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An ailuravine rodent from the lower Eocene Cambay Formation at Vastan, western India, and its palaeobiogeographic implications

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A new ailuravine rodent, *Meldimys musak* sp. nov. (Mammalia: Rodentia, Ischyromyidae), is recorded from the lower Eocene lignites of western India. It is the oldest record of Rodentia from India. *M. musak* is more derived than the earliest Eocene ailuravine *Euromys cardosoi* from Portugal and more generalized than late early Eocene *E. inexpectatus* and *Ailuravus michauxi* from France. Its dental morphology closely corresponds to the middle early Eocene species *M. louisi*, which lived about 52 Ma in Western Europe. *Meldimys* was previously known only from Europe, and ailuravines were previously reported only from Europe and North America. Its occurrence in India allows the first direct correlation between the early Eocene land mammal horizons of Europe and India, and raises the possibility of a terrestrial faunal exchange between India and Eurasia close to the Palaeocene–Eocene transition.

Key words: Mammalia, Ailuravinae, Rodentia, palaeobiogeography, Eocene, India.

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Introduction

Fossil rodent systematics and biochronology of South Asia have provided a fairly continuous record extending from the early Eocene to Neogene and Quaternary sediments. Among the best studied Palaeogene assemblages are the ones from the Eocene Subathu (India) and Kuldana (Pakistan) formations and coeval sediments (Hussain et al. 1978; de Bruijn et al. 1982; Hartenberger 1982a; Kumar et al. 1997a, b). The previously known Indian Palaeogene rodent assemblages were dominated by ctenodactyloids including the Chapattimyinae and the Baluchimyinae.

Here we describe a new early Eocene ailuravine rodent from the Vastan lignite mine (Rana et al. 2004, 2005; Rose et al. 2006; Sahni et al. 2006), which has interesting palaeobiogeographic implications since most plate tectonic reconstructions (Sahni and Kumar 1974; Klootwijk et al. 1991, 1992; Mattauer et al. 1999) place the Indian landmass as an island subcontinent in pre- or penecontemporaneous colliding phase at that time, and it has been argued that the India-Asia collision may have triggered some of the late Palaeocene–early Eocene global climatic and biotic events (Beck et al. 1998). The new rodent is based on isolated cheek teeth and incisor fragments and appears to have clear affinities with the early Eocene ailuravine (Ischyromyidae) rodents from Europe (Michaux 1968; Hartenberger 1975; Wood 1976; Escarguel 1999).

Prior to this report the ailuravine rodents were known only from Europe and North America. In Europe, they have been recorded from at least seven biochronological reference levels within the Eocene (Appendix 1). In North America, they are mainly known from the middle Eocene Uintan Land

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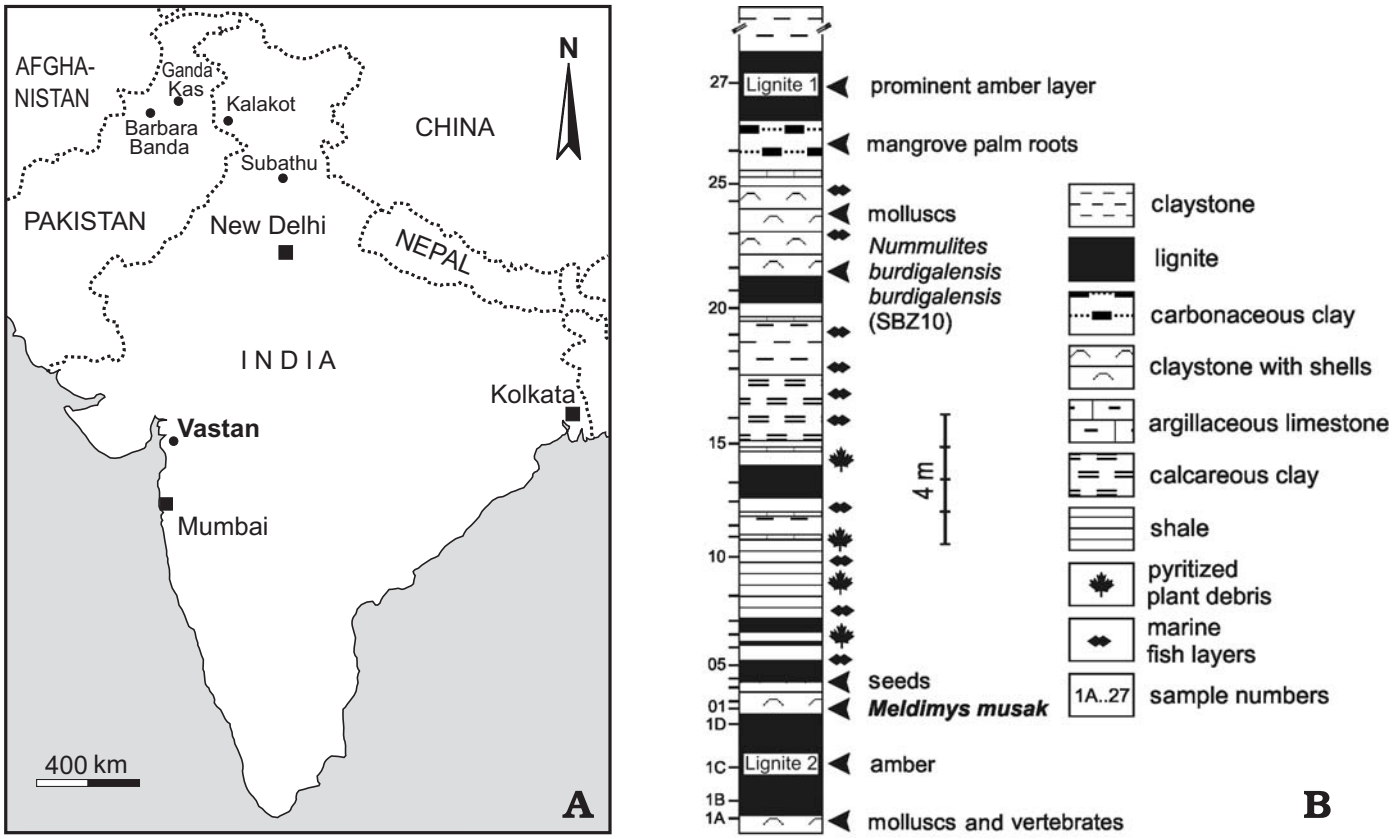

Fig. 1. **A**. Indian subcontinent with locations of ailuravine (Vastan) and other Eocene rodent sites (Ganda Kas and Barbara Banda in Pakistan, and Kalakot and Subathu in India). Squares represent major cities and black dots Eocene rodent localities. **B**. Lithological log of the Cambay Formation in the open cast lignite mine, Surat District, Gujarat, showing lignite seams, rodent-yielding level, other major fossiliferous levels, and the sample locations.

Mammal Age (ca. 46–41 Ma), with species ranging from the early Eocene (Wasatchian) to the late Eocene (Chadronian) (Wood 1962, 1980; Korth 1984, 1988, 1994).

The Vastan rodent represents a new species of the otherwise European ailuravine genus *Meldimys*. The common presence of the genus *Meldimys* in the Vastan as well as European sections is significant because (1) it allows for a biostratigraphic correlation between south Asia and Europe, and (2) it opens up exciting new possibilities for examining migration routes across the Tethys Sea which was still in existence during the early Eocene, enveloping most of the northern and northeastern margin of the Indian Plate (Sahni and Kumar 1974). Although such a connection with Asia had been proposed by several workers, including an early (near the Cretaceous/Tertiary Boundary) collision of India and Asia (Sahni et al. 1983; Jaeger et al. 1989; Klootwijk et al. 1991, 1992; Beck et al. 1995; Rage and Jaeger 1995; Rage et al. 1995), connections with Europe were considered to be more tenuous except of course for the presence of a few taxa, e.g., the dichobunid artiodactyl *Diacodexis*, and the ray fish *Igdabatis*, which were common to the two widely separated regions (Thewissen et al. 1983; Kumar and Jolly 1986; Soler-Gijon and López-Martínez 1998).

Institutional abbreviations.—GU/RSR/VAS, Garhwal University/R.S. Rana/Vastan catalogue numbers for the Department of Geology, H.N.B. Garhwal University, Srinagar, Uttaranchal, India; UM2, Université Montpellier 2, Montpellier, France; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MNHN-PL, Collection "Pierre Louis", Muséum National d'Histoire Naturelle, Paris, France.

