Palaeobiodiversity and Palaeoenvironments (2025) 106:211–227
https://doi.org/10.1007/s12549-025-00666-1

SENCKENBERG

ORIGINAL PAPER

Kayaca, a new vertebrate locality from the Upper Miocene of Türkiye and its importance for the Turolian biogeography of the eastern peri-Mediterranean region

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Received: 29 November 2024 / Revised: 18 March 2025 / Accepted: 22 May 2025 / Published online: 23 July 2025

Abstract

We present here a new Upper Miocene vertebrate locality, Kayaca, from the Beyağaç Basin in southwestern Türkiye that was discovered after surface survey and was subsequently systematically excavated. The locality yielded a diverse and rich vertebrate fauna notably including several complete cranial specimens. In this article we provide the first results on the taxonomy of the large mammal assemblage, and we discuss the biochronological implications. The Kayaca large mammal assemblage is dominated by hipparionine horses (*Hipparion dietrichi* morphotype, *Cremohipparion* sp.) and bovids (*Gazella* cf. *ancyrensis*, *Sporadotragus parvidens*, *Tragoportax* sp., *Palaeoryx pallasi* and the rare *Gangraia*), but includes also rhinocerotids (*Miodiceros neumayri*, *Diceros* sp.), suids (*Hippopotamodon major*), giraffids (*Palaeotragus rouenii*, *Samotherium major*), hystricids (*Hystrix* sp.), orycteropodids (*Amphiorycteropus gaudryi*), proboscideans (*Deinotherium* sp., Elephantimorpha indet.) and carnivorans. The latter are identified by some well-preserved specimens belonging to ictitheres (*Protictitherium* sp.), hyaenids (*Adcrocuta eximia*), felids (*Pontosmilus* sp. and a medium-sized felid) but also to the rare mustelid *Parataxidea maraghana*. The preliminary comparison with already known and well-studied faunal assemblages of Türkiye and the wider region, particularly the neighboring localities of Samos in Greece, suggest an age of ca. 7.4, close to the transition of early/middle Turolian (MN 11/12). Located at the western corner of Asia, Kayaca comprises a key location linking the vertebrate faunas of Asia and Europe and offers valuable insights into the Late Miocene terrestrial ecosystems of the eastern peri-Mediterranean region.

Keywords Neogene · Mammals · Biochronology · Biostratigraphy · Turolian · Türkiye

Introduction

At the crossroads of Europe, Asia and Africa, Türkiye and the eastern peri-Mediterranean region in general occupy a critical position for the dispersals of mammals. Indeed, the wider region has acted numerous times in the past, especially during the Neogene and the Quaternary (e.g. Rögl 1999; Koufos et al. 2005; Böhme et al. 2021) as a biogeographical landbridge among the three continents, highlighting the need for systematic and deeper investigations. Particularly during the Late Miocene, the geographic area that presently extends from the Balkans and Türkiye to the West until Iran and Afghanistan to the East, commonly referred to as "Greco-Irano-Afghan" or Balkano-Iranian palaeobiogeographic province (e.g. Bonis et al. 1992; Spassov 2002), although not homogenous (see e.g. Kostopoulos 2009a) hosted a particular mammal community that broadly inhabited savanna-like

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types of environments (e.g. Solounias et al. 1999; Spassov 2002; Koufos 2013; Merceron et al. 2016; Mirzaie Ataabadi et al. 2016; Böhme et al. 2017; Kaya et al. 2018; Spassov et al. 2018).

Several fieldwork campaigns carried out in Türkiye led to the discovery of numerous Upper Miocene vertebrate localities (see e.g. Sickenberg et al. 1975; Saraç 2003). However, in many of them the taxonomic identifications are limited and/or the fossil assemblages lack precise stratigraphic control, as common in older collections, obscuring their faunal composition and preventing a secure chronological assessment. The systematic field surveys and excavations that have been conducted in the last decades aimed to enrich the fossil record of Türkiye from well stratified contexts. They have enhanced significantly our knowledge of the local Late Miocene vertebrate faunas and underlined the importance of the country for taxonomic, palaeobiogeographic and palaeoenvironmental studies, including the evolution of hominoids (e.g. Sen 1994a, 2005; Fortelius et al. 2003; Geraads et al. 2005; Kaya et al. 2012; Erol et al. 2016; Yilmaz Usta et al. 2019; Aytek et al. 2022; Sevim-Erol et al. 2023).

The new Upper Miocene locality Kayaca (KYC), which is introduced for the first time here, constitutes a key site in the western corner of Asia, linking the vertebrate faunas of Asia and Europe. The locality was discovered after surface survey in 2018 (Aytek et al. 2022) and was subsequently systematically excavated during three field seasons in 2022–2024. Here we provide preliminary results about the stratigraphy, fauna and age of the site, based on the first collected material and its comparison with assemblages from other known Upper Miocene localities of the wider region. All specimens are stored at the Department of Anthropology of the Akif Ersoy University in Burdur (Türkiye).

Abbreviations: **d,** deciduous; **DAP,** anteroposterior diameter; **DT,** transverse diameter; **H,** height; **L,** length; **m/M,** lower/upper molar; ***n*****,** number of specimens; **p/P,** lower/upper premolar; **W,** width.

Geology and stratigraphy

Kayaca is located on the eastern margin of the Beyağaç Basin, one of the post-orogenic terrestrial basins of southwestern Anatolia (Figs. 1a, b, 2). The Beyağaç Formation (Upper Miocene–Lower Pleistocene) is divided into two distinct sedimentary units: the Yatağan beds at the base, comprising alluvial fan and fluvial deposits which thicken towards the basin boundary faults and show basinward thinning and fining trends, and the overlying Milet beds with

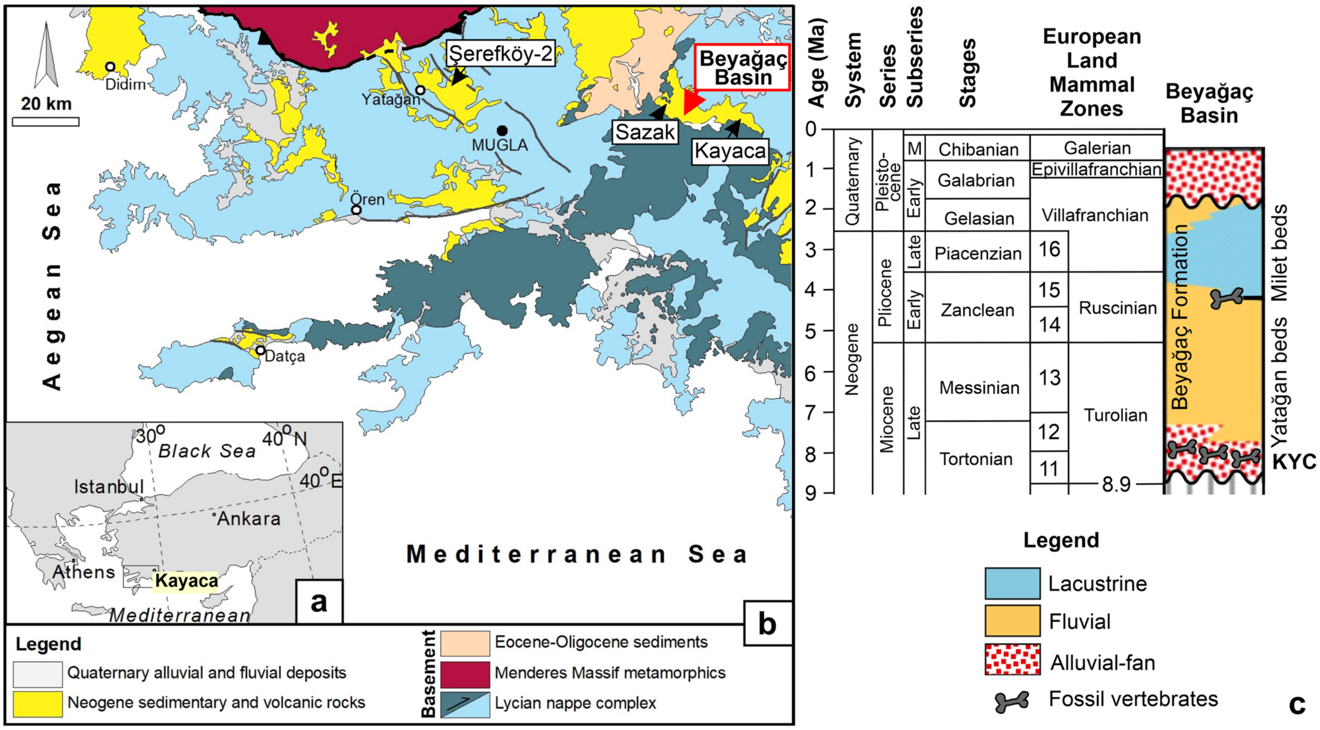

Fig. 1 **a** Geographic location of Kayaca locality in SW Türkiye. **b** Geological map (including the legend below it) of SW Anatolia indicating the Kayaca locality and nearby main fossil vertebrate localities in the Beyağaç and Yatağan Basins (based on Konak and Şenel 2002). **c** Stratigraphic log of the Beyağaç Basin showing the depositional environments of the Yatağan and Milet beds, and the position of Kayaca (KYC) locality (based on Alçiçek et al. 2019)

lacustrine sediments (Fig. 1c; Becker-Platen 1970; Alçiçek et al. 2019). The basin fill is unconformably overlain by younger alluvial fan deposits. The fossil vertebrate assemblage of Kayaca was accumulated within distal alluvial pond-lake deposits of the lower part of the Yatağan beds (Figs. 1c, 2). Higher up in the sequence, the alluvial fan deposits gradually pass upwards into the fluvial facies association and are eventually overlain by the lacustrine Milet unit with a coal seam at the bottom.

Other Upper Miocene localities in the Beyağaç Basin include Sazak at the western margin of the basin (Fig. 1b), which yielded a diverse vertebrate fauna, biochronologically dated to the middle Turolian (MN12; Kaya 1993; Tuna 1999; Oruç 2009; Koufos et al. 2018; Aytek et al. 2022; Konidaris et al. 2023), and the recently discovered site Kozlar (Alçiçek et al. 2019). At the nearby Yatağan basin, the Upper Miocene site of Şerefköy-2 (Fig. 1b) provided a diverse middle/late Turolian fauna, while several more localities are already known from the Yatağan region (e.g. Salihpasalar-Kemikalan; Sickenberg et al. 1975; Kaya et al. 2008, 2012; Kostopoulos and Karakütük 2015).

