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MAGNETOSTRATIGRAPHY AND PALEOECOLOGY OF THE HOMINID-BEARING LOCALITY ÇORAKYERLER, TUĞLU FORMATION (ÇANKIRI BASIN, CENTRAL ANATOLIA)

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ABSTRACT—*Ouranopithecus turkae*, from the late Miocene of Çorakyerler in Central Anatolia, is considered one of the last known occurrences of great ape in the eastern Mediterranean. The Çorakyerler fauna has previously been correlated with MN 11 to early MN 12 on the basis of biochronology, and its faunal composition has been found to contrast with those from contemporaneous sites. In this paper, we present the magnetostratigraphy of the Çorakyerler site and an expanded interpretation of its paleobiogeographical and paleoecological contexts. The paleomagnetic results reveal two intervals of normal polarity and an intervening interval of reversed polarity in the main fossiliferous section. Of the three likely age correlations spanning 8.13–7.15 Ma (MN 11–MN 12), we favor correlation with chron 4n, with a possible age range of the fossiliferous deposit between 8.11 and 7.64 Ma (late MN 11). The geographic distribution of genus-level faunal similarity and mean hypsodonty show that Çorakyerler is a typical representative of the Pikermian chronofauna with a wide range of faunal similarity, including late Miocene localities from the eastern Mediterranean, eastern Asia, and eastern Africa. Lithological and sedimentological characteristics of the fossiliferous horizon, however, indicate a lacustrine depositional environment and relatively humid local conditions within the more arid regional context. This special setting could explain the unexpected occurrence of a hominid primate at Çorakyerler.

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INTRODUCTION

Four different fossil hominid taxa have been discovered in the Miocene of Anatolia since 1955: *Griphopithecus alpani* from Paşalar (14–15 Ma; Alpagut et al., 1990; Casanovas-Vilar et al., 2011) and Çandır (13.1–14.1 Ma; Tekkaya, 1974; Begun et al., 2003a; Krijgsman, 2003; Casanovas-Vilar et al., 2011), *Kenyapithecus kizili* from Paşalar (14–15 Ma; Kelley et al., 2008), *Ankarapithecus meteai* from the Sinap Formation (Yassıören localities, 10 Ma; Ozansoy, 1955, 1965; Andrews and Tekkaya, 1980; Şen, 1991; Alpagut et al., 1996; Begun et al., 2003b; Kappelman et al., 2003a), and *Ouranopithecus turkae* from Çorakyerler (Fig. 1; Sevim et al., 2001; Güleş et al., 2007). *Griphopithecus* (from

Çandır and Paşalar) and *Kenyapithecus* (from Paşalar) are among the earliest hominid finds outside of Africa after Engelswies (Germany), with *Ankarapithecus* from Sinap believed to be closely related to pongines (Begun et al., 2003b). Aside from *Ouranopithecus*, the latest records of hominids in western Eurasia during the late Miocene include *Graecopithecus freybergi* (nomen vanum) from Pyrgos in Greece (Koufos, 2006), *?Udabnopithecus garedziensis* from Georgia (Gabunia et al., 2001), and the western Eurasian endemic ape *Oreopithecus bambolii* from Tuscany and Sardinia in Italy (Casanovas-Vilar et al., 2011; Rook et al., 2011). Hominids disappeared by the end of the Vallesian (around 9 Ma) in mainland Europe, but managed to survive into the middle Turolian (until almost 7 Ma) in the eastern Mediterranean (Casanovas-Vilar et al., 2011; Begun et al., 2012; Alba, 2012). In accordance with biochronological correlations to

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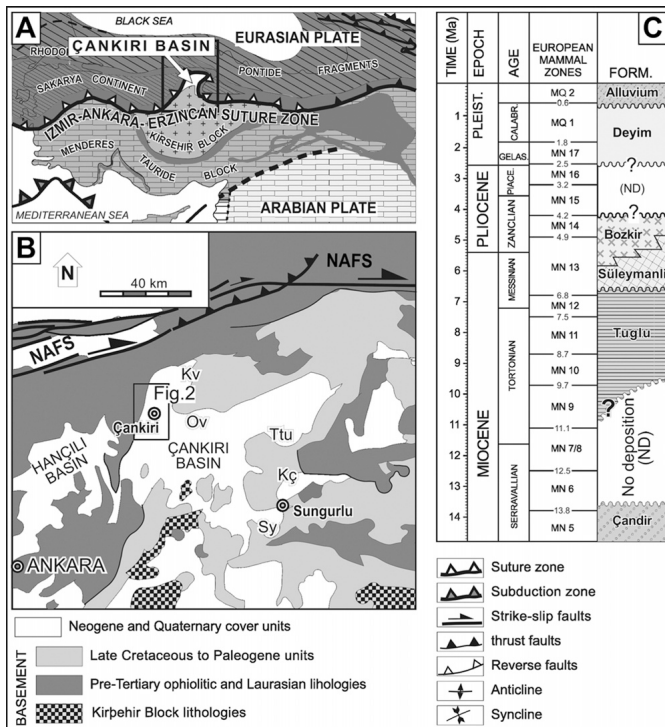


FIGURE 1. **A**, Simplified paleotectonic units in the eastern Mediterranean area (Şengör and Yılmaz, 1981; Görür et al., 1984). Rodope-Pontide fragments and the Sakarya Continent are of Laurasian affinity. Kırşehir Block and Menders-Tauride Block are of Gondwanan affinity; **B**, simplified map of Çankırı Basin and its surrounding; **C**, generalized columnar section of northwest part of the Çankırı Basin (modified from Kaymakçı, 2003; time scale is adopted from Hilgen et al., 2012; MN boundaries according to Agustí et al., 2001). **Abbreviations:** Kç, Karaçay; Kv, Kivçak; NAFS, Nort Anatolian Fault System; Ov, Ovacık; Sy, Saryaka; Ttu, Tuğlu.

European Neogene Mammal unit MN 11 or early MN 12 (Heissig, 1975; Köhler, 1987; Şen et al., 1998; Kaymakçı et al., 2000; Koufos, 2003; Ünay et al., 2006; Güleç et al., 2007; Kostopoulos, 2009; Casanovas-Vilar et al., 2011; Geraads, 2013), Çorakyerler represents one of the latest known occurrences of a hominid in the eastern Mediterranean. Güleç, et al. (2007) described the Çorakyerler *Ouranopithecus turkae* as the sister species to *O. macedoniensis*, but Begun (2009) has argued that several features distinguish the Çorakyerler specimens from *Ouranopithecus* and situate it closer to African Pliocene hominins. Ecological differences including hard and abrasive dietary components and better tolerance of low temperatures distinguish *Ouranopithecus* from extant hominins but align it with several African Plio-Pleistocene hominins (Ungar, 1996; Merceron et al., 2005; Merceron et al., 2013; de Bonis and Koufos, 2014; DeMiguel et al., 2014). The genus is also known from other eastern Mediterranean localities: Nikiti 1, Ravin de la Pluie, and Xirochori 1 from Greece (Koufos, 2006), with the youngest possible occurrence being the Azmaka quarry in Bulgaria (Spassov et al., 2012).

