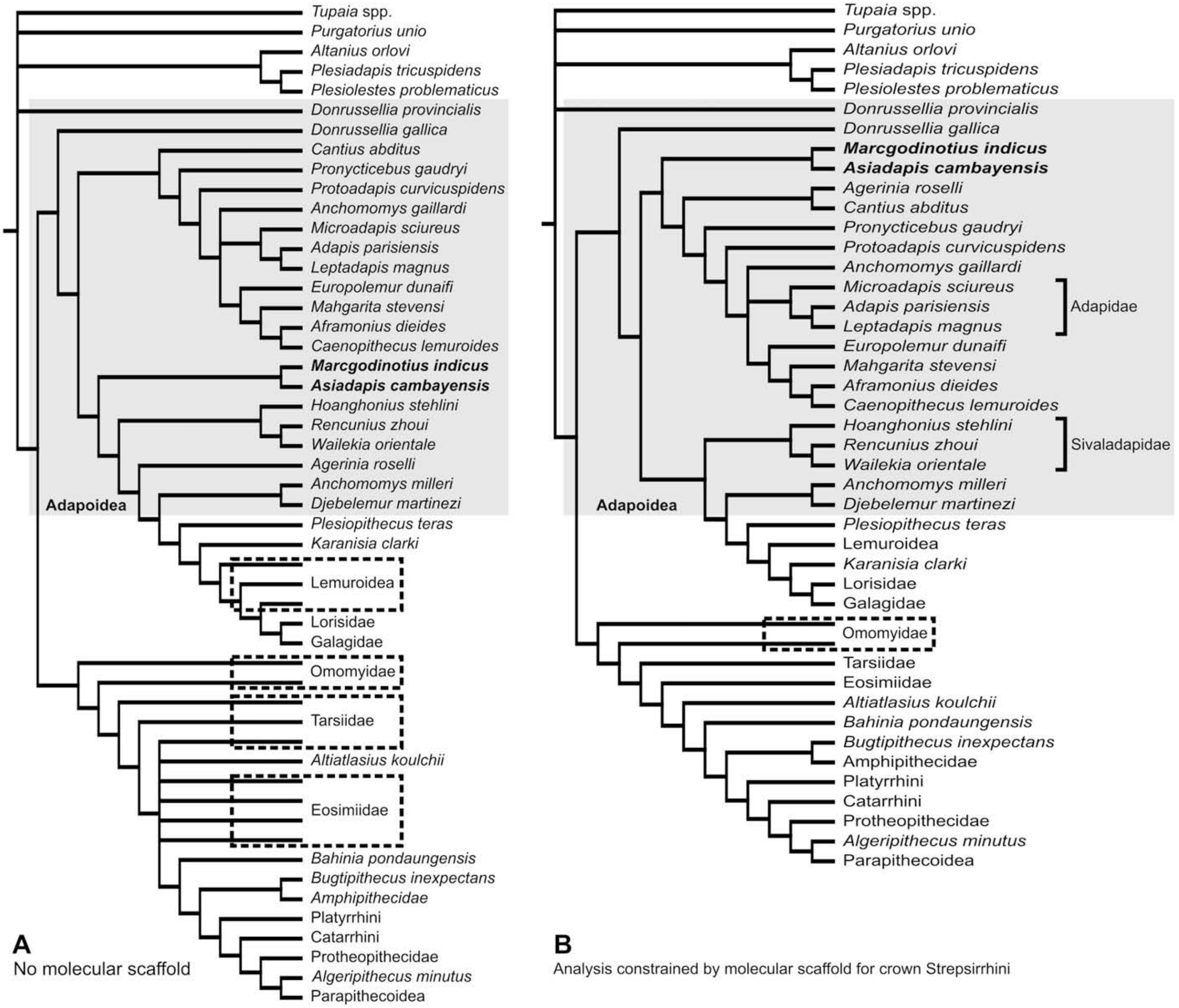

**Figure 23.** Cladograms showing relationships of the Vastan adapoids *Marcgodinotius indicus* and *Asiadapis cambayensis*. Analysis is based on the character-taxon matrix of Seiffert et al. (2005), which was rooted using *Tupaia*, mainly *T. glis* (Seiffert, pers. comm.). Many non-adapoid species in the analysis are here collapsed into family-level taxa for simplicity; uncondensed cladograms are shown in the online supplementary data. (A) Strict consensus of 253 equally most parsimonious trees obtained by analysis without the molecular scaffold; tree length: 2141.013; consistency index: 0.20; retention index: 0.59; homoplasy index: 0.80. (B) Strict consensus of 14 equally most parsimonious trees obtained by analysis with results constrained by the molecular scaffold; tree length: 2145.783; consistency index: 0.20; retention index: 0.59; homoplasy index: 0.80. Grey shading indicates the position of adapoid taxa.

surface is an irregularity (also seen in notharctines) that seems to be a remnant of the dorsal astragalar foramen.

The mean neck angle of the Vastan tali is 27.4° (ranging from 20°–32°; see Table 6), which is slightly less than in adapoids surveyed, and closer to omomyids and eosimiids. However, it should be noted that, aside from one specimen with an unusually low neck angle (GU 1640, angle = 20°), the mean angle is 29°, consistent with notharctids. In general, neck angle does not discriminate well among primates, although platyrrhines tend to have a more angled neck (Gebo et al., 2001). Neck length, however, can be more informative. Omomyids and eosimiids typically have longer talar necks than do notharctids, which in turn are longer than those of adapids. The Vastan tali group with notharctids in talar neck length. On the dorsolateral side of the neck of GU 747, just proximal to the navicular facet, is a tubercle (barely evident in the smaller tali) slightly smaller than that present at this position in notharctines. Gregory (1920) inferred that it served for attachment of a talo-ectocuneiform ligament.

The plantar aspect of the Vastan tali closely resembles that of notharctines, except that the posterior talocalcaneal (ectal) facet is shorter and wider in the Vastan tali. The facet is obliquely oriented and constricted near the middle (smaller tali) or toward the posterior end (GU 747). A wide talar sulcus separates the ectal and sustentacular facets. Near the posterior end of the sulcus is a plantar talar foramen (GU 749; not evident in the others). The sustentacular facet is ovoid and slightly convex transversely; proximodistally, it is flat in the smaller tali and very slightly convex in GU 747. As in other early euprimates, the sustentacular facet is continuous distally with the anterior talocalcaneal facet and the navicular facet, as well as with the surface supported by the plantar calcaneonavicular (spring) ligament. In GU 747, however, there is a nonarticular notch between the sustentacular facet and navicular facets on the lateral side, which is not present in the smaller tali. The talar head is ellipsoid and slightly flatter dorsoventrally than in notharctines. The long axis is oblique rather than horizontal and is oriented slightly dorsomedially (as in strepsirrhines, and not dorsolaterally as in omomyids; Godinot and Dagosto[1983]).

The long, narrow, and shallow trochlea, and the well-developed posterior trochlear shelf, are particularly characteristic of notharctid adapoids. Omomyids (except *Necrolemur*) generally differ in having a shorter, wider, and more deeply grooved trochlea and a smaller posterior trochlear shelf (Szalay, 1976; Gebo, 1988; Covert and Hamrick, 1993; Dagosto et al., 1999; Anemone and Covert, 2000). Most omomyids also have a longer talar neck and a well-developed "squatting facet" anterior to the trochlea. The sloping fibular facet and offset flexor sulcus present in the Vastan tali also indicate adapoid (and probably strepsirrhine) affinities and contrast with omomyids, which tend to have a more vertical talofibular facet and a flexor sulcus aligned with the trochlear groove (Gebo, 1988; Gebo et al., 2000; Seiffert and Simons, 2001). The talus of *Necrolemur* (Godinot and Dagosto, 1983) is similar to the Vastan tali and unusual among omomyids in having a distinct posterior trochlear shelf and a relatively long and narrow trochlea, but in *Necrolemur* the trochlea is more deeply grooved, the talar neck is shorter, and there is a distinct squatting facet. Tali of primitive anthropoids (eosimiids, *Proteopithecus*, *Catopithecus*) resemble those of omomyids and differ from the Vastan tali in having relatively short and wide trochleae, a reduced posterior trochlear shelf, a vertical talofibular facet, and a flexor sulcus aligned with the trochlea.

