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An omomyid primate from the Pontide microcontinent of north-central Anatolia: implications for sweepstakes dispersal of terrestrial mammals during the Eocene

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Abstract

A new genus and species of omomyid primate is described from the middle Eocene (Lutetian) Lülük Member of the Uzunçarşidere Formation, Orhaniye Basin, north-central Anatolia, Turkey. This is the first Eocene primate to be reported from the vast area between Switzerland and Pakistan. The new taxon is currently represented by a single dentary fragment, limiting the scope of morphological comparisons that can be made with related taxa. Nevertheless, its dentition differs fundamentally from that of contemporary European microchoerids. The new taxon most closely resembles North American middle Eocene omomyines such as *Mytonius hopsoni*, and it is therefore interpreted as a member of the Asian/North American omomyine radiation. Its occurrence on the Pontide microcontinent must have resulted from sweepstakes dispersal across the intervening Tethyan barrier that separated the Pontides from adjacent parts of Eurasia during the Lutetian. Sweepstakes dispersal by various terrestrial mammal clades, especially rodents and primates, was facilitated by Eocene greenhouse climatic conditions, which promoted extreme precipitation events and frequent flooding of major river drainages.

Keywords:
Eocene
Omomyidae
Sweepstakes dispersal
Pontides
Orhaniye Basin
Turkey

1. Introduction

Fossil primates are reasonably well-documented from the Eocene of western Europe and southern and eastern Asia (e.g., Szalay and Delson, 1979; Gebo, 2002; Gunnell and Rose, 2002; Beard, 2002; Godinot, 2014), but Eocene primates have never been reported from the vast territory between Pakistan and Switzerland (Fig. 1). This gap is significant because southwestern Asia would have been an appropriate staging ground for early anthropoids and other invasive mammals embarking for the island continent of Africa/Arabia prior to its collision with Eurasia near the Oligocene-Miocene boundary (Beard, 2016). Much of what is conventionally regarded as southwestern Asia, including the modern nations of Iraq and Syria, actually lies on the Afro-Arabian Plate (Stern and Johnson, 2010). During the Eocene, the margin of Eurasia that faced the impending collision with Africa/Arabia spanned what is now Iran and Turkey. The fossil record of Eocene mammals across this region is limited, but it has improved steadily in recent years. In Iran the Eocene record of mammals is currently restricted to trace fossils, including footprints of large taxa that have been identified as perissodactyls, proboscideans, and possibly pantodonts and/or dinoceratans (Ataabadi and Sarjeant, 2000; Abbassi and Lockley, 2004; Ataabadi and Khazaee, 2004; Abbassi et al., 2017). In contrast, Eocene mammals have been reported from multiple sites in Turkey, ranging from Süngülü near the international border with the Republic of Georgia (De Bruijn et al., 2003) to the Boyabat Basin near the central Black Sea coastline (Sanders et al., 2014) and the Orhaniye Basin and other sites in north-central Anatolia (Sen and Heintz, 1979; Kappelman et al., 1996; Maas et al., 1998, 2001; Métais et al., 2012, 2017, 2018; Maga and Beck, 2017; Jones et al., 2019).

By far the most diverse Eocene mammal fauna currently known from Turkey comes from the middle Eocene (44-43 Ma) Lülük Mb. of the Uzunçarşidere Fm., which outcrops in the Orhaniye Basin northwest of Ankara. The Eocene mammals of the Uzunçarşidere Fm. occupied a microcontinent known as the Pontides that was an island or an archipelago situated along the northern margin of the Neotethys Sea (Licht et al., 2017; Métais et al., 2017, 2018; Maga and Beck, 2017). The fauna that has been recovered to date from the Uzunçarşidere Fm. is characterized by a high degree of endemism and a unique combination of Laurasian and Gondwanan taxa. The most diverse and common ungulates in the fauna belong to an anachronistic radiation of pleuraspidotheriid "condylarths" comprising the genus *Hilalia* (Maas et al., 2001; Métais et al., 2017). Outside of Turkey, pleuraspidotheriids are only known from the late Paleocene of western Europe (Ladevèze et al., 2010), making their occurrence in the Orhaniye Basin ~13 Myr younger than their local extinction on the European mainland. The only large mammals documented so far from the Uzunçarşidere Fm. are embrithopods (Maas et al., 1998), an extinct clade showing phylogenetic and biogeographic affinities with African tethytheres (Sanders et al., 2010; Gheerbrant et al., 2018). Three taxa of metatherians (stem marsupials) are known from the Uzunçarşidere Fm., including both Laurasian and Gondwanan clades (Maga and Beck, 2017; Métais et al., 2018). Otherwise, a primitive bat pertaining to the stem chiropteran family Palaeochiropterygidae has recently been described (Jones et al., 2019). Notably absent from the Uzunçarşidere Fm. are several ecologically dominant mammalian clades that are otherwise ubiquitous across Eurasia by the middle Eocene. These include Rodentia, Carnivora, Creodonta, Artiodactyla and Perissodactyla. The anachronistic radiation of pleuraspidotheriids and the absence of so many common and widespread mammal taxa in the Uzunçarşidere Fm. corroborate the insular paleogeographic setting that has been inferred for the Eocene Pontides.

In June, 2014 the senior author collected a primate dentary fragment from the Uzunçarşidere Fm. in the Orhaniye Basin. Here, we describe a new taxon of Omomyidae based on this unique specimen. Given that Anatolia has often been cited as a potential corridor for the dispersal of Paleogene mammals between Africa, Asia and Europe (Kappelman et al., 1996; Maas et al., 1998; Sen, 2013), we also assess its phylogenetic and probable biogeographic affinities. Finally, we discuss how the discovery of this new taxon affects the broader issue of dispersal by terrestrial mammals across marine barriers during the Eocene.

2. Geological setting

Anatolia is a complex mosaic of Gondwanan and Laurasian microcontinents that collided from the Late Cretaceous through the Eocene (Şengör and Yilmaz, 1981). Until at least the late Eocene, this region formed an extended platform of islands and shallow tropical seas surrounded by wider seaways including the Neotethys to the South, the Paratethys to the North, the Carpathian Basin to the West, and the Fannuj, Sistan, and Katawaz Seaways to the east (Barrier and Vrielynck, 2008; Licht et al., 2017). Today, the majority of Anatolia is the product of a tectonic collision between two main terranes: the Pontides in the north and the Anatolide-Tauride Block (ATB) to the south. The timing of this collision has been constrained to the interval between the latest Cretaceous and late Paleocene (Ocakoğlu et al., 2019; Mueller et al., 2019).

