Dental anatomy, phylogenetic relationships and paleoecology of *Orhaniyeia nauta* (Metatheria, Anatoliadelphyidae), a Gondwanan component of the insular Eocene mammal fauna of Balkanatolia (north-central Turkey)

K. Christopher Beard[1,2] (corresponding author) email: chris.beard@ku.edu ORCID 0000-0002-6279-9837

Pauline M. C. Coster[3] ORCID 0000-0003-4015-252X

Faruk Ocakoğlu[4] ORCID 0000-0002-4619-5865

Alexis Licht[5] ORCID 0000-0002-5267-7545

Grégoire Métais[6] ORCID 0000-0002-4443-1801

[1] Biodiversity Institute, University of Kansas, 1345 Jayhawk Boulevard, Lawrence, KS 66045, USA

[2] Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045, USA

[3] Réserve naturelle nationale géologique du Luberon, 60 place Jean-Jaurès, 84404 Apt, France

[4] Department of Geological Engineering, Eskişehir Osmangazi University, Eskişehir, Turkey

[5] Centre Europeén de Recherche et d'Enseignement des Géosciences de l'Environnement, Aix-en-Provence, France

[6] Centre de Recherche en Paléontologie – Paris, UMR 7207 (CNRS, MNHN, UPMC), Sorbonne Université, Muséum National d'Histoire Naturelle, 8 rue Buffon, 75005 Paris, France

Abstract

Two new specimens of the anatoliadelphyid metatherian *Orhaniyeia nauta* are described from the middle Eocene Uzunçarşıdere Formation in the Orhaniye Basin, north-central Turkey. These specimens augment our knowledge of the dentition of this taxon, revealing that P3 and p3 of *Orhaniyeia* resemble those of its sister taxon *Anatoliadelphys* in being enlarged and highly inflated, suggesting that both taxa consumed a durophagous diet. The ancestral dental morphology of anatoliadelphyids likely approximated that of *Orhaniyeia nauta*, whereas the dentition of *Anatoliadelphys* is autapomorphous. A phylogenetic analysis incorporating the new data for *Orhaniyeia* reconstructs anatoliadelphyids as nested among a diverse, but generally poorly documented, assemblage of early Paleogene bunodont Gondwanan marsupials that are typically allied with polydolopimorphians. Alternative phylogenetic reconstructions based on *Anatoliadelphys* alone have suggested either peradectid or protodidelphid affinities for anatoliadelphyids, but these hypotheses are not supported by the new data from *Orhaniyeia*. Anatoliadelphyids likely colonized Balkanatolia from the south (Africa/Arabia), even though there is no current fossil record indicating that this Gondwanan bunodont marsupial clade ever inhabited Africa/Arabia. The durophagous diet of *Orhaniyeia* was probably eclectic, but with an emphasis on gastropods. A similar dietary reconstruction has been proposed for the Australian Miocene marsupial *Malleodectes*, the dentition of which is remarkably convergent with that of *Orhaniyeia*. *Orhaniyeia* and *Anatoliadelphys* appear to have exploited distinct ecological niches, because the autapomorphous dentition of *Anatoliadelphys* includes multiple specializations for enhanced carnivory. The colonization of Balkanatolia by anatoliadelphyids instigated a small endemic radiation, a pattern that was replicated by multiple other Balkanatolian mammal clades.

Keywords Lutetian, Marsupialia, Island biogeography, Endemic radiation, Durophagy, Polydolopimorphia

Statements and Declarations

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Introduction

Anatoliadelphyid metatherians are an endemic clade of mammals currently documented only from the fluvial Lülük Member of the Uzunçarşıdere Formation in the Orhaniye Basin, north-central Turkey. Two taxa of anatoliadelphyids have been described, including the highly autapomorphous and relatively large-bodied (3-4 kg) *Anatoliadelphys maasae* (Maga and Beck 2017) and the significantly smaller and dentally less specialized *Orhaniyeia nauta* (Métais et al. 2018). Beyond the holotype partial skeleton, additional specimens attributable to *Anatoliadelphys maasae* have not been recovered. However, field work in the Uzunçarşıdere Formation during the latter part of 2018 yielded two additional specimens of *Orhaniyeia nauta*, one of which is the most nearly complete specimen of this taxon recovered to date. These new specimens enhance our knowledge of the dental anatomy of *Orhaniyeia nauta* and provide further support for a sister group relationship between *Orhaniyeia* and *Anatoliadelphys* (Métais et al. 2018). Specifically, our knowledge of the highly specialized upper and lower distal premolars (P3 and p3) of anatoliadelphyid metatherians is augmented by relatively unworn examples of these distinctive tooth loci. Likewise, serially associated upper molars illuminate the upper dentition of *Orhaniyeia nauta*, previous knowledge of which was limited to two isolated upper molars.

The vertebrate fossils of the Lülük Member are found in pedogenic overbank, crevasse splay and channel lag deposits that have been dated to the middle Lutetian (~43-44 Ma) on the basis of paleomagnetic reversal stratigraphy and detrital zircon geochronology (Licht et al. 2017). This rock unit yields a mammalian fauna that is remarkable for several reasons. Several of the taxa known from the Lülük Member, notably including the Anatoliadelphyidae, are members

of endemic radiations, reflecting the insular paleogeogeographic conditions that prevailed across Balkanatolia at this time (Métais et al. 2017, 2018; Licht et al. 2017, 2022). Another distinctive feature of the mammalian fauna from the Lülük Member is the apparent absence of multiple mammal taxa, including Rodentia, Perissodactyla, Carnivora, Hyaenodontidae and Artiodactyla, that were otherwise ubiquitous across Laurasia during the Eocene. Instead, the Lülük Member hosts anachronistic mammals such as the pleuraspidotheriid *Hilalia* (Maas et al. 2001; Métais et al. 2017), which represents a clade that was extirpated elsewhere during the late Paleocene. Finally, the mammalian fauna of the Lülük Member is notable in that it comprises a biogeographic mélange of Laurasian (herpetotheriid metatherians, palaeochiropterygid chiropterans and omomyid primates) and Gondwanan (palaeoamasid embrithopods and anatoliadelphyid metatherians) taxa, many of which are unknown to co-occur outside of Balkanatolia (Maas et al. 1998; Métais et al. 2018; Jones et al. 2019; Beard et al. 2021).

The phylogenetic position of Anatoliadelphyidae is debated, with different hypotheses proposing that anatoliadelphyids are stem metatherians closely allied with Peradectidae (Maga and Beck 2017), crown marsupials allied with protodidelphids (Carneiro 2019), or crown marsupials allied with the extinct polydolopimorphian radiation (Métais et al. 2018). Part of the conflict among these competing phylogenetic analyses stems from different taxon sampling. That is, aside from the study of Métais et al. (2018), prior studies of anatoliadelphyid relationships have been founded upon *Anatoliadelphys maasae* alone. Because the dentition of *Anatoliadelphys* is highly autapomorphous with respect to that of its sister taxon *Orhaniyeia*, the inclusion of *Orhaniyeia* in character-taxon matrices exploring anatoliadelphyid relationships is highly desirable, particularly whenever dental characters are being heavily sampled. The new data regarding the dental morphology of *Orhaniyeia* reported here provides the basis for a new

analysis of anatoliadelphyid relationships that aims to test the conflicting tree topologies that have been published to date.

Our goals here are to describe the new specimens of *Orhaniyeia* and to leverage the new data provided by these specimens to interrogate the phylogenetic relationships of anatoliadelphyids, estimate the body mass of *O. nauta*, and reconstruct its dietary adaptations in order to achieve a more holistic picture of the evolutionary history of this endemic clade of Balkanatolian mammals.

