A New Omomyid Primate from the Earliest Eocene of Southern England: First Phase of Microchoerine Evolution

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A new omomyid primate from the earliest Eocene of southern England: First phase of microchoerine evolution

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A second species of the microchoerine omomyid genus *Melaneremia*, *M. schrevei* sp. nov. is described. It has been collected from the upper shelly clay unit of the Woolwich Formation, earliest Ypresian, Eocene, of Croydon, Greater London, UK. Phylogenetic analysis shows *M. schrevei* to be the most primitive member of the main clade of the Microchoerinae and demonstrates the initial dental evolution that separated this European subfamily from other omomyids. Calibration of the Woolwich upper shelly clay unit to the later part of the Paleocene–Eocene Thermal Maximum shows that speciation leading to the Microchoerinae took place within 170 ky of the beginning of the Eocene. Tentative identification of *M. schrevei* in the Conglomérat de Meudon of the Paris Basin suggests close time correlation with the upper part of the Woolwich Formation.

Key words: Mammalia, Primates, *Melaneremia*, evolution, phylogeny, Paleocene–Eocene Thermal Maximum.

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Introduction

In 1998 at Park Hill, Croydon, Greater London, a section in the Woolwich Formation of earliest Eocene age, originally exposed in 1882 during excavation of a railway cutting, was re-exposed when the cutting was widened for the Croydon Tramlink (Hooker et al. 2009). In 1882, the segment of the cutting known as Sandilands showed what is now identified as the upper shelly clay unit of the Woolwich Formation, overlying the Reading Formation and underlying the Blackheath Formation (Klaassen 1883; Hooker et al. 2009; Hooker 2010). Within apparently channelling blue clays (base not seen in 1998), Klaassen (1883) recorded three small channel fills. In the central of these three channels he found bones of the flightless bird *Gastornis* (Newton 1886) and an ulna of the pantodont mammal *Coryphodon* (Newton 1883). In 1998, thanks to Klaassen's accurate measurements, the central channel was relocated and bulk sampled. Among the small assemblage of mammals recovered (Hooker et al. 2009) were a lower jaw and three isolated lower molars of the omomyid *Melaneremia*. These differ from the only previously described species of the genus, *Melaneremia bryanti* Hooker, 2007, and here form the basis of a new species.

The annotation of the synonymy lists follows Matthews (1973). Scanning electron micrographs of casts of specimens were taken on a Philips XL30.

Institutional abbreviations.—CM, Carnegie Museum of Natural History, Pittsburgh, USA; NHMUK, Palaeontology Department, Natural History Museum, London, UK.

Other abbreviations.—PETM, Paleocene–Eocene Thermal Maximum; RHTS, Red Hot Truck Stop.

Systematic palaeontology

Order Primates Linnaeus, 1758
Family Omomyidae Trouessart, 1879
Subfamily Microchoerinae Lydekker, 1887
Genus *Melaneremia* Hooker, 2007

Type species: *Melaneremia bryanti* Hooker, 2007 from the Lessness Shell Bed, Blackheath Formation, Early Ypresian, Eocene, Abbey Wood, London, UK.

Included species: *Melaneremia schrevei* sp. nov.

Emended diagnosis.—Small microchoerine (mean m1 length 1.82 mm). Lower dental formula: ? ? 3 3. Cheek teeth relatively low-crowned and essentially without enamel wrinkling. P3 buccolingually long with short postmetacrista and tiny sublingual protocone (unique). p3 similar in size to p4, both with high, cuspate paraconids. p4 lacking exodaenodonty, with talonid relatively long and with lingual crown base horizontal. Upper molars transversely elongate with short, mesiodistally orientated postmetacrista, with distinct postcingulum and metacingulum, and without Nannopithex fold or mesostyle. Lower molars with paraconid as large as metaconid and with mesiodistally orientated pre-entocristid. m1 trigonid open lingually. m1–2 entoconid slightly lower than metaconid. m2 distinctly longer than broad. m3 as long as m2. m3 talonid narrower than

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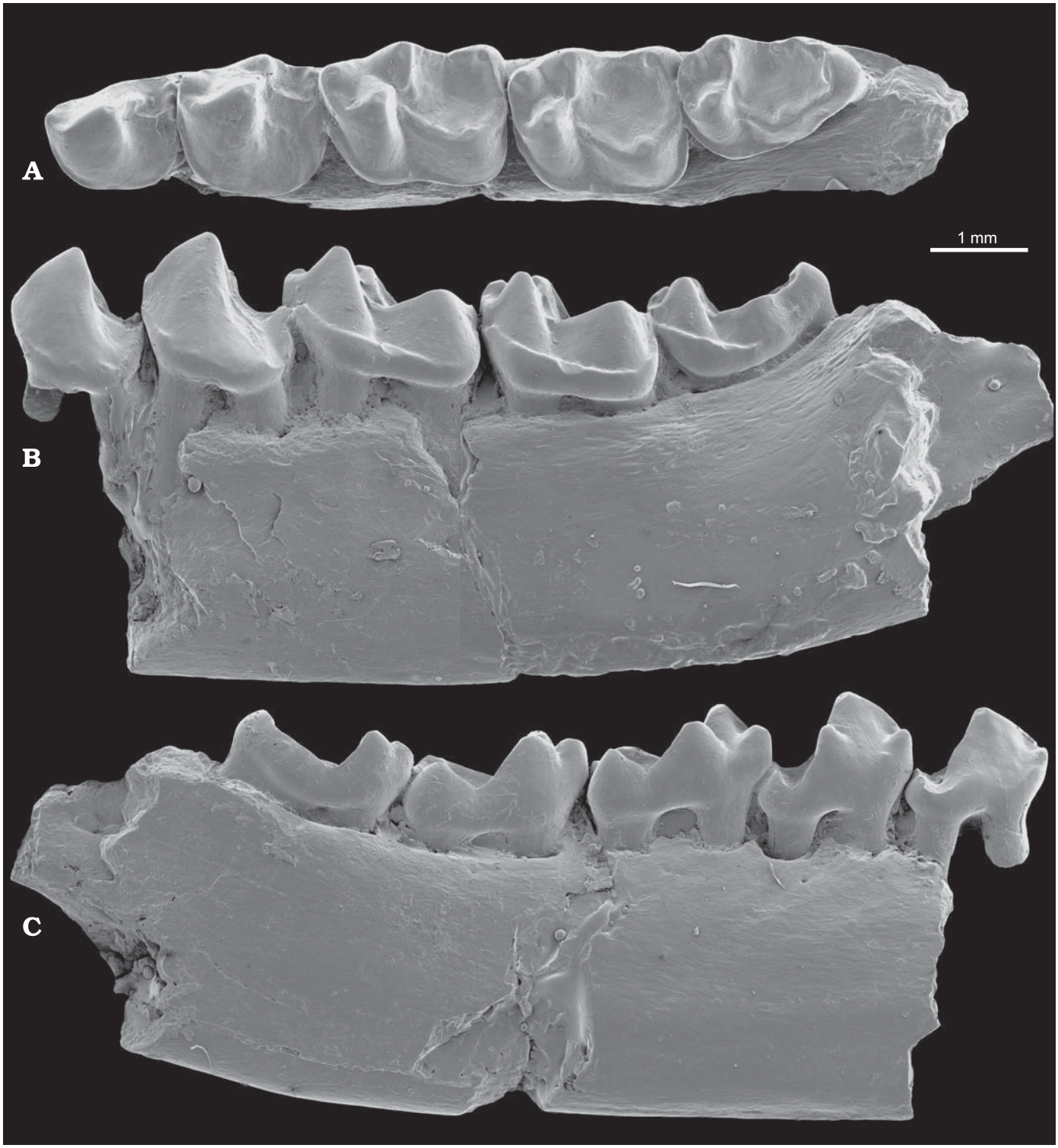

Fig. 1. Scanning electron micrographs of gold–palladium coated epoxy casts of the holotype left dentary of the omomyid primate *Melaneremia schrevei* sp. nov., NHMUK.M85501, central channel, upper shelly clays, Woolwich Formation, Sandilands cutting, Park Hill, Croydon, in occlusal (**A**), buccal/lateral (**B**), and lingual/medial (**C**) views.

trigonid, with entoconid not lingually salient. m3 hypoconulid lobe unicuspid, broadly open to rest of talonid.