Palaeontology

The vertebrate assemblage of Kayaca comprises reptiles (including a partial testudinid shell), birds and mammals. Here we focus on the larger mammals, which form the bulk of the present collection. These include hystricids, carnivorans, orycteropodids, proboscideans, rhinocerotids, equids, suids, giraffids and bovids.

Hystricidae: An almost complete cranium (KYC23.317; Fig. 3a) and the perhaps associated with it right and left hemimandibles (KYC23.276 and 195) preserve the complete cheek tooth dentition, which shows the typical occlusal pattern and outline of the porcupine *Hystrix*. Recent discoveries and the revision of older material from Türkiye and the Balkans highlight the diversity of Late Miocene *Hystrix* in western Eurasia (e.g. van Weers and Rook 2003; Kovachev 2012; Spassov et al. 2018; Halaçlar et al. 2024, 2025) and therefore the well-preserved Kayaca *Hystrix* is important for further taxonomic and palaeobiogeographic studies. For the moment we attribute the Kayaca porcupine to *Hystrix* sp.

Carnivora: A mustelid is known by an almost complete cranium (KYC22.73; Fig. 3c) bearing the left P4 (L × W = 7.9 × 7.8 mm), an isolated right P4 (KYC22.59; L × W = 8.1 × 7.9 mm) that most possibly belongs to the same individual, and a cranial fragment (KYC22.81) preserving the roots of the broken P4 and the right M1 (L = 12.7 mm). Cranial traits such as the short and rather wide muzzle, the oval narial opening, the weak sagittal crest and the elongated and narrow palate, and dental traits such as the short and wide P4 with strong protocone, and the large M1 with long lingual mesiodistal diameter, allow for an attribution to *Parataxidea* (Koufos 2022; Wang et al. 2023). The Kayaca specimens show morphological and metrical similarities with corresponding specimens of *Parataxidea maraghana* from Samos (Greece; Koufos 2009a) and can be ascribed to this species. Although *P. maraghana* is rare in western Eurasia, besides Samos it is known from the Middle Maragheh (Iran), and from Karaçahasan, Şerefköy-2 and Çorakyerler in Türkiye (e.g. Koufos 2009a; Kaya et al. 2012; Erol et al. 2016).

The presence of an ictithere is recognised by a mandibular fragment bearing the broken canine and the p2–p3 (KYC24.496; Fig. 3d). The dimensions of the premolars (L × W: p2 = 8.8 × 4.3; p3 = 10.8 × 5.6 mm) are larger than *Protictitherium cingulatum* and *Protictitherium gaillardi*, but smaller than *Ictitherium viverrinum*, and they are close to *Protictitherium crassum*, *Protictitherium aegaeum* and "*Protictitherium*" *arambourgi* (e.g. Schmidt-Kittler 1976; Koufos 2000; Kaya et al. 2005; Koufos et al. 2018). Pending new and more diagnostic material, we allocate it to *Protictitherium* sp.

A large-sized hyaenid is best identified by a complete hemimandible (KYC23.252; Fig. 3f) of an adult individual as well as from the right and left hemimandibles of a juvenile individual bearing the deciduous dentition (KYC22.94 and 99; Fig. 3e), and an isolated dp4 (KYC22.145). The adult mandible has a high and thick corpus with convex ventral margin and a relatively low ascending ramus. The cheek teeth are robust (L × W: p1 = 6.6 × 5.6; p2 = 16.2 × 11.1; p3 = 17.9 × 13.2; p4 = 21.6 × 12.5; m1 = 26.9 × 13.2; all in mm) and are characterised by the absence of anterior accessory cuspids in the p2 and p3, large posterior accessory cuspids that are attached to the main cuspids in the premolars, and well-developed bicuspid talonid in the m1. Morphologically and metrically the Kayaca specimen matches well with the large-sized, bone-cracking hyaenid, *Adcrocuta eximia* (see e.g. Koufos 2016; Spassov et al. 2018). The dimensions of the cheek teeth, and especially the large premolars and the wide m1, allow for an attribution to the subspecies *Adrcrocuta eximia eximia* (e.g. Koufos 2000, 2009a). Accordingly, the deciduous dentition is morphologically and metrically (L × W: dp3 = 13.1 × 6.3; dp4 = 18.6–20.1 × 6.9, *n* = 3; all in mm) similar to specimens of *Adcrocuta eximia* from Pikermi, Perivolaki and Nikiti-2 in Greece (Gaudry 1862–1867: pl. 12, fig. 6; Koufos 2006, 2016). *Adcrocuta* is a typical hyaenid during the Late Miocene of Eurasia and already known from several localities of Türkiye (e.g. Schmidt-Kittler 1976; Bonis 1994, 2005; Koufos et al. 2018).

A complete cranium of a felid belongs to a large-sized species. The cranium (KYC24.405; Fig. 3g) preserves the right P3–M1 and the left partially broken canine and P3–P4. The P3 is mesiodistally elongated (L × W = 17.0 × 8.1 mm), it bears a small mesial cusp and a well-developed distal one


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◂**Fig. 2** Kayaca locality and excavation photos. **a–c** General views of the locality (**a** and **b** captured from above with the use of a drone); arrows indicate the main excavation spot. **d** Close view of the trench; yellow circles indicate concentrations of fossils. **e–g** Skeletal remains *in situ*; **e** cranium of the bovid *Sporadotragus*. **f** Cranium of the felid *Pontosmilus*. **g** Accumulation of various skeletal remains belonging to several taxa

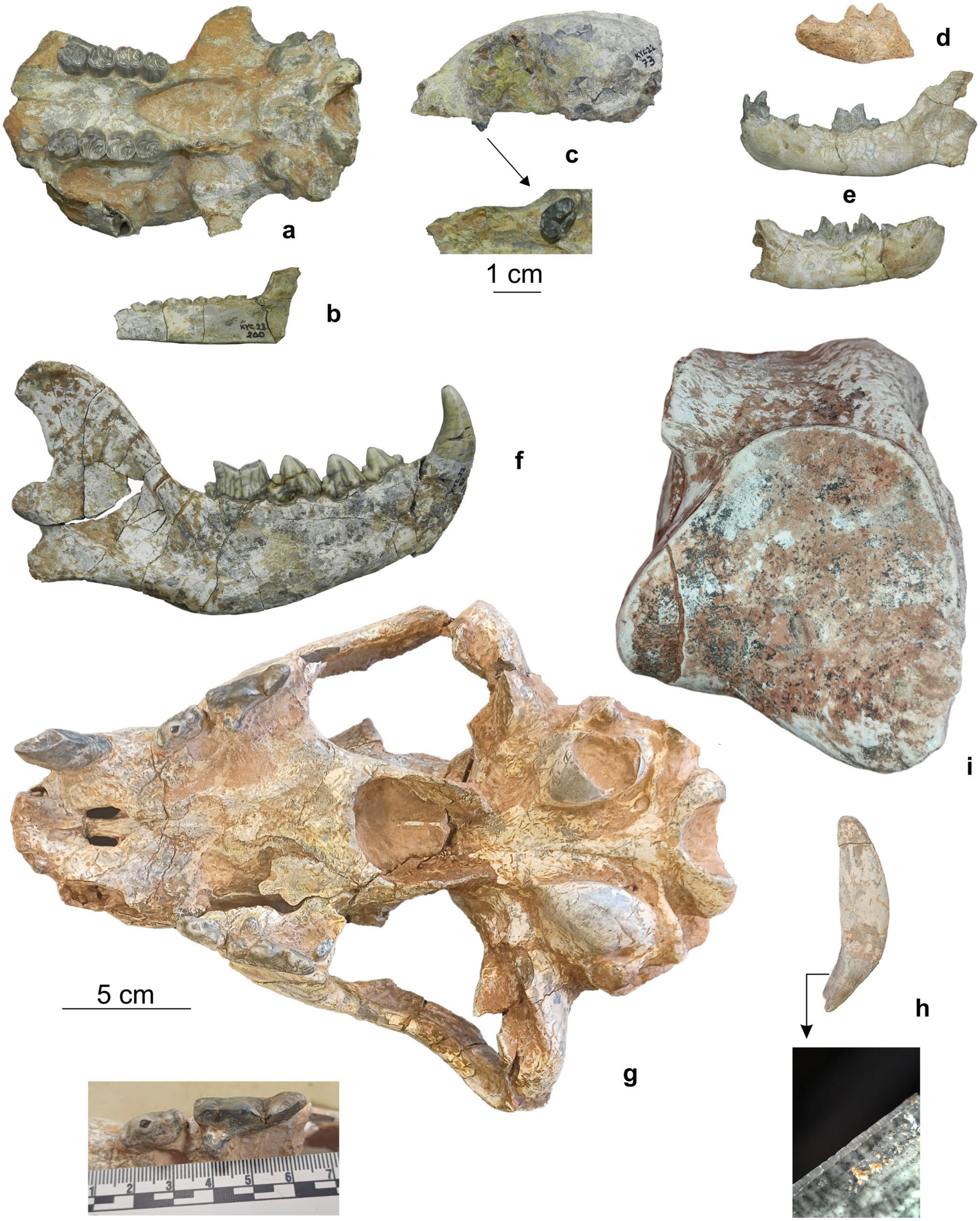
and has a middle–distal lingual convexity; the P4 (L × W = 26.4 × 14.5 mm) is serrated (Fig. 3g), has a mostly straight labial border and a somewhat reduced protocone; the M1 is transversely shortened. Such traits would fit with the diagnosis of *Paramachaeorodus* provided by Salesa et al. (2010). However, recently Jiangzuo et al. (2022) based on several craniodental traits considered that *Paramachaeorodus orientalis* belongs instead to *Pontosmilus orientalis* (type locality Maragheh; Kittl 1887; Salesa et al. 2010), while they resurrected the species *Paramachaeorodus schlosseri* (as the type species of *Paramachaeorodus* with Pikermi as the type locality) which encompasses European specimens previously attributed to *Metailurus major*. Following Jiangzuo et al. (2022), traits such as the serrated P4 of the Kayaca specimen point to *Pontosmilus* and although some features of the teeth (e.g. presence of a small mesial cusp in the P3) fit better with *Paramachaerodus* they may instead represent intraspecific variability or a more primitive evolutionary stage of *Pontosmilus*. Moreover, although the canine (L × W = 18.3 × 11.0 mm) of the cranium is not well-preserved, an isolated canine (KYC24.428; L × W = 17.8 × 11.3 mm; Fig. 3h) shows distinct serration, again pointing to *Pontosmilus*. As such the Kayaca large-sized felid is attributed to *Pontosmilus* sp., even if provisionally, pending more data to securely clarify the taxonomic distinction between *Pontosmilus* and *Paramachaerodus* (see also discussion in Tsoukala et al. 2024). If this attribution is correct, then the Kayaca specimen represents the most complete cranium of *Pontosmilus* to our knowledge. Finally, it should be noted that the Kayaca specimen exhibits certain similarities with the newly erected species *Paramachaerodus transasiaticus* from Hezheng (China) and Hadjidimovo (Bulgaria), which also shows weak serrations in the canines and cheek teeth (Li and Spassov 2017). Two femora (KYC22.89 and KYC24.376; H = 289.1, 292.5 mm) and one tibia (KYC23.190; H = 258.1 mm) from Kayaca correspond to a large-sized felid and could potentially also belong to *Pontosmilus*. All are smaller than *Amphimachairodus giganteus* (e.g. Roussiakis 2002; Koufos 2016) but close to "*Metailurus anceps*" from Hadjidimovo (Kovatchev 2001) that was later allocated to *Metailurus major* (Spassov 2002; Salesa et al. 2012; Spassov and Geraads 2015); recently, however, Jiangzuo et al. (2022) consider that the Balkan representatives of this species belong instead to *Paramachaerodus*.