Geological setting

The new rodent material described herein was recovered from the subsurface beds of the Cambay Formation (= Cambay Shale) dug out in an open cast lignite mine at Vastan, about 40 km (60 km road distance) NE of Surat (N 21°12', E 72°55') in Gujarat, western India (Fig. 1). In the Vastan mine, the Cambay Shale is 20–45 m thick but at the rodent site (N 21°25' 59", E 73°06' 59") only about 31 m thickness has been exposed so far (Fig. 1). It is composed of an alternating sequence of lignite, dark grey to black and greenish grey shales with vertebrate-rich sandy lenses, and clay-marls. There are two main lignite seams in the mine section: Lignite 1 at the top and Lignite 2 at the mine floor. The rodent-bearing level lies about a meter above the Lignite 2 (Fig. 1). The Cambay Formation overlies the Palaeocene–lower Eocene Vagadkhol Formation or its equivalent Olpad Formation, and is overlain by the upper Eocene nummulitic limestone and marl referred

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to as the Amravati Formation (sensu Sudhakar and Basu 1973) followed by Recent alluvium. Surface exposures of the Cambay Formation occur as thin strips to the east of the Gulf of Cambay (= Khambhat) and along the Saurashtra coast (Bhandari et al. 1991).

The Cambay Formation in the Vastan mine section is quite rich in animal as well as plant remains. Molluscs (mostly marine) are highly concentrated in the lower part of the section forming conspicuous shell bands, which are also rich in diverse vertebrates including fish (mainly sharks and rays), snakes, lizards, frogs, chiropterans, artiodactyls, anthracobunids, perissodactyls, rodents, insectivores, and primates (e.g., Rana et al. 2004, 2005; Bajpai et al. 2005; Rose et al. 2006; Sahni et al. 2006; Smith et al. 2007). Other major recorded groups are plants, ostracodes, and foraminifers. The foraminifera-rich interval lies about 10 m above the rodent-bearing horizon. The only index species in the Cambay Formation in general and the Vastan mine section in particular is the foraminifer *Nummulites burdigalensis burdigalensis*, which occurs ~18–20 m above the rodent-bearing horizon (Sahni et al. 2006). It assigns the section to the early Cuisian Shallow Benthic Zone SBZ 10 (= Planktonic Foraminiferal Zone P6b of Berggren et al. 1995 and tropical planktonic foraminiferal zone E4 of Berggren and Pearson 2006) corresponding to about early Ypresian (Serra-Kiel et al. 1998; Berggren and Pearson 2006).

Materials and methods

The rodent fossils from the Vastan lignite mine consist of 16 isolated cheek teeth as well as incisor fragments, all referable to a single genus and species. All were recovered from the same level and locality by screen-washing of matrix using only water. The quality of preservation of isolated teeth is variable but generally good. A few teeth have suffered damage which is ascribed to post-depositional breakage. The enamel surface in at least one tooth is deeply pitted probably from chemical erosion.

In this paper, the upper premolars and molars are indicated by P or M, respectively, lower molars by m, and deciduous teeth are preceded by d. The dental terminology adopted here follows Escarguel (1999).

Systematic palaeontology

Class Mammalia Linnaeus, 1758

Order Rodentia Bowdich, 1821

Superfamily Ischyromyoidea Alston, 1876

Family Ischyromyidae Alston, 1876

Subfamily Ailuravinae Michaux, 1968

Genus *Meldimys* Michaux, 1968

Type species: *Meldimys louisi* (Michaux, 1964), early Eocene (middle Ypresian) of Avenay, Paris Basin, France.

Revised diagnosis.—Smaller than *Ailuravus* and North-American ailuravines, and about the same size as the most primitive ailuravine *Euromys*. Differs from other ailuravines in having lower-crowned cheek teeth with more rounded cusps, noticeably less developed hypocone and less pronounced lingual sinus in P4–M3, more globular P4 with less developed anteroloph and posteroloph but better developed mesostyle, and p4 with metaconid markedly less developed than protoconid. Further differs from *Ailuravus* and *Euromys* in having upper molars with typical tetrahedral paracone and occlusal surface markedly more curved along the antero-posterior median line, and lower molars with hypoconulid nearly merged into posterolophid. Upper cheek teeth with short crest descending from protocone into trigon basin (this crest absent in *Ailuravus*). Lower cheek teeth with mesoconid connected to hypoconid, in contrast to *Euromys*, which has mesoconid completely separated from both hypoconid and metaconid.

Meldimys musak sp. nov.

Figs. 2–5; Table 1.

Derivation of the name: From Sanskrit *musak*, mouse.

Type material: Holotype: GU/RSR/VAS 609, an isolated right upper second molar (RM2). Paratypes: GU/RSR/VAS 608, RdP4; GU/RSR/VAS 606, LP4; GU/ RSR/VAS 449 RM1; GU/RSR/VAS 128 and 607 LM1; GU/RSR/VAS 450 and 454, RM2; GU/RSR/VAS 451–453, RM3; GU/RSR/VAS 455–456, LM3; GU/RSR/VAS 604, Rm1; GU/RSR/VAS 605, Lm1; GU/RSR/VAS 603, Lm2.

Horizon and locality: Lower Eocene (Ypresian) Cambay Shale, Vastan lignite mine (N 21°25’59”, E 73°06’59”), 40 km northeast of Surat, Gujarat, western India.

Table 1. Measurements (in mm) of isolated upper and lower cheek teeth of *Meldimys musak* sp. nov., from the lower Eocene of Vastan, Gujarat, western India (holotype in bold).

Specimen	Tooth	Length	Width	Trigonid width	Talonid width
GU/RSR/VAS 608	dP4	1.60	2.0	–	–
GU/RSR/VAS 606	P4	1.70	2.0	–	–
GU/RSR/VAS 128	M1	1.90	2.15	–	–
GU/RSR/VAS 449	M1	2.10	2.50	–	–
GU/RSR/VAS 450	M2	2.10	2.60	–	–
GU/RSR/VAS 454	M2	2.10	2.60	–	–
GU/RSR/VAS 609	M2	2.25	2.50	–	–
GU/RSR/VAS 451	M3	2.35	2.10	–	–
GU/RSR/VAS 452	M3	2.30	2.20	–	–
GU/RSR/VAS 453	M3	2.05	2.0	–	–
GU/RSR/VAS 455	M3	2.30	2.20	–	–
GU/RSR/VAS 605	m1	2.20	–	1.70	1.80
GU/RSR/VAS 604	m1	2.30	–	1.75	1.95
GU/RSR/VAS 603	m2	2.35	–	1.90	2.0

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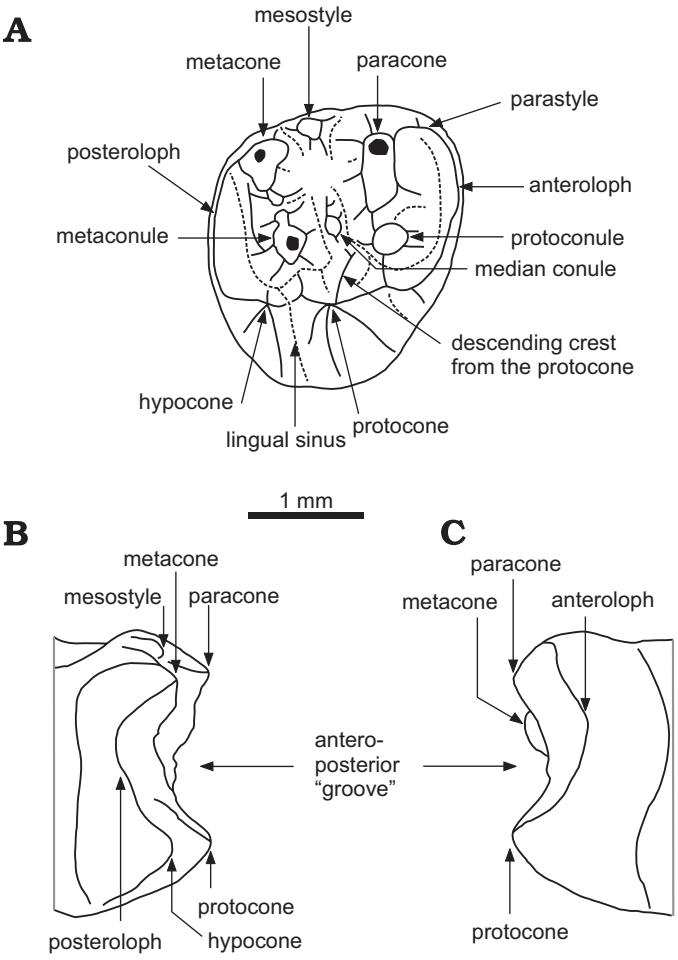

Fig. 2. Ailuravine rodent *Meldimys musak* sp. nov., GU/RSR/VAS 609 (holotype) from the lower Eocene Cambay Formation at Vastan (Gujarat, western India), upper molar showing described characters in occlusal (**A**), postero-lateral (**B**), and antero-lateral (**C**) views. Anterior is to the right in A.

