

The oldest Asian record of Anthropoidea

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Undisputed anthropoids appear in the fossil record of Africa and Asia by the middle Eocene, about 45 Ma. Here, we report the discovery of an early Eocene eosimiid anthropoid primate from India, named *Anthrasimias*, that extends the Asian fossil record of anthropoids by 9–10 million years. A phylogenetic analysis of 75 taxa and 343 characters of the skull, postcranium, and dentition of *Anthrasimias* and living and fossil primates indicates the basal placement of *Anthrasimias* among eosimiids, confirms the anthropoid status of Eosimiidae, and suggests that crown haplorhines (tarsiers and monkeys) are the sister clade of Omomyoidea of the Eocene, not nested within an omomyoid clade. Co-occurrence of Anthropoidea, Omomyoidea, and Adapoidea makes it evident that peninsular India was an important center for the diversification of primates of modern aspect (euprimates) in the early Eocene. Adaptive reconstructions indicate that early anthropoids were mouse-lemur-sized (≈ 75 grams) and consumed a mixed diet of fruit and insects. Eosimiids bear little adaptive resemblance to later Eocene-early Oligocene African Anthropoidea.

early Eocene | Eosimiidae | India | Primates | paleontology

The timing and geographic origins of the Anthropoidea (monkeys, apes, and humans) and the more inclusive crown clade Haplorhini (tarsiers and anthropoids) are poorly understood (1). Some hypothesize that crown haplorhines arose from a single common ancestor within a paraphyletic Eocene Omomyoidea (2) (Fig. 1A). Others suggest that tarsiers arose from a group of Eocene omomyoids, but that anthropoids stem from a separate group, the Eosimiidae, sister to omomyoids (Fig. 1B) (3). A third alternative, not previously advocated, is that crown haplorhines are sister to Omomyoidea as a whole (Fig. 1C). If the first hypothesis is correct, then the anthropoid stem could be as young as middle Eocene, when eosimiids first are recorded. However, if the second or third hypothesis is correct, haplorhine (and anthropoid) origins must be sought in the Paleocene or earlier. Here, we report the discovery of an early Eocene eosimiid anthropoid primate, named *Anthrasimias*, that is the first from peninsular India and extends the Asian fossil record of anthropoids by 9–10 million years. *Anthrasimias* occurs at the same stratigraphic level as basal representatives of Eocene primate groups Omomyoidea and Adapoidea (4–6), making it evident that India was an important center for the evolution of primates of modern aspect in the early Eocene. A new phylogenetic analysis supports the hypothesis that the Eosimiidae are stem anthropoids (7–9) and suggests that crown haplorhines are sister to a monophyletic Eocene Omomyoidea rather than being nested within omomyoids (10, 11).

As the antiquity of the anthropoid lineage deepens, questions about major adaptive shifts that are relevant to anthropoid origins are beginning to converge on questions about the origins of the Order Primates as a whole. It is becoming apparent that information about the basal members of each of the major Eocene groups, Anthropoidea, Omomyoidea, and Adapoidea, should contribute significantly to our reconstructions of ancestral primates. It has been hypothesized that the earliest primates dwelt in fine-branch thickets, were ≤ 200 g in body mass, and had a mixed diet of fruit and insects, gleaned by visual predation (12, 13). However, recent estimates based on extant arboreal primates place the ancestral body mass of crown primates at ≥ 1 kg

(14), which is outside the range of extant insectivorous primates (15). Body mass reconstruction of 1 kg for ancestral primates tends to rule out the visual predation hypothesis and supports, by implication, an alternative hypothesis that links novel primate adaptations with the coevolution of angiosperms (16). In addition to *Anthrasimias*, four other basal primates are known from the same stratigraphic level in the Vastan mine and represent Omomyoidea (*Vastanomys*, *Suratius*, compare with Omomyoidea) and Adapoidea (*Marcgodinotius* and *Asiadapis*) (4–6). Reconstructions of body mass and diet for these and other eosimiid taxa addressed in this article shed light on the alternative adaptive hypotheses.

Systematic Paleontology

Primates, Linnaeus, 1758; Anthropoidea, Mivart, 1864; Eosimiidae, Beard et al., 1994

***Anthrasimias*, Gen. Nov. Etymology.** After *anthra*, Greek for coal, because the fossils were found in a coal mine; *simias*, Latin for monkey or ape.

Diagnosis. As for type species.

