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THE KAYSERI HIPPARION HORSES: NEW INSIGHTS INTO EQUID EVOLUTION IN TÜRKIYE DURING THE EARLY AND MIDDLE TUROLIAN (MN11-12, LATE MIOCENE)

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Abstract. The Yamula Reservoir shores have yielded a series of vertebrate localities rich in diverse ungulates and carnivores which we refer to the Kayseri faunas, Türkiye. We report herein the geological context and hipparion horses excavated from fluvial and lake deposits Çevril, Taşhan, and Hırka sites. Published $^{40}Ar/^{39}Ar$ geochronologies place the deposits within the late Tortonian, respectively the late European Mammal Neogene (MN) Units late MN11– early MN12 (early to middle Turolian). These localities can therefore be correlated with others of the Greek–Türkish–Iranian region, as Pikermi and Samos (Greece) and Maragheh (Iran). We undertake both morphologic and morphometric analyses in identifying taxa and comparing them to a broad suite of taxa from Western Eurasian localities. Hipparion horses identified in this study include *Hippotherium brachypus*, *Hipparion dietrichi*, *Cremohipparion moldavicum*, *Cremohipparion* aff. *proboscideum* and *Plesiohipparion longipes*. Our paleoclimate reconstruction of Upper Miocene Western Eurasian faunas based on the mean ordinated hypsodonty analysis of fossil mammal assemblages from MN10–12 shows a substantial climate shift, expressed in the expansion and diversification of the classic Pikermian ungulate and carnivore "savanna-like" chronofauna.

INTRODUCTION

During the Late Miocene, the eastern Mediterranean and western Asia formed one of the most dynamic regions for terrestrial mammal evolution (Bernor 1984; Fortelius et al. 1996). Positioned at the intersection of Africa, Europe, and Asia, Anatolia played a critical role in shaping mammalian dispersal patterns and community structures across the broader Greek–Türkish–Iranian region (Kaya et al. 2018; Eronen et al. 2009; Kostopoulos 2009). Recent studies increasingly

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emphasize that Anatolia functioned not merely as a passive bridge but as an important center of faunal diversification and ecological restructuring during the Neogene (Kaya et al. 2018).

The Late Miocene mammalian assemblages of southeastern Europe, Anatolia, and northwestern Iran are often grouped within the so-called Pikermian chronofauna (Bernor, 1984), a widespread faunal complex characterized by diverse hipparionine horses, bovids, giraffids, rhinocerotids, and carnivores. Classic localities such as Pikermi and Samos in Greece, Maragheh in Iran, and Sinap in Türkiye have long served as reference points for understanding the composition and paleoecology of these communities. Together, these sites document the development of distinctive mammalian ecosystems across the Subparatethyan Turolian province as part of the Old World Savanna Paleobiome (here after OWSP) (Bernor 1984; Kaya et al., 2018), reflecting large-scale environmental transformations that affected much of the eastern Mediterranean during the Late Miocene. Despite the importance of this province, central Anatolian fossil sites are less studied when compared to the classical Greek and Iranian localities, which hampers biochronological correlations. The fossil localities discovered along the shores of the Yamula Reservoir near Kayseri provide a valuable opportunity to improve our understanding of mammalian community structure and equid evolution within this regional framework. The Kayseri assemblages occur within the Central Anatolian Volcanic Province (CAVP) and are stratigraphically constrained by radiometrically dated ignimbrites (Fig. 1), providing a well-dated record of mammalian faunas spanning the late MN11–early MN12 interval (>7.74–7.46 Ma) (Tholt et al., 2025; Meijers et al., 2018). Here, we use discrete character and morphometric analyses to identify hipparion taxa and compare them principally to Greek and Iranian Pikermian age localities. Kayseri hipparionin taxa that we formally recognize herein are: *Hippotherium brachypus* Hensel, 1862, *Hipparion dietrichi* Wehrli, 1941, *Cremohipparion moldavicum* Gromova, 1952, *Cremohipparion* aff. *proboscideum* and *Plesiohipparion longipes* Gromova, 1952. We further discuss the biogeography and paleoecology of these equids within the broader Greek–Turkish–Iranian Turolian Subparatehyan province.

GEOLOGY, GEOCHRONOLOGY, AND BIOCHRONOLOGIC CORRELATIONS

Geology and Geochronology of the Yamula Reservoir localities

Anatolia has been shaped by the convergence between the African (-Arabia) and Eurasian plates (Şengör & Yılmaz 1981) (Fig. 1A). Collision of Arabia with Eurasia led to the formation of the Anatolian microplate, which has been escaping westwards along the North and East Anatolian fault zones into the Aegean domain since ~5 Ma (Fig. 1A) (Whitney et al. 2023). The Central Anatolian Plateau (CAP), with a modern elevation of ~1.0–1.5 km is bordered by the Pontide and Tauride mountains to the north and south, respectively. The topography of the CAP formed since the Late Miocene, with mean elevations reaching ~1.5 km by 8 to 6 Ma (Meijers et al. 2025). The CAVP is located within the CAP and comprises an ignimbrite stratigraphy dated to a time window between ~9.4 and 2.7 Ma (Aydar et al. 2012; Higgins et al. 2015; Friedrichs et al. 2021; Tholt et al. 2025). The fluvial and lacustrine sedimentary deposits that are intercalated with the ignimbrites contain abundant mammalian fossils. The Yamula Reservoir fossil localities are located approximately 25 km north of Kayseri (Fig. 1). Fossil-bearing layers are exposed along the shoreline of the reservoir and were first discovered in 2018, following a report by a local shepherd, Murat Adıyaman. The elevation of the localities ranges from 1070 to 1100 m above sea-level and they are distributed across a wide region. The Yamula Reservoir fossil localities are found within fluvial and lacustrine sedimentary deposits that are exposed along the reservoir's shoreline. Three fossil localities have been discovered in the deposits of the Yamula Reservoir, Taşhan (TAS), Çevril (CEV), and Hırka (HIR) (Fig. 1B). Ongoing excavations at these fossil localities have uncovered faunal remains belonging to Equidae, Bovidae, Proboscidea, Carnivora, Rhinocerotidae, Giraffidae, Suidae, Testudines, and Rodentia. Species diversity is particularly notable among horses and elephants. In this study, we report the new hipparion remains from Taşhan, Çevril and Hırka.