Differential diagnosis.—All other microchoerine genera (*Nannopithex* Stehlin, 1916, *Vectipithex* Hooker and Harrison, 2008, *Necrolemur* Filhol, 1873, *Microchoerus* Wood, 1844, *Pseudoloris* Stehlin, 1916, but unknown in *Paraloris* Fahlbusch, 1995) have a P3 with a larger, lingually positioned protocone. All except *Paraloris* are higher-crowned and (where known) have a less transversely elongate M1. All ex-

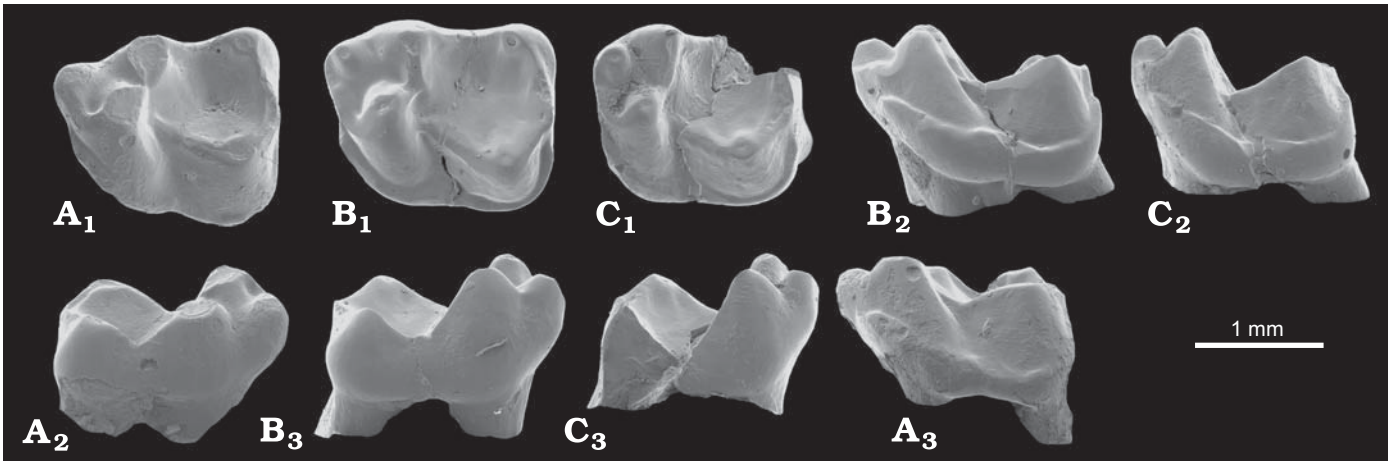

Fig. 2. Scanning electron micrographs of gold–palladium coated epoxy casts of lower molars of the omomyid primate *Melaneremia schrevei* sp. nov., central channel, upper shelly clays, Woolwich Formation, Sandilands cutting, Park Hill, Croydon. **A**. Right m1 (reversed), NHMUK.M85504. **B**. Right m2 (reversed), NHMUK.M85502. **C**. Left m2, NHMUK.M85503. Views are occlusal (A_1, B_1, C_1), buccal (A_3, B_2, C_2), and lingual (A_2, B_3, C_3).

cept *Pseudoloris parvulus* (Filhol, 1890) are larger. *Necrolemur* has an m3 shorter than m2. All except *Nannopithex zuccolae* have an M1–2 hypocone. All except *Pseudoloris*, *Vectipithex smithorum* Hooker and Harrison, 2008 and *V. ulmensis* (Schmidt-Kittler, 1971) have an upper molar Nannopithex fold. All except *Pseudoloris* and *Paraloris* have wrinkled enamel, intensely so in *Necrolemur* and *Microchoerus*. *Necrolemur* and *Microchoerus* have a larger, doubled upper molar metaconule, a bicuspid m3 hypoconulid lobe, and lack a paraconid on m2–3. Most *Microchoerus* have an upper molar mesostyle. *Nannopithex zuccolae* and *Vectipithex* have a p3 much smaller than p4. All except *Vectipithex* have a lower p3 paraconid. *Necrolemur*, *Microchoerus*, and *Paraloris* have a lower p4 paraconid. *Nannopithex* has an inflated p4. *Nannopithex* and *Vectipithex* have an exodaenodont p4. All except *Paraloris* have a p4 with a shorter talonid and with a mesially upward sloping lingual crown base. All except *Nannopithex* have lower molar paraconids distinctly smaller than metaconids and a lingually closed m1 trigonid. *Vectipithex raabi* (Heller, 1930), *Nannopithex*, *Necrolemur*, and *Microchoerus* have lower molars with pre-entocristid angled mesiobuccally. *Nannopithex*, *Vectipithex*, *Necrolemur*, and *Microchoerus* have an m2 nearly as broad as long. *Nannopithex*, *Vectipithex*, and *Microchoerus* have an m3 talonid wider than the trigonid; these plus *Necrolemur* have the m3 entoconid salient lingually. *Pseudoloris* has a longer, distobuccally angled M1 postmetacrista, an elongate p3, and an m1–2 entoconid as tall as the metaconid. *Paraloris* and *Pseudoloris* have a narrower m3 hypoconulid lobe.

The phenetically similar omomyine *Jemezius* Beard, 1987 differs from *Melaneremia* in having: a larger, lingually positioned P3 protocone; exodaenodont p4 with short talonid; M1–2 with distobuccally angled postmetacrista; buccolingually wide M3; lingually closed m1 trigonid; lower molar paraconid distinctly smaller than metaconid; m2–3 paraconid lingually situated and separated mesially from paracristid by a valley; and higher-crowned molars with a mesiobuccally angled pre-entocristid.

All species of the paraphyletic omomyid genus *Teilhardina* Simpson, 1940 differ in having: P3 with larger, lingually positioned protocone; M1–2 with distobuccally angled postmetacrista; taller p3–4; lower molars higher-crowned, with distal wall of trigonid steeper and paraconid distinctly smaller than metaconid; m1 with trigonid closed lingually and with straight, shallowly notched protocristid; m2–3 paraconid more lingually situated. For other differences from individual species of *Teilhardina* and from other primitive, non-microchoerine omomyids, see Appendices 1 and 2.

Melaneremia schrevei sp. nov.

Figs. 1–3.

?*1998* Omomyid primate; Godinot et al. 1998: pl. 11.1: k, l.
v. *2009 Melaneremia* sp.; Hooker et al. 2009: 79.

Etymology: Named after Pierre Schreve, who processed the large sample of Woolwich Formation clay and helped in numerous ways during the excavation at Croydon.

Type material: Holotype: Left dentary with p3–m3, NHMUK.M85501. Paratypes: Right m1, NHMUK.M85504; left m2 with broken entoconid, NHMUK.M85503; right m2, NHMUK.M85502.

Type locality: Sandilands cutting, Croydon, Greater London; National Grid Reference TQ339655.

Type horizon: Central channel, upper shelly clays, Woolwich Formation; mammal zone PE II, Neustrian European Land Mammal Age; Early Ypresian, Eocene (Klaassen 1883; Hooker et al. 2009). NHMUK. M85504 is from the middle to upper levels of the channel fill; the rest are from the base of the channel fill.