***Anthrasimias gujaratensis* Sp. Nov. Etymology.** After Gujarat state of western India, the provenance of this species.

Holotype. IITR/SB/VLM 1137, a left M¹ (Fig. 2A and C).

Hypodigm. IITR/SB/VLM 1100, a left M² (Fig. 2B–D), IITR/SB/VLM 1017, a right M₃ (Fig. 2E), IITR/SB/VLM 1201, a dP⁴ (Fig. 2E).

Horizon and locality. Early Eocene Cambay Shale, Vastan Lignite Mine, Surat District, Gujarat, western India (2). The *Anthrasimias* stratigraphic level contains a diverse early Eocene terrestrial mammalian fauna (1–3, 17, 18). Age-diagnostic dinoflagellate cysts indicate a basal Eocene (Sparnacian, ca. 54–55 Ma) age for the mammal horizon (19). This estimate is a revision of the earlier age assessment of basal Cuisian, ca. 53 Ma, from shallow benthic foraminifera (4, 6, 20).

Diagnosis. Equivalent in size to *Altiatlasius* (of Africa) and the smallest Asian eosimiids with described dental remains. Differs from eosimiids in having a more triangular occlusal outline (i.e., less transverse buccolingually) and in having a cusped hypocone (vs. absent to cristiform). Differs from other eosimiid primates (except *Phileosimias kamali*) and from *Altiatlasius* in having less well developed buccal and lingual cingulae. Conules slightly larger than in *Eosimias*, *Phenacopithecus*, and *Bahinia*, but smaller than in *Phileosimias*.

Comparisons. *Anthrasimias* shares with other eosimiids a suite of dental features noted by Beard and Wang (3) to be diagnostic of eosimiids but not found together in omomyoids, including strong

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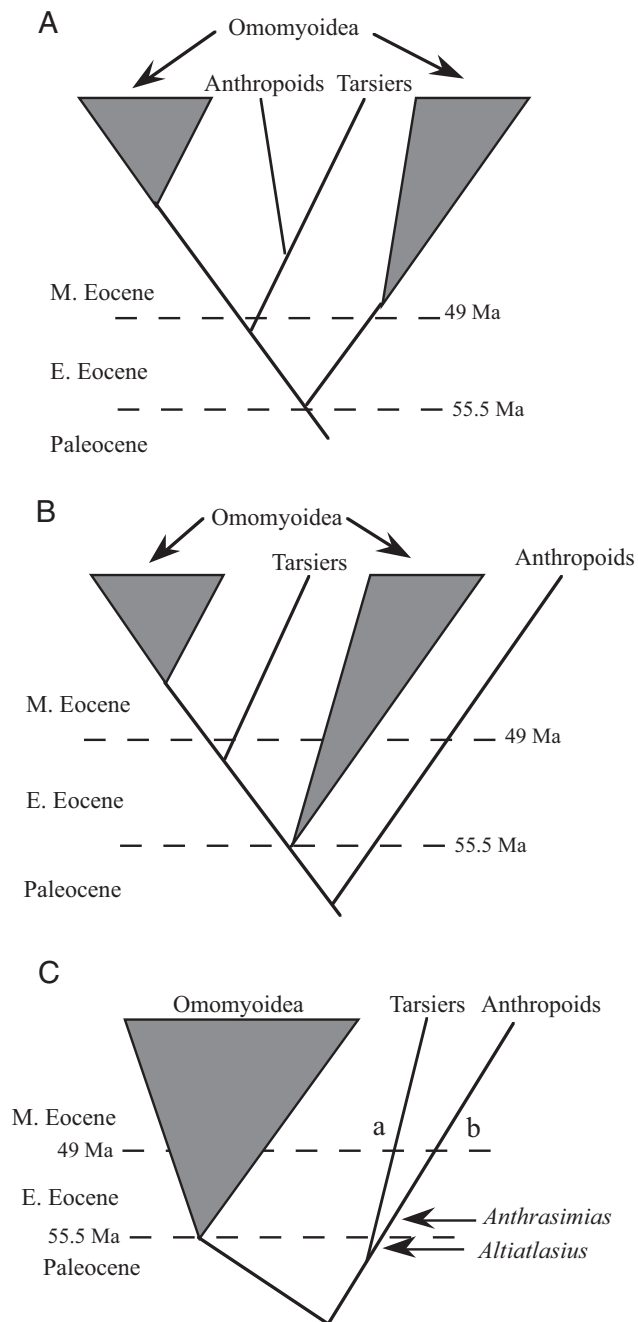


