PALÆO VERTEBRATA

ARTICLE

A late Eocene palaeoamasiine embrithopod (Mammalia, Afrotheria) from the Adriatic realm (Island of Rab, Croatia)

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Abstract: A cheek tooth recently unearthed in the Lopar Sandstone unit, of late Eocene age, in the northern part of Rab Island, Croatia, is one of the very few Eocene mammalian remains found in the Adriatic area. Thorough comparison of this tooth with those of Old-World Palaeogene mammalian orders suggests that it is a M3 belonging to an embrithopod afrothere. The specimen is referred to as *Palaeoamasia* sp. This genus was formerly known only in Eocene deposits of Anatolia but with close relatives in Romania among Palaeoamasiinae. The geographical distribution of this subfamily perfectly matches the recently-named Balkanatolian landmass, which experienced in-situ evolution of endemic mammals prior to the *Grande Coupure* event that occurred around the Eocene–Oligocene transition. This last event is characterised by massive Asian immigration in Western Europe and the supposed extinction of many endemic Central and Western European mammals, including Palaeoamasiinae.

Keywords: Great Adria, *Grande Coupure*, Palaeobiogeography, Balkanatolia, Systematics

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INTRODUCTION

The *Grande Coupure* event (GC) is well characterised in Western Europe at the Eocene-Oligocene Transition (EOT; Stehlin, 1910; Rage, 1984; Legendre, 1987; Hooker *et al.*, 2004; Pélissié *et al.*, 2021). During the abrupt cooling event marked by the Oi-1 glaciation (e.g., Westerhold *et al.*, 2020), many terrestrial mammals of Asian origin invaded Western Europe whereas endemic Western European taxa declined. This event has been proposed to be linked to landmass contact between Asian and European realms (Stehlin, 1910; Cavelier *et al.*, 1981) notably with the regression of the Turgai Strait (Pélissié *et al.*, 2021). Recent multidisciplinary research highlights the presence of a large landmass between these two realms, which could have played a critical role in the GC. This continental landmass, named Balkanatolia, is firstly evidenced by an original faunal composition well described over Eocene times in Anatolia (Licht *et al.*, 2022 and references therein). Clear faunal differences between Western Europe and Balkanatolia persist through the middle and late Eocene, suggesting an isolated landmass that could have connected episodically with Asia and Afro-Arabia.

A mammalian tooth was found embedded in upper Eocene deposits of the Lopar Sandstone unit, latest Bartonian–Priabonian in age, on Rab Island off the Croatian continental coast (Fig. 1). Terrestrial vertebrate remains are particularly scarce in the Palaeogene of Croatia due to extensive marine development in the area. Only remains of the anthracothere artiodactyl *Prominatherium dalmatinum* (Meyer, 1854) had been previously reported in the region; this taxon is included within the Balkanatolian fauna together with conspecific remains found in northern Italy and Romania (Grandi and Bona, 2017). Accordingly, any terrestrial fossils from this area are likely to provide key information to constrain the westernmost extension of Balkanatolia (Licht *et al.*, 2022) and to test the hypothesis of late Eocene endemism of European terrestrial faunas.

Here we describe this dental specimen and propose a taxonomic assignment for it, in a well-constrained geological context. More generally, this unexpected discovery provides new palaeobiogeographical constraints for the concerned area, just before the GC.

GEOLOGICAL SETTING

The tooth (RL-1486), belongs to the ProGEO-Croatia collection of Zagreb University, Croatia and is permanently exhibited in Public Open University Rab. It was found on a bedding plane of one layer of the Lopar Sandstone conglomerate interbed. During a field inspection, Marina Čalogović spotted it by accident. Further search for more fossil elements at the same location was unfortunately not successful thus far.

The conglomerates of Lopar, on the northern promontory of Rab Island (Fig 1A-B), are part of the middle to late Eocene marine clastic sedimentary succession of Lopar Sandstone and they either mark sequence boundaries between transgressive system tracts or occur as internal conglomerates (Marjanac and Marjanac, 2007; Fig. 1C-G). The thickness of the Lopar Sandstone unit reaches about 600 m (Marjanac and Marjanac, 2007). The composition of the conglomerates, dominated by various kinds of chert pebbles and locally sandstone from the basement, does not comply with the geology of the External Dinarides. Rather, their provenance must have been an area today known as Alps or even further north in Germany. Well-rounded pebbles of resistant material (chert) indicates a long fluvial transport (Fig. 1C-D), while associated plant debris indicates the presence of vegetated areas in the general vicinity. However, the majority of Lopar sandstones are well rounded sand deposits in a tide-dominated incised valley or estuary.

Based on identification of large foraminifers, Muldini-Mamužić (1962) interpreted the age of the Rab "Flysch" (now recognised as the San Marino Marls plus the overlying Lopar Sandstone) as latest middle Eocene and possibly earliest late Eocene. Benić (1983) discovered nannofossils of the *Discoaster tani nodifer* nannozone in the San Marino Marls (NP16, late Lutetian–earliest Bartonian) and no reworked forms were found in the studied samples. However, in the Lopar Sandstone, Benić (1983) found numerous reworked nannofossils, key-fossils of the zones NP 6–7, NP 7–9, NP 9–10 and NP 10–12 (Fig 1F). He therefore assumed that the Lopar sandstones overlie the San Marino marls and may also belong to the NP 16 or to a younger biozone. The age of the Lopar Sandstone is therefore only interpreted from the underlying formation, with deposition that started during the Bartonian, and probably lasted until the latest Priabonian, or even later (Fig. 1G).

Regarding the origin of the conglomerate which deposited in an estuarine environment, probably intersected by vegetated land areas, it is likely that the tooth was not transported from far away. Moreover, the tooth shows no sign of reworking or transport, but damaged upper surface of the tooth is due to long-term exposition to weathering at the bedding surface.