Diagnosis.—Teeth similar in size and occlusal morphology to *M. louisi*. Differs from *M. louisi* in having P4 with strong metaloph; upper molars with a small median conule between protoloph and metaloph and less buccally projecting mesostyle; M1 with less prominent parastyle positioned almost in line with paracone rather than being buccally extended; M2 with less rounded occlusal outline and a protocone usually more anteriorly situated compared to the more central protocone of *Meldimys louisi;* posterior width of M3 less short than in *M. louisi*; M3 with sub-complete metaloph and reduced lingual sinus (between hypocone and protocone); m1–2 with antero-posteriorly reduced trigonid and weaker anterolophid and "waist" (= slight constriction between trigonid and talonid), and no paralophid (= metalophulid I) and metalophulid II; talonid cusps considerably lower than trigonid cusps.

Description.—The dP4 and M1–M3 are triple-rooted; P4 is double-rooted, its postero-labial root fused with the lingual root. The m1–2 are double-rooted. The p4 and m3 are not represented in our collection. The dP4 is triangular, transversely elongated (L/W = 0.86), quite narrow lingually and somewhat heart-shaped with a faint notch (ectoflexus) in the labial margin. Its paracone is large, slightly labially placed in comparison to the metacone and also posteriorly shifted, leaving a wide shelf anterior to the protoloph. The hypocone represented by an elongated ridge is much lower than the protocone. The protoconule is anteriorly placed rather than aligned with the paracone and protocone.

P4 is somewhat globular with a convex anterior contour and a centrally slightly concave posterior contour. The protoloph is nearly transverse, the metaloph strong and oblique and the paracone posteriorly shifted as in dP4. It differs from dP4 in being more ovoid, and in having a thick and labially extended anteroloph, a short posteroloph restricted to the lingual half, and a more noticeable hypocone. Its lingual aspect is broad and rounded rather than narrow as in dP4.

Upper molars have occlusal surfaces somewhat concave in lateral profile, forming a shallow "groove" along their antero-posterior median line (Figs. 3, 4C–G, and 5A–D). M1 is narrow lingually, its labial half has a rounded contour. The anteroloph, posteroloph, protoloph, and metaloph are distinct. The protocone is the largest cusp; the paracone is massive and tetrahedral but slightly transversely elongated, much larger than the metacone, and medially shifted relative to the labial margin of the tooth. The protocone and paracone are equally high from the crown base. The parastyle is strong and extends more labially than the paracone. The mesostyle is also quite prominent and labially projecting relative to paracone and metacone. The hypocone is moderately developed and noticeably lower than the protocone. The metaconule is better developed than the protoconule. A long sloping shelf occurs anterior to the protoloph. In unworn teeth a short crest originates from the protocone and descends into the trigon; a distinct conule is present in the middle of trigon. A weak sinus is lingually situated between protocone and hypocone.

M2 is slightly larger than M1 with a somewhat rounded contour and better developed hypocone than in other upper teeth. The paracone is labio-lingually elongated, the parastyle and metastyle distinct and the mesostyle labially protruded. The metaconule is much larger than the protoconule. A crest arises from the protocone and descends into the trigon basin extending beyond the protoconule and metaconule and directed towards the mesostyle. A small conule in the trigon basin between the protoconule and metaconule is more distinct than in M1. It is usually isolated but lies close to the buccal end of the crest that descends into the basin. The anteroloph and posteroloph are prominent. The lingual sinus between the hypocone and protocone is more pronounced than in M1.

M3 is triangular with subequal length and width. Its paracone is large and labio-lingually elongated as in the more anterior molars. The hypocone is small but distinct in most teeth and slightly labially positioned relative to the protocone (Fig. 4B, C). Anteroloph and posteroloph are prominent; the latter is generally smooth but somewhat uneven in GU/RSR/VAS 452 and 455 (Fig. 4A, C, D). The difference in size of the metaconule and protoconule is less than in the anterior molars though the metaconule is still larger than the proto-

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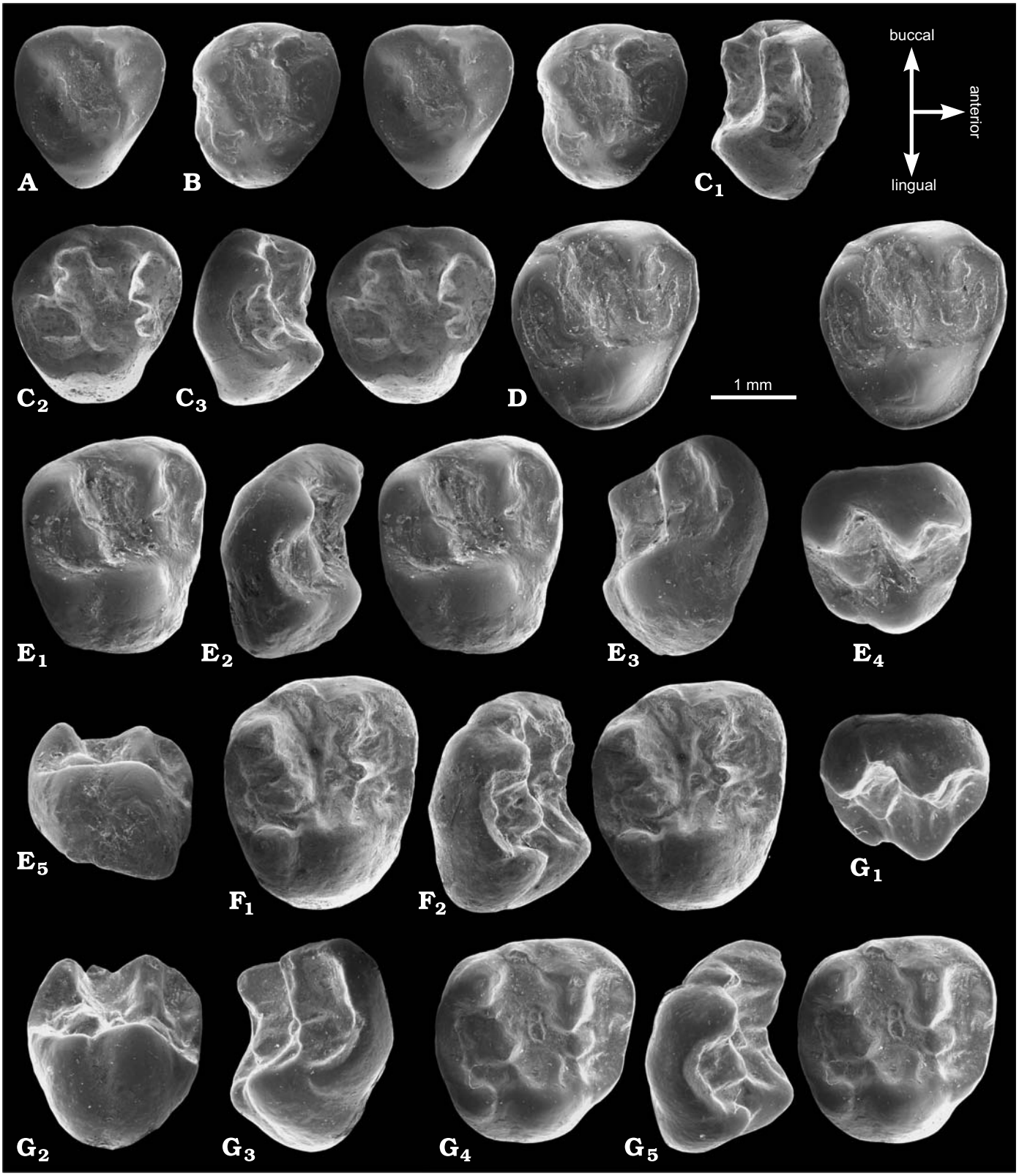

Fig. 3. Ailuravine rodent *Meldimys musak* sp. nov., from the lower Eocene Cambay Formation at Vastan (Gujarat, western India), isolated cheek teeth. **A**. GU/RSR/VAS 608, right dP4, paratype, stereo pair in occlusal view. **B**. GU/RSR/VAS 606, left P4 (reversed), paratype, stereo pair in occlusal view. **C**. GU/RSR/VAS 128, left M1 (reversed), paratype in anterior (C_1), occlusal (C_2 stereo), and posterior (C_3) views. **D**. GU/RSR/VAS 449, right M1, stereo pair in occlusal view. **E**. GU/RSR/VAS 454, right M2 in occlusal (E_1 stereo), posterior (E_2), anterior (E_3), buccal (E_4), and lingual (E_5) views; **F**. GU/RSR/VAS 450, right M2 in occlusal (F_1 stereo) and posterior (F_2) views. **G**. GU/RSR/VAS 609, right M2, holotype in buccal (G_1), lingual (G_2), anterior (G_3), occlusal (G_4 stereo), and posterior (G_5) views.