The Orhaniye Basin initially developed as a forearc basin along the southern margin of the Pontides during the Maastrichtian, before shifting to a retroarc foreland basin shortly after the collision between the Pontides and the ATB (Licht et al., 2017). The Uzunçarşidere Fm. is the first geological unit to be deposited in a foreland setting and consists of fluvio-lacustrine deposits sourced from the orogenic wedge (Ocakoğlu and Çiner, 1995). The Lülük Mb. is the fossiliferous and most basal member of the Uzunçarşidere Fm. and is dated to the late Lutetian (44-43 Ma) by a combination of magnetostratigraphy and U-Pb dating (Licht et al., 2017). It consists of red beds and fluvial channels, deposited under a seasonally wet, tropical climate (Licht et al., 2017). Vertebrate fossils are found in pedogenic carbonate nodules and red clays, or (more rarely) in channel lags.

3. Material and methods

The unique omomyid specimen described here is housed in the paleontological collections of the Department of Geological Engineering, Eskişehir Osmangazi University (EOU), Eskişehir, Turkey. Specimens collected from the Uzunçarşidere Fm. in the Orhaniye Basin are designated with the acronym UCF. Measurements were obtained using a Unitron Z Series binocular microscope equipped with Mitutoyo digimatic micrometers. We follow the dental nomenclature employed by Szalay and Delson (1979: fig. 6).

4. Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Primates Linnaeus, 1758

Suborder Haplorhini Pocock, 1918

Infraorder Tarsiiformes Gregory, 1915

Family Omomyidae Trouessart, 1879

Subfamily Omomyinae Trouessart, 1879

Genus ***Nesomomys*** nov. gen.

Derivation of the name: The generic name is derived from the Greek *nesos* (island), combined with the suffix -*omomys* commonly used for omomyid primates.

Type species: *Nesomomys bunodens* nov. gen., nov. sp.

Diagnosis: Differs from microchoerids and other omomyids in having the following combination of characters: P_4 roots elongated mesiodistally, especially in relation to M_1 length; M_1 trigonid cusps closely spaced, equidistant, and similar in size; M_1 paraconid present and relatively mesial in position; M_1 protoconid with expanded and inflated buccal margin; M_1 talonid cusps not distinctly cuspidate, with entoconid and hypoconulid lost or incorporated within elevated entocristid; lingual talonid notch on M_1 absent.

Nesomomys bunodens nov. gen., nov. sp.

Figs. 2, 3

Derivation of the name: The species name is derived from the Greek *bounos* (hill or mound) and Latin *dens* (tooth).

Holotype: EOU-UCF-9, left dentary fragment preserving the crown of M_1 and the roots of P_4 and M_2, only known specimen (Figs. 2, 3).

Type locality: Rejection Ravine locality, north of Memlik village, Orhaniye Basin, Ankara Province, Turkey (Fig. 4).

Known distribution: Middle Eocene (Lutetian) Lülük Mb. of the Uzunçarşidere Fm., central Anatolia.

Diagnosis: As for genus *Nesomomys*, by monotypy.

Description: The holotype and only known specimen is a left dentary fragment bearing the crown of a lower molar that is interpreted as M_1. On either side of the preserved molar crown, the roots for immediately adjacent tooth loci are preserved. Assuming that the molar crown is correctly identified as M_1, the ratio of the length of the roots of P_4 (3.24 mm) to the length of the crown of M_1 in this specimen is very unusual for an omomyid (Table 1; Fig. 5). It is therefore necessary to explain why the single crown is identified as M_1 rather than M_2. Four lines of evidence support this interpretation.

First, the cross-sectional dimensions of the roots of the (missing) mesial tooth are more consistent with it being P_4 than M_1 (length of mesial root: 1.31 mm; breadth of mesial root: 1.24 mm; length of distal root: 2.01 mm; breadth of distal root: 1.49 mm; for comparative purposes, similar data for the roots of the succeeding crown identified as M_1 are: length of mesial root, 1.13 mm; breadth of mesial root, 1.63 mm; length of distal root, 1.25 mm; breadth of distal root, 2.06 mm). Note that the individual roots of the missing mesial crown are each longer than wide, while the reverse is true for the roots of the intact molar crown. Also noteworthy is the disparity in the breadth of the distal (talonid) root of the tooth presumed to be P_4, which is only 1.49 mm, compared to the breadth of the distal (talonid) root of the presumed M_1, which is 2.06 mm, or roughly 38% greater than the same metric for the tooth immediately anterior to it. Among omomyid taxa in which the lower molar talonids are notably broad, such as *Nesomomys bunodens* nov. gen., nov. sp., *Mytonius hopsoni* and *Ourayia uintensis*, the width of the distal molar root is increased to match the expanded buccolingual breadth of the corresponding part of the crown. Having such dramatically different talonid widths in M_1 and M_2 would be unprecedented among omomyids, so the observed discrepancy in talonid root width in EOU-UCF-9 suggests that the loci in question are P_4 and M_1.

Second, the morphology of the lower molar trigonid is more consistent with it being M_1 than M_2. The trigonids of M_1 and M_2 in most omomyid taxa can be distinguished on the basis of the proximity of the paraconid and metaconid and whether the trigonid is open or closed lingually (e.g., Szalay, 1976; Beard, 1987; Bown and Rose, 1987; Gunnell, 1995). In EOU-UCF-9 the lower molar trigonid is not fully open lingually, but this is because of the development of neomorphic ridges connecting the paraconid and metaconid as opposed to close approximation or merging of the bases of these cusps, as would be expected if the tooth locus were M_2. Although all three trigonid cusps are closely spaced in EOU-UCF-9, the paraconid is relatively mesial (rather than lingual) in position, thereby being more similar to M_1 than M_2 in omomyid taxa such as *Mytonius hopsoni* and *Ourayia uintensis* (Robinson, 1968; Krishtalka, 1978; Williams and Kirk, 2008).

Third, the cross-sectional dimensions of the distal root for the (missing) distal tooth resemble those of M_2 instead of M_3. In most omomyids, M_3 retains a distally expansive hypoconulid lobe, and the distal root of M_3 is expanded distally as a result. Although the distal root for the missing distal tooth in EOU-UCF-9 is broken obliquely rather than transversely, it clearly lacks the distal extension that would be expected if the corresponding crown bore an expanded hypoconulid lobe.

Finally, there is no indication of swelling on the posterolateral side of the dentary that might correspond to the anterior margin of the masseteric fossa. If the (missing) distal tooth locus in EOU-UCF-9 were M_3 rather than M_2, at least minor swelling on the corpus of the dentary would be expected in this region. Based on the foregoing considerations, the sole crown preserved in EOU-UCF-9 is regarded as M_1.