Despite the interest in this late occurrence of an Anatolian hominid, several aspects of the age, environment, and biogeographic relationships of Çorakyerler within the eastern Mediterranean paleobioprovince remain unaddressed (Sickenberg et al., 1975; Ünay et al., 2006; Güleç et al., 2007; Casanovas-Vilar et al., 2011; Geraads, 2013). To investigate these relationships, we provide a new magnetostratigraphic age estimate and an ecometric-based paleoenvironmental reconstruction.

We then place the Çorakyerler fauna in the biogeographic context of contemporaneous sites of the Pikermian paleobiome, which at its greatest extent includes most of the middle latitudes of Eurasian and parts of (at least) North Africa (Bernor, 1983, 1984; Eronen et al., 2009; Kostopoulos, 2009; Solounias et al., 2013).

GEOLOGIC SETTING

The Çorakyerler fossil locality is located in north-central Anatolia, in the Tuğlu Formation of the Çankırı Basin (Fig. 1) (Kaymakçı, 2000; Kaymakçı et al., 2001; Mazzini et al., 2013). This Tertiary basin is one of the largest in Turkey, straddling the İzmir-Ankara-Erzincan Suture Zone and demarcating the former position of the northern Neotethys Ocean (Şengör and Yılmaz, 1981; Kaymakçı, 2000; Kaymakçı et al., 2000). It comprises more than 4 km of regressive marine to continental successions, intercalated with widely spread and thick evaporites that mobilized into salt domes during the Eocene to late Miocene. The middle Miocene of the basin is locally characterized by fluviolacustrine sequences, more than 500 m thick, known as the Çandır Formation (Koçyiğit et al., 1995; Kaymakçı et al., 2000, 2001, 2003; Krijgsman, 2003). The deposition of the Çandır Formation is associated with normal growth faults, mainly located in the western margin and central part of the Çankırı Basin (Figs. 1 and 2), where the Çandır Formation reaches its maximum thickness.

Unconformably overlying the Çandır Formation are the Tuğlu, Süleymanlı, and Bozkır formations (Fig. 3). At its lower levels, the Tuğlu Formation at Çorakyerler (Fig. 4) is characterized by red to pink nodular limestone and siltstone, marl alternations with sparse freshwater mollusks (Gastropoda, Bivalvia), and some vertebrate bones. This is succeeded by an approximately 6-m-thick white to pinkish clayey limestone intercalated with thin red mudstone lenses that are rich in vertebrate bones, including hominid fossils. The fossil-bearing horizon appears to reflect a distal alluvial fan to floodplain environment. The presence of freshwater mollusks, together with an alternation of gypsum, marls, laminated claystones, and shales, in the various levels of the section indicates lacustrine deposition with fluctuating lake levels. Organic-rich levels may indicate swampy areas at the periphery of the lake (cf. Walker and James, 1992; Talbot and Allen, 1996), whereas lenses of sandstones with conglomerates indicate fluvial settings, which probably drained the lake. Eastward thinning conglomerates, with subangular to subrounded pebbles and sandstone wedges intercalated with red mudstones and clayey limestones, indicate the presence of an alluvial fan that would have been temporarily inundated by the lake in the distal parts to the east (see also Kaymakçı et al., 2001). This is overlain by a dark brown to brick red moderately sheared mudstone, then by alternating red to green sandstone, siltstone, and mudstone, with very thin intercalations of conglomerate. Mesoscopic oblique-slip faults with centimeter to meter scale offset traverse the section.

METHODS

Magnetostratigraphy—The Çorakyerler section is covered by a 1-m-thick layer of colluvium, and the sampled section had to be exposed using a backhoe provided by the Çankırı Municipality. A large building complex has been constructed next to the base of the sampled section, and the upper 30 m of clastics, below a thick capping gypsum layer, could not be sampled due to steep slopes and thick soil cover. The thick capping gypsum, alternating with buff to yellowish-gray marls, in places extending more than 200 m, was not sampled. In total, 40 paleomagnetic samples were collected from 18 stratigraphic levels (at least two

samples per level) with a portable standard drill. Sample measurements were made at the Fort Hoofddijk Paleomagnetic Laboratory (Utrecht University, The Netherlands) using a horizontally mounted Cryogenic Squid magnetometer. The samples were sequentially heated to 580°C at 30°C intervals until the signal was almost completely diminished. Samples from 10 out of 18 levels yielded reliable polarities covering the central portion of the sampled section (Fig. 4). The remaining eight sampled levels come from the lowest and highest parts of the section and produced inconclusive results.

Paleoecology and Paleobiogeography—Numerous publications describe mammalian fossils from Çorakyerler, including Heissig (1975), Sickenberg et al. (1975), Gaziry (1976), Köhler (1987), Şen et al. (1998), Geraads and Güleç (1999), Pehlevan (2005), Ünay et al. (2006), Güleç et al. (2007), and Geraads (2013). Additionally, the Çorakyerler excavation team annually presents (in Turkish) the results of each excavation season at the Excavation Results Conferences held by the Turkish Ministry of Culture and Tourism (Sevim and Kiper, 2000, 2001, 2002; Sevim and Pehlevan, 2003, 2004; Sevim et al., 2005, 2006, 2007; Sevim Erol and Yiğit, 2009, 2010, 2011; Sevim Erol, 2011a; Sevim Erol et al., 2013, 2014). The current excavation project was initiated in 1997 and continues up to the present. The project is supported by the Turkish Ministry of Culture and Tourism and has yielded more than 3000 fossil specimens (mostly mammals) (Sevim Erol, 2011a).

In this study, we rely mainly on the Çorakyerler faunal list assembled by Geraads (2013), with reference also to the bovid list of Bibi and Savaş Güleç (2008). Although Geraads' (2013) report includes the description of the material collected between 1998 to 2001, in addition to his report, we take into account expanded material announced in the latest excavation reports by the project team (cited above). For other localities, we use data from the NOW database (Fortelius, 2015).

Hypsodonty comparisons relied only on the large mammals (orders: Artiodactyla, Perissodactyla, Proboscidea, and Primates) from sites encompassing MN 7/8 to MN 13 (12.5–4.9 Ma) (Agustí et al., 2001). All NOW localities from Eurasia and Africa were included in the study. Age of the African localities follows Werdelin (2010) and was matched to MN biochronological units (Agustí et al., 2001) according to age range. We calculated the genus-level Raup-Crick faunal resemblance index (GFRI) (Raup and Crick, 1979) between Çorakyerler and all available localities using PAST (Hammer et al., 2001). We followed the procedure of Eronen et al. (2009), including only localities with a minimum of seven large mammals identified to at least genus rank. The GFRI analyses reveal the extent of and large-scale similarity patterns within computational chronofaunas as well as their changes over time. They are used here as a heuristic tool to reveal Çorakyerler's paleobiogeographic position on the chronofaunal scale.