On the other hand, two femora (KYC23.179A and KYC22.90) and two tibiae (KYC23.179B and KYC22.95) with smaller dimensions (H femur: 234.7, 239.0 mm; H tibia: 222.9, 219.8 mm) belong to a smaller-sized felid. These could be attributed to a species of *Yoshi* (Spassov and Geraads 2015) but are referred to here as Felidae indet. (medium-sized).

Tubulidentata: Mandibular (KYC23.200, KYC24.341; Fig. 3b) and postcranial specimens (astragalus and calcaneus, KYC23.325, and several metapodials) belong to an orycteropodid. The available material is morphologically and metrically compatible with an attribution to *Amphiorycteropus gaudryi*, a species already known in Türkiye (e.g. Kemiklitepe, Şerefköy-2) and from the nearby localities of Samos in Greece and is well distributed in the Balkano-Iranian palaeobiogeographic province (e.g. Sen 1994b; Koufos 2009b; Kaya et al. 2012; Roussiakis et al. 2022).

Proboscidea: The proboscidean material is limited and pertains exclusively to postcranial specimens. Nonetheless, at least two taxa can be distinguished, an elephantimorph (carpals, metapodials) and a deinotheriid, which is identified by a distal extremity of an ulna (KYC22.148; Fig. 3i). The latter shows a distal articular facet for the ulnare morphologically distinct from that of elephantimorphs (e.g. Göhlich 1998). Although the available comparative material of deinotheres is limited, the outline and morphology match well with that of the *Deinotherium* ulnare and are markedly different from those of elephantimorphs (Konidaris et al. 2017). Pending the discovery of dental material, the Kayaca specimen can be ascribed to *Deinotherium* sp.

Rhinocerotidae: Rhinocerotids are well-represented by cranial, mandibular and several postcranial elements (humerus, astragali, calcanei, metapodials) that belong to two taxa, *Miodiceros neumayri* and *Dihoplus* sp. The former is identified by a maxillary fragment bearing the P2–M3 (KYC22.153; Fig. 4d), which is characterised by the presence of a weak paracone fold (better marked in the less worn M3), and the absence of a distal protocone groove, antecrochet, and metacone fold, traits that differentiate it from the upper dentition of *D. pikermiensis* (e.g. Geraads 1988; Giaourtsakis 2009, 2022). Metrically, the cheek teeth stand very close to the specimens of *M. neumayri* from Samos (Giaourtsakis 2009). To this species belong also two astragali (KYC23.271 and KYC22.77; Fig. 4e, f) with a high-oval outline of the sustentacular calcaneal facet, and a width of the bowed articular stripe for the lateral malleolus of the fibula that reduces gradually its width towards the proximal tip (Giaourtsakis 2009). On the other hand, another astragalus (KYC22.157; Fig. 4g, h) features different morphology (subcircular outline of the sustentacular calcaneal facet, and rather constant width of the bowed articular stripe for the lateral malleolus of the fibula), characters that are similar with *Dihoplus pikermiensis*, e.g. from Samos (Giaourtsakis 2009). Pending further material, we preliminarily assign this astragalus to *Dihoplus* sp.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◂**Fig. 3.** **a** *Hystrix* sp., cranium with right and left P4–M1, KYC23.317, ventral view. **b** *Amphiorycteropus gaudryi*, right hemimandible with p2 (broken)–m3, KYC23.200, medial view. **c** *Parataxidea maraghana*, cranium, KYC22.73, in lateral and detail of the left P4 in occlusal view. **d** *Protictitherium* sp., right mandibular fragment with the broken canine and the p2–p3, KYC24.496, lateral view. **e** *Adcrocuta eximia eximia*, left (above, KYC22.99) and right (below, KYC22.94) juvenile hemimandibles, lateral views. **f** *Adcrocuta eximia eximia*, right hemimandible with the canine and the p1–m1, KYC23.252, lateral view. **g** *Pontosmilus* sp., cranium with right P3–M1 and left canine and P3–P4, KYC24.405, in ventral view and detail of the left P3–P4. **h** *Pontosmilus* sp., canine, KYC24.428 showing the serrated enamel at the distal margin. **i** *Deinotherium* sp., distal extremity of left ulna, KYC22.148, distal view

Equidae: At least two hipparionine horses are present at Kayaca, a small-sized and a medium-sized one. The medium-sized form belongs to the *Hipparion prostylum* - *Hipparion dietrichi* lineage of Vlachou and Koufos (2009) or the *dietrichi*-morphotype of Vlachou (2013). It is represented by cranial, mandibular and postcranial remains, among them a complete cranium bearing the complete right and left P2–M3 (KYC22.7; Fig. 4a, b). The latter is characterised by a short and wide muzzle, slightly posteriorly pocketed and moderately deep preorbital fossa, which is situated far from the orbit. The tooth row length is 142.6 mm, the teeth are moderately plicated, and the protocone is elliptical to oval. The metatarsals are relatively long and slender with a mean slenderness index (100 × meas. 11/meas. 1; according to Eisenmann et al. 1988) 14.4. The small-sized form is known at least by a mandibular fragment (KYC22.67; Fig. 4c) with Lp = 64.8, Lm = 57.7, and Lpm = 122.1 (all in mm). Such dimensions are comparable to *Cremohipparion matthewi*/*C.* cf. *matthewi* from Kemiklitepe-A, B, Mahmutgazi and Samos (Koufos and Kostopoulos 1994; Vlachou and Koufos 2009; Geraads 2017), but the available material and especially the absence of cranial remains do not allow for a more precise attribution. We therefore refer to this equid as *Cremohipparion* sp. (small-sized).

Suidae: Although suids are represented by only few specimens so far, they are suitable for taxonomic identification, particularly the mandibular fragment that bears the well-preserved right and left cheek teeth rows (KYC23.336; Fig. 5e). The symphysis is partially preserved, yet the morphology of the mandible and the teeth is typical of *Hippopotamodon* (= *Microstonyx*). The p3 shows a simple morphology, whereas the p4 is more complex, and the metaconid and protoconid are equally high. The m1 and m2 have similar morphology and consist of four main cusps, but the m2 is longer and wider. The m3 (L × W: 47.2 × 21.1, 46.2 × 21.3 mm; right and left, respectively) is more complex; the first and second lophids are wider and have a complex talonid structure distally. The lingual notch is prominent between the metaconid and entoconid. The Kayaca suid material differs from *Hippopotamodon antiquus* in the narrower and shorter cheek teeth (especially the anterior premolars) and fits morphologically and metrically with *Hippopotamodon major* (= *Microstonyx erymanthius*) from Akkaşdağı, Şerefköy 2, Pikermi, Samos and some of the Çorakyerler specimens (Liu et al. 2005; Sylvestrou and Kostopoulos 2009; Pickford 2015; Tarhan 2021).

