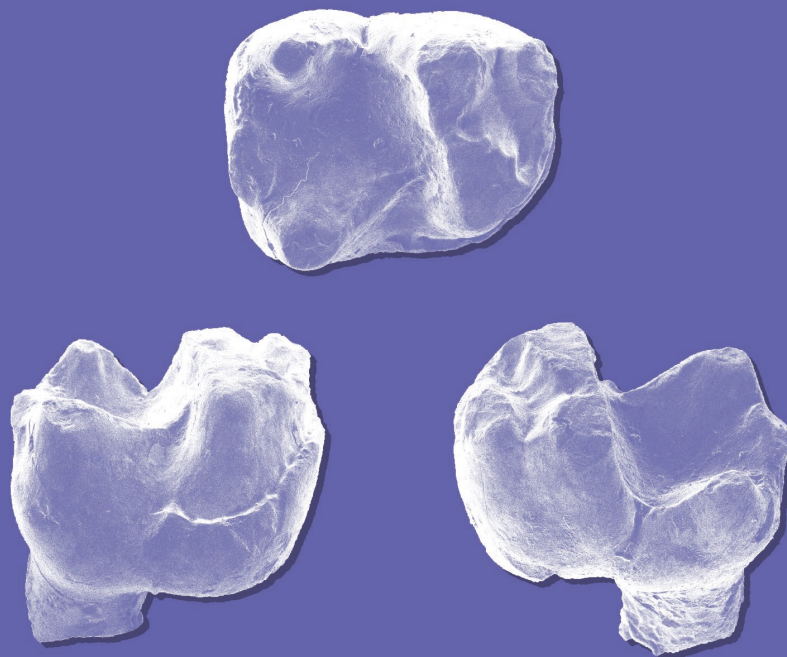


Additions to the late Eocene Süngülü mammal fauna in Easternmost Anatolia and the Eocene-Oligocene transition at the periphery of Balkanatolia

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Additions to the late Eocene Süngülü mammal fauna in Easternmost Anatolia and the Eocene-Oligocene transition at the periphery of Balkanatolia

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ABSTRACT

The Eocene-Oligocene transition marks a period of dramatic global climatic change correlated with pronounced mammalian faunal change. Fossil evidence is indispensable for studying the distribution of taxa through time, and determining how abiotic parameters shaped ancient biodiversity. Here we report ruminant artiodactyls and a new anthropoid primate from Süngülü, a locality in Eastern Anatolia that has yielded a diversified and largely endemic assemblage of rodents. Three taxa of

KEY WORDS
Balkanatolia,
Ruminantia,
anthropoid primate,
Eocene-Oligocene
transition,
new genus,
new species.

MOTS CLÉS
Balkanatolie,
Ruminantia,
primate anthropoïde,
transition Éocène-
Oligocène,
genre nouveau,
espèce nouvelle.

ruminants are recognized, the tragulid *Iberomeryx parvus* Gabunia, 1964, a larger species of *Iberomeryx* Gabunia, 1964, and a bachitheriid referred to cf. *Bachitherium* sp. A lower molar is identified as the new eosimiid primate *Sungulusimias unayae* n. gen., n. sp., which is the first occurrence of Paleogene anthropoids in western Asia. The lower molar of *Sungulusimias unayae* n. gen., n. sp. is characterized by protoconid and metaconid closely spaced and of similar height and volume, paraconid cuspidate and nearly connate with metaconid, strong mesiobuccal cingulid, and entoconid without strong connection to hypoconulid via the postcristid. The composition of this assemblage together with rodents indicates a probable Latest Eocene age for Süngülü, although an early Oligocene age cannot be completely ruled out. The rodent fauna from Süngülü suggests that endemism persisted at the periphery of Balkanatolia until the latest Eocene while Eastern Anatolia was situated in a strategic corridor for faunal exchanges between eastern Asia, Indo-Pakistan and Europe. During the Eocene-Oligocene transition, Balkanatolia probably functioned as a “holding pen” where various taxa were confined for significant intervals of time before proceeding to colonize Western Europe at the Grande Coupure.

RÉSUMÉ

Nouvelles données sur la faune de mammifères de l'Éocène supérieur de Süngülü en Anatolie orientale, et sur la transition Éocène-Oligocène à la périphérie de la Balkanatolie.

La transition Éocène-Oligocène est marquée par une période de changements climatiques globaux spectaculaires corrélés à des changements prononcés de la faune mammalienne. Les fossiles sont indispensables pour étudier la distribution des taxons dans le temps et comprendre comment les paramètres abiotiques ont façonné la biodiversité passée. Nous présentons ici les artiodactyles ruminants et un nouveau primate anthropoïde de Süngülü, une localité de l'Anatolie orientale qui a livré un assemblage diversifié et largement endémique de rongeurs. Trois taxons de ruminants sont identifiés, le tragulidé *Iberomeryx parvus* Gabunia, 1964, une espèce plus grande d'*Iberomeryx* Gabunia, 1964, et un bachithériidé laissé en cf. *Bachitherium* sp. Une molaire inférieure (probablement m2) est identifiée comme un nouveau primate eosimiidé *Sungulusimias unayae* n. gen., n. sp. qui est la première occurrence d'anthropoïde paléogène en Asie occidentale. La m2 de *Sungulusimias unayae* n. gen., n. sp. est caractérisée par un protoconide et métaconide rapprochés ainsi que de même hauteur et volume, un fort cingulide mésio-labial, et un entoconide sans forte postcristide reliée à l'hypoconide. La composition de cet assemblage de mammifères indique un âge probable de l'Éocène supérieur pour Süngülü, bien qu'un Oligocène basal ne puisse pas être complètement exclu. La faune de rongeurs de Süngülü suggère que l'endémisme a persisté à la périphérie de la Balkanatolie jusqu'à l'Éocène supérieur, tandis que l'Anatolie orientale était située dans un corridor stratégique pour les échanges de faune entre l'Asie, l'Indo-Pakistan et l'Europe. Au cours de la transition Éocène-Oligocène, la Balkanatolie a probablement fonctionné comme un sas où certains taxons ont été confinés durant l'Éocène supérieur avant de coloniser l'Europe de l'Ouest à la Grande Coupure.

INTRODUCTION

From the Late Cretaceous to the late Paleogene, the area spanning from the Balkans to Pakistan has experienced multiple collision and deformation events associated with the closure of the Neotethys Ocean and convergence between the Eurasian and African/Arabian Plates. These events have resulted in the formation of long, semi-continuous strips of land, bound by the Paratethys to the north and the Neotethys to the south, displaying a complex pattern of evolving seaways and land-bridges (e.g. Popov *et al.* 2004; Barrier *et al.* 2018). The complex and dynamically changing paleogeographic configuration of this area shaped its biogeographic history as well as faunal exchanges between Africa, Asia, Europe, and India. Paleontological data suggest that a low-topography land mass covering the Balkans and Anatolia—recently named Balkanatolia—existed during at least the early and middle Eocene, which was populated by endemic and anachronis-

tic mammals reflecting its isolation from mainland Eurasia (Kappelman *et al.* 1996; Métais *et al.* 2018; Licht *et al.* 2022; Beard *et al.* 2023). This geographic isolation seems to have ceased through various stages of biogeographic connection with Eurasia by the late Eocene.