We also calculated the mean ordinated crown height for each locality following Fortelius et al. (2002) for lists with at least two species with a hypsodonty value. Mean ordinated crown height is a robust proxy for humidity and productivity at the regional scale (Fortelius et al., 2002, Eronen et al., 2010a, 2010b; Liu et al., 2012). We plotted the results onto present-day maps and interpolated between the localities using MapInfo 11.5. For the interpolations, thematic mapping and grid interpolation was used, with the following settings: 20 km grid size; 800 km search radius; 800 grid borders. The interpolation method employed an inverse distance-weighted algorithm (IDW).

Abbreviations—ELMA, European land mammal ages; GFRI, genus-level Raup-Crick faunal resemblance index; MN, European Neogene land mammal units; NOW, New and Old World database of fossil mammals (Fortelius, 2015); PMAS, IMAS, DMAS, FMAS, primary, intermediary, dominant, and final mammal assemblages of Samos (Koufos et al., 2011).

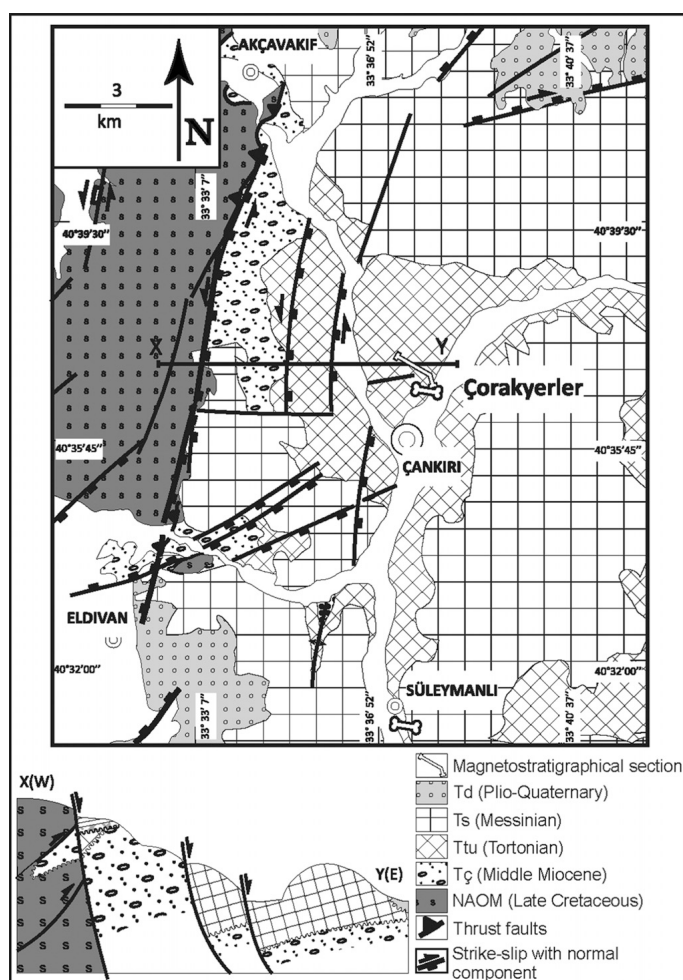


FIGURE 2. Geological map of northwest corner of Çankırı Basin and sketch of the cross-section along the line XY, which passes through the Çorakyerler fossil locality. Bone symbols indicate fossil localities.

RESULTS

Paleomagnetic Results

The 10 sampled levels yielded results indicating that the central portion of the sampled Çorakyerler section covers two normal and one reversed polarity intervals (Fig. 4).

Based on biostratigraphic correlations assigning the age of the Çorakyerler fauna to MN 11, or early MN 12, we propose three possible magnetostratigraphic correlations (Fig. 5). The first spans 7.30–7.15 Ma (middle chron 3B) with a possible age of the fossiliferous level of 7.29 Ma, the second spans 7.64–7.47 Ma (late chron 4n) with a possible age for the fossiliferous level of 7.64 Ma, and the third spans 8.13–7.55 Ma (early chron 4n) with a possible age for the fossiliferous level of 8.11 Ma. The first possible correlation (as well as an intermediate possibility at 7.50–7.22 Ma) is not supported given that the reversed polarity interval sampled at Çorakyerler is much thinner than the normal polarity interval below it (Fig. 5). We base this on the fact that there are no major changes in the mode of deposition throughout this part of the section (i.e., mainly fine clastics and carbonates), and mean sedimentation rates did not vary greatly. A long normal interval followed by a short reversed interval is a better fit with the second and third possible correlations, constraining the sampled sequence ranges to at least 8.13–7.47 Ma (Fig. 5). We therefore favor a possible age for Çorakyerler ranging between

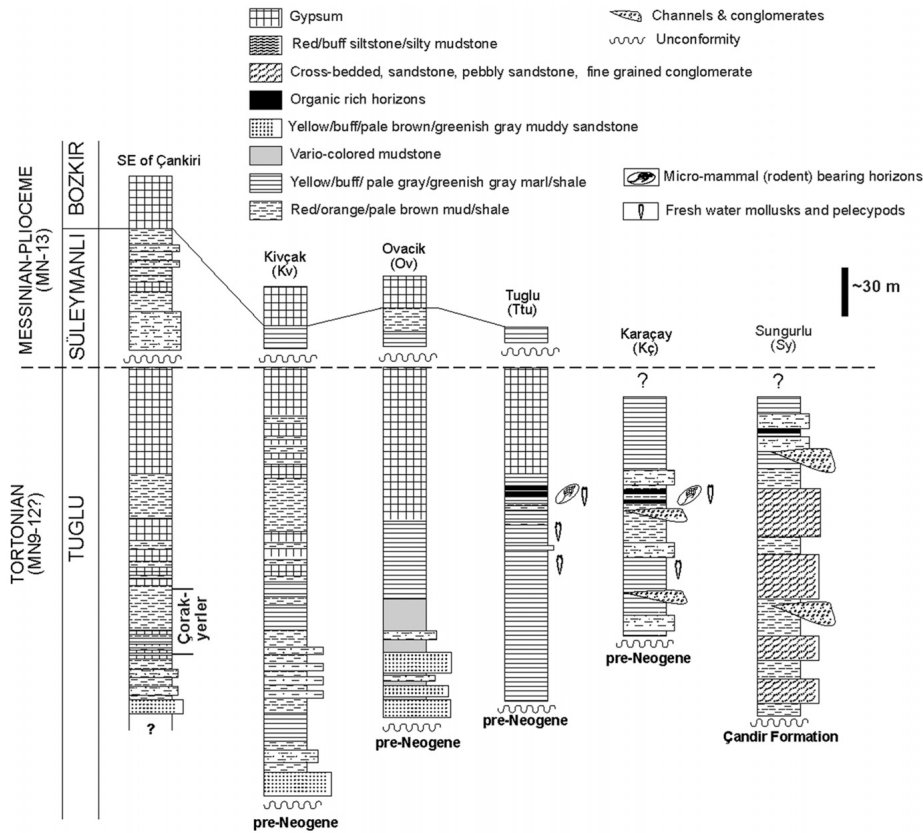


FIGURE 3. Correlation chart of the representative sections of the Tuğlu Formation.