Diagnosis.—p4 talonid with small, near vertical contact with m1. Lower molars high-crowned (within the generic range), with paraconids relatively erect. m1–2 with entoconid with steep distal wall. m2–3 with paraconids relatively close to protocristids. m2–3 metaconids with smooth mesial faces. m3 with angle of buccal crown base below protoconid and with postmetacristid straight.

Differential diagnosis.—*M. bryanti* differs in the following

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ways: p4 talonid with distal wall sloping, and with extensive contact with m1. Lower molars lower-crowned and with procumbent paraconids. m1–2 with entoconid with gently sloping distal wall. m2–3 with paraconids distant from protocristids. m2–3 metaconid mesial faces with accessory cuspules in some individuals. m3 with angle of buccal crown base behind protoconid and with postmetacristid concave.

Description.—The holotype dentary preserves p3–m3 complete and with light wear (Fig. 1). p3 was found isolated in the same sample bag as the dentary. It clearly fits the front of p4 and has been attached. Compared to other omomyids, except *M. bryanti*, all the cheek teeth have relatively low main cusps. This is particularly noticeable when compared to e.g., *Teilhardina belgica* (Teilhard, 1927), whose cusps are taller and more acute, especially those of p3–4. The same point has already been made about *M. bryanti* (Hooker 2007), although wear and slight corrosion of the p4 of that species have made the differences less clear. Although crown height is low in the genus, it is higher in *M. schrevei* than in *M. bryanti*. This difference shows most clearly in lingual view, especially in the shallower distal slope of the entoconid in *M. bryanti* (cf. Figs. 1, 2 herein with Hooker 2007: text-figs. 1C–F, 2C–F, 3C–F).

The low p3–4 protoconids create a distinctly backward curving paracristid in *M. schrevei* (Fig. 1B). The contact between p4 and m1 is small, resulting in the absence of the extensive, sloping distal talonid wall characterising *M. bryanti*, best seen in buccal view (Fig. 1B; Hooker 2007: text-fig. 2D). p3 lacks a metaconid, but a short distal crest from the protoconid, slightly lingual of the cristid obliqua, is the homologue of the metaconid developed in p4 (Fig. 1A–C). Both p3 and p4 have large, tall, cuspate paraconids, but these do not project mesially from the outline in buccal view (Fig. 1B). The p4 paraconid of *M. bryanti* is probably comparable in terms of its development, but abrasion or corrosion has reduced its size and extent (Hooker 2007: text-fig. 3E).

The two m1s show individual variation. That of the holotype shows a distinct step and notch in the protocristid, as well as a buccal metaconid buttress (Fig. 1A). This buttress does not join the cristid obliqua as it does in *Altanius*, *Washakius*, or *Trogolemur* (Szalay 1976; Dashzeveg and McKenna 1977). The structure is similar to that in m1s of *M. bryanti* and *Nannopithex zuccolae* Godinot, Russell, and Louis, 1992 (Hooker 1996b: pl. 4: 1, 2007: text-fig. 1E). The other *M. schrevei* m1 does not show this step in the protocristid (Fig. $2A_1$), indicating that the species may be at an intermediate stage in the acquisition of the derived stepped state. However, its presence in both of only two m1s of *M. bryanti* does not conclusively demonstrate that it is necessarily constantly present in that species either. NHMUK.M85504 differs from the m1 in the holotype also in having a much wider talonid. There is a complete ectocingulid, which is mainly strong, but which weakens around the hypoconid in both specimens. It is thus stronger than in *M. bryanti* m1s. The more erect orientation of the m1 paraconid in *M. schrevei* than in *M. bryanti* is consistent in both specimens (Figs. 1C, $2A_2$).

M_2 also shows this different orientation of the paraconid. The difference from *M. bryanti* is also more obvious in m2 because the paraconid is essentially the same height as the metaconid and much closer to it in *M. schrevei*. This difference is consistent across all specimens of each species. The ectocingulid is complete and strong in all three specimens, stronger than in *M. bryanti*, where it is also incomplete in one specimen around the hypoconid. There is slight variation in the position of the paraconid with respect to its distance from the protocristid. NHMUK.M85503 has the shortest distance, NHMUK.M85502 the longest, in this respect more closely resembling *M. bryanti*, whilst the holotype is intermediate (Figs. 1A, $2B_1$, C_1). However, the similarity between NHMUK.M 85502 and *M. bryanti* is less in lingual view (cf. Fig. $2B_3$ with Hooker 2007: text-fig. 3C).

The single m3 (of the holotype) is similar to those of *M. bryanti* in having a broadly open hypoconulid lobe and similar development of the ectocingulid, whose weakness around the hypoconulid is most like the holotype. It differs in having a straight, not concave, postmetacristid. It also differs in the position of angulation of the buccal crown base outline. In *M. schrevei* and in many other primitive omomyids, the buccal crown base descends steeply from the paraconid, then recurves below the protoconid and rises gradually to the hypoconulid lobe. By contrast, the shift in orientation, or angle, in *M. bryanti* is located distal of the protoconid. *N. zuccolae* and *Vectipithex raabi* are also like *M. bryanti*.

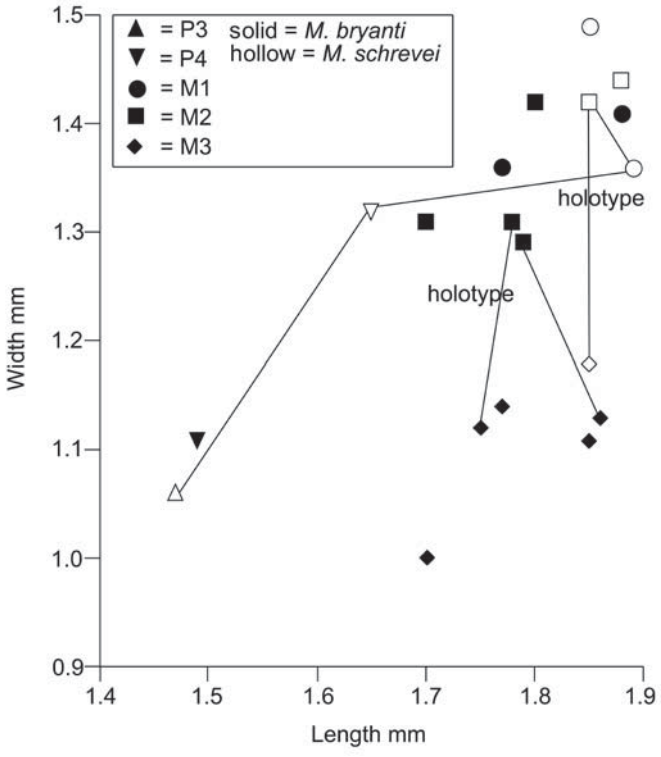

Fig. 3. Scatter diagram of length vs width (in mm) of lower cheek teeth of *Melaneremia schrevei* and *M. bryanti*. Lines join teeth of single individuals. The length dimension is measured lingually from the bulge of the distal crown base to the tip of the paraconid.

According to lower molar size, *M. schrevei* is slightly larger than *M. bryanti* (Fig. 3). However, coefficients of variation of the combined measurements (millimetres) are mainly low: m1 (4) length, 2.94; m1 (4) width, 4.35; m2 (7) length, 3.16; m2 (7) width, 6.58; m3 (6) length, 3.68; m3 (6) width, 5.46. This indicates that the size difference between the species is not statistically significant.

Anterior breakage of the dentary occurs below the front of p4. No mental foramen is preserved and therefore the posterior foramen of the two normally present must have existed more anteriorly, either below the junction of p3 and p4 as in *T. belgica*, or below p3 as in *Omomys* (Szalay 1976). It is thus unlike *N. zuccolae*, where the posterior mental foramen is located below p4 (Hooker 1996b). The most likely position in *M. schrevei* is below the junction of p3 and p4, the primitive state.