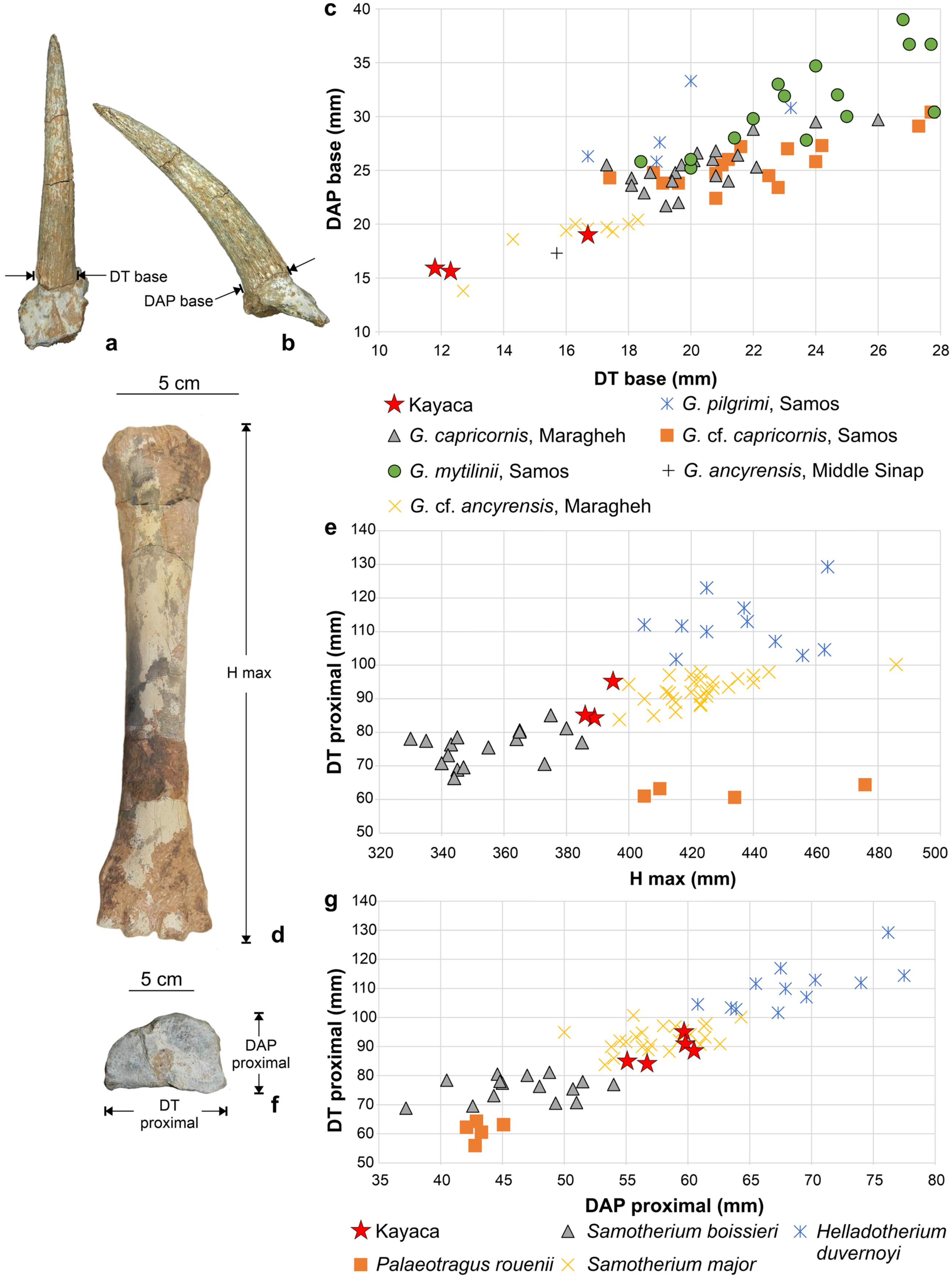
Giraffidae: Two giraffid species are recognised. The first and smaller-sized one is identified by a single specimen, a mandibular fragment that preserves the p3–m3 toothrow (KYC24.351; Fig. 5f) showing brachydont dentition and a molarized p4. The length of the molars (76.6 mm) matches well with that of *Palaeotragus rouenii* (e.g. Laskos and Kostopoulos 2022). This species is already known in Türkiye, e.g. Kemiklitepe-D, A, Akkaşdağı, Şerefköy-2 and Kavakdere (Geraads 1994; Kostopoulos and Saraç 2005; Kaya et al. 2012; Xafis et al. 2019a), as well as from the Samos localities, where it is also less frequent than *Samotherium* (Kostopoulos 2009b). The second and larger-sized giraffid is much better represented in the assemblage by both dental and postcranial specimens encompassing several completely preserved elements such as radius (KYC22.61), metacarpals (KYC23.213, 260, KYC22.136), tibia (KYC22.11), astragali (KYC22.3, 9, 112, 140, KYC23.301, 329, 339, and two surface ones), calcanei (KYC22.102, 110), metatarsals (KYC22.35, KYC23.272) and phalanges (KYC22.13, KYC22.100, 129). Metrically, the specimens are intermediate between those of the smaller-sized *Palaeotragus* and the larger-sized *Helladotherium* and match well with the *Samotherium* sample from Samos (Fig. 6d–g). Within *Samotherium*, the Kayaca specimens are larger than *Samotherium boissieri* and plot within or close the lower range of *Samotherium major* (Fig. 6e, g), permitting an attribution to this species.

Bovidae: Gazelles are represented by cranial, mandibular and some postcranial material, including complete/partially complete crania preserving the horncores. The basal dimensions of the latter (DT: 11.8–16.7 mm, DAP: 15.9–19.1 mm; *n* = 3–4) are smaller than *Gazella mytilinii*, *Gazella pilgrim* and *Gazella* cf. *capricornis* from Samos, as well as than *G. carpicornis* from Maragheh. By the short, small in basal diameters, rather straight and caudally inclined horncores the Kayaca taxon fits well with the small-sized gazelle from Middle Sinap, Kemiklitepe-D, Maragheh and Samos (Fig. 6a–c; Tekkaya 1973; Bouvrain 1994; Kostopoulos 2009c; fig. 6; Kostopoulos and Bernor 2011) attributed to *Gazella ancyrensis* or *G.* cf. *ancyrensis*. The Kayaca horncores are more curved than those from the type locality (Middle Sinap) of this species (but see Kostopoulos and Bernor 2011 for variability of this trait in gazelles) and fit better with those from Kemiklitepe-D, Maragheh and Samos. Apart from the horncore size, proportions and morphology, the species is considered to differ from *G. capricornis* also in the shorter molar row (Kostopoulos and Bernor 2011);

Fig. 4 **a–b** *Hipparion dietrichi*-morphotype, cranium, KYC22.7; **a** lateral view; **b** ventral view. **c** *Cremohipparion* sp. (small-sized), mandible fragment, KYC22.67, dorsal view. **d** *Miodiceros neumayri*, right maxillary fragment bearing the P2–M3, KYC22.153, ventral view. **e–f** *Miodiceros neumayri*, left astragalus, KYC23.271; **e** plantar view; **f** lateral view. **g–h** *Dihoplus* sp., right astragalus, KYC22.157; **g** plantar view; **h** lateral view

Fig. 5 **a** *Palaeoryx pallasi*, cranium, KYC24.352, right lateral view. **b** *Tragoportax* sp., female cranium, KYC22.117, right lateral view. **c** *Sporadotragus parvidens*, cranium with horncores, KYC24.451, right lateral view. **d** *Gangraia* sp., cranium, KYC24.411, right lateral view. **e** *Hippopotamodon major*, right hemimandible, KYC23.336, dorsal view. **f** *Palaeotragus rouenii*, left p3–m3 toothrow, KYC24.351, occlusal view

indeed, the molar row length in the Kayaca mandibles (32.1–33.9, mean = 33.1; *n* = 4) is smaller than in *G.* (cf.) *capricornis*, *G. pilgrimi* and *G. mytilinii* from Samos and Maragheh, and fits well with that of *G.* cf. *ancyrensis* from Kemiklitepe-D and Maragheh. Therefore, we attribute the gazelle from Kayaca to *Gazella* cf. *ancyrensis*.


a
b
DT base
DAP base
5 cm
H max
d
5 cm
DAP proximal
DT proximal
f
c
DAP base (mm)
DT base (mm)
10
15
20
25
30
35
40
10
12
14
16
18
20
22
24
26
28
Kayaca
G. pilgrimi, Samos
G. capricornis, Maragheh
G. cf. capricornis, Samos
G. mytilinii, Samos
G. ancyrensis, Middle Sinap
G. cf. ancyrensis, Maragheh
e
DT proximal (mm)
H max (mm)
50
60
70
80
90
100
110
120
130
140
320
340
360
380
400
420
440
460
480
500
g
DT proximal (mm)
DAP proximal (mm)
35
40
45
50
55
60
65
70
75
80
Kayaca
Samotherium boissieri
Helladotherium duvernoyi
Palaeotragus rouenii
Samotherium major

◂**Fig. 6** **a–b** *Gazella* cf. *ancyrensis*, cranial fragment with horncore, KYC22.46; **a** frontal view; **b** lateral view. **c** Bivariate plot of transverse diameter at the base (DT base) vs. anteroposterior diameter at the base (DAP base) for the horncores of *Gazella* spp. (data from Tekkaya 1973; Kostopoulos 2009c, and Kostopoulos and Bernor 2011). **d** *Samotherium major*, left third and fourth metacarpal, KYC23.213, anterior view. **e** Bivariate plot of maximum height (H max) vs. transverse diameter at the proximal end (DT proximal) for the third and fourth metacarpal of various giraffids. **f** *Samotherium major*, left third and fourth metacarpal, KYC23.260, proximal view. **g** Bivariate plot of anteroposterior diameter at the proximal end (DAP proximal) vs. transverse diameter at the proximal end (DT proximal) for the third and fourth metacarpal of various giraffids (data from Geraads 1994; Kostopoulos and Koufos 2006; Kostopoulos 2009b; Xafis et al. 2019a, b)

An almost complete cranium (KYC24.451; Fig. 5c) preserving the horncores belongs to a medium-sized bovid. The face is short, the braincase is angled on the face, the occipital forms an obtuse angle with the cranial roof, and the anterior margin of the orbit is placed above the M3. The upper premolar/molar ratio is 70.8 (LP = 30.6, LM = 43.2; LPM = 72.9). The horncores are long, sub-cylindrical and curved posteriorly, they show irregular furrows and lack torsion or keels. Five more pairs of horncores (KYC22.108, 126, KYC23.258, 287, 306) show the same morphology and dimensions (mean DT base = 40.1; mean DAP base = 47.8 mm; *n* = 6). Several mandibles show a short premolar row compared to the molars, with a premolar/molar ratio at 57.6–61.7 (*n* = 7) and length of the m3, Lm3 = 18.8–22.5 mm (*n* = 19). The morphology, size and proportions of the cranium, the horncores and the dentition match well with those of *Sporadotragus parvidens* from Samos, Pikermi and Şerefköy-2 (Geraads et al. 2006; Kostopoulos 2009c; Kostopoulos and Karakütük 2015).

A partial cranium with both horncores (KYC24.411) belongs to a medium- to large-sized bovid (Fig. 5d). The horncores are long, keelless, inserted widely apart, strongly diverged each other and slightly curved forwards (maximum × minimum basal diameters: 47.6 × 40.6 mm). Their surface shows clear developmental transverse ridges and irregular longitudinal furrows along their length. All these traits are diagnostic features of the recently erected genus *Gangraia* from Çorakyerler (Kostopoulos et al. 2021) and as such the Kayaca cranium is allocated to this genus.

Large-sized bovids are represented by two taxa, which are identified by cranial and mandibular material. An almost complete cranium (KYC22.117; LP: 50.0; LM: 60.2; LPM: 107.2; all in mm) shows a well-defined depressed area in the fronto-parietal surface, delimited laterally by well-marked temporal ridges and caudally by a step (Fig. 5b), a trait typical for the boselaphine *Tragoportax* (e.g. Spassov et al. 2004; Kostopoulos 2016). The cranium is hornless as known from several female individuals of *Tragoportax* further supporting an attribution to this genus. Several hornless, female, crania of *Tragoportax* are reported from various localities, e.g. from Maragheh, Samos, Axios Valley in Greece, and Molayan in Afghanistan (see discussion in Kostopoulos 2006 and Kostopoulos and Bernor 2011).