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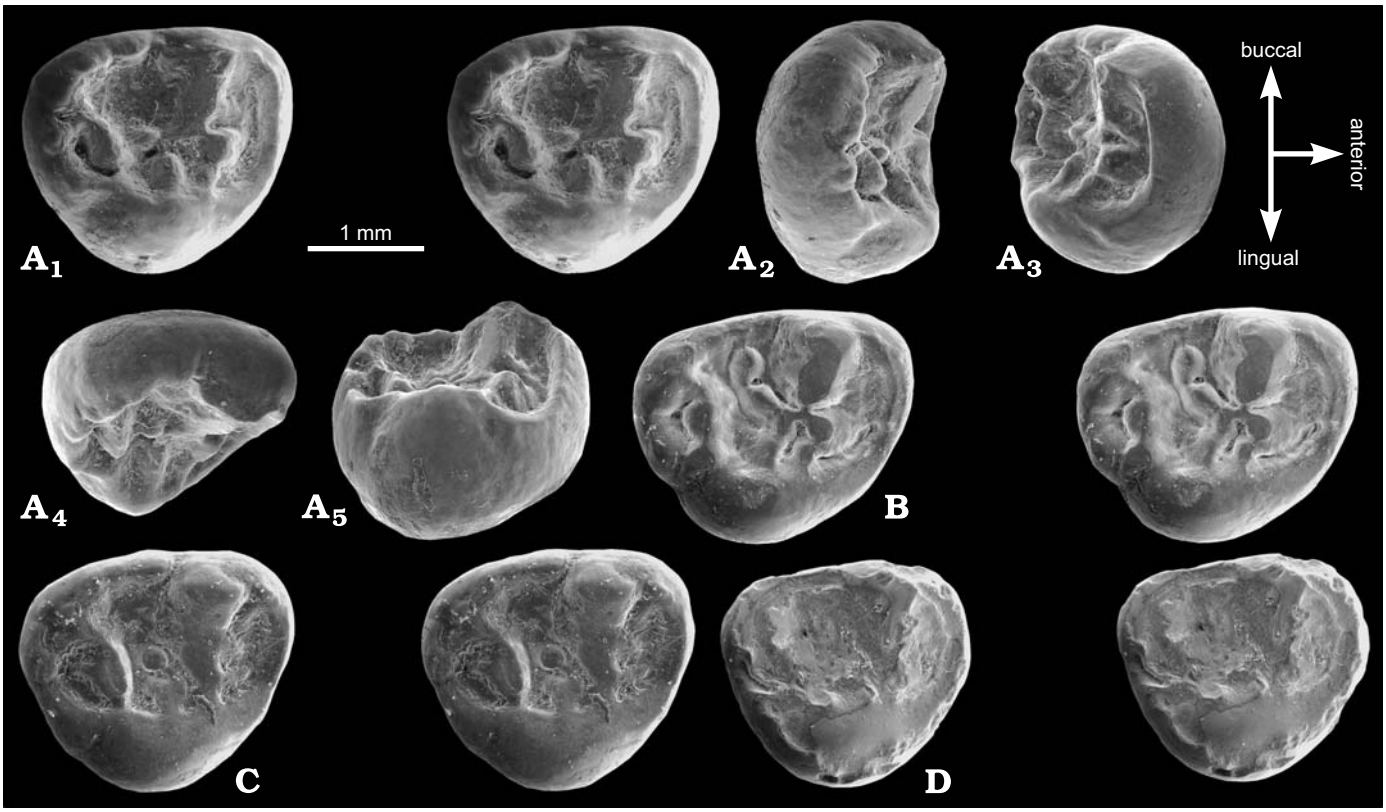

Fig. 4. Ailuravine rodent *Meldimys musak* sp. nov., from the lower Eocene Cambay Formation at Vastan (Gujarat, western India), isolated cheek teeth. **A**. GU/RSR/VAS 455, left M3 (reversed) in occlusal (A_1 stereo), posterior (A_2), anterior (A_3), buccal (A_4), and lingual (A_5) views. **B**. GU/RSR/VAS 451, right M3, paratype, stereo pair of occlusal view. **C**. GU/RSR/VAS 452, right M3, stereo pair of occlusal view. **D**. GU/RSR/VAS 453, right M3, stereo pair of occlusal view.

conule. The posterior part of the occlusal surface is characterized by the presence of a small depression bounded anteriorly by the metaloph and posteriorly by the posteroloph, both of which converge on the metacone on one side and the hypocone on the other. The median crest that descends into the trigon basin from the protocone and a small conule in the center of the trigon basin are generally very clearly seen in all M3s. The median crest extends almost up to the mesostyle in at least one tooth (GU/RSR/VAS 451; Fig. 4B), in which the central conule appears to be a part of this crest. The mesostyle and parastyle are nearly as distinct as in anterior molars. The lingual sinus between the hypocone and protocone is weak.

Our collection has only three lower cheek teeth, all of which are quite worn and or partly damaged. In m1, the trigonid is antero-posteriorly reduced, the anterolophid is weak, and talonid cusps are considerably lower than trigonid cusps. They lack a paralophid (= metalophulid I), while the metalophulid II is either absent or not discernible due to strong wear.

The m1 has a distinct "waist" (constriction) between the trigonid and the wider talonid (Fig. 5A). The metaconid is the highest cusp, and entoconid the smallest and lowest. The protoconid is larger than the metaconid and somewhat posteriorly placed in comparison to the latter. The hypoconid is massive, and hypoconulid tiny, almost merged into the posterolophid. An ectolophid is short but well developed, particularly posteriorly; it bears a distinct mesoconid which is connected to the hypoconid but separated from the protoconid. An anterolophid is poorly developed. A faint hypolophid can be seen in one of the two m1's (GU/RSR/VAS 604; Fig. 5A). A deep talonid notch is present between the entoconid and metaconid along the lingual margin of tooth.

The m2 differs from the m1 in having more widely separated protoconid and metaconid, a hypoconid smaller than the protoconid, better developed ectolophid and anterolophid, a much shallower talonid notch between entoconid and metaconid and a clearer yet weak hypolophid, and in lacking a "waist" between the trigonid and talonid. It has a faint metastylid.

Comparisons.—The new Indian rodent is referred to the subfamily Ailuravinae (Family Ischyromyidae) based on distinctive occlusal morphology of its cheek teeth—upper molars with relatively less developed hypocone (primitive character), tetrahedral paracone, strongly developed parastyle, distinct and externally extended mesostyle and a short crest ascending from the protocone into the trigon basin, and lower molars with a large mesoconid connected to the hypoconid by a strong ectolophid, and an isolated entoconid connected to a smaller hypoconulid. Most of these characters are not present in chapattimyids and yuomyids (Ctenodactyloidea), which include all middle Eocene rodents reported thus