The fossil-bearing layers at the CEV and TAS localities are laterally continuous and comprise two stratigraphically successive horizons (Fig. 1C). Here

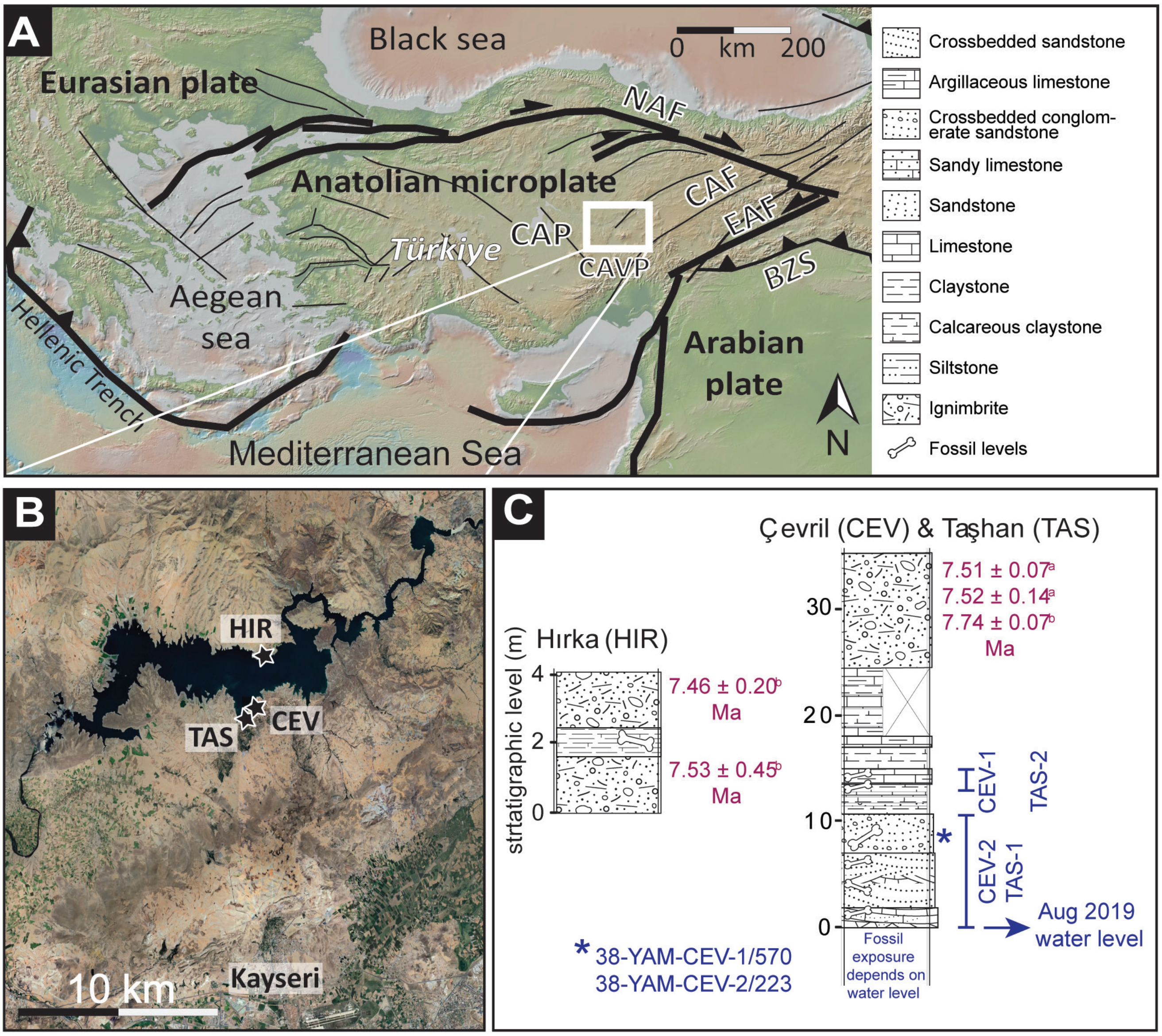

Fig. 1 - A) Geographic map of Anatolia including subduction zones and major fault zones. North Anatolian Fault Zone: NAFZ, Central Anatolian Fault: CAF, East Anatolian Fault: EAF, Bitlis Suture Zone (BSZ); B) Location of the localities HIR (Hırka), Taşhan (TAS1 and TAS2) and Çevril (CEV1 and CEV 2); C) Stratigraphies including ^{40}Ar/^{39}Ar ages of fossil-bearing sections at TAS, CEV and HIR (7.74-7.46 Ma). [a]: Meijers et al. (2018), [b]: Tholt et al. (2025).

we present a ~35 m stratigraphic section that extends from the reservoir shoreline level in August 2019, to the dated ignimbrite at the top (Fig. 1C). The area containing the TAS and CEV fossil finds starts with alternating cross-bedded siltstones, sandstones, gravels, and poorly sorted conglomerates interbedded with clayey and silty limestones. These are overlain by fine-grained sandstone, siltstone, and mudstone units, which are followed and capped by a thick ignimbrite layer (Fig. 1C). This 10 m thick ignimbrite was dated to 7.74 ± 0.07 Ma (plagioclase), 7.51 ± 0.07 Ma (amphibole), and 7.52 ± 0.14 Ma (plagioclase) using ^{40}Ar/^{39}Ar dating (Tholt et al. 2025; Meijers et al. 2018). Fossil sites Çevril 1 and 2 (CEV1–2) are found stratigraphically below this thick ignimbrite and are therefore older than 7.74 Ma. Hırka is located in an abandoned village (Hırka), which was submerged following Yamula Reservoir construction. Its fossil-bearing strata are located between ignimbrite layers. These ignimbrites were dated by Tholt et al. (2025): the lower (older) ignimbrite yields an ^{40}Ar/^{39}Ar age of 7.53 ± 0.45 Ma, and the upper (younger) ignimbrite was dated to 7.46 ± 0.20 Ma.

Biochronologic Correlations

We follow the $^{40}Ar/^{39}Ar$ radio-isotopic dating published by Meijers et al. (2018) and Tholt et al. (2025) for the Kayseri localities as reported in the previous section, which implies that the specimens from the Çevril and Taşhan sites are older than 7.74 Ma and the specimens from the Hırka site can be assigned an age of ~7.5 Ma. Based on the radiometric ages of the Yamula Reservoir localities, they can be biochronologically correlated to faunas from Samos, Greece (Kostopolous et al. 2003; Vlachou & Koufos 2009; Koufos 2024) and Maragheh, Iran (Bernor 1986; Steininger et al. 1996; Swisher 1996; Atabaadi et al. 2013), which were dated using integrated biostratigraphy and magnetostratigraphy or $^{40}Ar/^{39}Ar$ dating, respectively. In the present work, we use the biochronologic subdivision proposed by Hilgen et al. (2012), MN11–13. Critical are the limits for MN11 (8.9–7.6 Ma), MN12 (7.6–6.8) and MN13 (6.8–5.3 Ma) to which the Greek, Iranian and the Kayseri hipparion faunas are correlated, at least in part. A recent review of European Neogene Mammal zones based on an extensive study of magnetostratigraphic records of the Teruel Basin, Spain by Ezquerro et al. (2022) have placed the lower boundary of MN11 at 8.66 Ma (first occurrence of *Parapodemus lugdunensis*), MN12 lower boundary at 7.87 Ma (first occurrence of *Parapodemus gaudryi barbarae)* and MN13 at 6.88 Ma. However, we choose to continue to use the ages of Hilgen et al. (2012), because biogeographic provincialism can lead to severe diachrony between southwestern European and southeastern European/west Asian sites. Moreover, these rodent taxa defining Teruel Basin Late Miocene MN unit boundaries do not occur in the Greek, Turkish and Iranian localities, making MN unit correlations impossible using these taxa. Severe (up to 1 Myr) diachrony as a result biogeographic provincialism has been demonstrated between Late Miocene rodent faunas of Spain and France (Gómez-Cano et al., 2011). Moreover, Sen (1997) already provided a detailed commentary on the difficulties of correlating from eastern Mediterranean, Turkish and Iranian faunas (Subparatethyan faunas of Bernor (1983) and Bernor et al. (1996a)) to the Spanish mammalian faunas using the MN system. Moreover, our current investigation shows no known hipparion species-level comparisons between the Iberian Peninsula and Subparatethyan Turolian age faunas.