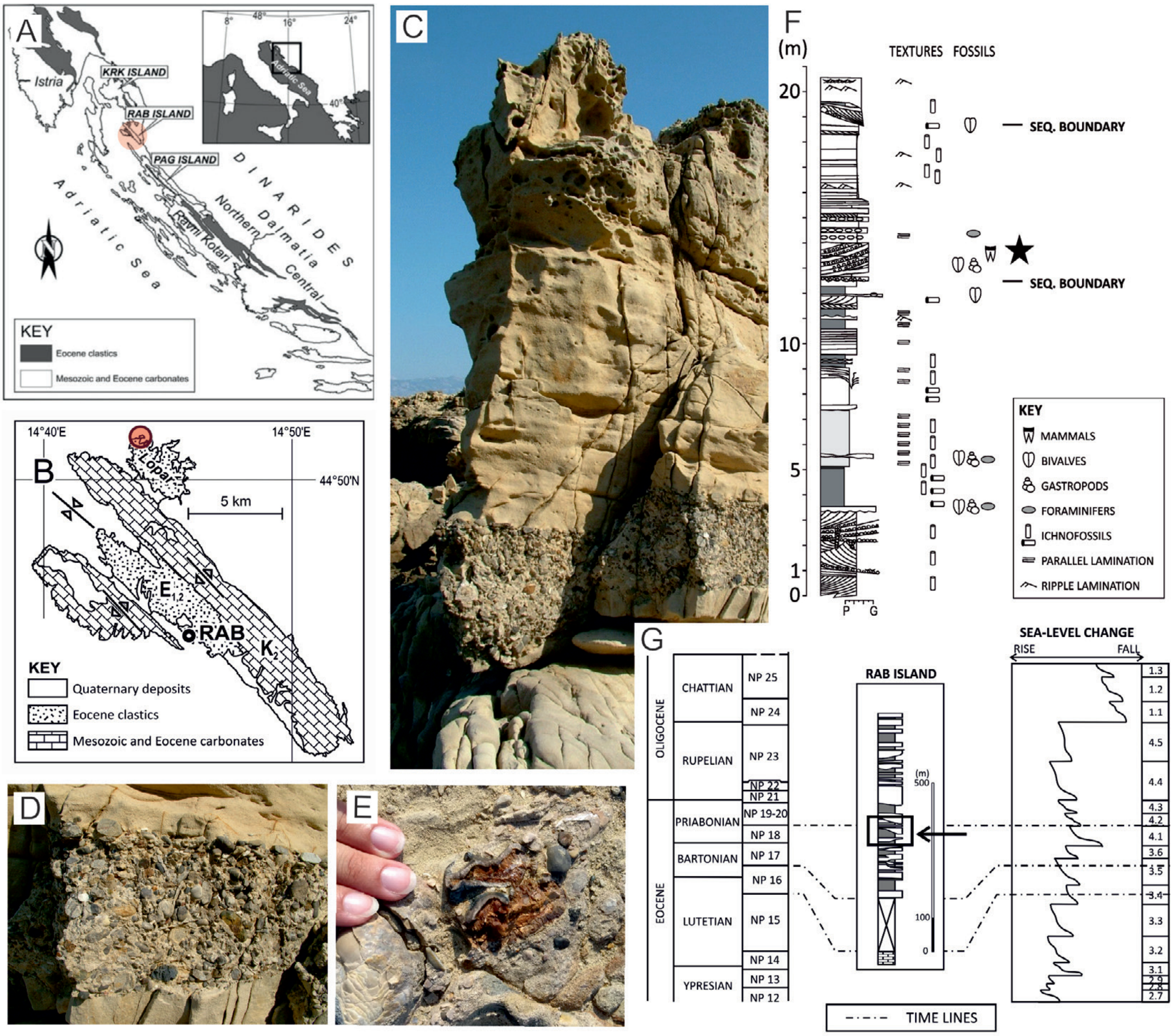

Figure 1. Geological context of the Eocene embrithopod molar from Rab Island. **A,** Localisation of the Rab Island in the Adriatic Sea. **B,** Position of the fossiliferous locality on Lopar peninsula on the Rab Island, Croatia. **C-D,** The upper Eocene conglomerates of Lopar. **E,** The fossil tooth embedded in the Lopar conglomerate. **F,** Sedimentary log of studied Lopar Sandstones with marked sequence boundaries and position of fossil tooth (asterisk mark). The interval with the tooth is a coarse-grained cross-bedded paraconglomerate with abundant oyster shells and chert pebbles. **G,** Stratigraphic position of studied Rab Island clastics in the synthetic geological column and correlation with relative sea-level changes (after Haq *et al*. 1987). The detailed log (F) is marked by an arrow.

Frequent oscillations in sea level forced basinward and landward shifts of facies with marls and conglomerate (Fig. 1F-G). We interpret the depositional environment as a paralic sea where a succession of incised valleys was formed during high frequency relative sea-level falls. Accordingly, the tooth must belong to a mammal having lived in a broad estuarine area.

SYSTEMATIC PALAEONTOLOGY

Class MAMMALIA Linnaeus, 1758

PAENUNGULATA Simpson, 1945

Order EMBRITHOPODA Andrews, 1906

Family ARSINOITHERIIDAE Andrews, 1904

Subfamily PALAEOAMASIINAE Sen and Heintz, 1979

Palaeoamasia Ozansoy, 1966

Type species. *Palaeoamasia kansui* Ozansoy, 1966

Palaeoamasia sp.

Specimen. RL-1486, a fragmentary right M3 with broken mesial and labial part; repository in Public Open University Rab, belonging to ProGEO-Croatia collection of Zagreb University, Croatia.

Locality and horizon. Lopar Peninsula on Rab Island, Croatia from the Lopar Sandstone unit, latest Bartonian–Priabonian in age.

Remarks on systematics. Palaeoamasiidae was first erected as a subfamily of Arsinoitheriidae (Paleoamasiinae Sen and Heintz, 1979) and then raised to the familial rank by Kaya (1995) based on the "numerous differences" between *Palaeoamasia* and *Arsinoitherium*, supposedly greater than those proposed by Sen and Heintz (1979). This thesis was supported by Maas *et al.* (1998), considering the Turkish diversity (three genera at that moment). It was then accepted by Gheerbrant *et al*. (2005) but without proposed diagnosis and, by Sanders *et al*. (2014) who indicated that "Eurasian and Afro-Arabian embrithopod radiations had long, separate phylogenetic histories, supporting the notion that they belong in different families (in Sanders *et al*. 2014: p1162)". Those arguments are not supported by phylogenies and the existing phylogenetic analyses do not validate the distinction between both families (see Gheerbrant *et al*. 2018, 2021). The phylogeny in Erdal *et al*. (2016) proposed *Namatherium* as sister group of Arsinoitheriidae that includes Arsinoitheriinae and Palaeoamasiinae whereas in Gheerbrant *et al*. (2021) *Palaeoamasia* is sister group of [*Namatherium* +*Arsinoitherium*+*Hypsamasia*+*Crivadiatherium*] thus preventing any separation between Eurasian and African taxa.

