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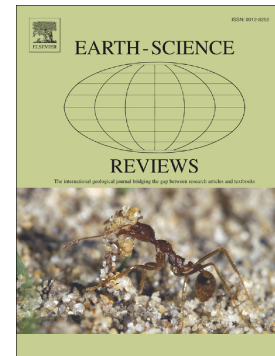
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Balkanatolia: the insular mammalian biogeographic province that partly paved the way to the Grande Coupure

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Abstract:

The Grande Coupure corresponds to a major episode of faunal turnover in western Europe around the Eocene-Oligocene boundary that is generally attributed to the influx of multiple clades of Asian mammals. However, Asian mammal clades begin to appear in the fossil record of southeastern Europe during the middle Eocene, 5-10 million years prior to the Grande Coupure. How and when these Asian mammal clades colonized southeastern Europe remains poorly understood, partly because the fossil record of mammals from nearby Anatolia is characterized by marked endemism and very limited exchanges with Asia during most of the Eocene. We resolve this apparent paradox by reviewing the age of existing paleontological sites from the Balkans to the Caucasus and documenting the oldest Asian perissodactyls found so far in central Anatolia, which date to the lower or middle Priabonian, 37.8 to 35 million years ago, on the basis of geochronological, magnetostratigraphic and biostratigraphic data. We show that the Eocene distribution of mammals across Eurasia supports a previously unrecognized biogeographic province, designated here as Balkanatolia, spanning the eastern and central segment of the Neotethyan margin. Isolated from mainland Eurasia during the early and middle Eocene, Balkanatolia

formed a low-topography archipelago where endemic and anachronistic mammals thrived. We show that the Eocene fossil record supports Balkanatolia having been colonized by Asian ungulates and rodents by the late Bartonian (mammalian Paleogene biohorizon MP16), following the establishment of a continuous terrestrial dispersal corridor across the central segment of the Neotethyan margin. This colonization event was facilitated by a drop in global eustatic sea level and a tectonically-driven sea retreat in eastern Anatolia and the Lesser Caucasus during the late middle Eocene. These paleogeographic changes instigated the demise of Balkanatolia as a distinct biogeographic province and paved the way for the dispersal of Asian endemic clades before and during the Grande Coupure in western Europe.

Keywords: Eocene, Anatolia, perissodactyls, Grande Coupure, Asian mammals, dispersal

1. Introduction

The mammalian biogeography of Eurasia during the Paleogene is commonly described as two distinct biogeographic provinces, western Europe and eastern Asia, separated by several epicontinental seaways acting as barriers (Brikiatis, 2014). For most of the Paleocene and Eocene, both regions display significantly different mammalian faunas with some level of intra-provincial endemism (Franzen, 2003; Menecart et al., 2021), punctuated by episodic long-distance exchanges with North America (Beard and Dawson, 1999; Beard, 2008) and Gondwana (Gheerbrant and Rage, 2006), and gradually increasing exchanges between eastern Asia and the Indian subcontinent (Klaus et al., 2016). The biotic provincialism shown in eastern and western Eurasia ended abruptly in the earliest Oligocene, 33.9 to 33.4 million years ago, with the decline of endemic Eocene animals in western Europe, such as adapiform primates, palaeotheriid perissodactyls and nyctitheriid laurasiatherians, and the rapid appearance of invasive taxa from eastern Asia, including crown clades of rodents (such as cricetids and castorids), perissodactyls (such as rhinocerotoids) and artiodactyls (such as anthracotheriids and hornless ruminants; Vianey-Liaud,

1991; Hartenberger, 1998; Hooker et al., 2004). This faunal turnover is often referred to as the “Grande Coupure” (Stehlin, 1909) and is roughly synchronous with the Oi-1 glaciation 33.5 million years ago (Hooker et al., 2004; Costa et al., 2011), the most dramatic episode of ice-sheet growth, eustatic sea level drop, and global cooling associated with the fall into the Oligocene Icehouse (Miller et al., 2009). However, this simple picture of two biogeographic provinces has been challenged by recent paleontological findings emphasizing the peculiarity of a third mammalian biogeographic region spanning from southeastern Europe to Anatolia, characterized by high endemism and earlier dispersal events (Tissier et al., 2018; Métais et al., 2018).

The discovery several decades ago of Eocene perissodactyls (amynodontids, hyracodontids, and bronthotheriids) and artiodactyls (anthracotheriids) in southeastern Europe showing Asian affinities had already underscored a clear biogeographic separation between western and southeastern European faunas prior to the Grande Coupure (Koch, 1897; Kretzoi, 1940; Nikolov and Heissig, 1985). Recent discoveries of additional Eocene mammals of Asian affinity, such as anthracotheriids in Italy (Grandi and Bona, 2017), amynodontids, bachitheriids (Menecart et al., 2018; Tissier et al., 2018) and cricetid rodents (de Bruijn et al., 2018) in the Balkans indicate that invasive mammals from Asia began to colonize southeastern Europe sometime between the Lutetian and the Priabonian, potentially as much as 10 million years before the Eocene-Oligocene transition (Tissier et al., 2018). However, when and how the first wave of Asian mammals reached to southeastern Europe remains poorly understood, because the ages of most of these fossil localities are associated with large uncertainties, as they are based on mammalian biostratigraphy and distant correlations between European and Asian fossil sites.

The geographic distribution of these early Asian immigrants spans a mosaic of Gondwana-derived and Laurasia-derived terranes assembled throughout the upper Cretaceous and lower Paleogene (van Hinsbergen et al., 2020). This amalgamation of terranes, designated here as Balkanatolia (Fig. 1), formed a low-elevation landmass from the Alpine region to the Lesser Caucasus for much of the Eocene.

Balkanatolia has a complex history of episodic drowning and emergence during the Eocene (Barrier et al.,

2018), and it has been depicted either as a discontinuous archipelago (Böhme et al., 2013) or a wide and continuous island (the Balkanian-Anatolian Island of Franzen, 2003). It has thus been proposed that Asia-derived mammals dispersed to southeastern Europe along a “southern route” through Balkanatolia, via island hopping and/or during episodes of quasi-complete emergence (Becker, 2009; Böhme et al.; 2013; Menecart et al., 2018, 2021).

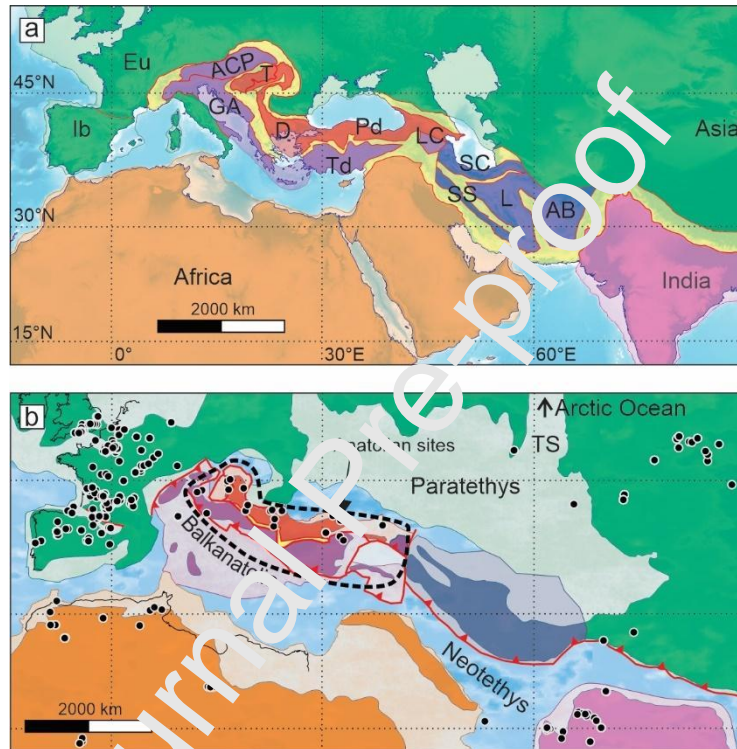


Figure 1. (a) The Neotethyan realm today, with major terranes highlighted as follows: Ib, Iberia; Eu, Western Europe; Asia (shown in green, comprising the core of mainland Eurasia); ACP, Alcapan; GA, Greater Adria; Td, Anatolide-Taurides (Gondwana-derived blocks shown in purple); T, Tisza; D, Dacia; Pd, Pontides; LC, Lesser Caucasus (Laurasian-derived blocks shown in red); SS, Sanandaj-Sirjan; SC, South Caspian; L, Lut; AB, Afghan Blocks (Middle Eastern Cimmerian blocks shown in blue). India is displayed in pink, Afro-Arabia in orange. Bright colors indicate emerged lands, faint colors indicate epicontinental seas; the approximate extent of oceanic seafloor is indicated in cyan blue. Sutures and accretionary complexes of the Paratethys and Neotethys are shown in yellow. (b) The Neotethyan domain during the middle Lutetian, 45 million years ago (color scheme similar to (a)); the areal extent of the

island or archipelago comprising Balkanatolia is highlighted by a dashed line; black dots are land mammal fossil sites of Eocene age. TS = Turgai Strait. See methods for the reconstruction procedure.