MATERIALS AND METHODS

Comparative samples

The Kayseri collection is housed at the Kayseri Bilim Merkezi (KBM**,** Kayseri Science Center), Türkiye. The Kayseri sample includes 201 studied specimens including crania, mandibles, teeth and postcranial elements. A complete list of specimens and their measurements is provided in Supplementary Table 1. The Kayseri equid sample is herein compared with a suite of Late Miocene North American, Eurasian and African hipparionine species of the genera *Cormohipparion* Skinner & MacFadden, 1977, *Hippotherium* Kaup, 1835, *Hipparion* sensu strictu de Christol, 1832, *Cremohipparion* Qiu et al., 1987, and *Plesiohipparion* Qiu et al., 1987 (Table 1). Table 1 is a complete list of hipparionine equids used in our analyses, including i) middle–late Claredonian North American *Cormohipparion* spp. as original source for the Afro-Eurasian hipparion horses, ii) the most relevant Vallesian (MN9–M10) Afro-Eurasian *Cormohipparion*, *Hippotherium* and *Hipparion* spp., iii) the main Turolian (MN11–M13) hipparion samples of the Subparatethyan region (Iran–Anatolia–Greece) including *Cormohipparion*, *Hippotherium*, *Hipparion*, *Cremohipparion* and *Plesiohipparion*, with the Çalta (MN15) sample for *Plesiohipparion longipes*.

Measurement and morphological protocol

Standard equid measurements on the Kayseri hipparions are given are given in Supplementary Table 1 following standards given by Eisenmann et al. (1988) and Bernor et al. (1997). Comparisons are undertaken on crania, third metacarpals and third metatarsals. We integrate the discrete characters of the crania, mandible and dentition for the specimens described here, following Bernor et al. (2022, 2024) and Kahya-Parıldar et al. (2025). The scoring values are reported in Supplementary Table 2.

Morphometric and statistical analyses

Measurements are all given in millimeters and rounded to 0.1 mm. Measurement numbers (M1, M2, M3, etc.) refer to those published by Eisenmann et al. (1988) and Bernor et al. (1997) for the crania and postcrania. Tooth measurement numbers refer to those published by Bernor et al. (1997). Principal component analysis (PCA) and Log10 ratio diagrams have been used here to analyze the Kayseri

Tab. 1 - Complete list of the Late Miocene hipparions used for comparative analyses in the present work listed by age, from older to younger.

Age	Species	Locality	Source
Late Miocene	*Cormohipparion fricki*	MacAdams Quarry, Texas; USA	Woodburne 2007 / Bernor Database
Late Miocene	*Cormohipparion occidentale*	X-Mas Quarry, Nebraska; USA	Woodburne 2007 / Bernor Database
Late Miocene	*Cormohipparion matthewi*	X-Mas Quarry, Nebraska; USA	Woodburne 2007 / Bernor Database
Late Miocene	*Cormohipparion africanum*	Bou Hanifia, Algeria	Bernor and White 2009
Late Miocene	*Cormohipparion sinapensis*	Sinap, Türkiye	Bernor et al. 2003
Late Miocene	*Cormohipparion kecigibi*	Sinap, Türkiye	Bernor et al. 2003
Late Miocene	*Cormohipparion* aff. *sinapensis*	Eşme Akçaköy, Türkiye	Bernor Database
Late Miocene	*Cormohipparion cappadocium*	Yeniyaylacık, Türkiye	Bernor et al. 2024
Late Miocene	*Cormohipparion sofularensis*	Sofular, Türkiye	Kahya-Parıldar et al. 2025
Late Miocene	*Hippotherium primigenium*	Inzersdorf, Austria	Bernor Database
Late Miocene	*Hippotherium primigenium*	Höwenegg, Germany	Bernor et al. 1997, 2022
Late Miocene	*Hippotherium primigenium*	Eppelsheim, Germany	Bernor Database
Late Miocene	*Hippotherium catalaunicum*	Hostalets de Pierola, Spain	Bernor Database
Late Miocene	*Hippotherium brachypus*	Pikermi, Greece	Bernor Database
Late Miocene	*Hippotherium brachypus*	Sofular, Türkiye	Kahya-Parıldar et al. 2025
Late Miocene	*Hippotherium* cf. *brachypus*	Middle Maragheh, Iran	Bernor et al. 2016
Late Miocene	*Hippotherium* aff. *brachypus*	Samos indet, Greece	Bernor Database
Late Miocene	*Hippotherium* aff. *brachypus*	Samos Q4, Greece	Bernor Database
Late Miocene	*Hippotherium* aff. *brachypus*	Akkaşdağı, Türkiye	Koufos and Vlachou 2005 / Bernor Database
Late Miocene	*Hipparion gettyi*	Kopran Maragheh, Iran	Bernor et al. 2016
Late Miocene	*Hipparion* aff. *gettyi*	Alban 13 Maragheh, Iran	Bernor et al. 2024
Late Miocene	*Hipparion prostylum*	Luberon, France	Bernor Database
Late Miocene	*Hipparion* sp.	Samos Q6, Greece	Bernor Database
Late Miocene	*Hipparion dietrichi*	Samos Q1, Greece	Bernor Database
Late Miocene	*Hipparion dietrichi*	Samos Q4, Greece	Bernor Database
Late Miocene	*Hipparion dietrichi*	Samos Q5, Greece	Bernor Database
Late Miocene	*Hipparion dietrichi*	Akkaşdağı, Türkiye	Koufos and Vlachou 2005 / Bernor Database
Late Miocene	*Hipparion dietrichi*	Sofular, Türkiye	Kahya-Parıldar et al. 2025
Late Miocene	*Hipparion* cf. *dietrichi*	Middle Maragheh, Iran	Bernor et al. 2016
Late Miocene	*Hipparion campbelli*	Upper Maragheh	Bernor et al. 2016
Late Miocene	*Cremohipparion moldavicum*	Taraklia, Moldavia	https://vera-eisenmann.com
Late Miocene	*Cremohipparion moldavicum*	Middle Maragheh, Iran	Bernor et al. 2016
Late Miocene	*Cremohipparion moldavicum*	Akkaşdağı, Türkiye	Koufos and Vlachou 2005 / Bernor Database
Late Miocene	*Cremohipparion moldavicum*	Sofular, Türkiye	Kahya-Parıldar et al. 2025
Late Miocene	*Cremohipparion mediterraneum*	Pikermi, Greece	Bernor Database
Late Miocene	*Cremohipparion* cf. *mediterraneum*	Samos Q1, Greece	Bernor Database
Late Miocene	*Cremohipparion proboscideum*	Samos indet	Bernor Database
Late Miocene	*Cremohipparion proboscideum*	Samos Q1, Greece	Bernor Database
Late Miocene	*Cremohipparion proboscideum*	Samos Q4, Greece	Bernor Database
Late Miocene	*Cremohipparion matthewi*	Samos Q5, Greece	Bernor Database
Late Miocene	*Cremohipparion matthewi*	Middle Maragheh, Iran	Bernor et al. 2016
Late Miocene	*Cremohipparion matthewi*	Sahabi, Libya	Bernor Database
Late Miocene	*Cremohipparion nikosi*	Samos Q5, Greece	Bernor Database
Late Miocene	*Plesiohipparion longipes*	Pavlodar, Kazakistan	https://vera-eisenmann.com
Late Miocene	*Plesiohipparion longipes*	Akkaşdağı, Türkiye	Koufos and Vlachou 2005 / Bernor Database
Late Miocene	*Plesiohipparion longipes*	Çalta, Türkiye	Bernor & Sen 2017

samples (Taşhan, Çevril and Hırka) and compare them with other Late Miocene fossil equid species. PCAs were calculated using R v. 4.5.1 (R Core Team 2025), implementing the packages "stats" v. 3.6.2 (Venables & Ripley 2008) and "ggplot2" v. 3.5.1 (Wickham 2016). PCAs were calculated on crania, third metacarpals and third metatarsals, having all the measurements selected. Incomplete specimens have been analyzed using Log10 Ratio Diagrams.