We do not want to rule on the systematics of the group in this study and thus prefer to keep the established relationships obtain in Erdal *et al*. 2016 which focus on Eurasian Embrithopods and that propose resolved relationships. Elevation of subfamily to the rank of family appear highly subjective in earlier studies and we prefer to keep the original term established by Sen and Heintz (1979) pending a thorough revision of the order.

Description

The only specimen known to date from Rab Island is interpreted as an upper right molar (RL-1486), distally unworn but broken labially and mesially. The very well-preserved distal cingulum and the absence of distal intertooth wear-facet suggest that this tooth is a last upper molar, i.e., M3 (Fig. 2A, C). The specimen displays two closely-associated distolingual cusps (Fig. 2B, D), interpreted here as the hypocone and the metacone. The hypocone is connected to a strong distolingual cingulum while the metacone connects the distal side by a mesiodistal crista, hence considered as a postmetacrista (Fig. 2). This postmetacrista reaches the distal cingulum, forming a spur that could thus be considered as a "metastyle" (Fig. 2A, C). A deep median valley is noticeable with the development of a large distomedial inflated base for the protocone, considering its origin and direction. The median valley is labially closed by a mesiodistal crista that connects the mesial loph to the metacone. This crista could be a postparacrista. Just lingual to this crista, the median valley is partially filled with some coronary cement (Fig. 2B, D). The labial part of the tooth is broken but is clearly organised in two separated transverse lobes (i.e., protoloph and metaloph). Enamel is thick, with a thickness variation between 1.9-2.5 mm.

Comparisons

In order to confirm the interpretation of the described features (dental homologies), we have chosen to first compare this tooth to all plausible mammalian orders, i.e., those with large bilophodont cheek teeth, of Old-World origin and Palaeogene in age. This is especially useful given i) the peculiar depositional context (marine setting) and ii) the absence or scarcity of previously-found mammal remains in the concerned area and time interval (late Eocene).

Comparison with Artiodactyla. In comparable marine deposits, also Priabonian in age, scarce anthracothere remains are known from Monte Promina in Croatia (Meyer, 1854), Grancona in Italy (Grandi and Bona, 2017) and Sacel in Romania (Patrulius, 1954). All of these Ante-GC specimens are assigned to *Prominatherium dalmatinum* (Fig. 3B), an early-diverging anthracotheriine probably not tightly linked to the European Oligocene *Anthracotherium* and *Paenanthracotherium* (Scherler *et al*., 2018). The specimen from Rab Island (Fig. 3A) clearly differs from large Eocene artiodactyls by the labiolingual well-developed bilophodont outline despite the heavily-damaged labial parts of the two lobes. The paracone and metacone are in median position instead of being labial as in anthracotheriines and in entelodontids.

Comparison with Perissodactyla. The strong development of lophs, as seen on the Rab specimen, is superficially consistent with Perissodactyla such as brontotheres, and notably *Embolotherium* (Fig. 3C), known and described from a large area extending from Slovenia to Turkey during the late Eocene (Licht *et al*., 2022), or coeval amynodontid rhinocerotoids (Fig. 3D) occurring in a handful of Eastern European localities (Tissier *et al*., 2018). The earliest rhinocerotids of the Adriatic realm do occur in the earliest Oligocene (Pandolfi *et al*., 2017). Nevertheless, some major features, such as the extremely thick enamel (especially in the lingual valley), the median notch on the labial side, the "metastyle" lingually displaced and oblique, and the undulated distal side of the metaloph, discard any assignment to perissodactyls. The specimen from Rab Island is far smaller than the Western European lophiodontids referred to as *Lophiodon* (the last ones are known from the late Bartonian (MP16) of Robiac, Southern France (Sudre, 1971). It is also larger and squarer than upper molars of palaeotheres (Rémy, 2015).

