



## Chapter 12

# New Specimens of *Frugivastodon* (Mammalia: Apatotheria) from the Early Eocene of India Confirm Its Apatemyid Status and Elucidate Dispersal of Apatemyidae

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**Abstract** We here describe 18 new specimens of the sole apatemyid mammal known outside North America and Europe: *Frugivastodon cristatus* from the early Eocene Cambay Shale Formation of Vastan Lignite Mine, Gujarat, India. This mammal was previously represented by a single isolated lower molar, which hindered the establishment of its relationships among Apatemyidae. The new fossils show that the Indian apatemyid is unique and represents a new morphotype among this family. It is notably characterized by mesiodistally elongated lower molars with a reduced m3, a small hypocone on the upper molars, and a transversely wider M1 than in other apatemyids. The new data supports the inclusion of the enigmatic Uintan *Aethomylos* within Apatemyidae. The Indian *Frugivastodon* and the North American *Aethomylos* might represent a distinct clade of Apatemyidae that originated around the Paleocene-Eocene boundary. A paleobiogeographic analysis suggests that *Frugivastodon* dispersed from Europe into India during the early Ypresian. We also review the dispersal events that characterized the history of Apatemyidae.

**Keywords** Insectivorous mammals • Eocene • Asia • Europe • North America • Dispersal

## Introduction

Apatemyids are small extinct mammals that have been known for approximately 150 years from both Europe (Gervais 1848–1852) and North America (Marsh 1872), but, until recently, almost exclusively from their highly specialized dentition. The dentition of apatemyids is characterized by the presence of an enlarged front tooth (generally considered to be the first incisor) in each quadrant, a reduced number of mostly small teeth between this front tooth and the first molar (the first premolar is lost, the third is greatly reduced or absent, and p2 is enlarged and bizarrely shaped), and rather low-crowned molars with broad, basined talonids (Matthew 1909; West 1973a; Gingerich 1982; Gingerich and Rose 1982).

The first skeletons were described from the lake deposits of Messel, Germany (Lutetian, MP 11 reference-level of the mammalian biochronological scale for the European Paleogene, BiochroM'97), thirty years ago (Koenigswald 1987; Koenigswald and Schierner 1987). Since this initial work, several skulls and complete articulated skeletons have been described from the Paleocene and Eocene of North America and Europe (Koenigswald 1990; Bloch and Boyer 2001; Kalthoff et al. 2004; Koenigswald et al. 2005, 2009; Silcox et al. 2010). A skull of *Sinclairella*, previously described by Jepsen (1934), was unfortunately lost more than 40 years ago (see discussion in Silcox et al. 2010). These mammals display numerous arboreal specializations (e.g., flexible ankle; unusually specialized elongate manual digits; short, deep and laterally compressed terminal phalanges; long bushy tail). More recently, cranial features including the morphology of the turbinates, bony labyrinth, and the endocranium of these mammals have been detailed thanks to

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the development of X-ray microtomography (Koenigswald et al. 2009; Armstrong et al. 2011; Silcox et al. 2011).

Apatemyids have been reconstructed as insectivorous mammals with foraging behaviours based on their peculiar features: the enlargement of the incisors and the modification of the second and third digits of the manus into elongate probes (Koenigswald 1987; Koenigswald and Schierner 1987; Bloch and Boyer 2001; Koenigswald et al. 2005). Consequently, paleomammalogists propose, in analogy with the extant lemuroid primate *Daubentonia* and the diprotodont marsupial *Dactylopsila*, that “apatemyids used their enlarged incisors to gouge into bark and rotten wood in search of wood-boring grubs and other insects, which they retrieved with their long, slender fingers” (Rose 2006, p. 104). Silcox et al. (2011) notably hypothesized a relationship between the acquisition of this specialized manual extractive feeding regime and the significant increase of brain size observed when comparing the two presently known endocasts of the Apatemyidae (the late Paleocene-early Eocene *Labidolemur kayi* and the late Eocene *Carcinella sigei*).

The relationships of the Apatemyidae among Mammalia are in dispute, with the most frequently suggested relationships being with primates or ‘insectivores’ (see notably the summaries of this debate in Jepsen (1934), McKenna (1963a), and Silcox et al. (2010)). The recent phylogenetic analysis performed by Silcox et al. (2010) suggests that apatemyids are members of Euarchontoglires rather than Laurasiatheria, a relationship previously proposed by Stehlin (1916), Heller (1930), and Simpson (1940). Silcox et al. (2010) also concluded that apatemyids do not seem to be a member of any living or fossil order and proposed that these mammals should be placed in their own order, Apatotheria, as originally suggested by Scott and Jepsen (1936).

Some 16 North American species (Gunnell et al. 2008a; Czaplewski and Morgan 2015) and 15 European species (Koenigswald et al. 2009) of apatemyids have been described so far, which are grouped among eleven genera (Fig. 12.1). Apatemyids are known from many fossil localities, but they are almost always represented by fragmentary material and are always rare faunal elements; very few localities contain specimens representing more than a few individuals (Simpson 1954; McKenna 1963a, b; Gingerich and Rose 1982). As a consequence, the morphological variability and the systematics of apatemyids have been subject to numerous debates (see the summaries of McKenna 1963a, and Russell et al. 1979), especially the number of species that can be recognized and included among *Apatemyids* (West 1973a; Gingerich and Rose 1982). Moreover,

there is little agreement regarding the relationships among apatemyids; the sole phylogenetic analysis that questioned the relationships among Apatemyidae included only the six best represented species (Silcox et al. 2010).

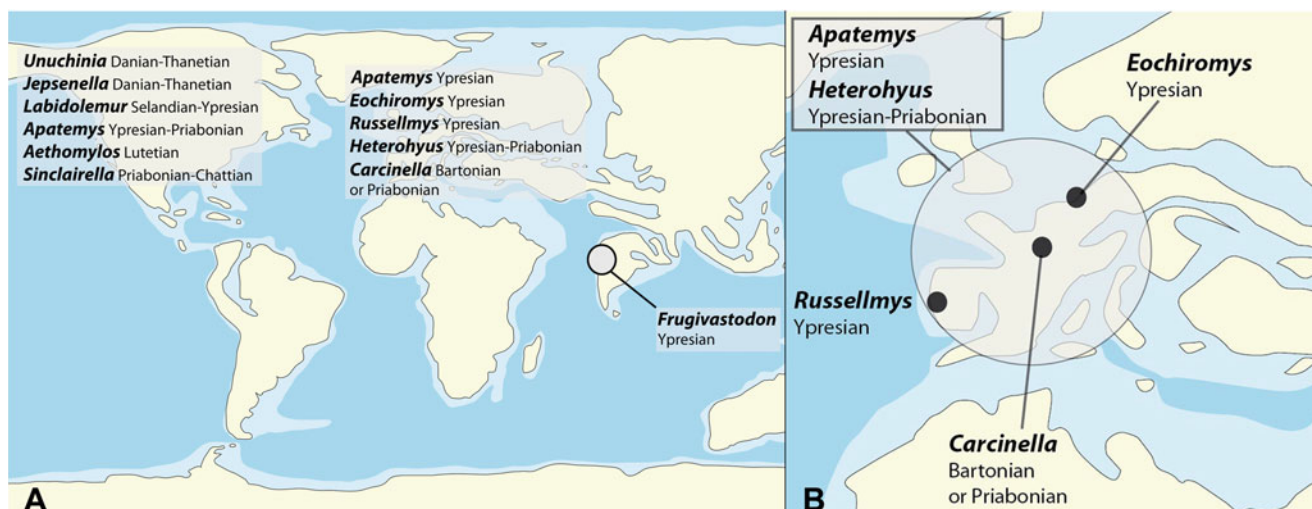
The Apatemyidae have been separated into two distinct subfamilies: Apatemyinae and Unuchiniinae. The latter subfamily includes only the Paleocene genus *Unuchinia*; Van Valen (1967) erected this subfamily because this genus represents a distinctive lineage characterized by the combination of very primitive molars for an apatemyid (molars relatively long anteroposteriorly and with tall trigonid, bladelike paracoid, and paralophid nearly straight in occlusal view) and a relatively advanced p4 (simple, and single-rooted – but *U. dysmathes* has a 2-rooted p4). However, Secord (2008) recently provided arguments that strongly support the inclusion of *Unuchinia* among Apatemyidae.

Apatemyids first appeared in the early Paleocene (Torrejanian; North American Land Mammal Age (=NALMA), To-3) of North America, represented by *Unuchinia* and the somewhat more advanced *Jepsenella* (Simpson 1937, 1940; McKenna 1963a; Szalay 1968; Gunnell 1988; Gunnell et al. 2008a). Apatemyids are recorded on this continent until the latest Oligocene (Arikarean NALMA, Ar-3) (Czaplewski and Morgan 2015). It is likely that the family originated in North America.

Apatemyids were also successful in Europe, where they underwent a moderate radiation (Russell et al. 1979). They appeared in Europe in the earliest Eocene, where they are first recorded in the locality of Dormaal (Belgium; MP7 reference-locality; Teilhard de Chardin 1927; Russell et al. 1979). Hooker (2015) recently proposed that the Dormaal fauna is latest Paleocene in age, which would imply that apatemyids have dispersed during the latest Paleocene in Europe; however, we disagree and here consider this fauna (and all the localities included among biozone PEIB *sensu* Hooker 2015) as earliest Eocene in age. The last occurrence of European apatemyids is from the late Eocene MP17b reference-level (Sigé 1975; Koenigswald et al. 2009; Hooker 2010a), and they are not known in Europe after the ‘Grande Coupure.’

The only apatemyid to be discovered in a locality situated outside North America and Europe is *Frugivastodon cristatus* from the early Eocene Cambay Shale Formation in Vastan Mine (Gujarat, India; Ypresian; c. 54.5 Ma; Bajpai et al. 2005: Fig. 1). Unfortunately, this taxon has until now been known from only a single isolated lower molar, and possibly because of the lack of information and uncertainty concerning its systematic position, it is rarely mentioned in the literature.

The Cambay Shale Formation, exposed at the Vastan open cast lignite mine near the Vastan village about 40 km



**Fig. 12.1** A Geographic and stratigraphic distribution of apatemyids, B focus on European apatemyids. Paleogeographic map adapted from Ron Blakey, Eocene (<http://www2.nau.edu/rcb7/050Marect.jpg>)

northeast of Surat, Gujarat, western India (Sahni et al. 2006: Fig. 1), is known for its well-preserved diverse fauna of terrestrial mammals as well as other vertebrates (Rana et al. 2004; Bajpai et al. 2005; Rose et al. 2006). The latter include marine and non-marine fishes (Rana et al. 2004; Nolf et al. 2006), the earliest ranid and bombinatorid frogs (Bajpai and Kapur 2008; Folie et al. 2013), agamid lizards (Prasad and Bajpai 2008; Rana et al. 2013), terrestrial and aquatic snakes (Rage et al. 2008), and oldest birds of the Indian subcontinent (Mayr et al. 2007, 2010, 2013). The mammalian fauna of the Cambay Shale Formation is represented by the earliest modern mammals from the Indian subcontinent, including the highest diversity of early bats (Rana et al. 2005; Smith et al. 2007), the earliest lagomorph (Rose et al. 2008), the first Asian ailuravine rodent (Rana et al. 2008), primitive adapoid and omomyid primates (Rose et al. 2009a; Dunn et al. 2016), primitive artiodactyls (Kumar et al. 2010), the first Indian tillodonts (Rose et al. 2009b, 2013), the oldest hyaenodontid in southern Asia (Bajpai et al. 2009; Rana et al. 2015), a primitive tapiroid perissodactyl (Smith et al. 2015), perissodactyl-like cambaytheres (Bajpai et al. 2006; Rose et al. 2014), and the first adapisoriculid from the Eocene of the Indian Subcontinent (Kapur et al. 2017).

We describe in the present paper new fossils from Vastan Lignite Mine that confirm the allocation of *Frugivastodon* to Apatemyidae, hence apatemyids were unambiguously present in southern Asia. Moreover, the new fossils suggest the presence of a new lineage of Apatemyidae in the Eocene, and enable reconstruction of the potential biogeographic origin of this Asian representative.

## Material and Methods

The material described here was discovered during several field seasons, between 2004 and 2012, at the Vastan Lignite Mine (Gujarat, India). The specimens were collected by screen-washing using a mesh size of 1 mm. The fossils have been prepared and studied at the RBINS, and are housed at Garhwal University (Srinagar, India) and at Wadia Institute of Himalayan Geology (Dehradun, India).

## Abbreviations

H = height; L = length; n = number of specimens; OR = observed range; W = width.

## Institutional Abbreviations

AMNH, American Museum of Natural History, New York, USA; CM, Carnegie Museum on Natural History, Pittsburgh, Pennsylvania, USA; GU/RSR/VAS, Garhwal University, Srinagar, India; IITR/SB/VLM, Indian Institute of Technology, Roorkee, India; MNHN.F.MU, Muséum National d'Histoire Naturelle, Mutigny Collection, Paris, France; UCMP, University of California, Museum of Paleontology, Berkeley, California, USA; YPM-PU, Princeton University collection, housed at Yale University Peabody Museum of Natural History, New Haven, Connecticut, USA; WIF/A: Wadia Institute of Himalayan Geology, Dehradun, India.

## Measurements

The measurements (in mm) follow Gingerich (1982).

## Systematic Paleontology

Apatotheria Scott and Jepsen, 1936.

Apatemyidae Matthew, 1909.

*Frugivastodon* Bajpai, Kapur, Das, Tiwari, Saravanan and Sharma, 2005.