Materials and methods

Abbreviations AÜJM, fossil specimens from the Uzunçarşıdere Formation at Ankara Üniversitesi Jeoloji Müzesi (Ankara, Turkey); **C**, upper canine; **EOU-UCF**, fossil specimens from the Uzunçarşıdere Formation at Eskişehir Osmangazi Üniversitesi (Eskişehir, Turkey); **L**, maximum mesiodistal length; **LMORL**, Lower Molar Occlusal Row Length; **M**, upper molar; **m**, lower molar; **P**, upper premolar; **p**, lower premolar; **PS**, Premolar Shape; **RBL**, Relative Blade Length; **RGA**, Relative Grinding Area; **RPL**, Relative Premolar Length; **RPS**, Relative Premolar Size; **TJL**, total jaw length; **UMORL**, Upper Molar Occlusal Row Length; **W**, maximum buccolingual width.

Specimens Anatoliadelphyid specimens reported here are permanently deposited in the collections of Eskişehir Osmangazi University (Eskişehir, Turkey). In addition to anatoliadelphyid specimens previously described by Maga and Beck (2017) and Métais et al. (2018), two newly recovered specimens of *Orhaniyeia nauta* are included in this study. EOU-UCF-13 is a left dentary fragment preserving the talonid of m3 and complete crown of m4

collected by Chris Beard at the type locality for *Orhaniyeia nauta.* EOU-UCF-14, is a left maxilla fragment preserving M2-4 and associated teeth including left C1, left P3, right M1, right M3, left p3, left m4, mesial fragment of right p3, right m2, and trigonids of right m3-4. EOU-UCF-14 was discovered by Pauline Coster at the Sheep Farm locality, ~2 km northwest of the type locality for *Orhaniyeia nauta*. Initially, a dentulous left maxillary fragment was found in situ as it was eroding out of a steeply weathering outcrop. Careful searching of the slopes and rills below the in situ maxillary fragment yielded multiple additional teeth and tooth fragments, all of which are interpreted as pertaining to the same individual based on the absence of any duplicated elements and the presence of complementary wear stages on all tooth loci. Subsequently, more teeth and tooth fragments were recovered by screen-washing weathered sediment from the slopes below the original discovery site.

Dental measurements and terminology Standard dental measurements were obtained using digital Mitutoyo micrometers paired with a measuring stage under a Unitron Z6 binocular microscope equipped with an ocular reticle (Table 1). Functionally significant dental indices, including PS, RBL, RGA, RPL, and RPS, were calculated following the methods of Zimicz (2012, 2014). Dental terminology follows the nomenclature employed by Métais et al. (2018).

Micro-CT scanning parameters EOU-UCF-14 was scanned at the University of Texas High-Resolution X-ray Computed Tomography Facility (UTCT), using an NSI scanner, Fein Focus High Power source, 130 kV, 0.12 mA, no filter, Perkin Elmer detector, 3000 projections, voxel size 10.2 µm. total slices = 1741. EOU-UCF-14 was scanned at the Duke University Shared Materials Instrumentation Facility using a Nikon XTH 225 ST scanner, 135 kV, 0.12 mA, 0.125 Cu filter, 2000 projections, voxel size 17.06 µm.

Body mass reconstruction Body mass estimates for *Orhaniyeia nauta* and *Anatoliadelphys maasae* were generated on the basis of predictive equations developed by Myers (2001) that estimate body mass from various craniodental variables in extant australidelphian marsupials (Table 2). Given the nature of available fossil specimens, two of the craniodental metrics employed by Myers (2001) were deemed appropriate for use in this study. LMORL and UMORL, both defined as the distance from the most anterior point on the first molar crown to the most posterior point on the fourth molar crown, were measured directly on high-resolution epoxy casts of the holotype of *Anatoliadelphys maasae*. Because serially associated complete upper and lower molar series remain unknown for *Orhaniyeia nauta*, these metrics were estimated in this taxon. Specifically, UMORL in *Orhaniyeia nauta* was calculated on the basis of EOU-UCF-14, by adding the length of its right M1 (3.35 mm) to the length of its serially associated left M2-4 (13.3 mm). LMORL in *Orhaniyeia nauta* was calculated on the basis of EOU-UCF-4 (the holotype), which preserves serially associated right m1-2 (L, 9.89 mm) and right m4 (L, 5.69 mm) and EOU-UCF-6, an isolated left m3 (L, 4.59 mm). Following Maga and Beck (2017), we estimated body mass for anatoliadelphyids using the body-mass equations derived from the dasyuromorphian dataset of Myers (2001: table 4).

Phylogenetic analysis Our phylogenetic analyses were based on a character-taxon matrix encompassing 51 morphological characters and 36 taxa (Online Resource 1). This matrix is based on the work of Chornogubsky and Goin (2015), supplemented by the addition of 6 characters noted by Métais et al. (2018). Two fossil metatherians (*Malleodectes* and *Protodidelphis*) and three extant marsupials (*Didelphis albiventris*, *Dasyurus hallucatus*, and *Dromiciops gliroides*) were added to the character-taxon matrix used by Métais et al. (2018). Taxa included in the matrix are the genotypic species, unless noted otherwise. In the case of

Malleodectes, we combined data from the upper dentition of *Malleodectes mirabilis* (Archer et al. 2016) with the lower dentition of *Malleodectes*? *Wentworthi* (Churchill et al., 2023), because no species of *Malleodectes* is currently documented by both upper and lower dentition. In order to account for genomic relationships among crown marsupials, we employed a molecular scaffold based on the results of Nilsson et al. (2010). The Cretaceous metatherian *Alphadon lulli* was designated as an outgroup. All characters except character 46 (cresting on StB and StD) were treated as unordered. Maximum parsimony analyses of this updated character-taxon matrix were performed with PAUP version 4.0a169 (Swofford 2002) using a heuristic search with 10,000 replicates and 100 trees saved by replication, and ACCTRAN character state optimization. A bootstrap analysis was carried out in PAUP to test the robustness of nodes. Full heuristic boostrap search was executed using 100 bootstrap replicates, 1000 addition sequence with 10,000 max trees for each replicate. Support values for clades represent absolute frequencies. Only Bootstrap values > 50% are represented.

Systematic paleontology

Class MAMMALIA Linnaeus, 1758

Subclass THERIA Parker and Haswell, 1897

Infraclass METATHERIA Huxley, 1880

Order POLYDOLOPIMORPHIA Archer, 1984

Family ANATOLIADELPHYIDAE Métais et al., 2018

Orhaniyeia nauta Métais et al., 2018

Holotype—EOU-UCF-4, associated dentary fragments and teeth preserving left m2 and m4 and right p2, m1-2, and m4. Note that the isolated lower premolar included as part of the holotype was originally identified as p3 rather than p2 (Métais et al. 2018).

Emended diagnosis—Much smaller than *Anatoliadelphys*. Distal premolars (P3 and p3) enlarged and highly inflated as in *Anatoliadelphys*, but larger relative to molars than in the latter genus. Upper and lower molars differ from those of *Anatoliadelphys* in being much less exodaenodont and in lacking the progressive size increase posteriorly found in that genus. Protoconid of m4 less hypertrophied in relation to paraconid and metaconid than in *Anatoliadelphys*.

Description

EOU-UCF-14 is the most nearly complete specimen of *Orhaniyeia nauta* recovered to date (Fig. 1a-u). However, because of the manner in which this specimen was collected (see "Materials and methods" above), our interpretation that the various teeth and bone fragments assigned here represent a single individual is open to debate. Our association of these elements is based on their compatible size, the absence of duplicated parts, and the paucity of fossil material that can be assigned to other taxa at this site. Dental metrics are provided in Table 1.

C1 is poorly preserved but closely resembles that of *Anatoliadelphys maasae* in terms of its morphology. The crown is single-rooted and anteroposteriorly longer than wide. Wear facets appear to be present on the anterolingual and posterior faces of the main cusp.