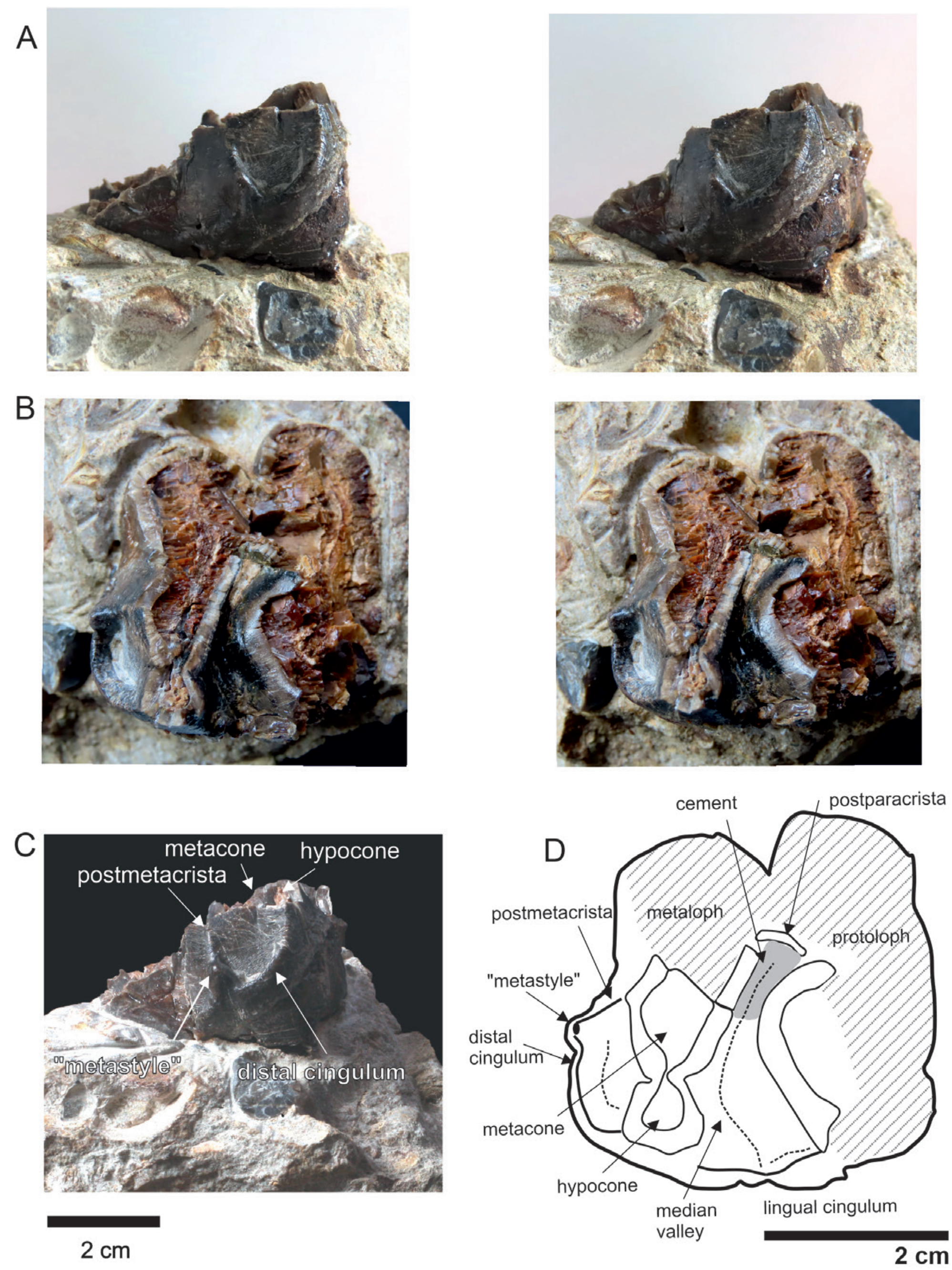

Figure 2. Right M3 of *Palaeoamasia* sp. (RL-1486) from Rab Island, Croatia. **A,** distal view. **B,** occlusal view. **C,** distal view with annotated structures. **D,** scheme in occlusal view with interpretations of the main preserved dental structures.

Comparison with Sirenia. Sirenians are well-known large marine tethytheres notably present in Mediterranean deposits during the late Eocene (Sagne, 2001). Compared to the Rab Island specimen, the paracone and metacone in sirenian teeth are in more labial position (Fig. 3E), the cusps are not organised in sharp lophs (buno-bilophodont teeth) and there is no crista such as in RL-1486, where a postmetacrista and a postprotocrista are well developed.

Comparison with Embrithopoda. This Paenungulate order originates from the Afro-Arabian landmass, with a Palaeocene–Oligocene time range (e.g., Gheerbrant *et al.*, 2018). However, some representatives of this clade, assigned to the palaeoamasiine subfamily, were described from Romania (Radulesco *et al*., 1976) and Turkey (e.g., Ozansoy, 1966; Erdal *et al.*, 2016). Their upper molars form two lobes with a well-developed labial part of ectoloph that implies a median position of the lingually-displaced labial cusps. Such hyperdilambdodont condition is unique in large herbivorous mammals (Gheerbrant *et al*., 2018). The development of the postmetacrista and the postparacrista and the lingual displacement of the labial cusps on the specimen from Rab Island fully match this occlusal pattern. The morphology of the distal cingulum and of the inflated distal protocone is also similar to that of *Palaeoamasia kansui* from Turkey (Fig. 3F; Erdal *et al.*, 2016). These unique features allow us to assign the Rab specimen to Embrithopoda, which in turn confirms our interpretation of dental structures as proposed in figure 2D. Moreover, the presence of a “metastyle”, absent in most of the

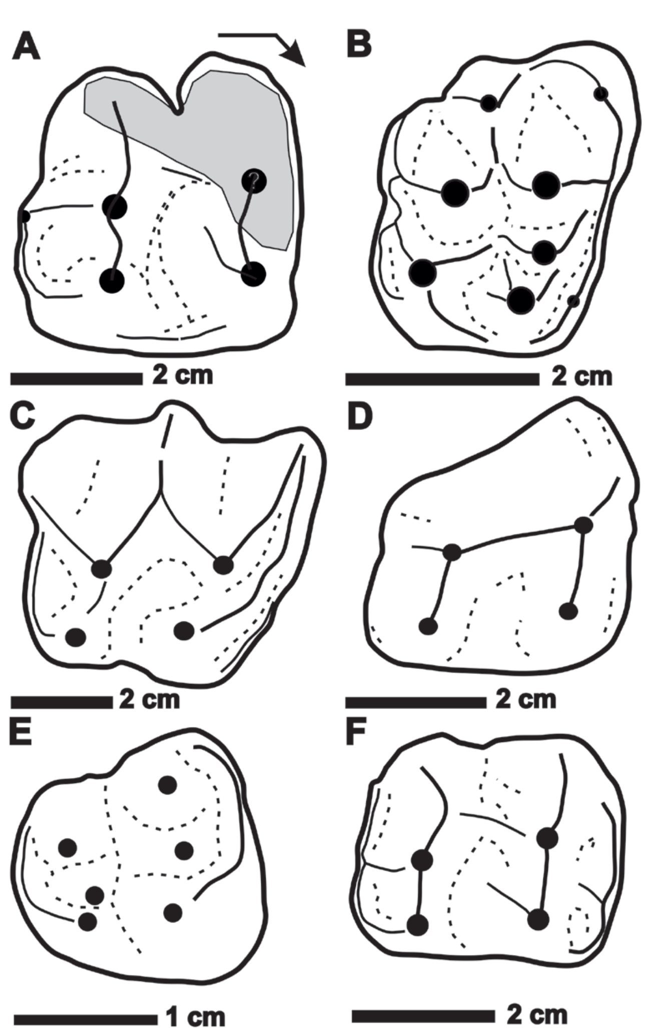

Figure 3. Comparison of occlusal schemes of M3/s among selected Palaeogene mammalian clades. **A,** RL-1486. **B,** the anthracotheriine *Prominatherium damaltinum* from Scherler, Lihoreau, and Becker (2018). **C,** the brontothere *Embolotherium andrewsi* from Osborn (1929). **D,** the amynodontid rhinocerotoid *Sellamynodon zimborensis* from Tissier *et al*. (2018). **E,** the sirenian *Halitherium taulannense* from Sagne (2001). **F,** the arsinoitheriid embrithopod *Palaeoamasia kansui* from Erdal, Antoine, and Sen (2016).

embrithopods, is noticed on the M3 MNHN-EÇ-6 (Erdal *et al*. 2016) and not on the M1 or M2 of MNHN-EÇ-4, which seems to confirm the assignment of RL-1486 to a M3.