Although a relatively flat talar head is typically associated with climbing in primates, many other traits of the Vastan tali have been considered to be leaping specializations. They include the long and high talar trochlea, nearly parallel trochlear rims, extended posterior trochlear shelf, and moderately long talar neck, all of which are traits comparable to notharctines (Godinot and Dagosto, 1983; Gebo, 1988).

Gebo et al. (2001) calculated numerous indices based on talar dimensions that appear to be informative about functional and/or phylogenetic relationships. As an exploratory tool for interpreting the Vastan tali, principal components analysis was performed using values of these indices in a variety of fossil and extant taxa, as provided by Gebo et al. (see Table 6). The analysis yielded three principal components with eigenvalues >1, which account for 78% of the variance (PC 1 = 45%, PC 2 = 19%, PC 3 = 14%). In this analysis, the Vastan tali group only with adapoids on PC 1 (at the negative end), and either closer to notharctids (GU 747, 749, 1640) or between notharctids and adapids (GU 748) on PC 2 (Fig. 21A). A plot of PC 1 vs. PC 3 did not reveal any other associations. Position along PC 1 was most strongly influenced by relatively shorter neck length and narrower trochleae in adapoids and the Vastan tali (Table 7A), compared to omomyids, platyrrhines, and basal anthropoids (eosimiids and protoanthropoids).

Several measurements appear in more than one of the indices in Gebo et al. (2001), which could bias the analysis. In order to avoid undue influence of those dimensions, a second PCA was performed on new indices representing the individual measurements scaled by talar length. In this analysis the first three principal components account for 81% of the variance (PC 1 = 41%, PC 2 = 28%, PC 3 = 12%), but only the first two principal components have eigenvalues above 1. The result (Fig. 21B) is similar to the first analysis, except that here the Vastan tali plot closest to notharctids (and distant from adapids) or equally close to notharctids and omomyids (GU 749). Talar body width, and head height and width, have the highest loadings on PC 1, with trochlear width also contributing (Table 7B). Neck length, trochlear length, and talar height have the highest loadings on PC 2. The position of the Vastan tali among notharctids reflects a narrower body and trochlea and a smaller talar head (PC 1), together with a relatively shorter neck, longer trochlea, and higher talar body (PC 2).

## *Discussion of postcrania*

Although only a small number of primate postcrania have been discovered at Vastan Mine, some are exceptionally well-preserved, and they impart considerable information to supplement the dentitions. All appear to belong to small, active, arboreal quadrupeds that were capable of leaping, but in which leaping was not the predominant locomotor behavior. The small calcaneus GU 710, however, represents an animal that appears to have been somewhat better adapted for leaping.

At least two taxa are represented, most likely the two asiadapines (*Marcgodinotius indicus* and *Asiadapis cambayensis*) whose teeth have been described above. It is probable that the femora, tali, and most of the calcanei represent these two species. Their anatomical features are similar to those of notharctids and are inconsistent with reference to Omomyidae, the most probable group they might otherwise represent. The humeri and radii are less confidently allocated to asiadapines. Their anatomy is certainly consistent with reference to Notharctidae, but most features seem to be primitive euprimate traits that do not definitively distinguish them from Omomyidae.

The three larger calcanei, though quite similar in size and in several details, show certain differences that imply either considerable intraspecific variation or more than one species. Unfortunately, without larger samples and a better understanding of variation in calcaneal anatomy, it is uncertain which interpretation applies to these calcanei. In view of the available dental evidence, they are here conservatively attributed to *Asiadapis cambayensis*. At least four of the smaller calcanei can be confidently referred to *Marcgodinotius indicus*, but some of the smaller calcanei are distally longer and proximally shorter than the others, resembling eosimiid calcanei in this regard (Rose et al., 2007b). These calcanei could constitute evidence supporting the eosimiid affinities of the recently described *Anthrasimias gujaratensis*. This would extend the range of Eosimiidae back to the early Eocene, as the oldest currently recognized representatives are from the middle Eocene of China (Beard et al., 1994; Beard and Wang, 2004). Eosimiids are now also known from the late middle Eocene of Myanmar (Jaeger et al., 1999; Gebo et al., 2002; Takai et al., 2005) and the Oligocene of Pakistan (Marivaux et al., 2005), making a range extension into the early Eocene of India more plausible. However, as discussed above, there are reasons to question the allocation of *Anthrasimias* to Eosimiidae. Moreover, the variation in the sample of calcanei is more or less continuous between the extremes, and does not support dividing the sample into two distinct morphs. Except for the calcanei, there is no other postcranial evidence of eosimiids from Vastan. Therefore, while we cannot exclude the possibility that one or more calcanei represent an eosimiid, the presence of Eosimiidae at Vastan is ambiguous based on present evidence.

The three known Vastan euprimate tali represent two sizes. Comparison of talar indices and principal components analysis of these indices support assignment of all three tali to Notharctidae and the interpretation of the animals they represent as active arboreal quadrupeds rather than slower climbers or specialized leapers. An additional result of interest is that the PCA corroborates the close similarity of eosimiid and protoanthropoid tali from China to those of Omomyidae, as observed by Gebo et al. (2000). However, no tali similar to those of either eosimiids or omomyids have been recovered yet at Vastan Mine.

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

## Body size

Estimates of body mass of the Vastan primates were made using first lower molar area (based on regressions in Conroy [1987]) and calcaneal dimensions (estimates provided by M. Dagosto [pers. comm.] based on equations of Dagosto and Terranova [1992]). Based on $M_1$ area, body mass of *Marcgodinotius indicus* was approximately 109 g (prosimian regression) or 118 g (all primate regression). Estimates drawn from the smaller adapoid calcanei, which probably represent *Marcgodinotius*, are closely comparable, ranging from 104–115 g based on length of the ectal facet (95% confidence intervals = 77–137 and 88–152, respectively) to 126 g based on calcaneal width at the sustentaculum (95% confidence interval = 99–162 g). Thus, *Marcgodinotius* was only a little larger than the biggest individuals of *Microcebus murinus* and *Galago demidoff* and smaller than *G. senegalensis* (Silva and Downing, 1995; Nowak, 1999).

The area of the $M_1$ of *Asiadapis cambayensis* yields body mass estimates of 220–297 g (based on the prosimian regression; lower estimate from the holotype, larger estimate from GU 745) and 258–359 g (all primate regression). These weights are comparable to those of *Mirza coquereli*, *Euoticus elegantulus*, and *E. pallidus* (Silva and Downing, 1995; Nowak, 1999). Estimates based on the larger adapoid calcanei, which are probably attributable to *Asiadapis*, are comparable or somewhat higher: length of the ectal facet yields an estimate of 300–325 g (95% confidence intervals = 249–362 and 271–390, respectively); body mass calculated from calcaneal width is 370–439 g (95% confidence intervals = 314–435 and 376–513, respectively). These estimates roughly span the size range of *Cheirogaleus* species.

The smallest calcaneus (GU 710), possibly representing an eosimiid, yields estimates of 80 g (95% confidence interval = 58–110) based on length of the ectal facet and 126 g (95% confidence interval = 99–162) based on calcaneal width. This is comparable to, or slightly smaller than, *Marcgodinotius*.

