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Rapid colonization and diversification of a large-bodied mammalian herbivore clade in an insular context: New embrithopods from the Eocene of Balkanatolia

*Grégoire Métais¹ (corresponding author), email : gregoire.metais@mnhn.fr ORCID 0000-0002-4443-1801

Pauline Coster² ORCID 0000-0003-4015-252X

Mustafa Kaya³ ORCID 0000-0003-2966-5092

Alexis Licht⁴ ORCID 0000-0002-5267-7545

Kristen Miller⁵ ORCID 0000-0002-8300-9590

Faruk Ocakoğlu⁶ ORCID 0000-0002-4619-5865

Kathleen Rust⁵ ORCID 0009-0008-9203-9987

K. Christopher Beard⁵ ORCID 0000-0002-6279-9837

(1) Centre de Recherche en Paléontologie – Paris (CR2P, UMR 7207), MNHN, CNRS, Sorbonne Université, Muséum national d’Histoire naturelle, 57 rue Cuvier, France

(2) Réserve naturelle nationale géologique du Luberon, Parc naturel régional du Luberon, Apt, France <pauline.coster@parcduluberon.fr>

(3) Department of Geological Engineering, Middle East Technical University, Ankara, Turkey <mustafayk@gmail.com>

(4) Aix Marseille University, CNRS, IRD, INRAE, CEREGE, Aix-en-Provence, France
<licht@cerege.fr>

(5) Biodiversity Institute and Department of Ecology and Evolutionary Biology, University of
Kansas, Lawrence, KS, USA chris.beard@ku.edu, k.miller9@ku.edu, k.rust@ku.edu

(6) Department of Geological Engineering, Eskişehir Osmangazi University, Eskişehir,
Turkey <focakoglu@gmail.com>

Abstract

Embrithopoda is an extinct clade of herbivorous placental mammals belonging to the afrotherian subclade Paenungulata. Early in their evolutionary history embrithopods colonized the insular terrane of Balkanatolia, presumably via dispersal across the Tethyan marine barrier that separated Africa from Eurasia during the early Cenozoic. Here we report new embrithopods from the early Eocene locality of Çamili Mezra, Çiçekdağı Basin, central Anatolia which document the early co-occurrence of two sympatric taxa of embrithopods, including *Crivadiatherium sevketseni* sp. nov. and *Crivadiatherium sahini* sp. nov. The genus *Crivadiatherium*, otherwise known only from the late Eocene of Romania, is reported for the first time in Anatolia. *Hypsamasia seni* from the middle Eocene of north-central Anatolia is interpreted as a nomen dubium. Embrithopod specimens previously described as *Palaeoamasia* sp. nov. from the Eocene-Oligocene transition of the Boyabat Basin in northern Anatolia are identified as a new genus and species, *Axainamasia sandersi*. The embrithopod fauna of Çamili Mezra indicates that this clade experienced at least a modest adaptive radiation after successfully colonizing Balkanatolia. The Balkanatolian record of embrithopod

evolution contrasts with the evolutionary history of this clade in its native Africa, where sympatric emrithopod taxa have never been documented.

Keywords: Afrotheria, Eocene, endemism, insularity, mammals, Paenungulata, Turkey

Statements and Declarations

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Introduction

The fossil record of large-bodied mammalian herbivores from island contexts is limited to Neogene (primarily Quaternary) proboscideans and hippopotamid artiodactyls, both of which invariably experienced phyletic dwarfing as part of their adaptation to insular conditions (van der Geer et al. 2013). During the early Paleogene, the former Tethyan island of Balkanatolia was colonized by a different clade of placental herbivores, the extinct Embrithopoda (Sen and Heintz 1979; Maas et al. 1998; Erdal et al. 2016). The Paleogene fossil record of Balkanatolia spans millions of years, enabling a broader picture of the macroevolutionary changes associated with the colonization of an insular terrane by large mammalian herbivores than is generally available in Quaternary island systems. Here, we report new data constraining the initial colonization of Balkanatolia by embrithopods and their early diversification there. These data underscore differences in the macroevolutionary patterns experienced by Balkanatolian embrithopods and large-bodied Quaternary mammalian herbivores, likely reflecting their divergent phylogenetic histories and paleogeographic settings.

Embrithopoda is an extinct clade of placental mammals that includes the iconic, graviportal taxon *Arsinoitherium* (Sanders et al. 2004; Sanders et al. 2010). Embrithopods have long been regarded as members of the afrotherian clade Paenungulata, which also includes Proboscidea, Hyracoidea and Sirenia (Simpson 1945; Court 1990, 1992; Gheerbrant et al. 2005; Seiffert 2007; Tabuce et al. 2007). An African origin for embrithopods is supported by their status as paenungulates, their relatively early appearance in the fossil record of Africa, and the basal phylogenetic position of the Moroccan embrithopod *Stylolophus* with respect to other known taxa (Gheerbrant et al. 2021). Despite the strong likelihood that embrithopods originated in Africa, this clade succeeded in colonizing the insular terrane of Balkanatolia sometime during the early Paleogene (Radulesco et al. 1976;

Sen and Heintz 1979; Radulescu and Sudre 1985; Maas et al. 1998; Erdal et al. 2016; Métais et al. 2018; Licht et al. 2022). Balkanatolian embrithopods persisted until roughly the Eocene-Oligocene boundary (Sanders et al. 2014), and during this interval they experienced at least a modest evolutionary radiation, as evidenced by *Crivadiatherium mackennai* from the Hateg Depression, Romania and a new taxon previously described as *Palaeoamasia* sp. nov. from the Boyabat Basin in north-central Turkey (Sanders et al. 2014).

Here we report new embrithopod material from the early Eocene locality of Çamili Mezra in the southern Çiçekdağı Basin of central Anatolia. Çamili Mezra is geographically close to an older locality known as Arabin Köyü, which yielded a large embrithopod dentary assigned to *Palaeoamasia kansui* by Sen and Heintz (1979). Çamili Mezra documents the co-occurrence of two sympatric taxa of embrithopods in the form of two new species of *Crivadiatherium*. *Crivadiatherium* is otherwise known only from the later Eocene of Romania, so the two new species from Çamili Mezra extend both the geographic and stratigraphic ranges of this genus. The embrithopod fauna of Çamili Mezra places new constraints on the timing of embrithopod colonization of Balkanatolia and the tempo and mode of their diversification on this insular terrane.

The new embrithopod material reported here indicates that this clade experienced a modest adaptive radiation after successfully colonizing Balkanatolia. The Balkanatolian record of embrithopod evolution contrasts with the evolutionary history of this clade in its native Africa, where sympatric taxa of embrithopods have never been documented. In situ diversification of embrithopods may have been facilitated by the endemic and unbalanced character of Balkanatolian biotas, particularly the absence of other large-bodied herbivores like proboscideans, which were diverse and abundant in the early Paleogene of Africa.

Material and methods

Geological setting and origin of the fossil material

In the Arabin Köyü area of the Çiçekdağı syncline (southern part of the Çiçekdağı Basin), the poorly constrained early Paleogene sedimentary sequence rests directly on the Central Anatolian Crystalline Complex (Erdogan et al. 1996; Gülyüz et al. 2012). Locally, the Baraklı Formation is the oldest Paleogene unit, consisting of ~300 m of greenish and brown sandstones and mudstones that are sometimes laminated, poorly cemented conglomerates, and lignite seams that are exploited in open mines. The fossils described here were found in one of these open mines, at a new locality designated as Çamili Mezra (named for a nearby village), from a dark greenish sandstone intercalated with bluish carbonaceous mudstone and coal seams (Fig. 1). The bluish mudstone has produced plant fragments, gastropods and unionid bivalves. This terrestrial unit is capped by beige, yellowish shales and sandstones with interbedded limestones. This uppermost part of the Baraklı Formation is transitional with the overlying Kocaçay Formation, which is composed of ~100 m of massive limestones alternating with thin marl beds. This unit has produced a benthic foraminiferal assemblage correlative with the late Ypresian SB-11–12 Zones (Schweitzer et al. 2007). Consequently, the beds of the Baraklı Formation that have produced vertebrate remains appear to be older than late Ypresian, pending further geochronological calibration of the age of the Baraklı Formation. It is worth noting that no detailed information is available regarding the exact provenance of the large embriothopod dentary assigned to *Palaeomasia kansui* by Sen and Heintz (1979: plate 3), but it was probably found in a laterally equivalent coal seam in the Baraklı Formation, suggesting an early Eocene age for that specimen as well. In Arabin Köyü, the continental red clastics of the Incik Formation rest unconformably on the late early Eocene limestones of the Kocaçay Formation. The age of the base of Incik Formation is still poorly constrained and may vary from place to place. In the northern part of the Çiçekdağı

Basin (Yerköy syncline), Licht et al. (2022) calculated $^{238}\text{U}/^{206}\text{Pb}$ zircon ages on tuffs and magnetostratigraphic correlations suggesting an early Priabonian age for the base of the Incik Formation there.

Abbreviations

EOU- ÇMZ, fossil specimens from the Çamili Mezra site in the Baraklı Formation are deposited at the Eskişehir Osmangazi University (Eskişehir, Turkey); L, maximum mesiodistal length; M, upper molar; m, lower molar; P, upper premolar; p, lower premolar.

Dental terminology, measurements and surface scanning

Terminology for the description of tooth morphology follows Sen and Heintz (1979) and Erdal et al. (2016). All measurements are given with an accuracy of 0.1 millimeters (mm) and were made with the same digital caliper, by the same operator. The fossil material was surface scanned with an EinScan Pro HD 3D scanner, and the 3D pictures were edited with MeshLab.

Systematic Paleontology

Class MAMMALIA Linnaeus, 1758

Infraclass PLACENTALIA Owen, 1837

Supercohort AFROTHERIA Stanhope et al., 1998

Superorder PAENUNGULATA Simpson, 1945

Order EMBRITHOPODA Andrews, 1906

Family PALAEOAMASIDAE Sen and Heintz, 1979

Included genera: *Palaeoamasia* Ozansoy, 1966; *Crivadiatherium* Radulescu, Iliescu and Iliescu, 1976; *Hypsamasia* Maas, Thewissen and Kappelman, 1998; *Axainamasia* gen. nov.