The Afro-Arabian Arsinoitheriidae (except *Namatherium*) have higher-crowned teeth than the specimen from Rab Island and the Palaeoamasiinae (Erdal *et al*., 2016). The postparacrista and the better-defined and larger hypocone of the Croatian specimen differ from what is observed in *Namatherium blackcrowense* and *Arsinoitherium* (Pickford *et al*., 2008). As for *Palaeoamasia kansui*, the Rab Island specimen (RL-1486) differs from *Arsinoitherium* and *N. blackcrowense* in the presence of a postmetacrista and of continuous mesial and lingual cingula on M3. RL-1486 further differs from the condition seen in *Arsinoitherium* in the presence of a distal cingulum on upper molars. The distolingual cingulum, which extends under the hypocone, is not connected to the lingual cingulum contrary to what defines *Namatherium* (Pickford *et al*., 2008).

Palaeoamasiinae comprise three genera: i) *Palaeoamasia* Ozansoy 1966 (Ypresian–Priabonian(/Rupelian); Turkey) described at Eski Çeltek (Ypresian?), Çiçekdağı (Lutetian), Yeni Fakili (Ypresian–Lutetian), Boyabat (Lutetian and late Priabonian/Rupelian), Bultu Zile (Lutetian) and Orhaniye basin (Upper Lutetian) (Sen and Heintz, 1979; Erdal *et al*., 2016; Licht *et al*., 2022) ; ii) *Crivadiatherium* Radulesco, Iliesco and Iliesco 1976, with two species from Hateg Formation in Romania (Lutetian; Radulesco and Sudre, 1985); iii) *Hypsamasia* from the Uzunçarşidere Formation of the Orhaniye sub-basin (upper Lutetian near 43 Ma; Maas *et al*., 1998; Sen, 2013; Licht *et al*., 2017, 2022; Métais *et al*. 2018). As a matter of fact, only *Palaeoamasia* nov sp. from Boyabat basin, from around the EOT (Sanders *et al*., 2014) could be coeval to the Croatian specimen, both records being the last attested occurrences of Palaeoamasiinae.

Unfortunately, upper teeth of *Crivadiatherium* are not known (Radulesco and Sudre, 1985) therefore comparison with RL-1486 is not possible except if we consider the very large size of lower molars of both *Crivadiatherium* species would imply upper molars strongly larger than RL-1486. The upper molar from Rab Island notably differs from the hypodigm of *Hypsamasia seni* in its more brachydont condition. *Hypsamasia* is larger than *Palaeoamasia* but with a M2 mesial width slightly smaller than the mesial width of the Croatian M3 (Table 1).

Table 1. Compared mesio-distal length and linguo-labial width of M3s of embrithopods in mm. e, estimated; (min-max). [1] Erdal *et al*. (2016), [2] Sen and Heintz (1979), [3] Sanders *et al*. (2014), [4] Pickford *et al*. (2008), [5] Gheerbrant *et al*. (2021).

Species	Locality	Specimen	Length	Width
***Palaeoamasia* sp.**	**Rab Island, Croatia**	**RL-1486**	**42.5**	**45.2**
Palaeoamasia kansui	Eski Ḉeltek, Turkey	MNHN-EḈ-4 UM cast	35.3	34.1
Palaeoamasia kansui [1]	Eski Ḉeltek, Turkey	MNHN-EḈ-6	33.5	28.1
Palaeoamasia kansui [2]	Eski Ḉeltek, Turkey	N=4/3	31.8 (28.4-36.5)	33.5 (32.3-34.5)
Palaeoamasia kansui [3]	Orhaniye Basin, Turkey	N= 2/1	39.9-40	37.2
Palaeoamasia nov. sp. [3]	Boyabat 2, Turkey	BOY-2	e30	e32
Namatherium blackcrowense [4]	Blackcrow, Namibia	N=2	40.8	40.7
Arsinoitherium zitteli [3]	Fayum, Egypt	N=1	60.5	55
Arsinoitherium giganteum [3]	Chilga, Ethiopia	N=2/2	71.8	61.2
Stylolophus minor [5]	Ouled Abdoun Basin, Morocco	OCP DEK/GE 667	15	16
Stylolophus major [5]	Ouled Abdoun Basin, Morocco	MNHN.FPM53	22.5	31

Most of the diagnostic features of *Palaeoamasia kansui sensu* Erdal *et al.* (2016) are not observable on the Croatian M3 due to the fragmentary nature of the specimen, such as the continuity between the mesial and lingual cingula on the mesio-lingual angle, the divided lingual roots and the root height that are greater than the crown height. However, the brachydonty, the strong development of the postmetacrista, the individualized hypocone and the distal cingulum extended lingually below the hypocone are shared features between the Turkish *Palaeoamasia* and the Croatian M3. Indeed, on the M3s of *P. kansui* MNHN-EÇ-4 and MNHN-EÇ-6 from Eski Çeltek, the lingual cingulum is continuous between the base of the fold of the protocone and the mesiolingual side of the hypocone as on RL-1486. On the distal side of the tooth, a strong postmetacrista joins the thick distal cingulum also as on RL-1486. At this junction we note that both RL-1486 and MNHN-EÇ-6, display a "cuspate metastyle", a structure that seems to vary within *P. kansui* (intra- and inter-individual) but that has never been observed in other embrithopods (Gheerbrant *et al*. 2018).