Eastern Anatolia consists of three terranes that are all attributed to the Balkanatolian landmass: the eastern Pontides, the eastern Taurides and the Armenia Block (van Hinsbergen *et al.* 2020). During the Eocene, the area was separated from other emerged lands further east (the Cimmerian blocks of Iran) by remnant seaways connecting the Neotethys to the Paratethys on both sides of the Lesser Caucasus. Eastern Anatolia hosts multiple intermontane pull-apart basins and grabens, the sedimentary fill of which is often attributed to “undifferentiated Neogene” in geological reports (Şengör *et al.* 2008). Older, Oligocene deposits commonly display an overall regressive trend, with shallow marine deposits passing upward to detrital and gypsiferous facies (Adamia *et al.* 2010);

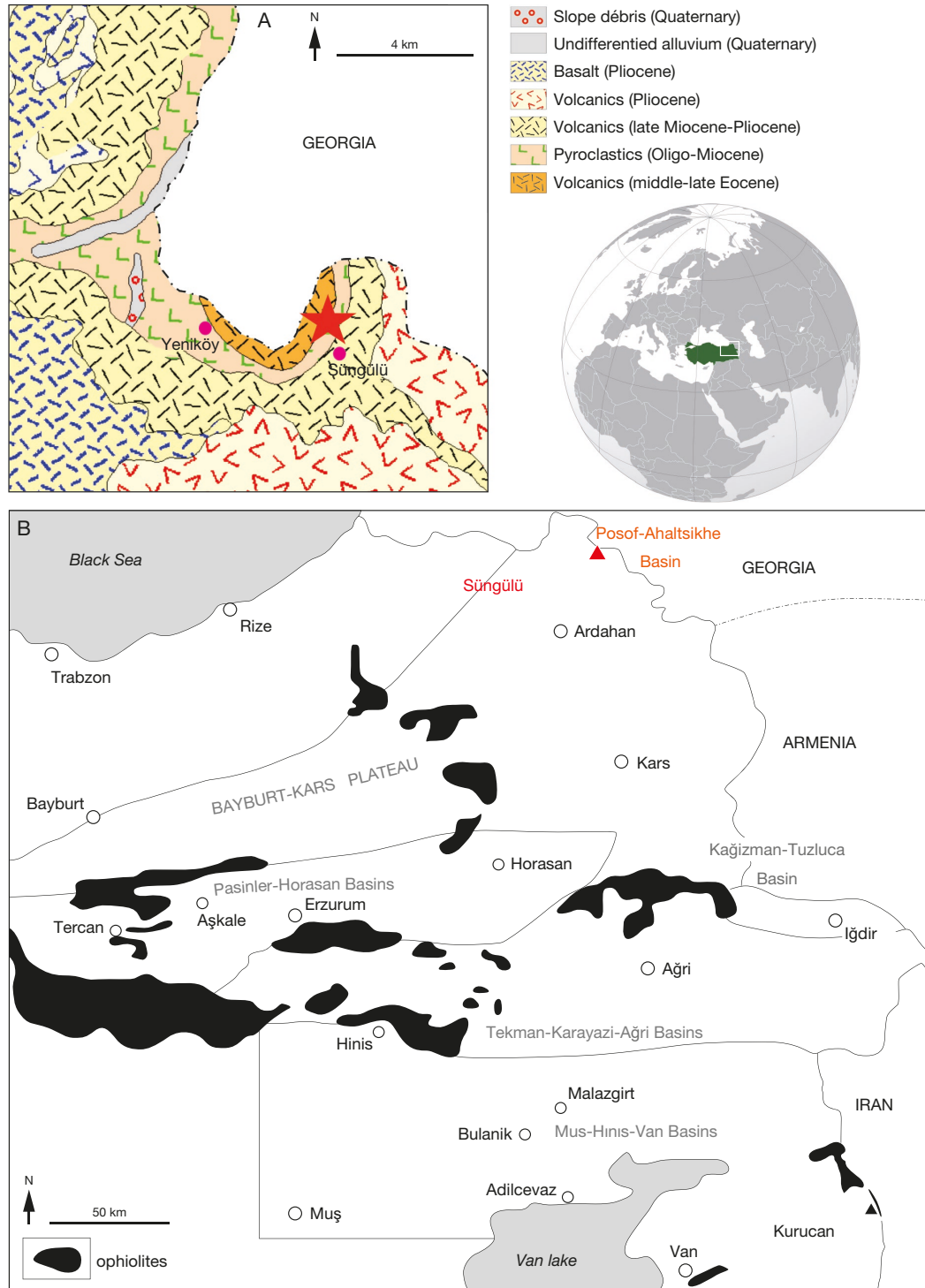


FIG. 1. — **A**, Location map of the Süngülü, Ardahan province, Eastern Anatolia; **B**, simplified geological map of the area redrawn after the 1/500 000 scale geological map of Turkey.

this trend is attributed to the onset of regional deformation following the final closure of the Neotethys and the drying-out of the remnant seaways.

The Posof-Ahalsikhe Basin (Fig. 1) lies at the edge of the eastern Pontides in the Lesser Caucasus and was filled with a detrital sequence dated as Oligocene based on marine molluscs (Yilmaz *et al.* 2001); the top of the sedimentary sequence consists of continental coal deposits and red clastics that have yielded the Benara mammal fauna generally considered as “middle” (Lucas & Emry 1999) or late Oligocene (Gabunia 1964). Only two other localities have yielded late Paleogene mammals in Easternmost Anatolia: 1) the late Oligocene Güngörmez Formation in the Kağızman-Tuzluca Basin has yielded sparse mammal remains, including large rhinos (Sen *et al.* 2011) and ruminants (Métais *et al.* 2015); and 2) the Süngülü locality, of debated late Eocene-early Oligocene age, in the Posof-Ahalsikhe Basin near the Turkish-Georgian border, has produced a diverse assemblage of small mammals, of which only the rodents have been described previously (de Bruijn *et al.* 2003). Paleogene mammals from Eastern Anatolia remain barely known, although they are of utmost significance for understanding the early evolution and distribution of modern faunas during an interval marked by strong climatic pulses. This dearth of paleontological data hampers attempts to reconstruct the complex biogeographic history of this region.

The aim of this paper is twofold: 1) describing the artiodactyl and primate fossils known from the Süngülü locality; and 2) analyzing their biochronological and paleobiogeographical implications in the context of the dismantling of Balkanatolia.

MATERIAL AND METHODS

The fossil material described herein was collected by screen washing about 3.5 tons of sediment (de Bruijn *et al.* 2003). The mammal remains have been collected from two successive beds: a $\pm$ 40 cm thick tuffite and the overlying $\pm$ 30 cm of white silty limestone with silicified nodules, but no significant difference in the faunal assemblages of these two beds has been detected (de Bruijn *et al.* 2003). The Süngülü mammal assemblage is dominated by rodents, and apart from artiodactyls and a single primate, it also includes insectivorous mammals and reptiles (de Bruijn *et al.* 2003). The specimens are permanently deposited in the collections of the MTA museum of Natural History, Ankara; casts of these fossils are available at the University of Utrecht (Netherlands). The measurements of teeth or postcrania are taken to measure the maximum length and width (maximum crown height was measured from the base of the crown to the tip of enamel for teeth). Measurements have been realized thanks to a caliper (precision 0.1 mm). The dental terminology follows Barmann & Rössner (2011) and Ni *et al.* (2016), the postcranial terminology follows Martinez & Sudre (1995).

ABBREVIATION

GABI Great American Biotic Interchange.

SYSTEMATIC PALAEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order ARTIODACTYLA Owen, 1848
Suborder RUMINANTIA Scopoli, 1777
Family TRAGULIDAE Milne-Edwards, 1864

Genus *Iberomeryx* Gabunia, 1964

Iberomeryx Gabunia, 1964: 179.

TYPE SPECIES. — *Iberomeryx parvus* Gabunia, 1964.

DIAGNOSIS (from Mennecart *et al.* 2021). — Small-sized ruminant with upper molars possessing the following combination of characters: well-marked parastyle and mesostyle in small-column shape; strong paracone rib; metacone rib absent; metastyle absent; unaligned external walls of metacone and paracone; strong postprotocrista stopping against the anterior side of the premetacrista; continuous lingual cingulum, stronger under the protocone. Lower dental formula is primitive (3-1-4-3) with non-molarized premolars. Tooth c is adjacent to i3. Tooth p1 is single-rooted, reduced and separated from c and p2 by short diastemata. The premolars have a well-developed anterior conid. Teeth p2-p3 display a distally bifurcated mesolabial conid. Tooth p3 is the largest premolar. Tooth p4 displays no mesolingual conid and a large posterior valley. Regarding the lower molars, the trigonid and talonid are lingually open with a trigonid more tapered than the talonid. The anterior fossa is open, due to a forward orientation of the preprotocristid and the presence of a paraconid. The internal postprotocristid is oblique and the external postprotocristid reaches the prehypocristid. The internal postprotocristid, postmetacristid and preentocristid are fused and Y-shaped. Protoconid and metaconid display a weak *Tragulus* Brisson, 1762 fold and a well-developed *Dorcatherium* fold, respectively. The mandible displays a regularly concave ventral profile in lateral view, a marked incisura vasorum, a strong mandibular angular process, a vertical ramus, and a stout condylar process.