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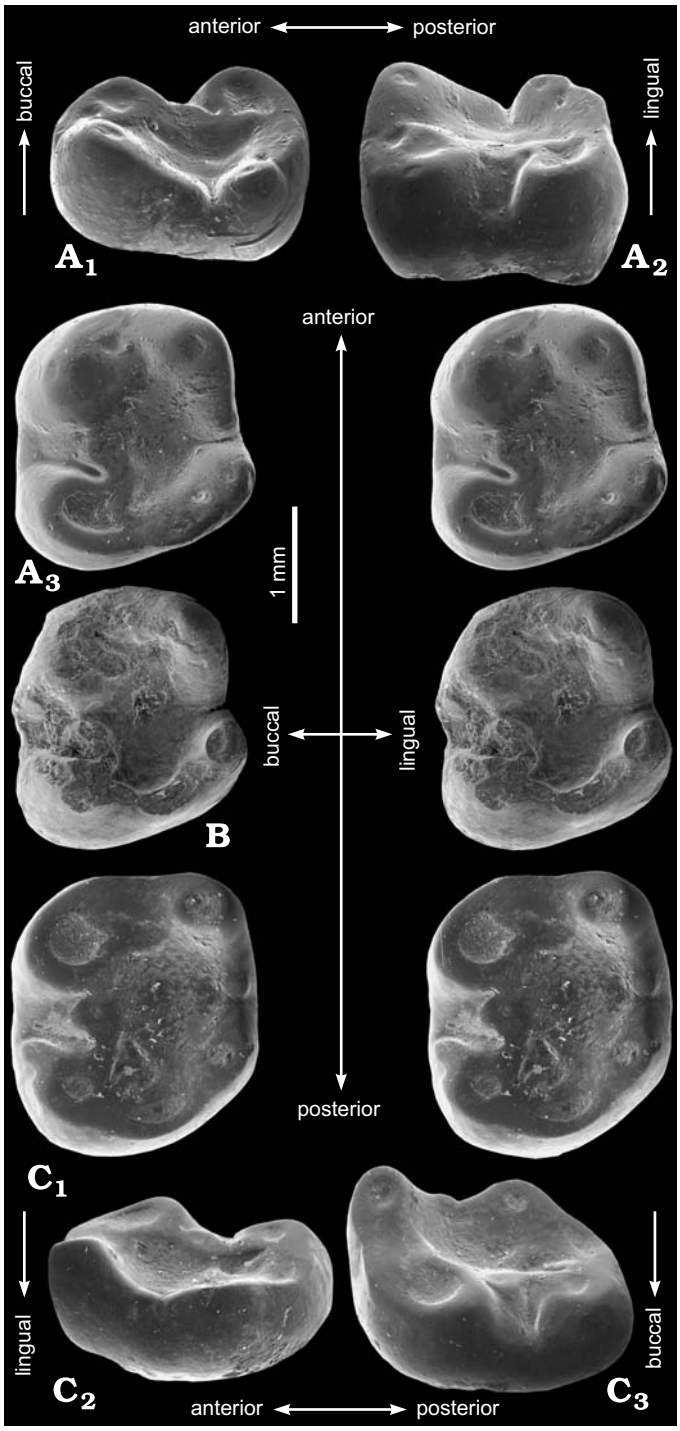

Fig. 5. Ailuravine rodent *Meldimys musak* sp. nov., from the lower Eocene Cambay Formation at Vastan (Gujarat, western India), isolated cheek teeth. **A**. GU/RSR/VAS 604, right m1, paratype in lingual (A_1), buccal (A_2, reversed), and occlusal (A_3 stereo, reversed) views. **B**. GU/RSR/VAS 605, left m1, stereo pair of occlusal view. **C**. GU/RSR/VAS 603, left m2, paratype in occlusal (C_1 stereo), lingual (C_2, reversed), and buccal (C_3) views.

far from India and Pakistan (Hussain et al. 1978; Kumar et al. 1997a, b). Similarly they are not seen in other contemporary ctenodactyloids such as ctenodactylids known from Central Asia (e.g., Dawson et al. 1984). Among the five known ailuravine genera (*Ailuravus*, *Euromys*, and *Meldimys* from Europe and *Mytonomys* and *Eohaplomys* from North America), the Indian ailuravine from Vastan is closer to European forms than to North American forms, and particularly closer to *Euromys* and *Meldimys* than to *Ailuravus*. It differs from *Ailuravus*, the type genus of Ailuravinae, in being smaller and having cheek teeth with rounded occlusal outlines and less sharp-pointed cusps. It shows relatively less developed parastyle and hypocone on upper cheek teeth and less developed trigonid basin and hypoconulid on lower teeth. *Ailuravus* is characterized by upper molars with very well developed parastyle and small but fairly developed and moderately high hypocone clearly separated from the protocone by a sinus (Escarguel 1999: pl. 1: a–c; pl. 2: a–h), and by lower molars with very well developed trigonids having distinct anterolophid and metalophulid II, a distinct hypoconulid and a lophulid between the hypoconulid and the entoconid (Escarguel 1999: pl. 1: j–r).

The Indian ailuravine is closely comparable to *Euromys* and *Meldimys* known from the lower Eocene localities of Mutigny (dated at 51.8±0.16 Ma; Escarguel et al. 1997), Avenay (dated at 52±0.17 Ma; Escarguel et al. 1997) and Condé-en-Brie (dated at 52.1±0.37 Ma; Escarguel et al. 1997) in the Paris Basin (France), and is most similar to the latter. Features including rounded occlusal outlines, lower crown height, a hypocone noticeably lower than the protocone, a markedly concave occlusal surface creating a "groove" along the antero-posterior median line, and protocone and tetrahedral paracone reaching nearly the same level above the crown base, are clearly indicative of its closer affinity to *Meldimys* than to *Euromys*. In contrast to *Euromys*, the Indian ailuravine has lower molars with a better developed trigonid and a hypoconulid more strongly connected to the hypoconid. The upper molars of the Indian ailuravine differ from those of *Euromys* mainly in having poorly developed hypocone and lingual sinus and in the relative size of the metaconule and protoconule; in the new taxon the metaconule is considerably larger than the protoconule whereas in *Euromys* the two conules appear subequal. Among the four known species of *Euromys*, *E. cardosoi* (Estravís, 2000) (for generic assignment see Escarguel 1999) is similar in tooth size to *M. musak* sp. nov., but *M. musak* appears morphologically more similar to *E. thaleri* (Michaux, 1964) (Escarguel 1999).

Prior to this report, *Meldimys* was represented by a single species, *M. louisi* (considering that the species *E. cardosoi* from the earliest Eocene of Silveirinha, Portugal, cannot be referred to this genus; Escarguel 1999, contra Estravís 2000), which has cheek teeth remarkably similar to those of the new Indian species *M. musak*. *M. musak* is presently represented by dP4, P4–M3, and m1 and m2 but m1–m2 are too worn or damaged to allow detailed comparisons with those of *M. louisi.* The dP4 of *M. musak*, though also quite worn, is almost indistinguishable from that of *M. louisi* (Fig. 6A) illustrated and described by Escarguel (1999: pl. 3: d) except in having a weaker central notch in the labial outline of the occlusal surface and a somewhat more posteriorly positioned paracone. The dP4 in

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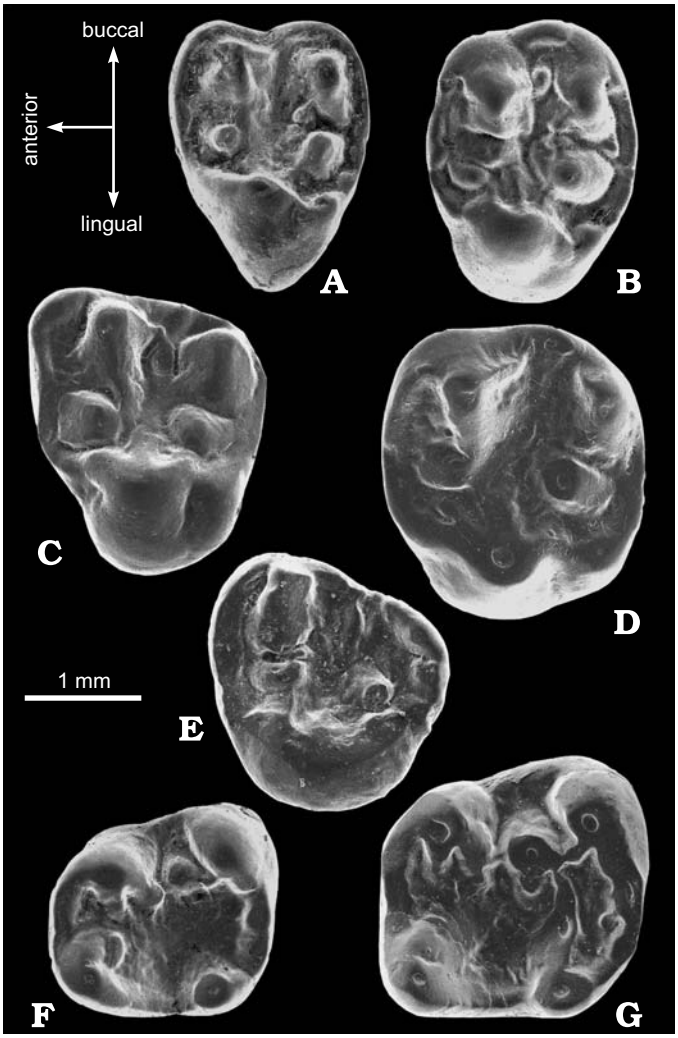

Fig. 6. Ailuravine rodent *Meldimys louisi* (Michaux, 1964) from the lower Eocene of Paris Basin (France) (from Escarguel 1999). Isolated cheek teeth in occlusal views. **A**. UM2-727, left dP4 from Avenay (Escarguel 1999: pl. 3: d). **B**. MNHN-PL-164, right P4 (reversed) from Avenay (Escarguel 1999: pl. 3: e). **C**. MNHN-PL-186, right M1 (reversed) from Mutigny (Escarguel 1999: pl. 3: a). **D**. MNHN-15799, right M2 (reversed) from Avenay (Escarguel 1999: pl. 3: g). **E**. MNHN-PL-1090, left M3 from Mutigny (Escarguel 1999: pl. 3: c). **F**. MNHN-PL-825, right m1 from Avenay (Escarguel 1999: pl. 3: m). **G**. MNHN-5737, right m2 (type) from Avenay (Escarguel 1999: pl. 3: n).