P3 is highly inflated, double-rooted and nearly circular in occlusal outline (Fig. 1a-c). Surprisingly, this tooth locus in *Orhaniyeia nauta* is nearly as large as its counterpart in the

holotype of *Anatoliadelphys maasae.* The anterior root of P3 is substantially smaller than its posterior root, particularly in the buccolingual dimension. Similar root proportions occur on P3 in the holotype of *Anatoliadelphys maasae*. The P3 crown shows primarily apical wear, which is moderate in contrast to the much heavier apical wear shown by P3 in the holotype of *Anatoliadelphys maasae*. As a result, details of P3 crown morphology are far more evident in EOU-UCF-14. The crown of P3 bears a single cusp, presumably homologous with the paracone, which is central in position. In buccal view P3 is slightly more inflated above each of the roots than near their junction. As a result, a vertically oriented crease occurs above the junction of the two roots, delimiting the more inflated buccal margins of the crown anteriorly and posteriorly. Barely discernible in occlusal view because of the extreme inflation of the crown are structures interpreted as vestigial remnants of the preparacrista and postparacrista. The former structure terminates at a tiny cuspule that may represent a vestigial parastyle. A short, weakly developed posterior cingulum occurs near the terminus of the postparacrista. Minor enamel crenulation occurs on this part of the P3 crown. In the holotype of *Anatoliadelphys maasae* P3 shows no evidence of a posterior cingulum. Instead, P3 in the latter specimen bears a weak cingulum anterobuccally that is not evident in EOU-UCF-14. Otherwise, P3 in EOU-UCF-14 is relatively shorter anteroposteriorly and broader buccolingually than that of *Anatoliadelphys maasae*, yielding a more nearly circular occlusal outline.

All four upper molar loci are represented in EOU-UCF-14. The crowns of M2-4 are included in serial association in a left maxillary fragment (Fig. 1s-u), while the much smaller M1 crown is documented from the opposite side (Fig. 1g-i). Having all four upper molar loci documented in a single individual facilitates the identification of isolated upper molars of *Orhaniyeia nauta*, which were previously the only data available for the upper dentition for this

taxon. Comparisons between EOU-UCF-14 and EOU-UCF-3, a well-preserved and lightly worn upper molar of *Orhaniyeia nauta* that was interpreted as M3 by Métais et al. (2018), indicates that the latter specimen more likely represents M2. AK95-19, an isolated upper molar that was figured and described by Maas et al. (1998), is interpreted here as M1 of *Orhaniyeia nauta*.

M1-3 in *Orhaniyeia nauta* show a progressive increase in size posteriorly, but M4 is clearly smaller than M3, particularly in the buccolingual dimension. All upper molars in EOU-UCF-14 show heavy wear, obscuring certain details of crown morphology. M1-3 are very similar in morphology, differing chiefly in terms of size. In occlusal outline M1-3 of *Orhaniyeia nauta* are more nearly quadrate than those of *Anatoliadelphys maasae* because the angulation between the pre- and postprotocristae on each upper molar is more obtuse in *Orhaniyeia*. As a result, the postprotocrista and the adjacent posterolingual wall of each upper molar are oriented more posteriorly in *Orhaniyeia*, while these upper molar structures are more posterobuccally oriented in *Anatoliadelphys*. M1-3 each bear five distinct stylar cusps that are arranged roughly anteroposteriorly and connected by a crest. In terms of their relative sizes, StD > StB > StE > StA > StC. Partly because of the narrow breadth of the stylar shelves on the upper molars, StB and StD are closely approximated to the bases of the paracone and metacone, respectively. StA is situated at the anterobuccal corner of the crown, near the buccal terminus of the anterior cingulum and the preparacrista. However, the preparacrista is not confluent with StA. StB is enlarged, being twinned with the paracone but separated from it by an anteroposteriorly oriented valley. StC is diminutive yet clearly present on right M1 and bilaterally on M3 in EOU-UCF-14; this structure is not clearly discernible on M2 in this specimen, possibly because of wear. Similarly, StC is extremely faint on EOU-UCF-3, likewise interpreted here as M2. StD and the adjacent metacone appear to be connected by a transversely oriented crest on M1-3 in EOU-

UCF-14, as was previously reported with respect to EOU-UCF-3 by Métais et al. (2018). StE is located posteriorly and slightly buccally with respect to StD. StE is not confluent with the postmetacrista, being situated slightly anterior to the buccal terminus of the latter structure.

There is variation in the development of an ectoflexus anteroposteriorly in EOU-UCF-14. M1 has a relatively straight buccal margin in occlusal view (Fig. 1g), while the buccal margin of M2 is modestly invaginated posterior to the level of StB (Fig. 1s) (the ectoflexus is deeper in EOU-UCF-3). The ectoflexus is most pronounced on M3 in EOU-UCF-14, but it remains only moderately developed even at this tooth locus. In buccal view, the bases of the crowns of M1-3 also vary with respect to their development of what can be called exodaenodont lobes (Fig. 1t), following the usage of this terminology for lower molars of *Anatoliadelphys maasae* by Maga and Beck (2017). Indeed, the development of exodaenodonty in upper molars of *Orhaniyeia nauta* closely tracks the expression of the ectoflexus. That is, there is little if any development of exodaenodonty on M1 (which lacks a significant ectoflexus), while M2 and especially M3 each show two exodaenodont lobes with lines of demarcation matching the position of the ectoflexus. On both M2 and M3 the posterior exodaenodont lobe is more massive and protrudes farther dorsally, away from the occlusal surface of the crown. Note that while the development of exodaenodonty on upper molars of *Orhaniyeia nauta* is significant, it pales in comparison to the much stronger exodaenodonty that occurs on upper molars of *Anatoliadelphys maasae* (Fig. 2c, d). As is the case for upper molars of *Orhaniyeia nauta*, exodaenodonty on upper molars of *Anatoliadelphys maasae* increases from M1-3, being best developed on the posterior lobe of M2 and especially that of M3.

The more lingual parts of M1-3 in EOU-UCF-14 are heavily worn, which obscures certain details of crown structure. What remains clear is that each of these upper molars bears a

continuous centrocrista, a metacone that is somewhat larger than the paracone, a postmetacrista that is longer than the preparacrista, a buccolingually narrow trigon, and an asymmetrical and anteriorly canted protocone yielding asymmetrical development of the protocone cristae, so that the postprotocrista is longer than the preprotocrista. Anterior and posterior cingula are present on M1-3, extending roughly from the buccal edges of the protocone to the antero- and posterobuccal corners of each molar. Heavy wear obscures the presence or absence of a metaconule on the upper molars in EOU-UCF-14, but a metaconule is well developed in EOU-UCF-3, which is lightly worn.

M4 is heavily worn in EOU-UCF-14, but it clearly shows different occlusal proportions with respect to M3 than is the case in *Anatoliadelphys maasae*, being relatively narrower buccolingually than in the latter taxon (Fig. 2a, b). A well-developed parastylar lobe is present, but this structure is less expansive and much less exodaenodont than its counterpart in *Anatoliadelphys maasae*. Partly because of heavy wear, it is not completely obvious how many stylar cusps are present on M4, nor is it clear how their homologies should be interpreted. StA was probably present near the anterobuccal corner of the tooth, but this area is heavily worn because of its proximity to the preparacrista, which was elongated and functionally important in *Orhaniyeia nauta*. An elevated, arcuate crest runs posteriorly from the vicinity of StA, tracing the buccal margin of the stylar shelf. At least one and possibly two stylar cusps occur on this crest, anterobuccal to the paracone. We identify the larger of these structures as StB. If a second distinct stylar cusp is present on M4, it is closely connate with StB and is likely homologous with StC. There is no clear development of either StD or StE on M4 in EOU-UCF-14, although wear may have obscured those structures. Farther lingually, much of the crown morphology of M4 is obscured by heavy wear. A paracone was present and was clearly the largest cusp. The area

surrounding the protocone and its cristae, as well as the metacone, is heavily worn. A distinct anterior cingulum is present, extending from roughly the level of the protocone to the anterobuccal corner of the tooth.