The past connectivity between individual Balkanatolian islands and the existence of this southern dispersal route remain debated because of the striking differences between Eocene mammal faunas on opposite sides of Balkanatolia, in southeastern Europe and Anatolia, respectively. Previously documented Eocene Anatolian mammal faunas from the Pontides and Anatolide-Tauride terranes indicate longstanding physical isolation from the rest of the world, because they comprise a unique mélange of endemic mammals including embrithopods (large afrotherian herbivores from Gondwana; Erdal et al., 2016; Gheerbrant et al., 2018), metatherians of Gondwanan origin (Métais et al., 2018), anachronistic survivors of an otherwise Paleocene European ungulate clade (Métais et al., 2017), with only bats (Jones et al., 2018) and primates (Beard et al., 2020) showing likely biogeographic affinities with Asia. Rodents have yet to be documented in Anatolia before the Eocene-Oligocene Transition (EOT; de Bruijn et al., 2003), and Asian ungulates remain undocumented before the late Oligocene (Métais et al., 2016). Yet the southern dispersal route through Anatolia cannot be ruled out because the temporal relationships among the endemic Eocene Anatolian faunas and the various Asia-derived fossils from Eocene sites in southeastern Europe remain poorly understood due to the poor geochronological resolution of many of the relevant fossil sites. That is, it remains unclear if these different faunal assemblages reflect biogeographic provincialism within Balkanatolia or different temporal stages within a single biogeographic province, before and after the establishment of a southern dispersal route linking Balkanatolia with adjacent parts of Asia.

This paper provides a synthesis of the biogeographic history of Balkanatolia and investigates the chronology of mammalian dispersal along the Neotethys margin preceding the Grande Coupure, based on new fossil material and an exhaustive review of Eocene fossil sites from central Europe to the Caucasus. We report here the discovery of the oldest ungulates from Anatolia showing clear biogeographic affinities with Asia, which constrain the arrival of invasive terrestrial vertebrates from Asia to Anatolia no later

than the early to middle Priabonian, at least 1.5 million years prior to the Grande Coupure. We show that current paleontological data from Balkanatolia do not require faunal provincialism to explain its various assemblages; regional fossil site chronology is consistent with an initial episode of colonization from Asia achieved by the late Bartonian, signaling the end of endemism in Balkanatolia. We show that this dispersal event possibly coincides with precursor faunal turnovers in western Europe predating the Grande Coupure, and thus indicates the initiation of a southern route for Eurasian dispersal as early as the late middle Eocene. The dispersal event is synchronous with a regional marine regression in Anatolia and the adjacent Caucasus, attributed to a combination of global eustatic drop and collisional tectonics along the central segment of the Neotethyan margin. This sea retreat established a continuous corridor for the dispersal of land mammals along the Neotethyan margin, triggering the demise of Balkanatolian endemism.

2. Materials and Methods

2.1 Regional context

Balkanatolia is defined as a semi-continuous strip of land during the Paleocene and Eocene between the western European craton and the Cimmerian terranes of the Middle East (Sanandaj-Sirjan, Lut and Afghan Blocks). To the north, the basement of Balkanatolia comprises Laurasia-derived terranes (Tisza, Dacia, Rhodope and Standja Massif, Pontides) that were separated from the core of Laurasia by back-arc spreading between the Late Jurassic and Late Cretaceous (Stephenson and Schellart, 2010). To the south, the basement of Balkanatolia incorporates individual terranes that rifted from Gondwana during the Jurassic (Alcapa, Greater Adria, Anatolide-Taurides, South Armenia) and accreted onto the Laurasia-derived terranes (van Hinsbergen et al., 2020). This accretion is the result of a long and protracted process that started in the Albian in western Balkanatolia (Dacia-Tisza accretion) and concluded in the late middle Eocene in eastern Balkanatolia with the final closure of the northern branch of the Neotethys (eastern Pontides-Taurides collision; Gürer et al., 2016). During the Paleocene and most of the Eocene, this

mosaic of terranes remained separated from other landmasses by expansive seaways of variable breadth: (1) from Africa by the southern branch of the Neotethys; (2) from the Western European Craton and Eurasia by the Paratethys (from west to east: Swiss Foreland Basin, Carpathian Basin, Luda Kamchia Trough, and the Black Sea); (3) from Middle Eastern Cimmerian terranes by remnant seaways connecting the Neotethys to the Paratethys on both sides of the Lesser Caucasus (Barrier et al., 2018; Palcu and Krijgsman, 2022). Balkanatolia experienced a complex deformation history during the Paleogene characterized by alternating stages of extension, thrusting and shortening, resulting in numerous local episodes of partial inundation and emersion (van Hinsbergen et al., 2020; Mueller et al., 2022). Balkanatolia was fragmented into numerous islands during most of the Paleocene and early Eocene (Alpine, Balkanian, Tisza and Dinaric Highs, Anatolian and Pontic lands of Popov et al., 2004). Many of the shallow seaways separating Balkanatolian islands retreated during the Lutetian, increasing land connectivity (Barrier et al., 2018). We estimate a maximum of ~950,000 km² emerged surface area for Balkanatolia during the middle Lutetian, roughly 1.6x the area of Madagascar, continuously spanning from the Alpine-Carpathian Basin to eastern Anatolia along the former suture of the northern branch of the Neotethys (see methods for the calculation). This wide area was once again partly inundated during the late Lutetian and early Bartonian, documented by the development of shallow reefs and carbonate platforms, particularly on the Pontics, Anatolide-Taurides, and lesser Caucasus. The late middle Eocene marine transgression retreated by the late Eocene (Okay et al., 2021). However, precisely when Balkanatolia achieved terrestrial continuity with Laurasia remains poorly constrained. To the east, seaways between Balkanatolia and the Cimmerian terranes of Iran gradually retreated between the late middle Eocene and the early Oligocene (Barrier et al., 2018). To the west, the Luda Kamchia Trough, which separates Balkanatolia from the Moesian Platform of southeastern Eurasia, became overfilled by continental deposits during the Priabonian (Doglioni et al., 1996).

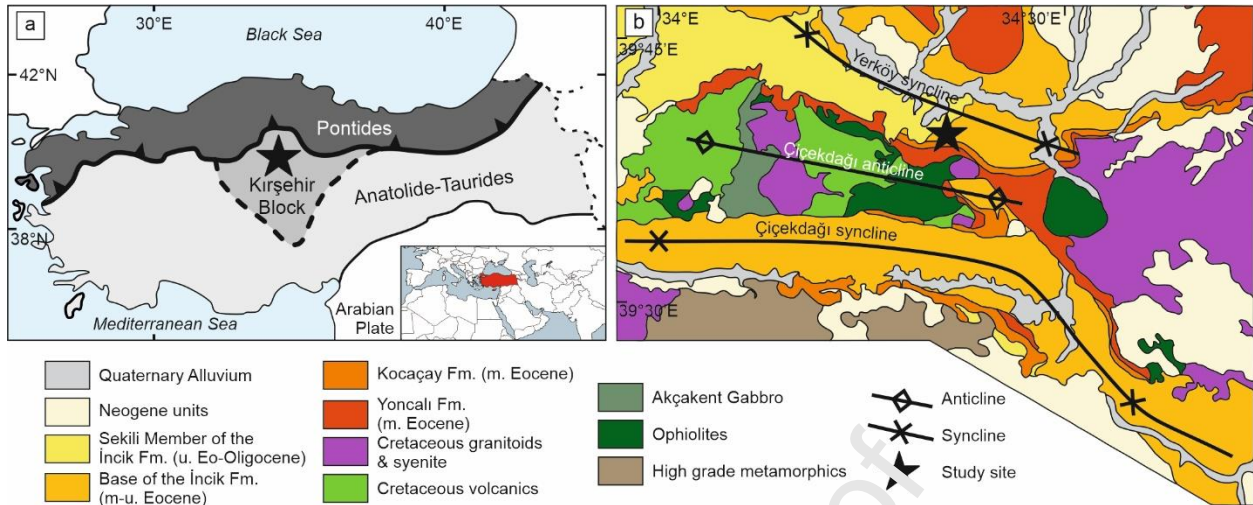


Figure 2. (a) Synthetic map of Anatolia, displaying its main tectonic units and the study area (Büyükteflek locality, shown with a star) modified from Licht et al., (2017). (b) Geological map of the Çiçekdağı region (after Dönmez et al., 2005; Gülyüz et al., 2013).