M. louisi is generally heart-shaped (Fig. 6A; Escarguel 1999: pl. 3: d; pl. 4: f) due to its narrow lingual aspect and a prominent central notch in the broader labial aspect, but this character (heart shape) is variable—dP4 of *Meldimys* is not always heart–shaped (Escarguel 1999: pl. 2: o). In fact a more or less heart-shaped dP4 is "archetypal" for the Ailuravinae and is probably plesiomorphic within rodents. This trait, amongst others (all plesiomorphic), led Hartenberger (1995) to propose inclusion of the Ailuravinae, together with *Alagomys* and *Tribosphenomys*, within the Alagomyidae. This proposition was based on a very limited cladistic analysis of selected taxa and characters and is now considered untenable (Dawson 2003; Marivaux et al. 2004).

The only known P4 of *M. musak* sp. nov., is more rounded than dP4 with a width/length ratio of 1.3. Compared to this, the P4 of *M. louisi* is generally ovoid with rounded margins and maximum length and width along the median lines (Fig. 6B; Escarguel 1999: pl. 2: p; pl. 3: e), but some are transversely elongated with high (1.4) width/length ratio and others rectangular with low (1.2) width/length ratio (Escarguel 1999: pl. 4: a, g). The anteroloph and posteroloph in P4 of the new species are marginally higher, the metaloph is stronger and the hypocone is clearly more lingually placed relative to the protocone than in *M. louisi*. In addition, in the single known P4 of *M. musak* the postero-labial root is fused with the lingual root, whereas in *M. louisi* the lingual root is separate and the two labial roots are fused together. However, based on a single specimen it is difficult to assess if this rather unusual configuration is really apomorphic in *M. musak* or just a teratological, unrepresentative state for this isolated tooth.

Among the anterior upper molars of *M. musak* sp. nov., M1 differs from that of *M. louisi* mainly in having a less prominent parastyle positioned almost in line with the paracone rather than being anterolabially extended (Fig. 3C). The M1 parastyle in *M. louisi* is so strong that the anterolabial aspect of tooth appears distinctly protruded or extended (Fig. 6C). M2 of *M. musak* differs from that of *M. louisi* in having a normally positioned protocone rather than a more centrally positioned one as in most specimens of *M. louisi* (Michaux 1968; Escarguel 1999). Moreover, in *M. louisi* these teeth have a more rounded occlusal outline than in *M. musak*. M3 differs in having posterior width less short than anterior width (Fig. 4) rather than considerably shorter posterior width in two out of three M3s of *M. louisi* (Fig. 6E; Escarguel 1999: pl. 3: c, i). The metaloph on M3 of the new species is more or less continuous and better developed than in *M. louisi*, in which the metaconule appears as an isolated cone. Further, in *M. musak* the metaloph and posteroloph converge on the metacone and hypocone to form a small enclosure (Fig. 4B), which is not seen in *M. louisi.* Most upper molars of *M. musak* possess a small but distinct conule in the middle of the trigon basin between the metaconule and paraconule (Figs. $3A_1$, $4F_1$, G_4, and 5A–D). This character is lacking in *M. louisi.* The m1–2 of *M. musak* differ from corresponding teeth of *M. louisi* mainly in having an antero-posteriorly reduced trigonid and in lacking a paralophid (= metalophulid I) and metalophulid II.

Discussion

The new ailuravine from Vastan is undoubtedly closer to European than to North American ailuravines and particularly to those known from the middle lower Eocene (reference level MP 8–9) localities of Mutigny, Avenay and Condé-en-Brie in the Paris Basin. Morphologically, its teeth appear more derived than teeth of earliest Eocene ailuravines such as *Euromys cardosoi* from Silveirinha (Portugal) and *Euromys* sp. from Dormaal (Belgium), and more primitive

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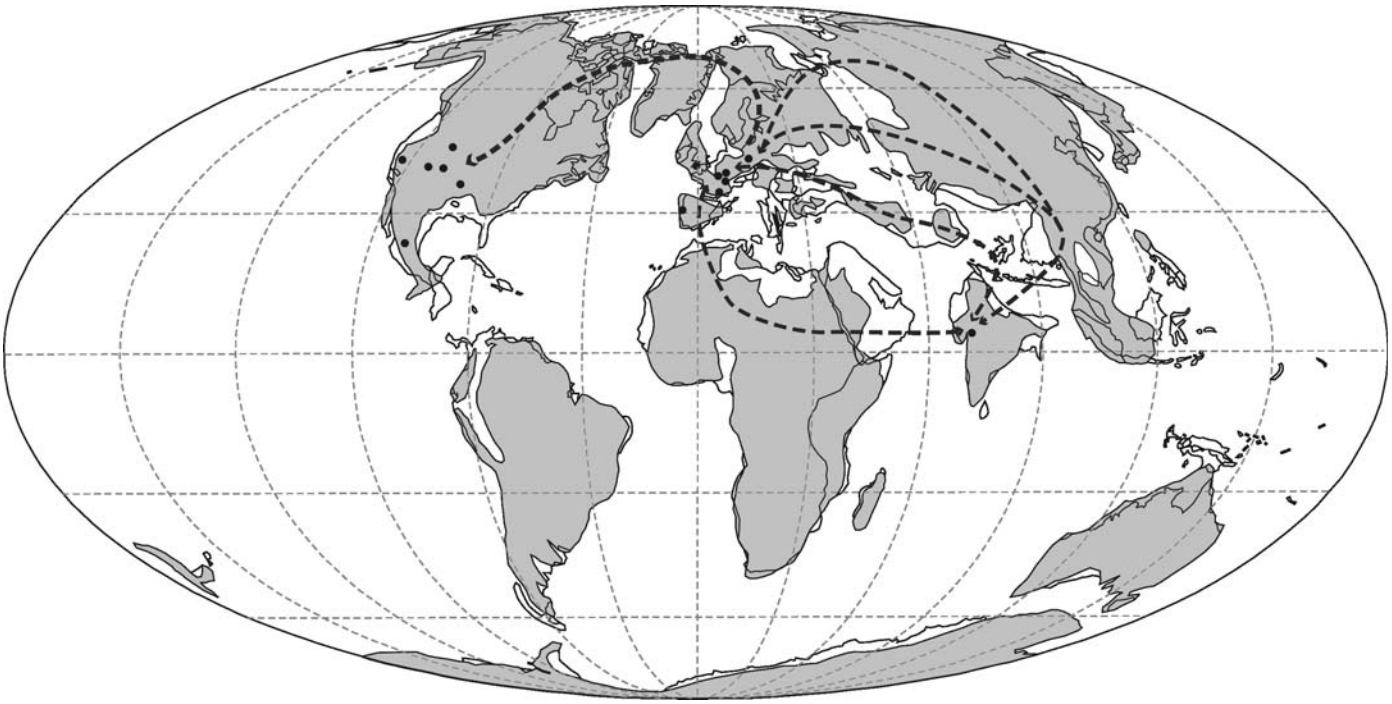

Fig. 7. Distribution of ailuravine rodents and possible routes of their dispersal during the early Eocene (based on Smith et al. 1994, with additional data mainly from Gaetani and Garzanti 1991; Gingerich et al. 1997). Black dots mark the position of Vastan in India and of ailuravine-yielding sites elsewhere; dashed lines indicate the possible/discussed dispersal routes, which include: Europe to Asia via the Turgai Strait and then to India via its leading edge (the favoured route); Europe to India via Africa and Madagascar; Europe to India directly through Turkey.