Medially, the dentary is 2.54 mm deep below m2, and thus within range of the two dentaries of *M. bryanti* (2.45 and 2.68 mm) at this locus. More anteriorly, the *M. schrevei* dentary deepens to 2.86 mm below p4. It is thus still deepening anteriorly at this point, which is close to the posterior margin of the symphysis, heralded by a sharpening of the ventral edge 1.5 mm before the anterior truncation. The most complete dentary of *M. bryanti*, which extends anteriorly to the position of the mesial edge of m1 (tooth missing) is also deepening anteriorly at this point (Hooker 2010: text-fig. 21g, h). In *N. zuccolae*, the dentary is 3.54 mm deep medially below p4 (still proportionally deeper than any of the *Melaneremia* dentaries despite its slightly larger tooth size) and probably deepens forwards no further as anterior dental and mandibular contraction has shifted the alveolus for the tip of a greatly enlarged i1 root to below p4 (Hooker 1996b: pl. 3). In *Teilhardina belgica*, the dentary begins shallowing anteriorly from just below the front of m1 (Teilhard 1927: pl. 4: 1, 2). As *T. belgica* has small incisors, the implication is that *M. schrevei* and probably *M. bryanti* had a somewhat enlarged i1, albeit smaller than in *N. zuccolae*, given its overall shallower dentary depth.

Geographic and stratigraphic range.—Later part of the PETM, earliest Eocene, London Basin and possibly Paris Basin.

Phylogenetic relationships

Choice of taxa.—*M. schrevei* is here included in a character-taxon matrix (Appendix 2) similar to that analysed when *M. bryanti* was described (Hooker 2007). As the aim of this paper is not to analyse the relationships of the Omomyidae as a whole, but to try to establish the relationships of the Microchoerinae to the rest, emphasis is placed on analysing the better known of the more primitive taxa. As the anaptomorphine tribe Trogolemurini has previously been implicated in microchoerine phylogeny (Ni et al. 2004), the primitive trogolemurins *Anemorhysis savagei* and *Teilhardina demissa* (see Tornow 2008) are also included here. Since the paper describing *M. bryanti* was accepted for publication, *Teilhardina magnoliana* Beard, 2008a has been named and *T. brandti* Gingerich, 1993 has become better known (Smith et al. 2006). In addition, Late Eocene *Paraloris bavaricus* Fahlbusch, 1995 was found to branch at the base of the Microchoerinae (Hooker and Harrison 2008). Being at the stem of omomyid evolution, these species are also included in the analysis here, with some modifications to and augmentation of the 2007 character list (see Appendix 1 for changes to the characters). Apart from the well-represented *Teilhardina asiatica* Ni, Wang, Hu, and Li, 2004, several other genera of primitive omomyids are now known from Asia, including: *Kohatius* Russell and Gingerich, 1980; *Vastanomys* Bajpai, Kapur, Thewissen, Das, Tiwari, Sharma, and Saravanan, 2005 (see also Rose et al. 2009); *Baataromomys* Ni, Beard, Meng, Wang, and Gebo, 2007; and *Indusius* Gunnell, Gingerich, Ul-Haq, Bloch, Khan, and Clyde, 2008b. However, these are currently too poorly known to be usefully included in this analysis. Other microchoerines included are *Nannopithex zuccolae* and *Vectipithex raabi* (Godinot et al. 1992; Hooker 1996b; Hooker and Harrison 2008). Once again *Purgatorius* Van Valen and Sloan, 1965 is chosen as outgroup, and in the PAUP 4.0b10 (Swofford 2002) analysis, this is treated as paraphyletic and the ingroup as monophyletic, thus characters found only in and throughout the ingroup have been excluded as having no influence on the result. As the morphological gulf between *Purgatorius* and the most primitive omomyids is large, two primitive adapiforms, *Cantius eppsi* and *Donrussellia*, are added to the ingroup to aid character polarity. They are not, however, treated as outgroup taxa, as they are potentially as derived in their own ways as omomyids.

Notes on characters.—Height of the p4 metaconid has previously been used in phylogenetic analyses (Hooker 2007: character 10; Smith et al. 2006: character 9). With the inclusion here of taxa with different overall relative heights of p4 (the protoconid being the tallest cusp), and given the substantial intraspecific variation in height of the metaconid in the well-represented species *Teilhardina americana* Bown, 1976 and *Tetonius matthewi* Bown and Rose, 1987 (Rose and Bown 1986), this character is abandoned.

Combining the relative sizes of the first incisor and canine (Hooker 2007: character 1) is also abandoned in favour of separate characters (1 and 2 herein). This accords with evidence for decoupling in several cases.

Taxa previously scored as having no p4 postmetacristid (Hooker 2007: character 11) are found to have faint basal development of this crest. The character is emended thus and the scoring slightly revised (character 16 herein).

Strength of the lower molar ectocingulid has also been used in previous analyses (e.g., Smith et al. 2006). However, it was considered too variable to be used here for the taxa involved.

Results.—Using the heuristic search and the stepwise addition option, random, with 1000 addition sequence replicates,

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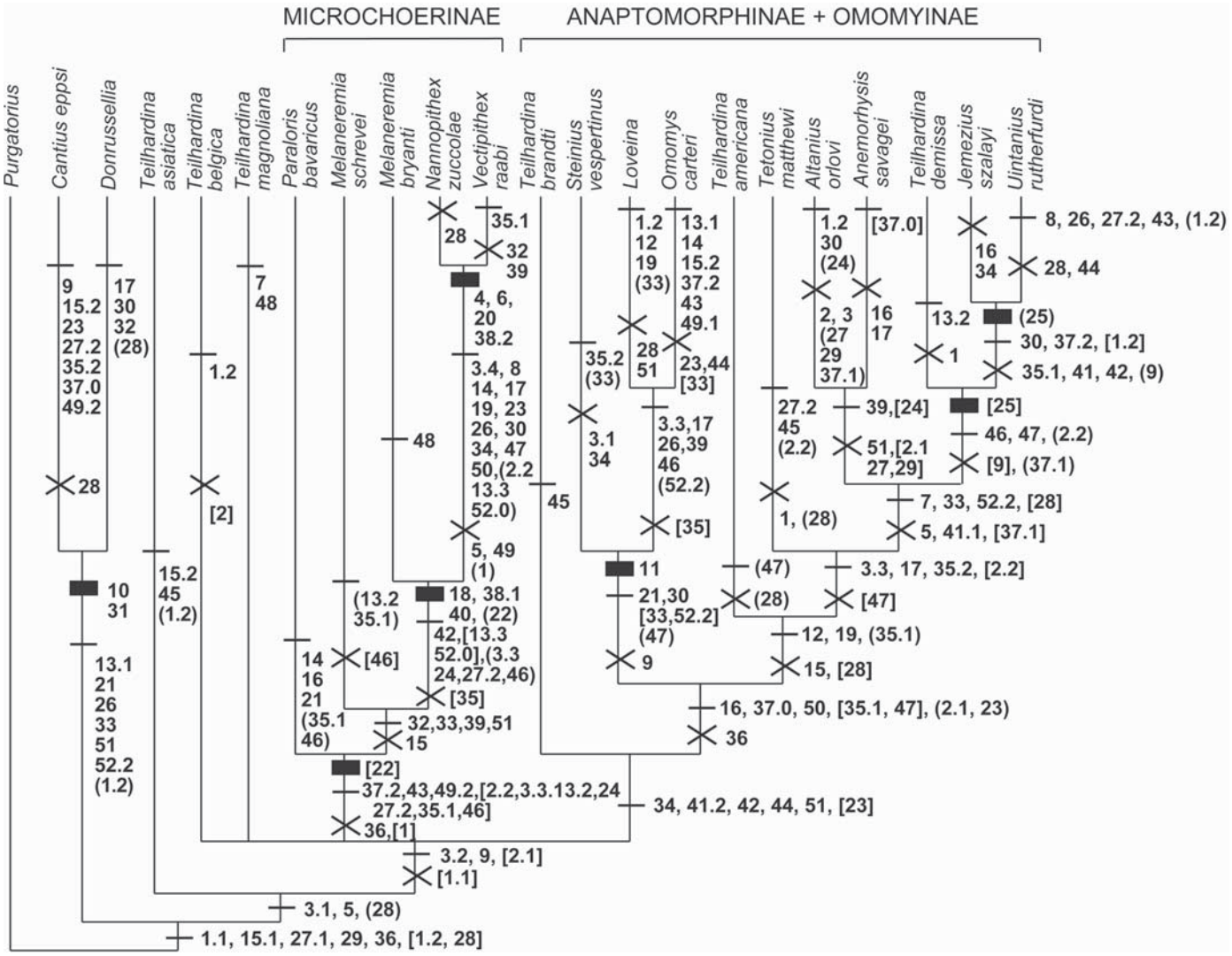