Our study area, the Büyükteflek locality in the Çiçekdağı region, falls within the eastern domain of Balkanatolia, at the edge of the Laurasian Pontides and Gondwanan Taurides (Fig. 2a). It is located ~ 200 km from some of the most iconic paleontological sites yielding Eocene Anatolian endemic fossils, such as embrithopods and pleuraspidotheriids (Çehaniye and Suluova Basins; Métais et al., 2012; 2018). The crystalline basement in the Çiçekdağı region belongs to the Kırşehir Block, a small block alternatively considered as a Cretaceous volcanic arc (Lefebvre et al., 2013) or as part of the central Taurides (van Hinsbergen et al., 2020) that was accreted onto the Pontides by the collision of the central Taurides in the latest Cretaceous-Paleocene (Licht et al., 2017). Cenozoic deposits in the Çiçekdağı region are exposed in two synclines located north and south of an E-W trending anticline exhuming Cretaceous ultramafic rocks and granitoids, the Çiçekdağı Anticline (Fig. 2b; Gülyüz et al., 2013). The stratigraphic sequence starts with the Yoncalı Formation made of middle Eocene basalts, volcanoclastic rocks and lignites (Akgün et al., 2002) that have yielded embrithopod remains (Erdal et al., 2016). They are overlain by late Lutetian limestones of the Kocaçay Formation, which are rich in nummulites (Gülyüz et al., 2013). The Kocaçay Formation is overlain by a molasse consisting of red beds, conglomerates and sandstone bodies deposited

following the folding, exhumation and denudation of the basin margin (Gülyüz et al., 2013). This molasse is mapped regionally as the İncik Formation, and it yields middle to late Eocene pollen assemblages (Akgün et al., 2002). In the southern syncline (the Çiçekdağı Syncline, also called the Çiçekdağı Basin), this molasse has been dated to the latest Bartonian-Priabonian by magnetostratigraphy (Gülyüz et al., 2013). In the northern syncline (the Yerköy Syncline), basal red beds and sandstones are overlain by unfossiliferous lacustrine deposits with marls, gypsum beds, and tuffs (Sekili Member of the İncik Formation) that are attributed to the Upper Eocene to Oligocene based on underlying and overlying units (Dönmez et al., 2005). In our study area, the contact with the Sekili Member is unconformable and marked by a continuous layer of conglomerates underlying a well-developed caliche; the base of the Sekili Member is then marked by ~ 200 m of conglomerates and sandstone bodies with reworked carbonate clasts and invertebrates from the Kocaçay Formation, regularly capped with caliches.

2.2 Methods

The vertebrate fossil specimens studied here were found in the basal red beds of the İncik Formation in the Yerköy Syncline, near the village of Büyükteflek. The fossil bed is a pedogenised red sandstone located ~ 50 m below an unconformity marking the transition to the Sekili Member. Specimens were prepared at the Muséum National d'Histoire Naturelle (Paris, France) and are housed in the paleontological collections of the Department of Geological Engineering, Eskişehir Osmangazi University (EOU), Eskişehir, Turkey. Measurements were obtained using a T&O digital caliper. Dental nomenclature follows Mhlbachler (2008). Detailed descriptions of the fossil specimens are available in Appendix A1.

We logged and sampled a 450 m sedimentary section spanning the fossil horizon, from the top of the Kocaçay Formation to the base of the Sekili Member. Rock samples for magnetostratigraphic dating were collected from 50 levels using a portable electric drill and orientated in situ, using standard paleomagnetic field equipment and procedures, with both magnetic and sun compasses. Most of the collected samples

are mudstones, siltstones and sandstones with preference for the finest grained layers whenever possible. Stepwise thermal demagnetization of the natural remanent magnetization (NRM) of each sample was conducted on a 2G cryogenic magnetometer hosted in a magnetically shielded room at the University of Rennes 1 (France); details about data acquisition procedure can be found in Westerweel et al. (2020) and in Appendix A2. The characteristic remanent directions (ChRMs) were determined after demagnetization by principal component analysis (Kirschvink, 1980) and corrected for basin tilt. Samples that were unstable during demagnetization or displayed a significant overprint of the present-day field (as observed on orthogonal demagnetization plots), resulting in poorly constrained ChRMs, were considered as low-confidence samples and not considered in our interpretations. Specimens with maximum angular deviations (MAD) above 15° were also rejected. The stable ChRMs were grouped in magnetozones based on polarity (normal or reverse) and compared with the Geomagnetic Polarity Timescale 2016 (Ogg et al., 2016). Detailed paleomagnetic results are given in Appendix A2.

Six samples from the uppermost layers of the Kocaçay Formation (levels 32-49 m) were selected for ostracod and foraminifera biostratigraphic dating. Micropaleontological identification was carried out at Dumlupınar University, Turkey; detailed results and microphotographs are available in Appendix A3. Four rock samples were selected for U-Pb dating of detrital/volcanic zircons. These include: one sandstone from the Kocaçay Formation (level 24 m, lowermost part of the section), one sandstone from the İncik Formation (level 100 m, ca. 25 m below the fossil bed), as well as two tuffs from the upper part of the section (level 355 and 455 m, above the unconformity). Zircon crystals were extracted by traditional methods of heavy mineral separation at the University of Washington, USA. U-Pb ages were generated using laser-ablation inductively-coupled-plasma mass-spectrometry (LA-ICPMS) with quadrupole and a laser spot diameter of 25 μm ; detailed methods for extraction, analysis, and data reduction can be found in Licht et al. (2020). Crystallization ages for volcanic samples were calculated using TuffZirc (Ludwig, 2003). The final age uncertainty around crystallization ages is the quadratic sum of the uncertainty of TuffZirc age calculation and of the systematic uncertainty ($\sim 2.67\%$ for the

$^{238}\text{U}/^{206}\text{Pb}$ ratios). We calculated the maximum depositional age for each detrital sample as the weighted average of the youngest zircon dates when the youngest three or more dates overlap (Dickinson and Gehrels, 2009). Detailed methods and U-Pb data are given in Appendix A4.

Paleogeographic maps for the Eocene (Fig. 1 and 5) were reconstructed with *Gplates* software for the paleo-position of Balkanatolian terranes and fossil sites, using the global plate rotation model provided by Poblete et al. (2021) and incorporating the high-resolution model of van Hinsbergen et al. (2020) for the Mediterranean domain, with fixed Eurasia. Paleo-shorelines are from Barrier et al. (2018) for the central and eastern Mediterranean domain and from Kovac et al. (2016) for the western Mediterranean domain, which were adapted to our plate rotation model using *Gplates* and *QGIS* software. Maps are displayed in Mercator ellipsoid projection (WGS84).

3. Results

Two taxa of fossil mammals, both of which pertain to Asian perissodactyl clades, have been recovered from basal red beds of the İncik Formation in the Yerköy Syncline. The first of these is documented by maxillary fragments (width x length: ca. 10x70 cm) with erupted molars (Fig. 3a) that pertain to a large brontothere, identified here as *Embolotherium* aff. *andrewsi* (see Appendix A1). The second taxon (Fig. 3b) is represented by an isolated upper molar pertaining to a hyracodontid rhinocerotoid, identified here as *Prohyracodon* sp. Brontotheriids are globally extinct by the end of the Eocene; the occurrence of *Embolotherium* in Anatolia considerably extends westward the distribution of the genus previously restricted to the Eocene of western China and Mongolia (Mihlbachler, 2008). Fossil specimens of *Prohyracodon* are described in the Bartonian-Priabonian (middle to upper Eocene) of East Asia (e.g. Chow and Xu, 1961) and southern Europe (Dacia-Tisza and Greater Adria terranes; Koch, 1897; Heissig, 1990) as well as from the late Oligocene of Georgia (Gabunia, 1964).

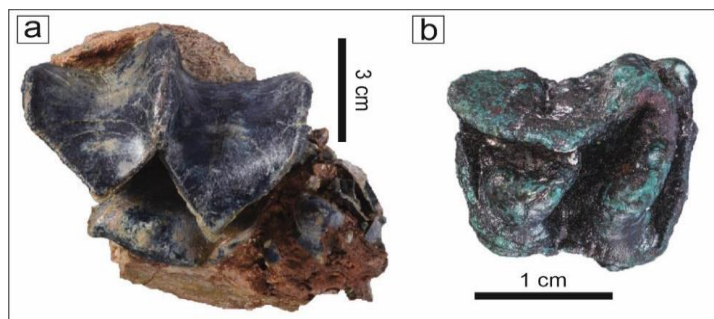


Figure 3. (a) Fragment of maxilla bearing a just erupted right M3 (hypocone missing) in occlusal view attributed to *Embolotherium aff. andrewsi*. (b) right M1 or M2 in occlusal view attributed to *Prohyracodon sp.* (additional images and systematic descriptions are provided in Appendix A1).