than those of the late early Eocene species *E. inexpectatus* Escarguel, 1999 and *Ailuravus michauxi* Hartenberger, 1975 from Prémontré in the Paris Basin. Occlusal surface characters of upper cheek teeth, such as trigon shape, relative size of protoconule and metaconule, transversely elongated paracone, and labially protruded mesostyle, are highly suggestive of the same evolutionary stage for *Meldimys musak* sp. nov., as seen in *M. louisi* and *E. thaleri* at ca. 52 Ma (middle early Eocene) in western Europe (Paris Basin localities). These ailuravine rodent assemblages are clearly different from those known at the same time in North America, which include the species ?*Mytonomys coloradensis* (Wood, 1962) from the lower to upper Wasatchian of Colorado and Wyoming, and *M. wortmani* (Wood, 1962) from the upper Wasatchian ("Lostcabinian") of Wyoming (Wood 1962; Korth 1984, 1988, 1994). ?*M. coloradensis* and *M. mytonensis* (Wood, 1962) from the Uintan and *M. robustus* (Peterson, 1919) from the Uintan and Duchesnean are noticeably more derived in their tooth morphology than *Euromys* and *Meldimys*. However, *M. wortmani* has rather primitive tooth morphology and shares many characteristics with the earliest Eocene species *Euromys cardosoi* and *E. thaleri* as well as with the middle to late early Eocene species *Ailuravus michauxi*. It cannot, however, be closely compared with *Meldimys louisi* and *M. musak*.

Eocene beds of the northern parts of the Indian subcontinent have produced a well known rodent fauna, most assemblages (e.g., Kalakot and Subathu in India and Ganda Kas in Pakistan) being of an early middle Eocene age and some levels (e.g., Barbara Banda in Pakistan) believed to be early Eocene in age. The middle Eocene assemblages comprise chapattimyids and yuomyids (ctenodactyloids), but the lower Eocene locality (Barbara Banda) has yielded only a few isolated teeth of indeterminate ctenodactyloids and a p4 of an ischyromyoid (de Bruijn et al. 1982: fig. 6). In the light of the new early Eocene ailuravine from India, the affinity of the ischyromyoid Rp4 from Barbara Banda must be reexamined here. A comparison of this tooth with p4's of known ischyromyoids from Europe and North America suggests that it is neither a paramyine nor a reithroparamyine (inclusive of *Microparamys*). The overall occlusal shape and arrangement of cusps, most particularly its anterior part, simple trigonid with well separated proto- and metaconid, a weak connection between the hypoconulid and the entoconid, a hypoconulid completely merged into the posterolophid, and presence of a mesostylid, which is variable but rather frequently observed tiny cusp in *Meldimys louisi* as well as *M. musak* (e.g., Escarguel 1999: pl. 3: j, and Fig. 5A, C herein) support an ailuravine affinity for this tooth. However, its smaller size [closely corresponding to p4 of *Pseudoparamys teilhardi* (Wood, 1962), but ca. 30% smaller than that of *M. louisi* and ca. 10% smaller than that of *Euromys cardosoi*, the smallest ailuravine species described to date], small length/width ratio, very strong anterior part of the ectolophid (posterior arm of the protoconid), a seemingly weak mesoconid totally fused with the ectolophid, and rectilinear (not rounded) posterior side favour a pseudoparamyine affinity (see *Pseudoparamys teilhardi*, Escarguel 1999: pl. 12: l). Al-

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though the possibility that this p4 belongs to a small ailuravine species cannot be eliminated, at present it seems more likely that it belongs to a species close to *Pseudoparamys teilhardi* than to an ailuravine. It is pertinent to mention here that both ailuravines and pseudoparamyines are likely to have shared the same biogeographical history. They are well diversified European groups known very early in the Eocene with a subsequent diversification in North America (*Mytonomys* and *Eohaplomys* for Ailuravinae and *Franimys* for Pseudoparamyinae). Now that there is an Indian ailuravine, also having a pseudoparamyine in the subcontinent makes a good working hypothesis rather than appearing unusual.

The occurrence of only chapattimyid and yuomyid (ctenodactyloids) rodents from the middle Eocene localities of the subcontinent and of some indeterminate cocomyids and paramyines from a single lower Eocene locality led several workers (Hussain et al. 1978; de Bruijn et al. 1982; Hartenberger 1982b; Kumar et al. 1997a, b) to believe that these mainly northern middle Eocene assemblages reflected the first immigrants from Central Asia following the Tethyan withdrawal, because similar forms had earlier been reported from the erstwhile USSR (Shevyreva 1976). However, the Vastan assemblage, which may be diachronous in age to the more northerly localities (e.g., Barbara Banda in Pakistan), offers evidence that ailuravine rodents were widespread across the Holarctic region. The presence of primitive ailuravines in lower Eocene strata of India is tantalizing and unexpected. It opens the possibility that the subfamily could have originated in southern Asia rather than Europe, as suggested by previous evidence. However, it does not provide further insight on rodent origins and dispersal because the Vastan material comes from a single horizon and there are no data for the basal-most Eocene or Palaeocene on the Indian subcontinent.The affinities of the pre-Palaeocene mammals known from India are also obscure.

Whether or not the Indian ailuravines were replaced by the chapattimyids when the latter appeared in India in the early middle Eocene (~48–47 Ma) is not known. From dental morphology it is apparent that ailuravines and chapattimyids (Ctenodactyloidea) did not share ancestor-descendant relationship, implying that at least two groups of Eocene rodents lived in the subcontinent, but whether they lived together at any point of time is not known. Judging by the European example the ailuravines lasted in Europe at least until the latest middle Eocene (MP 16 = late Bartonian), whereas they are not found in known early middle Eocene faunas of the Indian subcontinent. In North America, ailuravines are known throughout the Eocene, from Wasatchian to Chadronian Land Mammal Ages, showing the highest diversity during Uintan times (Wood 1962, 1980; Korth 1984, 1988, 1994).

The occurrence of a rodent genus common to two areas as widely separated as Europe and India during the early Eocene presents a palaeobiogeographic problem. We note that *Meldimys* is neither the first nor the only European genus that has been recognized in the Eocene of India. Another well known European (and North American) genus *Diacodexis,* a dichobunid artiodactyl, has been known from the lower middle Eocene beds of India and Pakistan for about a quarter of a century (Thewissen et al. 1983; Kumar and Jolly 1986). Recently diacodexeine material has also been recorded (Bajpai et al. 2005) from the same horizon which produced the new ailuravine described here. Though Bajpai et al. (2005) referred it to a new genus and species, *Gujaratia indica*, neither this species nor *G. pakistanensis* (Thewissen, Russell, Gingerich, and Hussain, 1983) (originally allocated to *Diacodexis*) is sufficiently distinct from *Diacodexis* to justify generic separation (see also Kumar 2006). Apart from *Meldimys* and *Diacodexis*, three genera (from three families) of chiropterans (*Hassianycteris*, *Archaeonycteris*, and *Icaronycteris*) are also common to India and Europe (Smith et al. 2006b, 2007).

The faunal similarity between Vastan in India and the Paris Basin in France at the middle–late early Eocene is somewhat comparable to the resemblance between Dormaal in Belgium and the Wasatchian-0 (Wa-0) interval in North America at the earliest Eocene (Smith et al. 2006a). In the context of this apparent similarity between Indian and European early Eocene mammal taxa, it is interesting to note that Godinot and Lapparent (2003) recently presented arguments favouring mammalian and reptilian dispersal from Asia to Europe during the Palaeocene/Eocene boundary interval. Earlier, Escarguel (1999: fig. 24) proposed a four-phase palaeobiogeographical hypothesis, based primarily on rodents, of which the first phase is of particular relevance here. It envisaged (1) migration of alagomyid and ischyromyid rodents (no ailuravines) at ca. 56.5 Ma, (Ti6/Cf1 limit, latest Palaeocene) from Asia to North America, and (2) arrival around the same time in Europe (exclusively in peri-Tethyan domain) from Asia of ailuravines, the incertae sedis *Corbarimys*, as well as artiodactyls, perissodactyls, and hyaenodontids. The latter hypothesis, consistent with the new evidence, offers an alternative to Beard's (1998, 2002) "East of Eden" hypothesis on origin and dispersal of mammals at the Palaeocene/ Eocene boundary.