The p3 is bulbous and enlarged in EOU-UCF-14 (Fig. 1d-f), approximating that of the holotype of *Anatoliadelphys maasae* in terms of size and morphology. The tooth is double-rooted and simple in construction, with a trigonid that is dominated by an inflated protoconid and an abbreviated talonid consisting of a diminutive hypoconid. The protoconid shows apical wear, but the degree of wear is much less than that on the holotype of *Anatoliadelphys maasae*, which is beveled nearly to the base of the crown (Maga and Beck 2017). The buccal margin of the trigonid is broadly rounded and convex in occlusal view, while the lingual margin of the trigonid is flatter, with a minor invagination above where the two roots converge at the base of the crown. The talonid deviates slightly lingually with respect to the long axis of the trigonid. Two very faint crests, separated by a shallow furrow, appear to climb the posterior face of the trigonid from the talonid. To the extent that p3 in EOU-UCF-14 can be compared with that of the holotype of *Anatoliadelphys maasae*, it differs in having a slightly longer, narrower and lingually invaginated trigonid and a better developed talonid.

Aspects of the lower molar morphology are preserved in EOU-UCF-13 and EOU-UCF-14. These specimens underscore differences in lower molar morphology between *Orhaniyeia nauta* and *Anatoliadelphys maasae*. Most of these differences have already been enunciated by Métais et al. (2018). Here, we highlight a few additional features, particularly regarding m4, which is the largest and most autapomorphous lower molar locus in *Anatoliadelphys maasae*. The m4 in *Orhaniyeia nauta* is primitive with respect to that of *Anatoliadelphys maasae* in several ways (Fig. 2e-h). While in both taxa the protoconid is the dominant trigonid cusp on m4,

in *Anatoliadelphys maasae* the protoconid is relatively taller, more voluminous, and slightly recurved posteriorly, while the metaconid is reduced to a vestigial structure. On m4 in *Orhaniyeia nauta* the paraconid and metaconid are larger and more lingual in position than they are in *Anatoliadelphys maasae*. As a result, in *Orhaniyeia nauta* the m4 paracristid and protocristid retain more of their primitive transverse orientation, while these crests in *Anatoliadelphys maasae* are longer and more vertically oriented. The m4 talonid is longer and slightly narrower in *Orhaniyeia nauta*, and the cristid obliqua runs anterolingually from the hypoconid so that it contacts the postvallid slightly lingual to the midpoint of the protoconid. In *Anatoliadelphys maasae* the cristid obliqua is anteroposteriorly oriented, forming a shearing crest that is more or less aligned with that formed by the paracristid. In EOU-UCF-13 two main cusps, interpreted as hypoconulid and entoconid, occur on the posterolingual side of the talonid of m4. Assuming that our interpretation of cusp homologies is correct, the hypoconulid occupies the posteriormost part of the m4 talonid, where it is connected to the hypoconid by a relatively straight postcristid. The hypoconulid and entoconid are closely twinned, as is frequently the case in metatherians. Multiple small neomorphic cuspules occur on the pre-entocristid, similar to the condition found in several palaeothentoid paucituberculatans. A short postcingulid occurs behind the hypoconid on m4 in EOU-UCF-13 (Fig. 1v, w), but wear has obscured this structure in EOU-UCF-14 (Fig. 1p, q). As already mentioned by Métais et al. (2018), the most distinctively autapomorphous features of m4 in *Anatoliadelphys maasae* include its enlargement with respect to the more anterior molars and its exaggerated degree of exodaenodonty. Both features occur in a far more muted form in *Orhaniyeia nauta*.

Results

Estimation of body mass Body mass estimates for *Orhaniyeia nauta* and *Anatoliadelphys maasae* are provided in Table 2, based on predictive equations developed by Myers (2001) that estimate body mass from various craniodental metrics in living dasyuromorphians. Maga and Beck (2017) estimated the body mass of *Anatoliadelphys maasae* as 3-4 kg on the basis of mandibular length (TJL). Because TJL is not determinable in *Orhaniyeia nauta* owing to the preservation of available fossil specimens, we applied other craniodental metrics developed by Myers (2001) to estimate body mass in both of these anatoliadelphyid taxa.

Our mean estimates of body mass in *Anatoliadelphys maasae* on the basis of its upper and lower molar occlusal length (UMORL and LMORL, respectively) are 3.6-3.8 kg or ~10% higher than Maga and Beck's (2017) mean estimate based on TJL, although our estimates fall within Maga and Beck's (2017) reported range of body mass estimates when percentage error is taken into account. One possible explanation for the slightly higher body mass estimates for *Anatoliadelphys maasae* that are derived from molar occlusal metrics is the autapomorphous enlargement of the posterior molars that occurs in this taxon.

Our mean estimates of body mass in *Orhaniyeia nauta* range from 1.0-1.4 kg, suggesting that this species is roughly similar in size to the extant eastern quoll (*Dasyurus viverrinus*). *Orhaniyeia nauta* probably attained roughly one-third the adult body mass of *Anatoliadelphys maasae*.

Phylogenetics PAUP recovered 105 equally most parsimonious trees (MPTs) having 180 steps, a consistency index of 0.42 and a retention index of 0.75. The distribution of character states for internal nodes and a complete list of synapomorphies are provided in Online Resource 2. The

strict consensus tree (Fig. 3) is well resolved and consistent with the phylogenetic results reported by Métais et al. (2018). *Anatoliadelphys* and *Orhaniyeia* are reconstructed as sister taxa (Anatoliadelphyidae) with strong bootstrap support. Our analysis recovered three synapomorphies for Anatoliadelphyidae, including a shift in the position of StB from in front of the paracone to behind the paracone (Character 45, 0=>1), loss of the paraconule on upper molars (Character 47, 1=>2), and presence of a reduced trigon on upper molars (Character 48, 0=>1). Anatoliadelphyids are nested among an assemblage of early Paleogene South American and Australian bunodont metatherian taxa including *Palangania*, *Chulpasia*, *Thylacotinga* and *Apeirodon* that have traditionally been regarded as basal polydolopimorphians (Goin et al. 2016; Babot et al. 2020). We recovered four synapomorphies supporting a clade including Anatoliadelphyidae and *Apeirodon*, including reduction and anteroposterior compression of the hypoconulid on m1-3 (Character 16, 0=>1), development of crests on both StB and StD (Character 46, 1=>2), enlargement of StD relative to StB (Character 49, 0=>1), and hypertrophy of the protoconid on m4 (Character 51, 0=>1). Two synapomorphies support a clade including Anatoliadelphyidae, *Apeirodon* and *Thylacotinga*, including loss of StC (Character 42, 0=>1), and development of crests on StB (Character 46, 0=>1). Three synapomorphies support a clade including Anatoliadelphyidae, *Apeirodon*, *Thylacotinga*, *Chulpasia* and *Palangania*, including hypertrophy of p3 (Character 5, 0=>1), addition of pre- and postmetaconule cristae on upper molars (Character 36, 1=>0), and progressive development of exodaenodonty on m1-4 (Character 50, 0=>1). More distantly related to anatoliadelphyids is a clade including "core" polydolopimorphian taxa such as Bonapartheriiformes (*Prepidolops* and *Bonapartherium*) and Polydolopiformes (*Polydolops*). Intriguingly, the recently described durophagous metatherian *Malleodectes* from the Miocene of Australia is reconstructed as the sister group of this most

inclusive clade of polydolopimorphians, rather than as a basal dasyuromorphian as previous analyses have suggested (Arena et al. 2011; Archer et al., 2016, Churchill et al. 2023).

Discussion

Phylogenetic relationships of *Orhaniyeia* and Anatoliadelphyidae The new specimens of *Orhaniyeia nauta* described here reveal that this taxon differs significantly in its dental anatomy from *Anatoliadelphys maasae*, supporting the generic-level distinction between these taxa. At the same time, the apparent sister group relationship between *Anatoliadelphys* and *Orhaniyeia* proposed by Métais et al. (2018) is corroborated by new data regarding the highly specialized P3 and p3 of *Orhaniyeia*, which closely resemble these autapomorphous tooth loci in *Anatoliadelphys*. A monophyletic Anatoliadelphyidae is among the most strongly supported nodes on our consensus tree topology, being recovered in 87% of bootstrapped trees (Fig. 3).