Remarks: *Palaeoamasia* and *Crivadiatherium* are reasonably well-documented and clearly distinct from one another, but *Hypsamasia* is highly problematic because the holotype and only known specimen of the type species, *H. seni*, is extremely fragmentary (Maas et al. 1998: fig. 2). The original diagnosis of *Hypsamasia* reads as follows: “Palaeoamasiid with high-crowned teeth. Protocone and hypocone are distinct and large, not fused into para- and metaloph” (Maas et al. 1998: p. 288). As Maas et al. (1998) acknowledged, retaining distinct protocone and metaconular hypocone that are not fused with the paraloph and metaloph, respectively, is also present in *Palaeoamasia*, so this is not a diagnostic character for *Hypsamasia*. Retention of distinct lingual cusps on the upper molars also occurs in *Stylolophus* and is undoubtedly primitive for embriothopods as a whole. The two most nearly complete teeth preserved in the holotype of *H. seni* are right P2-3, but these tooth loci are not well documented in the assemblage of *Palaeoamasia kansui* from its type locality of Eski Çeltek (Amasya Province, Turkey). Two Eski Çeltek specimens in which one or both of these tooth loci are preserved include ITU-EÇ-8 (Erdal et al. 2016: fig. 3C-D) and MNHN EÇ-4 (Sen and Heintz 1979: plate 1), both of which have smaller P2-3 than in the holotype of *H. seni*. However, without more adequate samples, it is impossible to estimate intraspecific variation in tooth size in either *H. seni* or *P. kansui*. More challenging for interpreting the status of *H. seni* is the fragmentary condition of the more distal cheek teeth in the holotype and only known specimen. None of the upper molar loci documented in the holotype of *H. seni* approaches completeness, and most are represented only by fragments (Fig. 2u). Some are chimeras, including the locus Maas et al. (1998: fig. 2A-B) interpreted as right M1, which consists of an anterior tooth fragment preserving part of the protocone and anterior cingulum

that may well pertain to this tooth locus and a second fragment interpreted as the distobuccal part of M1 that appears instead to be the talonid of a right lower premolar (probably p4, based on the width of the talonid). Likewise, tooth fragments interpreted by Maas et al. (1998: fig. 2C-D) as pertaining to left M3 include an anterolingual fragment preserving the protocone and adjacent areas that probably does pertain to left M3 and a fragment interpreted as representing the distobuccal part of left M3 that almost certainly includes the metacone and metaconular hypocone of right M3. Given the fragmentary condition of the holotype and the problems associated with its interpretation, we view the specimen as nondiagnostic and regard both the genus *Hypsamasia* and the species *Hypsamasia seni* as nomina dubia.

Genus *Crivadiatherium* Radulescu, Iliescu & Iliescu, 1976

Emended diagnosis: Differs from *Palaeoamasia* in having relatively longer and narrower lower premolars and molars, p4 with mesially oriented paralophid and elevated cristid obliqua, lower molars with columnar protoconid and hypoconid that are mesiodistally constricted so that the anterior flanks of the paralophid and cristid obliqua are always concave, lingually open lower molar trigonids, and exceptionally strong postcingulids on m1 and m2. Further differs from *Stylolophus* in its larger size, having higher-crowned and more lophate lower molars and premolars, mesiodistally elongated premolars with larger talonids and a cristid obliqua more lingually expanded on p3-4.

Included species: *Crivadiatherium mackennai* Radulescu, Iliescu and Iliescu 1976, *C. sahini* sp. nov., and *C. sevketseni* sp. nov.

Remarks: Radulescu and Sudre (1985) suggested that the concavity of the anterior wall of both the paralophid and cristid obliqua of the lower molars of *Crivadiatherium* was probably related to the development of the postmetacrista of M1 and the postparacrista of M2

respectively. The postparacrista and postmetacrista are very reduced in *Palaeoamasia kansui*, but they are more conspicuous in *Stylolophus* (Geerbrant et al. 2018, 2021) and the large new species of *Crivadiatherium* from Çamili Mezra described below. Among the material available for *Paleoamasia kansui*, only two specimens preserve a p4, i.e. ITU-EÇ-9, a left dentary fragment with p2-m1 (Erdal et al. 2016: fig. 3H-J), and MNHN-EÇ-5, a right dentary fragment with p4-m1 (Fig. 3d-f). The premolars of the former specimen are heavily worn, preventing detailed comparisons with those of *Crivadiatherium* from Çamili Mezra. The p4 preserved in MNHN-EÇ-5 provides more useful morphological information, although the distal part of its cristid obliqua is broken, making it difficult to estimate the true height of the p4 talonid. However, the breakage of the cristid obliqua well below the apex of the protoconid indicates that this crest was not as elevated as in *Crivadiatherium*, and the talonid is mesiodistally much shorter in *P. kansui*.

The holotype of *Crivadiatherium mackennai* consists of an association of three cheek teeth, including a high-crowned p4, moderately worn m1 (Fig. 4), and the trigonid of another molar that was identified by Iliescu and Iliescu (1976) as m3 but which is considered here as m2 based on its size. Radulescu and Sudre (1985) designated isolated lower m2 and m3 as the holotype of *C. iliescui*, which is otherwise known by isolated lower incisors and premolars. We concur with Sen (2013) that Radulescu and Sudre (1985) misinterpreted the premolar loci of *C. iliescui*, such that the tooth they interpreted as p3 is actually p4, their p2 is actually p3, and their p1 is actually p2. Moreover, the size of p4 in *C. iliescui* is comparable to that of *C. mackennai*, and they are also morphologically similar, differing only by the greater degree of wear on the p4 of *C. iliescui*. Likewise, the m1 referred to *C. mackennai* matches the expected size of m1 in *C. iliescui* (this tooth is lacking in the type series of the latter species), and the morphology of m1 in *C. mackennai* is consistent with that of m2-3 in *C. iliescui* (Fig. 4). We

consider *C. iliescui* as a junior synonym of *C. mackennai*, which should be retained as the only valid species of *Crivadiatherium* known from Romania.

Crivadiatherium sahini sp. nov.

Holotype: EOU-ÇMZ-6, right m3. **Paratypes:** EOU-ÇMZ-1, left upper cheek teeth of a single individual including P4, fragmentary M1, M2 and anterior part of M3; EOU-ÇMZ-4, left p3; EOU-ÇMZ-5, partial left m2 (trigonid broken).

Etymology: For Mr. Davut Şahin, in recognition of his dedication to field paleontology in the Çiçekdağı Basin of Turkey.

Diagnosis: Differs from *C. mackennai* in lacking buccal and lingual cingulids on p3 and having lower molar hypolophids more transversely oriented. Differs from *C. sevketsemi* in being much larger (Table 1) and having more arcuate cristid obliqua on p3, yielding shallower hyloflexid and broader talonid basin.

Horizon and locality: Lower part of the Baraklı Formation, ~1 km northeast of Çamili Mezra, Çiçekdağı Basin, Kırşehir Province, Turkey.

Description: The anatomical documentation of *C. sahini* is currently uneven. Its lower dentition is represented by isolated teeth and tooth fragments, while its upper dentition is represented by a specimen consisting of four associated cheek teeth and/or tooth fragments, the latter of which are the first upper cheek teeth to be described for *Crivadiatherium*.

Lower dentition. EOU-ÇMZ-4 (Fig. 2S-T) can be identified as p3 based on comparisons with serially associated lower dentitions of the small new species of *Crivadiatherium* described below. In contrast to p2 in the latter taxon, EOU-ÇMZ-4 bears a

more nearly molariform trigonid that includes a distinct metaconid and a stronger paraconid that is more lingual in position alongside a fully basined talonid with a small entoconid. In contrast to p4 in the latter taxon, EOU-ÇMZ-4 bears a more elongated and lingually open trigonid on which the metaconid is substantially smaller than the protoconid and positioned more distally than the latter cusp, so that the protolophid is obliquely oriented with respect to the mesiodistal axis of the tooth. EOU-ÇMZ-4 is relatively high-crowned, particularly with respect to its elevated cristid obliqua, which arcs mesiolingually to join the hypoconid with the protolophid near its junction with the metaconid. A relatively continuous buccal shearing surface is formed by the combination of the cristid obliqua and the fused trigonid crests, including the protolophid and paralophid. The buccal side of the tooth is moderately higher-crowned than the lingual side, owing to basal distensions of enamel beneath the trigonid and talonid. The unilaterally hypsodont construction of p3 can be appreciated in either mesial or distal view, where the basal distensions of enamel are readily apparent. A small, neomorphic cuspule occurs on the lingual side of the trigonid, in the open space between paraconid and metaconid. The hypoflexid is relatively shallow, and the talonid is broad and open lingually between the entoconid and the postvallid. There is no development of buccal or lingual cingulids.

EOU-ÇMZ-5 is interpreted as a fragmentary left m2 because of its large size. The trigonid is broken, but the talonid is reasonably well preserved (Fig. 2n-o). The postcingulid is very strong, and its lingual part rises toward the hypolophid but fails to join it. The hypolophid is high and transversely oriented. The cristid obliqua appears to arise from the hypolophid somewhat lingual to the hypoconid, making its pathway appear less oblique than on m2 in the small new species of *Crivadiatherium* described below. However, moderate wear may have obscured the unworn trajectory of the cristid obliqua.

EOU-ÇMZ-6 (the holotype) is a moderately worn right m3 (Fig. 2p-r). As preserved, the protoconid appears to be lower than the metaconid, but most or all of this disparity may be caused by wear along the protolophid. There is virtually no development of a mesiobuccal cingulid. As on EOU-ÇMZ-5, the hypolophid is remarkably transverse and the cristid obliqua appears to originate along the hypolophid, lingual to the hypoconid. A large, distally expansive hypoconulid bears a loop-like crest along its lingual half, while the buccal side of the hypoconulid slopes evenly toward the base of the hypoconid.