Previously a direct faunal dispersal between Asia and Europe was considered untenable because of the existence of the West Siberian Sea or Obik Sea and Turgai Strait acting as formidable physical barriers. However, recent studies of late Palaeocene–early Eocene dinoflagellate cysts and the sequence stratigraphy of the Turgai region have revived the possibility of such a dispersal owing mainly to drop in sea level as well as climatic factors (Iakovleva et al. 2001). Similarly, Hooker and Dashzeveg (2003), based on cladistic analysis and palaeogeographic reconstructions, recognized at least three cases of multiple land mammal dispersal across the Turgai Straits from Asia to Europe in the late Palaeocene and early Eocene. More recently Smith et al. (2006a) concluded that the earliest Eocene primate *Teilhardina*, known from all three northern continents, originated in Asia and quickly dispersed westwards to Europe and from there to North America.

In recent years several studies have favoured an "Out of India"/"Out of Asia" hypothesis for the origin and dispersal of various mammals, reptiles and amphibians as well as some plants (e.g., Krause and Maas 1990; Bossuyt and Milinkovitch

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2001; Bowen et al. 2002; Conti et al. 2002; Gower et al. 2002; Karanth 2006) based partly on other evidence suggesting Asia to Europe dispersal around the Palaeocene/Eocene boundary. Whether this dispersal was bidirectional or just one way is not known because other than the evidence of ailuravines and *Diacodexis*, there is little to suggest Europe to Asia dispersal around the same time. The problem with the presently available evidence from Vastan is that it comes from a single level and site. The assumption of ailuravines, diacodexines and other mammals reaching India from Europe raises the question of what route was taken—Europe to Asia via the Turgai Strait and then to India via its leading edge, Europe to India via Africa and Madagascar, or Europe to India directly through Turkey? So far *Meldimys* (and more generally ischyromyoids) and *Diacodexis* have neither been reported from central or western Asia nor from Africa-Madagascar to support either of the two possibilities (the validity of the record of diacodexeine from Asia by Gabunia 1973, is unknown). The middle Eocene mammalian faunas of the Indian subcontinent are known to be more endemic than cosmopolitan, though their migratory elements clearly show North American and Eurasian and particularly the Central Asian influx, and little or no African influence (Kumar 2001). Similarly the early Eocene mammalian fauna reported thus far from Vastan, does not show any notable relationship with African faunas. This may seem to weaken or negate the possibility of incoming migrants having taken the African route during the Eocene, but we know so little of the African Eocene record that negative evidence means a little. The Asia-North America connection, which is important for several other mammals at the beginning of the Eocene, is less pertinent for the Indian ailuravine, which is clearly more closely related to European than to the North American forms. Proponents of Asia to Europe dispersal around the Palaeocene/Eocene (PE) boundary generally cite global warming (the Palaeocene/Eocene Thermal Maximum or PETM) as the driving force for northward migration of faunas. This would support the origin of *Meldimys* and *Diacodexis* in India in the earliest Eocene and northward migration to Europe later, and at the same time would explain the lack of substantial Europe to Asia dispersal. At present there is no way to test any of these hypotheses, and waiting for new discoveries particularly in southeast and western Asia seems to be the only option. The distribution of Eocene ailuravine rodents and possible routes of their dispersal are depicted in Fig. 7.

While debating mammalian palaeobiogeography, the timing of India-Asia collision must also be considered. Presently there are two hypotheses, one favouring collision around the Palaeocene/Eocene boundary and the other around the Cretaceous/Tertiary (K/T) boundary. So far there is not enough palaeontological evidence to accept or negate definitively either of these hypotheses. Yet if faunal interchange between India and the northern continents and especially between India and Europe can be demonstrated in the early Eocene, it will be an argument favouring a land connection between India and Asia around the Palaeocene/Eocene boundary if not earlier.

Conclusions

Ailuravine rodents are reported for the first time from outside Europe and North America, indicating their widespread distribution in the Eocene. The Indian ailuravine, a new species of European genus *Meldimys*, is morphologically closer to European lineages than to North American lineages. *Meldimys musak* sp. nov., is more derived than the earliest Eocene ailuravines *Euromys cardosoi* and *Euromys* sp., which occur close to the Palaeocene/Eocene boundary in Portugal and Belgium respectively, and more primitive than the late early Eocene species *E. inexpectatus* and *Ailuravus michauxi* occurring during the late early Eocene in the Paris Basin. In grade of evolution it closely corresponds to *E. thaleri* and *M. louisi*, which occur at ~52 Ma in the Paris Basin (Western Europe).

Contrary to the earlier belief based on data from sub-Himalayan localities in India and Pakistan (Hussain et al. 1978; de Bruijn et al. 1982; Hartenberger 1982a; Kumar et al. 1997a, b), the oldest fossil rodents from India belong to the cosmopolitan Ischyromyidae rather than to the endemic Chapattimyidae, and so far there is no evidence to know whether these two groups lived together at any point of time.

The Indian ailuravine-yielding section at Vastan mine is chronologically closer to Paris Basin (France) sections than to Dormaal (Belgium) and Silveirinha (Portugal) as indicated by closely similar dental morphology of European *M. louisi* and Indian *M. musak* sp. nov., and the common presence of *Diacodexis* and some bat genera in the two sections. The faunal similarity between Vastan in India and the Paris Basin in France at the middle–late early Eocene is comparable to the resemblance between Dormaal in Belgium and the Wasatchian-0 (Wa-0) interval in North America at the earliest Eocene.

The presence of a rodent genus common to India and Europe allows the first direct correlation between Indian and European mammal-yielding sections. Further, it shows that generic level similarities in terrestrial mammalian palaeofaunas across continents are not uncommon. The Eocene mammalian fauna known so far from India seems to have more in common with Europe than with Asia, but this could simply reflect that contemporaneous faunas are otherwise unknown (or poorly known) from southern Asia.

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Appendix 1

Main European mammal fossil-bearing localities where ailuravine rodents have been recorded (names of type populations in bold).

Geological age	Level[1]	Locality	Species
Late Bartonian	MP 16	Mormont-Eclépens (CH)	***Ailuravus stehlinschaubi***
Late Bartonian	MP 16	Robiac (F)	*Ailuravus stehlinschaubi*
Early Bartonian	MP 14	Egerkingen (CH)	***Ailuravus picteti***
Late Lutetian	MP 13	Bouxwiller (F)	*Ailuravus picteti*
Late Lutetian	MP 13	Geiseltal oMK, OHM (G)	*Ailuravus* aff. *picteti*
Early Lutetian	MP 11	Messel (G)	***Ailuravus macrurus***
Late Ypresian/Early Lutetian	MP 10	Wittering Formation (E-PB)	*Ailuravus michauxi*
Late Ypresian	MP 10	Azillanet (F)	*Euromys inexpectatus*
Late Ypresian	MP 10	Prémontré (F-PB)	***Euromys inexpectatus***, *Ailuravus michauxi*
Late Ypresian	MP 10	Mas de Gimel (F)	*Ailuravus* aff. *michauxi*
Late Ypresian	MP 10	Grauves/Cuis (F-PB)	***Ailuravus michauxi***
Late Ypresian	MP 10	Saint-Agnan (F-PB)	*Euromys inexpectatus*, *Meldimys louisi*, *Ailuravus* aff. *michauxi*
Middle Ypresian	MP 8-9	Mutigny (F-PB)	***Euromys thaleri***, *Meldimys louisi*
Middle Ypresian	MP 8-9	Avenay (F-PB)	*Euromys thaleri*, ***Meldimys louisi***
Middle Ypresian	MP 8-9	Condé-en-Brie (F-PB)	*Euromys thaleri*, *Meldimys louisi*
Early Ypresian	MP 7	Pourcy (F-PB)	*Euromys thaleri*, *Ailuravus* cf. *michauxi*
Early Ypresian	MP 7	Rians/Bauduen (F)	*Euromys* aff. *thaleri*, *Meldimys louisi*, *Ailuravus* aff. *michauxi*
Early Ypresian	MP 7	Silveirinha (P)	***Euromys cardosoi***
Early Ypresian	MP 7	Dormaal (B-PB)	*Euromys* sp.

[1] Geological ages and European "Mammal Palaeogene" (MP) reference levels: BiochroM'97 1997.
Locality countries: B, Belgium; CH, Switzerland; E, England; F, France (PB, Paris basin); G, Germany; P, Portugal. Fossiliferous units at Geiseltal: oMK, obere Mittelkohle; OHM, Oberes Hauptmittel. Species description: Michaux 1968; Hartenberger 1975; Wood 1976; Hooker 1996; Escarguel 1999; Estravís 2000.

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