8.11 and 7.64 Ma based on the stratigraphic position of the fossiliferous level in the sampled sequence (Figs. 4 and 5), whereas the magnetic polarity ages of the second and third correlations range between 8.13 and 7.47 Ma. This also fits better with the Çorakyerler faunal assemblage, which is a closer match to MN 11 than MN 12 (below).

Mammal Biochronology

Artiodactyls, perissodactyls, carnivorans, primates, and proboscideans constitute the majority of the Çorakyerler faunal list (Table 1). The chronostratigraphic ranges of mammalian species from Çorakyerler are compared with those from other Late Miocene localities in Greece, Bulgaria, Anatolia, and Iran in Figure 6. Overall, the faunal composition of Çorakyerler matches those of Greco-Iranian sites of MN 11 and MN 12 ages. In particular, taxa such as *Majoreas woodwardi*, *Oioceros rothii*, *Plesiadax inundatus*, *Chilotherium kowalevskii*, and *Byzantia* spp. together favor a late MN 11 or early MN 12 age. Ünay et al. (2006) favored a correlation to MN 11 based on the occurrence of *Hansdebruijnia*, *Byzantinia*, and *Pseudomeriones*. The Çorakyerler *Hansdebruijnia* species displays a constellation of primitive and derived characteristics between *Hansdebruijnia perpusilla* (from middle Baodean or MN 11/12 of Baogedawulla, China) and *Hansdebruijnia pusillus* (from MN 13 of Ertemte 2, Inner Mongolia) (Ünay et al., 2006). However, *Hansdebruijnia neutrum* from Pikermi (Greece) and *Hansdebruijnia amasyaensis* from Amasya (Turkey) are more advanced than the Çorakyerler species in terms of occlusal morphology.

The relative taxonomic abundance of the Çorakyerler bovids is somewhat unusual. The abundance of *Majoreas* in particular distinguishes Çorakyerler from most contemporaneous Greco-Iranian sites, which are often rich in *Tragoptorax*,

Prostrepsiceros, and *Gazella*. In this regard, Çorakyerler strongly resembles Kemiklitepe D (Bouvrain, 1994; Bibi and Savaş Güleç, 2008; Geraads, 2013; Kostopoulos and Karakütük, 2013). The giraffids *Bohlinia* cf. *attica*, *Palaeotragus* cf. *rouenii*, and *Palaeotragus* cf. *quadricornis* are recorded at Çorakyerler according to Geraads (2013). *Bohlinia attica* is known from the early part of the late Vallesian to end of the late Miocene in the eastern Mediterranean, and has been reported from the Vallesian localities of Sinap Formation in Turkey and Ravin de la Pluie, Nikiti 1, and Pikermi in Greece, Maragheh in Iran, and Jebel Hamrin in Iraq (de Mecquenem, 1924–1925; Thomas et al., 1980; Koufos, 2003). *Bohlinia* survived until end of the Turolian, and its last appearance is reported from Dytiko 1 and 2 (MN 13) in Greece (de Bonis et al., 1992; Koufos, 2003).

The Çorakyerler rhinocerotid collection is characterized by a high number of specimens of *Chilotherium kowalevskii*, which differentiates it from Akkaşdağı, Upper Kavakdere, and some other localities dominated by *Ceratotherium neumayri*. The material of *Ceratotherium neumayri* from Çorakyerler shows similarities to the same species from Düzyayla, Mahmutgazi, Samos, Maragheh, Pikermi, Pentalophos 1, Akkaşdağı, and Kemiklitepe A-B-D. *Chilotherium kowalevskii* is known from MN 10–MN 12 of the eastern Mediterranean (Pehlevan, 2005; Geraads, 2013): Turkey (Garkın, Upper Kavakdere, and Karacahasan), Greece (Samos), Moldova (Poksheshty and Respeny), Bulgaria (Kalimantsi-Hadjidimovo) and Ukraine (Grebentki). The proboscidean material from Çorakyerler strongly resembles *Choerolophodon pentelici* from Akkaşdağı, while appearing more derived than Kemiklitepe D in terms of size and morphology (Şahin, 2005; Geraads, 2013). The Çorakyerler suid material is ascribed to *Microstonyx major*, because it resembles the material of this species from Akkaşdağı and Pikermi (Liu et al., 2005; Geraads, 2013; Van der Made

et al., 2013). Some dental characteristics of this species, such as a relatively long muzzle and medium-sized molars, are slightly more derived than those found at Pikermi and Grebeniki (Sevim Erol and Yiğit, 2011). Geraads (2013) suggested a middle Turolian age for the site considering the morphological characteristics of Çorakyerler suid material.

The Çorakyerler carnivoran collection includes mustelids, hyaenids, and felids (Sevim Erol and Yiğit, 2010). One significant discovery from Çorakyerler is the most complete skull known to date in Turkey of a lion-sized machairodontini (Sevim and Yiğit, 2008; Sevim Erol, 2011b, 2013). It appears that the skull is relatively well preserved, and its morphology resembles *Amphimachairodus giganteus* from Batallones 1 (Spain) (Antón et al., 2004), but merits more precise systematic description.

Paleobiogeography

Table 2 presents the genus-level faunal resemblance index (GFRI) for selected Eurasian and African large-mammal faunas

compared with the Çorakyerler large-mammal fauna. Twenty-three genera that Çorakyerler shares with selected localities, ordered most common to rarest, are *Hipparion*, *Gazella*, *Palaeotragus*, *Tragoportax*, *Microstonyx*, *Chilotherium*, *Miotragocerus*, *Choerolophodon*, *Ictitherium*, *Ceratotherium*, *Prostrepsiceros*, *Protoryx*, *Acerorhinus*, *Amphimachairodus*, *Oioceros*, *Bohlinia*, *Protragelaphus*, *Pliocervus*, *Criotherium*, *Nisidorcas*, *Plesiaddax*, *Ouranopithecus*, and *Majoreas*. Table 2, together with faunal resemblance maps (Fig. 7), shows that Çorakyerler firmly belongs to the Pikermian paleobiome (sensu Eronen et al., 2009).