**Type and Only Known Species:** *Frugivastodon cristatus* Bajpai et al., 2005.

*Frugivastodon cristatus* Bajpai et al., 2005.

(Figs. 12.2, 12.3 and 12.4).

**Holotype:** IITR/SB/VLM 507, left m2.

**Referred Specimens:** GU/RSR/VAS-533, left M1; GU/RSR/VAS-553, right M1; GU/RSR/VAS-704, right M1; GU/RSR/VAS-1512, left M1; GU/RSR/VAS-1545, right M1; GU/RSR/VAS-1661, left M1; GU/RSR/VAS-1761, right M1; WIF/A 2361, left M1; WIF/A 2362, right M1; GU/RSR/VAS-554, left M2; GU/RSR/VAS-1562, right mandible with m2, m3 and posterior alveoli of m1; GU/RSR/VAS-851, right mandible bearing m2 and alveoli of m1; GU/RSR/VAS-586, right m1; GU/RSR/VAS-1760, right m1; GU/RSR/VAS-587, right m2; GU/RSR/VAS-852, left m2; GU/RSR/VAS-1561, right m2; GU/RSR/VAS-853, right m3.

**Type Locality:** Vastan Lignite Mine (1–2 m above lower lignite: Lignite Seam 2), about 40 km northeast of Surat, Gujarat, Western India; Cambay Shale Formation, Ypresian, early Eocene.

**Emended Diagnosis:** Differs from *Apatemys*, *Heterohyus* and *Sinclairiella* by having m1 and m2 similar in length but m3 distinctly shorter, and by having higher-crowned molars. Paraconid very reduced on m2 and m3, in contrast to *Unuchinia*, *Labidolemur*, *Apatemys*, *Heterohyus* and *Sinclairiella*, in which the paraconid is more developed. Further differs from *Labidolemur*, *Apatemys*, *Heterohyus* and *Sinclairiella* in having a smaller hypocone and mesiodistally elongated lower molars. Differs from all other apatemyid genera in having a well-developed postprotocrista and a small metaconule, and transversely wide M1, and from *Aethomylos* in having a small metaconule.

**Measurements:** Tables 12.1 and 12.2.

**Description:** Eighteen new specimens (representing 5 loci: m1–m3; M1–M2) are referred to this apatemyid. The specimens, consisting mainly of isolated teeth, represent at least five individuals.

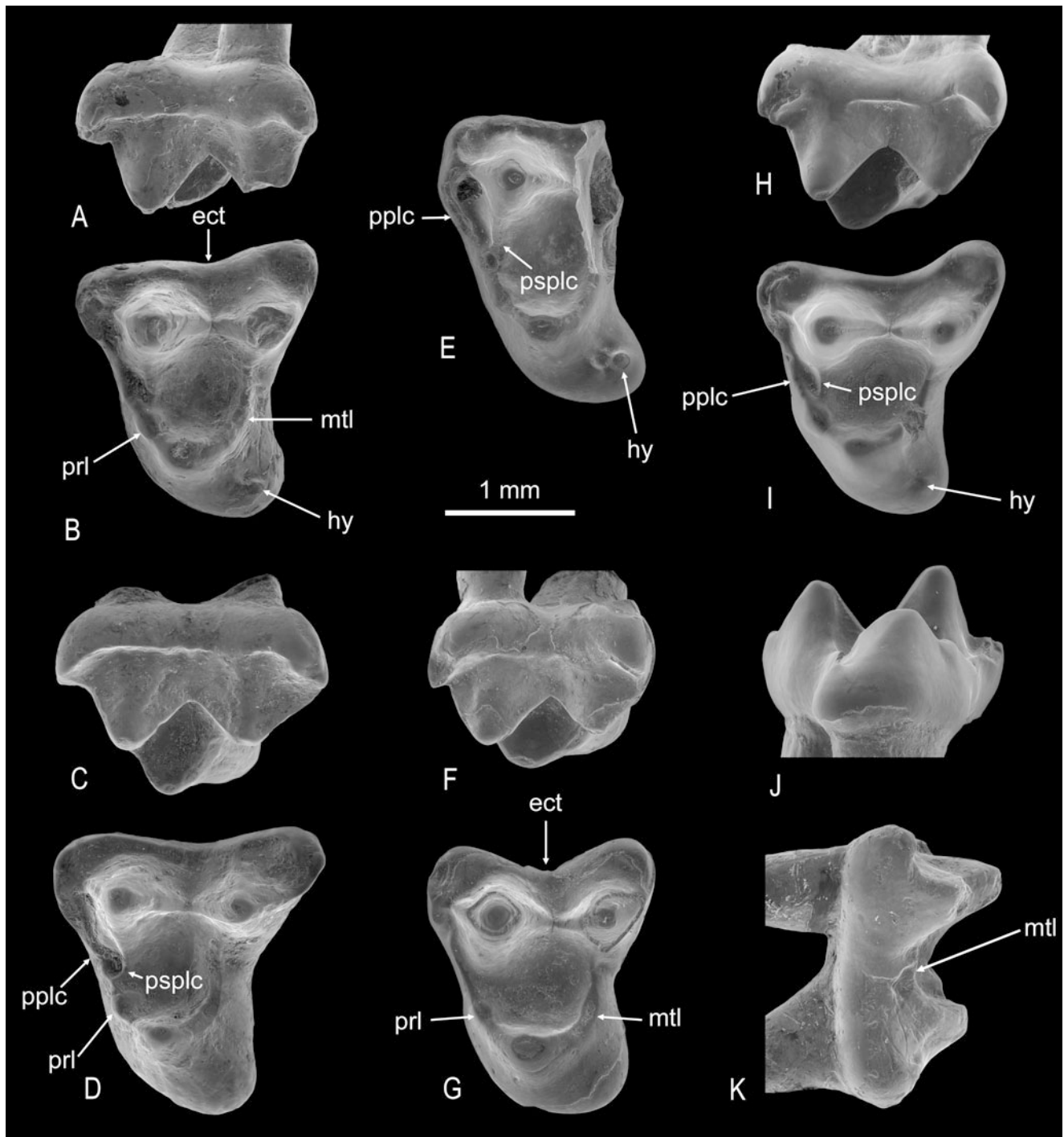
Nine M1s of *Frugivastodon* (Fig. 12.2A–E, H–K) have been discovered in the Vastan Lignite Mine. The paracone is larger and higher than the metacone on the M1, and the two

cusps are joined by a thin centrocrista. The protocone is prominent and shifted mesially (Fig. 12.2J). The trigon basin is deep. The paraconule and metaconule are present but weakly developed, corresponding rather to a thickening of the enamel than to distinct cusps (i.e., they are not separated from the protocone by a notch). Both cusps are situated closer to the protocone than to the buccal cusps. The preparaconule crista and premetaconule crista (Fig. 12.2K) are both distinct. The preparaconule crista joins the ectocingulum, while the premetaconule crista reaches the base of the metacone. The postparaconule crista is also clearly visible but there is no postmetaconule crista. The parastyle is short in length but the apex is clearly distinct and mesially projected. The postmetacrista appears as a short crest; it is more transversely oriented than the parastyle. The ectoflexus is variable but shallow. A moderate stylar shelf is present; it is wider labial to the metacone. GU/RSR/VAS-533, GU/RSR/VAS-553, GU/RSR/VAS-1512, and WIF/A 2361 (M1s) display a small but distinct hypocone (Fig. 12.2B, E, I); it is present on a ledge formed by a slight broadening of the postcingulum at the very base of the disto-lingual border of the protocone. The five other M1s have worn (e.g., GU/RSR/VAS-704; Fig. 12.2D) or broken hypocone area. The postcingulum is not continuous with the metacingulum.

Only one M2 can be referred to *Frugivastodon* (Fig. 12.2F, G). The tooth is similar to the M1s in having large paracone and metacone joined by a thin centrocrista, paracone taller than metacone, small paraconule and metaconule, prominent and mesially shifted protocone, deep trigon basin, distinct preparaconule and premetaconule cristae, and a moderate stylar shelf. The M2 differs from the M1s in having a deeper ectoflexus resulting in more labially projecting parastyle and metastyle, and the absence of the postparaconule crista. Unfortunately, the area where the hypocone might be present is damaged; it is thus impossible to determine if a hypocone was present.

All three lower molars appear to be represented in our sample. The m1 and m2 are approximately the same length, whereas m3 is distinguished by being distinctly smaller (Table 12.2). Moreover, the m1s and m2s discovered at Vastan Lignite Mine are conspicuously more transversely compressed and relatively more mesiodistally elongated than the m3s (Fig. 12.3A–C): the mean width/length ratio is 0.53 for the m1 (OR: 0.48–0.58, n = 2) and 0.56 for the m2 (OR: 0.51–0.60, n = 5), while it is 0.69 for the m3 (OR: 0.66–0.72, n = 2). The trigonid is higher than the talonid, as on all the molars. The protoconid is the tallest cusp, the metaconid slightly lower and more distal, and the paraconid low and greatly reduced but nevertheless more distinct on m1 and m2 than on m3. The preprotocristid and paracristid meet at an obtuse angle (nearly a right angle) at the mesiolabial margin of the tooth, where a small, low fourth trigonid cusp