Cirilli et al. (2021, 2023), Bernor et al. (2024) and Kahya-Parıldar et al. (2025) applied PCA to third metapodials to better discriminate the evolutionary relationships between genera and species of hipparions. The measurements included in our PCA of third metapodials include M1 (maximum length), M3 (midshaft width), M4 (depth of the diaphysis at level of M3), M5 (proximal articular width), M6 (proximal articular depth), M10 (distal maximum supra–articular width), M11 (distal maximum articular width), M12 (distal maximum keel depth), M13 (distal maximum depth of the lateral condyle), M14 (distal maximum depth of the medial condyle).

As applied in Bernor et al. (2024) and Kahya-Parıldar et al. (2025), we extend the application of PCA to crania to characterize the facial morphologies of the genera and species. The measurements used to develop the PCA on crania are: M7 (premolar row length), M8 (molar row length), M9 (upper cheek tooth length), M32 (distance between the orbit of the POF), M33 (length of the POF), M35 (height of the POF) and M36 (distance between the POF and the facial maxiallary crest). Due to the nature of fragmentary remains in hipparions, we created this dataset to analyze more specimens preserving the lateral facial morphology but lacking the snout, considering that no crania from Taşhan, Çevril and Hırka preserve a complete snout.

In several studies, Eisenmann, (see Eisenmann 1995 for a comprehensive summary), has used Log10 ratio diagrams to evaluate differences in hipparion metapodial proportions as a basis for recognizing taxa and their evolutionary relationships. This methodology has been applied to many other studies (among others Bernor & Armour–Chelu 1999; Bernor & Harris 2003; Bernor & Scott 2003; Bernor & Haile Selassie 2009; Bernor & White 2009; Bernor & Sen 2017; Bernor et al. 2003, 2005, 2010, 2013, 2016, 2020, 2022, 2024; Koufos & Vlachou 2005, 2016, 2019; Koufos 2016; Vlachou & Koufos 2009; Cirilli et al. 2020, 2021, 2023; Kahya-Parıldar et al. 2025), leading to a well-resolved context for Late Miocene, Pliocene and Pleistocene Eurasian and African hipparion assemblages. Log10 ratio graphs of mc3 and mt3 include the same measurements considered in the PCAs, together with M7 (maximum diameter of the articular facet for the third carpal/tarsal) and M8 (diameter for the anterior facet for the fourth carpal/tarsal), although these have always proven to be highly variable.

The Log10 ratio diagrams of third metapodials use the log-transformed mean values of the Höwenegg *Hippotherium primigenium* von Meyer, 1929 sample (Bernor et al. 1997) as our standard. The Höwenegg *Hippotherium primigenium* sample represents a well-studied, homogeneous quarry sample of a single primitive European species of Equinae, for which the full range of descriptive statistics (mean, standard deviation, confidence limits, minimum, maximum, and median values) are available for each bone, including the cranium, the mandible, teeth and postcranial elements (Bernor et al. 1997, 2022).

Mean ordinated hypsodonty maps

We assembled the large herbivorous mammals (Artiodactyla, Perissodactyla, Proboscidea and Primates) data from the NOW database (NOW 2025) and calculated the mean ordinated crown height for each locality from MN10–MN12 following Fortelius et al. (2002) for lists with at least two species with a hypsodonty value. All NOW localities between 9.9 Ma to 6.8 Ma from Western Eurasia and North Africa were included. Mean ordinated crown height is a robust proxy for humidity and productivity at the regional scale (Fortelius et al. 2002; Eronen et al. 2009; Kaya et al. 2018). We plotted the results onto present-day maps and interpolated between the localities using Quantum GIS 3.22.11. For the interpolations, thematic mapping and grid interpolation was used, with the following settings: 20 km grid size; 800 km search radius; 800 km grid borders. The interpolation method employed an inverse distance-weighted algorithm (IDW).

Anatomical abbreviations

POB, preorbital bar; **POF**, preorbital fossa; **UTR**, upper cheek tooth row; **LTR**, lower cheek tooth row; **I1**, premaxillary first incisor; **I2**, premaxillary second incisor; **I3**, premaxillary third incisor; **P2**, maxillary second premolar; **P3**, maxillary third premolar; **P4**, maxillary fourth premolar; **M1**, maxillary first molar; **M2**, maxillary second molar; **M3**, maxillary third molar; **i1**, mandibular first incisor; **i2**, mandibular second incisor; **i3**, mandibular third incisor; **p2**, mandibular second premolar; **p3**, mandibular third premolar; **p4**, mandibular fourth premolar; **m1**, mandibular first molar; **m2**, mandibular second molar; **m3**, mandibular third molar; **mc3**, third metacarpal; **mt3**, third metatarsal; **rt**, right; **lt**, left.

Repositories and institutional acronyms

AMNH, American Museum of Natural History, New York, USA; **AS**, Designation for specimens collected by the Sinap project, Alpagut et al. (1989–1995; published in 2003); **GIUM-SI**, Geologisch-Paläontologischen lnstitut der Universität of Münster, Germany, Samos Collection; **MDC**, Musée des Confluences, Lyon, France; **MNHN.F.PIK**, Museum National de Histoire Naturelle, Paris, France, Pikermi Collection; **MNHN.F.TRQ**, Museum National de Histoire Naturelle, Paris, France, Sinap Collection; **MMTT**, Muze Melli Tankh Tabei, Tehran, Iran; **NHMUKPVM**, Museum of Natural History of London, UK; **NHMW**, Natural History Museum in Wien, Austria; **PIN**, Paleontological Institut, Moskow; **PRCI**, Paleontological Research Center of Iran, Maragheh, 13Aban Locality, Lower Maragheh; **SEN MNHN.F.**, Museum National de Histoire Naturelle, Paris, France Collection made by Sevket Sen for Sinap *Cormohipparion sinapensis*; **SENK**, Senkenberg Museum, Frankfurt Germany; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart; **UCBL–FSL**, Université Claude Bernard–1, Paleontological Collection, Lyon, France; **SOF:** Sofular, Cappadocia, Türkiye.**YAM:** Yamula Central Anatolian Volcanic Province Türkiye; **KBM:** Kayseri Bilim Merkezi (Kayseri Science Center) Kayseri Türkiye.