## Phylogenetic analysis

In an attempt to place the Vastan asiadapines relative to other primates, we performed phylogenetic analyses using the recent character-taxon matrix of Seiffert et al. (2005), a comprehensive matrix that includes many of the probable adapoid relatives of *Marcgodinotius* and *Asiadapis. Vastanomys* was deemed too poorly known to be included in the analyses. The results should be regarded with caution because of the fragmentary evidence available for some taxa and because of the somewhat unstable topology, as shown by differences between the analysis results with and without a molecular scaffold. Nevertheless, several interesting relationships are indicated.

The first analysis, without a molecular scaffold, yielded 253 equally most parsimonious trees, and the strict consensus tree (Fig. 23A) has a length of 2141.013, a consistency index of 0.20, a retention index of 0.59, and a homoplasy index of 0.80. Most significantly, neither Adapoidea nor Notharctidae are monophyletic in this analysis (Fig. 23A). *Donrussellia* is divided, one species (*D. provincialis*) a plesiomorphic unresolved branch at the base of the tree, the other (*D. gallica*) the plesiomorphic sister taxon of all strepsirrhines in the analysis. *D. provincialis* and *Altanius orlovi* are the only taxa generally accepted as euprimates that fall outside the strepsirrhine-haplorhine dichotomy (although it was previously suggested that *Altanius* might be a plesiadapiform [Rose and Krause, 1984], which is consistent with this tree). Strepsirrhines appear as two clades, a notharctid-adapid clade and a clade of crown strepsirrhines together with several extinct taxa. Asiadapines form the sister group of the latter clade, with sivaladapids and *Agerinia* (usually considered a cercamoniine) nested successively closer to crown strepsirrhines. Some minor but potentially significant dental similarities between asiadapines and sivaladapids were mentioned above. Notably, within the crown strepsirrhine clade, Lemuroidea is paraphyletic in this analysis.

The second analysis, constrained by a molecular scaffold, yielded 14 equally most parsimonious trees, and a slightly longer strict consensus tree (length = 2145.783; see Fig. 23B) with similar consistency, retention, and homoplasy indices as in the first analysis. Although molecular data are unavailable for the fossil taxa, these constraints change the relationships within Lemuroidea and Lorisidae (recovering a monophyletic Lemuroidea), which has the effect of moving asiadapines from the base of the crown strepsirrhine clade to the base of the notharctid-adapid clade. This result is more congruent with the overall signal of the anatomical evidence presented here. Asiadapines thus appear as the sister taxon of a paraphyletic Notharctidae in which adapines are nested, an interpretation essentially consistent with the current consensus on adapoid relationships.

## Paleobiogeographic implications

Much has been written about the timing of the India-Asia collision and its significance for the distribution of ancient and modern biotas. As the only early Eocene—and the oldest Cenozoic—terrestrial assemblage from India, the Vastan local fauna is particularly relevant to this issue. In addition, the Vastan primates provide data pertinent to the geographic origin of primates.

India was part of Gondwana during most of the Mesozoic, most models indicating close contact with Madagascar well into the Late Cretaceous, with rifting between India and Madagascar occurring at about 90 Ma (e.g., Briggs, 2003). After separating from Madagascar, probably by the Campanian, India drifted rapidly northward until it collided with southern Asia in the Paleogene. It is now well-established that the rate at which the Indian plate approached Asia diminished abruptly near the Paleocene-Eocene boundary, which has usually been interpreted to indicate that collision had begun (e.g., Patriat and Achache, 1984; Gaetani and Garzanti, 1991; Beck et al., 1995) or even that suturing was complete (e.g., Klootwijk et al., 1992). Most estimates of the start of the collision range from the K-T boundary (Klootwijk et al., 1992) to well into the early Eocene. For example, Beck et al. (1995) placed the onset of collision in the Paleocene, Rowley (1996) dated it as late Ypresian (ca. 52 Ma), and Patriat and Achache (1984) fixed the collision at 50 Ma, coincident with magnetic anomaly 22. Clyde et al. (2003) pointed out that although the rate of northward movement slowed at about 55 Ma, a more significant decrease occurred ca. 50 Ma, which helps to explain the discrepancies. Thus, the collision has been variously considered to be older than, contemporary with, or slightly younger than the Vastan fauna. In any case, there is general agreement that the Indian plate rotated counterclockwise as it drifted northward, hence collision and suturing took place earlier to the northwest than to the east (e.g., Klootwijk et al., 1992; Rowley, 1996).

It is becoming apparent that India was probably less isolated during this drifting phase than is often supposed (Briggs, 2003; Ali and Aitchison, 2008), which has complicated attempts to understand its paleobiogeographic role. Paleontological evidence has been somewhat confusing and inconclusive. Although the presence of a gondwanatherian mammal and Gondwanan dinosaurs in Upper Cretaceous strata of India reflect a Late Cretaceous connection with Madagascar (e.g., Sahni, 2006), fossil frogs and eutherian mammals suggest ties between India and Laurasia at roughly the same time (e.g., Sahni and Bajpai, 1991; Rage and Jaeger, 1995).

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

Geophysical evidence certainly does not support a continuous land connection with Asia at that time, leaving the faunal similarities puzzling. In fact, Ali and Aitchison (2008: 158) recently concluded that India "reached its maximum level of isolation" at about 68 Ma (when it was still below the equator). Much of the land mass was submerged and surrounded by open ocean, but according to their model a discontinuous land connection between India and Madagascar persisted to the end of the Cretaceous. India was still widely separated from Asia in the Late Cretaceous, and any dispersal between the two land masses could only have occurred via an island arc believed to have existed in the Neotethys at that time, and across adverse oceanic currents (Aitchison et al., 2007; Ali and Aitchison, 2008). By the middle Eocene, however, India's mammalian faunas show clear Asian affinities, and dispersal is presumed to have taken place from Asia to India (e.g., Sahni et al., 1981; Kumar, 2001).

Until recently, data from the intervening and critical Paleocene and early Eocene epochs have been missing. The Vastan fauna, however, extends unequivocal evidence of faunal interchange with Laurasia back to the early Eocene. Besides the euprimates, occurrence at Vastan of the widespread Laurasian artiodactyl *Diacodexis*, the ailuravine paramyid rodent *Meldimys* (otherwise known only from western Europe), and a primitive lagomorph (whose older and more primitive sister group Mimotonidae is endemic to Asia), are clear indications of Eurasian faunal interchange that most likely required some kind of subaerial connection, even if discontinuous. The direction of this interchange is less certain, however, though most groups seem to have dispersed from Eurasia into India. Fossil chiropterans, though volant, also support this biogeographic connection. Among the families so far identified from Vastan, Hassianycterididae are otherwise known only from Europe and Palaeochiropterygidae only from Europe and China, whereas Icaronycteridae, like the artiodactyl *Diacodexis*, have a wider Holarctic distribution.

Perhaps the most intriguing paleobiogeographic hypothesis involving fossil primates and India is Krause and Maas's (1990) proposal that adapoids or omomyids (or both), together with other mammalian clades such as Perissodactyla and Artiodactyla, might have originated on India during its northward drift toward Asia. Upon collision, they would have dispersed into Asia and quickly spread throughout the northern continents. This notion was put forth as an explanation for the sudden appearance of these modern orders across the Holarctic region at the beginning of the Eocene. Nearly 20 years earlier, during the emergence of plate tectonics, McKenna (1973) had postulated India as a "Noah's Ark" that would have carried its evolving biota to Asia. The Vastan fauna provides the first early Eocene data, possibly predating the collision, pertinent to these hypotheses.