Thus, the molar RL-1486 can be assigned to the genus *Palaeoamasia* considering the differences with the other palaeoamasiine genera and the absence of strong differences (i.e., not subject to intraspecific variability) with *Palaeoamasia*. Considering its occlusal dimensions (Table. 1), however, it appears to be larger than most known *Palaeoamasia* M3s (Table 1) over ranking the specimen from Orhaniye basin from the late Lutetian and not far from the larger *Namatherium*. Unfortunately, intraspecific variation among palaeoamasiines is not well constrained, which does not allow us to state with any confidence on the specific assignment of the Rab tooth. Notably the strong development of the postmetacrista and the presence of a "metastyle" in RL-1486 might reflect intraspecific variability as it is also varying in the few specimens from Eski Çeltek. The presence of patchy coronary cement, filling part of the valley just lingual to the postparacrista, has never been described in palaeoamasines and, more generally, in embrithopods. The lack of cement in other palaeoamasiine specimens might be related to mechanical preparation and/or to distinct taphonomic/burial conditions, which hampers using this criterion with confidence to distinguish further the Rab embrithopod. Nevertheless, RL-1486 is larger than the youngest specimens known so far, from Boyabat (Table 1). Accordingly, we consider referring RL-1486 to as *Palaeoamasia* sp. This new discovery is likely to support an unsuspected specific diversity for Palaeoamasiinae, at the end of the Eocene in the Eastern Mediterranean.

DISCUSSION

Very few late Eocene vertebrate mammals have been found from the Adriatic realm (Greater Adria terrane; Fig. 4) and all of them consist of isolated teeth of large mammals. The specimens from Monte Promina (Croatia) and Grancona (Italy) match a dispersion event from Asia to Europe with the anthracotheriine *Prominatherium dalmatinum*. Scherler *et al.* (2018) showed that *Prominatherium* was not closely related to the Western European anthracotheriines (*Anthracotherium* and *Paenanthracotherium*), and thus have no direct relationship either with *Anthracotherium monsvialense* from Monteviale (Italy, earliest Oligocene; Ghezzo and Giusberti, 2016; Pandolfi *et al*., 2017). Their presence rather resulted from a dispersal from Southeast Asia occurring before the EOT. The geographical origin of *Prominatherium* is not clear but the latter taxon is an early-diverging offshoot of anthracotheriines, a subfamily the earliest representatives of which occurred in the Pondaung formation, Myanmar, with *Anthracokeryx birmanicus* (see Pilgrim and Cotter, 1916; Scherler *et al.*, 2018). *Prominatherium dalmatinum*, exclusively known from Southeastern Europe in Adria and Dacia-Tisza tectonostratigraphic terranes, has always been retrieved in marine-related deposits (Grandi and Bona, 2017), which is rare for anthracothere fossils but suggestive of hypothetical sweepstake dispersals via small islands, stopped westward by a wider and more sustainable waterbody. Other Palaeogene remains of the Greater Adria terrane are from Motnik in Slovenia, and consist of a hyracodontid rhinocerotoid (*Prohyracodon telleri/orientale*; see Heissig 1990) and an indeterminate artiodactyl named *Anthracohyus slovenicus*, considered either as an anthracothere (Heissig, 1990), an achaenodontid (Heissig, 2001) or a possible cebochoerid (Lihoreau and Ducrocq, 2007). This fossiliferous locality is not well constrained in age, extending possibly from Bartonian through Oligocene times. Considering those elements, the Eocene fauna from the Greater Adria is very elusive and does not permit a clear biogeographic characterisation. However, it is established that this terrane was connected to different microcontinents corresponding to other terranes that may have compounded a homogeneous Southeastern European bioprovince (Fig. 4). Indeed, Greater Adriatic microcontinental domain could belong to a large unit that also included the Alcapa, Tisza-Dacia, Taurides, Pontides, and lesser Caucasus terranes (van Hinsbergen *et al*., 2020; Licht *et al*., 2022).

The existence of a Southeastern European bioprovince corresponding to the aggregation of all those terranes has already been proposed (e.g., Sen, 2013; Licht *et al*., 2022) on the base of the very peculiar terrestrial Anatolian faunas with notably the presence of embrithopods, brontothere perissodactyls (Tissier *et al*., 2018), pleuraspidotheriid ungulates (Métais *et al*., 2012; 2016), Afro-Asian primates (Beard *et al*., 2021), and puzzling metatherians assigned to anatoliadelphyids (Métais *et al*., 2018). In the light of this faunal distribution, the interpretation of sediment distribution, and paleogeography, the concerned area, separated from both Western Europe and Asia, was renamed Balkanatolia (Licht *et al*., 2022). The embrithopod from Rab Island is the westernmost embrithopod found in Europe to date. It seems to validate a distribution within the western tip of Balkanatolia at least during the late Eocene. It also coincides with the most recent representative of the subfamily together with those from Boyabat in Turkey, for which a possible earliest Oligocene age has been hypothesised (Sanders *et al*., 2014).

Considering the megafaunal guild besides anthracotheres and embrithopods, some dispersal patterns can be inferred from the fossil record. As for rhinocerotoids, several hyracodontids (*sensu* Bai *et al.*, 2020) were recovered from Adria (*Prohyracodon telleri*; Slovenia), Dacia-tisza (*P. orientale*; Romania) and Taurides (*Prohyracodon* sp.; Turkey) during the Bartonian–Priabonian interval (Wood, 1929; Uhlig, 1999; Licht *et al*., 2022). This family, well represented in Asia at least since the late Eocene (Dashzeveg, 1991), has never been documented in any Western European localities predating the Oligocene. Similarly, the presence of Amynodontidae prior to the Oligocene in Europe (Fig. 4) is restricted to terranes of Alcapa (Pannonan basin in Hungary), Tisza, and Dacia (Transylvanian basin in Romania; Balkanide Nappes in Bulgaria). These Eocene amynodontids have either Asian (*Amynodontopsis* aff. *bodei*, middle–late Eocene of Romania and Hungary; *Cadurcodon ardynensis*, late Eocene