Taxonomic framework

The nomen *Hipparion* has been used in a variety of ways by different authors. We follow characterizations and definitions for hipparionine horses recently provided in Bernor et al. (1996b, 1997, 2021). Hipparion monographs by Gromova (1952) and Gabunia (1959) are cited after the French and English translations. The taxon *Hipparion* has been applied in a variety of ways by different authors. We utilize the following definitions in this work:

Hipparionini – a tribe of Equidae with an isolated protocone on maxillary premolar and molar teeth and, as far as known, tridactyl feet, including species of the following genera: *Cormohipparion*, *Neohipparion* Gidley, 1903, *Nannippus* Matthew, 1926, *Pseudhipparion* Ameghino, 1904, *Hippotherium*, *Cremohipparion*, *Hipparion* sensu strictu, *Sivalhippus* Lyddeker, 1877, *Eurygnathohippus* Van Hopen, 1930 (senior synonym of *Stylohipparion* Van Hopen, 1932), *Shanxihippus* Bernor et al., 2018, *Baryhipparion* Qiu et al., 1987, *Proboscidipparion* Qiu et al., 1987 and *Plesiohipparion*. These lineages have recently been reviewed by Qiu et al. (1987), Bernor & White (2009), Bernor et al. (2010, 2013, 2015, 2020, 2021, 2022, 2024), Armour–Chelu & Bernor (2011), Wolf et al. (2013), Bernor & Sun (2015), Koufos & Vlachou (2005), Vlachou & Koufos (2009), Koufos (2016), Koufos et al. (2022), Cirilli et al. (2020, 2021, 2023), Kahya-Parıldar et al. (2025). The morphological definition of these genera is provided in Bernor et al. (2021).

Cormohipparion. The genus represents the founding source for the Old World *"Cormohipparion* Datum" (MacFadden & Skinner 1981; Bernor et al. 2017, 2021, 2022). Woodburne (2007, 2009) proposed *Cormohipparion* sp. from the Punchbowl Formation (California) as a suitable antecedent morphotype for the Old World hipparion ancestor, although more recently Bernor et al. (2022) have proposed *Cormohipparion occidentale* Leidy, 1856 as the likely source for the Eurasian *Cormohipparion* radiation. *Cormohipparion* occurred in Türkiye (*Cormohipparion sinapensis* Bernor et al., 2003; *Cormohipparion kecigibi* Bernor et al., 2003, 2024; *Cormohipparion cappadocium* Bernor et al., 2024; *Cormohipparion sofularensis* Kahya-Parıldar et al., 2025), Pakistan (*Cormohipparion* sp., Bernor et al. 2021, 2025), Algeria (*Cormohipparion africanum* Arambourg, 1959; Bernor & White 2009, Bernor et al. 2021, 2024) and arguably Ethiopia (Bernor & White, 2009; Bernor et al. 2010, 2021). The genus *Cormohipparion* is characterized by: medium sized hipparion with long preorbital bar (POB); lacrimal extending slightly greater than half-way to preorbital fossa (POF) distal rim; well-developed POF, pocketed posteriorly with well-developed peripheral rim including a deeply recessed anterior rim; maxillary cheek tooth enamel ornamentation complex; mandibular cheek tooth metaconids and metastylids rounded; third metapodials moderately elongate and slender with reduced diaphysis, proximal and distal ends (Bernor et al. 2021).

Hippotherium - This is a distinct genus of Eurasian hipparionine horses known from Western, Central and Eastern Europe, Italy, the Eastern Mediterranean, Iran and China (Bernor et al. 2021). Species belonging to this genus are *Hippotherium primigenium, Hippotherium koenigswaldi* Sondaar, 1961*, Hippotherium catalaunicum* Pirlot, 1956*, Hippotherium intrans* Kretzoi, 1983*, Hippotherium microdon* Kormos, 1914*, Hippotherium kammerschmitti* Kaiser et al., 2003*, Hippotherium brachypus*, *Hippotherium malpassii* Bernor et al., 2011*,* perhaps *Hippotherium giganteum* Gromova, 1952 and *Hippotherium weihoense* Liu et al., 1978 (Bernor et al. 2011, 2021). It is a large hipparion with a long POB with lacrimal slightly more than half-way to POF distal rim; POF is large, dorsoventrally and medially deep; maxillary and mandibular cheek teeth have richly ornamented enamel plications; mandibular cheek tooth metaconids are rounded and metastylids squared; third metapodials are more robustly built than in *Cormohipparion, Hipparion* sensu strictu and *Cremohipparion* (Bernor et al. 2021).

Hipparion sensu strictu – The name is restricted to a specific lineage of hipparionine horses with the facial fossa positioned dorsally high on the face (MacFadden 1980, 1984; Woodburne & Bernor 1980; Woodburne et al. 1981; MacFadden & Woodburne 1982; Bernor 1985; Bernor & Hussain 1985; Bernor et al. 1987, 1990 a, 1990b, 2021; Woodburne 1989). The posterior pocket becomes reduced and eventually lost, and confluent with the adjacent facial surface (includes Group 3 of Woodburne & Bernor 1980). This issue was found to be even more complex in our analysis of the Cappadocia hipparions in that there has, to date, been an inadequate accounting of the genotype species *Hipparion prostylum* Gervais, 1959 postcranial size and proportions (Bernor et al. 2024). Bernor's definition departs from some investigators in not recognizing North American species of *Hipparion* sensu strictu. Bernor (1985) and Bernor (in Bernor et al. 1990 a, b) have argued that any morphologic similarity between North American "Hipparion" and Old World *Hipparion* s.s. is due to homoplasy. This hypothesis is here confirmed after work in collections on North American and Eurasian hipparions of two of the present authors (OC and RLB), suggesting that the early Barstovian "*Hipparion*" *shirleyi* MacFadden, 1984 deserves a different genus assignment than *Hipparion* s.s. *Hipparion* s.s. is characterized by a long POB; lacrimal extending slightly more than half -way to the POF posterior rim without penetrating the POFs interior; POF prominent to reduced, medially deep with posterior pocket, with a moderately well-developed peripheral rim, cheek teeth are moderately complexly ornamented, the metaconids and metastylids are rounded in mandibular dentitions and third metapodials are slender. The genus includes *Hipparion gettyi* Bernor, 1985*, Hipparion prostylum, Hipparion dietrichi, Hipparion campbelli* Bernor, 1985 and *Hipparion hippidiodum* Sefve, 1927 ranging from France, through Greece and Iran to China.

Cremohipparion – Representatives of this genus are medium- to small-sized hipparions recognized in the circum-Mediterranean area, Balkans, Ukraine, the Indian Subcontinent and China. *Cremohipparion* has a short POB with lacrimal suture invading or closely approaching the posterior rim of the POF; the POF is primitive in its dorsoventrally and medially deep with well-developed peripheral rim. *Cremohipparion mediterraneum* Roth & Wagner, 1855 *Cremohipparion proboscideum* Studer, 1911, *Cremohipparion forstenae* Zhegallo, 1971 and *Cremohipparion licenti* Qiu et al., 1987 usually express an intermediate fossa between the POF and buccinator fossae, other members of the group do not. This genus is characterized by moderately complex enamel plications, rounded mandibular cheek tooth metaconids and metastylids and elongate and slender metapodials. The genus includes *Cremohipparion macedonicum* Koufos, 1984, *Cremohipparion moldavicum*, *Cremohipparion mediterraneum*, *Cremohipparion proboscideum*, *Cremohipparion matthewi* Abel, 1926, *Cremohipparion nikosi* Bernor & Tobien, 1989, *Cremohipparion periafricanum* Villalta & Crusafont, 1957, *Cremohipparion antelopinum* Falconer and Cautley, 1846, *Cremohipparion forstenae* and *Cremohipparion licenti* (for complete summary see Bernor et al. 2021).

"Hipparion" – Several distinct and separate lineages of Old World hipparionine horses once considered to be referable to the genus *Hipparion*. We emphasize here the need to avoid confusion of well-defined hipparionine lineages with poorly characterized taxa of "Hipparion" sensu lato.