Upper dentition. The upper dentition is represented by a single specimen, EOU-ÇMZ-1, which comprises an associated series of left cheek teeth including complete P4 and M2 and broken M1 and M3. P4 (Fig. 2i-m) is rectangular in occlusal outline. The crown is asymmetrical in anterior or posterior view, because the buccal side of the crown is much taller (28.0 mm) than its lingual side (14.4 mm). Primarily, the increased height of the buccal side of P4 reflects dorsal or rootward extension of enamel buccally, while the anterior, lingual, and posterior margins of the crown lack similar basal extensions of enamel. Accordingly, P4 could be characterized as exodaenodont, but there is no inflation associated with the basal distension of enamel buccally, as frequently occurs on exodaenodont tooth loci. Rather, the buccal surface of P4 is relatively flat, with minor vertically oriented undulations occurring on either side of the paracone. In occlusal view, the buccal side of the crown bears a well-developed parastyle, a large and relatively cusped paracone, and a buccolingually compressed metacone that may be confluent with a metastyle. External crests connect the paracone with both the parastyle and the metacone, but the ectoloph is not linear because the pre- and postparacristae form an obtuse angle where they meet at the summit of the paracone. The lingual side of P4 is dominated by a centrally placed protocone. Arcuate pre- and postprotocristae link the protocone with more buccal structures. The shorter preprotocrista runs buccally from the protocone to merge with the base of the paracone, while the longer postprotocrista defines the

posterior border of a deep trigon basin before merging with the base of the metacone/metastyle. An inflated area on the postprotocrista may represent a small metaconule. There is no lingual cingulum, but the anterior cingulum is elevated and crestiform, running continuously from the anterior base of the protocone to the lingual base of the parastyle. A deep valley runs transversely, parallel to the anterior cingulum, separating it from the preprotocrista. A minor fold of enamel invades this valley from the anterolingual face of the paracone.

The upper molars (Fig. 2a-h) appear to increase in size posteriorly, and there is a clear wear gradient from M1 (heavily worn) to M2 (moderately worn) to M3 (little if any wear). The occlusal morphology of all three molars appears to be similar apart from wear, so only M2 is described in detail here. M1 is broken such that it is missing the parastyle, paraloph, paracone, and the adjacent part of the anterior cingulum. Its occlusal dimensions can only be estimated (Table 1). M2 is complete, although a minor transverse fracture runs from the deepest part of the ectoflexus buccally to the lingual side of the crown posterior to the protocone. The crown is basically rectangular in occlusal view, being longer than wide. The buccal side of the crown is dominated by two large, subvertically oriented ribs that are each canted anteriorly and which terminate at the parastyle and mesostyle, respectively. Between these ribs is the deep ectoflexus mentioned previously. The height of these buccal ribs (25.1 mm from the buccal base of the crown to the apex of the mesostylar rib) far exceeds that of the tallest structures on the lingual side of the crown (13.6 mm from the lingual base of the crown to the apex of the metaconular hypocone), making the entire crown unilaterally hypsodont. Well-developed paraloph (or preparacrista) and metaloph (or premetacrista) run diagonally across the occlusal surface of the crown, from parastyle to paracone and from mesostyle to metacone, respectively. Paracone and metacone are nearly connate with, but clearly separated from, the protocone and metaconular hypocone, respectively. Remnants of

the postparacrista and postmetacrista remain remarkably salient on M2, reflecting the ancestral embrithopod pattern of a more nearly dilambdodont ectoloph found in *Stylolophus*. Buccally, the spaces between the parastylar rib and the postparacrista and the mesostylar rib and the postmetacrista are deeply concave, reflecting the prominence of both the ribs and crests. Lingually, the protocone forms a blunt, anteroposteriorly elongated ridge that originates immediately lingual to the paracone. A low, blunt ridge that is topographically appropriate to be homologous with the postprotocrista joins the protocone with a mound-like structure in the middle of the trigon. The latter is apparently a neomorphic structure, based on character transformations indicating that the distolingual cusp or “hypocone” of embrithopod upper molars is actually a modified metaconule (Gheerbrant et al. 2016). The metaconular hypocone mimics the protocone in being low, blunt, and ridge-like. Posteriorly, the hypocone merges seamlessly with the posterior cingulum, which is raised and crestiform. The postmetacrista and posterior cingulum unite near the midline of the posterior margin of the crown, defining an excavated area between the two ridges. The anterior cingulum is broad and complete, running from the anterior base of the protocone to the lingual margin of the parastyle. Near its midline, a noticeable swelling of enamel forms a blunt cusp. M3 is broken, and only its anterior half remains.

Postcrania. A fragmentary proximal ulna EOU-ÇMZ-12 (Fig. 5a-c) is about 50% larger than EOU-ÇMZ-11 (Fig. 5d-g), which is attributed to the smaller species of *Crivadiatherium* described below, and except for its greater stockiness, is overall similar in morphology. The anterior part of the humero-ulnar joint is badly damaged so that it is impossible to estimate the relative sizes of the medial and lateral articular facets for the humerus. Likewise, no proximal notch for the radius is distinguishable, possibly because of the breakage. The most salient feature is the great development of the olecranon process which is oriented posteriorly with

respect to the long axis of the shaft. The anconeal process is laterally offset with respect to the proximo-distal axis of the diaphysis, and it overhangs the lateral articular lobe.

The distal part of a right femur suffers from postmortem deformation (Fig. 5h-j); the medial epicondyle is more prominent than the lateral epicondyle, which is partly damaged. The medial articular condyle is more voluminous than the lateral condyle, and is slightly more expanded posteriorly. The two articular condyles are separated posteriorly by a deep intercondylar notch which extends anteriorly to become continuous with the patellar trochlea which seems to extend ventrally.

Remarks: *C. sahini* from Çamili Mezra is best documented by upper cheek teeth, while the smaller species of *Crivadiatherium* described below from the same locality is represented primarily by two partial dentaries and two heavily worn upper molars. The virtual lack of correspondence in anatomical representation hinders direct comparisons between the two species, but the large difference in size makes it apparent that two taxa are represented (Table 2).

Assessing the generic affinities of *C. sahini* has not been straightforward. It can be readily distinguished from *Palaeoamasia* by its unilaterally hypsodont upper cheek teeth and the robust and anteriorly canted buccal ribs and relatively well-defined postparacrista and postmetacrista on its upper molars. EOU-ÇMZ-1 also differs from specimens of *Palaeoamasia kansui* (e.g., MNHN EÇ-4) from its type locality of Eski Çeltek in being 21-39% larger in linear measurements of P4 and M2. The only previously described embrithopod with vaguely comparable upper cheek tooth morphology is *Hypsamasia*. However, as noted previously, the holotype and only known specimen of the type species of *Hypsamasia* is highly fragmentary and plausibly nondiagnostic. Moreover, P4 in *C. sahini* clearly differs from P2-3 in the holotype of *H. seni* in showing very strong development of unilateral (buccal) hypsodonty, which is not present in P2-3 of *H. seni*. Comparing P4 in *C. sahini*

directly with the lingual fragment of P4 preserved in the holotype of *H. seni* reveals additional differences, including the presence of strong lingual and distolingual cingula on P4 in *H. seni* that are completely absent in *C. sahini*. Although we are unable to compare the highly specialized unilateral hypsodonty of P4 in *C. sahini* directly with P4 in the holotype of *H. seni* (owing to the fragmentary condition of the latter specimen), it would be extremely surprising if *H. seni* possessed a similarly hypsodont P4, based on the less specialized condition characterizing P2-3 of this specimen. The upper dentition of the type species of *Crivadiatherium* (Romanian *C. mackennai*) remains unknown, and it is possible that future discoveries will require *C. sahini* to be assigned to a genus other than *Crivadiatherium*. Here, we conservatively assign *C. sahini* to *Crivadiatherium*, because it cannot be placed in any other palaeoamasid genus. The retention of relatively well-developed postparacrista and postmetacrista on the upper molars of *C. sahini* conforms with the prediction made by Radulescu and Sudre (1985) that the (then unknown) upper molars of *Crivadiatherium* would bear these structures, based on the concavity of the paralophid and cristid obliqua on lower molars of *C. mackennai*.

Postcrania have not previously been reported for palaeoamasids, thus comparisons are necessarily limited to *Arsinoitherium*, the only embrithopod for which postcranial morphology is known. The postcranial anatomy (and particularly the appendicular skeleton) of *Arsinoitherium* display graviportal adaptations that limit comparisons with smaller palaeoamasids (Court 1993, Sanders et al. 2010). The ulna is the dominant element of the zeugopodium in *Arsinoitherium* (Court 1993) with a massive olecranon process arched posteriorly, forming almost a right angle with the shaft, and the two articular facets for the humerus are transversely expanded. Moreover, *Arsinoitherium* retains a proximal facet for the radius which is not ascertained on the ulnae from Çamili Mezra. The ulna EOU-ÇMZ-12, attributed here to *C. sahini* owing to its large size, is much more gracile than that of

Arsinoitherium, and it does not show the graviportal features found in the latter taxon including the orientation and massiveness of the olecranon process, and the transverse development of the articular facets for the humerus. The size of the distal femur is consistent with the size of the proximal ulna EOU-ÇMZ-12, and it also appears to belong to *C. sahini*.

Crivadiatherium sevketseni sp. nov.

Holotype: EOU-ÇMZ-2 (Fig. 7a-c), fragmentary right dentary with p2-m3 (p2 was recovered in association with the dentary preserving p3-m3, but the anterior part of the dentary was poorly preserved).

Paratypes: EOU-ÇMZ-3 (Fig. 7d-f), fragmentary right dentary preserving p2-3 and associated p4, m1, m2 and m3; EOU-ÇMZ-7, left m2; EOU-ÇMZ-8, right m3; EOU-ÇMZ-9, left M2 (Fig. 7i); and EOU-ÇMZ-10, left M1 (Fig. 7g-h).

Etymology: For Sevket Sen, in recognition of his outstanding contributions to vertebrate paleontology in Turkey, and particularly his early recognition of the ordinal affinities of *Palaeoamasia*.

Diagnosis: Differs from *C. mackennai* in being significantly smaller (about 30%), having p2-4 without buccal and lingual cingulids, and p4 less hypsodont.

Horizon and locality: Lower part of the Baraklı Formation, ~1 km northeast of Çamili Mezra, Çiçekdağı Basin, Kırşehir Province, Turkey.

Description: Dentary. The holotype dentary preserves serially associated p2-m3 of a young adult, based on the light wear on its molars and the unerupted status of the hypoconulid lobe of m3. There are no diastemata among the serially associated tooth loci preserved in this

specimen, and the symphysis reaches the anterior root of p3. The ascending ramus of the dentary is damaged and the processes are not preserved but the condyle must have been located well above the dental row. On the ventro-lingual border of the dentary, there is a circular hole of about 8 mm diameter that might correspond to the bite mark of a predator or a scavenger.