Fig. 1. Schematic representations of three hypotheses about anthropoid and tarsier origins. (A) Anthropoids and tarsiers share a common ancestor within a paraphyletic Omomyoidea. (B) Tarsiers arose from an omomyoid while anthropoids are sister to omomyoids. (C) The tarsier-anthropoid clade is the sister group of omomyoids. References to these views are in the text. Constraints on the branch times of the groups depicted in these schemes are approximate and based on the first appearance of (i) Omomyoidea [earliest Eocene (40)], (ii) Tarsiidae [middle Eocene (41)] or the omomyoid *Shoshonius*, its proposed sister taxon (22), and (iii) middle Eocene or earlier anthropoids, depending on the assumptions of various authors. Dashed lines represent the dates of the Paleocene-Eocene and early Eocene-middle Eocene boundaries (42). Temporal position of *Altiasius* and *Anthrasimias* are indicated. a, first appearance of Tarsiidae in Asia; b, hitherto first appearance on eosimiid anthropoids in Asia.

development of pre- and postprotocristae, absence of a *Nanopithec* fold, and reduced conules. The distolingual expansion of the talon, present in *Anthrasimias*, is common among eosimi-

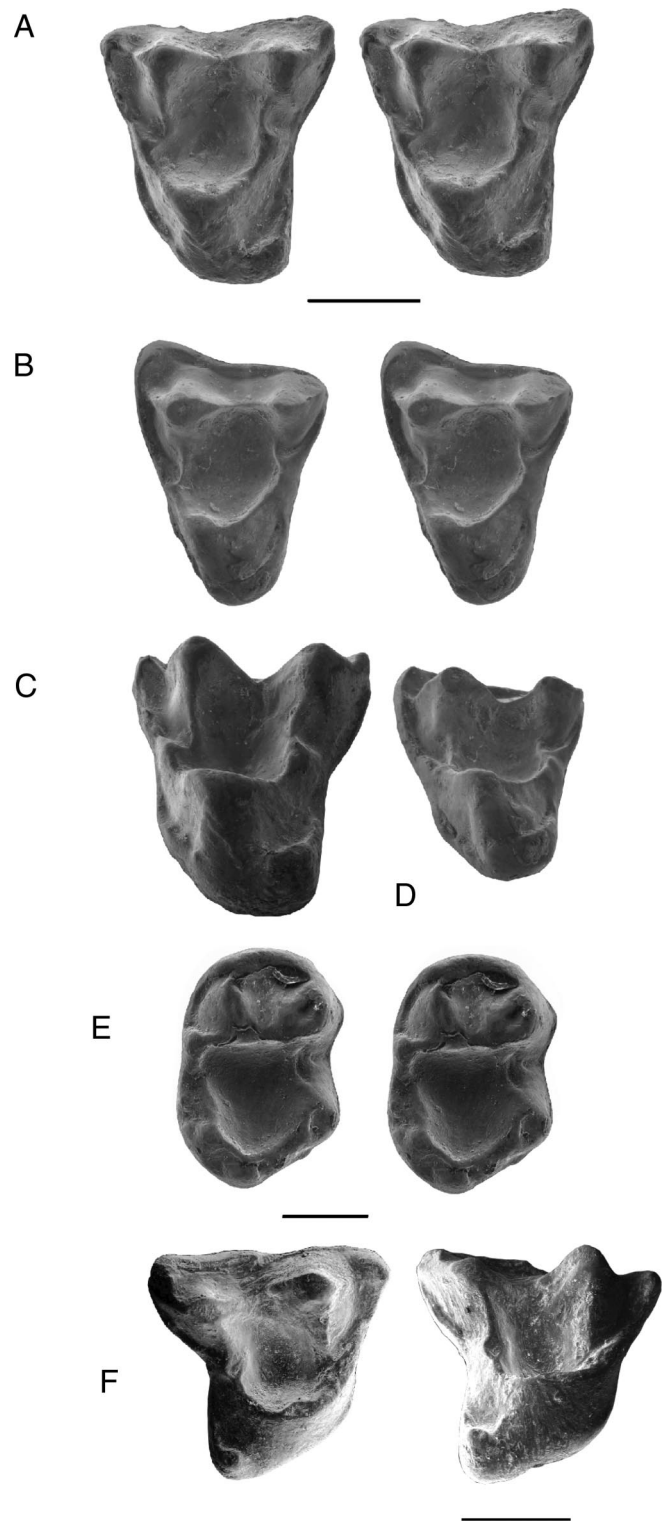


Fig. 2. The dentition of *Anthrasimias gujaratensis* sp. nov. (A) Occlusal stereopair of IITR/SB/VLM 1137, a left upper first molar. (B) Occlusal stereopair of IITR/SB/VLM 1100, a left upper second molar. (C) Lingual view of IITR/SB/VLM 1137. (D) Lingual view of IITR/SB/VLM 1100. (E) Occlusal stereopair of IITR/SB/VLM 1017, a right lower third molar. (F) occlusal and occluso-lingual view of IITR/SB/VLM 1201, a right dp⁴. (Scale bars, 1 mm.)

ids (21). The lingual cingulum of *Anthrasimias* is incomplete, unlike that of *Eosimias*, *Phenacopithecus*, *Bahinia*, and *Phileosimias brahuiorum*, but is similar to *P. kamali*.

The steep incline of the buccal wall of the paracone and metacone in *Anthrasimias* is common in eosimiids, particularly *Eosimias* and *Phenacopithecus*. Like other eosimiids, and especially like *Eosimias* (and unlike most omomyoids), the parastyle is a large distinct cusp, and the metastyle is present as a swelling along the postmetacrista. The protocone is canted mesially, such that it is closer to the mesial edge of the tooth, as in *Eosimias*, *Bahinia*, and *Phenacopithecus* but not *Phileosimias*. There is a distinct molar waisting, especially in the area of the metaconule, as in *Eosimias*, *Phenacopithecus*, and *Bahinia*, but less markedly in *Phileosimias*.