TYPE LOCALITY. — Benara, Georgia, late Oligocene.

Iberomeryx parvus Gabunia, 1964

Iberomeryx parvus Gabunia, 1964: 182.

TYPE MATERIAL. — **Holotype**. PIT-7-08, fragmentary maxilla preserving left M1-M3, Georgian National Museum, Tbilisi, Georgia.

Iberomeryx sp.
(Fig. 2P-Q)

REFERRED MATERIAL. — Sü-2016, left m3 (third lobe, hypoconulid lacking)

LOCALITY. — Outcrop of unnamed rock unit consisting of *c.* 40 cm thick tuffite bed containing gastropod operculae superposed by *c.* 30 cm thick white silty limestone with silicified nodules exposed in a streambed roughly two km northwest of Süngülü, Ardahan Province, Turkey (de Bruijn *et al.* 2003: fig. 1). Latest Eocene according to de Bruijn *et al.* (2018, 2019).

DESCRIPTION

The m3 is incomplete since the third lobe bearing the hypoconulid is damaged, and the mesial margin and labial flank of the protoconid are broken (Fig. 2). The molar is brachyo-



bars: A-I, P-S, 1 mm; J-O, 4 mm.

preentocristid that stops at the base of the posterior wall of the trigonid. The external postprotocristid is barely visible (but present) and fused with the distal portion of the prehypocristid. The metaconid displays a short and marked external postmetacristid. Although attenuated (on its labial side), the M-structure is present (Fig. 2). The entoconid is more mesially positioned than the hypoconid, it displays a strong wear facet on its posterior face, and it is not transversely compressed as in *Iberomeryx parvus*. The posthypocristid extends lingually and its distal extremity is connected to a mesio-distally extended pre-hypoconulid cristid. There is a crest extending mesio-

TABLE 1. — Measurements (in mm) of the ruminant dental material from Süngülü discussed in the text. The asterisks designates estimated values.

Taxon	Rank	Specimen	Length	Width
<i>Iberomeryx</i> sp. cf. <i>I. parvus</i>	p3	Sü-2002	3.8	1.4
	p4	Sü-2003	4	1.7
	p4 (talonid)	Sü-2005	—	1.6
	m1	Sü-2009	3.9	1.8-2.0
	lingual M1 or M2	Sü-2010	3.7*	—
<i>Iberomeryx</i> sp.	m3	Sü-2016	7.1*	3.6
cf. <i>Bachitherium</i> sp.	M1 or M2	Sü-2017	5.4	—
	p4	Sü-2019	—	2.5
<i>Sungulusimias unayae</i> n. gen., n. sp.	m2	Sü-2020	3	2.4

distally at the base of the posterior wall of the entoconid which is most probably a remnant of the internal pre-hypoconulid cristid, suggesting that the hypoconulid was connected to the rest of the talonid by two cristids.

TAXONOMIC ATTRIBUTION

Even considering intraspecific size variability, this m3 is roughly twice as large as would be expected for an m3 that would match the size of Sü-2009 (m1). The current sample from Süngülü does not allow us to estimate the size variability of *Iberomeryx* sp. cf. *I. parvus*, but the size of this m3 surpasses the size variability observable in the extant tragulid *Tragulus kanchil* (Raffles, 1821), for example (Meijaard & Groves 2004). Moreover, the morphology of this m3 is more bunodont and bulkier than the m1 of *Iberomeryx* sp. cf. *I. parvus* described below. The combination of an external postprotocristid, an internal postprotocristid, an internal postmetacristid and an external postmetacristid corresponds to the tragulid M-structure or Σ -structure, justifying identification of this molar as that of a tragulid (Mortl 1961; Rössner 2007). However, given the paucity of the present material and pending additional data, we prefer to assign this tooth to *Iberomeryx* sp.

cf. *Iberomeryx parvus* Gabunia, 1964
(Fig. 2A-I, J-O)

REFERRED MATERIAL. — Sü-2002, left p3; Sü-2003, left p4; Sü-2005, talonid of a left p4; Sü-2009, right m1; Sü-2010, lingual part of a right M1 or M2; Sü-2020, left p4; Sü-2013, right astragalus; Sü-2014, right astragalus.

LOCALITY. — Outcrop of unnamed rock unit consisting of c. 40 cm thick tuffite bed containing gastropod operculae superposed by c. 30 cm thick white silty limestone with silicified nodules exposed in a streambed roughly two km northwest of Süngülü, Ardahan Province, Turkey (de Bruijn *et al.* 2003: fig. 1). Latest Eocene according to de Bruijn *et al.* (2018, 2019).

DESCRIPTION

Dentition

The p3 is elongated with a small paraconid, and a hypoconid lower than the protoconid. A sharp crest joins the apex of the protoconid to the hypoconid, and is bifurcated distally, so that the two crests form a circular, postero-lingually opened

depression. The paraconid of p4 is more pronounced than on p3, and the crest joining the paraconid to the protoconid corresponds to a wear facet. Two crests extend backward from the apex of the protoconid; the better expressed labial crest joins the distal border of the tooth, whereas the weaker lingual crest stops at the mid-point of the posterior half of the tooth, leaving the talonid distolingually opened.

The lower molar is brachyodont, and only the hypoconid is completely crescent-shaped. The trigonid is narrower than the talonid, and the protoconid is taller than the metaconid. The anterior fossa is widely antero-lingually open due to the absence of a premetacristid. The preprotocristid extends mesially and is notched; it forms the anterior-most part of the lower molars. The internal postprotocristid is lingually oriented and short, and it joins the very short and posterolabially oriented internal postmetacristid to form a cristid at the rear of the trigonid which is oriented toward the mesially oriented preentocristid. The external postprotocristid is very faint and extends toward the prehypocristid without connecting it because of transverse breakage of Sü-2009. The metaconid is rounded mesially and displays a short external postmetacristid. The combination of an external postprotocristid, an internal postprotocristid, an internal postmetacristid and an external postmetacristid forms a M-structure or Σ -structure which is characteristic of tragulids. The posthypocristid is short and lingually oriented. The entoconid is labio-lingually compressed and its distal side is rounded (devoid of any crest), thus leaving the posterior fossa open on its postero-lingual corner. There are both mesial and distal cingulids and an ectostylid on Sü-2009.

The fragmentary upper molar (Sü-2010) only preserves the lingual part. The relatively large size of the metaconule suggests it is either a M1 or a M2. The postprotocrista is short, straight, and postero-labially oriented whereas the preprotocrista is labially oriented. The premetaconulecrista extends labially. There is a strong cingulum surrounding the protocone and extending along the mesial border of the tooth; however, there is no protoconule as in *Nalameryx* (Métais *et al.* 2009).

Postcranials

Two astragali of similar size are referred to this small taxon on the basis of both their size and morphology. The astragali display non-aligned proximal and distal trochlea, the distal one being slightly rotated medially. The distal trochlea does not show any ridge separating the articular surfaces of the

TABLE 2. — Measurements (in mm) of the ruminant postcranial material from Söngülü discussed in the text, and all referred to *Iberomeryx* sp. cf. *I. parvus*. The asterisks designates estimated values when material is slightly broken or heavily worn/digested.

Taxon	Specimen	Length	Mesio-lateral width	Dorso-plantar height
<i>Iberomeryx</i> sp. cf. <i>I. parvus</i>	Sü-2014	10	5.46	5.2*
<i>Iberomeryx</i> sp. cf. <i>I. parvus</i>	Sü-2013	9.2	5	5*

cuboid and the navicular. The astragalo-calcaneal facet is well-developed, and there is a deep fossa for the fibular condyle of the calcaneum. The distal astragalar facet is generally well-developed as it is in primitive Pecora (Métais *et al.* 2016). The distal part of the internal malleolus facet is wide. Sü-2013 is slightly smaller than Sü-2014, but they are similar in morphology, and we attribute these slight metric differences to intraspecific variation.

Measurements

Provided in Table 1 for the dental material, and in Table 2 for postcranial material.