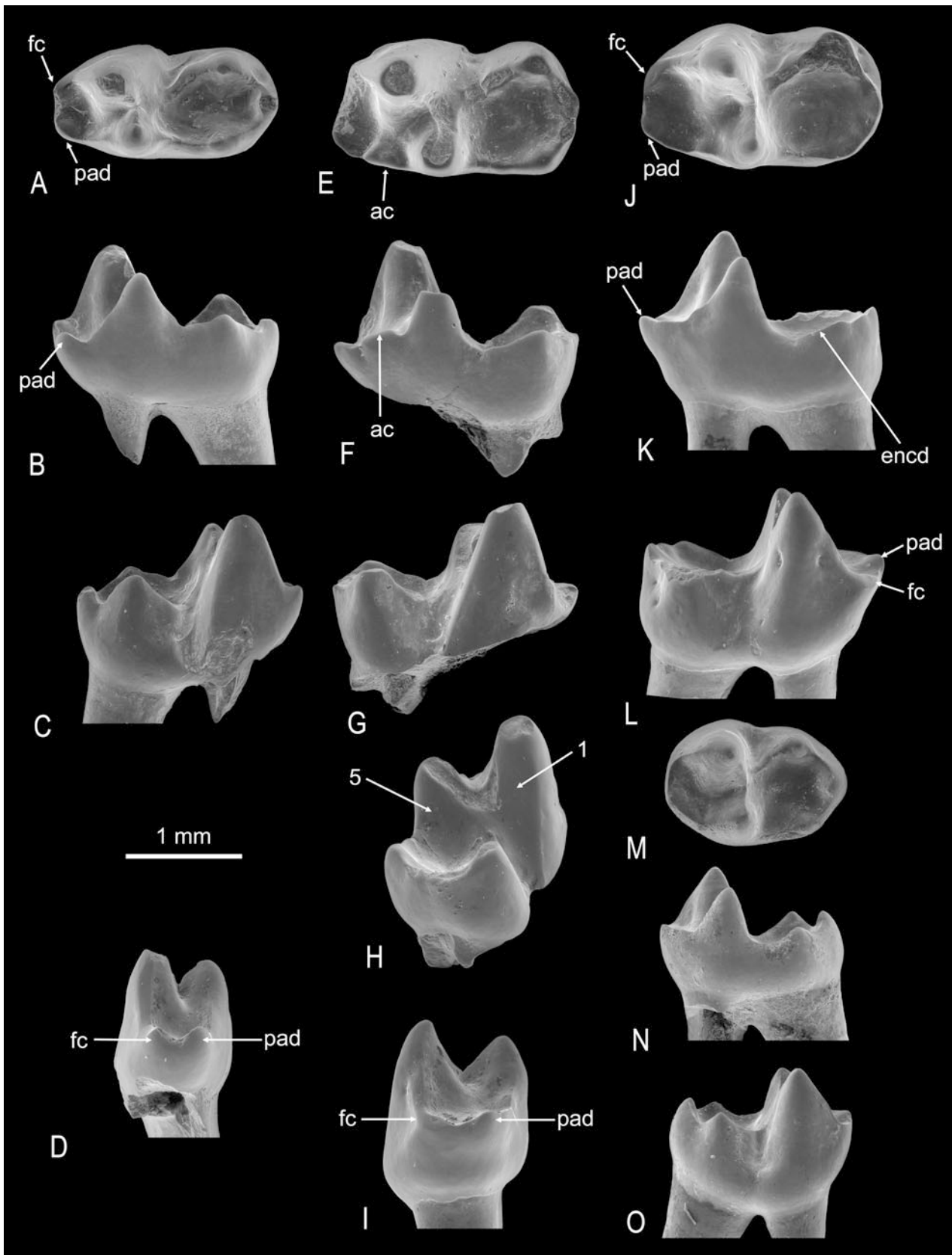




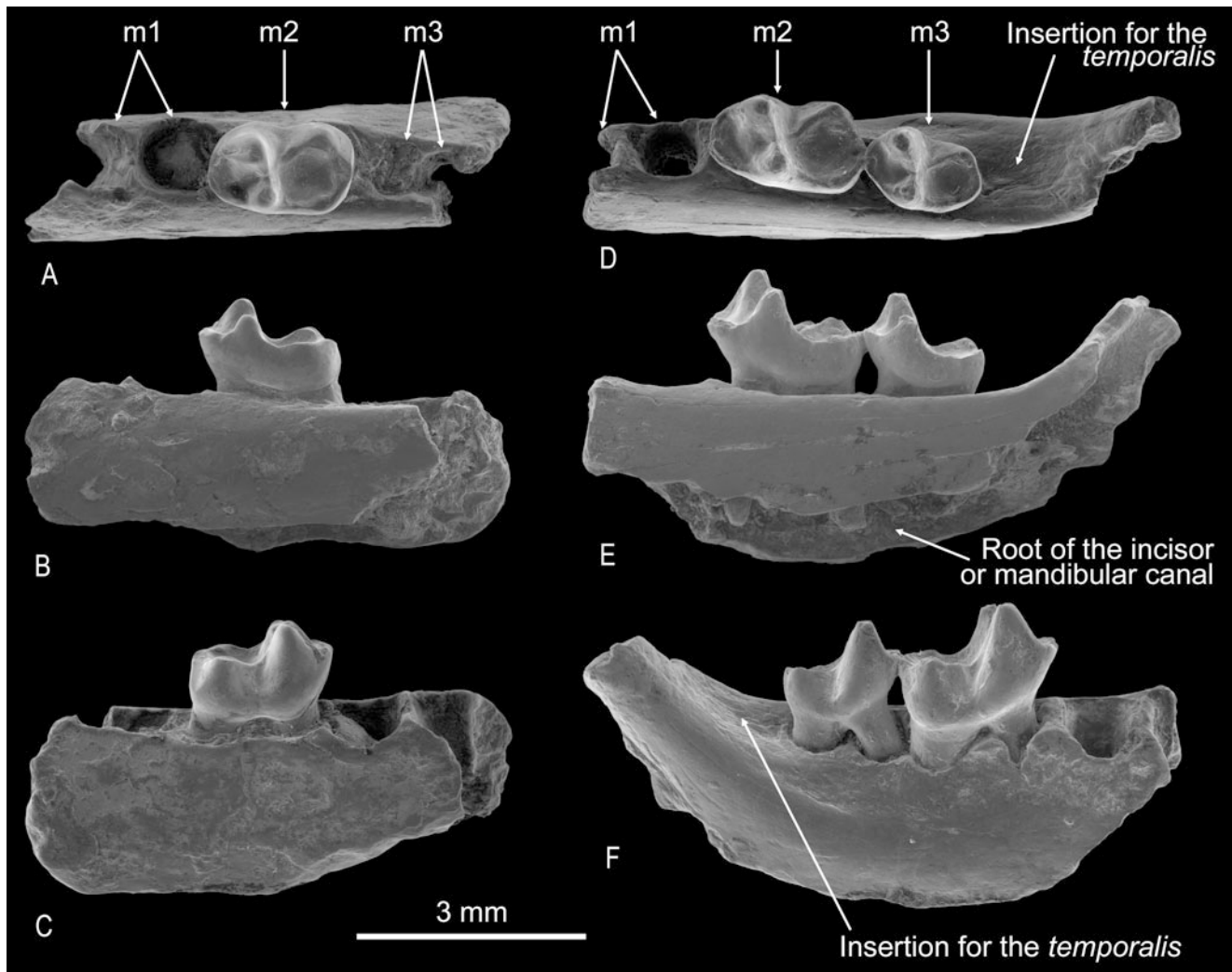
**Fig. 12.2** *Frugivastodon cristatus* from Vastan Lignite Mine (early Eocene; India). **A–B.** GU/RSR/VAS-1512, left M1; **A.** labial view; **B.** occlusal view; **C–D.** GU/RSR/VAS-704, right M1 (reversed); **C.** labial view; **D.** occlusal view; **E.** WIF/A 2361, left M1, occlusal view; **F–G.** GU/RSR/VAS-554, left M2; **F.** labial view; **G.** occlusal view; **H–K.** GU/RSR/VAS-553, right M1 (reversed); **H.** labial view; **I.** occlusal view; **J.** lingual view; **K.** distal view; Abbreviations: ect, ectoflexus; hy, hypocone; mtl, metaconule; pplc, preparaconule crista; prl, paraconule; psplc, postparaconule crista

(Fig. 12.3K, L) is present labial to the paraconid and separated from it by a notch. This fourth cusp is diagnostic of apatemyids. Nevertheless, the quadrilateral aspect of the trigonid in occlusal view, typical of other Eocene apatemyids

(e.g., *Apatemys*, *Heterohyus*), is less pronounced on the Indian specimens. A premetacristid descends to a notch behind the paraconid and is high enough to lingually enclose the trigonid basin. The talonid basin is enclosed by three



**Fig. 12.3** *Frugivastodon cristatus* from Vastan Lignite Mine (early Eocene; India). **A–D.** GU/RSR/VAS-586, right m1; **A.** occlusal view; **B.** lingual view; **C.** labial view; **D.** mesial view; **E–H.** GU/RSR/VAS-1561, right m2; **E.** occlusal view; **F.** lingual view; **G.** labial view; **H.** distal view; **I–L.** GU/RSR/VAS-852, left m2 (reversed); **I.** mesial view; **J.** occlusal view; **K.** lingual view; **L.** labial view; **M–O.** GU/RSR/VAS-853, right m3; **M.** occlusal view; **N.** lingual view; **O.** labial view. Abbreviations: ac, additional cusp?; encl, entocristid; fc, fourth cusp of the trigonid; pad, paraconid. 1 and 5 = indication of the wear facets 1 and 5



**Fig. 12.4** *Frugivastodon cristatus* from Vastan Lignite Mine (early Eocene; India). **A–C.** GU/RSR/VAS-851, right mandible bearing m2 and alveoli of m1; **A.** occlusal view; **B.** lingual view; **C.** labial view; **D–F.** GU/RSR/VAS-1562, right mandible with m2, m3 and posterior alveoli of m1; **D.** occlusal view; **E.** lingual view; **F.** labial view

cusps – hypoconid the tallest, entoconid slightly lower, and a low, posteriorly shifted hypoconulid – and their adjoining crests; however, the distal position of the hypoconid on m1 is only an impression conferred by the narrowness of the talonid. The cusps are situated on the periphery of the crown (i.e., there is no basal inflation). The crests joining these cusps are low, except for the somewhat higher entocristid, which closes the basin lingually. The morphology of m1 is closely similar to that of the m2 except for being narrower and having a more distinct paraconid (Fig. 12.3D, I), a narrow and somewhat extended trigonid and an elongate, basined talonid longer than the trigonid but about the same width, and a deeper notch between the hypoconulid and entoconid. The narrower width of m1 results in lingual and labial cusps that are less separated than on m2 (Fig. 12.3A, J), and consequently a more

distinctly notched crest that bridges the paraconid and the fourth cusp and mesially closes the shallow trigonid basin (Fig. 12.3D, I).

Apart from its greater width (and consequent wider separation between lingual and labial cusps; Fig. 12.3I), and the minor differences just noted, m2 is very similar to m1. The trigonid and talonid are approximately equal in length, and the distal margin of the talonid is rounded in occlusal view, somewhat more so than on m1. GU/RSR/VAS-1561 bears a small accessory cuspule (Fig. 12.3E, F) on the lingual part of the trigonid; this cuspule is not present in other specimens.

GU/RSR/VAS-1561 further differs from the other lower molars in having wear facets 1 and 5, on the distal surface of the trigonid (=postvallid), more distinctly offset (Fig. 12.3H). The cristid obliqua meets and partly ascends the middle

**Table 12.1** Measurements (in mm) of all the specimens of *Frugivastodon cristatus* Bajpai et al. 2005 from Vastan Lignite Mine (Ypresian; India)

Specimen	Locus	Length	Width	Height	Ratio L/W	Ratio W/L	Ratio H/L
IITR/SB/VLM 507 (holotype)	m2	1.92	1.03	–	1.86	0.54	–
GU/RSR/VAS-586	m1	1.97	0.95	1.6	2.07	0.48	0.80
GU/RSR/VAS-1760	m1	2.19	1.27	1.6	1.72	0.58	0.73
GU/RSR/VAS-587	m2	2.09	1.11	–	1.88	0.53	–
GU/RSR/VAS-852	m2	2.1	1.18	–	1.78	0.56	–
GU/RSR/VAS-1561	m2	2.16	1.1	1.7	1.96	0.51	0.77
GU/RSR/VAS-851	m2	1.93	1.13	1.4	1.71	0.59	0.74
GU/RSR/VAS-1562	m2	2.09	1.25	1.7	1.67	0.60	0.76
GU/RSR/VAS-1562	m3	1.48	1.07	1.4	1.38	0.72	0.93
GU/RSR/VAS-853	m3	1.56	1.03	1.4	1.51	0.66	0.88
GU/RSR/VAS-533	M1	–	2.51	–	–	–	–
GU/RSR/VAS-1761	M1	–	–	–	–	–	–
WIF/A 2362	M1	–	2.11	–	–	–	–
WIF/A 2361	M1	1.85	2.22	–	0.83	1.20	–
GU/RSR/VAS-1512	M1	1.91	2.07	–	0.92	1.08	–
GU/RSR/VAS-1661	M1	1.94	2.17	–	0.89	1.12	–
GU/RSR/VAS-1545	M1	1.97	2.27	–	0.87	1.15	–
GU/RSR/VAS-704	M1	2	2.24	–	0.89	1.12	–
GU/RSR/VAS-555	M1	1.84	2.21	–	0.83	1.20	–
GU/RSR/VAS-554	M2	1.72	2.08	–	0.83	1.21	–

**Table 12.2** Summary measurements (in mm) of *Frugivastodon cristatus* Bajpai et al. 2005 from Vastan Lignite Mine (Ypresian, India)

Locus		N	OR	Mean
M1	L	6	1.84–2	1.92
	W	5	2.07–2.51	2.23
M2	L	1	1.72	–
	W	1	2.08	–
m1	L	2	1.97–2.19	2.08
	W	2	0.95–1.27	1.11
m2	L	3	1.93–2.16	2.07
	W	3	1.10–1.25	1.15
m3	L	2	1.48–1.56	1.52
	W	2	1.03–1.07	1.05

of the postvallid, delimiting facet 1, on the distal surface of the protoconid, from facet 5, on the distal surface of the metaconid, as in some plesiadapiforms (Rose 1975).

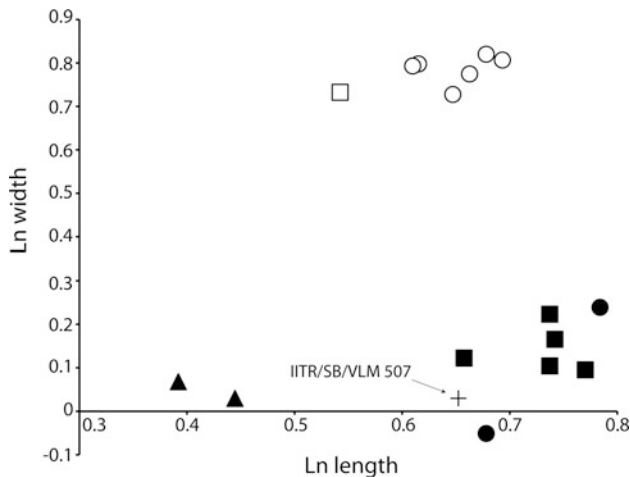
The m3 is quite different from m1 and m2 (Figs. 12.3M–O, 12.4D–F). It is short and elliptical in occlusal view and differs from m1 and m2 in having a less distinct paraconid, a shorter paracristid, and a weak or absent fourth cusp. The trigonid is slightly broader than the talonid. The hypoflexid is very shallow. The hypoconulid is relatively more distally located on m3 than on m2, comparable to its position on m1.

The ventral part of the mandible is broken just below the roots of the teeth on the two discovered dentaries (GU/RSR/VAS-1562 and GU/RSR/VAS-851; Fig. 12.4), so its depth cannot be determined. This breakage may result either from the presence of the root of a large incisor – a

characteristic of apatemyids – or from the presence of the mandibular canal (Fig. 12.4E). Indeed, as shown by radiographs of a specimen of *Apatemyis*, the incisor root may extend back to below m3 in Apatemyidae (Koenigswald et al. 2005). However, the Indian specimens are not adequately preserved to corroborate either hypothesis. The mandible of *Frugivastodon* was probably deep, as usually observed in apatemyids. There is a small fossa distal to the m3 for the insertion of part of the tendon of the temporalis muscle (Fig. 12.4D, F). The mandible is slightly expanded lateral to the m3 in GU/RSR/VAS-1562, but this enlargement is less pronounced in the second mandibular fragment described here (GU/RSR/VAS-851).

**Discussion.** *Frugivastodon cristatus* was described by Bajpai et al. (2005) based on a single lower molar





**Fig. 12.5** Comparison of the sizes Ln length (mm)  $\times$  Ln width (mm) of the holotype (IITR/SB/VLM 507) and the m1–m3 and M1–M2 of *Frugivastodon cristatus* described in the present paper. Circles are M1/m1, squares M2/m2, and triangles M3/m3; black symbols correspond to lower teeth, and white figures to upper teeth

(IITR/SB/VLM 507). Our fieldwork in the Cambay Shale Formation of Vastan Lignite Mine (Gujarat, India) has resulted in the discovery of numerous new dental elements for this species, including mandibular fragments and upper molars. The holotype probably corresponds to m2 based on its size ( $L = 1.92$ ;  $W = 1.03$ ); but its size is also close to that of one of the two m1s found by our team (Fig. 12.5; Table 12.1). The proportions and the poor development of the paracristid and paraconid, however, support its identification as an m2.

The fossils referred to *Frugivastodon* support the inclusion of this taxon within Apatemyidae based on the following combination of shared features: elongate M1 with the parastyle projecting forward; M2 with prominent styles; weak conules on upper molars; small hypocone present at the distal base of the protocone; lower molar trigonids with a reduced paraconid and a mesiolabial fourth cusp resulting in a quadrate trigonid; absence of labial and lingual cingulids; and rounded talonids on lower molars.