Eosimiids generally lack metaconule cristae and a postparaconule crista. Instead, the postprotocrista leads to the base of the metacone or to a small metaconule that connects in turn with a hypometacrista. *Anthrasimias* has an intermediate morphology: the postprotocrista is straight, not distally bowed, and connects with the metaconule, which sends a strong but buccally directed premetaconule crista up the lingual aspect of the metacone. We interpret this arrangement of the premetaconule crista as a precursor to the hypometacrista.

Several notable features of the M₃ are eosimiid-like: the trigonid is open lingually and supports a small centrally placed paraconid, the protocristid is transverse, and the hypoconulid is small and does not project posteriorly as a distinct distal lobe.

Altiatlasius (late Paleocene, Africa) exhibits some but not all of the above-mentioned symplesiomorphies with *Anthrasimias* and other eosimiids. Like eosimiids, the postprotocrista leads to the base of the metacone and the preprotocrista to the paracone. In both *Altiatlasius* and eosimiids, a *Nannopithecus* fold is absent, and like most eosimiids (but not *Anthrasimias*), there is a complete lingual cingulum. The steep incline of the buccal wall of the paracone and metacone in *Altiatlasius* also is common in eosimiids. Furthermore, like *Anthrasimias* and other eosimiids, especially *Eosimias* (and unlike most omomyoids), the preparacrista and postmetacrista are angled buccally and supported by a large parastyle and somewhat smaller metastyle, respectively. However, unlike *Anthrasimias* and other eosimiids, the talon of *Altiatlasius* is not noticeably expanded distolingually, the protocone is not canted mesially, and the molar waisting is indistinct. Further, *Altiatlasius* lacks a hypometacrista.

Phylogenetic analysis. A parsimony analysis was undertaken by using PAUP parsimony software (22) to determine the phylogenetic position of *Anthrasimias* and other Indian early Eocene primates (Fig. 3). A notable feature of all maximum parsimony trees is that crown Haplorhini is sister to all Omomyoidea, not nested within it as often argued (8, 11, 22).

All trees place *Marcgodinotius* near the base of Adapoidea. The latter is a sister taxon to crown Strepsirrhini. *Marcgodinotius* is similar to the European early Eocene adapoid *Donrussellia* in many primitive features (5). *Vastanomys* is placed near the base of the Omomyoidea. *Vastanomys* is primitive for omomyoids in retaining a large canine and a large, although single-rooted, P₂ (5). It appears to be more primitive than North American *Steinys*, argued by some to be the most primitive omomyoid (24).