TAXONOMIC ATTRIBUTION

The dental material displays the characteristics of the genus *Iberomeryx*, and the astragali strongly resemble those reported from the early late Oligocene Kızılırmak Formation, central Anatolia, Turkey (Métais *et al.* 2016). The genus *Iberomeryx* is known by three species: *I. miaoi* Mennecart, Aiglstorfer, Li, Li & Wang, 2021 recently described from material first identified as *Lophiomeryx gracilis* Miao, 1982 (Mennecart *et al.* 2021) and restricted to the late Eocene beds of the Shinao Basin, southern China; *I. minor* (Filhol, 1882) is known from early Oligocene (MP 23-24) localities of Western Europe (Mennecart *et al.* 2011); *I. parvus* is known from the late Oligocene of Georgia (Gabunia 1964) and Central Anatolia (Métais *et al.* 2016). The material from Söngülü is identified as pertaining to *I. parvus* on the basis of the combination of these diagnostic features: lower molars lack a metastylid, and show a thin mesial cingulum, p4 with a distinct disto-lingual notch. However, the teeth of type material of *I. parvus* are higher crowned than that of the material from Söngülü which is also slightly smaller. Therefore, owing to these morphological and size differences, and pending additional fossil data, we prefer to refer our fossil material to *Iberomeryx* sp. cf. *I. parvus*.

Family BACHITHERIIDAE Janis, 1987
Genus *Bachitherium* Filhol, 1882

cf. *Bachitherium* sp.
(Fig. 2R-S)

REFERRED MATERIAL. — Sü-2017, lingual half of a right molar (M1 or M2); Sü-2019, talonid of a left p4.

DIAGNOSIS (from Métais & Vislobokova 2007). — Elongated muzzle with small orbits placed relatively posteriorly (the anterior border of the orbit is situated above M2), postorbital bar partly formed by the jugal apophysis, sagittal crest developed and extending posteriorly

into temporal crests, small auditory bullae, lacrimal fossa absent, strong paraoccipital apophysis, limited postero-lateral exposure of the mastoid, ethmoidal fissure moderately developed, post-glenoid apophysis well-developed; the angular region of the mandible is extended posteriorly and upward, and the coronoid apophysis is much higher than the articular joint suggesting strong abductor muscles. Dental Formula: 0/3 1/1 3/4 3/3, upper canine tusk-like, slightly curved posteriorly, and occludes against the anterior side of the caniniform p1, P1 lost, very long diastema between C and P2, lower incisors as the incisiform canine are small, small diastema between c and p1, and long diastema between p1 and p2. Radius and ulna separate, tibia and fibula partially fused, distal extremity reduced to a malleolar bone, Mc III and IV unfused, Mt III and IV fused proximally, lateral metatarsals absent, astragalus with unparallel trochlea, crural index close to that of the extant genus *Moschus*.

LOCALITY. — Outcrop of unnamed rock unit consisting of c. 40 cm thick tuffite bed containing gastropod operculae superposed by c. 30 cm thick white silty limestone with silicified nodules exposed in a streambed roughly two km northwest of Söngülü, Ardahan Province, Turkey (de Bruijn *et al.* 2003: fig. 1). Latest Eocene according to de Bruijn *et al.* (2018, 2019).

DESCRIPTION

The lingual half of the molar preserves highly worn protocone and metaconule; there is no lingual cingulum or entostyle, and there is both a mesial and a distal cingulum; the enamel is relatively thick and smooth. The talonid of p4 which is tentatively referred to the same taxon as the fragmentary upper molar (mostly on the basis of large size) displays in occlusal view a pattern of crests that sets it apart from tragulids and lophiomerycids. The top of the protoconid is preserved and the transversely wide talonid is delimited by two crests extending posteriorly; the labial postprotocristid reaching the posterior margin, where it forms the posterior border of the tooth; the lingual postprotocristid seems to be interrupted at the level of a marked transverse crest which is connected to the labial postprotocristid but without totally reaching the lingual border of the tooth. The disto-lingual border of the tooth is badly damaged but it does not appear that a lingual opening existed. Posterior to the protoconid, there are enamel foldings.

TAXONOMIC ATTRIBUTION

The lack of a lingual cingulum on the upper molar Sü-2017 is a character seen in *Bachitherium* (Geraads *et al.* 1987). If the premolar Sü-2019 belongs to the same taxon as we hypothesize here, its morphology is also consistent with a p4 of *Bachitherium*. This “gutter-like” p4 showing transverse cristids subdividing the talonid into two basins is also present in the type species *Bachitherium curtum* Filhol, 1877 (MNHN-Qu3917-holotype), and in *Bachitherium insigne* Filhol, 1882 (MNHN-Qu3902; MNHN-Qu3918-holotype). However, the p4 of *B. curtum* and *B. insigne* display not

one but two neocristids extending transversely from the lingual and labial postprotocristids respectively, but they do not fuse and leave a notch, medially situated, between the extremities of these two crests. This morphology is not what is observed on Sü-2019, where a single transverse neocristid extends transversely from the labial postprotocristid to reach the lingual wall of the posterior valley, which is devoid of a neocristid. We consider that Sü-2017 and Sü-2019 are closer to *Bachitherium* than to any other ruminant taxon, but the morphology of Sü-2019 does not match any species of *Bachitherium* known so far. Given the paucity of the current fossil material, we refer Sü-2019 to cf. *Bachitherium* sp. The morphology of Sü-2019 is also unlike the p4 of *Bachitherium thracensis* Mennecart, Geraads, Spassov & Zagorchev, 2018a from the late Eocene of Bulgaria, in which the gutter-like talonid of p4 lacks a transverse cristid (Mennecart *et al.* 2018a). Thus, if our assumption is correct, it worth noting that there are two forms of bachitheriids in the late Eocene of Balkanatolia, suggesting a diversification of the family in this biogeographic province before its dispersal to Western Europe at MP 23 (“*Bachitherium* dispersal event” of Mennecart *et al.* 2018a, b).

Order PRIMATES Linnaeus, 1758

Suborder ANTHROPOIDEA Mivart, 1864

Family EOSIMIIDAE Beard, Qi, Dawson, Wang & Li, 1994

Genus *Sungulusimias* n. gen.

urn:lsid:zoobank.org:act:B7E863C3-4D08-4FFB-BF9D-C74C72927E23

TYPE SPECIES. — *Sungulusimias unayae* n. sp.

Sungulusimias unayae n. gen., n. sp.
(Fig. 3A–C)

urn:lsid:zoobank.org:act:F21B9D32-30F3-4A64-B0C7-F89DDB9ED92C

TYPE MATERIAL. — **Holotype.** Sü-2021, isolated right m2, only known specimen.

DIAGNOSIS. — Differs from *Eosimias* Beard, Qi, Dawson, Wang & Li, 1994, *Phenacopithecus* Beard & Wang, 2004 and *Bahinia* Jaeger, Thein, Benammi, Chaimanee, Soe, Lwin, Tun, Wai & Ducrocq, 1999 in having m2 with protoconid and metaconid more closely spaced and of similar height and volume, paraconid more cuspidate and more nearly connate with metaconid, stronger mesiobuccal cingulid, and entoconid without strong connection to hypoconulid via the postcristid. Differs from *Phileosimias* Marivaux, Antoine, Hassan Baqri, Benammi, Chaimanee, Crochet, de Franceschi, Iqbal, Jaeger, Métais, Roohi & Welcomme, 2005 in having M₂ with paraconid fully lingual in position and hypoconulid distobuccal in position, being located closer to the hypoconid than the entoconid.

ETYMOLOGY. — Generic name from the village of Süngülü and the Latin *simias* (ape). Specific name in recognition of Prof. Engin Ünay, who discovered the type locality and helped collect the holotype and associated fauna from Süngülü.

TYPE LOCALITY. — Outcrop of unnamed rock unit consisting of c. 40 cm thick tuffite bed containing gastropod operculae superposed by c. 30 cm thick white silty limestone with silicified nodules exposed in a streambed roughly two km northwest of Süngülü, Ardahan Province, Turkey (de Bruijn *et al.* 2003: fig. 1). Latest Eocene according to de Bruijn *et al.* (2018, 2019).