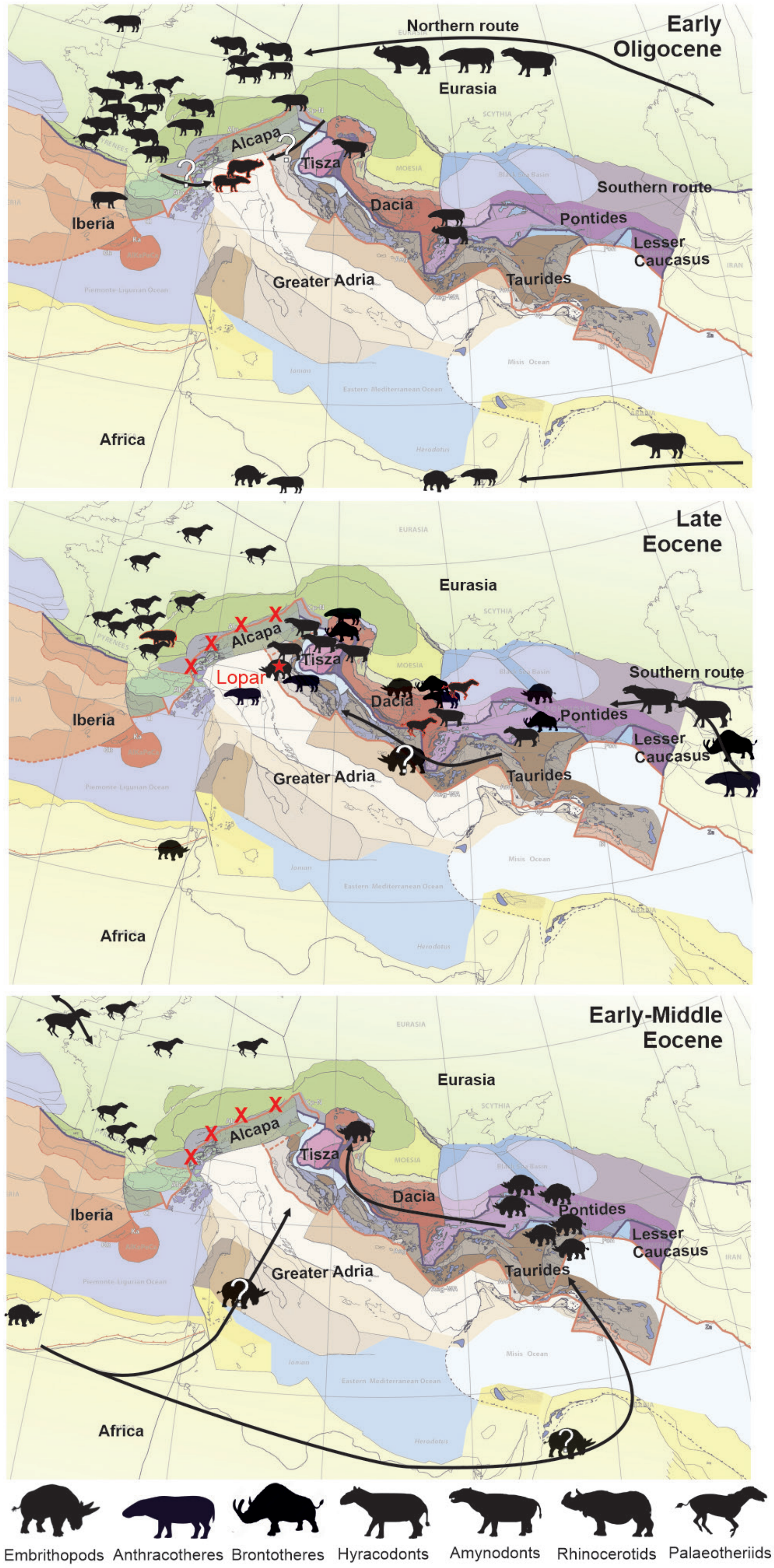

Figure 4. Spatiotemporal distribution of palaeoamasiine embrithopods and of main large mammalian families of the Palaeogene of Western Europe and Balkanatolia (references in the text). Tectonostratigraphic map from van Hinsbergen *et al*. (2020). Terranes Unit: Greater Adriatic, Alcapa, Tisza-Dacia, Anatolide-Tauride, Pontides and lesser Caucasus terranes. Small outlines are occurrences of taxa and larger ones indicate dispersal events; red outline are discussed occurences in the text; red star is Lopar fossil occurrence.

of Hungary; Tissier *et al.*, 2018; Wang *et al.*, 2020) or North American affinities (*Sellamynodon zimborensis*, late Eocene–early Oligocene of Romania; Tissier *et al.*, 2018; Veine-Tonizzo *et al.*, 2023). This Eocene wave of amynodontid dispersal to Eastern Europe (Balkanatolia) is fully distinct, both phylogenetically and temporally, from the second one, Oligocene in age, as documented by the conspicuous presence of *Cadurcotherium* (with two species) in the Oligocene of Western Europe (Veine-Tonizzo *et al.*, 2023). Indeed, the latter genus has earlier occurrences in South Asia (Antoine *et al.*, 2004; Métais *et al.*, 2009). Among rhinocerotoids, Paraceratheriidae (*sensu* Deng *et al.*, 2021) and Rhinocerotidae have also dispersed from East and South Asia to Asia Minor (Caucasus, Anatolia) and Eastern Europe (Bulgaria, Romania), but their records in Balkanatolia are all postdating the *Grande Coupure* (Saraç, 2003; Antoine *et al.*, 2008, in press; Sen *et al.*, 2011; Deng *et al.*, 2021). Another perissodactyl family, the Brontotheriidae, is known from Bartonian–Priabonian deposits of Tisza-Dacia terranes (*Brachydiastematherium transylvanicum* in Romania, and *Sivatitanops*? in Bulgaria; see Mihlbachler 2008) and a Priabonian locality of Taurides (*Embolotherium* aff. *andrewsi* from Turkey; Licht *et al*. 2022; Fig. 4). This family, well represented in the Eocene of North America and Asia and rarely found in eastern Europe, has never been recorded in Western Europe (e.g., Mihlbachler, 2008). Eastern European brontotheres have tight relationships with Asian taxa: *Brachydiastematherium* is gathered in a clade with the Mongolian and Chinese *Metatitan* spp. (Mihlbachler, 2008), the specimens from Bulgaria are close to *Sivatitanops birmanicus* from Myanmar, and *Embolotherium andrewsi* is mostly documented from China and Mongolia (Licht *et al*. 2022).