The 50% majority consensus tree places *Anthrasimias* at the base of the eosimiids. A plausible alternative places this taxon at the base of the tarsiid clade or in an unresolved trichotomy with tarsiids and eosimiids. The eosimiid placement is consistent with morphological characters, mentioned in the diagnosis above, considered most critical to reconstructing eosimiid evolution (3, 25). All trees also support placement of *Altiatlasius* with the Eosimiidae (10, 26, 27).

The phylogenetic position of late Eocene amphipithecids of Asia is a subject of considerable debate. Mandibular and dental similarities and the structure of an isolated talus suggest an anthropoid association (28, 29). In this analysis, we accept the view that some other isolated bones allocated to this taxon are not primate or belong to a large strepsirrhine (30, 31). Our

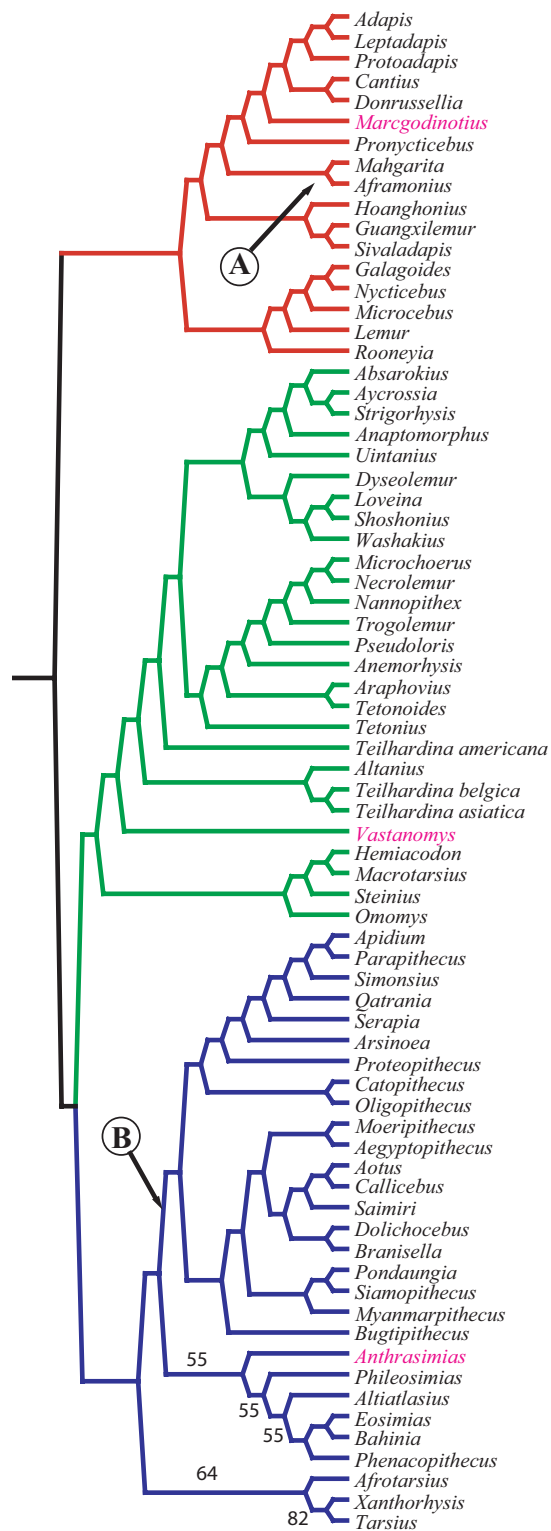


Fig. 3. The 50% majority consensus of 11 equally parsimonious trees. Tree length, 148,887; consistency index (CI), 0.230; retention index (RI), 0.554; rescaled CI (RCI), 0.127. Red, Adapoidea; green, Omomyoidea; blue, crown Haplorhini. Branching sequences are supported in 100% of the trees unless indicated by a percentage. *Suratius* and *Asiadapis* are not included on the tree. Circled letter A indicates branch placement of *Asiadapis* when it is run without *Suratius* included. Circled letter B indicates branch placement of *Suratius* when *Asiadapis* is not included. When *Suratius* and *Asiadapis* are run together, they are placed together at branch B. The list of characters and their states and character-taxon matrix is provided in [supporting information \(SI\) Text, Figs. S1–S3, and SI Appendices 1 and 2.](#)

Table 1. Body mass estimates for Eocene and early Oligocene South Asian primates (Thailand, Myanmar, Pakistan, India) and representative early taxa of early Eocene Omomyoidea and Adapoidea