DESCRIPTION

The holotype is an isolated right m2 (L = 3.0 mm; W = 2.4 mm). The crown is subrectangular in occlusal outline, although the trigonid is slightly narrower than the talonid. A relatively well-developed mesiobuccal cingulid extends from the base of the paraconid to the level of the hypoflexid. All three trigonid cusps are present, roughly similar in size, and distinctly cuspidate. The protoconid is situated internally rather than peripherally on the trigonid. As a result, the protoconid and metaconid are closely approximated. The metaconid is located slightly posterior to the level of the protoconid, and these two cusps are connected by a protocristid that runs somewhat obliquely with respect to the long axis of the tooth. A short but relatively trenchant paracristid arcs mesiolingually to connect the protoconid with the paraconid. The paraconid is fully lingual in position and almost connate with the metaconid. A short premetacristid fills the gap between the paraconid and metaconid. The postvallid is essentially vertical, separating the trigonid from the broader talonid. The hypoconid is the dominant talonid cusp, being situated near the distobuccal corner of the tooth. It gives rise to a straight, moderately trenchant cristid obliqua, which joins the postvallid near the lingual base of the protoconid. The hypoflexid is moderately deep but partly filled by the mesiobuccal cingulid. The lingual side of the talonid is marked by a relatively tall, isolated entoconid. A notch separates the lingual base of the postvallid from the entoconid, although a weak preentocristid is present. Distobuccally, the entoconid is not strongly connected to the hypoconulid by the postcristid. Instead, the hypoconulid projects slightly distally beyond the rest of the talonid and is more closely associated with the hypoconid than the entoconid.

COMPARISONS

Sü-2021 differs from primitive adapiform (e.g. *Donrussellia* Szalay, 1976) and omomyid primates (e.g. *Teilhardina* Simpson, 1940, *Steinius* Bown & Rose, 1984) in having the paraconid and metaconid of m2 closely approximated but not fully connate and in having an enlarged, distally expansive hypoconulid (Rose & Bown 1991). Most late early Eocene and younger adapiforms (adapids, notharctids, and sivaladapids) and stem lemuriforms (e.g. *Djebelemur* Hartenberger & Marandat, 1992) have reduced or completely lost the paraconid on m2 (Godinot 2014). Sivaladapid adapiforms (e.g. *Yunnanadapis* Ni, Li, Li & Beard, 2016, *Laomaki* Ni, Li, Li & Beard, 2016) retain a large hypoconulid on their lower molars, but this structure is invariably closely approximated with the entoconid in this clade, and it does not project distally beyond the rest of the talonid as it does in *Sungulusimias* (Ni *et al.* 2016). Anaptomorphine omomyids, best documented from the early and middle Eocene of North America, are much

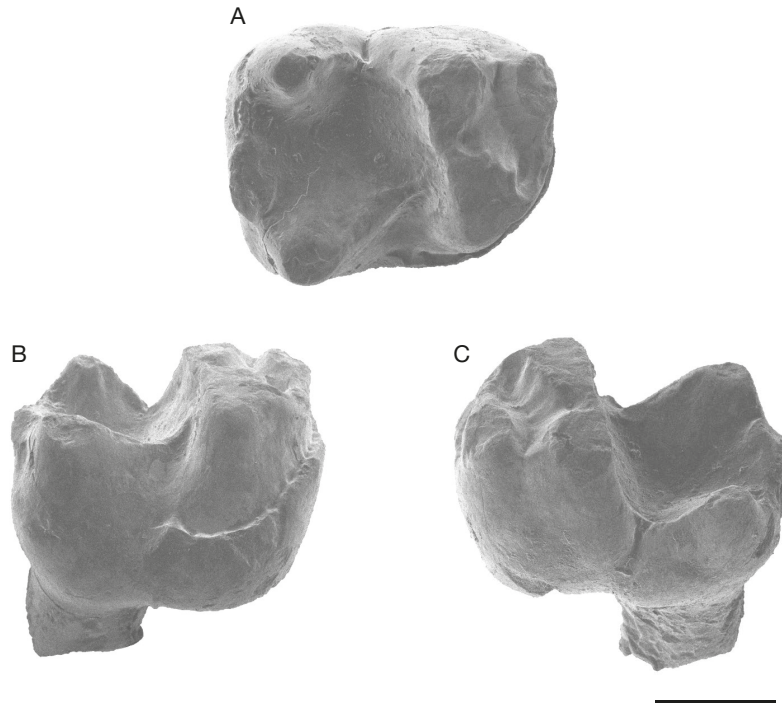


FIG. 3. — The eosimiid primate from Süngülü *Sungulusimias unayae* n. gen., n. sp.: **A–C**, Sü-2021, holotype, right m2, in occlusal (**A**), labial (**B**), and lingual (**C**) views. Scale bar: 1 mm.

more bunodont than *Sungulusimias* and they never possess the enlarged, distally expansive molar hypoconulid found in the latter taxon (Godinot 2014). North American and Asian omomyines, including the middle Eocene *Nesomomys* Beard, Métais, Ocakoglu & Licht, 2020 from Balkanatolia (Beard *et al.* 2021), are typically less bunodont than their anaptomorphine relatives, but they differ from *Sungulusimias* in having lower molars with trigonids much narrower than talonids (e.g. *Nesomomys*, *Hemiacodon* Marsh, 1872) and much smaller, less bulbous hypoconulids (e.g. *Shoshonius* Granger, 1910, *Mytonius* Robinson, 1968). The European microchoerid radiation, which persisted on the Iberian Peninsula as recently as the early Oligocene (Köhler & Moyà-Solà 1999), differs from *Sungulusimias* in having reduced both paraconid and hypoconulid on m2, with certain taxa (e.g. *Pseudoloris* Stehlin, 1916) showing enhanced molar shearing related to insectivory and others (e.g. *Microchoerus* Wood, 1846) developing heavily crenulated enamel in relation to frugivorous adaptations (Godinot 2014).

The distinctive trigonid and hypoconulid morphology of Sü-2021 allows it to be identified as an eosimiid rather than any other anthropoid clade. Like eosimiids, and in contrast to other stem anthropoids, Sü-2021 retains a lingual, distinctly cuspidate paraconid on m2. Certain stem anthropoids from Africa (e.g. *Biretia* de Bonis, Jaeger, Coiffait & Coiffait, 1988, *Proteopithecus* Simons, 1989) sometimes retain small paraconids on m1, but these taxa rarely retain even vestigial

paraconids on m2 and their overall molar morphology is more bunodont than that of *Sungulusimias* (Seiffert 2012). Among stem anthropoid taxa that are generally recognized as eosimiids, the trigonid morphology of Sü-2021 most closely resembles that of *Phileosimias* from the Oligocene of Pakistan (Marivaux *et al.* 2005), from which it differs in having a fully lingual paraconid. In other eosimiids (*Eosimias*, *Phenacopithecus* and *Bahinia*), the paraconid of m2 is typically less cuspidate and farther removed from the metaconid. The hypoconulid of Sü-2021 flares distobuccally, as it does in *Eosimias* and *Phenacopithecus*. In *Bahinia*, the talonids of m1–2 lack distinct hypoconulids. In *Phileosimias* and most early African anthropoids, the lower molar hypoconulids can be substantial and cuspidate, but they are located closer to the entoconid than the hypoconid, in contrast to the more central placement of the hypoconulid in *Sungulusimias*.

REMARKS

Sungulusimias is the first record of stem anthropoids in Anatolia and only the second example of Paleogene primates from there (Beard *et al.* 2021). Other eosimiids are known from China (Beard *et al.* 1994, 1996; Beard & Wang 2004; Ni *et al.* 2016), Myanmar (Jaeger *et al.* 1999) and Pakistan (Marivaux *et al.* 2005), so *Sungulusimias* is also the westernmost record of this group. Discovery of Anatolian eosimiids is not unexpected, given that eosimiids are well-documented from farther east along the Eurasian Neotethyan margin and

that eosimiiforms colonized the African/Arabian Plate prior to its tectonic collision with Eurasia near the Oligocene-Miocene boundary (Chaimanee *et al.* 2012). However, *Sungulusimias* is apparently younger than the oldest known African anthropoids, which date to the late middle or early late Eocene (Seiffert *et al.* 2005; Jaeger *et al.* 2010; Marivaux *et al.* 2014). What role, if any, *Sungulusimias* and its collateral relatives may have played in the colonization of Africa by early anthropoids must await better understanding of its anatomy and phylogenetic relationships.