Lower dentition. None of the lower premolars of *C. sevketzeni* bear buccal or lingual cingulids, in contrast to the condition in the Romanian material of *C. mackennai* (Fig. 4). Neither of the currently available specimens preserves the dentary anterior to p2, and the p1 (if present) is not preserved. The p2 is high-crowned and displays only mesiodistally oriented cristids that link three aligned cusps in occlusal view. From front to back, these include a tiny subconical paraconid, a prominent protoconid that is slightly mesially placed and canted anteriorly in lateral view, and a hypoconid that is more or less merged with the adjacent cristid obliqua. The hypoconid bears a marked interstitial wear facet on its posterior face. The p3 displays a trigonid mesiodistally longer than the talonid, oblique paralophid and cristid obliqua are subparallel, and the trigonid and talonid are widely open lingually. The short protolophid connects the protoconid to the metaconid whereas the paralophid extends mesially to connect a small paraconid; the cristid obliqua is relatively high and connects the hypoconid to the metaconid. The hypolophid is transverse and joins a small and low entoconid. The hypoflexid is deep and oblique in labial view. It arises from the distal part of the crown, just above the distal root, and it reaches the distal side of the metaconid. The depth of the hypoflexid increases from p2 to p4, contributing to a W-shape in occlusal view formed by the junction of paralophid, protolophid, cristid obliqua and hypolophid. This W-shaped occlusal pattern becomes more accentuated from p2 to p4. Wear facets are labio-distally ventrally oriented on premolars. The p4 is the most nearly molariform premolar, foreshadowing the morphology of the molars. The protolophid extends transversely, and the

paralophid is oriented mesially and does not reach the mesiolingual corner of the tooth, leaving a wider and deeper fossettid as compared to p2-3. The talonid is semi-circular, wide and deep. The mesiolabial side of the protoconid is faintly depressed. The talonid is longer than the trigonid in occlusal view. The labial wall of the protoconid is more convex and the hypoflexid much deeper than they are on the p3. Unlike the condition in p3, the cristid obliqua of p4 is less lingually oriented, at least on unworn teeth.

The lower molars are relatively high-crowned and rectangular in occlusal outline, the trigonid is mesiodistally shorter than the talonid, and the hypoflexid situated between the anterior and posterior roots is large and deep because of the columnar protoconid and hypoconid, which are mesiodistally constricted. Protoconid and hypoconid are slightly more mesial than the metaconid and entoconid, respectively. The paralophid is low and does not reach the mesial border of the metaconid, leaving the trigonid widely open lingually. The mesial wall of the paralophid is slightly concave, and the paraconid is low and reduced. A restricted cingulid occurs on the mesiolabial side of the lower molars, extending from below the mesial face of the protoconid to roughly the midpoint of the paralophid. The protolophid is high and bears a strong wear facet. At early wear stages, the labial cuspids are lower than the lingual cuspids because they are more heavily worn, but all cuspids become equally worn and of similar height at later stages of wear, exemplified by the condition of m1 in EOU-ÇMZ-3. The cristid obliqua is labially concave and is more lingual than it is on p4. The hypolophid is as high as the protolophid on unworn teeth. There is a very strong postcingulid on m1-2, which forms a shelf that is higher lingually than buccally. The extensive postcingulid on m1-2 was functionally significant, as attested by the prominent wear facet that develops on this structure with moderate to advanced stages of wear. The m3 displays a loop-like hypoconulid that is connected by its labial arm to the lingual base of the posterior wall of the talonid.

Upper dentition. Two isolated left upper molars are attributed to *C. sevketse*ni, but both are heavily worn. Based on differences in size, EOU-ÇMZ-10 is identified as M1, while EOU-ÇMZ-9 is identified as M2. Few details of occlusal morphology can be interpreted in these heavily worn molars, but both appear to show less trenchant development of the postmetacrista and less excavation of the area between the metastylar rib and the postmetacrista than in *C. sahini*.

Postcrania. Of the two palaeoamasid ulnae reported here, EOU-ÇMZ-11 (Fig. 5d-g) is the better preserved although its distal epiphysis and the proximal end of its olecranon are missing. The shaft is compressed medio-laterally and its proximal part is sub-triangular in section, its posterior border is concave in lateral view, and the diaphysis becomes slender distally. The olecranon is prominent, transversely compressed, and posteriorly oriented forming an acute angle of ~30° with the shaft. The medial articular facet for the humerus is oval in outline (the smaller diameter is medio-lateral) while the lateral facet for the humerus is lower than the medial facet and it is smaller and subcircular in outline. As a result, the coronoid process of the medial articular facet is much more salient anteriorly than the coronoid process of the lateral articular facet which is posteriorly situated. The two articular facets are separated by a ridge that appears to limit the lateral component of the humerus-ulna articulation, thus suggesting modest cursorial capacity like a pig. The anconeal process is laterally offset with respect to the proximo-distal axis of the diaphysis, and it overhangs the lateral articular lobe. Between and below the two facets for the humerus extends a deep notch along the shaft which receives the proximal head of the radius (Fig. 5d-e) which participated the lateral support of the humerus.

Comparisons: The most striking features of *C. sevketse*ni include the long and narrow occlusal outlines of its lower premolars and molars; strong postcingulids on m1-2, which are oblique in posterior view; the columnar protoconid and hypoconid on m1-3, which are

mesiodistally constricted; the lingually open lower molar trigonids; and the slight anterior concavity of the paralophid and cristid obliqua on the lower molars. All these characters distinguish *C. sevketseni* from specimens of *Palaeoamasia kansui* but are consistent with *Crivadiatherium mackennai*, which differs from *C. sevketseni* in being significantly larger, having lingual cingulids on lower premolars, and having more hypsodont p4. The proximal ulna EOU-ÇMZ-11 is somewhat similar to that of the pantodont *Coryphodon eocaenus*, although in the latter the olecranon process does not form an angle with the diaphysis, which is also not posteriorly concave as it is in EOU-ÇMZ-11. Among embrithopods, comparisons are limited to *Arsinoitherium*, which is highly derived postcranially because of its graviportal adaptations. Pending additional fossil data, we allocate EOU-ÇMZ-11 to the small species *C. sevketseni*, and the overall morphology of this ulna suggests moderate cursorial capability, perhaps comparable to a pygmy hippo.

Remarks: This report marks the first occurrence of *Crivadiatherium* in Turkey, and it extends the stratigraphic range of the genus into the early Eocene. As documented here, two species of *Crivadiatherium* co-occur at Çamili Mezra, marking the first example of sympatric embrithopods in the fossil record. A third Balkanatolian embrithopod, *Palaeoamasia kansui*, is known from Eski Çeltek in the Suluova Basin, ~200 km northeast of Çamili Mezra.

Achieving tighter geochronological and/or biostratigraphic constraints on the ages of Çamili Mezra and Eski Çeltek warrants further work, but available evidence suggests that these sites are close in age. If so, three palaeoamasid taxa would have coexisted during the early Eocene of Turkey, reflecting an insular radiation of embrithopods on the Balkanatolian terrane. Such unexpectedly high diversity among a dentally specialized clade of large, herbivorous mammals raises questions about niche partitioning and speciation in this insular context. While significant differences in dental morphology may have accommodated certain aspects

of niche partitioning, ecological segregation may also have been achieved through modifications of the postcranial skeleton and locomotor mode.

Axainamasia sandersi, gen. et sp. nov.

Holotype: BOY-2, right maxilla fragment preserving M2-M3.

Etymology: Generic name derives from *axaina* (indigo), a Scythian term describing the Black Sea, and suffix *-amasia*, referring to the modern city of Amasya, Turkey, located near the type locality for *Palaeoamasia kansui*. Species name recognizes the important contributions of William J. Sanders to our knowledge of embrithopod evolution and systematics.

Diagnosis: Upper molar occlusal proportions more transverse (mesiodistally shorter and buccolingually broader) than those of *Palaeoamasia* or *Crivadiatherium*, with paraloph and metaloph approximating a buccolingual orientation, as opposed to the more oblique orientation of these lophs in other palaeoamasids. Postparacrista and postmetacrista of upper molars highly vestigial, in contrast to the stronger expression of these crests on upper molars of *Stylolophus*. Postmetacrista of upper molars weaker than those of *Palaeoamasia* and (especially) *Crivadiatherium*. Upper molars smaller, more brachyodont, and retaining distinct protocone and metaconular hypocone, in contrast to those of *Namatherium* and *Arsinoitherium*.

Horizon and locality: Upper part of Cemalletin Formation, latest Eocene or earliest Oligocene, ~1.5 km northeast of Cemalletin köy, Boyabat Basin, Sinop Province, Turkey (see Sanders et al. 2014: figs. 2-3).

Description and comparisons: The holotype of *Axainamasia sandersi* was described in detail by Sanders et al. (2014), and this specimen is only briefly redescribed here. BOY-2 is a right maxilla fragment preserving the crowns of M2 and M3 (Fig. 7a-b), the latter of which is slightly damaged so that its distolingual cusp (metaconular hypocone) is missing. The occlusal proportions of M2 are highly distinctive because its buccolingual width (30.0 mm) is much greater than its mesiodistal length (21.9 mm). This contrasts with M2 proportions in other palaeoamasids, in which M2 length typically exceeds M2 width. For example, in *Palaeoamasia kansui* (MNHN EÇ-4), M2 length measures 31.6 mm, while M2 width is 28.9 mm. In *Crivadiatherium sahini* (EOU-ÇMZ-1), M2 length is 43.2 mm, while M2 width is 40.7 mm. In *Crivadiatherium sevketseni* (EOU-ÇMZ-9), M2 length is 28.8 mm, while M2 width is 28.5 mm. Associated with its modified occlusal proportions, major cusps and crests on M2 have been rearranged with respect to corresponding structures on M2 in *Palaeoamasia kansui*. Specifically, parastyle and protocone occur opposite one another, being aligned transversely with respect to the mesiodistal axis of the tooth. As a result, the paraloph (which is homologous with the preparacrista of less derived placental upper molars) is oriented buccolingually. Likewise, the mesostyle and metaconular hypocone are aligned more-or-less transversely, yielding a buccolingual orientation for the metaloph (which is homologous with the premetacrista of less derived placental upper molars). In association with the transverse orientation of the M2 crown, parastyle and mesostyle are extended buccally, yielding a mesiodistally short but deep ectoflexus near the central buccal margin of the crown. The postparacrista is relatively well-developed for an embrithopod, but the postmetacrista of M2 is extremely faint or vestigial. M3 shares similarly transverse occlusal proportions with M2 (mesiodistal length, 25.8 mm; buccolingual width, >30.0 mm). The same measurements in MNHN EÇ-4 are length, 34.6 mm; width 31.6 mm. Parastyle and mesostyle are buccally extended, thereby producing a short, deep ectoflexus on the buccal margin of the crown

between the latter structures. Postparacrista and postmetacrista are virtually imperceptible. Paraloph and metaloph are relatively transversely oriented.