Fossil ostracods and foraminifera indicate a Priabonian biostratigraphic age for the uppermost beds of the Kocaçay Formation in our study area (see Appendix A3), providing a maximum age of 38 Ma for the İncik Formation and the fossil mammal site (base of the Priabonian; Fig. 4). This maximum age is corroborated by the two maximum depositional ages of 38.7 ± 0.5 Ma (in the Kocaçay Formation) and 36.4 ± 2.3 Ma (below the fossil bed) from detrital zircon ages. The two tuffs in the uppermost part of the section (Sekili Member) yield ages of 32.6 ± 1.2 and 32.1 ± 1.1 Ma, indicating an early Oligocene age. These absolute ages allow us to correlate the upper 150 m of our magnetostratigraphic logs to chron C13.n and C12.r and C12.n (ca. 33.5 to 31 Ma). The conglomeratic, lowermost part of the Sekili Member (first 50 m) does not yield enough high-confidence ChRMs data for a clear correlation; below the unconformity, the magnetostratigraphic record does not display any clear magnetozone with multiple samples of reversed polarity that could be correlated to chron C13.r, straddling the Priabonian-Rupelian transition. This suggests two possible magnetostratigraphic correlations for the lower part of the section: (1) either the base of the Sekili Member and all the underlying İncik Formation are correlated to chron C13.n (lowermost Rupelian), or (2) Chron C13.r is recorded in the conglomeratic lower part of the Sekili Member and/or partly missing due to the underlying unconformity, while the basal İncik Formation (and the fossil bed) correlates with the normal chrons of the early and middle Priabonian (C17.n, C16.n and

C15.n, from 38 to 35 Ma). This second correlation is favored because it is compatible with (a) the middle to upper Eocene pollen biostratigraphic age for the İncik Formation (Akgün et al., 2002); (b) the middle to upper Eocene magnetostratigraphic age of the İncik Formation further south, in the Çiçekdağı syncline (Gülyüz et al., 2013); (3) the presence of a thick caliche (> 1m thick) below the unconformity, and numerous additional caliches in the lower 50 m of the Sekili Member, corroborating a sedimentary gap and/or lower accumulation rates favoring the absence of chron C13.r in the magnetostratigraphic record; and (4) the exclusively Eocene stratigraphic range of brontotheres. The stratigraphic level yielding the fossils is thus attributed a lower to middle Priabonian age (38 to 35 Ma, overlapping with Mammal Paleogene biohorizons MP17-MP18).

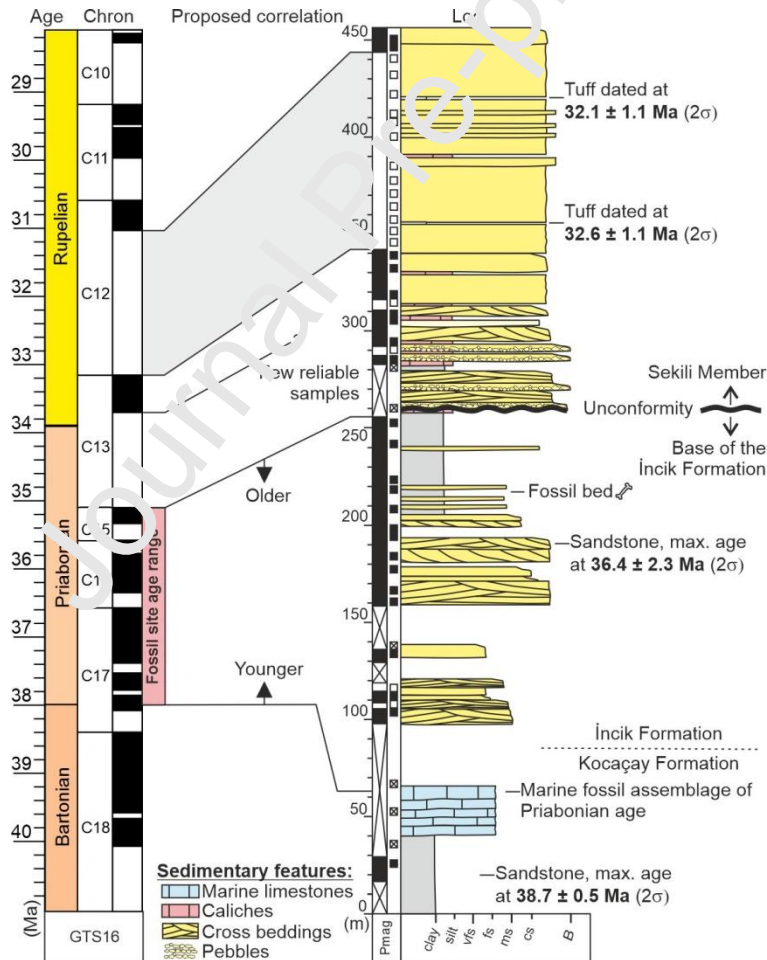


Figure 4. *Stratigraphic and magnetostratigraphic log of the Büyükteflek fossil locality in the Çiçekdağı Basin, and proposed correlation to the Geological Timescale (see main text for explanation).*

4. Discussion

4.1 A 2 stage-scenario for the biogeographic history of Balkanatolia

The discovery of late Eocene Asian ungulates in Anatolia provides a minimum age of middle Priabonian (>35 Ma) for the end of Anatolian biogeographic isolation. It shows that, like southeastern Europe, Asian ungulates reached Anatolia at least 1.5 million years before the Grande Coupure. In order to evaluate the relationship between Anatolian and southern European fossil localities, we compiled all published Balkanatolian sites with land mammals (all mammals excluding fossil sirenians, cetaceans and chiropterans) that have been attributed to the Eocene (31 in total). Age constraints at each locality (Table 1; Fig. 6) were updated following recent re-dating of several localities and excluding mammalian biostratigraphic constraints, to avoid the potential effects of island endemism on biostratigraphic correlations (e.g. Licht et al., 2017). Eocene terrestrial mammals of Balkanatolia consist mostly of embrithopods, artiodactyls, perissodactyls, pleuraspidothériid condylarths, anatoliadelphid metatherians, and rodents. Fossil assemblages are sorted according to the prominent biogeographic affinity of their respective faunas (Anatolian affinity: embrithopods, pleuraspidothériids, and anatoliadelphid metatherians; Asian affinity: hyracodontid, brontotheriid, amynodontid and rhinocerotid perissodactyls, bachitheriid and anthracotheriid artiodactyls, cricetid and murid rodents; European: palaeotheriid and hyrachiid perissodactyls).

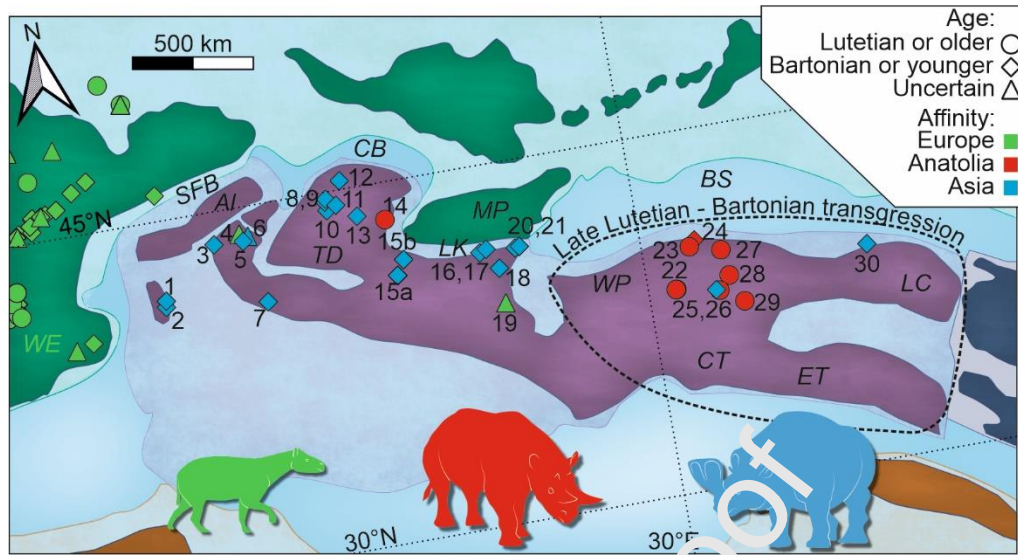


Figure 5: Synthetic paleogeographic map of Balkanatolia near the Bartonian-Priabonian Boundary, 38 million years ago. Color coding similar to Fig. 1; Laurasia and Gondwana-derived Balkanatolian terranes are shown in purple for simplicity. Fossil sites attributed to the Eocene are shown with circles (Ypresian-Lutetian), diamonds (Bartonian-Priabonian) or triangles (uncertain age); symbols are colored according to the dominant affinity of their fauna: European (in green), Asian (in blue), or Anatolian (in red). Site numbers relate to Table 1 and Fig. 5. See methods for the reconstruction. WE: Western Europe; SFB: Swiss Foreland Basin; Al: Alanya High; CB: Carpathian Basin; LK: Luda Kamcha Trough; MP: Moesian Platform; BS: Black Sea; TD: Tisza-Dacia; WP: Western Pontides; LC: Lesser Caucasus; CT and ET: Central and Eastern Taurides. Illustrations of key Eocene taxa are also displayed: European Palaeotherium (*palaeotheriid*, in green), Balkanatolian Palaeoamasia (*embrithopod*, in red), and Asian Embolotherium (*bronthoteriid*, in blue).