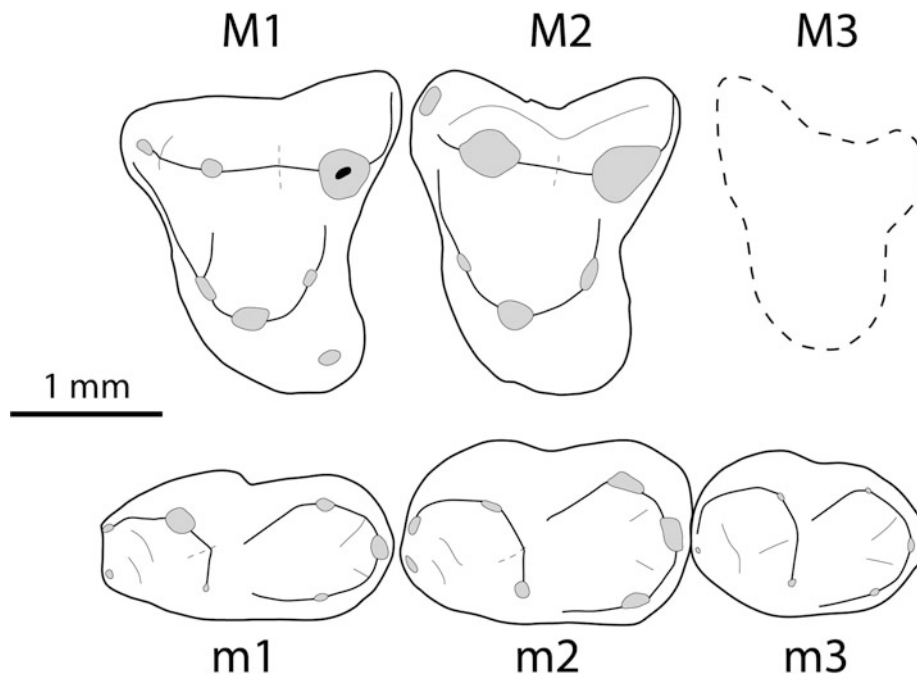
Based on the new fossils we have emended the diagnosis of *Frugivastodon cristatus*, adding further characteristics of the sole apatemyid species found outside Europe and North America. A large part of its molar dentition is now known (Fig. 12.6). Bajpai et al. (2005) considered that *Frugivastodon* differs from the other apatemyids by two major features: the lack of a paraconid and the low talonid cusps on the molars. The molars described and illustrated in the present article show that the paraconid is still present, if small, on the molars; therefore, its absence on the holotype may be explained by (1) the fact that the specimen corresponds to m2, in which the paraconid may be weaker than on m1; and (2) wear or erosion of the specimen. Nor do the new

specimens support the presence of talonid cusps lower than in other apatemyids. We believe that the low height of the talonid cusps compared to those of the trigonid on the holotype also results from wear or erosion of the specimen.

One of the most striking features of the new species is the relative size of the lower molars: m1 and m2 are approximately equal in length, but m3 is clearly shorter than m1 and m2 (Table 12.2). This contrasts with the situation observed in many North American and European Eocene apatemyids (*Unuchinia*, *Apatemys*, *Heterohyus*, *Sinclairiella*) where the m3 is usually longer than the m1 and m2 (Simpson 1936; West 1973a; Holtzman 1978; Russell et al. 1979) (Fig. 12.7). The three molars are, however, still very close in size in the North American Paleocene apatemyid *Labidolemur major*, the Paleocene-Eocene *Labidolemur kayi*, and the early Eocene *L. serus* and *Apatemys chardini* (McKenna 1963a; West 1972: Table 1; Gingerich and Rose 1982: Table 1; Gingerich 1982: Tables 1–3), and in the European *Apatemys mutiniacus* (Russell et al. 1979: Table 1). This is also the case for the Paleocene *Jepsenella praepropera*, the oldest apatemyid (Szalay 1968: Table 1; West 1973b: Table 1). Paleocene *Unuchinia* differs from other apatemyids in showing increase in molar length from m1 to m3 (Simpson 1936; Holtzman 1978).

*Frugivastodon* appears primitive relative to other early Eocene apatemyids in the morphology of the teeth. Morphological trends in apatemyids include a tendency for upper molars to expand the hypocone lobe posterolingually and become more squared and relatively narrower transversely; enlargement of the parastyle; reduction of the paraconid on lower molars and enlargement of the fourth trigonid cusp, which tends to extend mesially as far as or even farther than the paraconid (giving the trigonid a peculiar parallelogram aspect in occlusal view); talonid as wide as or wider than the trigonid; and talonid of m3 mesiodistally elongated (McKenna 1963a, b; West 1973a; Russell et al. 1979) (Fig. 12.7). For the majority of these features, *Frugivastodon* is more primitive than other Eocene apatemyids: the M1 is transversely wider and triangular in occlusal view because of the rudimentary hypocone, and it has a small parastyle. On the lower molars, the fourth trigonid cusp is small and not mesially displaced, consequently the trigonid is less oblique and parallelogram-shaped and more triangular in occlusal view than in other early Eocene apatemyids (Fig. 12.7). The talonid and trigonid are of approximately equal width, even on m1; the entocristid is high, closing the talonid basin lingually; the entoconid is almost as high as the hypoconid; and the talonid of m3 is mesiodistally short (Fig. 12.7).

The M1 of apatemyids is typically elongate mesiodistally and narrow transversely compared to M2 and M3 (McKenna 1963a) (Fig. 12.7). M1 of *Frugivastodon*, however, is transversely wide: the width/length (W/L) ratio for M1 is



**Fig. 12.6** Occlusal sketch of the dentition of *Frugivastodon cristatus*. M1, GU/RSR/VAS-1512; M2, GU/RSR/VAS-554; m1, GU/RSR/VAS-586; m2, GU/RSR/VAS-851; m3, GU/RSR/VAS-853. The outline of M3 is based on a specimen of *Aethomylos* (UCMP 101047) figured by Novacek (1976, Fig. 16D)

**Table 12.3** Width/length ratio of the M1 and M2 for several apatemyids. The values presented for *Jepsenella praepropera* are based on Szalay (1968: Table 1), *Labidolemur major* on West (1972), *Labidolemur kayi* on Gingerich (1982: Table 1), *Labidolemur serus* on Gingerich (1982: Table 2), *Apatemys chardini* on Gingerich (1982: Table 3), *Apatemys mutiniacus* on Russell et al. (1979: Table 1), and *Aethomylos simplicidens* on Novacek (1976: Table 6)

Taxa	Width/length ratio	
	M1	M2
<i>Frugivastodon cristatus</i>	1.13 (n = 6)	1.21 (n = 1)
<i>Aethomylos simplicidens</i>	0.98 <sup>a</sup> (n = 8)	
<i>Apatemys mutiniacus</i>	0.9 (n = 1)	–
<i>Apatemys chardini</i>	0.89 (n = 1)	1.12 (n = 1)
<i>Labidolemur serus</i>	0.98 (n = 2)	1.25 (n = 2)
<i>Labidolemur kayi</i>	0.95 (n = 1)	1.26 (n = 2)
<i>Labidolemur major</i>	–	1.29 (n = 1)
<i>Jepsenella praepropera</i>	0.96 (n = 1)	1.03 (n = 1)

<sup>a</sup>The deciduous premolars and molars (M1 and M2) were not discriminated by Novacek (1976)

1.15 (OR: 1.08–1.2, n = 6). M2 is also relatively wide (W/L = 1.21, n = 1). The relative width of the M1 of *Frugivastodon* is clearly unusual, while that of the M2 is frequently observed in apatemyids (Table 12.3).

The M1s of *Frugivastodon* are morphologically similar to those provisionally referred by Szalay (1968) to the Paleocene *Jepsenella praepropera* (Fig. 12.7). The similarities listed herein – triangular morphology, small hypocone, presence of both metacone and paracone, presence of postparacone crista – might be regarded as plausible support for Szalay's (1968) allocation of these isolated teeth to *Jepsenella*.

*Frugivastodon* shares with Eocene apatemyids the reduction of the paracone on the molars. However, it differs from the Eocene apatemyids *Apatemys* and *Heterohyus* in having higher-crowned molars, as seen in *Labidolemur*, *Jepsenella*, and *Unuchinia* (Table 12.4). The decrease in crown height was considered by McKenna (1963a) as a distinctive trend among apatemyids, and was documented in a limited sample by Gingerich (1982: Table 4). Crown height in *Frugivastodon* is actually greater than in early Eocene *Apatemys* and within the range of the *Labidolemur* species (*L. kayi* ranges from Tiffanian NALMA to early Wasatchian NALMA; *L. serus* is only known in the early

**Table 12.4** Relative crown height in mm (protoconid height above base of crown at mesial root/mesiodistal crown length; Gingerich 1982) in Ypresian *Frugivastodon* from Vastan Lignite Mine, Clarkforkian NALMA and Wasatchian *Labidolemur* and *Apatemys* from Clark's Fork and Bighorn basins. The values, except those for *Frugivastodon*, are from Gingerich (1982: Table 4)

Tooth position	Genus and species	N	OR	Mean
m1	<i>Frugivastodon cristatus</i>	2	0.73–0.8	0.77
	<i>Apatemys chardini</i>	2	0.63–0.69	0.66
	<i>Labidolemur kayi</i>	6	0.71–0.82	0.76
	<i>Labidolemur serus</i>	2	0.76–0.80	0.78
m2	<i>Frugivastodon cristatus</i>	3	0.74–0.77	0.76
	<i>Apatemys chardini</i>	4	0.59–0.67	0.63
	<i>Labidolemur kayi</i>	8	0.74–0.89	0.78
	<i>Labidolemur serus</i>	2	0.77	0.77
m3	<i>Frugivastodon cristatus</i>	2	0.88–0.93	0.90
	<i>Apatemys chardini</i>	1	0.59	–
	<i>Labidolemur kayi</i>	5	0.63–0.68	0.66
	<i>Labidolemur serus</i>	1	0.68	–

Wasatchian) (Table 12.4), presumably a plesiomorphic trait. However, because it has been demonstrated that modifications in molar crown height are closely related to diet (e.g., Boyer 2008), one can hypothesize that crown height might be a plastic trait in apatemyids (as generally in mammals) and therefore may not provide strong support for relationships.

In addition, *Frugivastodon cristatus* differs from all other apatemyids in one striking feature: the greater mesiodistal elongation of the lower molars. Because West (1973a) and Russell et al. (1979) hypothesized that there was a progressive lengthening of apatemyid lower molars through the Paleogene, we estimated the length/width (L/W) ratio for various apatemyids from the Paleocene, Eocene, and Oligocene, and for the Indian taxon (Table 12.5). The values calculated for *Frugivastodon* are much higher than those of the other apatemyids in being close to 1.9 for m1 (OR: 1.72–2.07; n = 2) and 1.74 for m2 (OR: 1.67–1.96; n = 5), while the values for these molars are between 1.2 and 1.6 in other apatemyids.

Thus *Frugivastodon* can be confidently assigned to the Apatemyidae, but it differs from contemporary apatemyids in several features that recall the Paleocene species (e.g., relative size of the lower molars, triangular M1 with a small hypocone, M1 transversely wide, high-crowned lower molars) and in displaying elongation of the lower molars and reduction of m3. However, *Unuchinia* differs among Paleocene apatemyids in having m3 longer than m1 and m2. *Frugivastodon* appears clearly less advanced than other Eocene apatemyids in numerous features and seems to belong to a separate lineage of Apatemyidae.

As discussed below (see *Relationships of Frugivastodon*), the closest taxon to *Frugivastodon* could be the enigmatic *Aethomylos simplicidens* from the middle Eocene (Uintan

NALMA). *Aethomylos* appears to be confined to the Uintan (Uinta-1) Friars Formation of southern California (Novacek 1976); the record from the Bridgerian Powder Wash locality in Utah (Krishtalka and Stucky 1984) is not certainly referable to this genus. Among the isolated teeth of *Frugivastodon* and *Aethomylos*, are a few narrow molariform teeth (Figs. 12.3A–C; 12.8D–F). Their trigonid is characterized by a low paraconid situated well mesial to the protoconid (though apparently more so in *Aethomylos*, to judge from Novacek's illustration). The talonid is a well-developed, deeply excavated basin, and the hypoconulid is distally located.

Novacek (1976) identified this peculiar tooth (Fig. 12.8 D–F) as either a p4 or dp4 but noted that no apatemyid has a molariform p4. The p4 is simple in known apatemyids, including the earliest taxa such as *Unuchinia*, *Jepsonella*, and *Labidolemur* (Simpson 1929, 1936; West 1972, 1973b), in which it is premolariform and displays only a high rounded trigonid cusp and a single talonid cusp. The morphology of the narrow tooth illustrated by Novacek (1976) (Fig. 12.8D–F), with its apparently extended trigonid, seems to be more consistent with dp4 of primitive placentals generally (e.g., Butler 1952; Zack 2012). The two narrow molariform teeth of *Frugivastodon* (GU/RSR/VAS-586 and GU/RSR/VAS-1760), however, have less extended trigonids and differ from m2 mainly in relative width; cusp positions are otherwise similar. For these reasons we regard them here as m1.

McKenna (1963a) listed the following differences between m1 and m2 of *Labidolemur kayi*: m2 has a relatively much wider trigonid with more separated cusps, a weaker fourth cusp, and a wider talonid. The same distinctions are found when comparing the teeth of *Frugivastodon* here identified as m1s and m2s.