Fig. 4. Maximum parsimony tree resembling the majority rule consensus (Fig. 5A), generated by PAUP 4.0b10 from the character–taxon matrix in Appendix 2, showing character state changes; see Appendix 1 for description of numbered characters. Broad bar, synapomorphy; narrow bar, normal polarity homoplasy; X, reversal. Characters that vary with different optimisations are enclosed between [ ] for Acctran and between ( ) for Deltran.

PAUP found four maximum parsimony trees (MPTs) of 186 steps, a consistency index (CI) of 0.3602 (all characters parsimony informative) and a retention index (RI) of 0.6007. The strict consensus is poorly resolved. Thus, essentially an omomyid polytomy, only resolved into the following clades, (*Altanius*, *Anemorhysis savagei*), (*Nannopithex zuccolae*, *Vectipithex raabi*) and (*Steinius vespertinus* (*Loveina*, *Omomys carteri*)), is sister group to *Teilhardina asiatica*. This omomyid clade is sister group to the adapiform clade (*Cantius eppsi* + *Donrussellia*).

In fact, there is little difference between the four MPTs. The largest difference is in the position of the *Nannopithex zuccolae* + *Vectipithex raabi* clade. In one tree it is nested successively with the North American *Uintanius rutherfurdi*, *Jemezius*, and *Teilhardina demissa*. This is an unlikely position on biogeographical grounds, given that the opening of the North Atlantic had cut off land routes between Europe and North America several million years earlier (Hooker 2007, 2010, and references therein). *Jemezius* is from Wasatchian Zone Wa-6 (52.9–53.5 Ma), whilst the earliest *Uintanius rutherfurdi* (Robinson, 1966) is from Bridgerian Zone Br-1a (52–52.4 Ma) (Beard 1987; Beard et al. 1992; Clyde et al. 2001; Luterbacher et al. 2004; Gunnell et al. 2008a, 2009).

In the other three trees, the *Nannopithex zuccolae* + *Vectipithex raabi* clade forms part of a monophyletic Microchoerinae. The only differences between these three trees involve the combination of two alternatives. The first is whether *Teilhardina belgica* is sister taxon to a trichotomous clade comprising *T. magnoliana*, a monophyletic Microchoerinae and North American and Asian omomyids (Omomyinae + Anaptomorphinae), or is part of that clade. The second is whether Microchoerinae plus North American and Asian omomyids form a clade independent of *T. belgica* and *T. magnoliana*, or separately form a polytomy with them.

One of these three MPTs resembles the majority rule consensus and is shown with its character transformations (Figs.

4, 5A). It shows Microchoerinae, Omomyinae + Anaptomorphinae, *Teilhardina belgica* and *T. magnoliana* forming a quadritomy, which is sister group to *T. asiatica*. The collapsing of *T. belgica* into this polytomy in this MPT by PAUP has created two extra steps and changed the CI to 0.3564 and the RI to 0.5940. *Teilhardina* is clearly paraphyletic as has been pointed out before (e.g., Hooker 2007; Tornow 2008), but three species in particular, *T. asiatica*, *T. belgica* and *T. magnoliana*, cannot be accommodated in any of the three currently named subfamilies.

Three key characters unequivocally support the *M. bryanti* + *N. zuccolae* + *V. raabi* clade. They are: p4 distal talonid wall sloping, with extensive contact with m1 (character 18); m3 metaconid with accessory cuspule in some individuals (character 38: unique, but insufficiently tested as only one *M. schrevei* m3 is known); and procumbent lower molar paraconid (character 40). A long M1–2 trigon basin (character 22) may also characterise this clade (Deltran). However, it could also have evolved at the base of the Microchoerinae clade (Acctran), but upper teeth are currently unknown for *M. schrevei* and *Paraloris*. The positioning of other characters here or at lower microchoerine nodes also varies according to the optimisation method, reflecting missing data in one or another taxon.

Five key characters support the *M. schrevei* + *M. bryanti* + *N. zuccolae* + *V. raabi* clade. They are: an open m1 trigonid (character 32); a stepped m1 protocristid (character 33); an enlarged lower molar paraconid (character 39); a wide m3 hypoconulid lobe (character 51); and secondary development of a tall p4 paraconid (character 15).

A concave postmetacristid is shown as an autapomorphy of *M. bryanti* (character 48), shared convergently only with *T. magnoliana*. Strict autapomorphies were not included in the analysis (see differential diagnosis of *M. schrevei* above). However, intermediate grade m2 paraconid separation from the protocristid (character 35), low-crowned p3–4 (character 13), both under Deltran, and angle of buccal m3 crown base shift to below protoconid (character 46), under Acctran, are shown as autapomorphies of *M. schrevei*. However, character state 35.1 may be the result of enlargement of the paraconid in the microchoerine clade and therefore in this case a transient feature, reversed by subsequent procumbent orientation of the paraconid (character 40). Character state 13.2 may also not really be an autapomorphy, since p3 is unknown in *M. bryanti* and *Paraloris*. The primitive state of character 46 is also an unlikely reversal for *M. schrevei*. However, the very small size and relatively buccal position of the P3 protocone (Hooker 2010) may be an autapomorphy of *M. bryanti* or of the genus *Melaneremia*, although the tooth type is unknown in *M. schrevei*. Therefore, with no unequivocal autapomorphies and in view of its stratigraphic occurrence, there is the possibility that *M. schrevei* and *M. bryanti* are stages in the evolution of a single biological species, as has been found in some North American omomyid species and genera (Rose and Bown 1986). However, in the absence of demonstrable character overlap, *M. schrevei* and *M. bryanti* are conservatively regarded as specifically distinct.

Three key characters support the *Paraloris* + *M. schrevei* *M. bryanti* + *N. zuccolae* + *V. raabi* clade (i.e., Microchoerinae). They are: a steep m2–3 trigonid back wall (character 37); m2–3 paraconid sublingually positioned (character 43); and reduction in molar crown height (character 49: reversed in the *N. zuccolae* + *V. raabi* clade).

The Omomyinae/Anaptomorphinae part of the tree differs from the results of previous recent analyses (e.g., Ni et al. 2004; Tornow 2008), although it is uncertain whether this is because of the addition of *Paraloris* and *Melaneremia* or because of the limited number of omomyine and anaptomorphine taxa used. However, the microchoerines included in the analyses of these authors were also limited (partly by what was available) to only derived members, whilst Asian *Altanius* was excluded from the analysis of Tornow (2008). Ni et al. (2004) included *Altanius*, but found that it grouped with plesiadapiforms. However, *Altanius* lacks the enlarged incisors, reduced canines and semimolariform last premolar of most plesiadapiforms. It was compared favourably with the carpolestid *Elphidotarsius* by Rose and Krause (1984) before the anterior dentition was known (Gingerich et al. 1991). However, unlike this genus, it has a well developed p4 trigonid, not an incipient slicing blade. Also, the paraconid of m2–3 is distally positioned with respect to the paracristid, subequal in height to the metaconid and has a strong buccal rib, which instead resembles the condition in *Teilhardina demissa*, *Tetonoides*, *Anemorhysis*, and *Arapahovius*. The molar similarities to *Elphidotarsius* can be largely accounted for by simple mesiodistal shortening.