M_1 (length, 3.62 mm; width, 2.70 mm) in the holotype is very low-crowned for an omomyid, with the trigonid being only slightly taller than the talonid, as is obvious in either buccal or lingual view (Figs. 2, 3). All three trigonid cusps are present, similar in terms of size and degree of basal inflation, and closely spaced so that they correspond to the apices of an equilateral triangle. As mentioned previously, the trigonid is not fully open lingually, because minor ridges run forward from the metaconid and backward from the paraconid to meet near the midpoint between these cusps. Nevertheless, a narrow and shallow valley marks the junction of these neomorphic ridges between the paraconid and metaconid. Buccally, a short, arcuate but continuous paracristid runs from the protoconid to the paraconid. The distal margin of the trigonid lacks a distinct or markedly notched protocristid because the inflated protoconid and metaconid are almost fused at their bases. A moderately developed mesiobuccal cingulid runs more or less parallel to the paracristid but lower on the trigonid crown. Ancestrally, this mesiobuccal cingulid probably extended distally to the level of the hypoflexid, as it does, e.g., in *Mytonius hopsoni*. However, in *Nesomomys bunodens* nov. gen., nov. sp., the buccal side of the M_1 protoconid is inflated and enlarged to the extent that it almost forms a separate neomorphic cusp. The latter structure blocks any continuity between the mesiobuccal cingulid and the short buccal cingulid, which occurs immediately buccal to the hypoflexid. The talonid of M_1 is broad, deeply excavated, and relatively open distally. While the position of the hypoconid can be ascertained by the junction of the cristid obliqua and the adjacent postcristid, the structure itself is not clearly cuspidate. More ambiguous are the locations of the hypoconulid and entoconid, the homologues of which appear to have been subsumed within the low crests marking the lingual and distolingual margins of the talonid. Although the entoconid itself is not readily identifiable, much if not all of the lingual talonid crest must be homologous with the entocristid. Notably, this structure is as elevated as the cristid obliqua on the buccal side of the talonid. There is no development of a lingual valley or talonid notch between the trigonid and talonid, as often occurs in Asian and North American omomyines (Beard and Wang, 1991; Gunnell, 1995). Rather, the entocristid is virtually confluent with a weak postmetacristid.

That which remains of the dentary is unremarkable (Fig. 3). Its depth appears to be fairly uniform throughout its preserved length (being 6.39 mm below the distal root of M_1). The preserved part of the dentary does not extend far enough anteriorly to provide evidence about the symphysis, mental foramina, or the lower dental formula. Likewise, the dentary does not extend far enough posteriorly to preserve aspects of the masseteric fossa or other structures on the posterior part of the bone.

Remarks: The unusually long P_4 of *Nesomomys bunodens* nov. gen., nov. sp. invites comparisons with primitive adapiform primates, which differ from most omomyids in retaining an uncompacted lower premolar series, including a double-rooted P_2 and mesiodistally elongated $P_{3\text{-}4}$ (Rose and Bown, 1991). However, the lower molar morphology of *Nesomomys bunodens* nov. gen., nov. sp. differs markedly from that of primitive adapiforms such as *Donrussellia* and *Cantius*. In particular, the lower molar trigonid cusps are situated peripherally in *Donrussellia* and *Cantius*, yielding a lingually open trigonid. In *Nesomomys* nov. gen., the trigonid cusps are internalized and closely spaced, so that the trigonid is nearly closed lingually. The paraconid of M_1 is fully lingual in primitive adapiforms, whereas this cusp is located mesially in *Nesomomys* nov. gen. The buccal cingulid is typically continuous mesiodistally on M_1 in primitive adapiforms, but this structure is broader and more massive in *Nesomomys* nov. gen., even though the buccal cingulid is interrupted near the base of the protoconid by the swollen enamel forming a nascent neomorphic cusp in that location. Finally, the protocristid in *Nesomomys* nov. gen. is oriented more or less transversely with respect to the long axis of M_1, while this structure in primitive adapiforms is decidedly oblique. There is little difference between the height of the trigonid and talonid in *Nesomomys* nov. gen., while in primitive adapiforms the trigonid projects well above the level of the talonid. The cristid obliqua of M_1 in primitive adapiforms joins the metaconid, yielding a deeply incised hypoflexid. In contrast, the cristid obliqua of M_1 in *Nesomomys* nov. gen. joins the buccal side of the trigonid, and the hypoflexid is shallow as a result. Three talonid cusps are discernible on the lower molars of primitive adapiforms, and the hypoconulid is located buccal to the midline, lying closer to the hypoconid than the entoconid. Both the hypoconulid and entoconid are indistinctly cuspidate on the talonid of M_1 in *Nesomomys* nov. gen., and there is no evidence that the hypoconulid was closely affiliated with the hypoconid. On the lingual side of the talonid of M_1 in *Nesomomys* nov. gen., an elevated entocristid is confluent with the lingual base of the trigonid. In primitive adapiforms such as *Donrussellia* and *Cantius*, the entocristid is very weakly developed and the entoconid is cuspidate, leaving a narrow lingual notch between the entoconid and postvallid. The clear and pervasive differences in lower molar morphology between *Nesomomys* nov. gen. and primitive adapiforms suggest that the relatively uncompacted P_4 that is shared among these taxa is a symplesiomorphy (Rose and Bown, 1991).

Because the mammalian fauna from the Uzunçarşidere Fm. contains a unique assemblage of Laurasian and Gondwanan taxa (Métais et al., 2018; Jones et al., 2019), it is worth comparing *Nesomomys bunodens* nov. gen., nov. sp. to other haplorhine primates from the Eocene of North America, Europe, Asia, and Africa. Omomyids and microchoerids (microchoerids are sometimes included as a subfamily of omomyids; cf. Szalay, 1976) were reasonably diverse and abundant across the three Laurasian continents during the middle Eocene (Szalay, 1976; Gunnell and Rose, 2002; Godinot, 2014). In contrast, there is no compelling evidence that haplorhines other than anthropoids ever inhabited Africa/Arabia (Beard, 1998). *Nesomomys* nov. gen. lacks all of the key derived features that occur in basal anthropoids, including the mesiodistal compaction and oblique orientation of the P_4 roots that characterize *Eosimias* and related basal anthropoids (Beard et al., 1994, 1996; Beard, 2002; Beard and Wang, 2004). Likewise, the lower molar morphology of *Nesomomys* nov. gen. differs from that of basal anthropoids in having trigonid cusps that are closely spaced and similar in size so that their apices describe an equilateral triangle, whereas in *Eosimias* and other basal anthropoids the protoconid is both more voluminous and taller than the other trigonid cusps and the trigonid cusps are situated more peripherally on the crown. These and other differences make it clear that *Nesomomys* nov. gen. is not an anthropoid, so detailed comparisons with African Eocene primates are unnecessary. In the following paragraphs, *Nesomomys* nov. gen. is compared with middle Eocene omomyids and microchoerids from Europe, Asia and North America. It should be noted at this point that multiple omomyid clades ranged across eastern Asia and western North America during the middle Eocene. Examples include the *Stockia* + *Asiomomys* clade (Beard and Wang, 1991), the genus *Macrotarsius* (Beard et al., 1994) and the subfamily Tarkadectinae (Ni et al., 2010). To the contrary, the European middle Eocene haplorhine primate fauna was restricted to microchoerids (Hooker and Harrison, 2008; Godinot, 2014).