**Table 12.5** Length/Width ratio for lower molars of several apatemyids from Europe, North America and India. Values of *H. nanus*, *A. sigogneaui*, *A. mutiniacus*, *A. teilhardi*, *A. uintensis*, *A. "bellus"*, and *Sinclairiella Apatemys* and Russell et al. (1979: Table 2). The values for the following taxa have been estimated by ourselves: *Aethomylos simplicidens* from Novacek (1976: Table 5), *Apatemys chardini* from Gingerich (1982: Table 3), *Jepsenella praepropera* (Szalay 1968: Table 1, type AMNH 3592), *Labidolemur kayi* from Gingerich and Rose (1982: Table 1), *Labidolemur serus* (Gingerich 1982: Table 2, holotype UM 69962), *Labidolemur soricoides* from West (1973a: Table 2, m1: holotype AMNH 17400, m2: PU 19992, m3: PU 19938), *Labidolemur major* from West (1972: Table 1), *Unuchinia dysmathes* (from Holtzman 1978: Table 23) and *Frugivastodon cristatus* (present paper); we used the mean values of the length and width when we did not have values for a particular specimen, and we used the maximal width estimated when the values of the trigonid and talonid were both available

	Europe			North America			India				
Eocene	m1	m2	m3		m1	m2	m3		m1	m2	m3
<i>Heteroyus nanus</i>	1.3	1.2	1.7	<i>Sinclairiella</i>	1.5	1.4	2	<i>Frugivastodon cristatus</i>	1.90 (n = 2)	1.74 (n = 5)	1.45 (n = 2)
<i>Apatemys sigogneaui</i>	1.3	1.4	1.6	<i>Apatemys uintensis</i>	1.4	1.4	1.6				
<i>Apatemys mutiniacus</i>	1.6	1.4	1.4	<i>Aethomylos simplicidens</i>	1.86 <sup>a</sup> (n = 2)	1.76 (n = 4) <sup>a</sup>	1.55 (n = 1)				
<i>Apatemys teilhardi</i>	1.65	1.6	–	<i>Apatemys "bellus"</i> (Bridgerian)	1.6	1.4	1.6				
				<i>Apatemys chardini</i>	1.45 (n = 2)	1.46 (mean)	1.55 (n = 1)				
				<i>Labidolemur serus</i>	1.47 (n = 1)	1.41 (n = 1)	–				
Paleocene				<i>Labidolemur kayi</i>	1.46 (mean)	1.27 (mean)	1.46 (mean)				
				<i>Labidolemur soricoides</i>	1.55 (n = 1)	1.38 (n = 1)	1.33 (n = 1)				
				<i>Jepsenella praepropera</i>	1.38 (n = 1)	1.27 (n = 1)	1.33 (n = 1)				
				<i>Labidolemur major</i>	1.3 (n = 1)	1.18 (n = 1)	1.25 (n = 1)				
				<i>Unuchinia dysmathes</i>	1.55 (n = 1)	1.5 (n = 1)	1.55 (n = 1)				

<sup>a</sup>Based on the study of *Frugivastodon*, the p4s (or dp4s) of *Aethomylos* (*sensu* Novacek 1976) are here considered as m1s, while the m1s are regarded as m2s

## Phylogenetic Analysis

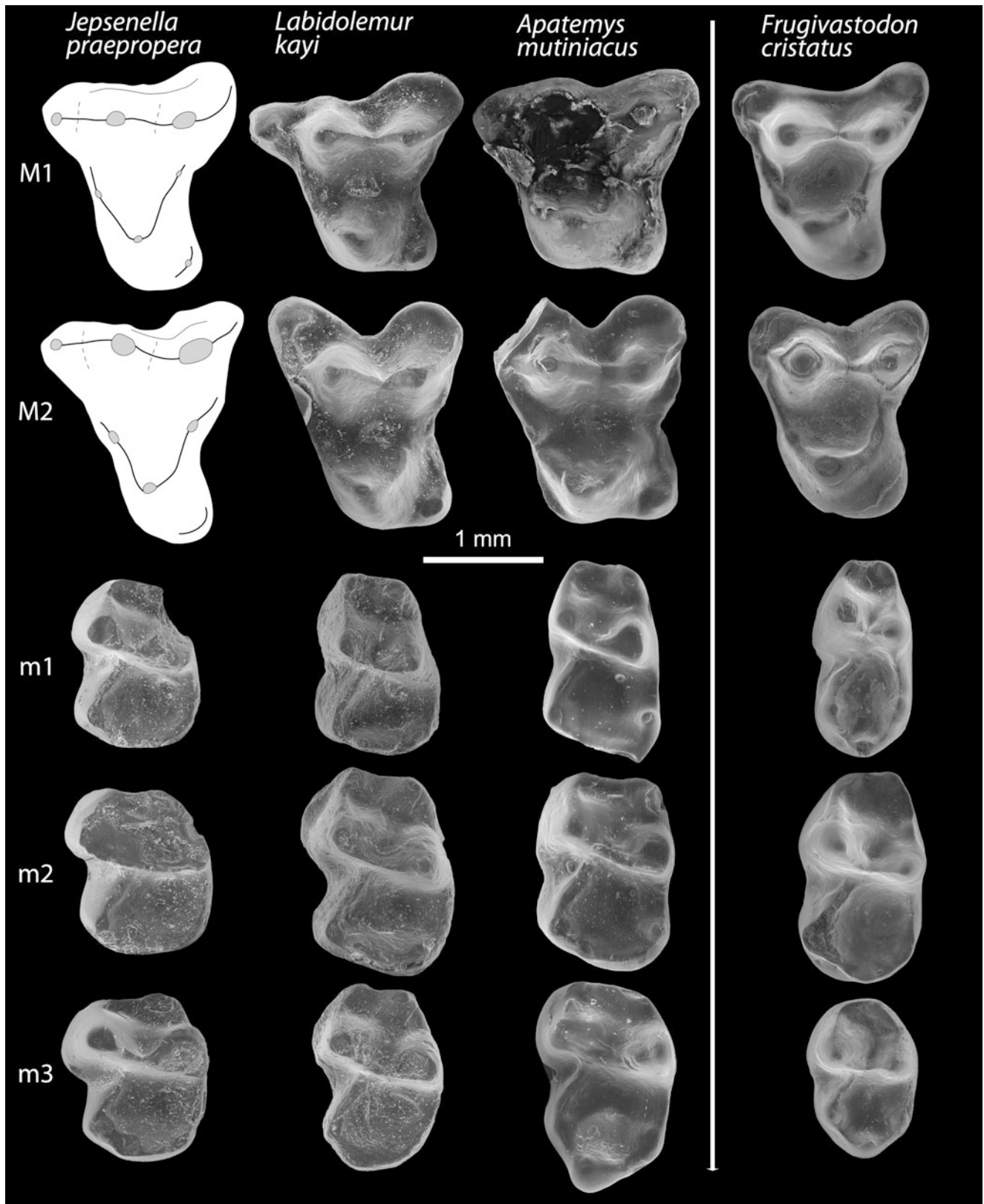
### Objectives and Methodology

The systematics and evolution of apatemyids have been controversial, largely because fossils are rare and tend to be very fragmentary; hence authors have focused on the description and validity of species rather than on the phylogenetic relationships among the approximately 30 described species. Silcox et al. (2010) provided the first matrix (240 morphological characters – 68 postcranial, 45 cranial, and 127 dental; 34 taxa) that includes numerous apatemyids. However, this large matrix was built in the attempt to study the broader relationships of these mammals among Placentalia, rather than to study the interrelationships among apatemyids. As a consequence, the matrix only includes six apatemyids: the North American *Jepsenella praepropera*, *Labidolemur kayi*, *Sinclairiella dakotensis*, and *Apatemys* sp., and the European *Carcinella sigei*, and *Heterohyus nanus*. The choice of taxa was based on their relative

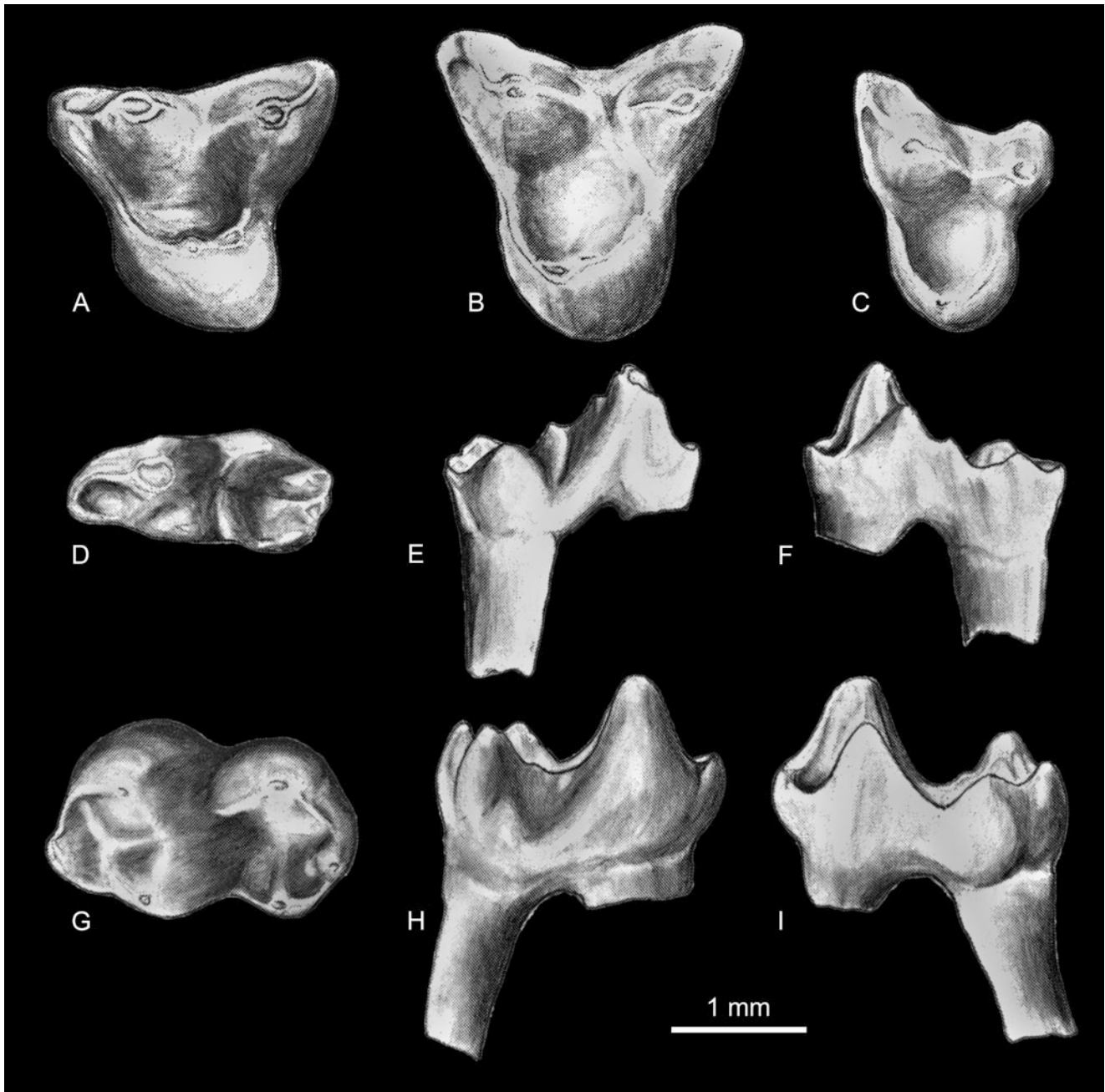
completeness (i.e., presence of skulls and, sometimes, of partial skeletons). This matrix, however, includes the most typical apatemyids: the only Eocene genera that are not represented are the European *Russellmys* and *Eochiromys*, but they are very poorly known and their systematic status is debated (Teilhard de Chardin 1927; Russell et al. 1979; Estravís 1990; Koenigswald et al. 2009). North American Paleocene *Unuchinia* was also excluded from the matrix, but this genus remains poorly known.

In order to test whether *Frugivastodon cristatus* and *Aethomylos simplicidens* are apatemyids, we added these taxa to the matrix of Silcox et al. (2010). Certain similarities shared by *Frugivastodon* and the enigmatic species *Aethomylos simplicidens* from the Uintan NALMA of North America (see *Relationships of Frugivastodon*), suggest that the latter species is a related apatemyid. We performed two analyses: in the first, we added only *F. cristatus* to the matrix, while we added both *F. cristatus* and *A. simplicidens* to the matrix for the second analysis. We performed these two distinct analyses in order to study the impact of *A. simplicidens* on the phylogenetic analysis.