As in the analysis originally including *M. bryanti* (Hooker 2007), neither Omomyinae nor Anaptomorphinae are monophyletic in the new analysis. However, by contrast, here it is the uintaniin omomyines *Jemezius* and *Uintanius* that nest within the Anaptomorphinae, with other omomyines (primitive members of the tribes Omomyini and Washakiini) remaining distinct, but with *Teilhardina brandti* being the sister taxon to the rest. The new analysis also shows *Altanius* as sister taxon to *Anemorhysis*. What are considered primitive characters of *Altanius*, such as large canines and the presence of a first premolar, are shown here as reversals to the primitive state. The absence of close relatives of *Altanius* suggests that there may be more homoplasy than currently recognised involving modification of the anterior dentition within Omomyidae. Such homoplasy is already increased (Hooker 2007, herein) by the addition of the primitive microchoerine *Melaneremia* to analyses, distancing derived microchoerines from a relationship with derived Trogolemurini (cf. Ni et al. 2004). Additional parallelism in this trend (if found) could result in retention of, rather than reversal to, various primitive states in *Altanius*.

Transformations of the anterior dentition.—Large canines and small incisors in mammals are universally regarded as the primitive states for size of these tooth types.

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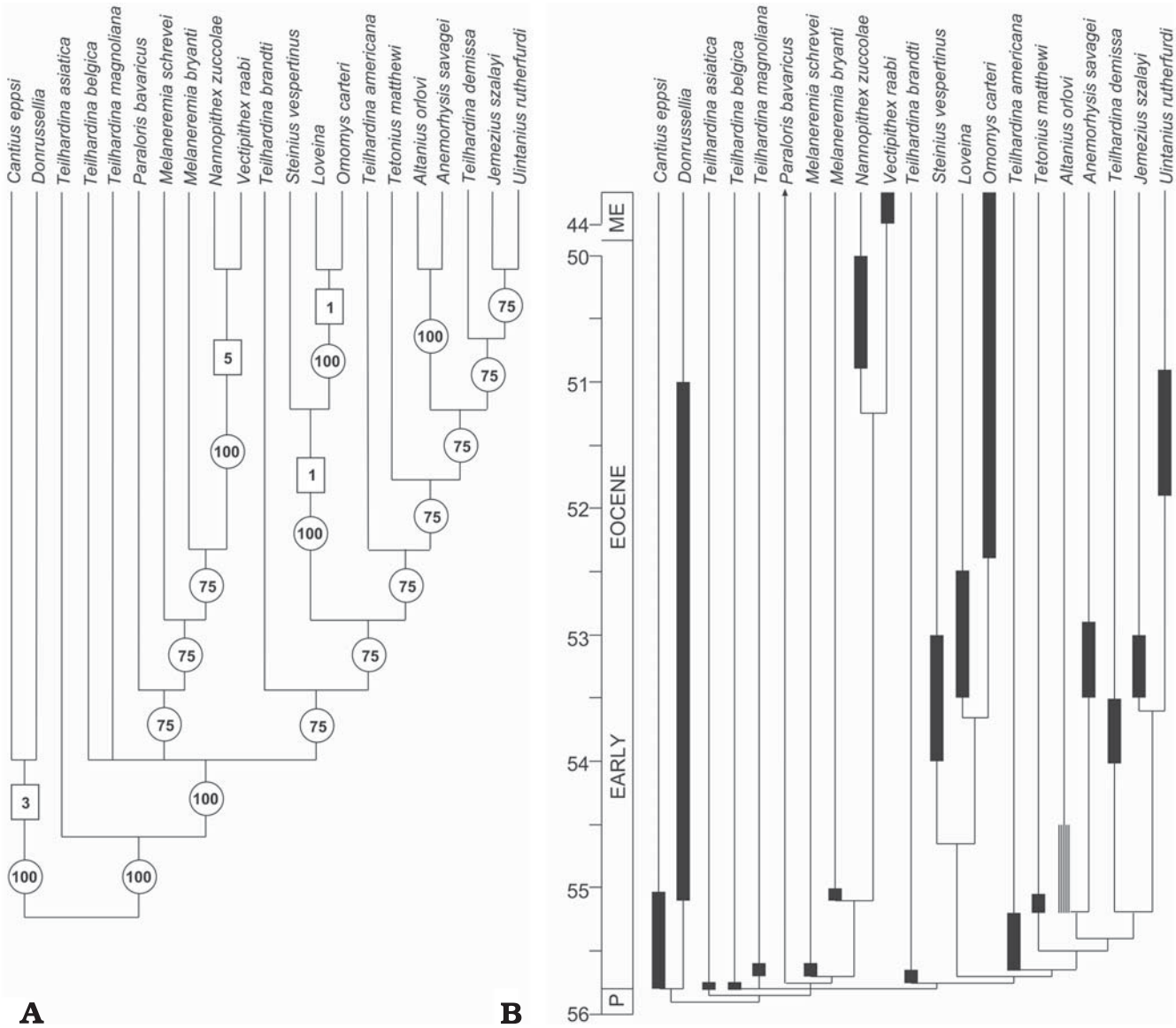

Fig. 5. **A**. 50% majority rule consensus of four maximum parsimony trees generated by PAUP 4.0b10, from the character–taxon matrix in Appendix 2. Numbers in square boxes delimiting nodes are decay indices (Bremer 1994), those in circles are consensus percentages. **B**. The same tree constrained by stratigraphic ranges of the taxa. Thickened sections of branches indicate stratigraphic ranges. Those shown as solid reflect the level of accuracy provided by the cited references and in some cases are known from only one horizon somewhere in that range. That shown as vertically hatched indicates uncertain age (see text). The timescale and correlation follow Luterbacher et al. (2004). Ranges are from: Rose and Bown (1986), Beard (1987, 2008b), Beard et al. (1992), Thalmann (1994), Hooker (1996b, 2010), Smith et al. (2006), Gingerich et al. (2008), Gunnell et al. (2008a, 2009), Beard and Dawson (2009), and herein. Abbreviations: Ma, millions of years before present; ME, Middle Eocene; P, Paleocene.

They are also usually treated as primitive when encountered in primates, e.g., the primitive omomyids *Teilhardina asiatica* and *T. belgica*, and the primitive adapiforms *Cantius* and *Donrussellia* (e.g., Rose and Bown 1991 and references therein). However, the Plesiadapiformes, the generally accepted sister group to primates (e.g., Bloch et al. 2007; Silcox 2003) universally have enlarged first incisors and usually reduced canines (except *Purgatorius*, where both teeth are large: Clemens 2004). Moreover, a similar pattern exists in the other two (and more remote) modern euarchontan orders, Scandentia and Dermoptera, which have enlarged incisors (in Dermoptera only in the lower jaw) and lack large canines (Butler 1980; Rose 2006). The extinct euarchontan families Mixodectidae, Plagiomenidae (Rose 2008) and Nyctitheridae (Sigé 1976; Hooker 2001) likewise have enlarged incisors and reduced canines. Therefore, use of any non-primate euarchontan as outgroup will produce a derived state for small incisors in primates. Herein, *Purgatorius* is used as outgroup, so large canine is nevertheless taken as primitive. However, small incisors in *Teilhardina asiatica* and *T. belgica* become derived.