Our results corroborate the phylogenetic analysis published by Métais et al. (2018) in finding anatoliadelphyids nested among taxa that have been widely regarded as basal polydolopimorphians. This result conflicts with prior interpretations of the phylogenetic position of *Anatoliadelphys* alone, in which *Anatoliadelphys* was interpreted either as a basal member of Marsupialiformes (Maga and Beck 2017) or as a protodidelphid (Carneiro 2019). A range of potential dental synapomorphies uniting *Anatoliadelphys* with various crown marsupial and metatherian clades was noted by Maga and Beck (2017), but these were generally dismissed as being convergent adpatations for a durophagous diet. Instead, the retention of seemingly primitive characters by *Anatoliadelphys* (including the presence of a small postcingulid on m3-4 and a simple, concave cuboid facet on the distal calcaneus) favored reconstructing

Anatoliadelphys outside of crown Marsupialia, while having a possible relationship with peradectids (Maga and Beck 2017; Beck 2023). Here, we emphasize that *Anatoliadelphys* shares no meaningful similarities in its dentition with peradectids, and unambiguous synapomorphies uniting *Anatoliadelphys* with peradectids have not been recovered (Maga and Beck 2017: table 6).

Part of the conflict between our phylogenetic results and those of prior workers undoubtedly owes to different taxon and character sampling regimes. In particular, phylogenetic analyses of the relationships of *Anatoliadelphys* that fail to include *Orhaniyeia* will inevitably be hampered by the highly autapomorphous nature of the dentition of the former taxon. Likewise, even though their anatomy remains poorly documented, various early Paleogene Gondwanan bunodont metatherians including *Palangania*, *Chulpasia*, *Apeirodon*, and *Thylacotinga* seem to be closely related to anatoliadelphyids, and their exclusion from phylogenetic analyses focusing on anatoliadelphyids will likely yield spurious results. However, certain caveats need to be considered with respect to our preferred phylogenetic result (Fig. 3). First, although anatoliadelphyids are reconstructed as being deeply nested among various basal, bunodont polydolopimorphians, bootstrap support for this part of the tree is quite low, indicating that several of these nodes are unstable. To some extent, all the taxa implicated in this part of our consensus tree topology (including *Palangania*, *Chulpasia*, *Apeirodon*, and *Thylacotinga*) are documented only by very fragmentary fossil remains (Sigé et al. 2009; Babot et al. 2020), an issue that undoubtedly contributes to the low bootstrap support mentioned previously. Also, the monophyly of Polydolopimorphia and its position with respect to other living and fossil metatherians has been challenged (Beck 2017, 2023), raising questions about where Anatoliadelphyidae and their closest bunodont Gondwanan relatives reside on the broader

metatherian tree. This uncertainty regarding the monophyly and broader relationships of Polydolopimorphia offers a plausible explanation for the seemingly contradictory interpretations of anatoliadelphyid affinities that have been proposed to date (Maga and Beck 2017; Métais et al. 2018; Beck 2023). In other words, it may be true that anatoliadelphyids are closely related to bunodont Gondwanan polydolopimorphians like *Apeirodon* (as available dental evidence would suggest) and that some or perhaps all polydolopimorphians lie outside the crown clade of Marsupialia (as the calcaneal evidence from *Anatoliadelphys* would suggest). Further anatomical data are required, especially bearing on the poorly documented bunodont Gondwanan taxa cited above, to solidify the monophyly of Polydolopimorphia and their affinities with respect to crown clade marsupials. Regardless of whether Anatoliadelphyidae and their bunodont Gondwanan relatives are crown marsupials or basal marsupialiforms, these taxa appear not to be closely related to either peradectids or protodidelphids.

Paleoecology The most surprising result from the discovery of EOU-UCF-14 is the new information this specimen reveals about P3 and p3 morphology in *Orhaniyeia nauta*. Previously, *Orhaniyeia nauta* was thought to differ from *Anatoliadelphys maasae* in lacking the hypertrophied and highly inflated P3 and p3 that typify the latter genus, an interpretation that was consistent with the smaller size and more primitive molar morphology characterizing *Orhaniyeia*. EOU-UCF-14 shows that P3 and p3 were actually more hypertrophied in *Orhaniyeia nauta*, at least in relation to the molars, than is the case in *Anatoliadelphys maasae*. The degree of hypertrophy of p3 in *Orhaniyeia nauta* is reflected by Zimicz's (2012, 2014) RPS index, which is larger in *Orhaniyeia nauta* (3.60; see Table 1) than it is in *Anatoliadelphys maasae* (2.89; see Maga and Beck 2017: table 3). According to Zimicz (2012), RPS values >2.6

signal adaptations for durophagy and/or bone-cracking behavior, so the high RPS values obtained for *Orhaniyeia nauta* suggest some type of durophagous diet in this species. Maga and Beck (2017) likewise interpreted *Anatoliadelphys maasae* as being durophagous, although they questioned whether this taxon could be a specialized bone-cracker, given its relatively small body size. Because *Orhaniyeia nauta* is substantially smaller than *Anatoliadelphys maasae* (Table 2), bone-cracking adaptations would appear to be even less likely in *Orhaniyeia*.

Further evidence for durophagy in *Orhaniyeia nauta* comes from the gross morphology and macroscopic wear patterns shown by P3 and p3 in EOU-UCF-14. These teeth in *Orhaniyeia nauta* are highly inflated, each being dominated by a basally broad and blunt cusp that approximates the optimal "design criteria" for propagation of cracks in brittle material (Sanson 1991). Both P3 and p3 in EOU-UCF-14 are moderately worn, but wear is restricted to the apices of the tooth crowns, including the paracone on P3 and the protoconid on p3 (Fig. 1a, d). The horizontally beveled nature of wear on these premolar crowns is caused by abrasive tooth-on-food contact rather than occlusion between complementary teeth, which instead yields attritional wear facets that are obliquely oriented (Ungar 2015). By way of comparison, P3 and p3 in the holotype of *Anatoliadelphys maasae* are highly beveled and more heavily worn than the corresponding teeth in EOU-UCF-14 (Maga and Beck 2017: figs. 2, 12). This wear pattern is consistent with durophagy in *Anatoliadelphys maasae* as well.

Although comparisons between *Orhaniyeia* and *Anatoliadelphys* are limited by the small available sample sizes, the differential patterns of wear across the tooth row shown by the most nearly complete known specimen of *Orhaniyeia nauta* (EOU-UCF-14) and the holotype of *Anatoliadelphys maasae* are striking (Fig. 2a-d). In the holotype of *A. maasae*, extremely heavy apical wear has beveled the crowns of P3-M1 and p3-m1 almost to the level of the roots. In

contrast, the posterior molars (particularly M3-4 and m3-4) are only lightly worn. Virtually the opposite pattern of wear characterizes the upper dentition of the EOU-UCF-14 specimen of *Orhaniyeia nauta*, in which the posterior molars (particularly M3-4) are heavily worn, yet P3 shows only a modest degree of beveling (Fig. 2a). Bearing in mind the caveat that these observations are limited by the paucity of available specimens, they nevertheless suggest that *Orhaniyeia* and *Anatoliadelphys* may have consumed different diets or deployed their masticatory apparatus in very different ways (and perhaps both).

Another functionally significant morphometric index that has been used to discriminate diets among carnivorous metatherians and eutherians is RGA or relative grinding area of the lower carnassial molar (m1 in carnivorans and m4 in metatherians) (Van Valkenburgh 1991; Friscia et al. 2007; Zimicz 2012). We follow Zimicz (2012) in discriminating among hypercarnivorous, mesocarnivorous, and hypocarnivorous taxa as follows: hypercarnivorous taxa focus almost exclusively on vertebrate tissues, mesocarnivorous taxa rely extensively on vertebrate tissues but also incorporate insects and other invertebrates into their diets, while hypocarnivorous taxa eat primarily invertebrates, fruits, and other items. Hypercarnivorous metatherians and eutherians emphasize shearing over grinding on their lower carnassial molars, and these taxa have relatively low (<0.5) RGA values as a result. Mesocarnivores retain moderately large talonids on their lower carnassial molars, yielding intermediate RGA values (0.5<RGA<0.8). Hypocarnivores or omnivores lack the extreme emphasis on shearing shown by hypercarnivores, and these taxa therefore show the highest RGA values (>0.8) among carnivorous metatherians and eutherians. The available sample of m4 for *Orhaniyeia nauta* (n = 5) exhibits a mean RGA of 0.9 (range = 0.84-1.03; see Table 1), suggesting an omnivorous or

hypocarnivorous diet for this taxon. In contrast, *Anatoliadelphys* has a lower RGA value of 0.65 (Maga and Beck, 2017: table 3), consistent with a mesocarnivorous diet.