The lower dentition of European microchoerids such as *Melaneremia* (Hooker, 2012), *Pseudoloris* (Minwer-Barakat et al., 2015a), *Nannopithex* (Godinot et al., 1992), *Vectipithex* (Hooker and Harrison, 2008), *Necrolemur* (Minwer-Barakat et al., 2015b) and *Microchoerus* (Minwer-Barakat et al., 2013) differs fundamentally from that of *Nesomomys* nov. gen. Most notably, P_4 in all microchoerids aside from *Melaneremia* is mesiodistally compressed so that the roots of this tooth are closely spaced, in marked contrast to the condition in *Nesomomys* nov. gen. Early Eocene *Melaneremia* retains relatively primitive or uncompacted P_4 proportions, but its P_4 roots are more closely spaced in relation to M_1 than is the case in *Nesomomys* nov. gen. (Hooker, 2012). The trigonid of M_1 in relatively primitive microchoerids such as *Melaneremia*, *Vectipithex* and *Nannopithex* differs from that of *Nesomomys* nov. gen. in having cusps that are spaced farther apart, yielding a lingually open trigonid and a more oblique, rather than transverse protocristid. The talonid of M_1 in *Melaneremia*, *Vectipithex* and *Nannopithex* retains a distinctly cuspidate entoconid, lacks the elevated entocristid that occurs in *Nesomomys* nov. gen., and bears a continuous buccal cingulid that extends from the base of the paracristid to the base of the hypoconid. *Pseudoloris* differs appreciably from *Nesomomys* nov. gen. in having a mesiodistally compacted P_4 and M_1 that is much less bunodont, retaining a lingually open trigonid, obliquely oriented protocristid, angular hypoconid, distinctly cuspidate entoconid, and a strong lingual valley between the postvallid and the entoconid. *Necrolemur* and *Microchoerus* share little in common with *Nesomomys* nov. gen. in terms of their comparable dental morphology. Like most other microchoerids, their P_4 is strongly compacted mesiodistally. M_1 in *Necrolemur* and *Microchoerus* is more bunodont than that of *Pseudoloris*, but it differs from that of *Nesomomys* nov. gen. in many ways, notably in having: a complete buccal cingulid; a paraconid that is more lingual in position; a protoconid that is typically taller than the metaconid; trigonid cusps more widely spaced, often with a shelf-like mesial fovea between the protoconid and paraconid; more angular hypoconid; cristid obliqua invariably taller than entocristid; entoconid distinct and cuspidate; entocristid weakly developed (when present), with lingual talonid notch present between postvallid and entocristid; and variably crenulated molar enamel. The lack of any close morphological correspondence between *Nesomomys* nov. gen. and members of the European microchoerid radiation allows us to exclude the possibility of any special phylogenetic relationship between these taxa.

North American and Asian omomyids are more diverse than European microchoerids, and this diversity encompasses a much broader range of dental morphologies (Szalay and Delson, 1979; Bown and Rose, 1987; Beard, 1987; Beard et al., 1992; Gunnell, 1995; Gunnell and Rose, 2002; Ni et al., 2010; Godinot, 2014). Like microchoerids, most omomyids are characterized by mesiodistal compaction of their lower premolars, including P_4 (Fig. 5). Exceptions to this general rule fall into two main categories. Among relatively small-bodied omomyids (with M_1 length <3 mm), taxa such as *Uintanius*, *Absarokius*, and the *Tetonius* + *Pseudotetonius* clade bear hypertrophied, exodaenodont P_4 crowns that are not strongly compacted mesiodistally (Bown and Rose, 1987; Gunnell, 1995). On the other hand, certain larger-bodied omomyids such as *Ourayia uintensis* and *Hemiacodon gracilis* have relatively uncompacted P_4 roots, with P_4 crowns that are neither exodaenodont nor hypertrophied in terms of their height with respect to M_1 (Robinson, 1968; Szalay, 1976). With respect to its M_1 length, *Nesomomys bunodens* nov. gen., nov. sp. clusters with larger-bodied omomyids, but its P_4 roots are longer than those of any of the omomyid taxa sampled in Fig. 5. Moreover, although the crown of P_4 remains unknown in *Nesomomys bunodens* nov. gen., nov. sp., the narrow breadth of its distal root (see above) makes it very unlikely to have supported an exodaenodont, hypertrophied crown. Omomyids such as *Uintanius* that possess exodaenodont, hypertrophied P_4 crowns have extraordinarily broad distal P_4 roots to support the exodaenodont lobe above it. Accordingly, we would expect the unknown P_4 crown of *Nesomomys bunodens* nov. gen., nov. sp. to be proportionally similar to that of *Ourayia uintensis* and closely related omomyines (Gunnell, 1995).

The M_1 morphology of *Nesomomys bunodens* nov. gen., nov. sp. is unique among omomyids, but it most closely approximates conditions found in North American middle Eocene omomyines such as *Mytonius hopsoni* (Robinson, 1968; Krishtalka, 1978; Williams and Kirk, 2008). Notable similarities include the close spacing of the lower molar trigonid cusps, which in their position approximate the apices of an equilateral triangle; the relatively slight difference in height of the trigonid and talonid; the extremely broad talonid; the absence of a lingual talonid notch; and the indistinct nature of the entoconid, which is more or less incorporated into the entocristid. Despite these intriguing similarities, important differences exist between *Nesomomys bunodens* nov. gen., nov. sp. and *Mytonius hopsoni*. For example, M_1 of *Mytonius* has a paraconid that is more lingual in position than that of *Nesomomys* nov. gen.; it bears a stronger, mesiodistally continuous buccal cingulid; it lacks the buccal inflation of the protoconid found in *Nesomomys* nov. gen.; and it has a taller, more angular hypoconid and cristid obliqua.

5. Discussion

5.1. Body weight and diet of Nesomomys bunodens *nov. gen., nov. sp.*

Body weight is closely related to many aspects of behavior and ecology, and these relationships have been extensively investigated among Eocene primates (e.g., Gingerich, 1981; Conroy, 1987; Dagosto and Terranova, 1992; Payseur et al., 1999; Gebo et al., 2000; Egi et al., 2004). Using regression equations provided by Gingerich (1981) and Conroy (1987), we can estimate the body weight of *Nesomomys bunodens* nov. gen., nov. sp. based on its M_1 dimensions. Estimates of the body weight of *Nesomomys bunodens* nov. gen., nov. sp. obtained in this manner vary depending on the taxonomic sampling employed to generate the original regression equations. For example, Gingerich (1981) noted that extant tarsiers are megadont relative to other primates of similar body weight, apparently because of their uniquely faunivorous diet. As a result, using Gingerich's (1981) tarsioid regression equation yields the lowest estimated body weight for *Nesomomys bunodens* nov. gen., nov. sp.