It is tempting to speculate that a primitive African euprimate stock dispersed to Madagascar and then to India, giving rise to adapoids (and possibly even omomyids and anthropoids) while India drifted toward Asia. The primitive anatomy of asiadapines, and the antiquity of the eosimiid (if its identity can be corroborated), are plausibly consistent with this scenario. This alone, however, is hardly compelling evidence. Several recent developments allow a reevaluation of this hypothesis.

(1) New tectonic models indicate that India retained a discontinuous land connection with Madagascar (via island chains) as late as the Paleocene/Eocene boundary (Aitchison et al., 2007; Ali and Aitchison, 2008). The distances between islands would have been considerably less than that presumed to have been crossed by taxa that reached Madagascar during the Cenozoic. Nevertheless, tectonic evidence indicates that Madagascar has been widely separated from Africa since the mid-Early Cretaceous, well before even the oldest molecular dates for the origin of primates. Thus, any scenario involving Madagascar would have required multiple water crossings to reach India, reducing its probability.

(2) Some paleogeographic models situate India relatively close to, or even in contact with, northeast Africa during its drift northward (e.g., Besse and Courtillot, 1988; Briggs, 2003; Ali and Aitchison, 2008). According to these models, a possible land connection (probably discontinuous) existed between India and northeast Africa or Arabia as late as the Cretaceous-Tertiary boundary. Dispersal of a stem euprimate from Africa to India near the K-T boundary via this route seems more palatable than a much earlier dispersal to Madagascar and thence to India. The presence of the oldest known probable euprimate, *Altiatlasius*, in the late Paleocene of North Africa makes such a scenario more plausible.

(3) While the fossil record continues to indicate that a Paleocene origin of euprimates is most probable, molecular phylogenies and some other models that place the origin of primates in the Late Cretaceous at least 80 Ma (e.g., Tavaré et al., 2002; Springer et al., 2003; Murphy et al., 2007) are consistent with the evolution of euprimates from a stem group that reached India in the Late Cretaceous or early Paleocene.

(4) Several lines of evidence (e.g., molecular, paleogeographic) already support an "Out of India" hypothesis of origin for various plants, fishes, frogs (at least 3 lineages of Ranidae, including *Rana* itself), and perhaps other groups (e.g., Bossuyt and Milinkovitch, 2001; Conti et al., 2002; Karanth, 2006)—which postulates that these groups entered India across land or island arcs from Madagascar or Africa, evolved there, and dispersed into Laurasia when contact was possible.

(5) A new tectonic model (Aitchison et al., 2007; Ali and Aitchison, 2008) postulates that India did not collide with Asia until the end of the Eocene (~35 Ma), but that peripheral contact between northeastern Greater India and southeast Asia (Sumatra to Myanmar) prior to the collision was possible at least intermittently from 55–35 Ma. According to the model, contact would have involved the Dazhuqu island arc or perhaps a transient land bridge, either of which would have provided a potential route for exchange of faunal elements between Laurasia and India during the Eocene. Contrary to this model, however, the presence of nonmarine sediments from the middle Eocene onward in the Himalayas suggests that some degree of suturing had already occurred by that time along the northwestern margin of the Indian plate. In any case, faunal exchange with Asia was established by the middle Eocene.

For Krause and Maas's (1990) hypothesis to be valid for primates (i.e., euprimates or at least adapoids originated in India), asiadapines, and possibly eosimiids, would have to be remnants of an older primate radiation that was present on India throughout the Paleocene. This radiation should include more primitive euprimates than have been found anywhere else. No Paleocene fossils have been found in India to test this possibility, but the Vastan primates shed some light on the matter. Older and more primitive omomyids than *Vastanomys* are known from across Laurasia (Smith et al., 2006), so the origin of Omomyidae on India can be rejected on present evidence. If omomyids did not originate in India, it suggests that euprimates did not originate in India, and it weakens the argument that adapoids originated there. Asiadapines, though very primitive, are not demonstrably more primitive than the older *Donrussellia*. Thus, it seems that the prevailing evidence does not support an Indian origin of any of these groups. Of course, the evolutionary steps leading to the most primitive adapoids and omomyids remain largely unknown, and discovery in India of older or more primitive euprimates than are now known could have

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

a dramatic impact, requiring a reconsideration of Krause and Maas's (1990) hypothesis.

Even if euprimates or adapoids did not originate on India, limited evidence suggests that asiadapines and possibly an eosimiid-like lineage evolved in India from basal euprimates that entered India perhaps around the Paleocene-Eocene boundary. Their possible descendants (sivaladapids, eosimiids) could have dispersed to southeast Asia via the newly proposed land connection mentioned above.

How, then, do the Vastan primates relate to the biogeographic origin of euprimates? Several lines of evidence have been marshaled to support an Asian origin of the clade (Beard, 1998; Silcox, 2008), but other factors argue for an African, European, or North American origin. In the decade since Beard's (1998) "East of Eden" hypothesis, Asia has produced *Teilhardina asiatica*, the oldest and one of the most primitive omomyids (Ni et al., 2004; Smith et al., 2006), providing further support for an Asian origin. Asiadapines are the most primitive Asian adapoids, but they are not the oldest adapoids and probably not the most primitive. European *Donrussellia* is most plesiomorphic, whereas North American *Cantius* is the oldest. Unless it can be corroborated that *Marcgodinotius* diverged from the euprimate stem before *Donrussellia*, as suggested by a few dental traits, an Asian (Indian) origin of adapoids seems unlikely.

## Conclusions

The Cambay Formation at Vastan Mine yields the oldest fossil primates known from India. The age of the fossils is early Eocene (early Cuisian), at least 53 Ma, based on foraminiferal evidence from above the vertebrate-bearing layer, and possibly 54–55 Ma based on dinoflagellates. The only primate-bearing deposit of comparable age on the Indian subcontinent is the upper Ghazij Formation of Pakistan, which has produced possibly related adapoids referable to *Panobius*. Sedimentologic and tectonic evidence indicates that the Vastan primates inhabited a nearshore, tropical equatorial forest.

At least five primate taxa have been identified at Vastan Mine based on dental evidence, and another could be indicated by calcanei and isolated teeth. Adapoids, represented by the related taxa *Marcgodinotius indicus* and *Asiadapis cambayensis*, and a third asiadapine known from a single tooth, are the most common primates in the Vastan local fauna. They compare most closely in dental features with primitive Notharctidae, especially European Cercamoniinae such as *Donrussellia* and *Protoadapis*, but they are distinct enough in various traits to warrant their recognition as a new subfamily of notharctids, here designated Asiadapinae. Various postcranial elements are tentatively allocated to Asiadapinae, based on their combination of notharctid features; but, like the dental resemblances, these features are largely primitive euprimate traits that shed little additional light on the precise relationships of asiadapines, except to exclude them from clear relationship to omomyids or tarsiids. The postcrania, if correctly assigned, indicate that asiadapines were small bushbaby-sized primates adapted for active arboreal quadrupedal locomotion, including occasional leaping, comparable to notharctids.