**Fig. 12.7** Comparison of the M1–M2 and m1–m3 of several apatemyids from the Paleocene and early Eocene. *Jepsenella praepropera*; M1, AMNH89513 (redrawn from Szalay 1968: Fig. 8A); M2, AMNH89512 (redrawn from Szalay 1968: Fig. 8B); m1–m3, YPM-PU19184 (cast). *Labidolemur kayi*, M1–M2, UM73496 (cast); m1–m3, CM11703 (cast); *Apatemys mutiniacus*; M1, MNHN.F.MU115-L; M2, MNHN.F.MU6680 (cast); m1, MNHN.F.MU6332 (cast); m2, MNHN.F.MU6248 (cast); m3, MNHN.F.MU6024 (cast). *Frugivastodon cristatus*; M1, GU/RSR/VAS-553; M2, GU/RSR/VAS-554; m1, GU/RSR/VAS-586; m2, GU/RSR/VAS-852; m3, GU/RSR/VAS-853. Reversed views: AMNH89512, UM73496, MNHN.F.MU1274, MNHN.F.MU6332, GU/RSR/VAS-553, GU/RSR/VAS-586, GU/RSR/VAS-853



**Fig. 12.8** Drawings of several specimens referred to *Aethomylos simplicidens* (early-middle Eocene; North America). **A.** UCMP 99429, right M1?, occlusal view. **B.** UCMP 104178 (holotype), left M2?, occlusal view. **C.** UCMP 101047, left M3, occlusal view. **D–F.** UCMP 101077, left m1; **D.** occlusal view; **E.** labial view; **F.** lingual view. **G–I.** UCMP 101119, right m2; **G.** occlusal view; **H.** labial view; **I.** lingual view. Reversed views: **A, D–F** reproduced from Novacek (1976: Figs. 16B–D and 18A–F)

The coding of *Frugivastodon cristatus* is based on the fossils described and illustrated in the present paper. *Aethomylos simplicidens* has been scored only based on the drawings and the description provided by Novacek (1976).

The data matrix was assembled with WinClada 1.00.08 (Nixon 1999, Appendix S1) and the parsimony analysis was performed with TNT 1.5 (Goloboff and Catalano 2016). The

search strategy followed that of Spaulding and Flynn (2012). We analysed the data under the ‘New Technology search’ option, selecting the sectorial search, ratchet and tree-fusing search methods, all with default parameters. Under these settings, replications were run until the minimum length tree was found in 500 separate replicates. The trees generated were then analysed under typical search options (using TBR)

to explore fully the tree islands discovered. As in Silcox et al. (2010), all characters were equally weighted and treated as unordered. Results were examined with Winclada 1.00.08 using strict consensus and majority-rule consensus. Bremer support indices were determined using TNT: they have been calculated with TNT for 10 supplementary steps. Bootstrap values were calculated using TNT (10,000 bootstrap replicates).

## Results

The first phylogenetic analysis (*Frugivastodon* added to the matrix) yielded three equally parsimonious trees, with a tree length of 1095 steps, CI of 0.29 and RI of 0.52. Such low indices suggest substantial homoplasy. The strict consensus of these three trees is 1101 steps long with a CI = 0.29 and RI = 0.51 (Fig. 12.9). In the strict consensus, two nodes are collapsed. The values of Bremer support index that TNT has found are between one and seven (only one node); three nodes have a Bremer support higher than ten. Seven nodes have a Bootstrap value higher than 50.

The second phylogenetic analysis (*Frugivastodon* and *Aethomylos* added to the matrix) yielded nine equally parsimonious trees, with a tree length of 1099 steps, and CI of 0.29 and RI of 0.52. The strict consensus tree is 1138 steps long with a CI = 0.28 and RI = 0.50 (Fig. 12.10A). In the strict consensus, ten nodes are collapsed. The majority-rule consensus is 1099 steps long (Fig. 12.10B). Its CI and RI equal 0.29 and 0.52, respectively. As in the first analysis, the values of Bremer support index that TNT has found are generally between one and seven, while three nodes have a Bremer support higher than ten (Fig. 12.10A). Seven nodes have a Bootstrap value higher than 50 (Fig. 12.10A).

## Discussion

As in Silcox et al. (2010), there are two areas of disagreement among the trees of the first phylogenetic analysis (Fig. 12.9): the relationships of Leptictida and Paleoryctidae to the other major clades and the branching order among the Paleoryctidae (*Pararyctes pattersoni*, *Paleoryctes* sp., *Otteryctes winkleri*). The relationships among the taxa are the same as those found by Silcox et al. (2010), and they are thus not discussed here. Notably, the addition of *Frugivastodon* to the matrix did not change the relationships among the taxa already analysed.

The node that unites the apatemyids has a Bremer support index of 5 (Fig. 12.9). The Paleocene *Jepsenella praepropera* is the most basal apatemyid; this agrees with the results of Silcox et al. (2010) and previous hypotheses that consider this species as one of the most primitive apatemyids

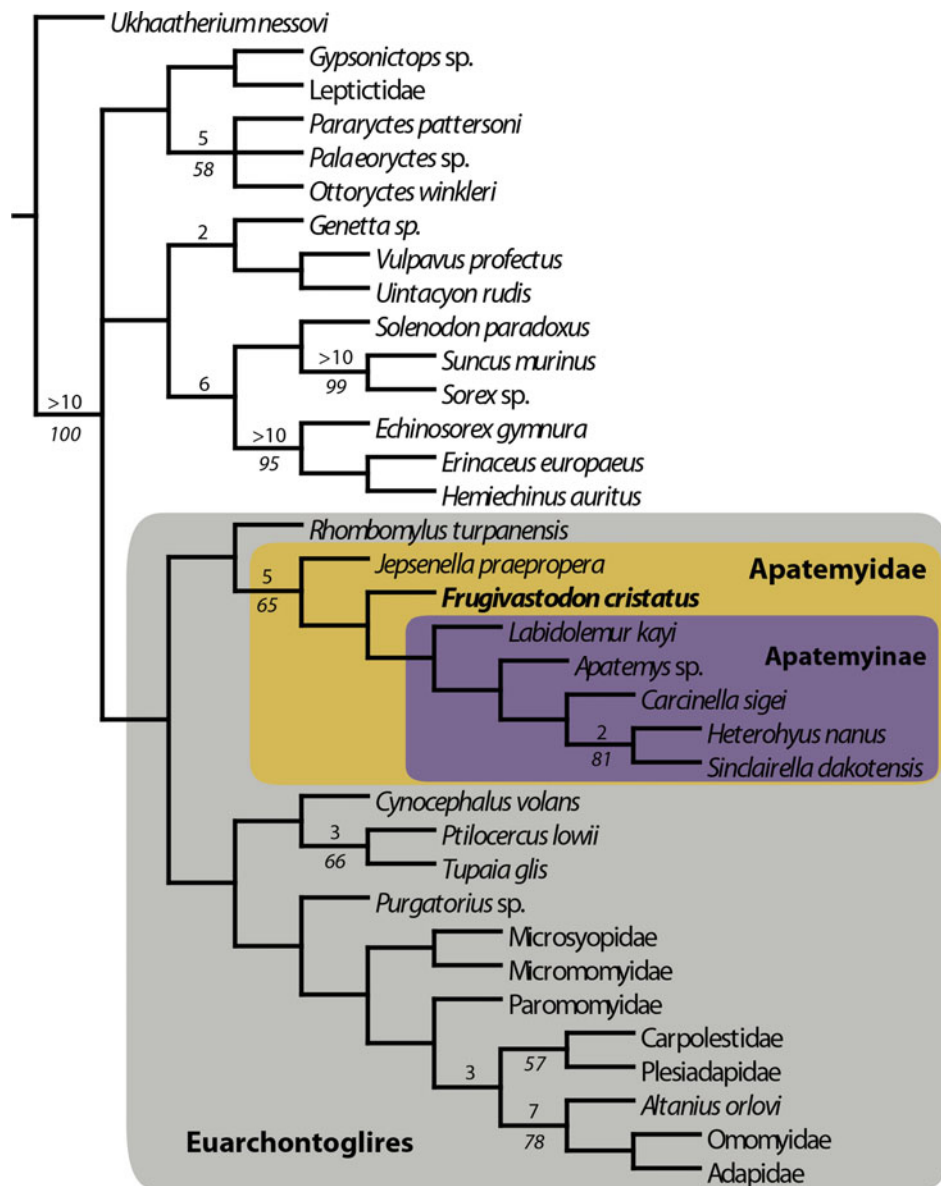
(Simpson 1940; McKenna 1963a; Szalay 1968). *Frugivastodon* is included among Apatemyidae and is the sister taxon to all the other apatemyids in the analysis: *Labidolemur kayi*, *Apatemys* sp., *Carcinella sigei*, *Heterohyus nanus*, and *Sinclairiella dakotensis*. This relationship is supported by the following synapomorphies: 159(1) (straight preparacrista on M1); 206(1) (moderate crown height on m1); 214(1) (metaconid positioned well behind the level of the protoconid on m1); 223(1) (mesiolabial projection present on m2); 235(3) (labial cingulid absent on lower molars).

The node that includes *L. kayi*, *Apatemys* sp., *C. sigei*, *H. nanus*, and *S. dakotensis* is only supported by the character 153(1) (M1 more elongate relative to transverse width than M2 or M3). This feature is an unusual character among placental mammals and is therefore phylogenetically highly significant. This group of genera is essentially the subfamily Apatemyinae of McKenna and Bell (1997), excluding *Jepsenella* (Fig. 12.9). The relationships among this clade are similar to those found by Silcox et al. (2010); as a consequence, the addition of *Frugivastodon* to the analysis did not change the relationships among Apatemyinae. *Labidolemur kayi* is the most basal member, while the European *C. sigei* is closely related to the European *H. nanus* and to the North American *S. dakotensis*. Silcox et al. (2010) noted that the relationship between *Carcinella* (from the ?late Eocene of the ‘Phosphorites du Quercy’) and *Heterohyus*+*Sinclairiella* is poorly supported (two dental characters are related to the P4 in the present analysis). The close relationship between the North American *S. dakotensis* and the European *H. nanus* – a relationship that suggests, as noted by Silcox et al. (2010), that *Sinclairiella* may have been a European migrant (see *Geographic origin of Frugivastodon and the dispersal of apatemyids*) – is well supported (seven synapomorphies; Bremer support = 2; Bootstrap value = 81) (Fig. 12.9). This relationship is supported by several cranial and postcranial features, as well as numerous dental ones.

The strict consensus of the second phylogenetic analysis, which included *Frugivastodon* and *Aethomylos*, is less resolved than the one produced by the first analysis (Fig. 12.10A). However, the Bremer support and Bootstrap values are very similar to those found in the first analysis; the clades that were well supported in the first analysis are supported in the second.

We found the two areas of disagreement as in the first analysis and Silcox et al. (2010). However, the results of the second analysis display several important differences from that of Silcox et al. (2010). We only list here the differences in the topology with the first analysis and that of Silcox et al. (2010) because the relationships among Euarchontoglires have already been discussed by Silcox et al. (2010). It is worth noting that our phylogenetic analysis does not support Euarchonta (Fig. 12.10), which is a clade that is well supported in molecular analyses (e.g., Springer et al. 2004).





**Fig. 12.9** Strict consensus of 3 equally parsimonious trees from the first analysis, adding only *Frugivastodon* to the dataset of Silcox et al. (2010) (L = 1095 steps; CI = 0.29; RI = 0.52): 1101 steps long with a CI = 0.29 and RI = 0.51. Bremer supports (above node) and bootstrap values greater than 50% (below node)

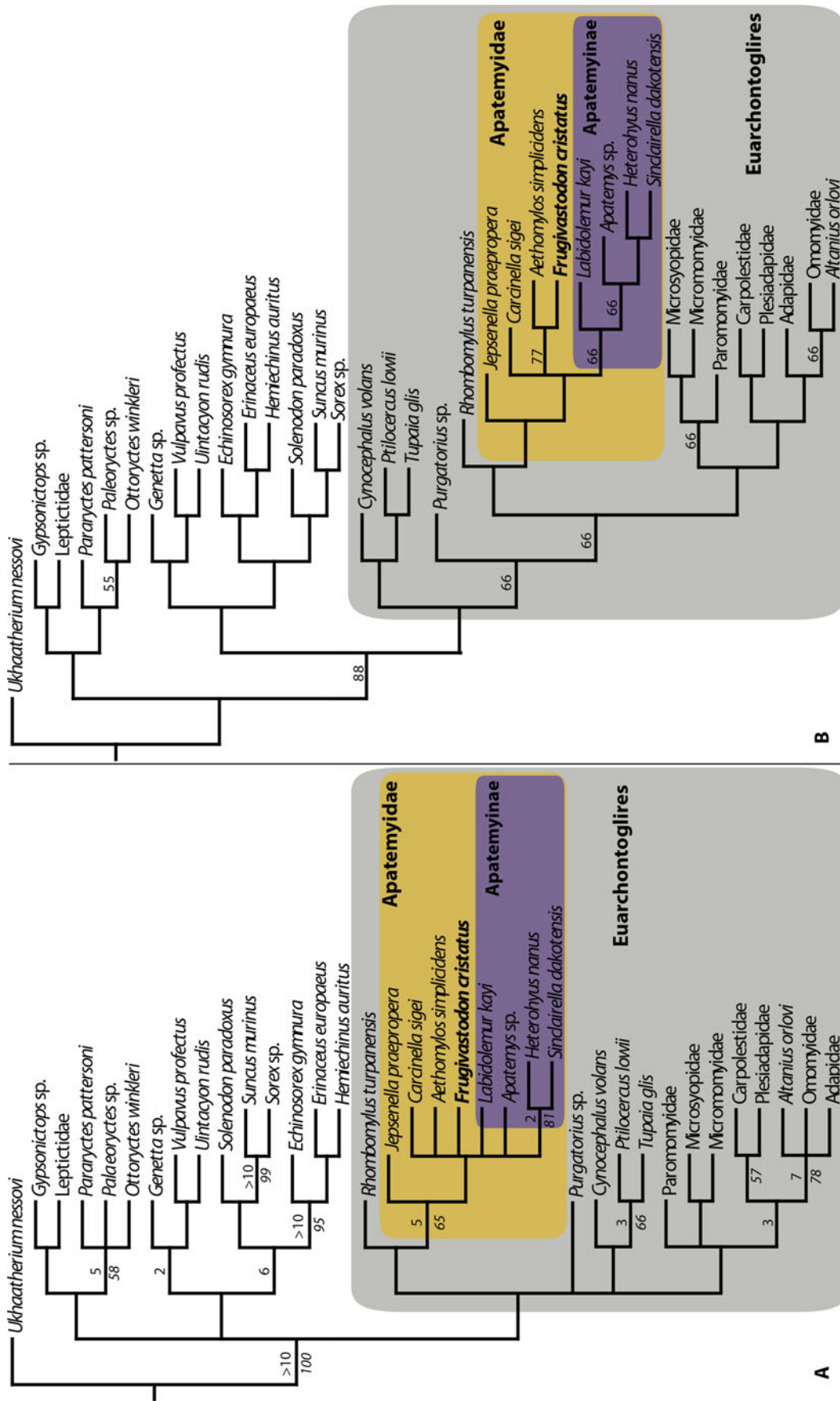
In the strict consensus tree of the second analysis, the majority of the polytomies are localized among the Euarchontoglires (Fig. 12.10A). The primate *Altanius orlovi* is in a polytomy with the Omomyidae and Adapidae (Fig. 12.10A); it was the sister taxon of the two families in the first analysis. However, in the majority-rule consensus of the second analysis, *Altanius orlovi* is more closely related to Omomyidae (Fig. 12.10B).