(217 g). In contrast, Gingerich's (1981) regression equation based on a wide range of living primates yields the highest estimated body weight for *Nesomomys bunodens* nov. gen., nov. sp. (897 g). Conroy's (1987) equations yield intermediate body weight estimates for *Nesomomys bunodens* nov. gen., nov. sp. (572 g using Conroy's "prosimian" regression equation and 740 g using Conroy's "all primates" regression equation). Because postcranial elements of *Nesomomys bunodens* nov. gen., nov. sp. have yet to be found, it is currently impossible to assess which of these dental estimates for the body weight of *Nesomomys bunodens* nov. gen., nov. sp. is most consistent with the size and proportions of its appendicular skeleton (Dagosto and Terranova, 1992). However, both dental and postcranial estimates of body weight are available in the case of *Omomys carteri* (Payseur et al., 1999), which is another member of the North American/Asian radiation of omomyines that also includes *Nesomomys bunodens* nov. gen., nov. sp. Dental estimates for the body weight of *Omomys carteri* derived from Conroy's (1987) regression equations coincide with those based on postcranial dimensions (Payseur et al., 1999), indicating that *Omomys carteri* was not megadont like modern tarsiers. Assuming that *Nesomomys bunodens* nov. gen., nov. sp. resembled *Omomys carteri* in this regard, we can suggest an estimated body weight of 500-800 g for the Turkish taxon, approximating that of the extant northern greater galago *Otolemur garnettii*. This places *Nesomomys bunodens* nov. gen., nov. sp. slightly above Kay's threshold of 500 g body weight (Kay, 1975; Gingerich, 1981), which separates primates that specialize on insectivorous diets (below) from committed primate folivores (above). The low topographic relief of M_1 in *Nesomomys bunodens* nov. gen., nov. sp. suggests that this taxon was primarily frugivorous.

5.2. Phylogenetic and biogeographic affinities of Nesomomys *nov. gen.*

Given the fragmentary nature of the single specimen currently available for *Nesomomys bunodens* nov. gen., nov. sp., we refrain from undertaking a formal phylogenetic analysis for this taxon at this time. However, our comparisons with potentially related taxa make it clear that *Nesomomys* nov. gen. is not specially related to European microchoerids. Its affinities appear to lie more closely with North American and Asian omomyines. Certain middle Eocene omomyines, notably including *Ourayia uintensis*, resemble *Nesomomys bunodens* nov. gen., nov. sp. in retaining relatively uncompacted P_4 (Robinson, 1968: fig. 22), a feature that is plausibly interpreted as a symplesiomorphy shared with early Eocene *Steinius vespertinus* and middle Eocene *Omomys carteri* (Rose and Bown, 1991). The lower molar morphology of *Nesomomys bunodens* nov. gen., nov. sp. most closely approximates that of *Mytonius hopsoni*, although the latter taxon appears to be derived in having a more mesiodistally compacted P_4 (Robinson, 1968: fig. 23). *Mytonius hopsoni* and *Ourayia uintensis* are generally regarded as being closely related (Robinson, 1968; Krishtalka, 1978; Gunnell, 1995) or even conspecific (Szalay, 1976). Based on the limited anatomical evidence currently available, it can be hypothesized that *Nesomomys bunodens* nov. gen., nov. sp. is closely related to a clade of omomyines that contains *Ourayia* and *Mytonius*. Robinson (1968) erected the subfamily Mytoniinae for *Ourayia* and *Mytonius*, while Gunnell (1995) subsequently proposed the tribe Ourayiini for a broader grouping of omomyines that also includes *Wyomomys*, *Ageitodendron*, *Utahia* and *Stockia*. Without necessarily endorsing the monophyly of this assemblage, we note parenthetically that Gunnell's Ourayiini is a junior subjective synonym of Robinson's Mytoniinae, because both are family-group taxa containing *Mytonius hopsoni* (which Gunnell regarded as a species of *Ourayia*). A potential problem with hypothesizing a close relationship between *Nesomomys bunodens* nov. gen., nov. sp. and the omomyines included in either Mytoniinae or Ourayiini is that the latter taxa are documented almost exclusively from western North America, while *Nesomomys bunodens* nov. gen., nov. sp. is known only from the Pontide microcontinent in northern Anatolia. However, *Asiomomys changbaicus* from the middle Eocene of Jilin Province in northeastern China is very closely related to *Stockia powayensis* from California and Montana (Beard and Wang, 1991; Dawson and Constenius, 2018), so at least one member of the group that Gunnell (1995) called Ourayiini has been documented from Asia. In general, omomyines are more extensively documented in North America than they are in Asia, but the presence of multiple omomyine clades on each side of the North Pacific Ocean indicates that these primates dispersed repeatedly across Beringia during the middle Eocene (Beard and Wang, 1991; Beard et al., 1994; Ni et al., 2010).

Nesomomys nov. gen. is unusual among the mammalian taxa known from the Uzunçarşidere Fm. because it represents one of the modern clades appearing across Laurasia at or near the Paleocene-Eocene boundary. Métais et al. (2018) noted that perissodactyls, artiodactyls, creodonts, carnivorans and rodents remain unknown from the Uzunçarşidere Fm., and the absence of these otherwise ubiquitous mammal taxa constitutes powerful evidence for an extended interval of geographic isolation for the Pontides prior to the middle Eocene. Geographic isolation of the Pontides must have commenced during the latter part of the Paleocene in order to explain the persistence of archaic ungulates such as pleuraspidotheriids and the absence of modern ungulates like perissodactyls and artiodactyls there (Métais et al., 2018). Given this context, it is virtually impossible to interpret the occurrence of *Nesomomys* nov. gen. on the Pontides as resulting from vicariance. In other words, it is difficult to imagine the ancestors of *Nesomomys* nov. gen. being stranded on the Pontides prior to its isolation from adjacent parts of Eurasia during the late Paleocene, because euprimates in general are not known to occur prior to the earliest Eocene (e.g., Rose and Bown, 1991; Smith et al., 2006; Beard, 2008; Ni et al., 2013). Moreover, although the phylogenetic position of *Nesomomys* nov. gen. remains somewhat enigmatic, there is no reason to interpret *Nesomomys* nov. gen. as a particularly basal member of the omomyid/microchoerid radiation. Accordingly, we hypothesize that *Nesomomys* nov. gen. dispersed from Asia to the Pontides by traversing one or several of the seaways separating both landmasses during the middle Eocene. This is the first clear evidence that omomyid primates were capable of transoceanic dispersal by rafting and/or island-hopping across marine barriers, although anthropoids did so repeatedly during the Eocene (Beard, 2016).