Preliminary phylogenetic analyses—preliminary because of the limited nature of the evidence for asiadapines—indicate unambiguously that asiadapines are primitive strepsirrhines. However, their precise relationship to other strepsirrhines varies in the analyses according to whether or not extant strepsirrhines are constrained by a molecular scaffold. When no scaffold is imposed, Asiadapinae, rather than grouping with most other adapoids, are placed at the base of a clade containing crown strepsirrhines, sivaladapids, and *Agerinia* (usually considered either a cercamoniine or an adapid). This outcome is revealing in that certain dental resemblances suggest that asiadapines could be related or ancestral to sivaladapids. Should the position of asiadapines at the base of this clade be corroborated, they would provide an important link between European notharctids and Sivaladapidae. A relationship to crown strepsirrhines, however, seems more tenuous and will require additional evidence to be convincing. When the data are reanalyzed with a molecular scaffold, asiadapines fall where expected based on the preponderance of anatomical evidence: at the base of the (paraphyletic) Notharctidae, between *Donrussellia* and *Cantius*. That Notharctidae and even Adapoidea as generally conceived appear as paraphyletic groups is no surprise, as they have long been considered primitive strepsirrhines plausibly related to extant lemurs and lorises. Asiadapines thus appear to be among the most primitive known adapoids and are the most primitive Adapoidea so far reported from Asia.

In addition to asiadapines, the Vastan fauna includes the omomyid *Vastanomys*, with two species, one of which is new and named above. Both species remain very poorly known. The basal inflation of $M_2$ and its centrally situated paraconid, together with the absence of $P_1$, indicate that *Vastanomys* is more derived than the basal omomyid *Teilhardina*. However, the minimal evidence available permits little further speculation about its precise phylogenetic or paleogeographical relationships.

A possible sixth primate taxon is represented by one or two calcanei whose proportions (relatively longer anterior arm and shorter posterior arm) resemble those of eosimiids, together with four isolated teeth recently described as a new eosimiid, *Anthrasimias gujaratensis*. They are potentially significant since they would constitute the oldest record of Anthropoidea. While the evidence is not quite strong enough to deny the presence of eosimiids at Vastan, for reasons detailed above, we regard the eosimiid affinities of these specimens to be equivocal. Indeed, if these specimens do represent eosimiids, then they appear to intergrade morphologically with the adapoids in the fauna, which could have interesting implications for the relationships of Eosimiidae or the origin of Anthropoidea.

The presence of the asiadapine clade in central western India indicates that primitive cercamoniine-like notharctids, though currently known only from western Europe, had a much broader distribution. Together, the anatomical and paleogeographic evidence suggests that ancestors of the Vastan primates most likely dispersed from southern Asia into India sometime near the Paleocene-Eocene boundary.

## Acknowledgments

We thank Marc Godinot, Philip Gingerich, Gregg Gunnell, Chris Beard, and Richard Kay for sharing their knowledge of early euprimates and opinions about the Vastan primates, and for providing comparative casts that were essential in determining the relationships of the specimens described here. Chris Beard pointed out similarities between *Marcgodinotius* and sivaladapids. We are grateful to Marian Dagosto and Dan Gebo for offering critical advice concerning interpretation of postcrania. In addition, Dr. Dagosto provided the body mass estimates of Vastan primates based on calcaneal measurements, using her expanded database. We thank Gregg Gunnell for allowing us to cite the forthcoming manuscript on Eocene primates from Pakistan. Mark Teaford provided helpful advice on multiple issues. Special appreciation is extended to Valerie Burke DeLeon for running and helping to interpret the principal components analyses, preparing Figs. 20 and 21, and providing advice on preparation of other figures. L. Gordon and R.W. Thorington, Jr. (National Museum of Natural History, Smithsonian Institution), kindly provided access to recent primates for comparison. We are grateful to Annelise Folie, François Gould, Gina McKusick, and Hukam Singh for assisting in the field work, and to personnel of the Gujarat Industrial Power Corporation Ltd. for facilitating our excavations at Vastan Mine. We also thank Julien Cillis (Brussels) for assisting with the SEM images and preparation of figures, and Jonathan Bloch and two anonymous reviewers for constructive comments on the manuscript. Field work and research were supported by the National Geographic Society (grants 6868-00, 7938-05, and 8356-07 to K.D.R. and A.S.); Department of Science and Technology, Government of India (ESS/23/Ves092/2000 to R.S.R.); the Council for Scientific and Industrial Research of India (ES grant 560, 21/EMR-II to A.S.); the Director, Wadia Institute of Himalayan Geology, Dehradun, India (to K.K.); and the Belgian Federal Science Policy Office (MO/36/011 and MO/36/020 to T.S.).

## Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi: 10.1016/j.jhevol.2009.02.008

## Note added in proof

After this paper was accepted, the report on Eocene primates of Pakistan by Gunnell et al. was published (Contrib. Mus. Paleontol. Univ. Michigan 32 [1], 1–14, 2008). These authors described new material of the notharctid adapiform *Panobius*, including two new species, reinforcing the differences observed here between that genus and *Marcgodinotius*. It should be noted that the holotype of *P. afridi*, originally identified as $M_1$ and considered as such herein, is reinterpreted to be $M_2$ by Gunnell et al. If this is correct, the trigonid structure of $M_2$ contrasts with that of asiadapines even more markedly than first thought.

## References

Aitchison, J.C., Ali, J.R., Davis, A.M., 2007. When and where did India and Asia collide? J. Geophys. Res., Solid Earth 112, B05423, doi:10.1029/2006JB004706.

Alexander, J.P., 1994. Sexual dimorphism in notharctid primates. Folia. Primatol. 63, 59–62.

Ali, J.R., Aitchison, J.C., 2008. Gondwana to Asia: plate tectonics, paleogeography and the biological connectivity of the Indian sub-continent from the Middle Jurassic through the latest Eocene (166–35 Ma). Earth-Sci. Rev. 88 (3–4), 145–166, doi:10.1016/j.earscirev.2008.01.007.

Anemone, R.L., Covert, H.H., 2000. New skeletal remains of *Omomys* (Primates, Omomyidae): functional morphology of the hindlimb and locomotor behavior of a middle Eocene primate. J. Hum. Evol. 38, 607–633.

Bacon, A.-M., Godinot, M., 1998. Analyse morphofonctionnelle des fémurs et des tibias des "*Adapis*" du Quercy: mise en évidence de cinq types morphologiques. Folia. Primatol. 69, 1–21.

Bajpai, S., Kapur, V.V., Das, D.P., Tiwari, B.N., 2007. New Early Eocene primate (Mammalia) from Vastan Lignite Mine, District Surat (Gujarat), western India. J. Palaeontol. Soc. India 52 (2), 231–234.

Bajpai, S., Kapur, V.V., Das, D.P., Tiwari, B.N., Saravanan, N., Sharma, R., 2005a. Early Eocene land mammals from Vastan Lignite Mine, District Surat (Gujarat), western India. J. Palaeontol. Soc. India 50 (1), 101–113.

Bajpai, S., Kapur, V.V., Thewissen, J.G.M., Das, D.P., Tiwari, B.N., 2006. New Early Eocene cambaythere (Perissodactyla, Mammalia) from the Vastan Lignite Mine (Gujurat, India) and an evaluation of cambaythere relationships. J. Palaeontol. Soc. India 51 (1), 101–110.

Bajpai, S., Kapur, V.V., Thewissen, J.G.M., Das, D.P., Tiwari, B.N., Sharma, R., Saravanan, N., 2005b. Early Eocene primates from Vastan Lignite Mine, Gujarat, western India. J. Palaeontol. Soc. India 50 (2), 43–54.

Bajpai, S., Kay, R.F., Williams, B.A., Das, D.P., Kapur, V.V., Tiwari, B.N., 2008. The oldest Asian record of Anthropoidea. Proc. Natl. Acad. Sci. USA 105, 11093–11098.

Beard, K.C., 1998. East of Eden: Asia as an important center of taxonomic origination in mammalian evolution. In: Beard, K.C., Dawson, M.R. (Eds.), Dawn of the Age of Mammals in Asia. Bull. Carnegie Mus. Nat. Hist, vol. 34, pp. 5–39.