The dentition of *Orhaniyeia nauta* is generally plesiomorphous with respect to that of *Anatoliadelphys maasae* (Métais et al. 2018), providing guidance on character state polarities in the dentition of anatoliadelphyids and evolutionary trends in their dietary adaptations. Some of the most salient differences in the dentition of *Orhaniyeia* and *Anatoliadelphys* are localized in the posterior molars, which function as the primary carnassial teeth among marsupials. In the upper dentition, *Anatoliadelphys* differs most obviously from *Orhaniyeia* in having M3-4 relatively larger (Fig. 2a, b). Much of the difference in the relative size of these tooth loci in *Anatoliadelphys* is concentrated on the parts of those teeth that bear important carnassial shearing crests, specifically the postmetacrista of M3 and the preparacrista of M4, as well as adjacent mesiodistally oriented crests on their stylar shelves. Additionally, in buccal view it is clear that these parts of the upper carnassial dentition in *Anatoliadelphys* exhibit a higher degree of exodaenodonty than occurs in *Orhaniyeia* (Fig. 2c, d). Similar differences are observed on m4 of *Anatoliadelphys* and *Orhaniyeia*, in which the trigonid of *Anatoliadelphys* has been transformed by increasing the height and basal circumference of the protoconid, reducing the paraconid and metaconid to vestigial structures, and reorienting the trajectory of the paracristid so that it lies in a nearly mesiodistal, as opposed to more oblique, plane (Fig. 2e-h). Like the upper carnassial molars, m4 of *Anatoliadelphys* shows an exaggerated degree of exodaenodonty compared to the condition in *Orhaniyeia* (Fig. 2g, h). Finally, the talonid of m4 is reduced with respect to the trigonid in *Anatoliadelphys*, yielding the divergent RGA scores documented for these taxa. These autapomorphous features of the upper and lower carnassial dentition of

Anatoliadelphys result in longer shearing crests and enhanced puncture-crushing capacity, while *Orhaniyeia* retains a greater emphasis on grinding.

The overall pattern that emerges for reconstructing the dietary adaptations of *Orhaniyeia nauta* is that this taxon was apparently an omnivore or hypocarnivore with important adaptations for durophagy. A compelling model for the dietary adaptations of *Orhaniyeia nauta* is that recently proposed for the Australian Miocene metatherian *Malleodectes*, which shares many convergent dental adaptations with *Orhaniyeia* (Archer et al. 2016). Like *Orhaniyeia*, *Malleodectes* has a greatly enlarged and highly inflated P3 combined with upper molars retaining a generally primitive tribosphenic pattern, including substantial capacity for shearing. Compelling evidence that the highly inflated and enlarged P3 of *Orhaniyeia* and *Malleodectes* is convergent comes from the recent discovery of the lower dentition of a new malleodectid species, *Malleodectes*? *wentworthi*, in which p2 rather than p3 is enlarged and inflated (Churchill et al. 2023). Moreover, *Orhaniyeia nauta* is roughly the same size as two of the three described species of *Malleodectes*, although the recently published *Malleodectes*? *wentworthi* is about an order of magnitude smaller. We interpret *Orhaniyeia nauta* as a durophagous metatherian with an eclectic diet that may have specialized on snails, opercula of which are remarkably abundant in screen-washed sediment of the Lülük Member of the Uzunçarşıdere Formation.

Relative to *Orhaniyeia nauta*, *Anatoliadelphys maasae* shows multiple derived aspects of its dentition indicating a greater commitment to carnivory. These features include the relative increase in size of the posterior upper and lower molars, where the carnassial function of the metatherian dentition resides; development of enhanced shearing through lengthening of the postmetacrista of M3, preparacrista of M4, mesiodistally oriented stylar crests on M3-4, and paracristid of m4; development of exaggerated exodaenodonty on M3-4 and m4; reduced talonid

basin and associated lower RGA scores on m4; and hypertrophy of the protoconid and reduction of the paraconid and metaconid on m4. Like *Orhaniyeia*, *Anatoliadelphys* was apparently specialized for durophagy, but these two closely related taxa were able to occupy distinct ecological niches and achieve sympatry on Balkanatolia through a combination of their divergent dental specializations and a roughly three-fold difference in body mass. The exploitation of a more carnivorous niche by *Anatoliadelphys* would have been facilitated by the apparent absence of carnivorous eutherian taxa during Balkanatolia's insular phase represented by the Uzunçarşıdere Formation, where remains of Carnivoramorpha, Hyaenodonta and Oxyaenidae have not been recovered (Métais et al. 2018; Licht et al., 2022).

Evolutionary history of anatoliadelphyids Our data suggest that *Anatoliadelphys* and *Orhaniyeia* evolved from a single anatoliadelphyid ancestor that colonized Balkanatolia sometime in the early Paleogene (prior to the middle Lutetian). There are no known Laurasian metatherians that either resemble anatoliadelphyids or appear to share a particularly close phylogenetic relationship with them, even though the fossil record of early Paleogene and older metatherians across Laurasia is considered to be reasonably good (Eldridge et al. 2019). To the contrary, multiple taxa of bunodont metatherians known from the early Paleogene of South America and Australia share a range of dental synapomorphies with Anatoliadelphyidae, even though these taxa are typically documented by nothing more than isolated teeth (Babot et al. 2020). Biogeographically, we interpret these data as supporting a Gondwanan origin for Anatoliadelphyidae. This raises the interesting prospect of requiring a geographic ghost range extension for Gondwanan bunodont metatherians to include Africa/Arabia during the early Paleogene, where they remain unknown so far as fossils, because it is difficult to envision how

this clade could have colonized Balkanatolia directly from any other Gondwanan landmass. Examples of vertebrate taxa colonizing Africa from South America during the early Paleogene are rare, but the metatherian *Kasserinotherium* and the flightless "terror birds" or Phorusrhacidae may provide such examples (Angst et al. 2013; Crespo and Goin 2021).

Once anatoliadelphyids colonized the insular terrane of Balkanatolia during the early Paleogene, they encountered an unbalanced ecosystem that was apparently devoid of mammalian predators. Like other mammalian taxa that colonized Balkanatolia from either Africa (palaeoamasid embrithopods) or Europe (pleuraspidotheriid "condylarths"), anatoliadelphyids responded by undergoing an endemic radiation. *Orhaniyeia* likely retained many plesiomorphic features inherited from the original anatoliadelphyid colonist to invade Balkanatolia, while *Anatoliadelphys* evolved larger body mass and developed dental specializations for a more carnivorous diet. Anatoliadelphyids probably succumbed to extinction soon after Balkanatolia became reconnected to Asia during the late Bartonian (Licht et al. 2022), but adequately documenting the stratigraphic range of anatoliadelphyids in Balkanatolia requires a denser fossil record than is currently available.