Another almost complete cranium (KYC24.352; Fig. 5a) with relatively short opisthocranium, horncores (DT base = 44.5; DAP base = 51.6 mm) inserted in the postero-dorsal part of the orbit, rather brachyodont cheek teeth, and upper premolar/molar ratio 70.0 (LP = 45.3, LM = 64.7; LPM = 107.2; all in mm) is ascribed to the large-sized antilopine *Palaeoryx pallasi* (see e.g. Kostopoulos 2009c, 2016). A larger (DT base: 56.6 mm; DAP base: 70.5 mm), isolated, horncore fragment (KYC23.297) with almost rounded cross-section at the base also fits well with *Palaeoryx* from Samos and Pikermi (Kostopoulos 2009c: fig. 7). Additionally, a hemimandible fragment (KYC22.109) bearing the complete cheek tooth dentition has morphology and dimensions (Lp = 55.3; Lm = 79.5; Lpm = 135.0; Lm3 = 34.8; Wm3 = 15.9; all in mm) similar to those of from Samos and Şerefköy-2 and allow for attribution also to *Palaeoryx* (Kostopoulos 2009c; Kostopoulos and Karakütük 2015).

Biochronology

The preliminary faunal list of Kayaca is given in Table 1. Most of the mammalian taxa that are documented at Kayaca have a biostratigraphic range within the Turolian and only few species (e.g. *Miodiceros neumayri*, *Gazella* cf. *ancyrensis*, *Hippopotamodon major*) are recorded also within the Vallesian, confirming the Turolian character of the Kayaca large mammal fauna (Fig. 7). Several taxa (e.g. *Parataxidea maraghana*, *Tragoportax*, *Palaeoryx pallasi*, *Hipparion dietrichi* morphotype) restrict the age to the early–middle Turolian. The presence of *G. ancyrensis* clearly indicates an age older than the Dominant Mammal Assemblage of Samos (7.2–6.9 Ma; Koufos et al. 2009a). This mostly Vallesian species is present in the early Turolian of Kemiklitepe-D (7.7. Ma; Bouvrain 1994; Sen et al. 1994), the Middle Maragheh (Kostopoulos and Bernor 2011) and the Primary Mammal Assemblage of Samos (7.8–7.4 Ma; Kostopoulos 2009c; Koufos et al. 2009a). The giraffid material is also biochronologically informative as based on Samos and the upper levels of Kemiklitepe *Samotherium major* is thought to have replaced its forerunner *S. boissieri* at ca. 7.4 Ma (Kostopoulos 2009b). The smaller dimensions of *S. major* from Kayaca than those from the Dominant Mammal Assemblage of Samos (see also Kostopoulos 2009b: fig. 19) might hint at an age close to this replacement, i.e. close to the MN 11/12 boundary, which would also fit better with the presence of *G. ancyrensis* as well as with the occurrence of *Gangraia*, otherwise known so far only from Çorakyerler (8.7 Ma, MN 10/11; Kostopoulos et al. 2021; Sevim-Erol et al. 2023).

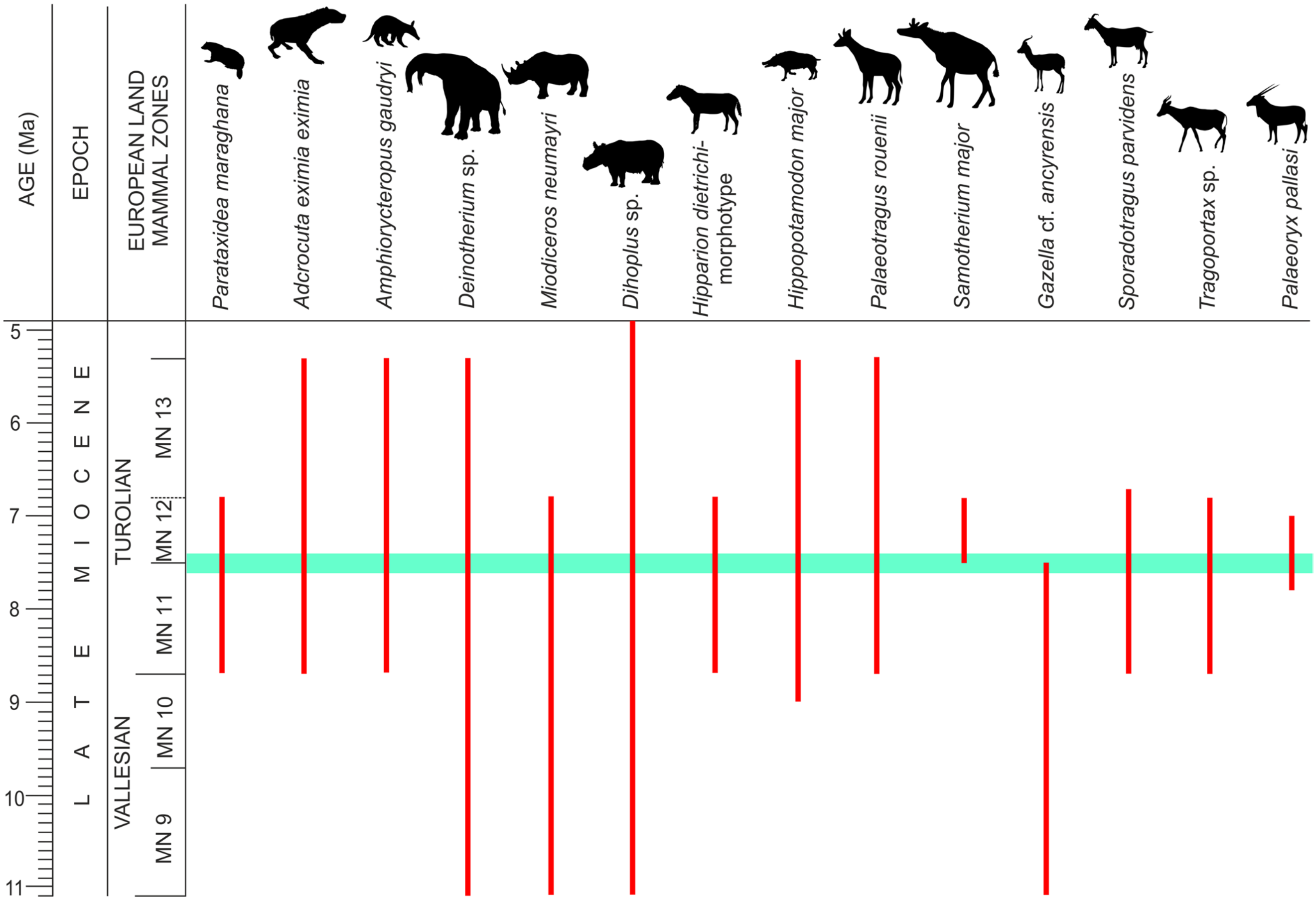


Fig. 7 Biostratigraphic range of selected mammal taxa documented at Kayaca and proposed biochronologic placement of the locality (green box). The boundaries of the MN zones are according to Kostopoulos (2009a); the upper boundary of MN 12 remains controversial and is marked with a dashed line. Silhouette images from PhyloPic, phylopic.org

Overall, based on the biostratigraphic range of the Kayaca large mammals and their comparison with well-studied mammal faunas from Anatolia and Greece, an age close to 7.4 Ma, i.e. close to the transition between the early and middle Turolian, is proposed for Kayaca (Fig. 7). This age renders Kayaca as chronologically younger than Çorakyerler and older than Akkaşdağı (ca. 7.1 ± 0.1 Ma, MN 12; Sen 2005; alternatively, MN 12/13 *sensu* Spassov et al. 2018), and is possibly dated between the lower (KTD) and upper (KTA, KTB) levels of Kemiklitepe (7.7 Ma, MN 11 and 7.2 Ma, MN 12, respectively; Sen et al. 1994), and at the transition between the Primary and the Intermediate Mammal assemblage of Samos (ca. 7.4 Ma; Koufos et al. 2009a).

Conclusions

Kostopoulos (2009a) and Koufos et al. (2009b) pointed out the faunal resemblance in terms of taxonomic composition and abundance of specific taxa (hipparionine horses, antelopes, gazelles, giraffids) and accordingly the biogeographic similarities between the Turolian mammal faunas of Samos in Greece (which was part of today's Asia Minor during the Late Miocene) and the western Anatolian ones. Considering the taxonomic resemblance of the first collected material from Kayaca with the geographically adjacent faunas of Samos this interpretation is further confirmed. Based on the palaeoecological study of the Samos mammals (including dental micro- and mesowear analyses in order to illuminate their feeding preferences), the majority of the Kayaca ungulates are considered as mixed-feeders or grazers indicating possibly a similar palaeolandscape of an open bushland with a well-developed grassy floor.

In addition to the taxonomic, biochronologic and palaeobiogeographic perspectives, another interesting aspect of the Kayaca assemblage is its taphonomic context, which deserves further investigation. For instance, the presence of bones preserving evidence of carnivore gnawing (e.g. tooth marks; Fig. 8) suggests that carnivorans played a role in the modification of the bone assemblage to a certain degree.