As no anterior dentitions (incisors and canine) or even alveoli are known for either species of *Melaneremia*, characters 1 and 2 are coded as "?" (Appendix 2). Therefore, the position

at which canine size reduced to small in *N. zuccolae* and *V. raabi* varies between the basal microchoerine node in one step (Acctran) and the node subtending *N. zuccolae* and *V. raabi* in two steps (Deltran). The same situation exists for the enlargement of the incisors. The enlarged state of i1 is unlikely in either species of *Melaneremia* for two reasons. The dentary in *M. schrevei* is shallower than in *N. zuccolae* or *V. raabi*. However, it is still deepening slightly, anteriorly below p4, unlike in *T. belgica* and *Paraloris*, where anterior shallowing begins just in front of m1 (Teilhard 1927; Fahlbusch 1995). This suggests that *M. schrevei* had an i1 that was larger than in *T. belgica* or *Paraloris*, but smaller than in *N. zuccolae* or *V. raabi* (i.e., state 1 of character 1), as well as probably a slightly reduced canine. The dentary of *M. bryanti* is also shallower than that of *N. zuccolae,* and its p2 is procumbent with the mesial interstitial facet underneath the mesial overhang. This contrasts with e.g., *T. americana*, where the anterior premolars are well spaced and there is little or no contact between the canine/p1 and p2, and suggests crowding in *M. bryanti*, consistent with incipient enlargement of i1 and incipient reduction of the canine as suggested for *M. schrevei*. Therefore, the implication is that incisor enlargement and canine reduction in Microchoerinae took place in two steps, to states 1.1 and 2.1 at the node above *Paraloris*, and to states 1.0 and 2.2 at the node above *M. bryanti*.

Stratigraphic issues.—Figure 5B shows the majority rule consensus from Fig. 5A plotted against stratigraphy. It reflects the absence of an early record of Omomyinae (nothing in the first nearly 2 million years of the Eocene: Gunnell et al. 2008a) and a gap of 4 million years in the early record of Microchoerinae between the youngest known *Melaneremia* and the oldest known *Nannopithex*. The most incongruent stratigraphic range, however, is that of *Paraloris bavaricus* Fahlbusch, 1995, which is known only from the holotype dentary from Priabonian strata in southern Germany. The cladistic analysis shows it to be the most primitive microchoerine, with the implication of a ghost record for its clade of about 20 million years. Only the discovery of more material of this enigmatic taxon and its earlier relatives will resolve the questions surrounding its evolution. *Melaneremia* remains the key genus at the root of mainstream microchoerine evolution as recorded in most of Europe.

The dating of *Teilhardina magnoliana* from the Red Hot Truck Stop site (RHTS), Meridian, Mississippi, is controversial (Beard 2008b; Gingerich et al. 2008). The presence of the dinocyst *Apectodinium augustum* reported by Beard and Dawson (2001) is relevant. This species is restricted to the Paleocene–Eocene Thermal Maximum (PETM), which records an *Apectodinium* acme (Bujak and Brinkhuis 1998). However, acme percentages for the RHTS have not been given by Beard and Dawson (2001, 2009). Moreover (contra Beard 2008b), it is the onset of the *Apectodinium* acme, not the acme itself, which at some sites antedates the PETM Carbon Isotope Excursion (Sluijs et al. 2007b). There is a major sequence boundary between the top of the Tuscahoma Formation (slightly above the RHTS mammal horizon, the T4 channel) and the overlying Bashi Formation (Ingram 1991). However, the Bashi Formation belongs to calcareous nannoplankton zone NP10 (Frederiksen et al. 1982), which begins at least 700ky after the end of the PETM (Luterbacher et al. 2004). Thus, if the T4 channel does date from the PETM, it implies a larger hiatus than usually considered present below the Bashi Formation (e.g., Frederiksen et al. 1982). The basal Bashi sequence boundary in any case (contra Beard 2008b) is younger than the Tht-5 sequence boundary, which underlies the Dormaal Sand Member in Belgium (Steurbaut et al. 1999). The former instead probably equates with that of Ypr-2 in Europe (Bujak and Brinkhuis 1998). Accepting that the T4 channel does indeed belong to the PETM, the presence of typical Eocene pollen taxa well below in the upper Tuscahoma Formation (Harrington 2003a, b, 2004; Harrington and Jaramillo 2007) implies that the T4 channel should belong to the later part of the PETM. The range given for *T. magnoliana* (Fig. 5B) attempts to reflect current knowledge.

Dating of *Altanius orlovi* Dashzeveg and McKenna, 1977 within the Early Eocene is largely speculative (Fig. 5B). There is no clear evidence that it is from strata as old as the PETM, as there are no species in common with those from the documented PETM Carbon Isotope Excursion at Lingcha, China (Ting et al. 2011).

Relevance of *Melaneremia* to European biostratigraphy

The Woolwich Formation is spanned by an acme of the dinoflagellate *Apectodinium* that proxies the PETM (Collinson et al. 2009). Underlying this formation locally in Kent is the Cobham Lignite Bed, which records a negative carbon isotope shift that marks the onset of the PETM (Collinson et al. 2003; Pancost et al. 2007). The occurrence of *Melaneremia schrevei* in the upper part of the Woolwich Formation, the upper shelly clay unit (Hooker et al. 2009), therefore links its occurrence to the later part of the PETM.

Two isolated teeth, a p4 and an m2, from the Conglomérat de Meudon, Vaugirard Formation of Meudon, Paris Basin, figured by Godinot et al. (1998: pl. 11.1: k, l) bear a striking resemblance to the same teeth of *M. schrevei*, suggesting that they are conspecific. The m2 in particular shows spacing of the paraconid and protocristid identical to that of *M. schrevei*. The p4 differs slightly in having a crestiform paraconid. The mammal fauna of Meudon formed the basis of mammal Biozone PE II (Hooker 1996a), and the apparent occurrence of *M. schrevei* at both Meudon and Croydon suggests attribution of the Croydon fauna to the same zone. The underlying Biozone PE I is based on the mammal fauna of Dormaal, Belgium, which is correlated to the early part of the PETM (Steurbaut et al. 1999). Dormaal and other PE I sites contain a different, more primitive omomyid, *Teilhardina belgica*. The more derived species of *Melaneremia*, *M. bryanti*, occurs in the Black-

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heath Formation, which overlies the Woolwich Formation in the London Basin and whose mammal fauna has formed the basis of Biozone PE III (Hooker 1996a, 2010). Zone PE II is therefore tentatively anchored to the later part of the PETM, correlating approximately with the lower part of Wasatchian Zone Wa-1 of the Bighorn Basin, Wyoming, USA. As the omomyids at this time in Europe and North America are more different than in the early part of the PETM, this appears to be when a restriction to dispersal and the beginning of differentiation took place. This is rapid given the 170 ky extent (Sluijs et al. 2007a) of the Paleocene–Eocene Thermal Maximum.