Upper molars of *Palaeoamasia kansui* and *Crivadiatherium sahini* differ from those of *Axainamasia sandersi* in being longer and narrower in occlusal proportions, with parastyle and mesostyle clearly situated farther mesially than protocone and metaconular hypocone, respectively. As a result, protoloph and metaloph are more obliquely oriented, as opposed to transverse, in *Palaeoamasia* and *Crivadiatherium* than in *Axainamasia*. In upper molars of *Palaeoamasia* and *Crivadiatherium*, parastyle and mesostyle do not project as strongly buccally as in *Axainamasia* (Fig. 7). The ectoflexus of M2-M3 is accordingly broader and shallower in *Palaeoamasia* and *Crivadiatherium* than in *Axainamasia*. Finally, the postmetacrista on M2-M3 is extremely reduced in *Axainamasia*, while this structure remains trenchant on M2 of *Crivadiatherium sahini* and is faint but clearly discernible on upper molars of *Palaeoamasia*. In general, the upper molars of *Axainamasia* closely approximate a bilophodont condition, within the stringent constraints imposed by basic embriothopod tooth structure, whereby paracone and metacone have shifted strongly lingually to become approximated with the protocone and metaconular hypocone, respectively (Court, 1992).

Remarks: BOY-2 was originally described by Sanders et al. (2014), who recognized its morphological distinctiveness with respect to *Palaeoamasia kansui* by referring to it as “*Palaeoamasia* sp. nov.” Parenthetically, Sanders et al. (2014) mistakenly reported that the upper molars preserved in BOY-2 overlap in size with the sample of *Palaeoamasia kansui* from Eski Çeltek near Amasya (the type locality for *Palaeoamasia kansui*). In fact, upper molars of BOY-2 range between 23-44% shorter (mesiodistally) than their counterparts in *Palaeoamasia kansui*, although their upper molars are comparable in terms of buccolingual width. Given its small size, unique occlusal proportions, and the novel position of major cusps and crests on its upper molars, we do not hesitate to erect a new genus and species for it here.

The fundamental embrithopod molar pattern involved shifting the upper molar paracone and metacone strongly lingually so that they approximate the protocone and metaconular hypocone, while at the same time enhancing the size and functional importance of the parastyle and mesostyle, so that they assume the role of the main buccal cusps (Court, 1992). This dramatic reorganization of molar structure canalized subsequent dental evolution in embrithopods, limiting the range of additional transformations that might occur within this clade. Essentially, given a molar bauplan like that of *Stylolophus*, embrithopods can become larger or smaller, more or less hypsodont (or unilaterally hypsodont) and more or less bilophodont, with little additional latitude in terms of potential morphospace to explore. Given these constraints, the upper molar morphology of *Axainamasia* must be interpreted as highly autapomorphous, justifying erection of the new genus.

Sanders et al. (2014) indicate that the type specimen (BOY-2) was found in a fluvial paleochannel in the upper part of the Cemalletin Formation. These paleochannels form the lowest part of a normal-regressive highstand systems tract that directly overlies a transgressive systems tract yielding calcareous nannoplankton of the biozones NP 19-20/21. This occurrence of *Axainamasia sandersi* in transitional Eocene-Oligocene deposits of the Boyabat Basin constitutes the youngest occurrence of a palaeoamasid in Balkanatolia. In the Çiçekdağı Basin, Licht et al. (2022) demonstrated that by the early Priabonian, typically Asian mammal taxa such as brontotheriids and hyracodontids were present in Balkanatolia while Balkanatolian endemic taxa (such as palaeoamasids) remain unknown there. At this stage, we cannot rule out the possibility that Balkanatolian palaeoamasids cohabitated with Asiatic newcomers during the Eocene-Oligocene transition, but current data suggest that palaeoamasids went extinct during the early Oligocene (if not earlier) since they have never been recovered from the well-sampled middle and late Oligocene faunas of the Çankiri Basin (Antoine et al. 2008; Métais et al. 2016; Van de Weerd et al. 2021). Alternatively, the

Boyabat area may have been geographically isolated from the main Balkanatolian landmass, enabling relict populations of Balkanatolian taxa to persist beyond their extirpation on the Balkanatolian mainland, probably during the late middle or late Eocene (Licht et al. 2022). Further paleontological data are required to test these different hypotheses.

Discussion

The large-bodied mammal fauna of Balkanatolia during the middle Eocene

Crivadiatherium and *Palaeoamasia* are medium-sized to large herbivorous mammals restricted to Turkey and Romania, but two (and perhaps three) other medium-sized to large perissodactyls have been reported from areas that are structurally in Balkanatolia (Licht et al. 2022). If these perissodactyls made their way to Balkanatolia most probably during the middle Eocene, they apparently never diversified there.

Dental remains referred to the basal ceratomorph *Hyrachyus* sp., cf. *H. stehlini* have been reported from the middle Eocene shallow marine marls and limestone of the Csernye Formation in the Gerecse Hills, Hungary (Kocsis 2002). This fossil was found in marine beds that yielded a nannoplankton assemblage corresponding to the NP16 zone (Kocsis 2002), which correlates with the second half of the Lutetian and early Bartonian (Martini 1970). Additional sampling of the horizon yielding *Hyrachyus* would be useful to establish its age according to the more precise calcareous nannofossil CN zonation (Agnini et al. 2014), in which NP16 is subdivided into four zones of approximately 1.5 Ma each. *Hyrachyus* is a medium-sized ceratomorph perissodactyl that has a wide distribution across Laurasia during the early and middle Eocene (Bai et al. 2017). Additionally, Tissier et al. (2018) suggested that remains of the amynodontid *Amyndontopsis* aff. *bodei* may possibly come from the

Dorog Coal Formation in the vicinity of Budapest, which is dated to biozone NP16 (Upper Lutetian - Bartonian), although one cannot rule out that these fossils actually come from nearby Priabonian coals of the Kosd Formation (Licht et al. 2022).

Métais and Sen (2017) reported tarsal bones referred to *Palaeotherium* sp., cf. *P. magnum* from late Lutetian or Bartonian strata of the Thrace Basin in easternmost Greece. *P. magnum* is the largest species of *Palaeotherium* and approximates the size of a large tapir. It is worth noting that the palaeotheriid *Plagiolophus* sp., cf. *P. minor* has been reported from the middle/late Eocene of Tscherno More in Bulgaria (Nikolov and Heissig 1985), suggesting at least intermittent faunal exchanges between western Europe and Balkanatolia during the Eocene-Oligocene remodeling of fauna in Europe which culminates at the Grande Coupure (Stehlin 1909; Métais et al. 2023). Palaeotheriids first appeared in Western Europe at MP13 (middle Eocene; see Franzen 2003), and they experienced a significant adaptive radiation there during the middle and late Eocene until their extinction during the early Oligocene (MP22). While long thought to be restricted to Western Europe, stem palaeotheriids are now known from the middle Eocene of China (Bai 2017).

The occurrence of *Hyrachyus* and *Palaeotherium* suggests that peripheral areas of Balkanatolia were at least intermittently connected to Western Europe and mainland Asia during the middle Eocene. This is consistent with the sudden arrival of several mammal taxa in Europe at MP13 (Franzen 2003) and MP14, probably from eastern and Central Asia. Recently, Bai et al. (2023) reported remains of tapirulid artiodactyls from the middle Eocene (Irdinmanhan ALMA) of China, a family that was long considered to be endemic to Western Europe, where it appeared suddenly at MP13 (Erfurt and Métais 2007). These sporadic faunal exchanges between Western Europe (and to a lesser extent with Balkanatolia) and Eastern Asia are consistent with palaeogeographic data from Central Asia during the middle Eocene (Iakovleva 2011) showing potential terrestrial dispersal pathways north of the Turgai Strait.

The precise dispersal routes between Eastern Asia and Europe remain speculative, but Bai *et al.* (2023) erroneously suggested a southern dispersal route along the northern margin of the Neotethys, which is inconsistent with the endemic and highly isolated fauna of Central Anatolia (Métais *et al.* 2018).

Ecological interaction and niche partitioning among large bodied mammals in Balkanatolia

The areal extent of Balkanatolia must have fluctuated dynamically with eustasy and tectonics, creating and reconnecting islands with the Balkanatolian mainland. Although the endemic fauna of Balkanatolia remains poorly known, no evidence of dwarfing related to insular conditions has been detected among embrithopods. *Palaeoamasia kansui*, *Crivadiatherium sahini* sp. nov., and *Crivadiatherium mackennai* approximate the size of the Sumatran rhinoceros (*Dicerorhinus sumatrensis*), *Axainamasia sandersi* gen. and sp. nov. that of the extant Malayan tapir (*Tapirus indicus*) and *Crivadiatherium sevketseni* sp. nov. was about the size of a bushpig (*Potamochoerus larvatus*). All of these Balkanatolian palaeoamasids are substantially larger than species of the basal embrithopod *Stylolophus* known from Africa (Gheerbrant 2021), and smaller than the African *Arsinoitherium*, and to a lesser degree, *Namatherium* (Pickford *et al.* 2008). However, because we lack detailed information regarding the body mass of the embrithopod taxon that originally colonized Balkanatolia, assessing the evolution of body size among Balkanatolian embrithopods remains somewhat problematic. By the time of deposition of the Çamili Mezra quarry, Balkanatolian embrithopods had radiated into larger and smaller taxa, as represented by *C. sahini* and *C. sevketseni*.