Table 1 Preliminary faunal list of the large mammals from Kayaca

Order	Family/Clade	Genus	Species/Subspecies
Rodentia	Hystricidae	*Hystrix*	sp.
Carnivora	Mustelidae	*Parataxidea*	*maraghana*
	"Ictitheres"	*Protictitherium*	sp.
	Hyaenidae	*Adcrocuta*	*eximia eximia*
	Felidae	*Pontosmilus*	sp.
		indet. (medium-sized)	
Tubulidentata	Orycteropodidae	*Amphiorycteropus*	*gaudryi*
Proboscidea	Deinotheriidae	*Deinotherium*	sp.
	Elephantimorpha	indet.	
Perissodactyla	Equidae	*Hipparion*	*dietrichi* (morphotype)
		Cremohipparion	sp. (small-sized)
	Rhinocerotidae	*Miodiceros*	*neumayri*
		Dihoplus	sp.
Artiodactyla	Suidae	*Hippopotamodon*	*major*
	Giraffidae	*Palaeotragus*	*rouenii*
		Samotherium	*major*
	Bovidae	*Gazella*	cf. *ancyrensis*
		Sporadotragus	*parvidens*
		Gangraia	sp.
		Tragoportax	sp.
		Palaeoryx	*pallasi*

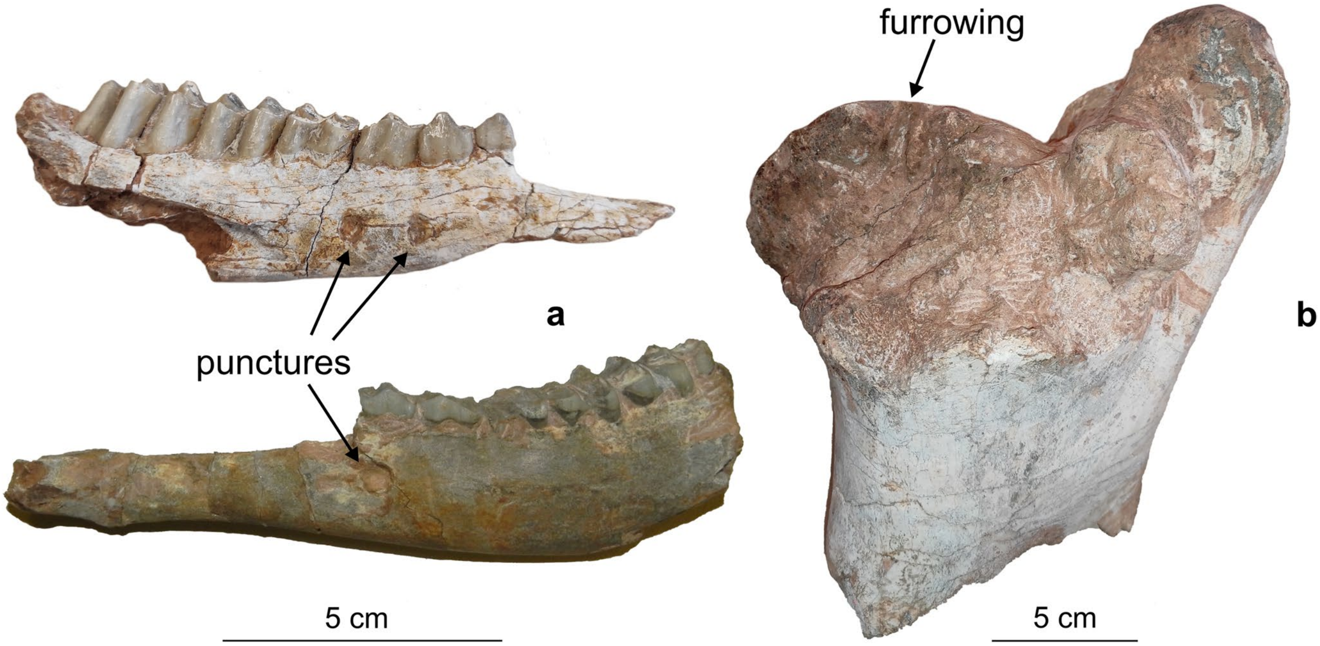


Fig. 8 Carnivore gnawing on ungulates. **a** Punctures on mandibles of medium-sized bovids. **b** Furrowing (deletion of cancellous tissue) on the proximal epiphysis of a rhinocerotid humerus

The fact that the modified bones belong to ungulates ranging in size from small-/medium-sized bovids to rhinocerotids (megafauna; Fig. 8) indicates a wide spectrum of prey by formidable predators (e.g. *Adcrotuta* and the felids present at the site), while the relatively high number of juvenile individuals (particularly bovids, and hipparions, but also rhinocerotids) might be related to specific foraging strategies and selection of prey.

Although research at Kayaca is just at its beginning, the already collected material shows a rich and diversified vertebrate fauna (to date more than 700 specimens collected and 21 taxa of large mammals as yet identified), important in terms of completeness and preservation of specimens, that has the potential to contribute to the identification of the faunal, evolutionary and palaeoenvironmental changes at both local and regional scale. As such, the discovery of new material from Kayaca is deemed essential in order to i) enrich the collection and enhance our knowledge on the evolution and taxonomy of several vertebrate taxa and mammal turnovers, ii) add further data for a more detailed age estimation, iii) lead to the precise biostratigraphic correlation between Kayaca and other Upper Miocene sites of Türkiye and the wider region of western Eurasia, and iv) provide additional palaeobiogeographical, taphonomic and palaeoecological information, offering overall valuable insights into the Late Miocene terrestrial ecosystems of the eastern peri-Mediterranean region.

Acknowledgements Excavations at Kayaca were supported by the Republic of Türkiye Ministry of Culture and Tourism, and with funds from the DFG Leibniz prize awarded to KH. We thank the Tavas Directorate of National Education and the Özay Gönlüm Science High School for providing accommodation for the team members. Many thanks to all field team members for their valuable contribution in the fieldwork and the preparation of the material. We also thank G. Koufos and T. Vlachou for discussions on some of the specimens. G.K. was supported by the Deutsche Forschungsgemeinschaft Project no. 463225251 ("MEGALOPOLIS"). KH is also supported by the European Research Council (ERC-AdG-101019659). We thank N. Spassov and one anonymous reviewer for the constructive comments and suggestions that improved the manuscript.

Funding Open access funding provided by HEAL-Link Greece.

Data availability All specimens are stored at the Department of Anthropology of the Akif Ersoy University in Burdur (Türkiye).

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

References

Alçiçek, M. C., Mayda, S., ten Veen, J. H., Boulton, S. J., Neubauer, T. A., Alçiçek, H., Tesakov, A. S., Saraç, G., Hakyemez, H. Y., Göktaş, F., Murray, A. M., Titov, V. V., Jiménez-Moreno, G., Büyükmeriç, Y., Wesselingh, F. P., Bouchal, J. M., Demirel, F. A., Kaya, T. T., Halaçlar, K., Bilgin, M., & van den Hoek Ostende, L. W. (2019). Reconciling the stratigraphy and depositional history of the Lycian orogen-top basins, SW Anatolia. In L. W. van den Hoek Ostende, S. Mayda, & T. Kaya (Eds.), *Taking the Orient Express? The role of Anatolia in mediterranean Neogene palaeobiogeography. Palaeobiodiversity and Palaeoenvironments*, *99*(4), 551–570.

Aytek, A. I., Yavuz, A. Y., Mayda, S., Tarhan, E., Aladağ, B., Vialet, A., & Alçiçek, M. C. (2022). Denizli İli omurgalı fosil yatakları tespiti yüzey araştırması 2019-2020 (Vertebrate fossil locality survey in Denizli 2019-2020). In C. Keskin (Ed.), *2019-2020 Yili Yüzey Araştırmaları* (Vol. 193, pp. 133–144). Kültür Varlıkları ve Müzeler Genel Müdürlüğü. [in Turkish]

Becker-Platen, J. D. (1970). *Lithostratigraphische Untersuchungen im Känozoikom Südwest- Anatoliens (Türkei). (Känozoikum und Braunkohlen der Türkei. 2.)* (Vol. 97). Beihefte zum Geologischen Jahrbuch. Hannover: Bundesanstalt für Bodenforschung.

Böhme, M., Spassov, N., Ebner, M., Geraads, D., Hristova, L., Kirscher, U., Kötter, S., Linnemann, U., Prieto, J., Roussiakis, S., Theodorou, G., Uhlig, G., & Winklhofer, M. (2017). Messinian age and savannah environment of the possible hominin *Graecopithecus* from Europe. *PLoS ONE*, *12*, e0177347.

Böhme, M., Spassov, N., Majidifard, M. R., Gärtner, A., Kirscher, U., Marks, M., Dietzel, C., Uhlig, G., El Atfy, H., Begun, D. R., & Winklhofer, M. (2021). Neogene hyperaridity in Arabia drove the directions of mammalian dispersal between Africa and Eurasia. *Communications Earth & Environment*, *2*, 85.

Bonis, L. de (1994). Les gisements de mammifères du Miocène supérieur de Kemiklitepe, Turquie: 2. Carnivores. *Bulletin du Muséum National d'Histoire Naturelle*, *16*, 19–39.

Bonis, L. de (2005). Carnivora (Mammalia) from the late Miocene of Akkaşdağı, Turkey. In S. Sen (Ed.), *Geology, mammals and environments at Akkaşdağı, late Miocene of Central Anatolia. Geodiversitas, 27,* 567–589.

Bonis, L. de, Brunet, M., Heintz, E., & Sen, S. (1992). La province greco-irano-afghane et la réparition des faunes mammaliennes au Miocène supérieur. *Paleontologia i Evolució*, *24–25*, 103–112.

Bouvrain, G. (1994). Les gisements de mammifères du Miocène supérieur de Kemiklitepe, Turquie: 9. Bovidae. *Bulletin du Muséum National d'Histoire Naturelle*, *16*, 175–209.

Eisenmann, V., Alberdi, M. T., Giuli, C. d., & Staesche, U. (1988). Methodology. In M. Woodburne & P. Sondaar (Eds.), *Studying fossil horses* (pp. 1–71). Leiden: E. J. Brill.

Erol, A. S., Kaya, T. T., Yavuz, A. Y., Mayda, S., Cihat Alçiçek, M., & van den Hoek Ostende, L. W. (2016). *The late Miocene (early Turolian, MN 11) fauna of Corakyerler (Turkey): New collection of large mammals.* XIV Annual Meeting of the European Association of Vertebrate Palaeontologists, Haarlem, The Netherlands.

Fortelius, M., Kappelman, J., Sen, S., & Bernor, R. L. (Eds.). (2003). *Geology and Paleontology of the Miocene Sinap Formation, Turkey*. New York: Columbia University Press.

Gaudry, A. (1862–1967). *Animaux fossiles et géologie de l'Attique*. Paris: F. Savy.

Geraads, D. (1988). Révision des Rhinocerotinae (Mammalia) du Turolien de Pikermi. Comparaison avec les formes voisines. *Annales de Paléontologie*, *74*, 13–41.

Geraads, D. (1994). Les gisements de mammifères du Miocène supérieur de Kemiklitepe, Turquie: 8. Giraffidae. *Bulletin du Muséum National d'Histoire Naturelle*, *16*, 159–173.