Arguably the oldest Balkanatolian ungulate showing Asian affinities, the amynodontid *Amyndontopsis* aff. *bodei* (site #6 on Fig. 5) was originally attributed to the upper Lutetian Dorog Coal near Budapest, but its exact provenance is unclear (Tissier et al., 2018) and Priabonian coal mines are present in the immediate vicinity of the Dorog Coal (Kozd Formation; Körmös et al., 2020). All other Balkanatolian fossil ungulates and rodents showing Asian affinity have been attributed to the Bartonian and/or

Priabonian stages of the Eocene. The temporal distribution of Asian ungulates in Balkanatolia is thus compatible with a dispersal event in the late middle Eocene, sometime during the latest Lutetian or Bartonian (42-38 Ma). Biogeographic affinities between late Eocene ungulates and rodents of Balkanatolia and East Asia suggest the persistence of a southern route for dispersal along the Neotethys since then (Böhme et al., 2013; Tissier et al., 2018).

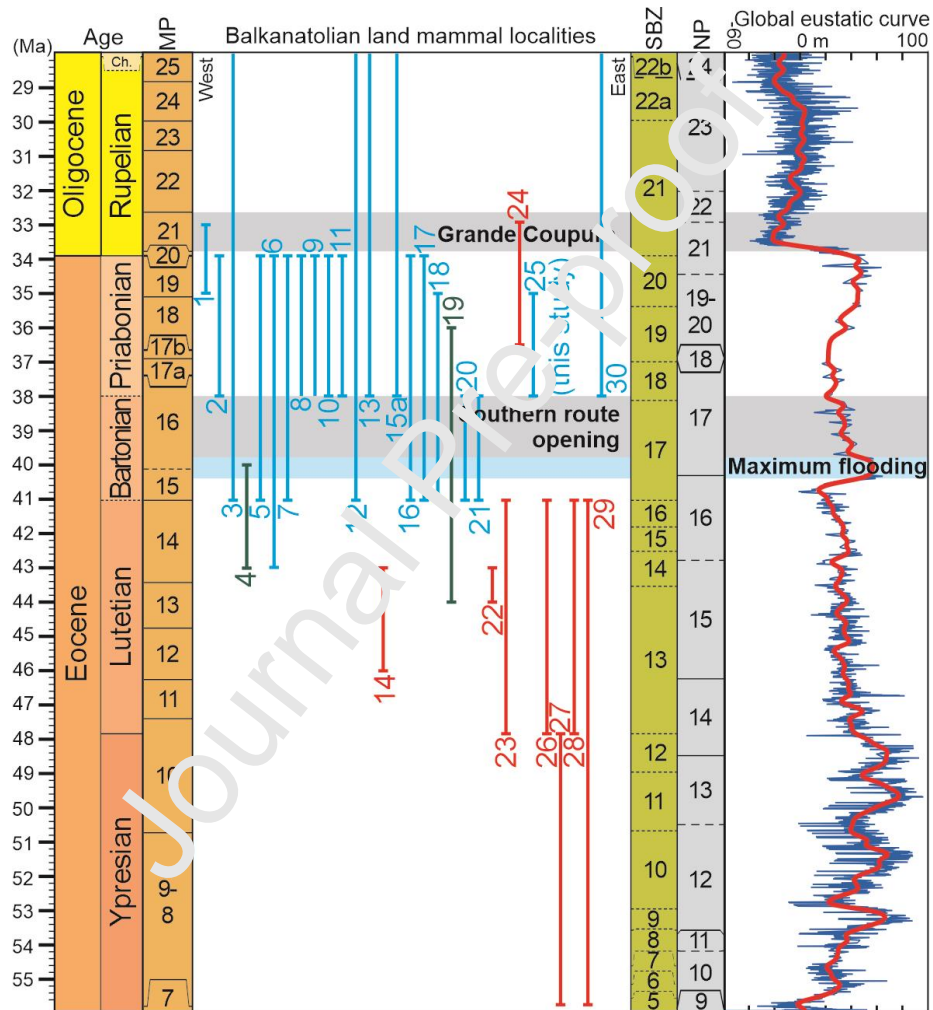


Figure 6: Age uncertainty of individual Balkanatolian localities sorted from east to west and according to their geographic affinity (in blue: Asia-derived; in green: Europe-derived; in red: Balkanatolia-derived); color coding and numbering similar to Fig. 5. European Mammalian Paleogene biohorizons (MP), large foraminifera Shallow Benthic Zones (SBZ), Nannoplankton zones (NP) from Ogg et al.

(2016) and the global eustatic curve of Miller et al. (2020) are displayed for comparison. The maximum flooding of eastern Balkanatolia is highlighted in light blue shading; the minimum age for the opening of the southern route and the timing of the Grande Coupure are shown in grey shading. With the apparent exception of the Boyabat Basin (site #24), there is no temporal overlap between Balkanatolia- and Asia-derived fauna.

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Table 1: Synthesis of Balkanatolian Fossil sites

Location #	Locality name	Terrane	Chronostratigraphic Age	Geochronological Age	Age constraints	Fossil land mammals	Fauna Affinity	References
1	Monteviale locality (Italy)	Adria	Upper Priabonian - lower Rupelian	35-33 Ma	Lignite with upper Priabonian marine microfossils. Pandolfi et al. (2017) and previous authors have proposed an early Oligocene age based on land mammal affinity.	Pantolestia (<i>Epapheliscus italicus</i> , ? <i>Dyspterna helbingi</i>), Rhinocerotidae (<i>Epiaceratherium bolcense</i>), Anthracotheriidae (<i>Anthracotherium mansvalense</i> , <i>Anthracocherus stehlini</i> , <i>Anthracocherus fabianii</i> , Anthracotheriidae ind.) and Paleocheridae (? <i>Propalaeocherus paronae</i>)	Asia	Böhme et al. (2014), Pandolfi et al. (2017)
2	Grancona locality (Italy)	Adria	Priabonian	37.8-33.9 Ma	Fossil bed attributed to the Priabonian based on its marine microfossils.	Anthracotheriidae (<i>Prominatherium dalmatinum</i>)	Asia	Grandi and Bona (2017)
3	Mottnig locality (Slovenia)	Adria	Bartonian-Oligocene	41-23 Ma	Late middle Eocene to Oligocene based on the age of nearby units. Correlation with Asian ungulate localities suggest a Bartonian-Priabonian age.	Anthracotheriidae (<i>Anthracochyus</i> sp.), Perissodactyla, Brontotheriidae (<i>Probrachytherium orientale</i>)	Asia	Heissig (1990)
4	Csordakut Locality, Pannonian Basin (Hungary)	Alcapa	Upper Lutetian - Bartonian	43-40 Ma	Unit attributed to marine biozone NP16 (Upper Lutetian - Bartonian).	Hyracodontidae (<i>Hyrachyus cf stehlini</i>)	Europe	Kocsis (2002)
5	Tapioszele locality, Pannonian Basin (Hungary)	Alcapa	Bartonian-Priabonian	41-33.9 Ma	Location of the sample is unsure. Attributed to the "Late Eocene" by Kretzoi (1940), expanded to the upper middle to upper Eocene based on the age of nearby units.	Amynodontidae (<i>Amynodon hungaricus</i>)	Asia	Kretzoi (1940), Tissier et al. (2018)
6	Dorog? locality, Pannonian Basin (Hungary)	Alcapa	Upper Lutetian - Priabonian	43-33.9 Ma	Location of the sample is unsure. Named as "Dorog substratum" in Budapest Museum collections; attributed to the Dorog Coal Formation near Dorog city by Tissier et al. (2018), which is dated on biozone NP16 (Upper Lutetian - Bartonian), but could also come from nearby Priabonian coals (Kosd Formation).	Amynodontidae (<i>Amynodontopsis</i> aff. <i>bodei</i>)	Asia	Tissier et al. (2018), Körmös et al. (2020)
7	Mt. Promina locality (Croatia)	Adria	Bartonian-Priabonian	41-33.9 Ma	Unit above Bartonian Flysch deposits, regional correlations suggest an Eocene age.	Anthracotheriidae (<i>Prominatherium dalmatinum</i>)	Asia	Vlahovic et al. (2012), Grandi and Boni (2017)
8	Bociu locality, Transylvanian Basin (Romania)	Dacia-Tisza	Priabonian	37.8-33.9 Ma	Unit above and below Priabonian limestones.	Cricetidae (<i>Atavocricetodon</i> cf. <i>nanooides</i>)	Asia	Baciu and Hartenberger (2001)
9	Treznea locality, Transylvanian Basin (Romania)	Dacia-Tisza	Priabonian	37.8-33.9 Ma	Unit above and below Priabonian limestones.	Cricetidae (<i>Pseudocricetodon</i> sp.)	Asia	Baciu and Hartenberger (2001)
10	Morlaca locality, Transylvanian Basin (Romania)	Dacia-Tisza	Priabonian	37.8-33.9 Ma	Unit above and below Priabonian limestones.	Perissodactyla, Amynodontidae (<i>Amynodontopsis</i> aff. <i>bodei</i>)	Asia	Tissier et al. (2018), Filipescu (2011)
11	Radaia/Andrashaza/Mera locality (Romania)	Dacia-Tisza	Priabonian	37.8-33.9 Ma	Unit above and below Priabonian limestones.	Hyracodontidae (<i>Prohyracodon orientale</i>), Brontotheriidae (<i>Brachydiastematherium transylvanicum</i>)	Asia	Koch (1897), Filipescu (2011)
12	Sacel locality (Romania)	Dacia-Tisza	Bartonian-Oligocene	41-23 Ma	No information on the site, but the basin is dominated by marine deposits until the Bartonian. Grandi and Bona (2017) attribute the site to the Eocene based on correlation with other anthracotheriids localities.	Anthracotheriidae (<i>Prominatherium dalmatinum</i>)	Asia	von Meyer (1854) in Grandi and Boni (2017)
13	Dobârca locality, Transylvanian Basin (Romania)	Dacia-Tisza	Priabonian to Oligocene	37.8-23 Ma	Locality of the fossil is unclear, and attributed to Priabonian-Chatian deposits.	Amynodontidae (<i>Sellamynodon zimborensis</i>)	Asia	Tissier et al. (2018)
14	Hateg Depression (Romania)	Dacia-Tisza	Middle to upper Lutetian	46-43 Ma	Unit correlated to nearby deposits attributed to Biozone NP15.	Embrithopoda (<i>Crivadioatherium Mackennai</i> , <i>C. Iliescu</i>)	Balkanatolia	Radulesco and Samson (1987), Proust and Hosu (1996)
15a	Buštranje Locality, Pčinja Basin (Serbia)	Dacia-Tisza	Priabonian to Oligocene	37.8-23 Ma	Regional correlations suggest a Priabonian - Oligocene age for the unit. The rodent assemblage suggests an Eocene age.	Muridae (<i>Pseudocricetodon</i> cf. <i>heissigi</i> , <i>Paracricetodon stajanovici</i> , <i>Witenia europa</i> , <i>Bustrania dissimile</i> , <i>Mogilia miloshi</i> , <i>Edirnella</i> sp.), Insectivora (<i>Erinaceidae</i> gen. et sp. ind.), Marsupialia (<i>Peratherium</i> sp.)	Asia (+ Balkanatolian marsupial?)	de Bruijn et al. (2018), van de Weerd et al. (2018), Markovic et al. (2018)