The fauna from the early Eocene Baraklı Formation remains poorly known, but Çamili Mezra marks the first instance that two species of embrithopods have been recorded at the same locality. This situation stands in contrast to the African record of embrithopod evolution, where sympatric embrithopods have never been documented (Sanders et al. 2010). The question of precisely when embrithopods reached Balkanatolia remains unresolved, but they apparently colonized this insular terrane not long after their first appearance in the fossil record of Africa during the early Eocene (Gheerbrant et al. 2018, 2021). In contrast to their longstanding failure to radiate in Africa, Balkanatolian embrithopods diversified rapidly, as evidenced by the coexistence of two species of *Crivadiatherium* at Çamili Mezra and the roughly contemporaneous *Palaeoamasia kansui* at Eski Çeltek. Possible explanations for why embrithopods diversified in Balkanatolia, but not in their African homeland, fall into two major categories. Biological explanations include the absence of potential ecological competitors for embrithopods on Balkanatolia, whereas African embrithopods evolved alongside multiple clades of proboscideans and giant hyracoids. Likewise, potential mammalian predators in the form of Hyaenodonta were prevalent in Africa, while on Balkanatolia the only predatory mammals documented so far were anatoliadelphid metatherians, which clearly posed no threat to Balkanatolian embrithopods (Maga and Beck 2017; Métais et al. 2018; Beard et al. 2023). Alternatively, the diversification of Balkanatolian embrithopods may be explained by multiple shifts in eustasy during the Ypresian, which likely had the effect of repeatedly converting a fairly contiguous Balkanatolian mainland into an archipelago, thereby stimulating speciation among embrithopods and other mammals that were stranded on separate islands.

These taxa certainly exploited similar ecological niches and in regard to their dental morphology, they probably exhibited overlap in diet. The few postcranial data available for *C. sahini*, and *C. sevketse* do not indicate a graviportal posture like that of *Arsinoitherium*, and

rather suggest that these sympatric palaeoamasids practiced a more generalized locomotor pattern characterized by prolonged walking or running. These four palaeoamasids plus *Palaeotherium magnum* have never been found in association, and they document different time intervals of the large mammals' diversity in Balkanatolia during approximately 20 Ma. Consequently, it is difficult at this stage to assess niche partitioning among these herbivores at different time slices. Licht et al. (2022) estimate the merged surface of Balkanatolia during the middle Eocene as roughly 1.6 times the size of Madagascar, which leaves space for various ecological niches for large herbivores. Madagascar's mammalian fauna today displays low diversity at high taxonomic levels, in concert with a remarkable endemic species-level variety within those depauperate major clades (Tattersall 1999). This is the case for the pleuraspidotheriid *Hilalia* from the middle Eocene Uzunçarşidere Formation (Maas et al. 2001), which is known by at least four species of different size and perhaps locomotor adaptation. This adaptative radiation of *Hilalia* involves occupying or creating novel niches, possibly producing morphologies different from that of their ancestral forms. Mammalian predators in Balkanatolia are so far restricted to the endemic metatherian *Anatoliadelphys*, the weight of which did not exceed 4 kg (Maga and Beck 2017), and rare small-sized crocodylians have been recovered from the Uzunçarşidere and the Barakli formations. It is thus likely that even the smaller *C. sevketseni* lacked significant predation pressure, and there is no clear evidence of dwarfing in these herbivores suggesting that the competition for resource access was low, at least in Central Anatolia during the middle Eocene. These observations must be considered preliminary because ecological interactions, particularly intraguild competition, which is the major driver of evolution in insular communities, including change in body size (Palombo 2009), remain poorly understood in Balkanatolia.

Conclusion

New paleontological data from Çamili Mezra augment our knowledge of the embrithopods of Balkanatolia. The genus *Crivadiatherium* is reported for the first in the early-middle Eocene of Central Anatolia, extending its geographic range beyond the Hateg Depression in Romania (Radulescu et al. 1976; Radulescu and Sudre 1985). The embrithopod fauna of Çamili Mezra indicates that this clade experienced a modest adaptive radiation after successfully colonizing Balkanatolia. The Balkanatolian record of embrithopod evolution contrasts with the evolutionary history of this clade in its native Africa, where sympatric taxa of embrithopods have never been documented. In situ diversification of embrithopods may have been facilitated by the endemic and unbalanced character of Balkanatolian faunas, particularly the absence of other large-bodied herbivores like proboscideans, which were diverse and abundant in the early Paleogene of Africa. While it is generally accepted that embrithopods colonized Balkanatolia by dispersing across Tethys (Sen 2013), precisely when embrithopods colonized Balkanatolia remains poorly constrained. In part, this arises from gaps in the early Paleogene record of fossil vertebrates across Balkanatolia, but it also reflects fairly weak geochronological constraints on the various embrithopod-bearing localities that are currently known. From a broader perspective, increased knowledge of the early evolutionary history of Balkanatolian embrithopods would also advance our understanding of how insular biotas are assembled across Deep Time. For example, the relative significance of different processes contributing to faunal assembly in an insular context—notably including colonization, in situ diversification, and vicariance—can only be assessed in light of relevant data on the evolutionary history of each clade comprising the fauna.

Competing interests

The authors declare that there are no conflicts of interest.

Data availability

The datasets generated during and/or analysed during the current study are published in this article.

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Figure captions.

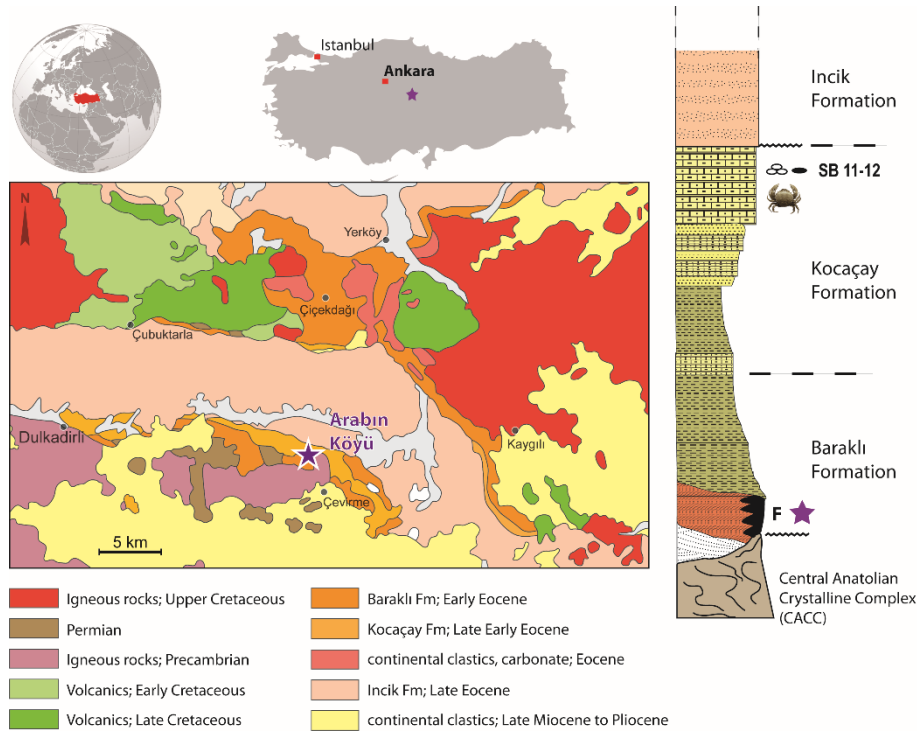


Fig. 1 location maps (left) and simplified stratigraphic column (right). In the map of Turkey (above) and the simplified geological map (below), the locality is indicated by a violet star. The stratigraphic position of the embriothopod-yielding horizon is also indicated by a violet star in the stratigraphic column of the Arabin Köyü-Çamili Mezra area. The stratigraphic position of fossil crabs and benthic forams reported by Schweitzer et al. (2007) is indicated near the top of the Kocacay Formation.