Therefore, the large mammal distribution (anthracotheres, rhinocerotoids, brontotheres, and embrithopods) suggests both a continuity in the Balkanatolian bioprovince at least during the late Eocene and a lack of connection with Oligocene Western European large mammals. Afro-Arabian born Embrithopoda dispersed toward Balakanatolia via the greater Adria terrane and/or the Taurides terrane (see Sen, 2013; Gheerbrant *et al.*, 2018). Thereafter their evolution and subsequent dispersions suggest an early/middle Eocene isolation of Anatolia (Licht *et al*., 2022). Indeed, the presence of latest middle–late Eocene brontotheriids, amynodontids, hyracodontids and anthracotheres of Asian origin in Balkanatolia suggests the presence of pathways over late middle–late Eocene times (Tissier *et al*., 2018; Licht *et al*., 2022). The newly-described distribution of embrithopods all over Balkanatolia (Adria, Tisza-Dacia, Taurides, and Pontides) is congruent with a late Eocene westward dispersal within Balkanatolia, likely related to the gradual aggregation of the terranes, and further matching the anthracothere westward dispersal (Grandi and Bona, 2017). Unfortunately, the lack of older fossil-yielding localities in the western part of Balkanatolia impedes refining palaeobiogeographical scenarios for the evolution of bioprovincialism on this continent.

Nevertheless, the discovery of a palaeoamasiine in the Great Adria substantiates the western extension of Balkanatolia during the late Eocene, and the lack of faunal exchanges with Western Europe during the late Eocene (late Bartonian and Priabonian; Fig. 4). Embrithopods, rhinocerotoids, and brontotheres are not known from late Eocene Western European localities (long-studied, well-sampled, and species-rich), and Oligocene anthracotheres and amynodontids from Western Europe are not phylogenetically linked to their earlier or coeval Balkanatolian counterparts. Based on this observation it can be hypothesized that Balkanatolia is not implied in the dispersal way from Asia to western Europe related to the *Grande Coupure* event (e.g., Stehlin, 1910; Pélissié *et al.*, 2021). The only putative exchanges between Western Europe and Balkanatolia during late Eocene times should be taken with caution. An astragalus from Greece discovered in the mid-19th century was tentatively attributed to *Palaeotherium* cf. *magnum* (Métais and Sen, 2017), a representative of a Western European endemic family of hippomorph perissodactyls (Danilo *et al*., 2013), but some doubt exists for the age of this specimen (Métais and Sen, 2017). Also claimed as belonging to a palaeotheriid, a fragmentary mandible attributed to *Plagiolophus* cf. *minor* has been described from Tscherno More, Bulgaria (Nikolov and Heissig, 1985). This locality, previously considered to be late Eocene/ early Oligocene in age, was recently ascribed a late middle–early late Eocene age (Mennecart *et al*., 2018). Another possible Eocene intrusion of Asian mammals through Western Europe – eventually via Balkanatolia coincides with the recognition of the anthracothere *Elomeryx crispus* at La Debruge (MP18, Priabonian), in southern France (Bonis, 1964). This single specimen (dP4-M1, Gervais, 1849; Bonis, 1964; Hellmund, 1991) is also the only known specimen of this species/family in Western Europe prior to the EOT and it originates from a very rich locality (both species-rich and in terms of specimens collected). This species displays clear phylogenetic relationships with Asian relatives and notably east Asian *Elomeryx* (Ducrocq and Lihoreau, 2006). It could also be linked to *Bakalovia*, an early-diverging bothriodontine taxon also described from Tscherno More, Bulgaria (Nikolov and Heissig, 1985; Hellmund, 1991) and Na Duong in Vietnam (Böhme *et al*., 2013). The last exceptions consist of three isolated remains of late Eocene Ruminants from Western Europe. One corresponds to a unique specimen of a gelocid, *Phaneromeryx gelyensis*, found by Gervais (1848) in Eocene lignite from St Gely du Fesc near Montpellier (Blondel, 2001). Some doubts were raised on its systematic attribution (see Métais and Vislobokova, 2007) and the exact location of this fossiliferous level is unknown as many lignite levels exist in the Eocene and Oligocene strata of this area. The two other ruminant remains present equivalent problems (Mennecart, 2012): only one specimen with dubious location. Besides those six cases, each represented by a unique specimen with possible confusion on its age, there is no evidence for late Eocene exchanges of large mammals between Western Europe and Balkanatolia.

Interestingly, Embrithopoda seemingly did not survive the EOT, when connectivity between Eastern and Western bioprovinces was efficient. This is also the case for hyracodontids, the first wave of amynodontids (see above), and brontotheres. It looks like Balkanatolia, despite a first colonisation from Asia during the late Eocene, did not display the typical fauna that would later disperse toward Western Europe, notably including the Rhinocerotidae, the amynodontid *Cadurcotherium*, the large anthracotheriids *Anthracotherium* and *Paenanthracotherium*, the Entelodontidae, and Ruminantia (Mennecart *et al*., 2018; Scherler *et al*., 2018). In other words, Eocene Balkanatolian taxa had no close phylogenetic affinities with those who invaded Western Europe after the EOT. Would the southern route have been a dead end, physically separated from Western Europe by a sea barrier? In that context, the exceptional fauna from Monteviale, in Northern Italy, perhaps result from a dispersal from Western Europe to Adria (Fig. 4). If so, it may have been favoured by a terrestrial connection, whereas a separation existed east of Monteviale during the early Oligocene interval due to the deepening of the Greater Adria continent under the Balkan (van Hinsbergen *et al*., 2020). This hypothesis should be confronted to a better-established early Oligocene fossil record for the Adria terrane.

CONCLUSIONS

The geographical distribution of palaeoamasiine embrithopods over Eocene times is relevant for mammalian history in Eastern Europe and Asia Minor. During this period, north- and westward dispersals of African and Asian land mammals are confined to an isolated continent, recently named as Balkanatolia (Fig. 4). This landmass has not been connected to Western Europe until the earliest Oligocene and might be critical in the framework of the underlying *Grande Coupure* Event by the Eocene–Oligocene Transition. By its presence on Rab Island, the specimen from Lopar confirms the western extension of this Eocene landmass that included the Adriatic realm. Conversely, it also underlines the lack of exchange with Western Europe for large mammals until the Eocene–Oligocene Transition. Future prospection of this area and formation could lead to new discoveries likely to further our knowledge of Balkanatolian mammalian communities from the Adriatic area. Ultimately, it may allow to understand mammalian distribution of this landmass and to highlight its potential role in the *Grande Coupure* Event.

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