SYSTEMATIC PALEONTOLOGY

Class **MAMMALIA** Linnaeus, 1758
Order **Perissodactyla** Owen, 1848
Family Equidae Gray, 1821
Tribe Hipparionini Quinn, 1955
Hippotherium Kaup, 1835

Hippotherium brachypus Hensel, 1862

Neotype: NHMUKPVM11240, third metacarpal. Figured in Koufos 1987b, Pl. VII, fig. 2.

Topotype: NHMUKPVM 11265, third metatarsal. Figured in Koufos 1987b, Pl. VIII, fig. 2.

Remarks on the Neotype and Topotype. Some metapodials from Pikermi were preliminarily described by Hensel (1862), who was the first to classify the Pikermi hipparion horses into two groups. The one with short and robust metapodials was referred to as *Hippotherium brachypus*. This name must be the specific name of the large hipparion of Pikermi whose metapodials have the same morphology and dimensions as those described by Hensel. The location of this material is unknown. In Munich, there is a cast of a forefoot, figured by Abel (1927), which following Koufos could possibly be considered as the lectotype of *Hippotherium brachypus*. Should the original of the cast be lost as well as the rest of Hensel's syntypes, Koufos proposed BMNH, M.11240 (here

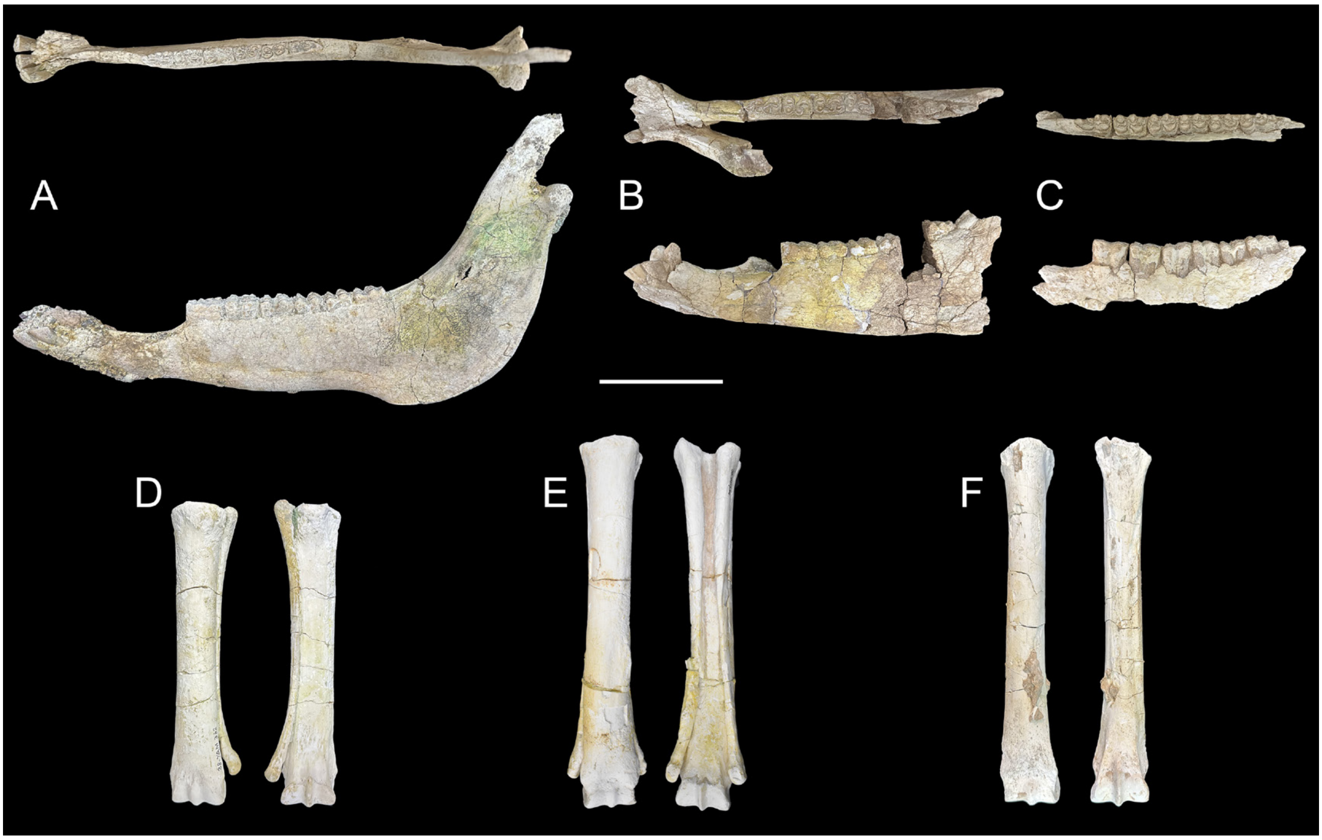

Fig. 2 - Mandibular and postcranial remains of the Kayseri *Hippotherium brachypus*. A) 38-YAM/275, mandible in occlusal and lateral view; B) 38-YAM/561, mandible in occlusal and lateral view; C) 38-YAM/614, mandible in occlusal and lateral view; D) 38-YAM/362 mc3 in dorsal and palmar view; E) 38-YAM/486, mt3 in dorsal and plantar view; F) 38-YAM/432, mt3 in dorsal and plantar view. Scale bar 10 cm.

NHMUKPVM11240) (pl. VIJ.2) as the Neotype and the associated metacarpals BMNH, M.11265 (here NHMUKPVM11265) as Topotype, the associated metatarsals and some metapodials of the Gaudry collection of the Museum National d'Histoire Naturelle: MNHN.F.PIK42, MNHN.F.PIK4 6, NHN.F.PIK48, MNHN.F.PIK52, MNHN.F.P IK54, MNHN.F.PIK59, MNHN.F.PIK104.

We follow the proposal for the Neotype and Topotype of Koufos (1987a, 1987b).

Referred Specimens: See Supplementary Table 1.
Type Locality: Pikermi, Greece
Age: Late Miocene, MN11-12
Geographic Range: Greece, Bulgaria, Türkiye and Iran.
Diagnosis (modified from Koufos, 1987a):

Size large; skull elongated with a wide muzzle; preorbital fossa situated far from the orbits separated by a long preorbital bar (POB); narrow choanae; mandible with a long, narrow muzzle and an elongated symphysis; complexly plicated maxillary cheek teeth; elliptical protocone usually not connected with the protoloph; often multiple small pli caballins; elliptical hypocone; lower cheek teeth with protostylids; crenelated or plicated borders of the flexids; rare pli caballinid; first upper deciduous premolar (dP1s) may be present both in young and adult individuals; bones robust with large dimensions; metapodials elongated and stout.

Description

Mandibles. The Hırka 1 left mandible, YAM/275 (Fig. 2A) is of a large individual. The mandible is very well preserved, including an elongate symphysis and pristine ascending ramus. The incisor arcade is arcuate, preserves left i2–i3 with the remaining teeth absent or poorly preserved. The mandible has a very long symphysis (M2 = 124.7 mm), elongate p2–m3 dimension (M5 = 151.4 mm) and shallow mandibular corpus (M11 = 64.8 mm; M12 = 45.2 mm; M13 = 56.8 mm) (Fig. 2A). Salient cheek tooth characters include: p2 anterostylid is elongate; premolar metaconids are rounded (the p2 has a very small metaconid subequal in size to the metastylid) as is the molar metaconid; molar metastylids are also rounded with "incipient" squaring occurring; there are no premolar or molar metastylid spurs; premolar ectoflexid does not separate metaconid and metastylid; pli caballinid is absent; there are no ectostylids. The dimensions of p2-m3 (M5) falls above the range reported by Koufos & Vlachou (110.9-130.0 mm) but the length of the symphysis is within the range for the 7.1 Ma assemblage of *Hippotherium* aff. *brachypus* (see results) from Akkaşdağı, Türkiye (Koufos and Vlachou 2005).