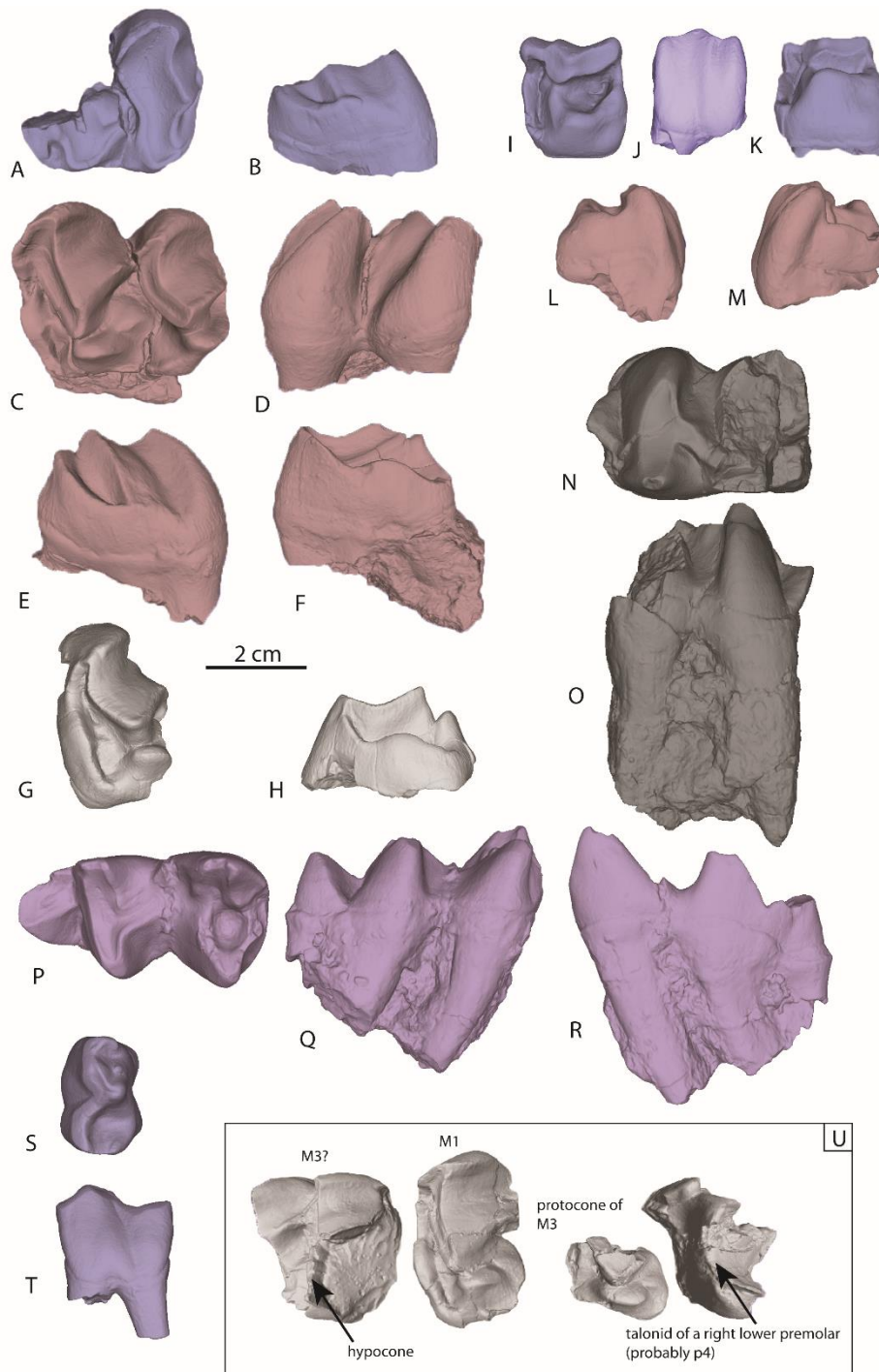


Fig. 2 Surface scans of the dental material of *Crivadiatherium sahini*, sp. nov. from Çamili Mezra (a-t). Specimen EOU-ÇMZ-1, incomplete left M1 (mesio-labial part is missing) in occlusal (a) and distal (b) views; left M2 in occlusal (c), labial (d), distal (e) and mesial (f) views; anterior part of a left M3 in occlusal (g) and mesial (h) views; left P4 in occlusal (i), labial (j), lingual (k), distal (l) and mesial (m) views. Specimen EOU-ÇMZ-5, left m3

(trigonid missing) in occlusal (n), and labial (o) views. Holotype specimen EOU-ÇMZ-6, right m3 in occlusal (p), labial (q), and lingual (r) views. Specimen EOU-ÇMZ-4, left p3 in occlusal (s), and labial (t) views. Holotype of *Hypsamasia seni* from the middle Eocene Uzunçarşidere Formation (u). Scale bar equals 2 cm.

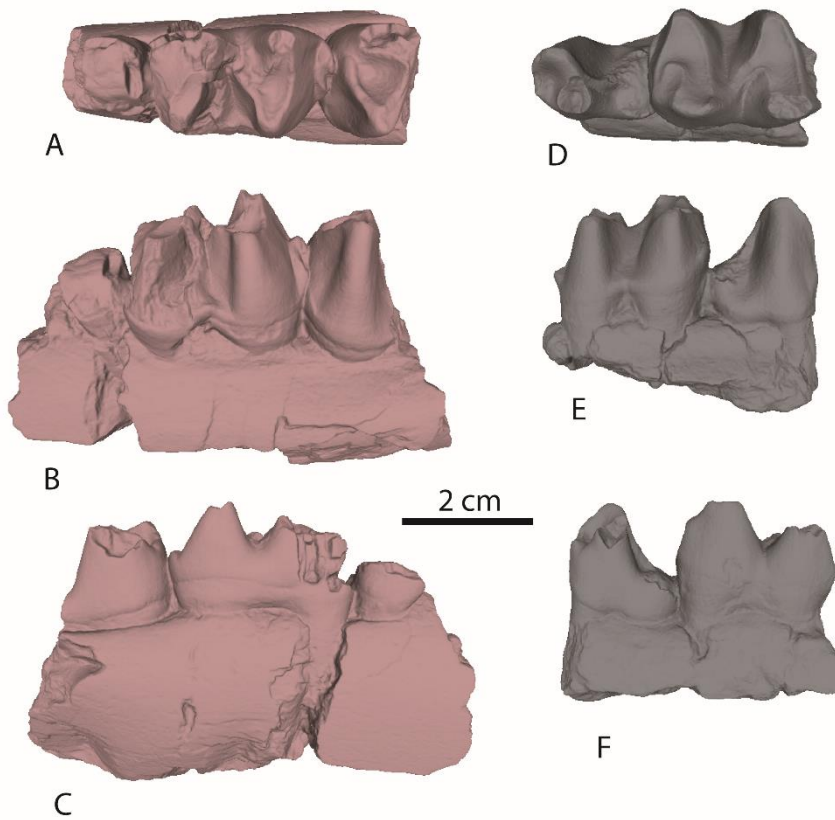


Fig. 3 *Palaeoamasia kansui* Ozansoy, 1966 from the lignite mine of Eski Çeltek (Amasya Province). Holotype specimen MNHN-EÇ-1, fragmentary left lower jaw with damaged talonid of m1, m2 (trigonid damaged), and the trigonid of m3 in occlusal (a), labial (b) and lingual (c) views; specimen MNHN-EÇ-5, fragmentary right lower jaw with p4 (cristid obliqua partly missing)-m1 in occlusal (d), labial (e) and lingual (f) views. Scale bar equals 2 cm.

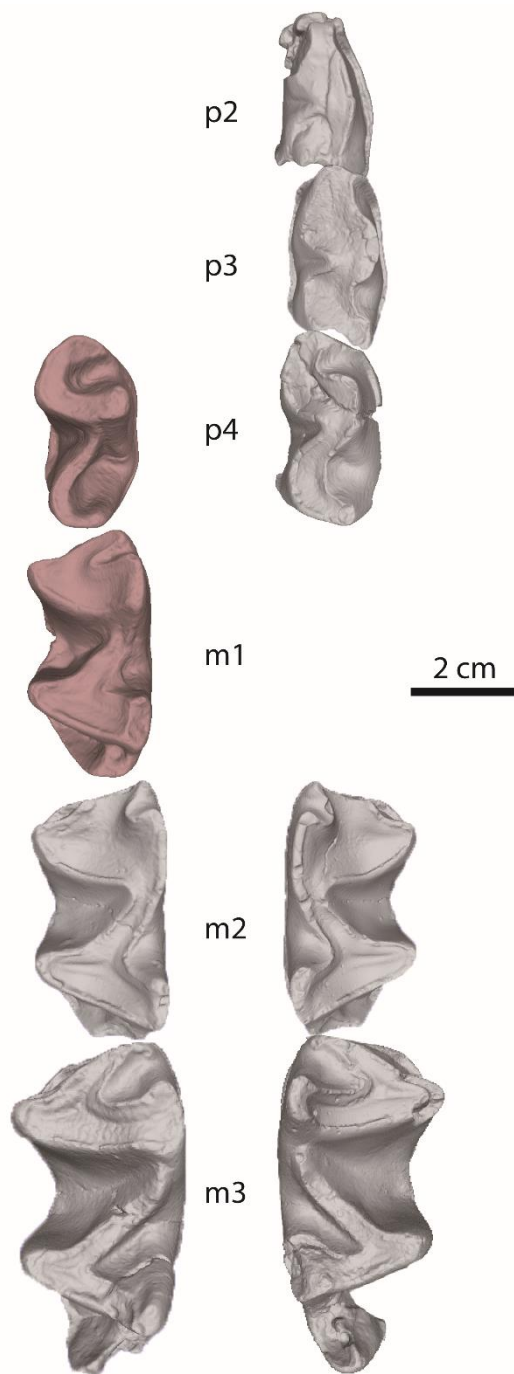


Fig. 4 *Crivadiatherium mackennai*, from the middle Eocene of Crivadia, Hateg Basin, Romania. Reconstructed dental row of *C. mackennai* from the teeth referred to *C. iliescui* (in grey) by Radulescu and Sudre (1985), and the p4 and m1 of the holotype of *C. mackennai* (in light red color). Radulescu and Sudre (1985) designated the left m2 and m3 as the holotype of *C. iliescui*. The two species cannot be distinguished by size or dental morphology; thus, we consider them synonymous. Scale bar equals 2 cm.