Table 1 (second page): Synthesis of Balkanatolian Fossil sites

Location #	Locality name	Terrane	Chronostratigraphic Age	Geochronological Age	Age constraints	Fossil land mammals	Fauna Affinity	References
15b	Zvonce Locality, Babušnica-Koritnica Basin (Serbia)	Dacia-Tisza	Eocene - Oligocene	56-23 Ma	Regional correlations suggest an Eocene - Oligocene age for the unit. The rodent assemblage suggest an Eocene age.	Muridae (<i>Edirnella</i> sp., <i>Mogilia miloshi</i> , ?Spalacinae), Insectivora indet., Artiodactyla indet., Carnivora indet	Asia	de Bruijn et al. (2018), van de Weerd et al (2018)
16	Nikolaevo Locality, Balkanide Nappes (Bulgaria)	Dacia-Tisza	Bartonian-Priabonian	41-33.9 Ma	Fossil site roughly correlated to the Tscherno More locality based on pollen assemblages, but originally attributed to the Priabonian based on correlations with Asian perissodactyl localities.	Amynodontidae (<i>Cadurcodon ardynensis</i>)	Asia	von Nikolov and Heissig (1985), Tissier et al. (2018)
17	Borov Dol locality (Bulgaria)	Dacia-Tisza	Bartonian-Priabonian	41-33.9 Ma	Fossil site roughly correlated to the Tscherno More locality based on pollen assemblages, but originally attributed to the Priabonian based on correlations with Asian perissodactyl localities.	Hyracodontia (<i>Forstercooperia</i> sp.)	Asia	von Nikolov and Heissig (1985), Menecart et al. (2018)
18	Thrace Basin (Bulgaria)	Dacia-Tisza	Bartonian to lower Priabonian	41-35 Ma	Unit below Priabonian marine beds. No maximum age for the unit, but sedimentation starts regionally in the uppermost Lutetian and the unit is stratigraphically high in the basin sequence.	Artiodactyla, Bacnitheriidae (<i>Bachitherium thracensis</i>)	Asia	Menecart et al. (2018)
19	Balouk Keui locality, Thrace Basin (Greece)	Dacia-Tisza	Upper Lutetian-lower Priabonian	44-36 Ma	Exact location of the fossil is unsure, two possible ages are proposed: upper Lutetian or Bartonian-lower Priabonian based on correlation with local units (dated with marine biostratigraphy and volcanics).	Palaeotheriidae (<i>Palaeotherium magnum</i>)	Europe	Metais and Sen (2017)
20	Kameno Locality, Balkanide Nappes (Bulgaria)	Dacia-Tisza	Bartonian	41-37.8 Ma	Fossil site near the Tscherno More locality and attributed to the same age.	Brontotheriidae (<i>Sivatitanops ?rumelicus</i>), Amynodontidae (<i>Cadurcodon ardynensis</i>)	Asia	von Nikolov and Heissig (1985), Menecart et al. (2018)
21	Tscherno More locality (Bulgaria)	Dacia-Tisza	Bartonian	41-37.8 Ma	Unit attributed to the Bartonian based on pollen assemblages and planktonic foraminifera.	Anthracotheriidae (<i>Bakalovia palaeopontica</i> , <i>B. asticus</i>), Brontotheriidae (<i>Sivatitanops ?rumelicus</i>), Palaeotheriidae (<i>Plagiolophus minor</i>)	Asia (+ European palaeotheriid)	Nikolov and Heissig (1985), Böhme et al. (2014)
22	Orhaniye Basin (Turkey)	Pontides	Upper Lutetian	44-43 Ma	Age constrained by detrital zircon ages and magnetostratigraphy.	Embrithopoda (<i>Palaeoamasia</i> sp., <i>Hypsamasia seni</i>) Pleuraspidotheriidae (<i>Hilalia saribeya</i> , <i>H. robusta</i> , <i>H. sezerorum</i> , <i>H. Selanneae</i>), Marsupialia (<i>Anatoliadelphys maasae</i> , <i>Galatiadelphys minor</i> , <i>Orhaniyeia nauta</i>), Primate (<i>Nesomomys bundens</i>)	Balkanatolia (+ Asian primate)	Licht et al. (2017), Metais et al., (2018)
23	Boyabat Basin (Turkey)	Pontides	Lutetian	48.6-41 Ma	Unit unconformably overlying upper Maastrichtian deposits and below uppermost Lutetian limestones, correlated to nearby Lutetian units.	Embrithopoda (<i>Palaeoamasia kansui</i>)	Balkanatolia	Ozansoy (1966), Sen and Heintz (1979)
24	Boyabat Basin (Turkey)	Pontides	Upper Priabonian - lower Rupelian	37-33 Ma	Fossil site located a few meters above marine beds attributed to biozone NP19-21.	Embrithopoda (<i>Palaeoamasia kansui</i>)	Balkanatolia	Sanders et al. (2014)
25	Büyükteflek locality, Southern Cankiri Basin (Yerköy syncline; Turkey)	Taurides	Lower to middle Priabonian	37.8-35 Ma	Age constrained by detrital zircon ages and magnetostratigraphy.	Brontotheriidae (<i>Embolotherium aff. andrewsi</i>), Hyracodontidae (<i>Prohyracodon</i> sp.)	Asia	This study
26	Cicekgadgi mine, Southern Cankiri Basin (Yerköy syncline, Turkey)	Taurides	Lutetian	48.6-41 Ma	Unit above Ypresian basalts and below uppermost Lutetian limestones, yield middle Eocene pollen assemblages.	Embrithopoda (<i>Palaeoamasia kansui</i>)	Balkanatolia	Akkiraz et al. (2008), Gülyüz et al. (2013), Erdal et al. (2016)
27	Eski-Celtek Mine, Suluova Basin (Turkey)	Pontides	Paleocene to Ypresian	56-48.6 Ma	Unit unconformably overlying upper Maastrichtian deposits and below lower Lutetian limestones, correlated to nearby Lutetian units.	Embrithopoda (<i>Palaeoamasia kansui</i>), Pleuraspidotheriidae (<i>Parabunodon anatolicum</i>)	Balkanatolia	Metais et al. (2012), Erdal et al. (2016)
28	Southern Cankiri Basin (Yozgat area, near Bultuzile; Turkey)	Taurides	Lutetian	48.6-41 Ma	Unit yielding middle to upper Eocene pollen assemblages and is below Lutetian limestones.	Embrithopoda (<i>Palaeoamasia kansui</i>)	Balkanatolia	Kaya (1995), Akkiraz et al. (2008)
29	Bogazliyan-YeniFakili locality (Turkey)	Taurides	Ypresian - Lutetian	56-41 Ma	Unit unconformably overlying upper Maastrichtian deposits and below Lutetian limestones, correlated to nearby Ypresian to Lutetian units.	Embrithopoda (<i>Palaeoamasia kansui</i>)	Balkanatolia	Ozankoy (1966), Sen and Heintz (1979)
30	Süngülü locality, Lesser Caucasus (Turkey)	Pontides	Priabonian - Rupelian	37.8- 28.1 Ma	Unit above middle Eocene volcanoclastic below upper Oligocene lignite-rich deposits.	Ctenodactylidae (<i>Ottomania proavita</i> , <i>Confiniummys sidiki</i>), Dipodidae (<i>Heosminthus minutus</i>), Muridae (<i>Paracricetodon wentgesi</i> , <i>Witenia fusca</i> , <i>Witenia flava</i> , <i>Edirnella kempeni</i> , <i>Pseudocricetodon aff. Montalbanensis</i> , <i>Eucricetodon kurthi</i> , cf. <i>Lignitella suemengeni</i>). Remains of Artiodactyla and Insectivora (ind.)	Asia	de Bruijn et al. (2003)