The relationships of the Paromomyidae in the second analysis are different from those found by the first analysis and by Silcox et al. (2010). In the latter study, the family was the sister taxon of the clade that comprises the Carpolestidae,

Plesiadapidae, *Altanius*, Omomyidae, and Adapidae (i.e., Euprimateformes). In our second analysis (majority-rule consensus; Fig. 12.10B), Paromomyidae are closely related to Microsyopidae and Micromomyidae. This relationship, however, seems less probable – based on the current morphological and stratigraphic data – than the relationships found by Silcox et al. (2010) and our first analysis.

In the second analysis there is a lack of resolution concerning the phylogenetic position of the primitive plesiadapiform *Purgatorius* (Fig. 12.10A); its position in our analysis does not support the monophyly of the Primates. *Purgatorius* is indeed more basal among Euarchontoglires





**Fig. 12.10** Consensus of 9 equally parsimonious trees from the analysis adding *Frugivastodon* and *Aethomylos* to the dataset of Silcox et al. (2010) (L = 1099 steps; CI = 0.29; RI = 0.52). **A** Strict consensus with Bremer supports (above node) and bootstrap values greater than 50% (below node); 1138 steps long with a CI = 0.28 and RI = 0.50. **B** Majority-rule consensus; 1099 steps long with a CI = 0.29 and RI = 0.52

than in the first analysis and Silcox et al. (2010) (Fig. 12.10B).

Apatemyids and *Rhombomylos turpanensis* are less basal among Euarchontoglires in the majority-rule consensus of the present analysis than in the strict consensus tree of the first analysis and that of Silcox et al. (2010): they are the sister group to Primates (they are even more inclusive than *Purgatorius*) (Fig. 12.10B). In this topology, they are included among Euarchonta. Finally, the Sundatheria (and thus Scandentia) are more basal in the majority-rule consensus than in the first analysis and Silcox et al. (2010).

The relationships listed above, based on our analysis including both *Frugivastodon* and *Aethomylos*, seem less likely than the results of the first analysis and Silcox et al. (2010), based on our current knowledge of the evolution of the Euarchontoglires. Because the present study focused on apatemyids, only further studies will determine if there is merit to any of these rearrangements. However, one can conclude that the inclusion of the fragmentary *Aethomylos* introduces instability into the resulting trees and strongly modifies the relationships among Euarchontoglires. We also performed analyses with the fragmentary possible apatemyids *Eochiromys* and *Russellmys*, but the results were less resolved and the analyses were not informative.

Nevertheless, the second phylogenetic analysis supports allocation of *Aethomylos* to Apatemyidae. The node that unites apatemyids has a Bremer support index of 2 (Fig. 12.10A); it equals five in the first analysis (Fig. 12.9), even though there is little resolution among apatemyid genera. The Paleocene *Jepsenella praepropera* is again the most basal apatemyid (Fig. 12.10). In the strict consensus, only the close relationship between *H. nanus* and *S. dakotensis* is found (Bremer support = 2; Bootstrap value = 81) (Fig. 12.10A). The other apatemyids form a polytomy. In the majority-rule consensus tree (Fig. 12.10B), relationships among some Apatemyidae are resolved. *Apatemys* sp. is closely related to *H. nanus* and *S. dakotensis*. *Labidolemur kayi* is related to *Sinclairiella*, *Heterohyus*, and *Apatemys*. This topology is partially similar to that of the first analysis – only *Carcinella* is excluded from this group.

The newly added taxa, *Frugivastodon* and *Aethomylos*, form a monophyletic clade in the majority-rule consensus (Fig. 12.10B). This relationship is supported by the similarities noted above. *Frugivastodon* and *Aethomylos* thus might represent a distinct clade of apatemyids. The position of *Carcinella* is still uncertain. It shares with *Aethomylos* the absence of a hypocone, but some features distinguish *Carcinella* from *Frugivastodon* and *Aethomylos* (see section “Relationships of *Frugivastodon*”).

Therefore, our phylogenetic results indicate that two groups of apatemyids might have evolved independently during the Eocene. The Paleocene age of *Labidolemur kayi* implies that the two groups may have separated during the

Paleocene. They both root in Paleocene *Jepsenella*, and as a result, the primitive apatemyid *Jepsenella* should be excluded from the Apatemyinae.

## Discussion

### Relationships of *Frugivastodon*

To further assess the affinities of *Frugivastodon*, we compared it to the apatemyids present in Europe and North America at the time it was present in India (c. 54.5 Ma). In North America, two distinct genera are known. *Labidolemur*, first recorded in the Tiffanian, is represented in the early Eocene by *L. kayi* (Cf-1/Wa-6) and *L. serus* (Wa-1/Wa-5). *Apatemys* is represented by *A. pygmaeus* (Wa-0), *A. chardini* (Wa-0/Wa-7), *A. rodens* (Wa-0/Br-3), and *A. bellulus* (Wa-0/Br-3) (Gingerich 1982; Gunnell et al. 2008a; Beard and Dawson 2009).

In Europe, the genus *Apatemys* is known only in the early Eocene, when it was already diverse. Four species are known: *A. teilhardi* at Dormaal (MP7; c. 56 Ma) (Teilhard de Chardin 1927; Russell et al. 1979), *A. sigogneui* at Pourcy (MP7) and Mutigny and Avenay (MP8+9; Avenay ≈ 51–52 Ma) (Russell et al. 1979), *A. prouti* at Abbey Wood (MP8+9; c. 55.12 Ma) (Hooker 2010b), and *A. mutiniacus* at Mutigny and Avenay (MP8+9) (Russell et al. 1979). A second apatemyid genus, *Heterohyus*, is well diversified in Europe. It is represented in early Eocene localities by indeterminate species: at Silveirinha (MP7), Mutigny, and Avenay (MP8+9), Grauves, and Cuis (MP10) (Russell et al. 1979; Estravis 1992). The genus is far better known in the middle and late Eocene where nine species are presently recorded (Koenigswald et al. 2009; Table 2). In addition to *Apatemys* and *Heterohyus*, there are two poorly known genera in the earliest Eocene of Europe: *Eochiromys landenensis* from Dormaal (two specimens) and *Russellmys denisae* from Silveirinha (one specimen) (Russell et al. 1979).

As discussed in the Systematics section above, the Indian taxon is unusual compared to the typical Eocene apatemyids *Apatemys* and *Heterohyus* due to the relative size and morphology of the molars (M1 transversely elongated and bearing only a small hypocone; high postprotocrista; presence of metaconule; tiny fourth trigonid cusp; paraconid not distally located; trigonid not parallelogram-like; talonid not wider than the trigonid; high entocristid; entoconid only slightly smaller than the hypoconid; reduced m3; talonid mesiodistally short on the m3). As mentioned above, some of the distinctive features of *Frugivastodon* (e.g., morphology of the M1) are more typical of Paleocene apatemyids such as *Labidolemur* and *Jepsenella* than of

contemporaneous apatemyids. The Indian taxon notably shares with *Labidolemur* and *Jepsenella* the high crown and the relative size of the molars (primitive features among apatemyids), except the shorter m3. However, the morphology of the Indian fossils clearly distinguishes *Frugivastodon* from *Labidolemur* and *Jepsenella*: the Indian taxon differs from these genera in having more mesiodistally elongated molars, less mesiodistally compressed trigonids, less distally located paraconid, smaller fourth cusp, narrower talonid, higher entocristid, wider M1, and less developed hypocone. *Frugivastodon* is more similar to *Jepsenella* than to *Labidolemur* in having wider, triangular upper molars (a primitive feature). Moreover, *Frugivastodon* and *Jepsenella* possess M1 and M2 that have close L/W ratios – other apatemyids have very different ratios between M1 and M2 (Table 12.3).

Comparison of *Frugivastodon* with the better known apatemyids from the Paleocene and Eocene highlights the numerous unusual features shown by the Indian apatemyid, which suggest that *Frugivastodon* represents a clade separate from that of *Labidolemur*, *Apatemys*, and *Heterohyus*. Among the particular features of *Frugivastodon* is the small hypocone (a primitive feature). This feature is rare among apatemyids, but it characterizes the Paleocene *Jepsenella* (Szalay 1968). It is also found in two European apatemyids known in the Eocene: *Russellmys denisae* from the locality of Silveirinha (Portugal, MP7; Estravís 1990) and *Carcinella sigei* from the ‘Phosphorites du Quercy’ (France; ?late Eocene; Koenigswald et al. 2009).

*Russellmys denisae*, from the earliest Eocene of Silveirinha, was described based on a left maxillary fragment bearing the almost intact crown of M2 and bases of M1 and M3. As only one molar is known, the inclusion of this genus among Apatemyidae is problematic (Estravís 1990, 1992). If correctly attributed to this family, it would represent one of the smallest apatemyids recorded in Europe (Estravís 1990; Koenigswald et al. 2009). As in *Frugivastodon*, but unlike other Eocene apatemyids, the hypocone of M2 is either very small or absent; wear makes its presence ambiguous. *Russellmys* also differs from other apatemyids in having a protocone that is less mesially located (resulting in a triangular aspect in occlusal view), a high postprotocrista, and a metaconule. *Frugivastodon* and *Russellmys* share the triangular morphology of the upper molars in occlusal view, the presence of a small metaconule and a distinct postprotocrista (the trigon is distally open in other Eocene apatemyids due to the absence of this structure), and a weak hypocone. The styles are shorter in the Portuguese fossil than in *Frugivastodon* (as well as in all the other apatemyids). Moreover, the area where the hypocone may be situated is somewhat more labially located than in *Frugivastodon* and apatemyids in general – the postcingulid actually extends lingually in apatemyids. As a consequence, the comparison between

*Frugivastodon* and *Russellmys* does not evidence similarities between these two taxa, leaving open the question of the systematic status of *Russellmys*.

Estravís (1990) noted similarities between *Russellmys* and *Aethomylos*. Koenigswald et al. (2009, p. 62) followed Estravís (1990) and considered that *Aethomylos* is “almost certainly an apatemyid.” *Aethomylos* was initially considered as *Insectivora incertae sedis* because of the peculiar morphology of its upper and lower molars (Novacek 1976; Gunnell et al. 2008b), although Novacek considered the possibility that it could represent an apatemyid. He listed several similarities with apatemyids, including the bowl-shaped structure of the talonid basin, the high entocristid, the morphology of the angular mesiolabial corner of the trigonid (position of the fourth cusp of the trigonid), the low profile of the trigonids, and the more posterior position of the metaconid relative to that of the protoconid (Novacek 1976) (Fig. 12.8). At the same time, however, he noted several important differences: the mesiolabial corner of the trigonid is farther posterior than the paraconid (hence the trigonid lacks the typical parallelogram occlusal outline of Eocene apatemyids), and the upper molars differ in lacking a distinct hypocone (Fig. 12.8). In these differences *Aethomylos* resembles *Frugivastodon*. *Frugivastodon* and *Aethomylos* also share the presence of a distinct postprotocrista that closes the trigon distally, a high entocristid, an entoconid almost as high as the hypoconid, mesiodistally elongated molars (Table 12.5), talonids of similar width to the trigonids (the talonid is wider than the trigonid, at least on the m1, in other Eocene apatemyids), and an m3 shorter than the m1 and m2. Because the teeth of *Aethomylos* are isolated, and upper loci were not identified with confidence, it is premature to reach any conclusions about similarity to *Frugivastodon* in upper molar proportions. The similarities shared by *Frugivastodon* and *Aethomylos* support the conclusions of Estravís (1990) and Koenigswald et al. (2009) that *Aethomylos* is probably an apatemyid. Moreover, the results of the phylogenetic analysis presented herein support a close relationship between *Frugivastodon* and *Aethomylos* despite the great geographic separation between the two taxa (see above; Fig. 12.10B). More complete specimens of both taxa would obviously help to test this hypothesis.