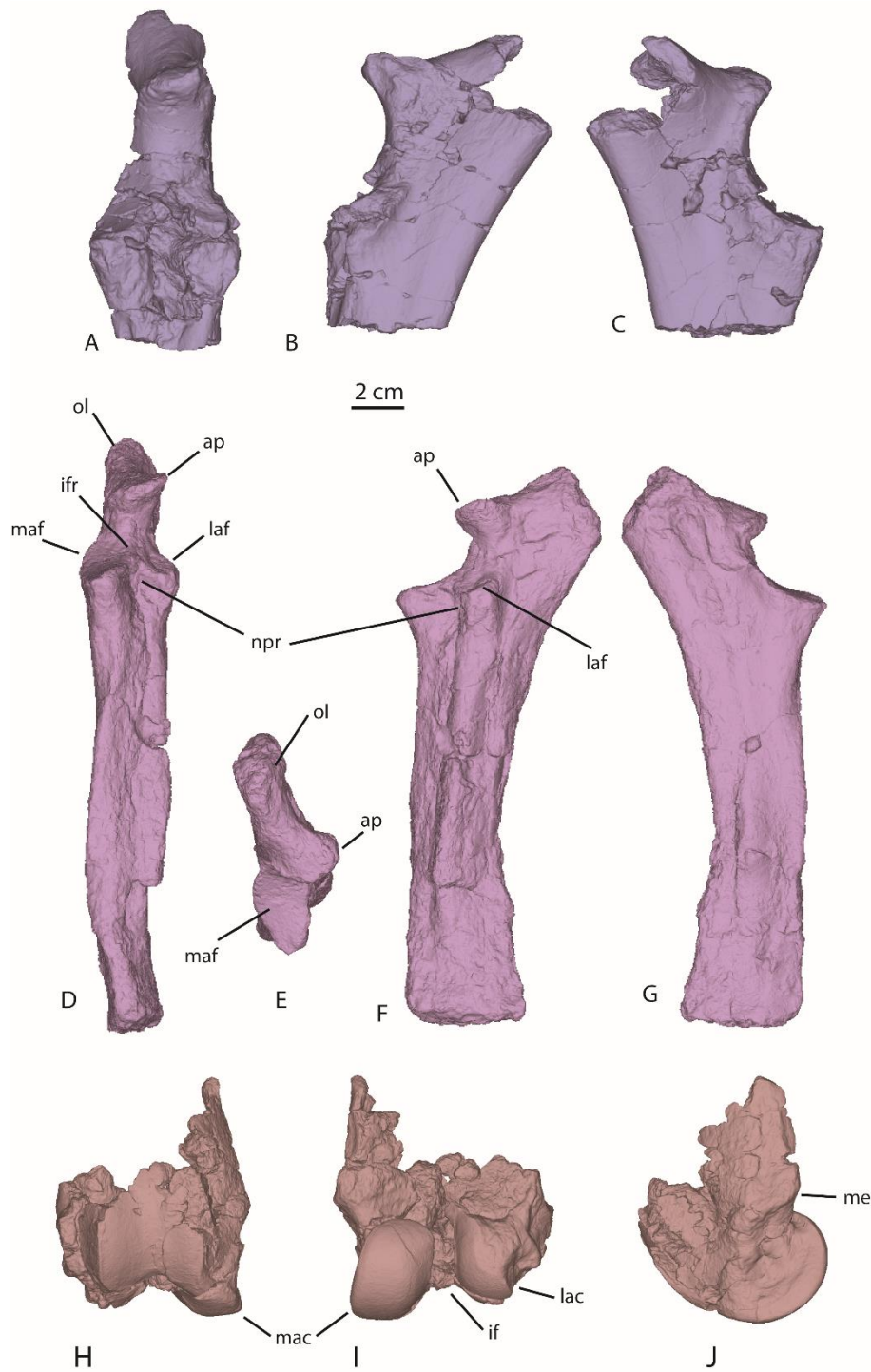


Fig. 5 Postcranial remains of embranchopods from Çamili Mezra. *Crivadiatherium sahini*, sp. nov. Specimen EOU-ÇMZ-12, proximal ulna in anterior (a), lateral (b), and medial (c) views. Specimen EOU-ÇMZ-13, distal femur in anterior (h), posterior (i), and medial (j) views. *Crivadiatherium sevketsemi*, sp. nov. Specimen EOU-ÇMZ-11, ulna (distal epiphysis is missing) in anterior (d), mesial (e), lateral (f), and medial (g) views. Abbreviations: **ap**,

anconeal process (beak of the olecranon); **if**, intercondylar fossa; **ifr**, inter facet ridge; **lac**, lateral articular condyle; **laf**, lateral articular facet; **maf**, medial articular facet; **mac**, medial articular condyle; **me**, medial epicondyle; **npr**, notch for the proximal radius; **ol**, olecranon.

Scale bar equals 2 cm.

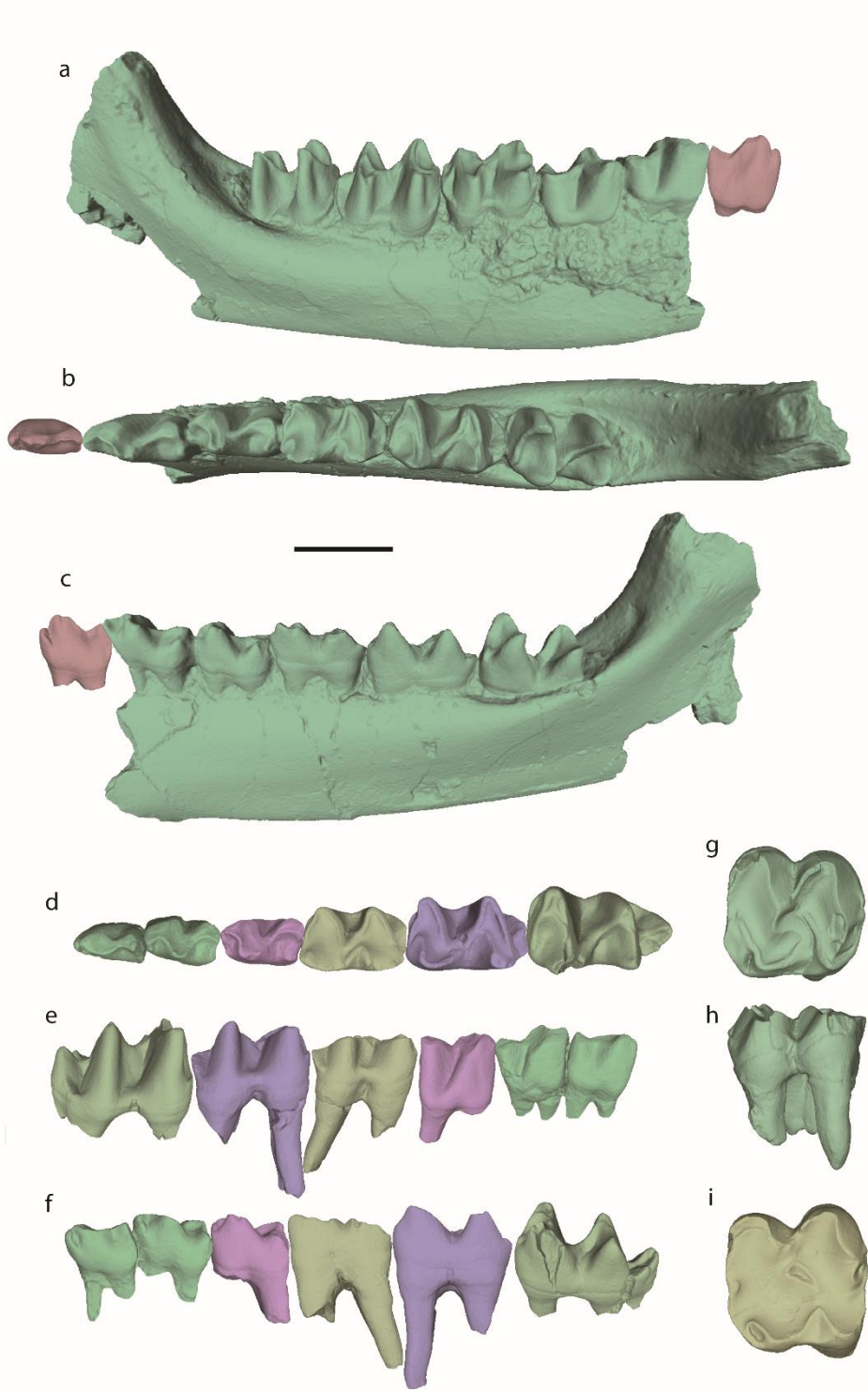


Fig. 6 *Crivadiatherium sevketseni*, sp. nov. from Çamili Mezra. Holotype specimen EOU-ÇMZ-2, fragmentary right lower jaw with p2-m3 (p2 was recovered in association with the dentary preserving p3-m3) in labial (a), occlusal (b) and lingual (c) views; paratype specimen EOU-ÇMZ-3, fragmentary right dentary preserving p2-3 and associated p4, m1, m2 and m3 in occlusal (d), labial (e) and lingual (f) views. Specimen EOU-ÇMZ-10, left M1 in occlusal (g), and labial (h) views. Specimen EOU-ÇMZ-9, left M2 in occlusal (i) view. Scale bar equals 2 cm.

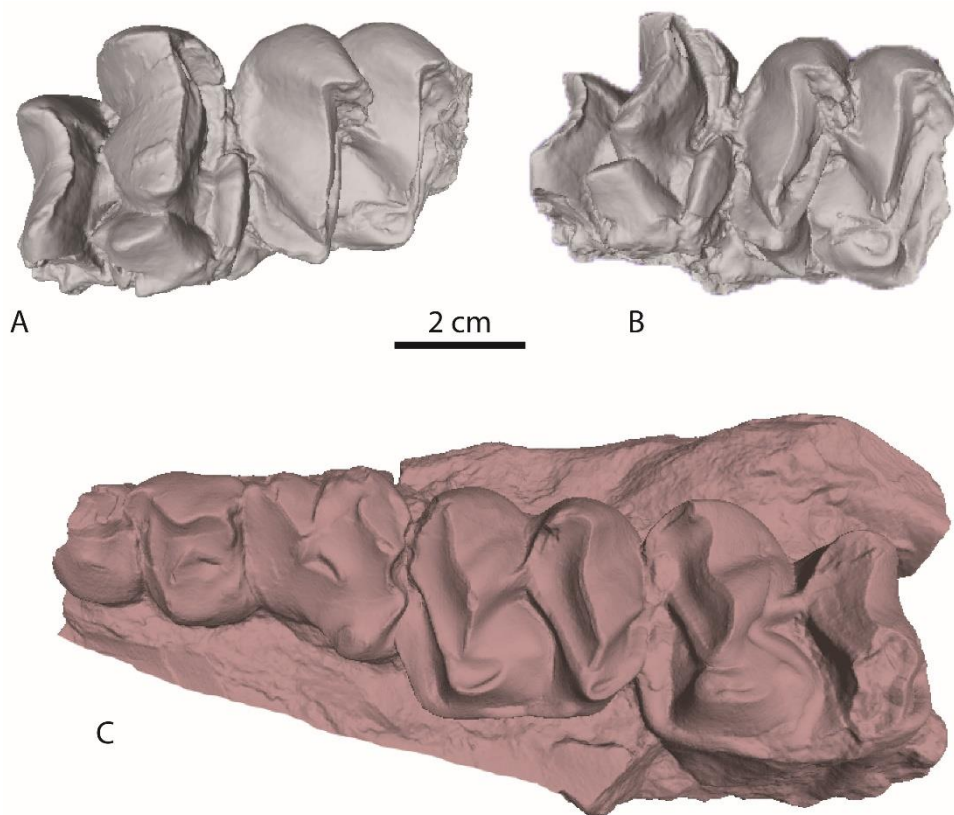


Fig. 7 a-b. *Axainamasia sandersi*, gen. et sp. nov. from the upper part of Cemalletin Formation, Boyabat Basin, Sinop Province. Holotype specimen BOY-2, fragmentary right maxilla with M2-M3 with the specimen in slightly different occlusal views in **a** and **b** because of the distortion of the specimen; the roots of M1 and posterior roots of P4 are also present but not figured here (see Sanders et al. 2014: fig. 3). **c.** *Palaeoamasia kansui* Ozansoy 1966,

MNHN-EÇ-4 (in part), fragment of palate with left P3-M3 in occlusal view. Scale bar equals 2 cm.