Beard, K.C., Wang, B., 1991. Phylogenetic and biogeographic significance of the Tarsiiform primate *Asiomomys changbaicus* from the Eocene of Jilin Province, People's Republic of China. Am. J. Phys. Anthropol. 85, 159–166.

Beard, K.C., Wang, J., 2004. The eosimiid primates (Anthropoidea) of the Heti Formation, Yuanqu Basin, Shanxi and Henan Provinces, People's Republic of China. J. Hum. Evol. 46, 401–432.

Beard, K.C., Marivaux, L., Tun, S.T., Soe, A.N., Chaimanee, Y., Htoon, W., Marandat, B., Aung, H.H., Jaeger, J.-J., 2007. New sivaladapid primates from the Eocene Pondaung Formation of Myanmar and the anthropoid status of Amphipithecidae. In: Beard, K.C., Luo, Z.-X. (Eds.), Mammalian Paleontology on a Global Stage: Papers in Honor of Mary R. Dawson. Bull. Carnegie Mus. Nat. Hist, vol. 39, pp. 67–76.

Beard, K.C., Qi, T., Dawson, M.R., Wang, B., Li, C.-K., 1994. A diverse new primate fauna from middle Eocene fissure-fillings in southeastern China. Nature 368, 604–609.

Beck, R.A., Burbank, D.W., Sercombe, W.J., Riley, G.W., Barndt, J.K., Berry, J.R., Afzal, J., Khan, A.M., Jurgen, H., Metje, J., Cheema, A., Shafique, N.A., Lawrence, R.D., Khan, M.A., 1995. Stratigraphic evidence for an early collision between northwest India and Asia. Nature 373, 55–58.

Beck, R.A., Sinha, A., Burbank, D.W., Sercombe, W.J., Khan, A.M., 1998. Climatic, oceanographic, and isotopic consequences of the Paleocene India-Asia collision. In: Aubry, M.-P., Lucas, S.G., Berggren, W.A. (Eds.), Late Paleocene-Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records. Columbia University Press, New York, pp. 103–117.

Berggren, W.A., Aubry, M.-P., 1998. The Paleocene/Eocene Epoch/Series boundary: chronostratigraphic framework and estimated geochronology. In: Aubry, M.-P., Lucas, S.G., Berggren, W.A. (Eds.), Late Paleocene-Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records. Columbia University Press, New York, pp. 18–36.

Besse, J., Courtillot, V., 1988. Paleogeographic maps of the continents bordering the Indian Ocean since the Early Jurassic. J. Geophys. Res. 93 (B10), 11791–11808.

Bossuyt, F., Milinkovitch, M.C., 2001. Amphibians as indicators of Early Tertiary "Out-of-India" dispersal of vertebrates. Science 292, 93–95.

Bown, T.M., Rose, K.D., 1987. Patterns of dental evolution in early Eocene anaptomorphine primates (Omomyidae) from the Bighorn Basin, Wyoming. Paleontol. Soc. Mem. 23, 1–162.

Briggs, J.C., 2003. The biogeographic and tectonic history of India. J. Biogeog. 30, 381–388.

Clyde, W.C., Khan, I.H., Gingerich, P.D., 2003. Stratigraphic response and mammalian dispersal during initial India-Asia collision: evidence from the Ghazij Formation, Balochistan, Pakistan. Geology 31, 1097–1100.

Conroy, G.C., 1987. Problems of body-weight estimation in fossil primates. Int. J. Primatol. 8, 115–137.

Conti, E., Eriksson, T., Schönenberger, J., Sytsma, K.J., Baum, D.A., 2002. Early Tertiary out-of-India dispersal of Crypteroniaceae: evidence from phylogeny and molecular dating. Evolution 56, 1931–1942.

Covert, H.H., Hamrick, M.W., 1993. Description of new skeletal remains of the early Eocene anaptomorphine primate *Absarokius* (Omomyidae) and a discussion about its adaptive profile. J. Hum. Evol. 25, 351–362.

Cuozzo, F.P., 2008. Using extant patterns of dental variation to identify species in the primate fossil record: a case study of the middle Eocene *Omomys* from the Bridger Basin, southwestern Wyoming. Primates 49, 101–115.

Dagosto, M., 1983. Postcranium of *Adapis parisiensis* and *Leptadapis magnus* (Adapiformes, Primates). Folia. Primatol. 41, 49–101.

Dagosto, M., 1993. Postcranial anatomy and locomotor behavior in Eocene primates. In: Gebo, D.L. (Ed.), Postcranial Adaptation in Nonhuman Primates. Northern Illinois Univ. Press, DeKalb, Illinois, pp. 199–219.

Dagosto, M., Schmid, P., 1996. Proximal femoral anatomy of omomyiform primates. J. Hum. Evol. 30, 29–56.

Dagosto, M., Terranova, C.J., 1992. Estimating the body size of Eocene primates: a comparison of results from dental and postcranial variables. Int. J. Primatol. 13, 307–344.

Dagosto, M., Gebo, D.L., Beard, K.C., 1999. Revision of the Wind River faunas, early Eocene of central Wyoming. Part 14. Postcranium of *Shoshonius cooperi* (Mammalia: Primates). Annals Carnegie Mus. 68, 175–211.

Decker, R.L., Szalay, F.S., 1974. Origins and function of the pes in the Eocene Adapidae (Lemuriformes, Primates). In: Jenkins Jr., F.A. (Ed.), Primate Locomotion. Academic Press, New York, pp. 261–291.

Folie, A., Rana, R., Sahni, A., Rose, K., Smith, T., 2008. Frogs (Anura) from the early Eocene of Vastan Lignite Mine, Gujarat, India. J. Vert. Paleont. 28, 79A.

Ford, S.M., 1988. Postcranial adaptations of the earliest platyrrhine. J. Hum. Evol. 17, 155–192.

Gaetani, M., Garzanti, E., 1991. Multicyclic history of the northern India continental margin (northwestern Himalaya). Amer. Assoc. Pet. Geol. Bull. 75, 1427–1446.

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

Gebo, D.L., 1987. Humeral morphology of *Cantius*, and early Eocene adapid. Folia. Primatol. 49, 52–56.

Gebo, D.L., 1988. Foot morphology and locomotor adaptation in Eocene primates. Folia. Primatol. 50, 3–41.

Gebo, D.L., Dagosto, M., Beard, K.C., Qi, T., 2001. Middle Eocene primate tarsals from China: implications for haplorhine evolution. Am. J. Phys. Anthropol. 116, 83–107.

Gebo, D.L., Dagosto, M., Beard, K.C., Qi, T., Wang, J., 2000. The oldest known anthropoid postcranial fossils and the early evolution of higher primates. Nature 404, 276–278.

Gebo, D.L., Dagosto, M., Rose, K.D., 1991. Foot morphology and evolution in early Eocene *Cantius*. Am. J. Phys. Anthropol. 86, 51–73.

Gebo, D.L., Gunnell, G.F., Ciochon, R.L., Takai, M., Tsubamoto, T., Egi, N., 2002. New eosimiid primate from Myanmar. J. Hum. Evol. 43, 549–553.

Gingerich, P.D., 1974. Size variability of the teeth in living mammals and the diagnosis of closely related sympatric fossil species. J. Paleontol. 48, 895–903.

Gingerich, P.D., 1995. Sexual dimorphism in earliest Eocene *Cantius torresi* (Mammalia, Primates, Adapoidea). Contrib. Mus. Paleontol. Univ. Michigan 29, 185–199.

Gingerich, P.D., 2003. Stratigraphic and micropaleontological constraints on the middle Eocene age of the mammal-bearing Kuldana Formation of Pakistan. J. Vert. Paleontol. 23, 643–651.