5.3. Broader implications for mammalian dispersal by rafting during the Eocene

The discovery of *Nesomomys bunodens* nov. gen., nov. sp. on the Pontides adds to a growing record of dispersal by terrestrial mammals across marine barriers during the Eocene. These dramatic colonization episodes transformed the endemic faunas occupying the Gondwanan landmasses of Africa, South America and (most likely) Madagascar. At least three Asian mammal clades, including anomaluroid and hystricognath rodents and anthropoid primates, colonized Africa sometime near the Bartonian-Priabonian boundary (Sallam et al., 2009; Jaeger et al., 2010; Seiffert, 2012; Marivaux et al., 2014; Coster et al., 2015; Beard, 2016). Two of these three Asian mammal clades, hystricognath rodents and anthropoid primates, dispersed slightly later in the Paleogene across the South Atlantic to colonize the island continent of South America (Antoine et al., 2012; Bond et al., 2015; Seiffert et al., 2020). In contrast, the colonization of Madagascar by its relatively impoverished extant mammalian fauna involved different clades, notably including lemuriform primates, tenrecoid afrotherians, feliform carnivorans, and nesomyine rodents

(Poux et al., 2005). The timing of the mammalian colonization of Madagascar is unconstrained by the virtually nonexistent Cenozoic fossil record of that island, but molecular estimates of the diversification of some endemic Malagasy mammal clades, notably including tenrecs (Poux et al., 2008) and lemurs (Yoder and Yang, 2004; Gunnell et al., 2018), are consistent with colonization having occurred during the Eocene.

Given the geographic location of the Pontides along the northern margin of Neotethys, a potential role for this landmass during the trans-Tethyan dispersal of the Asian mammal clades that colonized Africa near the Bartonian-Priabonian boundary cannot be dismissed. However, paleontological data from the Uzunçarşidere Fm. indicate that, during the Lutetian, the Pontide microcontinent was a biogeographical cul-de-sac rather than a launching pad for dispersal across Tethys (Métais et al., 2018). None of the mammal clades that are known to have dispersed across Tethys a few million years later have been recovered so far on the Pontides during the Lutetian. Hence, if anthropoid primates and hystricognath and anomaluroid rodents traversed the Pontides and adjacent parts of Anatolia as part of their colonization of Africa, they must have done so later in the Eocene. Recovery of younger Eocene mammal faunas in Anatolia will be necessary to evaluate a possible role for this region in the trans-Tethyan dispersal of anthropoid primates and anomaluroid and hystricognath rodents.

Current examples of terrestrial mammal dispersal across marine barriers during the Eocene now include the colonization of the Pontides by omomyid primates, the colonization of Africa and subsequently South America by anthropoid primates, the colonization of Africa and subsequently South America by hystricognath rodents, the colonization of Africa by anomaluroid rodents, and probably the colonization of Madagascar by lemurs and tenrecs. These dispersal events involved multiple mammal clades, although primates and rodents are particularly well represented. Moreover, phylogenetic evidence suggests that in some cases, such as the colonization of Africa by anthropoid primates and hystricognath rodents, the endemic radiations that ensued were not monophyletic, implying that multiple anthropoid and hystricognath taxa colonized Africa at roughly the same time (Beard, 2016; Jaeger et al., 2019). The recent discovery of a parapithecid anthropoid in South America likewise indicates that multiple African anthropoid clades colonized that continent, although the timing of the initial colonization of South America by early anthropoids is relatively weakly constrained (late Eocene or early Oligocene; Seiffert et al., 2020).

In contrast to the multiple Eocene examples cited above, few if any clear examples of terrestrial mammal dispersal across marine barriers are known during the Oligocene, despite the generally narrower marine obstacles caused by lower eustatic sea levels and ongoing tectonic convergence between Africa and Eurasia. The discrepancy between the ability of terrestrial mammals to traverse marine barriers repeatedly during the Eocene and the difficulty of doing so during the Oligocene suggests that climatic factors must have played a pivotal role in facilitating Eocene "sweepstakes" dispersal. Eocene greenhouse climates were characterized by elevated pCO_2, the initiation of monsoonal climate regimes, and extreme climate variability including extreme precipitation events that were mediated by increased temperatures (Berg et al., 2013; Pagani et al., 2014; Licht et al., 2014). Frequent flooding of major rivers caused by these extreme precipitation events would have promoted sweepstakes dispersal by rafting across marine barriers, especially among small mammals such as rodents and primates (Beard, 2016). The discovery of *Nesomomys bunodens* nov. gen., nov. sp. on the Pontides indicates that sweepstakes dispersal of terrestrial mammals across marine barriers began as early as the Lutetian and took place as far north as the northern margin of Neotethys. Better known examples of Eocene sweepstakes dispersal occurred later in time and farther to the south, being particularly well documented by the colonization of Africa and South America by anthropoid primates and hystricognath rodents.

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Table and Figure captions

Table 1. Metric data (in mm) for specimens used to generate bivariate plot shown in Fig. 5.

Fig. 1. Major Eocene primate-bearing localities of Eurasia, superimposed on paleogeographic reconstruction published by Métais et al. (2018: fig. 4B). Numbers correspond to localities as follows: 1, Silveirinha (Portugal); 2, Creechbarrow (United Kingdom); 3, London Basin (multiple sites, United Kingdom); 4, Casa Ramón (Spain); 5, Capella (Spain); 6, Mazaterón (Spain); 7, Sossís (Spain); 8, Dormaal (Belgium); 9, Mormont Entreroches (Switzerland); 10, Paris Basin (multiple sites, France); 11, Roc de Santa (Spain); 12, Quercy fissure-fillings (multiple sites, France); 13, Sant Jaume de Frontanyà (Spain); 14, Lissieu (France); 15, Robiac (France); 16, Bouxwiller (France); 17, Les Alleveys (Switzerland); 18, Euzet (France); 19, La Débruge (France); 20, Fordones (France); 21, Rians (France); 22, La Verrerie de Roches (Switzerland); 23, Egerkingen (Switzerland); 24, Gösgen canal (Switzerland); 25, Geiseltal (Germany); 26, Herrlingen (Germany); 27, Oberaudorf (Germany); 28, Orhaniye Basin (Turkey); 29, Chorlakki (Pakistan); 30, Gandhera Quarry (Pakistan); 31, Vastan lignite mines (India); 32, Pondaung (multiple sites, Myanmar); 33, Naran Bulak (Mongolia); 34, Krabi lignite mines (Thailand); 35, Erlian Basin (Inner Mongolia, China); 36, Yongle Basin (Guangxi, China); 37, Songzi (Hubei, China); 38, Yuanqu Basin (Shanxi and Henan, China); 39, Lingcha (Hunan, China); 40, Shanghuang fissure-fillings (Jiangsu, China); 41, Huadian (Jilin, China).