In contrast, all but one of the endemic Balkanatolian fossil assemblages showing Anatolian affinity (Boyabat Basin, site #24, late Eocene to early Oligocene; Sanders et al., 2014) are attributed to the Lutetian and/or the Ypresian, and thus mostly predate the appearance of Asia-derived mammals (Fig. 6). Continental Lutetian deposits are scarce in southeastern Europe, and the only unequivocally Lutetian site there (site #14, Romania) yields embriothopod fossils of Anatolian affinity (Radulesco and Samson, 1987). It is thus likely that the Anatolian endemic fauna once roamed over most, if not all, of Balkanatolia at the time of maximum terrestrial emergence (middle Lutetian). The arrival of Asian ungulate clades is synchronous with a quasi-disappearance of endemic Anatolian taxa in the fossil record, suggesting that the dispersal event roughly coincided with their decline. The embriothopod specimens from the Boyabat Basin (site #24; Sanders et al., 2014) and a possible marsupial specimen in the Pčinja Basin of Serbia (site #15a; de Bruijn et al., 2018), both post-dating the Bartonian suggest that some Anatolian endemic taxa may have persisted for several million years after the opening of the dispersal corridor.

These observations show that the marked differences in biogeographic affinities among Eocene faunas of Balkanatolia can be interpreted as reflecting temporal ordering rather than provincialism within Balkanatolia. The biogeographic history of Balkanatolia remains to be written in detail, because many of these sites lack precise age controls, and sites older than the Lutetian are particularly rare. However, our observations suggest at least two phases characterized by distinctive mammalian faunas: an endemic phase during the Ypresian and Lutetian, and an invasive phase defined by multiple first appearances of Asian taxa during the Bartonian-Priabonian. This 2-stage scenario is compatible with some degree of provincial endemism within Balkanatolia (Pandolfi et al., 2017), considering its complex history of inundation.

The faunal turnover on Balkanatolia is roughly coeval with the second Eocene Intra-European turnover of mammalian fauna of Franzen (2003), which spans over mammalian Paleogene biohorizons MP16-MP18 (middle Bartonian to middle Priabonian; Fig. 6) and is associated with the appearance of new artiodactyls (anthracotheriids, cainotheriids, and anoplotheriids), creodonts and carnivorans of Asian and Gondwanan

affinity in western Europe (Solé et al., 2014; Scherler et al., 2019). Anthracotheriids are documented as early as the Bartonian in southeastern Europe (Tscherno More, site #21, Bulgaria; Nikolov and Heissig, 1985); Eocene fossil specimens of these other newcomers remain to be documented on Balkanatolia. It is possible that the second Eocene Intra-European faunal turnover is a ripple effect of the dispersal of Asian immigrants to Balkanatolia, with some Asian newcomers as well as endemic Anatolian taxa pushing up to the western European shorelines. The presence of palaeotheriids at two southern European sites attributed to the latest Lutetian to early Priabonian (sites #4 and #19; Kocsis, 2002; Métais and Sen, 2017) and in the predominantly Asia-derived faunal assemblage of Tscherno More corroborate some degree of exchange between Europe and western Balkanatolia during the Eocene. On the eastern side of Balkanatolia, the presence of at least one fossil omomyid primate in the Lutetian fauna of the Orhaniye Basin also suggests limited, episodic exchanges between eastern Balkanatolia and East Asia before the opening of the terrestrial dispersal corridor, although fossil primates are known for their ability to cross maritime barriers more readily than other mammals (Beard, 2016; Beard et al., 2020). The penetration of Balkanatolian mammals into Asia during the Eocene remains undocumented if it occurred at all. However, the closest known Eocene land mammal fossil localities east of Balkanatolia are in Pakistan, and it is possible that the Cimmerian tethyanes hosted a mixed fauna having both Asian and Balkanatolian affinities.

4.2 Geological controls on the end of Balkanatolian endemism

The opening of a terrestrial dispersal corridor between Balkanatolia and Asia is synchronous with a series of dramatic paleogeographic changes at the eastern edge of Balkanatolia. While narrow epicontinental seaways on the eastern Pontides and on both sides of the Lesser Caucasus formed a buffer zone between Balkanatolia and Asia during the Ypresian and Lutetian (Barrier et al., 2018), the Bartonian is a time of tectonically-driven paleogeographic reconfiguration that eventually promoted regional sea retreats and land connectivity.

Most of the iconic endemic mammals (embrithopods, pleuraspidotheriid condylarths, anatoliadelphid metatherians) of Anatolia are found in coal seams, floodplain fines, or channel lags in continental clastic rocks directly below late middle Eocene limestones and marls (Erdal et al., 2016; Licht et al., 2017; Métais et al., 2018). These marine deposits represent the last Cenozoic transgression in the Pontides and Lesser Caucasus, preceding the establishment of a continuous terrestrial corridor from western Anatolia to the Middle East (Okay et al., 2021). In western and central Anatolia, these marine deposits are found in most Eocene sedimentary basins where they overlie sutures and basement rocks: the Güvenç Formation in the western Pontides (Oçakoğlu, et al., 2018), the Orhaniye Formation in the central Pontides (Licht et al., 2017), the Kocaçay Formation on the Kırşehir Block (including in our study area), and the Bolbeztepe Formation in the central Taurides (Gürer et al., 2016). The timing of transgression and later sea retreat varies from one basin to another, but these different units overlap the shallow benthic zones (SBZ) 14-17 and indicate a maximum flooding period during the uppermost Lutetian - lower Bartonian, sometime between 43 and 38 Ma (Licht et al., 2017). Further east, similar marine deposits are also found but have been less studied: in the eastern Taurides, most sedimentary basins are covered by marine carbonate platforms from the mid Lutetian to the Bartonian (Asartepe and Akpınar Formations; Gürbüz and Gül, 2005; Booth et al. 2014); in the eastern Pontides, the marine transgression reaches its maximum extent during the Bartonian (nannoplanktonic biozone NP 17; Hippolyte et al., 2017); in the Lesser Caucasus, shallow marine limestones are superimposed unconformably over sutures and topographic highs; these deposits are also attributed to the Bartonian (NP 17; Sosson et al., 2016). This regional high-stand likely corresponds to the ca. 500 kyr global eustatic high of the middle Eocene, dated at the base of biozone NP17 around 40 Ma (Miller et al., 2020). It is highly unlikely that Asian ungulates dispersed into Balkanatolia during this eustatic high. A precocious and possibly ephemeral dispersal episode from Asia to Balkanatolia before the high-stand and during the latest Lutetian-earliest Bartonian is possible but not required to explain the temporal distribution of Asia-derived taxa (Fig. 6). The transgression maximum is short-lived and most of the flooded basins and sutures return to fully continental conditions by the late Bartonian (Okay et al., 2021). By 37.7 Ma (earliest Priabonian), the onset of euxinic conditions on the

Paratethys side of the Caucasus indicates an abrupt decrease of water circulation between the Paratethys and Neotethys (van der Boon et al., 2017). We thus suggest a middle to upper Bartonian age (upper NP17 and SBZ17 biozones, ca. 39 - 38 Ma) for the opening of the dispersal corridor from Asia to Balkanatolia, which is compatible with the temporal distribution of Asia-derived fossils and the onset of the second Eocene Intra-European turnover during MP16 times (Fig. 6; Franzen, 2003).