Taxon	Age	M ₂ length	M ¹ area	Our estimate body weight, g	Previous estimates (Ref.)
Adapoidea					
<i>Marcgodinotius indicus</i> (n = 2)	Early Eocene	2.23	—	132	—
<i>Asiadapis cambayensis</i>	Early Eocene	2.83	—	270	—
<i>Donrussellia provincialis</i>	Early Eocene	2.3	5.67	144, 74	40 g (43)
Superfamily affinity uncertain					
<i>Suratius robustus</i>	Early Eocene	2.75	—	248	—
<i>Altanius orlovi</i>	Early Eocene	1.2	1.78	17, 10	10 g-30 g (44)
Omomyoidea					
<i>Teilhardina belgica</i>	Early Eocene	1.73	4.29	61, 46	30–90 (44)
<i>Teilhardina asiatica</i>	Early Eocene	1.78	4.68	67, 54	28 g
<i>Steinivus vespertinus</i>	Early Eocene	2.18	—	122	298 g
<i>Vastanomy gracilis</i>	Early Eocene	2.06	5.90	103, 80	—
Eosimiidae					
<i>Altiatlasius koulchii</i>	Late Paleocene	1.76	3.38	31, 64	—
<i>Anthrasimias gujaratensis</i>	Early Eocene	—	5.68	75	—
<i>Eosimias sinensis</i>	Middle Eocene	1.85	—	75	67–137 (3); 140 (45)
<i>Eosimias centennicus</i>	Late middle Eocene	2.07 (n = 5)	6.23	105, 88	64–131 (3); 160 (45)
<i>Eosimias dawsonae</i>	Late middle Eocene	2.40	—	164	107–276 (3)
<i>Bahinia pondaungensis</i>	Late middle Eocene	—	12.25	279	570 g (45)
<i>Phenacopithecus xueshii</i>	Late middle Eocene	2.70	—	235	163–316 g (3)
<i>Phenacopithecus krishtalkai</i>	Late middle Eocene	—	8.50	149	163–316 g (3)
<i>Phileosimias brahuiorum</i>	Early Oligocene	2.60	7.26	114, 209	250 g (25)
<i>Phileosimias kamali</i>	Early Oligocene	2.60	8.60	152	250 g (25)
Amphipithecidae					
<i>Siamopithecus eocaenus</i>	Late Eocene	6.26 (n = 2)	43.7	—	5.9 kg (45)
<i>Pondaungia</i> spp.	Late middle Eocene	6.92	33.8	—	5,900 g (45)
<i>Myanmarpithecus yarshensis</i>	Late middle Eocene	4.17	18.8	870, 583	1,800 g (45)
<i>Bugtipithecus inexpectans</i>	Early Oligocene	—	7.82	129	350 g (25)

A new body mass is not proposed for *Pondaungia* and *Siamopithecus*, because such an estimate would be an extrapolation from the size range on which the size estimates are based. The formulae for estimation of body mass in grams for 10 genera of prosimians: from lower second molar length: $(3.019 \times \ln m_2 \text{ length}) + 2.459$ with an r^2 of 0.458; from upper first molar area: $(1.716 \times \ln M_1 \text{ area}) + 1.333$ with an r^2 of 0.55.

analysis using dental, gnathic, and talar characters supports placement of amphipithecids within Anthropoidea.

The analysis is equivocal concerning placement of *Asiadapis* and *Suratius*. Phylogenetic analysis of all taxa in our dataset links the two and places them at the base of the noneosimiid Anthropoidea. In separate analyses, however, *Asiadapis*, considered alone without *Suratius*, falls with adapoids *Aframoni* and *Mahgarita*, whereas *Suratius*, run alone without *Asiadapis*, is linked with eosimiids.

Adaptations. Our findings of very small body size in basal members of all radiations indicate that insects rather than plants were the primary source of protein for early primates (Table 1) (32). There is no support for the hypothesis that basal Anthropoidea were large, despite the relatively large size of most Oligocene-Recent species (15). *Anthrasimias*, at 75 g, was smaller than all living primates with the exception of some species of *Galagoides* (the dwarf galago) and *Microcebus* (the mouse lemur) (Table 1). No size trends are evident among eosimiids. *Anthrasimias* (and African *Altiatlasius*) were slightly smaller than middle to late Eocene Asian eosimiids known from dental material (85–150 g), but some tarsal bones suggest that some middle Eocene eosimiids may have been shrew-sized (33). Likewise, Vastan omomyoids and adapoids were very small animals: *Vastanomy* and *Marcgodinotius* ranged up to 130 g. *Suratius* and *Asiadapis* were slightly larger, up to 270 g. Thus, early Eocene members of the three radiations of crown primates, omomyoids, stem strepsirrhines, and crown haplorhines also weighed <300 g.