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

Godinot, M., 1983. Contribution à l'étude des Primates Paléogènes d'Europe – Systématique, Locomotion. Thèse d'Etat, Université des Sciences et Techniques du Languedoc, Montpellier II, France.

Godinot, M., 1992. Apport à la systématique de quatre genres d'Adapiformes (Primates, Eocène). Comptes Rendu Acad. Sci. Paris 314 (série II), 237–242.

Godinot, M., 1994. Early North African primates and their significance for the origin of Simiiformes (= Anthropoidea). In: Fleagle, J.G., Kay, R.F. (Eds.), Anthropoid Origins. Plenum, New York, pp. 235–295.

Godinot, M., 1998. A summary of adapiform systematics and phylogeny. Folia. Primatol. 69 (Suppl. 1), 218–249.

Godinot, M., Dagosto, M., 1983. The astragalus of *Necrolemur* (Primates, Microchoerinae). J. Paleontol. 57, 1321–1324.

Gregory, W.K., 1920. On the structure and relations of *Notharctus*, an American Eocene primate. Mem. Amer. Mus. Nat. Hist. 3, 49–243.

Gunnell, G.F., Gingerich, P.D., ul-Haq, M., Bloch, J.I., Khan, I.H., Clyde, W.C., 2008. New euprimates (Mammalia) from the early and middle Eocene of Pakistan. Contrib. Mus. Paleontol. Univ. Michigan. 32, 1–14.

Hershkovitz, P., 1988. The subfossil monkey femur and subfossil monkey tibia of the Antilles: a review. Int. J. Primatol. 9, 365–384.

International Commission of Zoological Nomenclature (ICZN), 1999. International Code of Zoological Nomenclature. International Trust for Zoological Nomenclature. The Natural History Museum, London.

Jaeger, J.-J., Thein, T., Benammi, M., Chaimanee, Y., Soe, A.N., Lwin, T., Tun, T., Wai, S., Ducrocq, S., 1999. A new primate from the middle Eocene of Myanmar and the Asian early origin of anthropoids. Science 286, 528–530.

Jernvall, J., 2000. Linking development with generation of novelty in mammalian teeth. Proc. Natl. Acad. Sci. USA 97, 2641–2645.

Jouffroy, F.-K., 1962. La musculature des members chez les lémuriens de Madagascar. Etude descriptive et comparative. Mammalia 26 (Suppl. 2), 1–326.

Kangas, A.T., Evans, A.R., Thesleff, I., Jernvall, J., 2004. Nonindependence of mammalian dental characters. Nature 432, 211–214.

Karanth, K.P., 2006. Out-of-India Gondwanan origin of some tropical Asian biota. Curr. Sci. 90 (6), 789–792.

Kay, R.F., Schmitt, D., Vinyard, C.J., Perry, J.M.G., Shigehara, N., Takai, M., Egi, N., 2004. The paleobiology of Amphipithecidae, South Asian late Eocene primates. J. Hum. Evol. 46, 3–25.

Klootwijk, C.T., Gee, J.S., Peirce, J.W., Smith, G.M., McFadden, P.L., 1992. An early India-Asia contact: paleomagnetic constraints from Ninetyeast Ridge, ODP Leg 121. Geology 20, 395–398.

Krause, D.W., Maas, M.C., 1990. The biogeographic origins of late Paleocene-early Eocene mammalian immigrants to the Western Interior of North America. In: Bown, T.M., Rose, K.D. (Eds.), Dawn of the Age of Mammals in the Northern Part of the Rocky Mountain Interior, North America. Geol. Soc. Amer. Spec. Paper, 243, pp. 71–105.

Krishtalka, L., Stucky, R.K., Beard, K.C., 1990. The earliest fossil evidence for sexual dimorphism in primates. Proc. Natl. Acad. Sci. USA 87, 5223–5226.

Kumar, K., 2001. Distribution and Migration of Paleogene Terrestrial Mammal Faunas in the Indian Subcontinent. Internat. Conf. on Distribution and Migration of Tertiary Mammals in Eurasia. Univ. Utrecht, pp. 29–31.

Kumar, K., Hamrick, M.W., Thewissen, J.G.M., 2002. Middle Eocene prosimian primate from the Subathu Group of Kalakot, northwestern Himalaya, India. Curr. Sci. 83 (10), 1255–1259.

Luterbacher, H.P., Ali, J.R., Brinkhuis, H., Gradstein, F.M., Hooker, J.J., Monechi, S., Ogg, J.G., Powell, J., Röhl, U., Sanfilippo, A., Schmitz, B., 2004. The Paleogene Period. In: Gradstein, F.M., Ogg, J.G., Smith, A.G. (Eds.), A Geologic Time Scale 2004. Cambridge Univ. Press, Cambridge, pp. 384–408.

Marivaux, L., Antoine, P.-O., Baqri, S.R.H., Benammi, M., Chaimanee, Y., Crochet, J.-Y., de Franceschi, D., Iqbal, N., Jaeger, J.-J., Metais, G., Roohi, G., Welcomme, J.-L., 2005. Anthropoid primates from the Oligocene of Pakistan (Bugti Hills): data on early anthropoid evolution and biogeography. Proc. Natl. Acad. Sci. USA 102, 8436–8441.

Marivaux, L., Welcomme, J.-L., Ducrocq, S., Jaeger, J.-J., 2002. Oligocene sivaladapid primate from the Bugti Hills (Balochistan, Pakistan) bridges the gap between Eocene and Miocene adapiform communities in southern Asia. J. Hum. Evol. 42, 379–388.

Mayr, G., Rana, R.S., Sahni, A., Smith, T., 2007. Oldest fossil avian remains from the Indian subcontinental plate. Curr. Sci. 92 (9), 1266–1269.

McKenna, M.C., 1973. Sweepstakes, filters, corridors, Noah's Arks, and beached Viking funeral ships in palaeogeography. In: Tarling, D.H., Runcorn, S.K. (Eds.), Implications of Continental Drift to the Earth Sciences, vol. 1. Academic Press, London and New York, pp. 295–308.

Murphy, W.J., Pringle, T.H., Crider, T.A., Springer, M.S., Miller, W., 2007. Using genomic data to unravel the root of the placental mammal phylogeny. Genome Res. 17, 413–421.

Ni, X., Beard, K.C., Meng, J., Wang, Y., Gebo, D.L., 2007. Discovery of the first early Cenozoic euprimate (Mammalia) from Inner Mongolia. Amer. Mus. Novit. 3571, 1–11.

Ni, X., Wang, Y., Hu, Y., Li, C., 2004. A euprimate skull from the early Eocene of China. Nature 427, 65–68.

Nowak, R.M. (Ed.), 1999. Walker's Mammals of the World. Johns Hopkins Univ. Press, Baltimore.

Patriat, P., Achache, J., 1984. India—Eurasia collision chronology has implications for crustal shortening and driving mechanism of plates. Nature 311, 615–621.

Qi, T., Beard, K.C., 1998. Late Eocene sivaladapid primate from Guangxi Zhuang Autonomous Region, People's Republic of China. J. Hum. Evol. 35, 211–220.

Rage, J.-C., Jaeger, J.-J., 1995. The sinking Indian raft: a response to Thewissen and McKenna. Syst. Biol. 44, 260–264.

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

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

Rana, R.S., Kumar, K., Singh, H., 2004. Vertebrate fauna from the subsurface Cambay Shale (Lower Eocene), Vastan Lignite Mine, Gujarat, India. Curr. Sci. 87 (12), 1726–1733.

Rana, R.S., Singh, H., Sahni, A., Rose, K.D., Saraswati, P.K., 2005. Early Eocene chiropterans from a new mammalian assemblage (Vastan Lignite Mine, Gujarat, Western Peninsular Margin): oldest known bats from Asia. J. Palaeontol. Soc. India 50 (1), 93–100.