The middle Bartonian global sea drop alone cannot explain the newly-acquired land connectivity between Balkanatolia and Asia, because later Eocene global sea-level remained roughly similar or even higher than Lutetian levels (Fig. 6). Interestingly, the temporal window centered around NP17 is also associated with a major change of tectonic regime in Anatolia and the Caucasus. Along the area spanning from central Anatolia to central Iran, the early to middle Eocene is a period of basin subsidence associated with crustal extension and arc and intra-plate magmatism. Both of these processes have been associated with either delamination following final suturing between the Pontides and Taurides (Schleiffarth et al., 2018), or back-arc extension related to Neotethyan slab roll back (Vincent et al., 2005). In the eastern and central Pontides, where extension is absent and shortening is active following the onset of the Pontide-Tauride collision at ca. 60 Ma, subsidence has been attributed to local flexural loading (Hippolyte et al., 2017; Ballato et al., 2018). The onset of sea retreat in the latest middle Eocene is associated with two regional events, emphasized in numerous geochronological and thermochronological studies: (1) the shut-down of arc magmatism in a wide belt spanning from the western Pontides to Iran, dated at ca. 39-37 Ma (Hippolyte et al., 2017; Schleiffarth et al., 2018); (2) the end of the extensional regime, replaced by renewed thrusting and exhumation along former fault zones, with associated molassic input, dated in low-temperature thermochronology between 40 and 36 Ma (Darin et al., 2018; Ballato et al., 2018). Both events have been attributed to a shift to a new compressional regime along the Neotethyan margin (Vincent et al., 2005; Gürer et al., 2016; Darin et al., 2018; Ballato et al., 2018). This new compressional regime has been explained either as reflecting the final suturing of the northern branch of the Neotethys in eastern Anatolia (Gürer et al., 2016; van Hinsbergen et al., 2020) or the onset of Africa-Asia collision and

the closure of the southern branch of the Neotethys (Vincent et al., 2005; Darin et al., 2018; Ballato et al., 2018). As a result, it uplifted regional marine basins or overfilled them with molassic material (Gülyüz et al., 2013; Okay et al., 2021), enhancing the regional sea retreat and thus directly contributing to the shrinking and removal of the marine barriers isolating Balkanatolia from the Cimmerian blocks located farther east. This new deformation regime thus promoted land connectivity along the Neotethyan margin, instigating the colonization of Balkanatolia by Asian mammals.

4.3 Implications

Aside from the occurrence of a late-surviving embriothopod in the latest Eocene of Anatolia (Sanders et al., 2014), the fossil record of Balkanatolia suggests that Asian immigrants rapidly replaced endemic faunal assemblages there, as also occurred during the Grande Coupure in western Europe. In contrast to the Grande Coupure, it is unclear from available evidence if a changing climate coincided with faunal turnover in Balkanatolia. Terrestrial Eocene paleoenvironments of Balkanatolia remain poorly documented and the evolution of their diversity and fragmentation requires a great deal of further study; nonetheless, pollen and stable isotopic data suggest a gradual trend toward more arid and seasonal floral assemblages along the Mediterranean margins during the late Eocene (Collinson and Hooker, 2003; Kocsis et al., 2014; Pound and Saltzman, 2017). This environmental stress could have enhanced the decline of Balkanatolian endemic taxa; however, it would also have favored the fragmentation of (sub)tropical forested habitats and wetlands associated with many of the incoming Asian ungulates (Böhme et al., 2013). In this sense, this climatic trend alone fails to explain the establishment of a southern dispersal corridor from Asia to Balkanatolia and eventually western Europe. Our current understanding of late Eocene climate evolution thus favors eustasy, tectonics, and associated paleogeographic changes as the primary triggers for dispersal and faunal turnover. That is, biotic interactions between endemic Balkanatolian taxa and invasive Asian clades, in the form of competition or predation or both, is the most probable causal factor underlying the extinction of Balkanatolian endemics and Balkanatolian faunal turnover more generally. It is well established, especially from Quaternary

records, that insular ecosystems and their endemic taxa are highly susceptible to invasive taxa (Cooke et al., 2017; van der Geer et al., 2017). Given the apparent absence of modern clades of ungulates, carnivorans and rodents in Balkanatolia prior to the establishment of a terrestrial dispersal corridor linking it with Asia during the late middle Eocene, the effects of the biotic interactions between these invasive Asian clades and endemic Balkanatolian mammals must have been substantial.

The seaways separating Balkanatolia and Europe all persisted until the earliest Oligocene except the Luda Kamchia Trough, which dried out sometime in the late Bartonian (Doglioli et al., 1996). This sea retreat episode connected Balkanatolia to the Moesian Platform but remained isolated from western Europe by shallow epicontinental seaways (Fig. 5). Most of these epicontinental seaways regressed following the eustatic drops of the early Oligocene (Barrier et al., 2018; Pálcu and Krijgsman, 2022) and incipient Alpine uplift (Kocsis et al., 2014), completing the land connection between Asia and Europe through Balkanatolia. The early Oligocene paleontological record of Balkanatolia is almost as scarce and poorly dated as the Eocene record and it is difficult to assess a potential increase of biotic exchanges with western Europe following the Oi-1 glaciation. We nevertheless suggest that Balkanatolia and the southern route served as a stepping stone to western Europe during the Grande Coupure as higher-latitude routes appear less favorable for large-scale dispersals. Indeed, the late Eocene and Oligocene plains of central Asia were dominated by desert steppe, semi-arid environments, cool temperate and boreal forests where some of the incoming Asian ungulates were not particularly favored (Barbolini et al., 2020; Tardif et al., 2021). Faunal exchanges between Europe and Asia through higher latitudes, such as evidenced by Mennecart et al. (2021) for some artiodactyls, were likely limited to taxa adapted to temperate or colder, drier environments; these high latitude bridges are yet inadequate for taxa adapted to wetter and warmer environments, such as anthracotheriids and possibly some rhinocerotoids (Böhme et al., 2014). The Turgai Strait, which connected the Arctic Sea to the Paratethys and is frequently proposed as the main biogeographic barrier between Europe and East Asia (Fig. 1), completely receded by 37 Ma, well before the Oi-1 glaciation, and experienced earlier events of closure during the Eocene (Kaya et al., 2019;

Poblete et al., 2021). If high-latitude dispersals barely occurred earlier in the Eocene when the climate was milder, they are less likely to have occurred after the transition into the Oligocene icehouse and the aridification of central Asia (Barbolini et al., 2020). The numerous late Eocene faunal turnovers of the Neotethyan domain thus occurred in multiple stages, starting in the middle Bartonian with the end of Balkanatolian endemism and eventually leading to the opening of the southern route to western Europe. These events can be seen as a long-term domino effect of the last stages of closure of the Neotethys, which commenced in the late middle Eocene and favored increased land connectivity between Balkanatolia, Europe, Asia, and eventually Africa. In this light, the convergence between Asia and Africa first favored dispersals parallel to the Neotethyan shorelines, between Asia and Europe, well before the first exchanges across the Neotethyan suture (Sen, 2013).

Precisely when Balkanatolia emerged as an independent mammalian biogeographic province remains unknown considering the paucity of its fossil record prior to the middle Eocene. Embrithopods and pleuraspidotheriids are found on Balkanatolia since at least Ypresian times (Suluova Basin, site #27) and nowhere else in Laurasia, suggesting isolation since at least the early Eocene. Métais et al. (2018) argue for a well-marked isolation since the late Paleocene as pleuraspidotheriids found in late Lutetian Anatolian deposits had disappeared everywhere else world-wide by the late Paleocene. The Gondwanan affinity of embrithopods (Glebehrant et al., 2018) and anatoliadelphid metatherians (Métais et al., 2018) indicates some degree of faunal exchange with Africa during the early times of Balkanatolian isolation. The late Paleocene-early Eocene time window also marks the assembly of Balkanatolia as a large archipelago with significant subaerial continental landmass, in response to a phase of increased deformation and uplift in Anatolia (Mueller et al., 2022). Middle Eocene Balkanatolia recalls in many ways the Indo-Australian Archipelago between Sundaland and the Australia-Papua shelf, and its associated biogeographic province, spanning respectively east and west of the Wallace and Weber's lines, coined "Wallacea" by Dickerson (1928). Both biogeographic provinces share a similarly complex geological history, marked by accretion between Gondwana-derived blocks and Laurasia fragments rifted

by back-arc processes. Both share highly endemic mammalian faunas, with limited penetration of foreign taxa. This endemism is a long-standing feature persisting for millions of years, despite the proximity of much wider biogeographic provinces, separated by narrow seaways. For both middle Eocene Balkanatolia (Métais et al., 2018; Beard et al., 2020) and Wallacea (Lohman et al., 2011), episodic dispersals and in-situ diversification seem to contribute equally to insular biodiversity. This simple analogy is only built on mammalian fossils and a more complete picture of past Balkanatolian biodiversity remains to be drawn. The fossil record of mammals and other vertebrates living on islands is remarkably poor, mainly consisting of examples from <100,000 years ago (van der Geer et al., 2011); the rich terrestrial fossil record of Balkanatolia thus provides a unique opportunity to document the evolution and demise of island biotas in deep time.

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Conflict of Interest

The authors declare that they have no competing interests.

Data availability statement

Detailed paleontological descriptions, geochronological and paleomagnetic results, and the synthesis of Balkanatolian taxa are provided in the appendices.

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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