Faunal resemblance maps (Fig. 7) indicate that localities with high similarity during MN 7/8 (12.5–9.7 Ma) were situated in present-day Turkey, Georgia, central Asia, and northeast China. At that time, there was no indication of similarity to sites in western, eastern, and central Europe and south Asia. During MN 9 (11.1–9.7 Ma), similarity to Çorakyerler became more prominent in the eastern Mediterranean and northeast China, with a lower resemblance occurring in

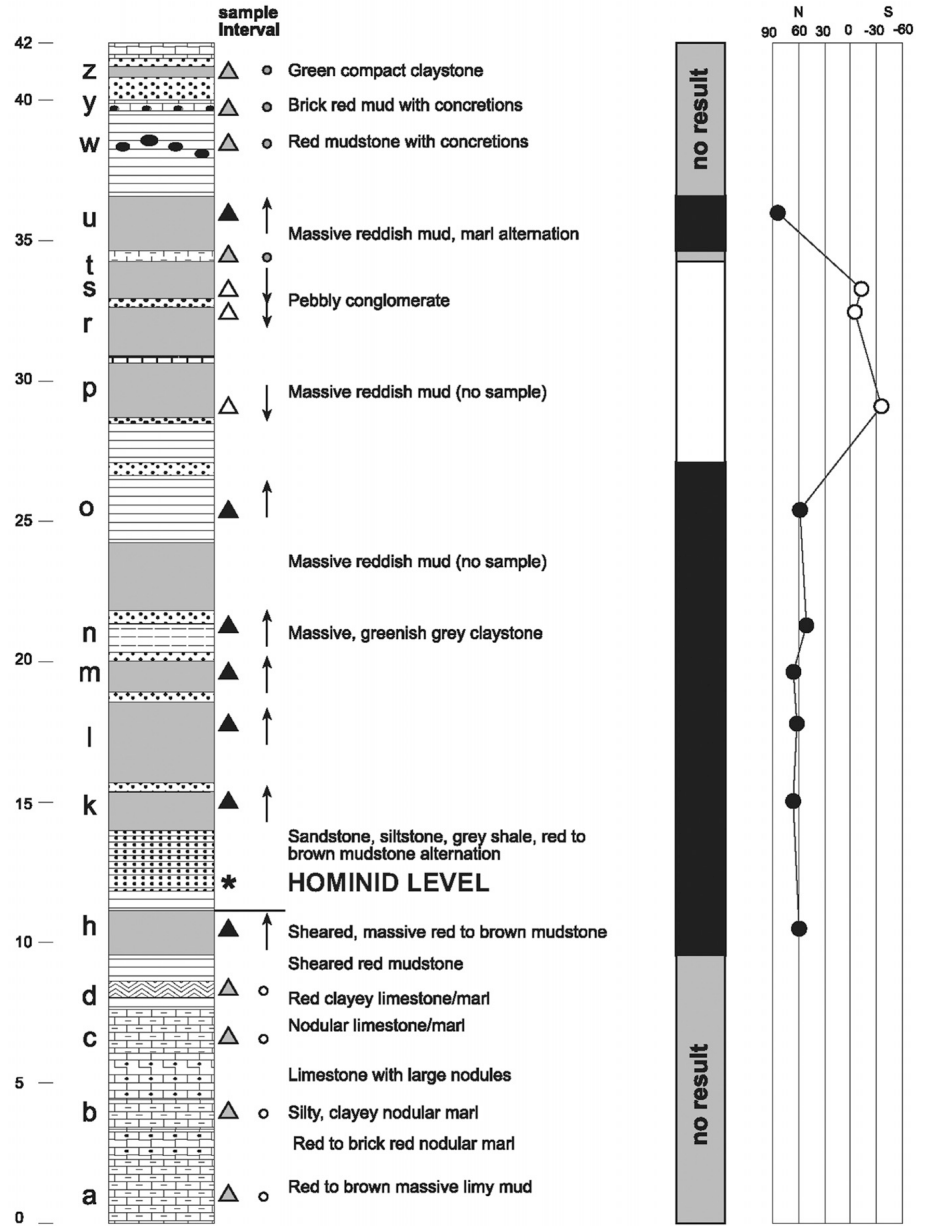


FIGURE 4. Log of Çorakyerler section and magnetostratigraphic results. Black areas are normal polarities, white areas are reversed polarities, and gray areas indicate levels with no results. Letters on the left section indicate the sampled levels, and triangles indicate the sampled levels with polarity results.

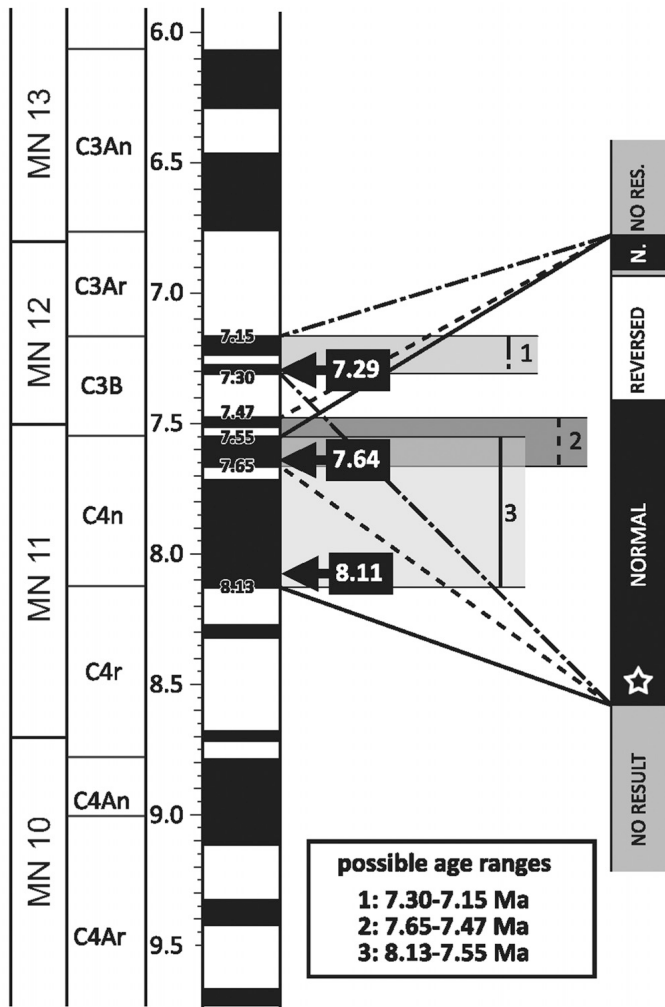


FIGURE 5. Magnetostratigraphic correlation of the Çorakyerler section. The ages of the MN boundaries are according to Agustí et al. (2001), and the geomagnetic polarity time scale is adopted from Hilgen et al. (2012). The star indicates estimated location of fossiliferous horizon.