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Appendix 1

Description of numbered characters

1. i1 (and where known I1): large (0); medium-sized (1); small (2). (Modified from Hooker 2007: character 1 in part).
2. Canine: large (0); medium (1); small (2). (Modified from Hooker 2007: character 1 in part).
3. p1 present, p2 2-rooted (0); p1 present, p2 1-rooted (1); p1 present in some individuals, where squeezed buccally, p2 1-rooted (2); p1 absent, p2 1-rooted (3); p1–2 absent (4). (Modified from Hooker 2007: character 2 in part).
4. p3 (and where known P3) large (0); small (1). (Modified from Hooker 2007: character 2 in part).
5. P3 with mesiodistally short protocone lobe (0); longer, nearly as long as buccal half (1). (Hooker 2007: character 3).
6. P3 with postmetacrista short (0); long (1). (Hooker 2007: character 4).
7. P3 parastyle small (0); large (1).
8. P3 buccolingually long (0); short (1).
9. P4 parastyle large (0); small (1). (Hooker 2007: character 5).
10. p3–4 canted mesially (0); not canted mesially (1).
11. p3 postmetacristid (or homologous crest when metaconid is missing) weak, trending distally (0); strong, trending distolingually to lingually (1). (Hooker 2007: character 8).
12. p3 paraconid low (0); high (1). (Hooker 2007: character 9).
13. p3–4 tall (0); p3 tall, p4 low (1); p3–4 low (2); p4 tall, p3 low (3). STEPMATRIX.
14. p4 paraconid cuspate (0); crestiform (1).
15. p4 paraconid tall (0); intermediate (1); low (2). (Hooker 2007: character 15).
16. p4 postmetacristid restricted basally (0); complete (1). (Modified from Hooker 2007: character 11).
17. p4 talonid long (0); short (1). (Hooker 2007: character 12).
18. p4 distal talonid wall with small near vertical contact with m1 (0); with more extensive, sloping contact with m1 (1). (Modified from Hooker 2007: character 13).
19. p4 not exodaenodont (0); exodaenodont (1). (Modified from Hooker 2007: character 14).
20. p4 lingual crown base horizontal (0); sloping up mesially (1). (Modified from Hooker 2007: character 16).
21. p4 without distobuccal crest (0); with distobuccal crest (1). (Hooker 2007: character 17).
22. M1–2 trigon basin short (0); long (1). (Hooker 2007: character 18).
23. Upper molar Nannopithex fold absent (0); present (1). (Hooker 2007: character 19).
24. M1–2 with hypocone shelf (0); postcingulum only (1). (Hooker 2007: character 20).
25. M1–2 protocone lobe mesiodistally long (0); short relative to buccal half (1). (Hooker 2007: character 21).
26. M1–2 with distinct postcingulum and metacingulum (0); fused to form distal cingulum, bypassing postmetaconule crista (1). (Hooker 2007: character 22).
27. M1–2 postmetacrista long (0); intermediate (1); short (2). (Hooker 2007: character 24).
28. M2 tapering distally (0); not tapering distally (1). (Hooker 2007: character 25).
29. Upper molar preparacrista oblique (0); mesiodistally orientated (1). (Hooker 2007: character 26).
30. M3 crown and m3 talonid buccolingually narrow (0); wide (1). (Hooker 2007: character 27).
31. m1–2 trigonid symmetrical (0); with distolingual torsion (1).
32. m1 trigonid closed lingually (0); open (1). (Hooker 2007: character 28).
33. m1 protocristid straight and shallowly notched (0); deeply notched, stepped, with buccal metaconid buttress tending to join cristid obliqua (1).
34. m2 distinctly longer than broad (0); nearly as broad as long (1). (Hooker 2007: character 29).
35. m2–3 paraconid separation from protocristid distant (0); intermediate (1); close (2). (Hooker 2007: character 30).
36. m2 entoconid tall (0); low (1).
37. m2–3 back wall of trigonid gently sloping (0); intermediate (1) PRIMITIVE; steep (2). (Hooker 2007: character 31).
38. m2–3 metaconid with mesial face smooth (0); with accessory cuspule in some individuals (1); consistently with accessory cuspule (2). (Hooker 2007: character 32).
39. Lower molar paraconid distinctly smaller than metaconid (0); subequal to metaconid (1). (Modified from Hooker 2007: character 33).
40. Lower molar paraconid relatively erect (0); procumbent (1).
41. m2–3 paraconid and metaconid ribs: weakly projected buccally and separate (0); strongly projected buccally and separate (1); strongly projected buccally and connate buccally, leaving groove between metaconid and protocristid (2). (Modified from Hooker 2007: character 34, to accommodate additional taxa).
42. m2–3 paraconid and metaconid not joined by crest (0); joined by crest (1). (Hooker 2007: character 35).
43. m2–3 paraconid lingually situated (0); sublingual (1). (Hooker 2007: character 36).
44. m2–3 paracristid flush with paraconid mesially (0); passes in front of paraconid leaving valley (1). (Hooker 2007: character 37).
45. m3 as long as or longer than m2 (0); shorter (1). (Modified from Hooker 2007: character 38).
46. Angle of m3 buccal crown base, where it shifts from oblique mesially to horizontal distally: below protoconid (0); behind protoconid (1). (Modified from Hooker 2007: character 39).
47. m3 entoconid not salient lingually (0); salient lingually (1). (Hooker 2007: character 40).
48. m3 postmetacristid straight (0); distally concave (1).
49. Lower molar crown height relatively high (0); trigonid low (1); trigonid and talonid low (2). UNORDERED. (Modified from Hooker 2007: characters 41–42).
50. Lower molar pre-entocristid mesiodistally orientated (0); angled mesiobuccally, making lingual concavity where meets postmetacristid (1). (Hooker 2007: character 43).
51. m3 hypoconulid lobe narrow (0); wide (1).
52. Posterior mental foramen below p4 (0); between p3 and p4 (1) PRIMITIVE; below p3 (2).

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Appendix 2

Character-taxon matrix of primitive anaptomorphine, omomyine, microchoerine and undifferentiated omomyids.

Information is drawn from originals, casts and the following published sources: Szalay (1976), Bown and Rose (1984, 1987), Rose and Krause (1984), Rose and Bown (1986, 1991), Beard (1987), Gingerich et al. (1991), Beard et al. (1992), Gunnell (1995), Clemens (2004), Ni et al. (2004), Smith et al. (2006). M_3 is judged unknown for *Jemezius szalayi*, as CM.34844 is removed from that species as it has the characters of *Steinius vespertinus* (see Beard 1987). Nearly all multistate characters are ordered, since they represent morphological transformation series. Exceptions are character 13, which is partially ordered as a stepmatrix (Appendix 3), and character 49, which is unordered. N.B., Although the posterior mental foramen is not preserved, *Melaneremia schrevei* is coded "1" for character 52 as the most likely state (primitive), having excluded state "0".

	0000000001111111111222222222233333333334444444444555
	1234567890123456789012345678901234567890123456789012
Purgatorius	000000?00000000000000000000000000001000000000000001
Altanius orlovi	20000010100100011010001100010100112010101101000001 02
Teilhardina asiatica	20101000000000200000000000111000000110000000100000 0?
Teilhardina belgica	20201000100000100000000000111000000110000000000000 01
Teilhardina magnoliana	????101010???0100?00000000111000000110000000000100 0?
Teilhardina brandti	??????????0???0100000?????????000010110002101100000 1?
Teilhardina americana	1120????100100010010001000101000011000002101001001 11
Teilhardina demissa	0230?????001200110100????????000112010001101011001 1?
Loveina	2130????001100111010101001101100110000102101011001 02
Steinius	11101000001000110000101000111100102000002101001001 1?
Omomys carteri	11301000001011211000100001111100010020102110011011 12
Jemezius szalayi	?2300010000??????0010100010101111001010200000 1????01??
Uintanius rutherfurdi	22300011000100011010001011201100111020000010011001 12
Tetonius matthewi	02301000100100011010001000201000012000002101100001 11
Anemorhysis savagei	1130?????001000000100????????000112000101101000001 0?
Melaneremia bryanti	??301000?0???000010001010 02?100110002111011001012 01?
Melaneremia schrevei	???0?????000200000000????????001101020100010000020 11
Nannopithex zuccolae	02410101100031001111011101201101110022110110011001 10
Vectipithex raabi	02410101100031001111011101211100111022010110011001 10
Paraloris	??????????0???11100001????????000001020000010010020 0?
Cantius eppsi	20000000110010200000101001201010102100000000000020 12
Donrussellia	2000????01?0101010001000011111111001100000000000001 2

Appendix 3

Stepmatrix for character 13.

0	1	2	3
–	1	1	1
1	–	1	2
1	1	–	1
1	2	1	–