DISCUSSION

AGE OF THE SÜNGÜLÜ FAUNA

The ruminant fauna from Süngülü does not bring definitive arguments about the age of this important fossil assemblage. The earliest occurrences of tragulids are known from the late Eocene of Southeast Asia with *Archaeotragulus krabiensis* Métais, Chaimanee, Jaeger & Ducrocq, 2001 from Krabi (Métais *et al.* 2001), and *Iberomeryx miaoi* is now reported from the late Eocene of China (Mennecart *et al.* 2021). The two other species of *Iberomeryx*, *I. minor* and *I. parvus*, are known from the early and late Oligocene, respectively. Lucas & Emry (1999) suggested that the age of the Benara locality, which has yielded the type of *I. parvus*, may equally be correlated with MP 23 (early Oligocene), which is consistent with the occurrence in the Benara fauna of taxa such as the ruminant *Lophiomeryx* Pomel, 1854 and the anthracotheriid *Anthracotherium* Cuvier, 1822, which are known in western Europe from MP 22 and MP 21, respectively (BiochronM'97 1997). Gabunia (1964) assigned a late Oligocene age to the Benara mammals largely because they immediately overlie and are interbedded with marine to brackish water sandstones that contain a *Corbula*-dominated bivalve assemblage which is supposed to record a well-documented early Chattian marine transgression in the eastern Paratethys. The primate *Sungulusimias* likewise provides an ambiguous biostratigraphic signal. Most eosimiids (including *Eosimias*, *Phenacopithecus* and *Bahinia*) are middle Eocene in age, but *Phileosimias* from Pakistan is Oligocene (Marivaux *et al.* 2005). *Sungulusimias* combines molar features that occur separately in Eocene eosimiids (such as its distinctive hypoconulid morphology) and Oligocene *Phileosimias* (particularly its trigonid morphology). It is possible that *Sungulusimias* is a primitive relative of *Phileosimias*, but this hypothetical relationship cannot be tested adequately until additional material of *Sungulusimias* is recovered.

The rodent assemblage from Süngülü consists of a mixture of endemic and mostly Asian taxa showing a dominance of muroids and ctenodactylids (de Bruijn *et al.* 2003). It is worth noting that the typically European theridomyids, pseudosciurids and glirids are missing in Süngülü, suggesting an absence of biogeographic relationships with western Europe at that time. The endemic character of rodents from Süngülü makes biochronological correlations with faunas from Central Asia very difficult. According to de Bruijn *et al.* (2003), the cricetid *Eucricetodon* (*Atavocricetodon*) *kurthi*

from Süngülü matches in size and morphology *A. minusculus* from Caijiachong (southern China), which is now considered to be late Eocene in age (Mennecart *et al.* 2021). In their chronostratigraphic scheme of Paleogene faunas from Anatolia, the Balkans and Southern Asia, van de Weerd *et al.* (2021) and Marković *et al.* (2018: fig. 8) considered Süngülü as latest Eocene.

THE LEAKY BALKANATOLIAN HOLDING PEN AND ITERATIVE FAUNAL CHANGE AROUND THE GRANDE COUPURE

The newly recognized Balkanatolian biogeographic province is defined on the basis of multiple Eocene sites in the Balkans and central Anatolia (Licht *et al.* 2022). During the middle Eocene, central Anatolia hosted strongly endemic faunas characterized by a mélange of anachronistic taxa such as the pleuraspidotheriid *Hilalia* and invasive clades including embrithopods and anatoliadelphid metatherians (Métais *et al.* 2017, 2018; Beard *et al.* 2023). The insular nature of these middle Eocene Balkanatolian faunas is underscored by the absence of artiodactyls, perissodactyls, carnivorans, hyaenodontids and rodents, which are otherwise ubiquitous across Laurasia at this time (Métais *et al.* 2018). The only insular Balkanatolian mammal showing Asian affinities is the omomyid primate *Nesomomys*, which is thought to have reached Balkanatolia by rafting (Beard *et al.* 2021). We currently lack middle Eocene paleontological sites between central Anatolia and South Asia (Pakistan), and therefore the eastward extent of Balkanatolian endemism remains unknown. The eastern boundary of Balkanatolia is hypothetically placed in the Lesser Caucasus, where remnant seaways separated Anatolian terranes from the Cimmerian blocks of Iran during most of the Eocene (Popov *et al.* 2004; Barrier *et al.* 2018; Palcu & Krijgsman 2023). While no body fossils of mammals have been so far reported from the Eocene of Iran, several late Eocene localities have yielded mammal footprints organized in trackways that have been interpreted as being made by perissodactyls and proboscideans (Abbassi *et al.* 2016). The Süngülü locality, on the eastern Pontides, would have been west of these seaways and thus part of Balkanatolia, although its younger age and relatively cosmopolitan fauna shows that it postdates the height of Balkanatolian endemism. Licht *et al.* (2022) have proposed that the progressive retreat of adjacent seaways in the late middle Eocene, *c.* 40–38 Ma, opened a terrestrial pathway for faunal exchanges between Balkanatolia and the Cimmerian blocks, favoring the dispersal of East Asian mammals as far as western Balkanatolia (i.e., Romania, Bulgaria). Moreover, Licht *et al.* (2022) hypothesized that subsequent westward prolongation of this dispersal pathway could have instigated the Grande Coupure roughly 34 Ma, when mammals of East Asian affinity invaded western Europe. Although there is currently no overlap in faunal composition between the central Anatolian Büyükteflek fauna reported by Licht *et al.* (2022), which is dominated by large ungulates, and the eastern Anatolian Süngülü fauna dominated by micromammals and small ruminants that we focus on here, this overall scenario is equally applicable to both of these late Eocene Anatolian faunas.

It is instructive to compare the pattern of faunal turnover observed in western Europe on either side of the Grande Coupure with that which has been documented for the Great American Biotic Interchange (GABI) during the late Neogene (e.g. Woodburne 2010). In both cases mammalian faunal turnover was severe, and in both cases it was caused by paleogeographic changes linked to tectonics, eustasy, and/or climate change. However, the nature and complexity of potential pathways for dispersal were very different. In the case of GABI, dispersal ultimately entailed traversing the Panamanian Isthmus connecting North and South America. In the case of the Grande Coupure and closely related dispersal episodes in Eurasia, potential pathways for dispersal are more numerous, reflecting the dynamic paleogeography of Eurasia during the latter part of the Eocene and Oligocene. For example, Mennecart *et al.* (2018b: 9) have stressed that two dispersal episodes are discernible across Eurasia during the late Eocene-early Oligocene, while emphasizing that associated dispersal pathways may have been different in each case. Classically, it is postulated that the earlier dispersal episode – the Grande Coupure *sensu stricto* – utilized a northern dispersal pathway linking Central Asia with western Europe across northern latitudes (mainly comprising the modern Russian Federation), while a more recent dispersal episode – designated the *Bachitherium* event by Mennecart *et al.* (2018b) – traversed a more southern pathway that included Balkanatolia. Likewise, the mechanisms underlying these two events are postulated to be different – including the drying out of the Turgai Strait with respect to the Grande Coupure and tectonic uplift associated with the Alpine orogeny connecting Balkanatolia with western Europe in the case of the *Bachitherium* event. However, several authors (Heissig 1979; Böhme *et al.* 2013) suggested that the alpine tectonics created intermittent land bridge that probably connected the Island Europe and Southwestern Asia, and thus another potential dispersal pathway to explain the sudden appearance of Asian mammals at MP 21 in Western Europe.

Closer examination of faunal changes in western Europe during the late Eocene and early Oligocene suggests a more complex pattern of mammalian dispersal that probably included at least four separate “events” (Table 3). The first of these, which occurred prior to the Grande Coupure during MP 18, records the first appearance in western Europe (La Débruge, France) of the anthracothere *Elomeryx*, which is also known from Balkanatolian terranes to the east (de Bonis 1964; Nikilov & Heissig 1985). A separate anthracothere, *Prominatherium*, is relatively widely distributed across western Balkanatolia during the late Eocene. The Grande Coupure itself comprises the second event, characterized by the first appearances in western Europe at MP 21 of a large number of small- to large-bodied mammals (Table 3), which share only 7% of common genera with the late Eocene Balkanatolian mammal fauna, possibly suggesting a different geographic source for the MP 21 fauna of Western Europe. The third and fourth dispersal events are relatively minor inputs of Asian taxa of much lower magnitude than the major MP 21 turnover that was initially documented in the Paris Basin by Stehlin (1909).