northwest and eastern Africa, the Balkans, and southwestern Europe (Fig. 7). In eastern Africa, India, northeast China, central Asia, the Balkans, and the eastern Mediterranean, faunal similarity greatly increased in MN 10 (9.7–8.7 Ma), but similarity to central and western Europe remained low. During MN 11 (8.7–7.9/7.5 Ma) and MN 12 (7.9/7.5–6.8 Ma), faunal similarity to Çorakyerler peaked in a wide area including the Balkans, the eastern Mediterranean, the Middle East, North Africa, Arabian Peninsula, Afghanistan, Pakistan, and northeast China. In contrast, there was only intermediate similarity to central and western Europe during MN 11 (Fig. 7). This pattern reflects maximum development of the late Miocene Pikermian paleobiome (sensu Eronen et al., 2009), which extended eastwards across the Greco-Iranian region, through central Asia, to northeastern China, was taxonomically distinct from European areas just to the west, and reached its peak development during MN 11–12. Towards the end of the Miocene (MN 13, 6.8–4.9 Ma), similarity to the Çorakyerler fauna becomes concentrated in the eastern Mediterranean, central Asia, and northeast China, with a slightly lower presence in the Iberian Peninsula and North Africa. Central and eastern Europe, sub-Saharan Africa, and south Asia show a low similarity value by the end of the Miocene (Fig. 7).

Paleoenvironment

The Çorakyerler large-mammal assemblage suggests approximately equal proportions of browsers, grazers, and mixed feeders (35%, 30%, and 35%, respectively). In terms of hypsodonty, the Çorakyerler fauna is dominated by mesodont forms, followed by brachyodont and hypsodont species.

The hypsodonty maps (Fig. 8) reveal that molar crown height begins to increase in Anatolia during MN 7/8, a trend that continues through the late Miocene, driven by the expansion of the Pikermian paleobiome and the radiation of open-adapted ungulate clades, especially bovids and hipparionine equids. In the late Miocene (MN 9–MN 13), Anatolia was occupied by an increasingly hypsodont fauna. Similar hypsodonty trends were seen in central Asia and northeast China. More humid areas with low or intermediate hypsodonty values persisted north of the Paratethys, in eastern Africa, and continental Europe (save the fauna from southern France during MN 11). By the end of the Miocene, mean hypsodonty indicates more arid conditions in central Anatolia, Inner Mongolia, southwest of the Tibetan Plateau, and northwestern Africa. Although humid patches persisted in

TABLE 1. Fauna list of Çorakyerler locality.

ARTIODACTYLA	PERISSODACTYLA	RODENTIA**
<i>Miotragocerus</i> sp. ¹	<i>Ceratotherium neumayri</i> ³	<i>Protoallactaga major</i>
cf. <i>Tragoportax</i> ¹	<i>Chilotherium kowalevskii</i> ³	<i>Keramidomys</i> indet.
<i>Majoreas</i> cf. <i>woodwardi</i> ¹	<i>Acerorhinus</i> , n. sp. ¹	<i>Myomimus</i> indet.
cf. <i>Nisidorcas</i> sp. ²	<i>Hipparion</i> sp. ¹	<i>Allocritacus aylasevima</i>
<i>Oioceros rothi</i> ¹	<i>Hipparion</i> cf. <i>prostylum</i> ¹	<i>Byzantinia hellenicus</i>
<i>Gazella</i> sp. ¹	PROBOSCIDEA	<i>Byzantinia pikermiensis</i>
<i>Protragelaphus</i> cf. <i>skouzesi</i> ²	<i>Choerolophodon pentelici</i> ⁴	<i>Hansdebruijnina erksinae</i>
cf. <i>Prostrepsiceros</i> sp. ¹	CARNIVORA	<i>Hansdebruijnina neutrum</i>
<i>Plesiadax inundatus</i> ¹	<i>Amphimachairodus giganteus</i> ⁵	<i>Pliospalax</i> indet.
cf. <i>Criotherium</i> sp. ¹	<i>Ictitherium</i> indet. ⁵	<i>Rhinocerosodon</i> indet.
<i>Protoryx</i> sp. ¹	Mustelidae indet. ⁵	<i>Pseudomeriones latidens</i>
<i>Pliocervus</i> sp. ¹	PRIMATES	Muridae indet.
<i>Bohlinia</i> cf. <i>attica</i> ¹	<i>Ouranopithecus turkae</i> ⁶	EULIPOTYPHILA**
<i>Palaeotragus</i> cf. <i>rouenii</i> ¹		Soricidae indet.
<i>Palaeotragus</i> cf. <i>quadricornis</i> ¹		
<i>Microstonyx major</i> ¹		

¹Geraads, 2013; ²Bibi and Güleç, 2008; ³Pehlevan, 2005; ⁴Şahin, 2005; ⁵Sevim Erol and Yiğit, 2010; ⁶Güleç et al., 2007.

*Description based on our preliminary interpretations considering Sevim and Yiğit, 2008.