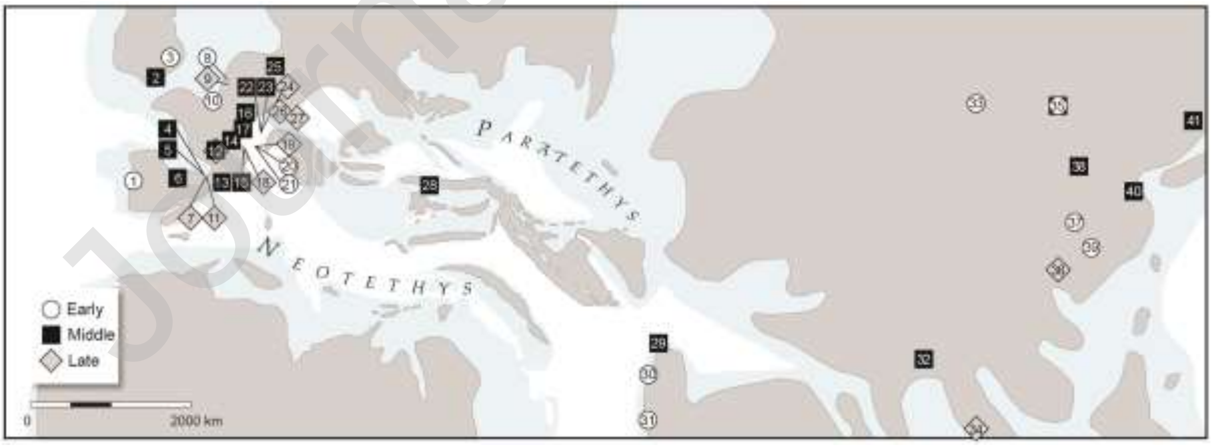

Fig. 2. *Nesomomys bunodens*, nov. gen., nov. sp., holotype left dentary fragment (EOU-UCF-9) preserving the crown of M_1 in occlusal (A) and buccal (B) views. Images are scanning electron microphotographs. Scale bar: 4 mm.

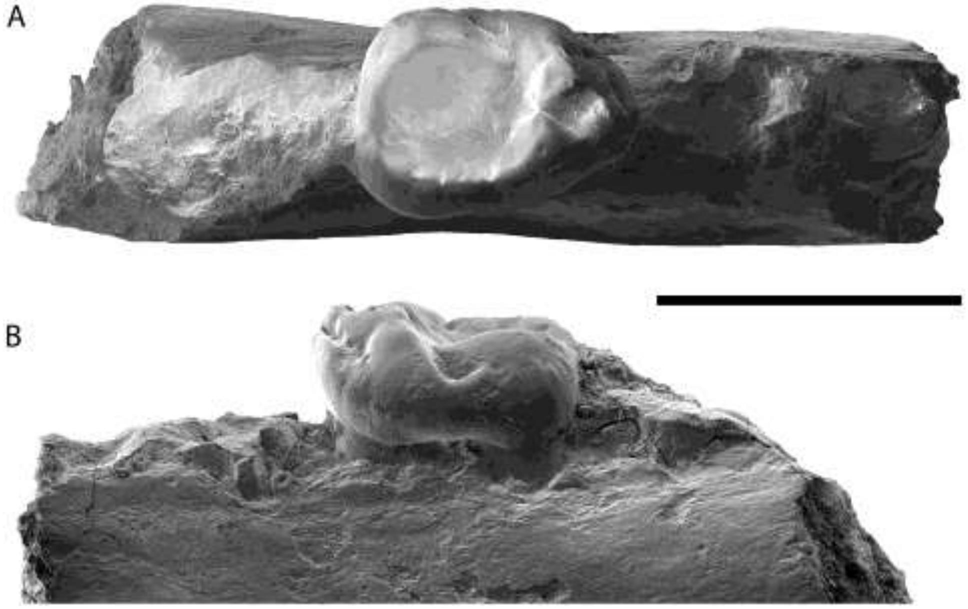

Fig. 3. *Nesomomys bunodens*, nov. gen., nov. sp., holotype left dentary fragment (EOU-UCF-9) preserving the crown of M_1 in occlusal (A), buccal (B), and lingual (C) views. Occlusal view is stereopair. Scale bar: 4 mm.

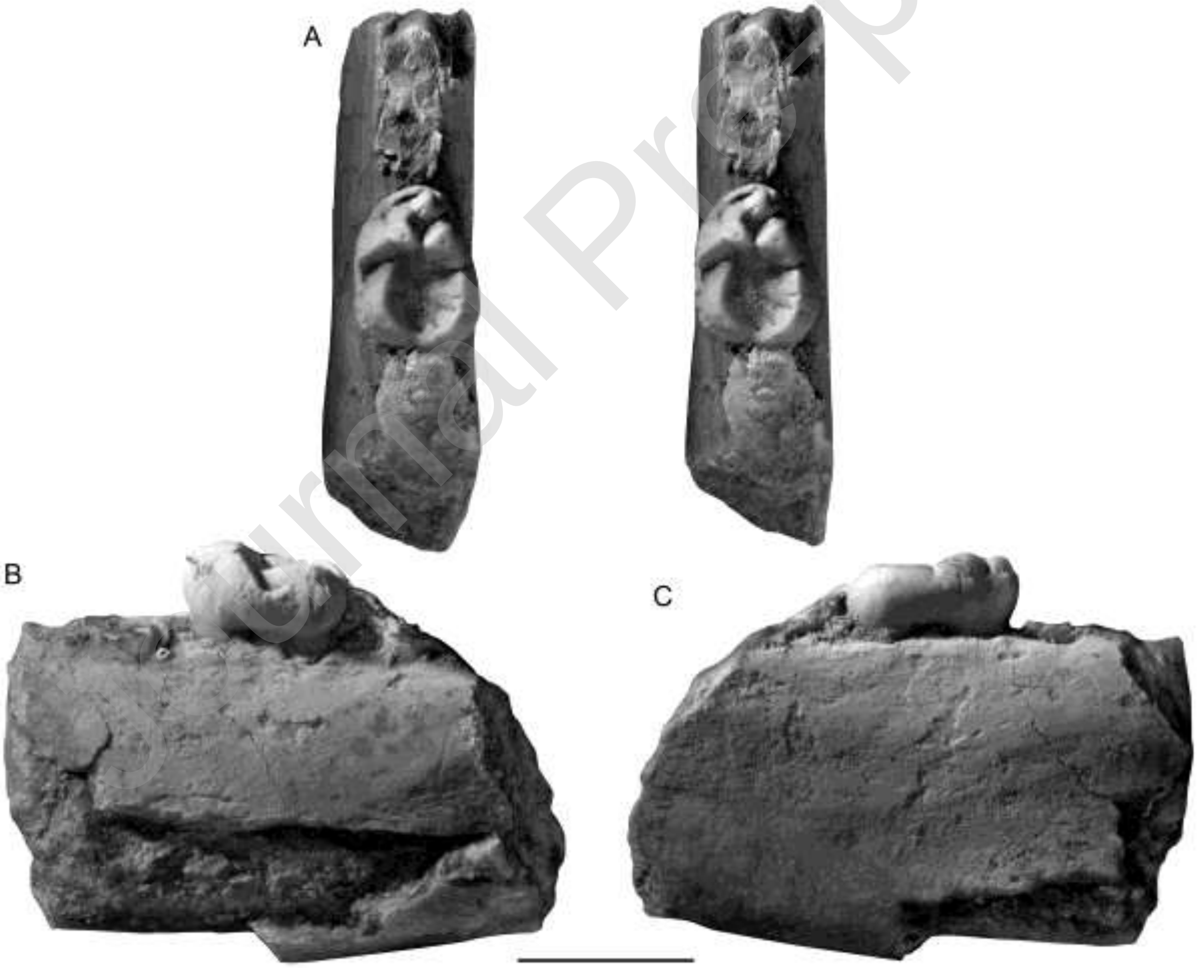

Fig. 4. Type locality (Rejection Ravine) for *Nesomomys bunodens* nov. gen., nov. sp. in the Lülük Member of the Uzunçarşidere Formation, Orhaniye Basin, Turkey.