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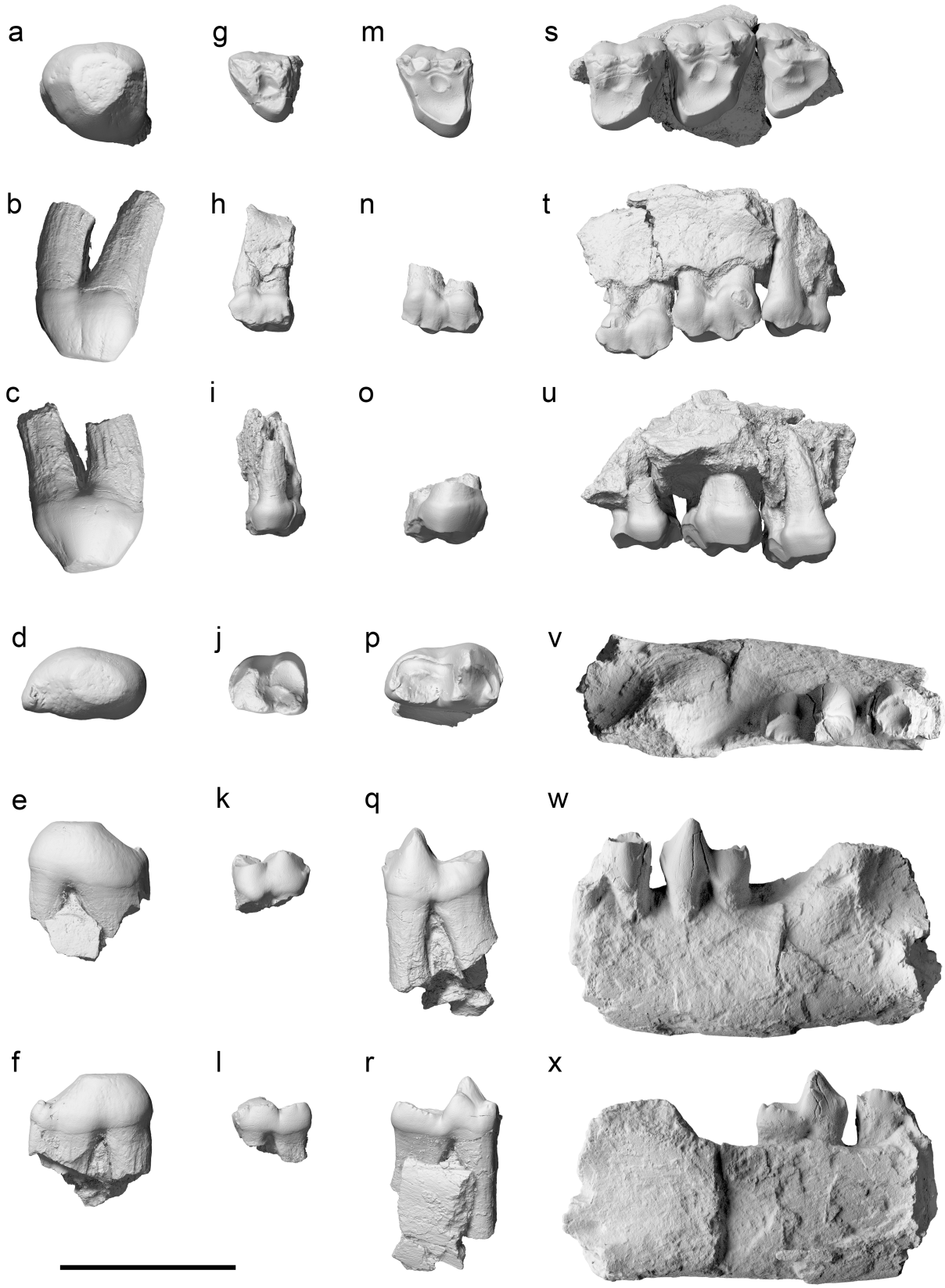
Figure Captions

Fig. 1 New specimens of *Orhaniyeia nauta* from the Uzunçarşıdere Formation, middle Eocene of north-central Turkey. **a-u.** EOU-UCF-14, associated teeth and left maxillary fragment including left P3 in **a.** occlusal; **b.** buccal; and **c.** lingual views; left p3 in **d.** occlusal; **e.** buccal; and **f.** lingual views; right M1 in **g.** occlusal; **h.** buccal; and **i.** lingual views; right m2 in **j.** occlusal; **k.** buccal; and **l.** lingual views; right M3 in **m.** occlusal; **n.** buccal; and **o.** lingual views; left m4 in **p.** occlusal; **q.** buccal; and **r.** lingual views; and left maxillary fragment preserving M2-4 in **s.** occlusal; **t.** buccal; and **u.** lingual views. **v-x.** EOU-UCF-13, left dentary fragment preserving the talonid of m3 and the crown of m4 in **v.** occlusal; **w.** buccal; and **x.** lingual views. Scale bar equals 1 cm

Fig. 2 Comparison of dental features in *Orhaniyeia nauta* (EOU-UCF-14) and the holotype of *Anatoliadelphys maasae* (AÜJM 2002-25). **a.** left P3-M4 (M1 reversed from the right side) of *O. nauta* in occlusal view; **b.** left P3-M4 of *A. maasae* in occlusal view. Note the divergent wear patterns across the toothrow in these taxa. Grayscale gradient reflects degree of occlusal wear at each tooth locus, with lighter colors indicating lighter wear and darker colors indicating heavier wear. **c.** left P3-M4 of *O. nauta* in buccal view; **d.** left P3-M4 of *A. maasae* in buccal view. Note the different degrees of exodaenodonty in these taxa (see white stippling on M3). **e**. left m4 of *O. nauta* in occlusal view; **f.** left m4 of A. maasae in occlusal view. Note the different trigonid morphology in these taxa. **g.** left m4 of *O. nauta* in buccal view; **h.** left m4 of *A. maasae* in buccal view. Note qualitative differences in exodaenodonty. Specimens are scaled to have similar mesiodistal lengths; scale bars equal 1 cm. Images of the holotype of *A. maasae* are adapted from Maga and Beck (2017)