**Çorakyerler's Rodentia and Eulipotyphla specimens described by Ünay et al., 2006.

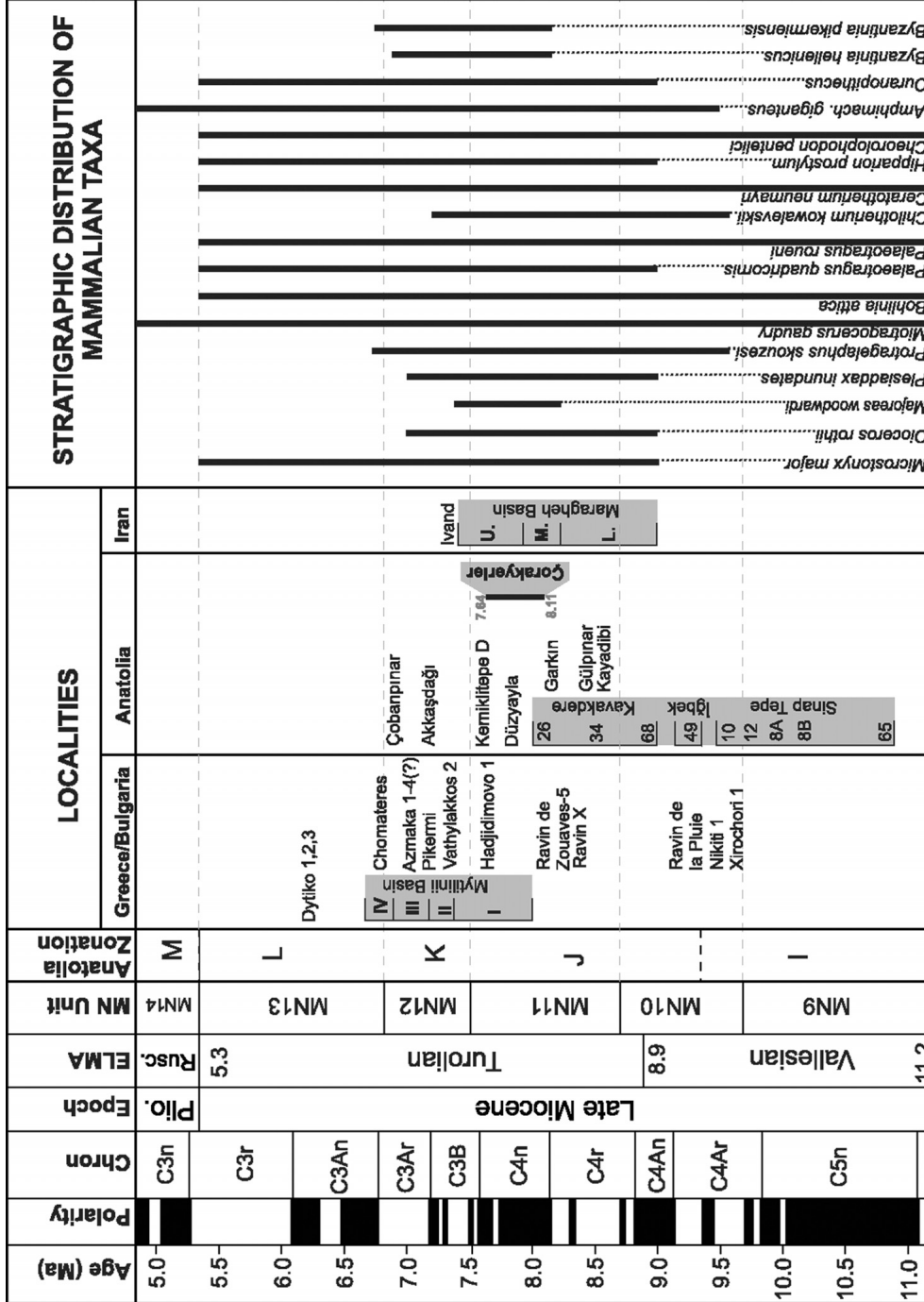


FIGURE 6. Stratigraphical and spatial distributions of selected mammalian species from Çorakyerler with correlation to the other reference localities from the late Miocene of Greece, Bulgaria, Anatolia, and Iran. In Mytilini Basin, I: PMAS, II: IMAS, III: DMAS, and IV: FMAS levels. MN boundaries according to Agustí et al. (2001), and the geomagnetic polarity time scale is adopted from Hilgen et al. (2012), Anatolian zones from Ünay et al. (2003).

TABLE 2. List of selected eastern Mediterranean and other localities used in this study.

Locality name	Present-day location	Age (Ma)*	N	Raup-Crick FRI	Mean hypsodonty
Samos FMAS	Greece	6.9–6.7	19	1	2
Azmaka 1–4	Bulgaria	7	24	1	1.6
Akkaşdağı	Turkey	7.1	28	1	1.7
Samos DMAS	Greece	7.2–6.9	33	0.9995	1.8
Pikermi	Greece	7.2	49	1	1.5
Samos IMAS	Greece	7.4–7.2	23	1	2
Vathylakkos 2	Greece	±7.5	13	1	1.6
Samos PMAS	Greece	7.8–7.4	22	1	1.8
Çorakyerler	Turkey	8.11–7.64	25	1	1.9
Middle Maragheh	Iran	8.2–7.1	39	1	1.9
Nikiti 1	Greece	9.3–8.7	12	1	1.7
Sinap 12	Turkey	9.735	23	1	2
Kemiklitepe D	Turkey	±7.6	11	0.9995	2
Udabno I	Georgia	8.8–8.5	11	0.9975	1.5
Xirochori 1	Greece	9.4	10	0.9895	1.8
Yushe	China	8–7	43	0.997	1.3
Baynunah	United Arab Emirates	8.2–7.1	15	0.9955	1.6
Wudu-Longjiagou	China	8–7	30	0.978	1.7
Ravin de la Pluie	Greece	9.1	20	0.9815	1.7
Nakali	Kenya	9.9–9.8	15	0.9565	1.6
Samburu Hills (Namurungule)	Kenya	9–9.5	16	0.9515	1.7

*References for ages of localities: Çorakyerler (this study); Pikermi (Solounias et al., 2013); Akkaşdağı (Şen et al., 2005); Nikiti 1, Ravin de la Pluie, and Xirochori 1 (Koufos, 2006); Udabno I (Gabunia et al., 2001); Azmaka 1–4 (Spasov et al., 2012); Vathylakkos 2 (Koufos et al., 2004); Middle Maragheh (Ataabadi et al., 2013); Kemiklitepe D (Şen et al., 1994); Samos (PMAS, DMAS, IMAS, and FMAS) (Koufos et al., 2011); Sinap 12 (Kappelman et al., 2003b); Baynunah (Bibi et al., 2013); Yushe (Opdyke et al., 2013); Wudu- Longjiagou (Xue et al., 2006); Nakali (Kunimatsu et al., 2007); and Samburu Hills (Sawada et al., 1998).

northern parts of Europe, northern India, and central eastern Africa, intermediate hypsodonty values indicate a less arid environment in Iberia and the Balkans, northern, central, and eastern Africa, Saudi Arabia, western central Asia, and northeastern China by the end of the late Miocene.

DISCUSSION AND CONCLUSIONS

Ouranopithecus turkae at Çorakyerler has been considered one of the last occurrences of a hominid from the eastern Mediterranean, but the age of this find has never been well constrained. Our magnetostratigraphic age correlation brackets the Çorakyerler fauna between 8.11 and 7.64 Ma. This is based primarily on the relative thicknesses of the sampled normal and

reversed polarity intervals, and on a preference for a late MN 11 age from certain faunal elements.

Similarity analyses indicate that the Çorakyerler large-mammal fauna is similar to localities from MN 10–MN 13 in the eastern Mediterranean, central Asia, and northeast China (Table 2; Fig. 7). Maximum faunal similarity to Çorakyerler occurs during MN 12 with an average FRI of 0.92 and is followed by MN 11 (FRI = 0.88), MN 10 (FRI = 0.81), MN 13 (FRI = 0.68), MN 9 (FRI = 0.56), and MN 7/8 (FRI = 0.3) (Fig. 7). Pikermi, Akkaşdağı, Maragheh, Kemiklitepe D, and Samos represent the highest similarity values to the Çorakyerler fauna, and the changes in the similarity index values from MN 7–8 to MN 13 follows the general trend of Pikermian chronofauna (Eronen et al., 2009).

Faunal similarity between the eastern Mediterranean and east Asian large mammals first appears from MN 9 and continues with an increasing ratio until the end of the Miocene (Fig. 7). Interestingly, the late Miocene fauna of Yushe Basin in east Asia shows a particularly high similarity to Çorakyerler. The mean hypsodonty value for the Yushe fauna indicates the presence of more humid conditions compared with the Pikermian and Baodean faunas (cf. Kurtén, 1952), suggesting the possibility that the faunal resemblance between Yushe and Çorakyerler might be related to taxonomic effects of local rather than regional humidity.