38-YAM/561 (Fig. 2B) is an adult male right mandible from Çevril 1. Length of the symphysis (M2) is 116.1 mm and the length of p2–m3 is very long, 163.5 mm. The mandible is fragmentary in preserves the mandibular symphysis and both horizontal rami which are separated by a break. The right mandibular ramus includes the symphysis, right horizontal ramus and mesial portion of the left horizontal ramus. The anterior dentition includes a large left i3 and worn i2, i3 and c. The right mandible has p2–m1 preserved, m2 missing and mesial portion of m3 present. The left horizontal ramus has p3–m3 present (Fig. 2B); p2–m3 has a length (M5) of 163.5 mm; length of symphysis (M2) is 116.1 mm. The mandibular cheek tooth morphology has the following salient features: p2 anterostylid is elongate; premolar and molar metaconids are rounded; premolar and molar metastylids are likewise rounded; there is no premolar or molar metastylid spur; premolar ectoflexids are moderately deep but do not separate metaconid from the metastylid; there are no pli caballinids or ectostylids.

38-YAM/614 (Fig. 2C) is a large mandible with complete cheek teeth of an older individual from Çevril 1. The length of the symphysis is 61.8 mm (M2) and p2–m3 is 155.9 mm (M5). The p2 anterostylid is elongate; premolar metaconid is rounded and the molar metaconid is rounded; premolar metastylid is angular on the distal surface; premolar metastylid spur is absent and molar metastylid is angular on the distal surface; there are no molar metastylid spurs; premolar ectoflexid does not separate metaconid and metastylid; pli caballinids are absent as are the ectostylids.

Metapodials. One third metacarpal (38-YAM/362, Hırka 1; Fig. 2D) and two third metatarsals (YAM/486, Hırka 1, Fig. 2E; 38-YAM/432, Hırka 1, Fig. 2F) are here referred to *Hippotherium brachypus*. The mc3s and the mt3s are characterized by a large and stout shape, with an expanded diaphysis and large proximal and distal width.

Hipparion de Christol, 1832

Hipparion dietrichi Wehrli, 1941

Holotype: GIUM-SI/7 Munster, cranium. Figured in Wehrli 1941, Pl. XVII, fig. 4.

Type Locality: Samos, Greece, unknown locality

Age: Turolian, MN11-13

Diagnosis: Cranium of medium size; POF is placed high on the maxilla with a long to moderately long POB; POF is C-shaped, elongate with reduced medial depth, posterior pocketing reduced most often with distinct posterior POF rim; medial depth is usually moderate but reduced peripheral rim; nasal notch placed above P2 anterostyle or sometimes mesostyle; cheek teeth with moderately complex plications of the fossettes; protocone round to oval and sometimes flattened lingually; mc3s and mt3s are elongate and slender.

Description

Crania. 38-YAM/423 (Fig. 3A) is a male skull from Hırka 1 with premaxilla, maxilla, anterior orbit and frontal bones; right and left I1–I3, canine, left P2–M3 and right P2–M2. Snout length is 106.2 mm (M1), P2–M3 length is 146.2 mm (M9) and the POB is long, 45.8 mm (M32). Other POF measurements are: M33 = 48.4 mm; M34 = 43.7 mm; M35 = 29.8 mm; M36 = 47.5 mm; M37 = 35.3 mm; M38 = 80.0 mm. Salient morphological features include: (POB) with the anterior edge of the lacrimal placed more than half the distance from the anterior orbital rim to the posterior rim of the fossa; POF C-shaped and anteroposteriorly oriented; POF not pocketed but with a small posterior rim; POF has a moderate depth, 10–15 mm in deepest place; POF peripheral outline weakly defined around periphery; POF anterior rim absent; nasal notch absent; maximum crown height 40–60 mm; cheek tooth ornamentation moderately complex with fewer, more shortly amplified, thinly banded plications; there is no linkage of adjacent fossette borders; protocone shape varies from oval to lingually flattened and labially rounded to rounded; protocones are isolated from the protoloph; P2 anterostyle is elongate.

38-YAM/367 (Fig. 3B) is a partial skull from Hırka 1 including proximal snout, facial region, anterior orbit and forehead, right and left P2–M3. Length of the P2–M3 is 145.2 mm (M9) and POB length is 31.8 mm. Other POF measurements are: M33 = 68.4 mm; M34 = 60.5 mm; M35 = 34.4 mm; M36 = 24.6 mm; M37 = 41.4 mm; M38 = 70.1 mm; M39 = 54.1 mm. Salient morphological features include: preorbital bar (POB) long with the anterior edge of the lacrimal placed more than half the distance from the anterior orbital rim to the posterior rim of the fossa; POF is C-shaped and anteroposteriorly oriented; POF is not pocketed but with a distinct posterior rim; POF medial depth is approximately 10 mm.; POF peripheral outline is weakly defined around periphery; anterior rim is absent; nasal notch is absent; maximum crown height is 40–60 mm; cheek tooth ornamentation is moderately complex with fewer, more shortly amplified, thinly banded plications; adjacent fossettes are not linked; protocones are oval to rounded and isolated from the protoloph; protoconal spur is reduced (on right P2 only) to absent; P2 anterostyle is elongate.

38-YAM/409 (Fig. 3C) is a partial skull of an old adult individual from Hırka 1 including facial region, anterior orbit and forehead, right P2–M2 and left P3–M3. Length of P2–M3 is 142.1 mm (M9) and POB length is 41.4 mm (M32). Other POF measurements are: M34 = 53.7 mm; M35 = 25.4 mm; M36 = 50.9 mm; M37 = 40.7 mm; M38 = 76.5 mm; M39 = 60.5 mm. Salient morphological features include: preorbital bar (POB) long with the anterior edge of the lacrimal placed more than half the distance from the anterior orbital rim to the posterior rim of the fossa; POF C-shaped and anteroposteriorly oriented; POF not pocketed but with a posterior rim; POF of moderate depth, 10–15 mm in deepest place; POF weakly defined around periphery; anterior rim absent; nasal notch not present; maximum crown height 40–60 mm; maxillary cheek teeth moderately complex with fewer, more shortly amplified, thinly banded plications; there is no linkage of adjacent fossette borders; protocone shape varies from oval to rounded to lingually flattened and labially rounded; protocone is isolated from the protoloph except in the worn right P2 and M1; there are no protoconal spurs; P2 anterostyle is elongate.