Previous studies on the diet of fossil anthropoids have relied

on comparative evidence from living taxa and the morphology of the lower teeth of anthropoid taxa from the Fayum of Egypt dating back to the late Eocene (34). Those late Eocene anthropoids show a diet that was predominantly frugivorous, but their >750 g body size suggests leaves, not insects, as an important source of dietary protein. However, the 20-million-year separation of Fayum anthropoids from basal members of the anthropoid clade makes them poor candidates from which to infer possible adaptive shifts at the base of the group.

Body mass alone may tell us something about the likely source of dietary protein, but tooth structure gives further details about the relative importance of fruit vs. animal prey. Among small-bodied extant prosimians, a strong relationship exists between the summed lengths of shearing crests of the lower molar teeth and the amount of animal prey in the diet (32). A similar phenomenon occurs with the upper molars (Fig. 4, Table 2). From dental anatomy (combined with small size), we infer that *Anthrasimias* had a mixed diet of fruit and some insects similar to that of the mouse lemur *Microcebus*. The development of shearing crests on the upper and/or lower teeth of *Asiadapis*, *Vastanomy*, and *Marcgodinotius* likewise suggests a mixed frugivorous/insectivorous diet. Unlike proposed reconstructions of body mass >1 kg, our body mass and dietary reconstructions of taxa basal to Eocene primate clades provide broadly based evidence that the earliest primates relied, at least in part, on insects or other animal prey. Our conclusion is consistent with the visual predation hypothesis but does not rule out coevolution with angiosperms. There is no evidence to indicate that changes in body mass or diet accompanied the

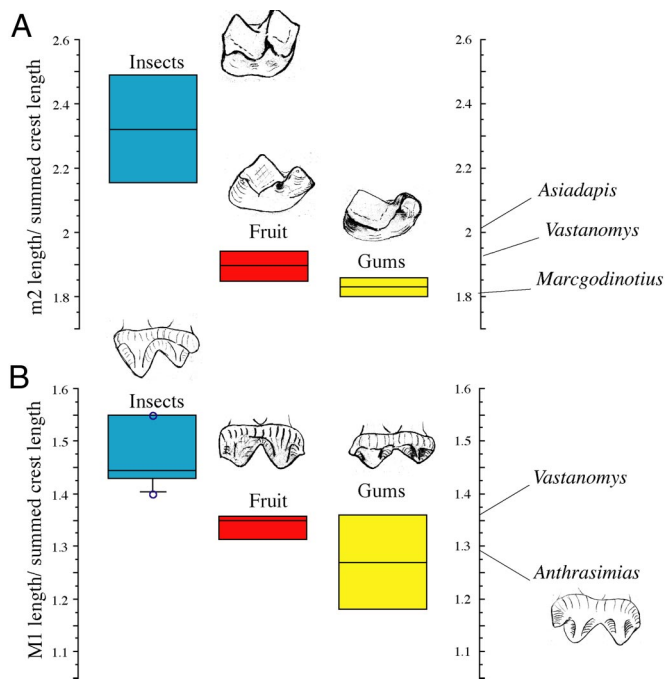


Fig. 4. Measurements of shearing crest development on the molar teeth of Vastan primates. (A) Ratio of second lower molar length to summed lengths of six principal M_2 shearing crests. (B) Ratio of first upper molar length to summed lengths of four principal buccal shearing crests. Color-coded bars (blue, insects; red, fruit; yellow, gums) indicate principal dietary item (34). *Asiadapis*, *Vastanomyys*, and *Marcgodinotius* fall within the range of extant prosimian fruit and gum eaters such as the extant mouse lemur *Microcebus*, which also eats a substantial amount of insects (Table 2).

cladogenic splitting of haplorhines from strepsirrhines or anthropoids from omomyoids.