Geraads, D. (2017). Late Miocene large mammals from Mahmutgazi, Denizli province, Western Turkey. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, *284*, 241–257.

Geraads, D., Kaya, T., & Mayda, S. (2005). Late Miocene large mammals from Yulaflı, Thrace region, Turkey, and their biogeographic implications. *Acta Palaeontologica Polonica*, *50*, 523–544.

Geraads, D., Spassov, N., & Kovachev, D. (2006). A new *Sporadotragus* (Bovidae, Mammalia) from the late Miocene of Bulgaria. *Rivista Italiana di Paleontologia e Stratigrafia*, *112*, 473–479.

Giaourtsakis, I. (2009). The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 9. Rhinocerotidae. In G. D. Koufos & D. Nagel (Eds.), *The Late Miocene Mammal Faunas of Samos*. *Beiträge zur Paläontologie, 31*, 157–187.

Giaourtsakis, I. (2022). The fossil record of rhinocerotids (Mammalia: Perissodactyla: Rhinocerotidae) in Greece. In E. Vlachos (Ed.), *Fossil Vertebrates of Greece Vol. 2: Laurasiatherians, Artiodactyles, Perissodactyles, Carnivorans, and Island Endemics* (pp. 409–500). Springer.

Göhlich, U. B. (1998). Elephantoidea (Proboscidea, Mammalia) aus dem Mittel- und Obermiozän der Oberen Süβwassermolasse Süddeutschlands: Odontologie und Osteologie. *Münchner Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie*, *36*, 1–245.

Halaçlar, K., Erol, A. S., Köroğlu, T., Rummy, P., Deng, T., & Mayda, S. (2024). A new Late Miocene *Hystrix* (Hystricidae, Rodentia) from Turkey. *Integrative Zoology*, *19* 548–563.

Halaçlar, K., Rummy, P., Mayda, S., & Deng, T. (2025). A newly discovered *Hystrix primigenia* specimen from the Kemiklitepe collection at Ege University Natural History Museum: insights into paleobiogeography in Eurasia. *Integrative Zoology*, *20*, 73–87.

Jiangzuo, Q., Niu, K., Li, S., Fu, J., & Wang, S. (2022). A diverse metailurine guild from the latest Miocene Xingjiawan fauna, Yongdeng, Northwestern China, and generic differentiation of metailurine felids. *Journal of Mammalian Evolution*, *29*, 845–862.

Kaya, T. (1993). The Late Miocene Perissodactyla in Sazak (Kale-Denizli). *Bulletin of the Mineral Research and Exploration*, *115*, 23–30.

Kaya, T., Geraads, D., & Tuna, V. (2005). A new Late Miocene mammalian fauna in the Karaburun Peninsula (W Turkey). *Neues Jahrbuch für Geologie Paläontologie - Abhandlungen*, *236*, 321–349.

Kaya, T., Mayda, S., & Tan, A. (2008). *New fossil records from the Late Miocene mammalian localities from Muğla-Yatağan region* IX. Paleontology-Stratigraphy Workshop, Denizli-Turkey.

Kaya, T. T., Mayda, S., Kostopoulos, D. S., Alcicek, M. C., Merceron, G., Tan, A., Karakutuk, S., Giesler, A. K., & Scott, R. S. (2012). Şerefköy-2, a new Late Miocene mammal locality from the Yatağan Formation, Muğla, SW Turkey. *Comptes Rendus Palevol*, *11*, 5–12.

Kaya, F., Bibi, F., Žliobaitė, I., Eronen, J. T., Hui, T., & Fortelius, M. (2018). The rise and fall of the Old World savannah fauna and the origins of the African savannah biome. *Nature Ecology & Evolution*, *2*, 241–246.

Kittl, E. (1887). Beiträge zur Kenntnis der fossilen Säugethiere von Maragha in Persien. *Annalen des K.K. Naturhistorischen Hofmuseums*, *2*, 317–338.

Konak, N., & Şenel, M. (2002). *Geological map of Turkey in 1/500.000 scale: Denizli sheet*. Mineral Research and Exploration Directorate of Turkey (MTA).

Konidaris, G. E., Roussiakis, S. J., Athanassiou, A., & Theodorou, G. E. (2017). The huge-sized deinothere *Deinotherium proavum* (Proboscidea, Mammalia) from the Late Miocene localities Pikermi and Halmyropotamos (Greece). *Quaternary International*, *430*, 5–21.

Konidaris, G. E., Aytek, A. I., Yavuz, A. Y., Tarhan, E., & Alçiçek, M. C. (2023). First report of "*Mammut*" (Mammalia, Proboscidea) from the Upper Miocene of Turkey. *Journal of Vertebrate Paleontology*, e2222784.

Kostopoulos, D. S. (2009a). The Pikermian Event: Temporal and spatial resolution of the Turolian large mammal fauna in SE Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *274*, 82–95.

Kostopoulos, D. S. (2009b). The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 13. Giraffidae. In G. D. Koufos & D. Nagel (Eds.), *The Late Miocene mammal faunas of Samos* . *Beiträge zur Paläontologie, 31*, 299–343.

Kostopoulos, D. S. (2009c). The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 14. Bovidae. In G. D. Koufos & D. Nagel (Eds.), *The Late Miocene mammal faunas of Samos* (Vol. 31, pp. 345–389). Beiträge zur Paläontologie.

Kostopoulos, D. S. (2016). Artiodactyla. In G. D. Koufos & D. S. Kostopoulos (Eds.), *Palaeontology of the upper Miocene vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece)*. *Geobios 49,* 119–134.

Kostopoulos, D. S., & Bernor, R. L. (2011). The Maragheh bovids (Mammalia, Artiodactyla): systematic revision and biostratigraphic-zoogeographic interpretation. *Geodiversitas*, *33*, 649–708.

Kostopoulos, D. S., & Karakütük, S. (2015). Late Miocene bovids from Şerefköy-2 (SW Turkey) and their position within the sub-Paratethyan biogeographic province. *Acta Palaeontologica Polonica*, *60*, 49–66.

Kostopoulos, D. S., & Koufos, G. D. (2006). The late Miocene vertebrate locality of Perivolaki, Thessaly, Greece. 9. Cervidae and Bovidae. *Palaeontographica Abt. A*, *276*, 151–183.

Kostopoulos, D. S., & Saraç, G. (2005). Giraffidae (Mammalia, Artiodactyla) from the late Miocene of Akkaşdağı, Turkey. In S. Sen (Ed.), *Geology, mammals and environments at Akkaşdağı, late Miocene of Central Anatolia*. *Geodiversitas, 27,* 735–745.

Kostopoulos, D. S., Sevim Erol, A., Yavuz, A. Y., & Mayda, S. (2021). A new late Miocene bovid (Mammalia: Artiodactyla: Bovidae) from Çorakyerler (Turkey). *Fossil Record*, *24*, 9–18.

Koufos, G. D. (2000). Revision of the late Miocene carnivores from the Axios valley, Macedonia, Greece. *Münchner Geowissenschaftliche Abhandlungen*, *39*, 51–92.

Koufos, G. D. (2006). *The late Miocene vertebrate locality of Perivolaki, Thessaly, Greece. 4. Carnivor*a (pp. 39–74). Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung.

Koufos, G. D. (2009a). The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 5. Carnivora. In G. D. Koufos & D. Nagel (Eds.), *The Late Miocene mammal faunas of Samos. Beiträge zur Paläontologie, 31,* 57–105.

Koufos, G. D. (2009b). The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 6. Tubulidentata. In G. D. Koufos & D. Nagel (Eds.), *The Late Miocene Mammal Faunas of Samos*. *Beiträge zur Paläontologie 31*, 107–125.

Koufos, G.D. (2013). Neogene mammal biostratigraphy and chronology of Greece. In X. Wang, L. J. Flynn & M. Fortelius (Eds.), *Fossil mammals of Asia. Neogene biostratigraphy and chronology* (pp. 596–621). New York: Columbia University Press.

Koufos, G. D. (2016). Carnivora. In G. D. Koufos & D. S. Kostopoulos (Eds.), *Palaeontology of the upper Miocene vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece)*. *Geobios*, 53–67.

Koufos, G. D. (2022). The fossil record of mustelids (Mammalia: Carnivora: Mustelidae) in Greece. In E. Vlachos (Ed.), *Fossil Vertebrates of Greece Vol. 2: Laurasiatherians, Artiodactyles, Perissodactyles, Carnivorans, and Island Endemics* (pp. 641–659). Springer.

Koufos, G. D., & Kostopoulos, D. S. (1994). Les gisements de mammifères du Miocène supérieur de Kemiklitepe, Turquie: 3. Equidae. *Bulletin du Muséum National d'Histoire Naturelle*, *16*, 41–80.

Koufos, G. D., Kostopoulos, D. S., & Vlachou, T. D. (2005). Neogene/Quaternary mammalian migrations in Eastern Mediterranean. *Belgian Journal of Zoology*, *135*, 181–190.

Koufos, G. D., Kostopoulos, D. S., & Vlachou, T. D. (2009a). The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 16. Biochronology. In G. D. Koufos & D. Nagel (Eds.), *The Late Miocene mammal faunas of Samos*. *Beiträge zur Paläontologie 31*, 397-408.

Koufos, G. D., Kostopoulos, D. S., & Merceron, G. (2009b). The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 17. Palaeoecology - Palaeobiogeography. In G. D. Koufos & D. Nagel (Eds.), *The Late Miocene mammal faunas of Samos. Beiträge zur Paläontologie 31,* 409–430.

Koufos, G. D., Mayda, S., & Kaya, T. (2018). New carnivoran remains from the Late Miocene of Turkey. *PalZ*, *92*(1), 131–162.

Kovachev, D. (2012). A porcupine skeleton of *Hystrix (Hystrix) primigenia* (Wagner) from the Upper Maeotian (Turolian) near Hadzhidimovo, SW Bulgaria. *Geologica Balcanica, 41*, 3–20.

Kovatchev, D. (2001). Description d'un squelette complet de *Metailurus* (Felidae, Carnivora, Mammalia) du Miocène supérieur de Bulgarie. *Geologica Balcanica*, *31*, 71–88.