The fourth dispersal event corresponds to the *Bachitherium* event of Mennecart *et al.* during MP 23, when *Bachitherium* and *Iberomeryx* first appear in Western Europe.

Finer resolution of the GABI dispersals during the late Neogene of North and South America has also resulted in recognition of four separate dispersal episodes within GABI (Woodburne 2010). These iterative dispersal events are thought to have been facilitated by fluctuations in eustatic sea level and oscillating climatic conditions, which would have rendered Central America more or less porous to invasive taxa hailing from higher latitudes in either North or South America. At times, Central America and adjacent southern Mexico functioned as a “holding pen” where various taxa were confined for significant intervals of time before proceeding to colonize higher latitudes (Woodburne 2010). Here, we propose that the concept of a holding pen also applies to Balkanatolia during the late Eocene and early Oligocene, thereby posing a biogeographically simpler hypothesis than that of Mennecart *et al.* (2018b) to explain the iterative pattern of dispersal observed in western Europe during this interval.

The new data presented here and by Licht *et al.* (2022) show that Balkanatolia was colonized by multiple clades of Asian mammals by the late Eocene. Although these late Eocene Asian mammals were virtually on Europe’s doorstep, with the notable exception of *Elomeryx* and *Phaneromeryx* (Table 3), very few of them were immediately able to overcome the biogeographic barrier posed by remnant peri-Alpine seaways blocking unfettered access to western Europe. Some taxa, including brontotheres and eosimiid anthropoids, apparently never colonized western Europe, either succumbing to extinction or being regionally extirpated before leaving the Balkanatolian holding pen. Indeed, Balkanatolia seems to have functioned as a biogeographic cul-de-sac for many of its late Eocene mammalian taxa that never reached Western Europe (Table 3). Most of the taxa that first appeared in Western Europe at MP 21 have no direct ancestry among the late Eocene taxa known so far from Balkanatolia, thus suggesting that another pathway was used for these MP 21 newcomers to reach Western Europe. However, we cannot rule out that this hypothesis may be biased by the relatively poor fossil data currently available for the late Eocene faunas from Balkanatolia. The impact of the Eocene-Oligocene boundary on the Balkanatolian mammal fauna is difficult to evaluate because earliest Oligocene faunas are poorly represented there, with the exception of an early Oligocene rodent assemblage from Serbia (de Bruijn *et al.* 2018, 2019, 2023; Marković *et al.* 2018; Wessels *et al.* 2020). However, as in the case of GABI, the Balkanatolian holding pen must have been porous to some degree, and its proximity to Western Europe may explain most, if not all, of the iterative dispersal events outlined in Table 3, including the Grande Coupure. The Balkanatolian holding pen continued to function into the early Oligocene, as suggested by the recent discovery of diatomyid rodents from the early Oligocene of Southeastern Serbia (Marković *et al.* 2018), a family that is common in Oligocene faunas of Pakistan (Marivaux & Welcomme 2003), India (Nanda &

TABLE 3. — First appearance of mammal genera in Balkanatolia and Western Europe around the Grande Coupure. Four phases can be differentiated in the faunal turnover that occurred during the Eocene-Oligocene transition. Taxa in **bold** are those reported from Süngülü. References refer to recent publications regarding systematic revision or updated occurrences of each taxon.

First appearance					
Phase	Western Europe	Balkanatolia	Family	Reference	Locality
Phase 0					
Bartonian (MP16-17?)	Hyaenodontinae [Solé <i>et al.</i> (2022)]	<i>Sivatitanops</i>	Brontotheriidae	Nikolov & Heissig (1985)	Kameno, Tchernomore
		<i>Cadurcodon</i>	Amynodontidae	Nikolov & Heissig (1985), Tissier <i>et al.</i> (2018)	Kameno
		<i>Elomeryx</i> <i>Bakalovia</i>	Anthracotheriidae Anthracotheriidae	Nikolov (1967) Nikolov & Heissig (1985)	Tchernomore Tchernomore
Phase 0-1					
Localities that could be either Bartonian or Priabonian		<i>Prohyracodon</i>	Hyracodontidae	Heissig (1990)	Mottnig
		<i>Anthracohyus</i>	Anthracotheriidae	Heissig (1990)	Mottnig
		<i>Amynodontopsis</i>	Amynodontidae	Tissier <i>et al.</i> (2018)	Dorog
		<i>Amynodon</i>	Amynodontidae	Tissier <i>et al.</i> (2018)	Tapioszele
		<i>Prominatherium</i>	Anthracotheriidae	Grandi & Bona (2017)	Mt Promina
		<i>Forstercooperia</i> <i>Bachitherium</i>	Hyracodontidae Bachitheriidae	Mennecart <i>et al.</i> (2018a, b) Mennecart <i>et al.</i> (2018a, b)	Bobov Dol Thrace Basin
Phase 1					
MP18-20 (early late Eocene)	<i>Elomeryx</i> [de Bonis (1964)] <i>Phaneromeryx</i> [Métais & Vislobokova (2007)] <i>Cynodictis</i> [Le Verger <i>et al.</i> 2020]	cf. <i>Bachitherium</i> sp.	Bachitheriidae	this study	Sungulu
		<i>Iberomeryx</i>	Tragulidae	this study	Sungulu
		<i>Sellamynodon</i>	Amynodontidae	Tissier <i>et al.</i> (2018)	Dobarca
		<i>Embolotherium</i>	Brontotheriidae	Licht <i>et al.</i> (2022)	Büyükteflek
		<i>Brachydiastematherium</i>	Brontotheriidae	Mihlbachler <i>et al.</i> (2004)	Mera
		<i>Debruijnina</i>	Spalacidae	de Bruijn <i>et al.</i> (2023)	Zvonce
		<i>Bustrania</i>	Muroidea	de Bruin <i>et al.</i> (2019)	Buštranje
		<i>Mogilia</i>	Muroidea	Wessels <i>et al.</i> (2018)	Buštranje, Zvonce
		<i>Pseudocricetodon</i>	Muroidea	de Bruijn <i>et al.</i> (2003, 2018); Baciú & Hartenberger (2001)	Süngülü, Buştranje
		<i>Paracricetodon</i>	Muroidea	de Bruijn <i>et al.</i> (2003, 2018)	Süngülü, Buştranje
		<i>Witenia</i>	Muroidea	de Bruijn <i>et al.</i> (2003, 2018, 2019)	Süngülü, Buştranje
		<i>Edirnella</i>	Muroidea	de Bruijn <i>et al.</i> (2003, 2018)	Süngülü, Zvonce
		<i>Eucricetodon</i>	Muroidea	de Bruijn <i>et al.</i> (2003); Baciú & Hartenberger (2001)	Süngülü
		cf. <i>Lignitella</i>	Muroidea	de Bruijn <i>et al.</i> (2003)	Süngülü
		<i>Heosminthus</i>	Dipodidae	de Bruijn <i>et al.</i> (2003)	Süngülü
		<i>Ottomania</i>	Baluchimyine	de Bruijn <i>et al.</i> (2003)	Süngülü
		<i>Confiniummys</i>	Baluchimyine	de Bruijn <i>et al.</i> (2003)	Süngülü
		<i>Sungulusimias</i>	Eosimiidae	this study	Süngülü
Phase 2					
MP21 (earliest Oligocene)	<i>Gelocus</i>	–	Geolocidae	Blondel (2001)	–
	<i>Paragelocus</i>	–	Geolocidae	Blondel (2001)	–
	<i>Pseudogelocus</i>	–	Geolocidae	Blondel (2001)	–
	<i>Anthracotherium</i>	–	Anthracotheriidae	Pandolfi <i>et al.</i> (2016)	–
	<i>Anthracochœrus</i>	–	Anthracotheriidae	Pandolfi <i>et al.</i> (2016)	–
	<i>Bothriodon</i>	–	Anthracotheriidae	Brunet & Vianey-Liaud (1987)	–
	<i>Propalaeochoerus</i>	–	Suidae	Pandolfi <i>et al.</i> (2016)	–
	<i>Cadurcotherium</i>	–	Amynodontidae	Tissier <i>et al.</i> (2018)	–
	<i>Eggsodon</i>	–	Hyracodontidae	Brunet (1979); Becker (2009)	–
	<i>Ronzotherium</i>	–	Rhinocerotidae	Brunet (1979); Tissier <i>et al.</i> (2021)	–
	<i>Epiaceratherium</i>	–	Rhinocerotidae	Pandolfi <i>et al.</i> (2016)	–
	<i>Entelodon antiquus</i>	–	Entelodontidae	Brunet (1979)	–
	<i>Feliformia</i>	–	Carnivora	Solé <i>et al.</i> (2022)	–
	<i>Caniformia</i>	–	Carnivora	Solé <i>et al.</i> (2022)	–
	<i>Eucricetodon</i>	–	Muroidea	Dienemann (1987); Freudenthal (1988)	–
	<i>Pseudocricetodon</i>	–	Muroidea	Dienemann (1987)	–
	<i>Eomys</i>	–	Eomyidae	Bosma <i>et al.</i> (2023)	–
	<i>Steneofiber</i>	–	Castoriidae	Smith (2003)	–
	<i>Ephemerolagus</i>	–	Lagomorpha	Vianey-Liaud & Lebrun (2013)	–
	<i>Percygale</i>	–	Talpidae	Hugueney & Maridet (2018)	–
	<i>Oligonyctia</i>	–	Nyctitheriidae	Smith & van den Hoek Ostende (2006)	–