Fig. 3 Strict consensus tree produced by maximum parsimony analysis of our character-taxon matrix (Online Resource 1). Bootstrap values >50% are shown above nodes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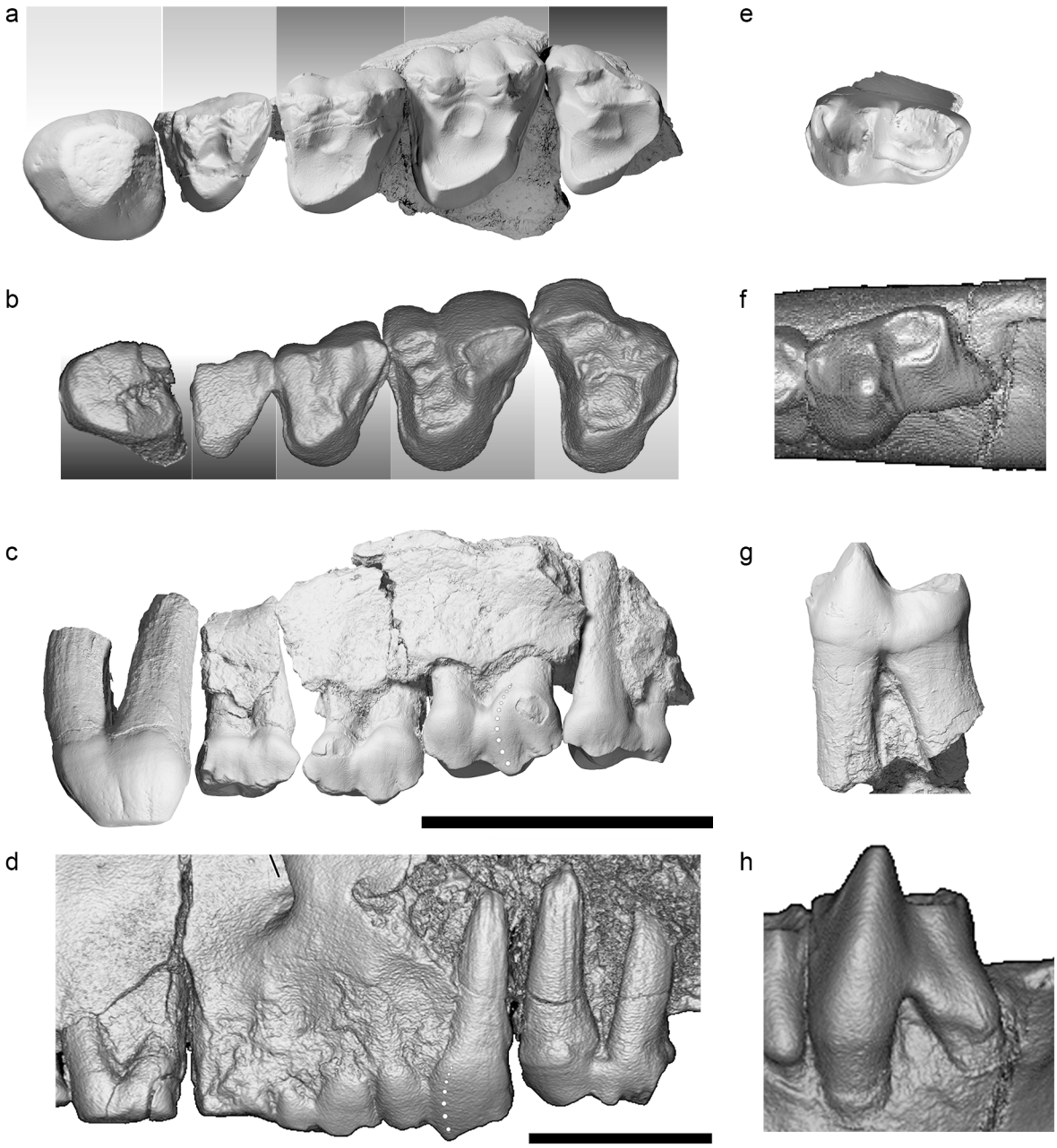
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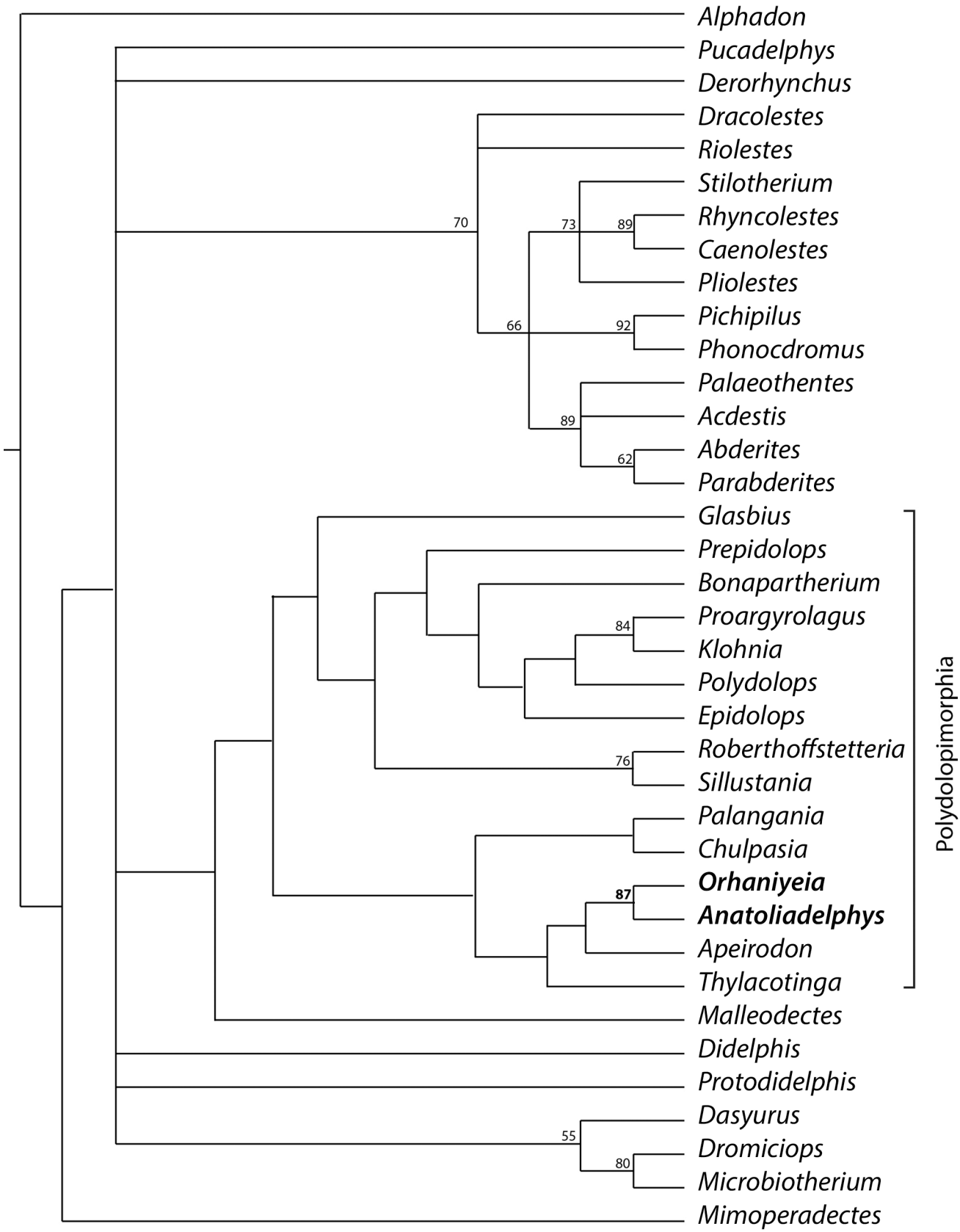
Alphadon
Pucadelphys
Derorhynchus
Dracolestes
Riolestes
Stilotherium
Rhyncolestes
Caenolestes
Pliolestes
Pichipilus
Phonocdromus
Palaeothentes
Acdestis
Abderites
Parabderites
Glasbius
Prepidolops
Bonapartherium
Proargyrolagus
Klohnia
Polydolops
Epidolops
Roberthoffstetteria
Sillustania
Palangania
Chulpasia
Orhaniyeia
Anatoliadelphys
Apeirodon
Thylacotinga
Malleodectes
Didelphis
Protodidelphis
Dasyurus
Dromiciops
Microbiotherium
Mimoperadectes
70
73
89
66
92
89
62
84
76
87
55
80
Polydolopimorphia

Table 1. Metric data (in mm) for newly collected specimens of *Orhaniyeia nauta* and associated morphofunctional dental indices of Zimicz (2014).

Specimen	Tooth locus	L	W	Trigonid L	Talonid L	Talonid W	RGA	RPS	PS	RPL	RBL
EOU-UCF-13	L m4	5.79	3.34	3.10	2.69	2.87	0.90				0.54
EOU-UCF-14	L P3	5.44	5.46								
EOU-UCF-14	R M1	3.35	4.05								
EOU-UCF-14	L M2	4.30	4.70								
EOU-UCF-14	L M3	4.94	5.64								
EOU-UCF-14	R M3	4.89	5.68								
EOU-UCF-14	L M4	4.18	5.24								
EOU-UCF-14	L p3	6.84	4.00					3.60	0.58	1.11	
EOU-UCF-14	R m2	4.62	3.90								
EOU-UCF-14	L m4	6.18	3.76	3.12	3.06	3.35	1.03				0.50
EOU-UCF-4	L m4	5.75	3.06	3.04	2.71	2.54	0.86				0.53
EOU-UCF-4	R m4	5.70	3.26	2.98	2.72	2.59	0.89				0.52
EOU-UCF-5	R m4	6.08	3.38	3.31	2.77	2.80	0.84				0.54

Table 2. Body mass estimates for anatoliadelphyid metatherians based on predictive equations developed by Myers (2001).

Taxon	Metric	Measurement (mm)	Body mass estimate (g)	Source
Anatoliadelphys maasae	TJL	88.2	3370	Maga and Beck (2017)
Anatoliadelphys maasae	LMORL	27.25	3766	This study
Anatoliadelphys maasae	UMORL	24.5	3640	This study
Orhaniyeia nauta	LMORL	20.17	1380	This study
Orhaniyeia nauta	UMORL	16.65	998	This study