Roos, C., Schmits, J., Zischler, H., 2004. Primate jumping genes elucidate strepsirrhine phylogeny. Proc. Natl. Acad. Sci. USA 101, 10650–10654.

Rose, K.D., Krause, D.W., 1984. Affinities of the primate *Altanius* from the early Tertiary of Mongolia. J. Mammal. 65, 721–726.

Rose, K.D., Walker, A., 1985. The skeleton of early Eocene *Cantius*, oldest lemuriform primate. Am. J. Phys. Anthropol. 66, 73–89.

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

Rose, K.D., MacPhee, R.D.E., Alexander, J.P., 1999. Skull of early Eocene *Cantius abditus* (Primates: Adapiformes) and its phylogenetic implications, with a re-evaluation of "*Hesperolemur*" *actius*. Am. J. Phys. Anthropol. 109, 523–539.

Rose, K.D., Rana, R.S., Sahni, A., Smith, T., 2007a. A new adapoid primate from the early Eocene of India. Contrib. Mus. Paleontol. Univ. Michigan 31, 379–385.

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

Rose, K.D., Smith, T., Rana, R., Singh, L., Sahni, A., 2007b. Early Eocene primates from peninsular India. J. Vert. Paleontol. 27, 136A.

Rose, M.D., 1988. Another look at the anthropoid elbow. J. Hum. Evol. 17, 193–224.

Rowley, D.B., 1996. Age of initiation of collision between India and Asia: a review of stratigraphic data. Earth Planet. Sci. Lett. 145, 1–13.

Russell, D.E., Gingerich, P.D., 1980. Un nouveau primate omomyide dans l'Eocène du Pakistan. Comptes Rendu Acad. Sci. Paris 291 (série D), 621–624.

Russell, D.E., Gingerich, P.D., 1987. Nouveaux primates de l'Éocène du Pakistan. Comptes Rendu Acad. Sci. Paris 304 (série II), 209–214.

Sahni, A., 2006. Biotic response to the India-Asia collision: changing palaeoenvironments and vertebrate faunal relationships. Palaeontographica Abt. A 278, 15–26.

Sahni, A., Bajpai, S., 1991. Eurasiatic elements in the Upper Cretaceous nonmarine biotas of peninsular India. Cretaceous Res. 12, 177–183.

Sahni, A., Bhatia, S.B., Hartenberger, J.-L., Jaeger, J.-J., Kumar, K., Sudre, J., Vianey-Liaud, M., 1981. Vertebrates from the Subathu Formation and comments on the biogeography of the Indian subcontinent during the early Paleogene. Bull. Soc. Géol. France sér. 7, 23 (6), 689–695.

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

Sauther, M.L., Cuozzo, F.P., 2008. Somatic and dental variation in living, wild ring-tailed lemurs. Folia. Primatol. 79, 55–78.

Schaub, H., 1981. Nummulites et Assilines de Téthys paléogène. Taxinomie, phylogenèse et biostratigraphie. Mém. Suisses Pal. 104–106, 1–236.

Schettino, A., Scotese, C.R., 2005. Apparent polar wander paths for the major continents (200 Ma to the present day): A palaeomagnetic reference frame for global plate tectonic reconstructions. Geophys. J. Internat. 163, 727–759.

Schmitt, D., 1996. Humeral head shape as an indicator of locomotor behavior in extant strepsirhines and Eocene adapids. Folia. Primatol. 67, 137–151.

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008

Seiffert, E.R., Simons, E.L., 2001. Astragalar morphology of late Eocene anthropoids from the Fayum Depression (Egypt) and the origin of catarrhine primates. J. Hum. Evol. 41, 577–606.

Seiffert, E.R., Simons, E.L., Clyde, W.C., Rossie, J.B., Attia, Y., Bown, T.M., Chatrath, P., Mathison, M.E., 2005. Basal anthropoids from Egypt and the antiquity of Africa's higher primate radiation. Science 310, 300–304.

Serra-Kiel, J., Hottinger, L., Caus, E., Drobne, K., Ferrandez, C., Jauhri, A.K., Less, G., Pavlovec, R., Pignatti, J., Samso, J.M., Schaub, H., Sirel, E., Strougo, A., Tambareau, Y., Tosquella, J., Zakrevskaya, E., 1998. Larger foraminiferal biostratigraphy of the Tethyan Paleocene and Eocene. Bull. Soc. Géol. France 169, 281–299.

Silcox, M.T., 2008. The biogeographic origins of Primates and Euprimates: east, west, north, or south of Eden? In: Sargis, E.J., Dagosto, M. (Eds.), Mammalian Evolutionary Morphology: A Tribute to Frederick S. Szalay. Springer, Dordrecht, The Netherlands, pp. 199–232.

Silva, M., Downing, J.A., 1995. CRC Handbook of Mammalian Body Masses. CRC Press, Boca Raton.

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

Smith, T., Rose, K.D., Gingerich, P.D., 2006. Rapid Asia-Europe-North America geographic dispersal of earliest Eocene primate *Teilhardina* during the Paleocene-Eocene Thermal Maximum. Proc. Natl. Acad. Sci. USA 103, 11223–11227.

Springer, M.S., Murphy, W.J., Eizirik, E., O'Brien, S.J., 2003. Placental mammal diversification and the Cretaceous-Tertiary boundary. Proc. Natl. Acad. Sci. USA 100, 1056–1061.

Swofford, D.L., 2002. Phylogenetic Analysis using Parsimony (*and Other Methods), Ver. 4.0b10. Sinauer, Sunderland, MA.

Szalay, F.S., 1976. Systematics of the Omomyidae (Tarsiiformes, Primates), Taxonomy, Phylogeny, and Adaptations. Bull. Amer. Mus. Nat. Hist. 156, 157–450.

Szalay, F.S., Dagosto, M., 1980. Locomotor adaptations as reflected on the humerus of Paleogene primates. Folia. Primatol. 34, 1–45.

Szalay, F.S., Delson, E., 1979. Evolutionary History of the Primates. Academic Press, New York.

Takai, M., Sein, C., Tsubamoto, T., Egi, N., Maung, M., Shigehara, N., 2005. A new eosimiid from the latest middle Eocene in Pondaung, central Myanmar. Anthropol. Sci. 113, 17–25.

Tardieu, C., 1983. L'articulation du genou. Analyse morpho-fonctionnelle chez les primates et les hominidés fossils. In: Cahiers de Paléoanthropologie. Éditions du Centre National de la Recherche Scientifique, Paris, pp. 1–108.

Tattersall, I., Schwartz, J.H., 1983. A revision of the European Eocene primate genus *Protoadapis* and some allied forms. Amer. Mus. Novit. 2762, 1–16.

Tavaré, S., Marshall, C.R., Will, O., Soligo, C., Martin, R.D., 2002. Using the fossil record to estimate the age of the last common ancestor of extant primates. Nature 416, 726–729.

Thewissen, J.G.M., Hussain, S.T., Arif, M., 1997. New *Kohatius* (Omomyidae) from the Eocene of Pakistan. J. Hum. Evol. 32, 473–477.

Thewissen, J.G.M., Williams, E.M., Hussain, S.T., 2001. Eocene mammal faunas from northern Indo-Pakistan. J. Vert. Paleontol. 21, 347–366.

Trouessart, E.L., 1879. Catalogue des mammifères vivants et fossils. Revue et Magasin de Zoologie, Paris 7 (sér. 3), 223–230.

Please cite this article in press as: Kenneth D. Rose et al., Early Eocene Primates from Gujarat, India, J Hum Evol (2009), doi:10.1016/j.jhevol.2009.01.008