Temporal and biogeographic implications. Hitherto, the oldest undisputed eosimiids were recovered from the Chinese middle Eocene (≈ 45 Ma) (3, 35). *Anthrasimias* is the first eosimiid from the Indian subcontinent and extends the Asian fossil record of anthropoids by 9–10 million years. *Anthrasimias* may also be the oldest anthropoid in the world. However, our analysis supports the hypothesis that *Altiatlasius* from the late Paleocene of Africa is possibly an eosimiid anthropoid (10, 26, 27). Nevertheless, others consider it to be an omomyoid (36), a plesiadapoid (37), or of indeterminate subordinal affinities (1). In any event, the cooccurrence of an anthropoid taxon alongside adapoid and omomyoid primates in the early Eocene of Asia gives further evidence that the cladogenesis of crown haplorhines and strepsirrhines was ancient, in the Paleocene or even Cretaceous, as molecular evidence suggests (14, 38).

The Vastan Indian fauna shows strong links with Laurasian early Eocene faunas (5, 6, 17, 18). The presence of an anthropoid in India before 54 million years ago and possibly even earlier in Africa (if *Altiatlasius* is an anthropoid) fleshes out the picture of early Cenozoic interchange between Laurasia and Africa (26, 39) and between the Indian and Asian plates, the latter in the context of their tectonic collision (17). The Vastan anthropoid testifies to the early importance of India as an important center for the differentiation of all of the major groups of primates.

Materials and Methods

For the phylogenetic analysis, our dataset consists of 75 taxa and 343 characters of the skull, postcranium, and dentition. It includes a wide

Table 2. Diet and shearing crest lengths of extant and extinct primates used in the text

Taxon	Principal dietary item	Upper molar shearing ratio	Lower molar shear ratio
<i>Arctocebus calabarensis</i>	Insects	1.55	2.18
<i>Galagoides demidoff</i>	Insects	1.4	2.13
<i>Galago maholi</i>	Insects	1.43	2.46
<i>Loris tardigradus</i>	Insects	1.49	2.01
<i>Tarsius spectrum</i>	Insects	1.46	2.52
<i>Tarsius syrichta</i>	Insects	1.43	
<i>Tarsius bancanus</i>	Insects	1.55	
<i>Galago alleni</i>	Fruit	1.3	1.94
<i>Microcebus murinus</i>	Fruit	1.35	1.85
<i>Microcebus rufus</i>	Fruit	1.36	
<i>Perodicticus potto</i>	Fruit	1.11	1.71
<i>Otolemur crassicaudatus</i>	Fruit	1.22	1.69
<i>Eooticus elegantulus</i>	Gums	1.36	1.86
<i>Phaner furcifer</i>	Gums	1.18	1.8
<i>Vastanomyys gracilis</i>		1.32	1.91
<i>Anthrasimias gujaratensis</i>		1.33	
<i>Marcgodinotius indicus</i> ($n = 2$)			1.81
<i>Asiadapis cambayensis</i>			2.06

Principal dietary item as defined by Kirk and Simons (34). Sample sizes for extant taxa for the lower molar shearing listed in Kay *et al.* (46). The means of two specimens were used for each upper molar shearing ratio.

representation of Adapoidea, Omomyoidea, Tarsiidae, Eosimiidae, and other stem and crown Anthropoidea. We include *Anthrasimias* and other early Eocene Indian primates from Vastan: *Marcgodinotius*, *Vastanomyys*, *Suratius*, and *Asiadapis*. We ran the character–taxon matrix in PAUP 4.0b10 (22) with all multistate characters scaled. As described by Swofford (22), weights are assigned to all characters, such that the minimum possible length of each character is 100 (the default “base weight”). Binary characters and unordered characters are assigned a weight of 100, three state ordered characters a weight of 50, and so on. Findings are detailed in Fig. 2.

Previous estimates of body mass in small-bodied fossil primates have been based on regressions derived from a wide range of prosimian taxa, including such large-bodied primates as *Propithecus* and *Varecia*. A more appropriate model for these extremely small primates should be based on a sample of small-bodied taxa. To estimate the body mass of *Anthrasimias* and other eosimiid and amphipithecoid taxa, we used a formula derived from the molar size and body mass of 10 genera of extant prosimians weighing < 600 g.

To reconstruct diet in our Eocene species, we selected 10 genera of extant tarsiers, galagos, lorises, and dwarf lemurs (14 genera for the lower teeth). We compared the ratio of the summed lengths of six principal lower second molar shearing crests to M_2 length. Likewise, we took the ratio of the sum of the four principal buccal shearing crests (preparacrista + postparacrista + premetacrista + postmetacrista) of the upper first molar to M^1 length. Findings for Vastan primates are detailed in Fig. 4. Data are summarized in Table 2.

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