TABLE 3. — Continuation.

Phase	First appearance		Family	Reference	Locality
	Western Europe	Balkanatolia			
	<i>Belgicashorex</i>	–	Heterosoricidae	Smith & van den Hoek Ostende (2006)	–
	<i>Butselia</i>	–	Plesiosoricidae	Smith & Smith (2012)	–
	<i>Tetracus</i>	–	Erinaceidae	Smith (2004)	–
Phase 3					–
MP22 (early Oligocene)	<i>Lophiomyx</i>	–	Lophiomyxidae	Brunet & Sudre (1987); Fejfar (1987)	–
	<i>Paenanthracotherium</i>	–	Anthracotheriidae	Scherler <i>et al.</i> (2018)	–
Phase 4					–
MP23 (early Oligocene)	<i>Dolichochoerus</i>	–	Suidae	Sudre (1995)	–
	<i>Iberomyx</i>	–	Tragulidae	Mennecart <i>et al.</i> (2011)	–
	<i>Bachitherium</i>	–	Bachitheriidae	Sudre (1986); Blondel (2001)	–

Sahni 1998) and Thailand (Marivaux *et al.* 2004), but which is lacking from Oligocene faunas from the Thrace Basin of Turkey and from Kazakhstan. Likewise, diatomyids are absent from the abundant rodent fauna recovered from Söngülü, suggesting either taphonomic/paleoecological biases within Balkanatolia or relatively late colonization of this terrane by diatomyids during the early Oligocene (after the time of deposition of Söngülü).

Although paleobiogeographic obstacles remained, a leaky Balkanatolian holding pen may be preferable to dispersal across high latitudes for those Asian mammal taxa that colonized western Europe during the Grande Coupure. From a purely paleontological perspective, there is virtually no record of late Eocene mammals across the broad geographic expanse from western Europe to China and Mongolia, making this dispersal pathway theoretically possible but entirely conjectural. This dearth of paleontological data contrasts with the broad range of late Eocene Asian mammals in the Balkanatolian holding pen (Table 3). Moreover, recent geological assessments of Eurasian paleogeography highlight the precocious (Priabonian) drying out of the Turgai Strait (Kaya *et al.* 2019), an event that has been considered pivotal for establishing a northern dispersal pathway for Asian mammals to colonize western Europe at the Grande Coupure (Mennecart *et al.* 2018b). As Licht *et al.* (2022) emphasized, if high-latitude dispersal between Asia and western Europe was insignificant during the late Eocene when climate was relatively mild, it is difficult to conceive how dispersal across this pathway would have been significantly enhanced during the Grande Coupure, when central Asia would have been cooler and drier (Oi-1, Zachos *et al.* 2001; Barbolini *et al.* 2020). Likewise, regardless of the timing of regression of the Turgai Strait, a second marine barrier to dispersal persisted between western Europe and central Asia in the form of an epicontinental seaway that connected the North Sea with Paratethys across what is now the Baltic region (see Kaya *et al.* 2019; fig. 12).

The Söngülü fauna lacks the endemic elements known from older (Lutetian) sites of central Anatolia, where the most iconic Balkanatolian mammals have been described

(Métais *et al.* 2018); and the site postdates the proposed age for the end of Balkanatolian endemism (*c.* 40–38 Ma; Licht *et al.* 2022). The Söngülü fauna shows clear Asian affinities and corroborates regional exchanges between East and southern Asia and eastern Anatolia during the late Eocene. This assemblage therefore corroborates the existence of a dispersal route between East Asia and Europe along the Neotethys via the Middle East and Balkanatolia, although late Eocene mammals from Balkanatolia remain highly dissimilar at the generic level from those known in MP 21 in Western Europe (Table 3). This dispersal route has previously been invoked to explain the appearance of Asian taxa in the Balkans prior to the Grande Coupure (Heissig 1979; Böhme *et al.* 2013). Several large or medium-sized mammal families that arrived in Central or Western Europe after the Grande Coupure were already present in Balkanatolia during the late Eocene, including ruminants (Mennecart *et al.* 2018a, b), rhinocerotoids (Nikolov & Heissig 1985; Tissier *et al.* 2018; Licht *et al.* 2022), anthracotheriids (Böhme *et al.* 2013), and Hyaenodonta (Solé *et al.* 2022). This is also true for small mammals, especially muroids which are known from Söngülü and various late Eocene localities in the Balkans (Baciu & Hartenberger 2001; de Bruijn *et al.* 2018, 2019).

Finally, the presence of an anthropoid primate in the Söngülü fauna, showing affinities with *Phileosimias* and related taxa from the Eocene and Oligocene of South Asia, indicates some degree of continuity for forested ecosystems along the Eurasian Neotethyan margin. This continuity is consistent with palynological data (Kayseri Özer 2017), but at odds with late Eocene climate simulations indicating desertic conditions along a significant part of the Neotethyan domain (Tardif *et al.* 2021). We suggest that coastal mangrove forests, which can develop despite dry conditions inland, could have played a significant role in favoring the dispersal of arboreal mammals from East Asia to Anatolia. This is also consistent with the occurrence in Söngülü of small tragulids which are currently restricted to tropical forested environments (Meijaard & Groves 2004). Interestingly, the end of Balkanatolian endemism, dated at 40–38 Ma, is roughly synchronous with the arrival of eosimiiform primates in

Africa (Jaeger *et al.* 2010). We thus suggest that eosimiiform primates might have arrived in Anatolia as early as 40–38 Ma and used Balkanatolia as a stepping stone to pursue their dispersal to Africa. Precisely how and when they reached Africa from Balkanatolia remains unknown.

CONCLUSION

New paleontological data from the latest Eocene-earliest Oligocene of Balkanatolia reveal a complex biogeographic province that remained separated from Europe until the later Paleogene while being connected to Asia. Regional small mammal assemblages indicate that major differences in faunal composition between western Europe and Balkanatolia persisted until the early part of the late Oligocene (van der Weerd *et al.* 2021, 2023), suggesting the persistence of a substantial geographic (and possibly climatic) barrier, related to the persistence of several seaways in eastern Europe and/or the early growth of the Alpine orogeny. The assembly of the Balkanatolian paleobiogeographic province during the early Paleogene remains an enigma and its demise is barely better documented. In that regard, the fauna from Söğütözü offers an important snapshot for documenting the Eocene-Oligocene transition in Eastern Anatolia, along a strategic corridor for faunal exchanges between Europe, South and East Asia. Intensive screen washing efforts carried out at Söğütözü has produced remains of additional and so far unstudied taxa that may provide supplementary biochronologic or paleoenvironmental data. According to the data provided by de Bruijn *et al.* (2003), including the nature of the lithological sequence containing the fossil locality, the application of modern geochronological methods to this section may help constrain the age of Söğütözü.

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