A high faunal similarity was observed between Çorakyerler and Baynunah (United Arab Emirates) localities during MN 12. Our FRI analyses at the genus level reveal that Baynunah shows high similarity to Pikermian, south Asian, and eastern African faunas, probably because of its location at the contact of the three paleobiogeographic provinces (Bibi et al., 2013).

In eastern Africa, the early late Miocene (MN 9 equivalent) hominoid-bearing Samburu Hills (Namurungule) and Ngorora show intermediate similarity to Çorakyerler. The slightly younger (MN 10 equivalent) Nakali (9.9–9.8 Ma) shows higher similarity, and the Nakali hominid itself, *Nakalipithecus nakayamai*, also shows strong similarities to *Ouranopithecus turkae* in size and some morphological characteristics (Kunimatsu et al., 2007). The hominoid locality Chorora (Ethiopia)

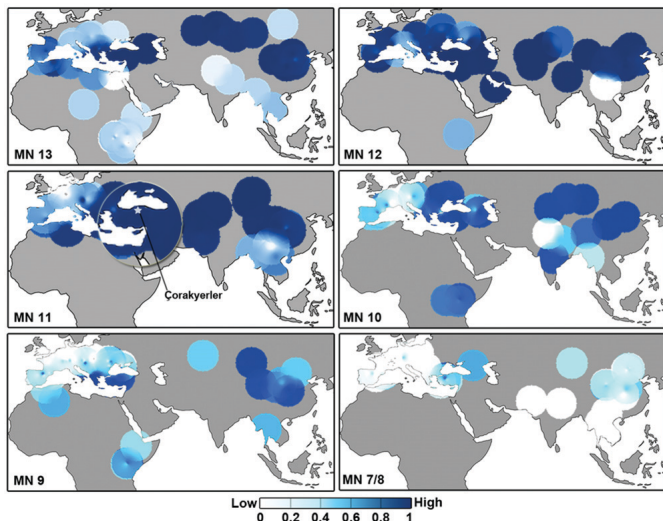


FIGURE 7. Raup-Crick genus-level faunal similarity maps to Çorakyerler. High similarity indicated by blue and low similarity by white.

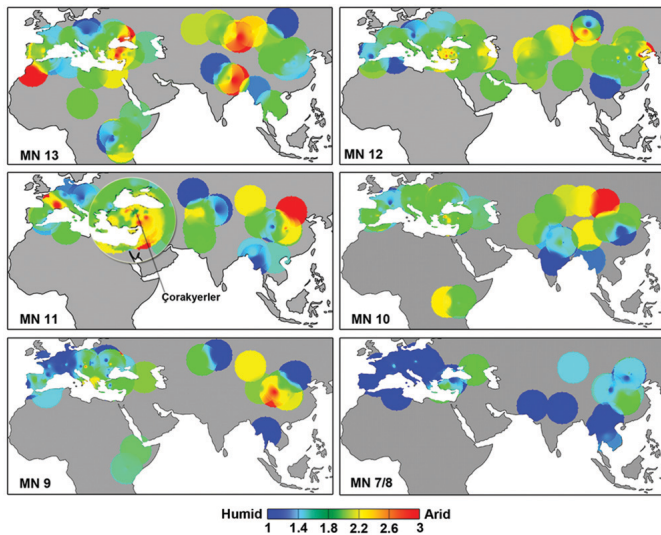


FIGURE 8. Map of mean ordinated hypsodonta of the ungulates from MN 7–8 to MN 13. Arid conditions (high hypsodonta) indicated by red, humid conditions (low hypsodonta) by blue, green, and yellow.

also shows high similarity to Çorakyerler. Mean ordinated hypsodonta map patterns indicate that Samburu Hills and Çorakyerler large-mammal faunas occupied drier, probably more open areas than those of Nakali and Chorora, which is in accord with previous paleoenvironmental reconstructions (Kunimatsu et al., 2007; Suwa et al., 2015). Çorakyerler has the highest taxonomic similarity to localities with lower mean hypsodonta rates such as Nakali.

A high similarity value was also observed between Çorakyerler and the Georgian MN 11–equivalent locality Udabno I, which has yielded the hominid *Udabnopithecus garedziensis*. Once again, the hypsodonta value of Udabno I suggests more humid environmental conditions than the *Ouranopithecus*-bearing localities.

Çorakyerler fauna shows high faunal resemblance similarity with European *Ouranopithecus*-bearing localities, including Nikiti 1, Ravin de la Pluie, Xirochori 1, and possibly Azmaka 1–4 (Table 2). Investigations at these sites (Nikiti 1 [MN 10], Xirochori 1 [MN 10], and Ravin de la Pluie [MN 10] in Greece and Azmaka [MN 12] in Bulgaria) indicate that *Ouranopithecus* may have occupied a range of relatively dry habitats, from woodlands to open areas with some trees, bushes, and thick grass (de Bonis et al., 1992; Spassov et al., 2012; de Bonis and Koufos, 2014). Reconstructions of *Ouranopithecus* as a possible terrestrial hominid specialized for abrasive diet (Ungar, 1996; Merceron et al., 2005; de Bonis and Koufos, 2014; DeMiguel et al., 2014) fit such a range of relatively dry, non-forest habitats.

Geraads and Güleç (1999) have suggested that sites such as Çorakyerler might reflect a period of increased provincial endemism in central Anatolia during the late Vallesian to early Turolian. Kostopoulos and Bernor (2011) noted that conditions toward the center of the sub-Paratethyan province may have been different from those at the eastern and western edges. According to the mean hypsodonta proxy, central Anatolia was a more arid region throughout the late Miocene than was eastern Europe (Fortelius et al., 2014) and would have offered even more challenging living conditions for hominid primates. The Çorakyerler large-mammal fauna shows the highest similarity (GFRI = 1.0) to localities from MN 11 and MN 12 that have significantly lower mean

hypsodonta than that of Çorakyerler ($P = 0.016$ for MN 11 localities; $P = 0.0009$ for MN 12 localities).

We have shown here that the lacustrine deposits at Çorakyerler contrast strongly with the mostly fluvial or alluvial fan deposits at other Turolian localities in the Greco-Iranian region. Sedimentological and faunal differences both suggest that the fossil assemblage of Çorakyerler represents habitats at an ancient lake shore. The evidence supports the view that its community is somehow ‘more humid’ than expected from its mean hypsodonta, reflecting a locally humid setting in a more arid regional context. Çorakyerler therefore shows local taxonomic and paleoenvironmental differences from the regional average, as a typical Pikermian fauna and environment with a local twist favorable to hominids.

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