Laskos, K., & Kostopoulos, D. S. (2022). The Vallesian large *Palaeotragus* Gaudry, 1861 (Mammalia: Giraffidae) from Northern Greece. *Geodiversitas*, *44*, 437–470.

Li, Y., & Spassov, N. (2017). A new species of *Paramachaerodus* (Mammalia, Carnivora, Felidae) from the late Miocene of China and Bulgaria, and revision of *Promegantereon* Kretzoi, 1938 and *Paramachaerodus* Pilgrim, 1913. *Paläontologische Zeitschrift*, *91*, 409–426.

Liu, L., Kostopoulos, D. S., & Fortelius, M. (2005). Suidae (Mammalia, Artiodactyla) from the late Miocene of Akkaşdağı, Turkey. In S. S. (Ed.), *Geology, mammals and environments at Akkaşdağı, late Miocene of Central Anatolia. Geodiversitas 27,* 715–733.

Merceron, G., Novello, A., & Scott, R.S. (2016). Paleoenvironments inferred from phytoliths and Dental Microwear Texture Analyses of meso-herbivores. In G. D. Koufos & D. S. Kostopoulos (Eds.), *Palaeontology of the upper Miocene vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece). Geobios 49,* 135–146.

Mirzaie Ataabadi, M., Kaakinen, A., Kunimatsu, Y., Nakaya, H., Orak, Z., Paknia, M., Sakai, T., Salminen, J., Sawada, Y., Sen, S., Suwa, G., Watabe, M., Zaree, G., Zhaoqun, Z., & Fortelius, M. (2016). The late Miocene hominoid-bearing site in the Maragheh Formation, Northwest Iran. In M. M. Ataabadi, & M. Fortelius (Eds.), *The Late Miocene Maragheh mammal fauna; results of recent multidisciplinary research*. *Palaeobiodiversity and Palaeoenvironments*, *96*(3), 349–371.

Oruç, S. (2009). *Denizli (Sazak) neojen memeli faunasının Bovidae (Artiodactyla) fosilleri ve biyokronolojik, paleobiyocoğrafik ve paleoklimatolojik anlamları* [*The fossils of Bovidae (Artiodactyla) from Denizli (Sazak) Neogene mammalian fauna and their biocronological, paleobiogeographic and paleoclimatologic meanings*] Izmir: Department of Biology, Ege University.

Pickford, M. (2015). Late Miocene Suidae from Eurasia: the *Hippopotamodon* and *Microstonyx* problem revisited. *Münchner Geowissenschaftliche Abhandlungen Reihe A: Geologie und Paläontologie*, *42*, 1–126.

Rögl, F. (1999). Circum-Mediterranean Miocene paleogeography. In G. E. Rössner & K. Heissig (Eds.), *The Miocene land mammals of Europe* (pp. 39–48). München: Verlag Dr. Friedrich Pfeil.

Roussiakis, S. J. (2002). Musteloids and feloids (Mammalia, Carnivora) from the late Miocene locality of Pikermi (Attica, Greece). *Geobios*, *35*, 699–719.

Roussiakis, S., Kargopoulos, N., Kampouridis, P., Svorligkou, G., & Theodorou, G. (2022). The fossil aardvark *Amphiorycteropus gaudryi* (Forsyth Major, 1888) from the late Miocene of Kerassia (Euboea, Greece). *Historical Biology*, *34*, 493–506.

Salesa, M. J., Antón, M., Turner, A., Alcalá, L., Montoya, P., & Morales, J. (2010). Systematic revision of the Late Miocene sabre-toothed felid *Paramachaerodus* in Spain. *Palaeontology*, *53*, 1369–1391.

Salesa, M. J., Pesquero, M. D., Siliceo, G., Antón, M., Alcalá, L., & Morales, J. (2012). A rich community of Felidae (Mammalia, Carnivora) from the late Miocene (Turolian, MN 13) site of Las Casiones (Villalba Baja, Teruel, Spain). *Journal of Vertebrate Paleontology*, *32*, 658–676.

Saraç, G. (2003). *Türkiye Omurgalı Fosil Yatakları. MTA (Mineral Research and Exploration, Ankara, Turkey) Report, No. 10609*. unpublished.

Schmidt-Kittler, N. (1976). Raubtiere aus dem Jungtertiär Kleinasiens. *Palaeontographica Abt. A*, *155*, 1–131.

Sen, S. (Ed.). (1994a). Les gisements de mammifères du Miocène supérieur de Kemiklitepe, Turquie. *Bulletin du Muséum National d'Histoire Naturelle 16,* 1–240.

Sen, S. (1994b). Les gisements de mammifères du Miocène supérieur de Kemiklitepe, Turquie: 5. Rongeurs, Tubulidentés et Chalicothères. *Bulletin du Muséum National d'Histoire Naturelle*, *16*, 97–111.

Sen, S. (Ed.). (2005). Geology, mammals and environments at Akkaşdağı, late Miocene of Central Anatolia. *Geodiversitas 27*(4), 513–836.

Sen, S., Bonis, L. de, Dalfes, N., Geraads, D., & Koufos, G. D. (1994). Les gisements de mammifères du Miocène supérieur de Kemiklitepe, Turquie: 1. Stratigraphie et magnétostratigraphie. *Bulletin du Muséum National d'Histoire Naturelle*, *16*, 5–17.

Sevim-Erol, A., Begun, D. R., Yavuz, A., Tarhan, E., Sözer, Ç. S., Mayda, S., van den Hoek Ostende, L. W., Martin, R. M. G., & Alçiçek, M. C. (2023). A new ape from Türkiye and the radiation of late Miocene hominines. *Communications Biology*, *6*, 842.

Sickenberg, O., Becker-Platen, J. D., Benda, L., Berg, D., Engesser, B., Gaziry, W., Heissig, K., Hünermann, K. A., Sondaar, P. Y., Schmidt-Kittler, N., Staesche, K., Staesche, U., Steffens, P., & Tobien, H. (1975). Die Gliederung des höheren Jungtertiärs und Altquartärs in der Türkei nach Vertebraten und ihre Bedeutung für die internationale Neogen-Stratigraphie. *Geologisches Jahrbuch*, *15*, 1–167.

Solounias, N., Plavcan, J. M., Quade, J., & Witmer, L. (1999). The paleoecology of the Pikermian Biome and the savanna myth. In J. Agustí, L. Rook & P. Andrews, P., *Hominoid evolution and climatic change in Europe. Volume 1. The evolution of Neogene tereestrial ecosystems in Europe* (pp. 436–453). Cambridge University Press.

Spassov, N. (2002). The Turolian megafauna of West Bulgaria and the character of the Late Miocene "Pikermian biome". *Bolletino della Società Paleontologica Italiana*, *41*, 69–81.

Spassov, N., & Geraads, D. (2015). A new felid from the Late Miocene of the Balkans and the contents of the genus *Metailurus* Zdansky, 1924 (Carnivora, Felidae). *Journal of Mammalian Evolution*, *22*, 45–56.

Spassov, N., Geraads, D., & Kovachev, D. (2004). *Tragoportax* Pilgrim, 1937 and *Miotragocerus* (*Pikermicerus*) Kretzoi, 1941 (Mammalia, Bovidae) from the Turolian of Bulgaria. *Geologica Balcanica*, *34*, 89–109.

Spassov, N., Geraads, D., Hristova, L., Markov, G.N., Garevska, B., & Garevski, R. (2018). The late Miocene mammal faunas of the Republic of Macedonia (FYROM). *Palaeontographica Abt. A*, *311*, 1–85.

Sylvestrou, I., & Kostopoulos, D. S. (2009). The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 12. Suidae. In G. D. Koufos & D. Nagel (Eds.), *The Late Miocene Mammal Faunas of Samos.*. Beiträge zur Paläontologie, *31*, 283–297.

Tarhan, E. (2021). *Palaeontological analysis of Late Miocene Anatolian suids* [Ph.D. thesis, Ankara University]. Ankara.

Tekkaya, I. (1973). Une nouvelle èspece de gazella de Sinap moyen. *Bulletin of the Mineral Research and Exploration of Turkey*, *80*, 118–143.

Tsoukala, E., Nagel, D., Youlatos, D., Crégut-Bonnoure, E., Vlachos, E., & Spassov, N. (2024). Primates and carnivores from Late Miocene and earliest Late Pliocene sites of Macedonia, Northern Greece. *Fossil Imprint*, *80*, 362–389.

Tuna, V. (1999). Yukarısazak (Kale-Denizli) Geç Miyosen Artiodactyl'leri (Mammalia). *MTA Dergisi*, *121*, 73–82.

Vlachou, T. D. (2013). *Palaeontology, biochronology and palaeoecology of the Greek hipparionine horses*. Ph.D. thesis. Thessaloniki: Aristotle University of Thessaloniki..

Vlachou, T. D., & Koufos, G. D. (2009). The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 11. Equidae. In G. D. Koufos & D. Nagel (Eds.), *The Late Miocene Mammal Faunas of Samos*. Beiträge zur Paläontologie, *31*, 207–281.

Wang, D., Xing, L., Rothschild, B. M., Persons Iv, W. S., & Liu, J. (2023). A palaeopathological specimen of the Late Miocene *Parataxidea* sp. (Mammalia: Carnivora) from the Linxia Basin, China. *Historical Biology*, *35*, 1255–1260.

Weers, D. J. van, & Rook, L. (2003). Turolian and Ruscinian porcupines (genus *Hystrix*, Rodentia) from Europe, Asia and North Africa. *Paläontologische Zeitschrift*, *77*, 95–113.

Fossil Giraffidae (Mammalia, Artiodactyla) from the early Turolian of Kavakdere (Central Anatolia, Turkey). *Comptes Rendus Palevol*, *18*, 619–642.

Xafis, A., Tsoukala, E., Solounias, N., O., M., Harzhauser, M., Grímsson, F., & Nagel, D. (2019b). Fossil Giraffidae (Mammalia, Artiodactyla) from the late Miocene of Thermopigi (Macedonia, Greece). *Palaeontologia Electronica*, *22.3.67*, 1–38.

Yilmaz Usta, D. N., Mayda, S., & Kaya, T. T. (2019). Yeni Buluntular Işığında Yalvaç (Isparta / Türkiye) Neojen Devir Omurgalı Fosil Yatakları. *SDÜ Fen-Edebiyat Fakültesi Sosyal Bilimler Dergisi*, *47*, 79–96.