*Carcinella* was described by Koenigswald et al. (2009) based on a well-preserved skull found in the ‘Phosphorites du Quercy’. This small apatemyid is possibly late Eocene in age; its precise locality and age are unknown. It differs from *Heterohyus* (Eocene of Europe) by having a remnant hypocone on M1 and no hypocone on M2 (derived features?). This genus differs from *Frugivastodon* in the loss of the postprotocristid and metaconule (derived features), resulting in a distally open trigon as in most Eocene apatemyids. The protocone area of the M1 and M2 is also reduced compared to *Frugivastodon*. This feature also characterizes the Eocene

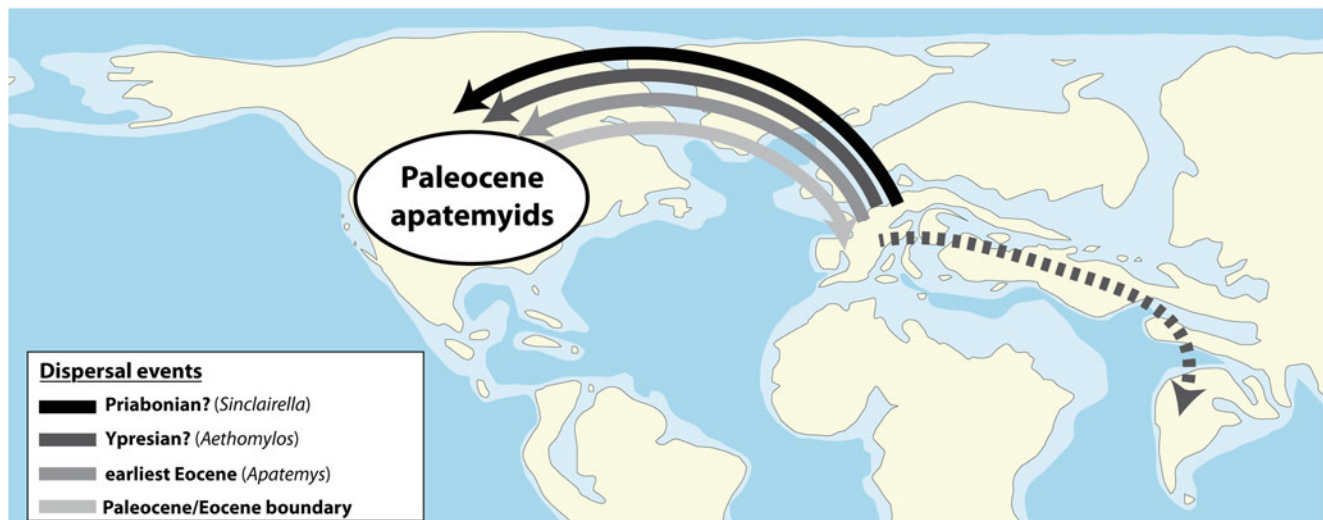
*Apatemys*, *Heterohyus* and *Sinclairiella*. The lower dentition of *Carcinella* is unfortunately unknown, which prevents comparison to the lower molars of *Frugivastodon*. However, the large size of the M3 – notably of its protocone – indicates that the m3 was probably mesiodistally elongated, as seen in *Apatemys* and *Heterohyus*, and probably as long as the m1 (a derived feature), rather than reduced as in *Frugivastodon*. Thus, although *Carcinella* seems to be potentially close to *Frugivastodon* based on the absence of a hypocone, the overall morphology of the dentition recalls the apatemyines (*Heterohyus*, *Apatemys*, *Sinclairiella*). If *Carcinella* is indeed closely related to *Apatemys* and *Heterohyus*, this would imply that at least two groups of apatemyids independently greatly reduced or lost the hypocone.

### Geographic Origin of *Frugivastodon* and the Dispersal of Apatemyids

Apatemyidae first appear in the early Paleocene of North America (Torrejonian, To-3), but are not known in Europe until the earliest Eocene. Consequently, it seems reasonable to postulate that the family originated in North America and dispersed into Europe around the Paleocene-Eocene boundary (e.g., during the PETM, Fig. 12.11). European and North American faunas were very similar (at the genus and family levels) during the earliest Eocene (e.g., Simpson 1947; McKenna 1975; Krause and Maas 1990). Dispersals from North America into Europe have been evidenced for

numerous mammalian groups (e.g., Nyctitheriidae, Oxyaenidae, Palaeonodonta, Pantodonta, Rodentia) (Russell 1975; Smith 1996; Lucas 1998; Smith and Smith 2001; Gheerbrant et al. 2005; Solé et al. 2011), whereas several mammals may have followed the opposite direction (e.g., Artiodactyla, Carnivoraformes, Hyaenodonta, Perissodactyla, Primates) (Gingerich 1989; Smith and Smith 2001; Godinot and de Broin 2003; Hooker and Dashzeveg 2003; Smith et al. 2006; Solé et al. 2014). The dispersals that are inferred to have occurred at that time have been recently summarized by Hooker (2015).

The presence of three species referred to *Apatemys* and four or possibly five lineages of apatemyids in the early Eocene of Europe led Russell et al. (1979) to conclude that apatemyids experienced a rapid and important radiation when they arrived in Europe. As a consequence, some paleontologists have also suggested that they were already present in Europe in the Paleocene. Szalay (1968) discussed this possibility based on an upper molar figured by Russell et al. (1966) as *Aboletylestes* sp. that he considered similar to those he referred to *Jepsenella*; however, this isolated tooth is now considered to be a pantolestian, *Nosella europaea* (López-Martínez and Peláez-Campomanes 1999). The absence of apatemyids in the Paleocene fossil record of Europe could result from the scarcity of fossiliferous localities known in Europe during this epoch and the rarity of apatemyids. It has recently been suggested that European mammals from the Paleocene document several episodes of dispersal from North America into Europe (De Bast and Smith 2017).



**Fig. 12.11** Schematic map showing the hypothetical geographic dispersion of apatemyids. Apatemyidae dispersed between North America and Europe via the Greenland Bridge and Thulean route; they dispersed from Europe to India probably through the Turgai Strait and/or along the Tethyan shore. Oldest apatemyids are recorded in the Paleocene of North America (Torrejonian) (Simpson 1940; McKenna 1963a; Szalay 1968; West 1973b). See text for explanations of the dispersal events. The exact timing of the dispersals of Apatemyidae in India is unknown but probably occurred in the Ypresian. Paleogeographic map adapted from Ron Blakey, Eocene (<http://www2.nau.edu/rcb7/050Marect.jpg>)



Apatemyids seem to have dispersed between Europe and North America in the earliest Eocene. Gingerich (1982) postulated that *Apatemys chardini* may have dispersed from Europe into North America (Fig. 12.11; earliest Eocene) as part of the Wasatchian faunal cohort that arrived in North America in the earliest Eocene (Gingerich 1989; Woodburne et al. 2009; Hooker 2015). Therefore, European apatemyids may have been closer to the centre of origin of *Apatemys* than North American ones. If *A. chardini* evolved from a European taxon, this would imply rapid radiation of apatemyids in Europe, followed by dispersal back into North America in the earliest Eocene. Unfortunately, the few isolated teeth from the earliest Eocene (Wa-0) of North America (*A. pygmaeus* from the Red Hot local fauna of Mississippi [Beard and Dawson 2009], and *Apatemys* sp. from the southern Bighorn Basin of Wyoming [Strait 2001]) are insufficient to shed light on the geographic origin of *Apatemys*. It may be noted that Sluijs et al. (2014) proposed an age younger than Wa-0 for the Red Hot fauna.

None of the early Eocene apatemyids found in the Belgium, London and Paris basins (=Northwestern European Province) (e.g., Dormaal, Abbey Wood, Mutigny, Avenay) and in the south of France and Iberian Peninsula (=Southwestern European Province) (e.g., Silveirinha, Rians) seem to be related to *Frugivastodon*. Even *Apatemys teilhardi*, the oldest European apatemyid (together with the very fragmentary *Eochiromys*) and the slightly younger *A. mutinicus*, appear too derived to be closely related to *Frugivastodon* (Fig. 12.7): the difference in width between the (wider) talonid and the trigonid on m1 is greater than in *Frugivastodon*; the position of the entoconid is more distal; the talonid is open lingually; the paraconid is more distally located (giving a pronounced trapezoidal aspect to the trigonid in occlusal view); the M1 is narrower transversely (Table 12.3); and the internal crests, paraconule, metaconule and postparaconule crista are reduced. However, lower molar proportions of *A. teilhardi* are intermediate between those of the late Paleocene-early Eocene apatemyids from North America and *Frugivastodon* (Table 12.5). The oldest European apatemyids might have undergone a mesiodistal elongation of the lower molars similar to *Frugivastodon*.

Because apatemyids were restricted to Europe and North America before the discovery of *Frugivastodon*, the presence of this latter taxon in southern Asia is intriguing. How can we explain the presence of *Frugivastodon* in India? Two hypotheses can be envisaged: (1) apatemyids dispersed from North America into Asia and thus into India via the Bering Land Bridge; (2) they dispersed first from North America into Europe via the Greenland Bridge and Thulean route, and then from Europe to India via land connections across the Turgai Strait and/or along the Tethyan shore – the southern route being more likely. As suggested above, the Indian apatemyid shares mesiodistal elongation of the

molars (a possible derived character) with *A. teilhardi* from the earliest Eocene of Europe. Certain other particular features of *Frugivastodon* are shared only with some North American apatemyids from the Paleocene or the Paleocene-Eocene boundary (*Jepsenella*, *Labidolemur*). Since apatemyids are otherwise unknown from Asia, the hypothesis of a direct dispersal from North America into Asia seems less likely. Consequently, present evidence suggests Europe as the potential geographic source of *Frugivastodon*.

The possibility of dispersal from Europe into India is strengthened by the presence of several mammal taxa in the Vastan local fauna (bats, rodents, primates, tilodonts) that strongly suggest faunal connections between Europe and India during the early Eocene (Smith et al. 2007, 2016; Rana et al. 2008; Rose et al. 2009a, b). The direction of this dispersal is, however, still uncertain. By contrast, the Vastan fauna displays only a few similarities to Asian faunas (Rose et al. 2008). The timing of this dispersal is uncertain but it presumably occurred during the early Ypresian or even earlier (Fig. 12.11; Ypresian).

The European endemic genus *Heterohyus*, which is mainly characterized by its incisor morphology (Russell et al. 1979) and the development of the hypocone, is first recorded in Europe at Mutigny (MP8+9), a locality of the Paris Basin that ranges in age between 55.12 Mya (age of Abbey Wood; Hooker 2010b) and 52–51 Mya (age of Avenay; Smith and Smith 2013) – while Vastan age is considered to be around 54.5 Ma (Bajpai et al. 2005; Adatte et al. 2014; Samanta et al. 2016; Smith et al. 2016). As a result, *Heterohyus* and *Frugivastodon* appeared almost at the same time, but in different Laurasian regions. These two endemic lineages can be viewed as representing a phase of local evolution that followed the dispersal that occurred around the Paleocene-Eocene boundary and in the early Ypresian from North America to Laurasia.

As discussed above, certain molar features suggest that *Frugivastodon* could be closely related to North American *Aethomylos*. However, because of the geographic and temporal separation between the two taxa (India vs North America, early Eocene vs middle Eocene), and the very limited fossil evidence on which their possible relationship is based, the following interpretations are largely speculative. Given the older age of *Frugivastodon*, and some features that might be interpreted as more primitive, it may be postulated that the ancestors of *Aethomylos* could have dispersed from Europe (or from India through Europe) into North America either during the Bridgerian (i.e., during the Ypresian) or around the Brigerian/Uintan boundary (Fig. 12.11; Ypresian?). It is worth noting that the Uintan, like the Bridgerian, experienced only minor immigrations (Woodburne et al. 2009). In the absence of evidence, a dispersal route through Asia and across the Bering land bridge cannot be ruled out.

The beginning of the Bridgerian records a new evolutionary diversification of the mammals, probably related to the Early Eocene Climatic Optimum (EECO) (Woodburne et al. 2009). However, none of the 'new' taxa recorded in the Bridgerian are immigrants according to Woodburne et al. (2009). Once again, because apatemyids, except for *Frugivastodon*, are unknown in Asia, a dispersal from Europe into North America appears to be equally as likely as dispersal directly from Asia to North America across Beringia. Finally, the sudden appearance of *Aethomylos* in the North American fossil record implies that the group that includes *Aethomylos* and *Frugivastodon* may have survived at least until the Uintan.

Another possible dispersal of European apatemyids into North America has been recently discussed by Silcox et al. (2010). As shown by these authors, *Sinclairiella dakotensis* and the European *Heterohyus nanus* have a close relationship that suggests *Sinclairiella* may have been a European migrant. In this case, the dispersal may have occurred during the Priabonian (*Sinclairiella* is first recorded in the Chadronian NALMA, Ch-3) (Fig. 12.11; Priabonian).

The dispersals reconstructed here imply that apatemyids dispersed several times from Europe into North America. Conversely, one can hypothesize that parallel evolution could have occurred in Europe (or India) and North America. As is often the case, more definitive conclusions on the dispersal of apatemyids will require an improved fossil record.

## Conclusions

The new fossils discovered at Vastan Lignite Mine confirm the reference of *Frugivastodon* to Apatemyidae. The Apatemyidae were thus present in the Indian subcontinent as well as in Europe and North America. The morphology of the teeth discovered in the early Eocene of India differs from that of most Apatemyidae known from the Eocene of North America and Europe. Similarities between the teeth of *Frugivastodon* and those of *Aethomylos*, from the early and middle Eocene of western North America, strengthen the interpretation that *Aethomylos* is an apatemyid. Further, the resemblances suggest that *Frugivastodon* and *Aethomylos* represent a separate clade of apatemyids, which probably originated during the late Paleocene or, at least, around the Paleocene-Eocene boundary, although where this clade originated is uncertain.

The numerous differences in the dental anatomy of *Frugivastodon* compared to apatemyines (*Labidolemur*, *Apatemyis*, *Heterohyus*, *Sinclairiella*) indicate that the early Eocene

radiation of Apatemyidae was more complex than has been envisioned, but the history and phylogeny of the apatemyids remain poorly understood. Europe appears to have been a crucial area for deciphering the evolution of these insectivorous mammals.

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