Fig. 5. Bivariate plot showing mesiodistal length of P_4 roots vs. mesiodistal length of M_1 crown (in mm) among various omomyids and microchoerids. Line is least squares regression through individual data points. Raw data and the identity of taxa and specimens used to generate the bivariate plot are provided in Table 1.

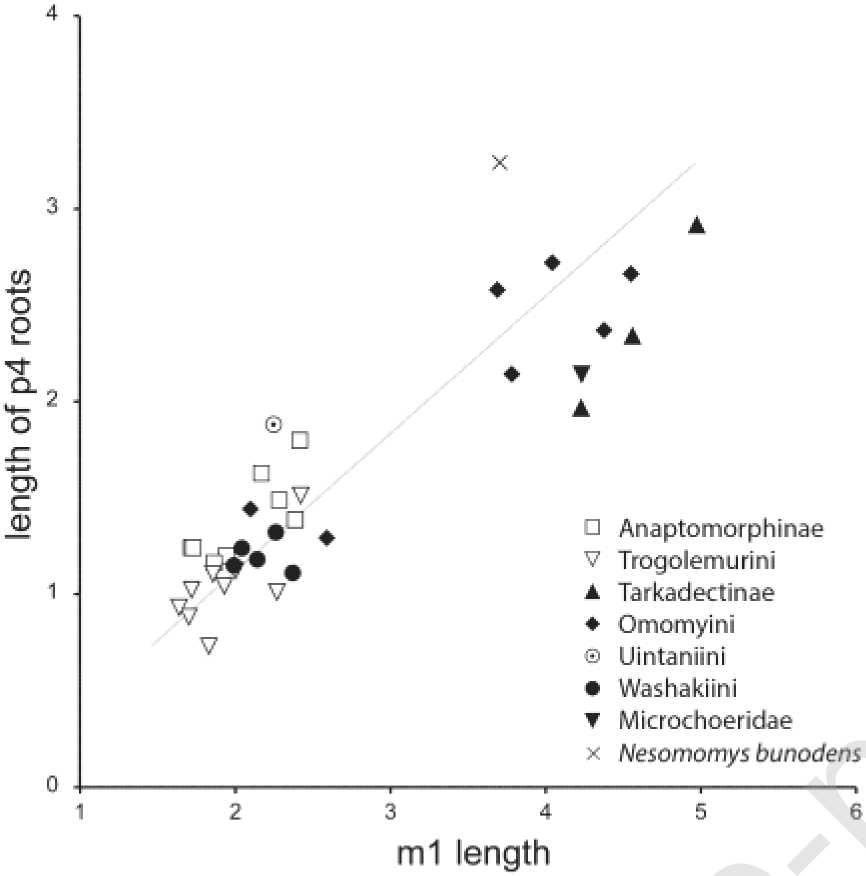
length of p4 roots
m1 length
0
1
2
3
4
1
2
3
4
5
6
□ Anaptomorphinae
▽ Trogolemurini
▲ Tarkadectinae
◆ Omomyini
⊙ Uintaniini
● Washakiini
▼ Microchoeridae
× *Nesomomys bunodens*

Table 1.

Clade	Taxon	Specimen	L p4 roots	L m1
Anaptomorphinae	*Teilhardina asiatica*	IVPP V12060	1.24	1.71
Anaptomorphinae	*Teilhardina belgica*	MMRHNB L+M64	1.24	1.72
Anaptomorphinae	*Teilhardina americana*	UW 6896	1.20	1.94
Anaptomorphinae	*Teilhardina brandti*	USNM 493913	1.17	1.86
Anaptomorphinae	*Tetonius matthewi*	CM 12190	1.80	2.41
Anaptomorphinae	*Pseudotetonius ambiguus*	UW 10212	1.63	2.17
Anaptomorphinae	*Absarokius* sp.	UCM 42009	1.49	2.28
Anaptomorphinae	*Aycrossia lovei*	USGS 250563	1.39	2.38
Trogolemurini	*Trogolemur amplior*	CM 40069	1.01	2.28
Trogolemurini	*Trogolemur myodes*	AMNH 12599	0.73	1.84
Trogolemurini	*Anemorhysis savagei*	UCM 56410	0.88	1.71
Trogolemurini	*Anemorhysis pattersoni*	USGS 15403	1.12	2.01
Trogolemurini	*Anemorhysis sublettensis*	USNM 19205	0.93	1.65
Trogolemurini	*Anemorhysis natronensis*	CM 41137	1.10	1.87
Trogolemurini	*Arapahovius gazini*	UCM 56419	1.51	2.43
Trogolemurini	*Tetonoides pearcei*	USNM 22426	1.02	1.73
Trogolemurini	*Arapahovius advena*	USNM 491907	1.04	1.94
Tarkadectinae	*Tarkops mckennai*	IVPP V16424	2.34	4.55
Tarkadectinae	*Tarkadectes montanensis*	CM 40818	1.97	4.22
Tarkadectinae	*Tarka stylifera*	AMNH 113133	2.92	4.97
Omomyini	*Mytonius hopsoni*	YPM 15266	2.14	3.78
Omomyini	*Ourayia uintensis*	YPM-PU 11236	2.72	4.04
Omomyini	*Omomys lloydi*	CM 6417	1.44	2.10
Omomyini	*Steinius vespertinus*	USGS 25027	1.29	2.59
Omomyini	*Hemiacodon gracilis*	YPM 11806	2.58	3.69
Omomyini	*Macrotarsius siegerti*	CM 21990	2.37	4.38
Omomyini	*Macrotarsius montanus*	CM 9592	2.66	4.55
Uintaniini	*Uintanius ameghini*	UW 1566	1.88	2.25
Washakiini	*Loveina minuta*	ACM 3365	1.24	2.04
Washakiini	*Loveina zephyri*	AMNH 32517	1.32	2.26
Washakiini	*Shoshonius cooperi*	CM 60594	1.11	2.37
Washakiini	*Utahia kayi*	CM 6488	1.15	1.99
Washakiini	*Dyseolemur pacificus*	LACM-CIT 1395	1.18	2.14
Microchoeridae	*Microchoerus erinaceus*	BMNH M30346	2.14	4.24
Omomyidae	*Nesomomys bunodens*	EOU-UCF-9	3.24	3.62