YAM/579 Fig. 3D is a skull with snout, cheek teeth and facial features preserved from Çevril 1. Preorbital bar is moderately long (M32 = 35.1 mm) with the anterior edge of the lacrimal placed more than half the distance from the anterior orbital rim to the posterior rim of the fossa; The POF is elongate and dorsoventrally high, subtriangularly shaped and anteroposteriorly oriented (M33 = 58.5 mm; M35 = 28.9 mm; M36 = 40.1 mm; M39 = 59.7 mm); POF is not pocketed but with a posterior rim; POF is moderately deep, about 10 mm in the deepest place; POF outline is developed posteriorly and ventrally, more faint dorsally; there is a faint anterior rim; nasal notch would appear to be above P2; snout is long (M1 = 93.8 mm); crown height is 40–60 mm; cheek tooth row is long (M9 = 151.2 mm); cheek tooth occlusal fossette ornamentation has simple complexity with few, shortly amplified plications; there is no linkage of adjacent fossette plications; protocone shapes are oval and lingually flattened-labially rounded; protocones are isolated from the protoloph; there are no protoconal spurs; P2 anterostyle is elongate.

38-YAM/592 (Fig. 3E) is a fragmentary skull of a very old male individual from Çevril 1 with frontal bone, maxilla and most of the premaxilla present, fragmentary left male canine and P3–M3, and right P4–M2 very worn. Length of POB is 39.8 mm (M32); premaxilla length (M1) and cheek tooth row length (M9) measurements are not possible because of missing bone and teeth. Salient morphological features of the skull include: preorbital bar (POB) long with the anterior edge of the lacrimal placed more than half the distance from the anterior orbital rim to the posterior rim of the fossa; POF egg-shaped and anteroposteriorly oriented; POF not pocketed but with a highly reduced posterior rim; POF with shallow depth, less than 10 mm in the deepest place; POF peripheral outline absent with no remnant depression; nasal notch may be at or near the anterior border of P2; maximum crown height 40–60 mm; maxillary cheek teeth with simple complexity due to extreme wear; right M1 shows evidence of adjacent fossette borders being linked; protocones rounded; protocone isolated from protoloph except right M2 which shows linkage due to advanced wear; protocone spur is absent; P2 not preserved.

38-YAM/86 (Fig. 3F) is a skull fragment from Çevril 1. It is an old individual with worn cheek teeth. The preorbital bar appears to be long; the POF is C-shaped and is anteroposteriorly oriented; the POF is not pocketed but has a distinct posterior rim; the POF has a shallow depth, less than 10 mm in deepest place; POF peripheral border outline is absent with a remnant depression; POF anterior rim is absent; nasal notch would appear to be at or near the anterior border of P2.

38-YAM/590 (Fig. 3G) is a skull fragment from Çevril 1. The POF is of moderate length (M32 = 29.4 mm), vestigial but the lacrimal is still placed more than half distance to the posterior rim of the fossa; the POF is C-shaped and anteroposteriorly oriented; the POF is not pocketed but with a posterior rim; the POF has a shallow depth, less than 10 mm in its deepest place; there is no peripheral outline preserved; anterior rim is absent; nasal notch is not preserved. Teeth are worn with only fragmentary right C and P4–M3 present; maximum crown height was 40–60 mm; occlusal morphology of cheek teeth had simple complexity with few, shortly amplified plications; there is no linkage of opposing fossettes; protocone shape is rounded to lingually flattened-labially rounded; all four cheek teeth have protocone connected to the protoloph due to advanced wear; protoconal spurs are absent.

38-YAM/630 (Fig. 3H) is a fragmentary old adult skull from Çevril 1. P2–M3 length is 141.9 mm (M9). Salient morphological features include: POF vestigial without C-shape outline but a shallow depression less than 10 mm. in its deepest place and lacking peripheral rim; nasal notch not preserved; maximum crown height 40–60 mm; maxillary cheek tooth fossette ornamentation with simple complexity; right P2 and P4 have fossette linkage; protocones are round; P2 and M1 are so worn that protocone is linked to protoloph; there are no protocone spurs; P2 has elongate anterostyle, even in this late stage-of-wear.

38-YAM/580 (Fig. 3I) is a partial cranial fragment from Çevril 1. The POF has a long preorbital bar (M32 = 46.8 mm) with the anterior edge of the lacrimal placed more than half the distance from the anterior orbital rim to the posterior rim of the fossa; the POF is vestigial but with a C-shaped or egg-shaped outline; the POF is not pocketed but with a posterior rim; peripheral outline is lacking with no remnant depression; there is no anterior rim or nasal notch preserved; crown height is 40–60 mm; cheek tooth plications are moderately complex with fewer, more shortly amplified, thinly banded plications; there is no linkage of adjacent fossette plications; protocone shape varies from oval to elongate to rounded; protocones are not flattened lingually.

Mandibles. 38-YAM/199 (Fig. 3J) is a fragmentary female late state juvenile mandible from Hırka 1. The mandible has right i1–i2, a small canine and p2–m2; left i3 is still in the crypt but exposed labially; the right m3 is absent. Also present are left i1 and both canines which are small and diagnostic of the gender identification. The mandibles symphysial length is 79.7 mm (M2). Salient morphological features include: p2 anterostylid elongate; premolar and molar metaconids rounded; premolar metastylids rounded; premolar metastylid spurs absent; molar metastylids are rounded; premolar ectoflexid separates metaconid and metastylid in p2 and in the molars; there are no molar metastylid spurs, nor are there any pli caballinids nor any ectostylids.

38-YAM/295 (Fig. 3K) is a fragmentary adult female left mandible from Hırka 1. The mandible includes right and left i1–i3, a small right c, broken left c and right p2–m3. Length of the symphysis is 100.1 mm (M2) and p2–m3 length is 146.1 mm (M5). Salient morphological features include: p2 anterorstylid is elongate premolar and molar metaconids are rounded; premolar metastylids are rounded; there is no premolar metastylid spur; molar metastylids vary from rounded to square shaped; molar metastylid spurs are absent; premolar ectoflexid does not separate metaconid and metastylid.

38-YAM/666 (Fig. 3L) is a right mandible from Çevril 1. The length of p2–m3 is 140.7 mm (M5) and the mandibular depth is not great (M11 = 49.4 mm; M12 = 41.0 mm) indicating that the maximum crown height was between 40–60 mm. Salient morphological features include: p2 anterostylid is elongate; premolar and molar metaconids are rounded; premolar metastylids are rounded while the molar metastylids are square-shaped; there are no premolar metastylid spurs; only m3 has a small metastylid spur; premolar ectoflexid does not separate metaconid and metastylid; there are no pli caballinids nor ectostylids.

Metapodials. There are several mc3s and mt3s of *Hipparion dietrichi* from the Kayseri localities (Taşhan, Çevril and Hırka; see Supplementary Table 1). The mc3s and the mt3s are elongated and slender, with a moderately expanded diaphysis, proximal and distal width. A representative sample of the metapodials from these localities is shown in Fig. 4.

Fig. 3 - Cranial and mandibular remains of the Kayseri *Hipparion dietrichi*. A) 38-YAM/423, cranium in lateral and ventral view; B) 38-YAM/367, cranium in lateral and ventral view; C) 38-YAM/409, cranium in lateral and ventral view; D) 38-YAM/579, cranium in lateral and ventral view; E) 38-YAM/592, cranium in lateral and ventral view; F) 38-YAM/86, cranium in lateral and ventral view; G) 38-YAM/590, cranium in lateral and ventral view; H) 38-YAM/630, cranium in lateral and ventral view; I) 38-YAM/580, partial cranium in lateral and ventral view; J) 38-YAM/199, mandible in occlusal and lateral view; K) 38-YAM/295, mandible in occlusal and lateral view; L) 38-YAM/666, mandible in occlusal and lateral view. Scale bar 10 cm.

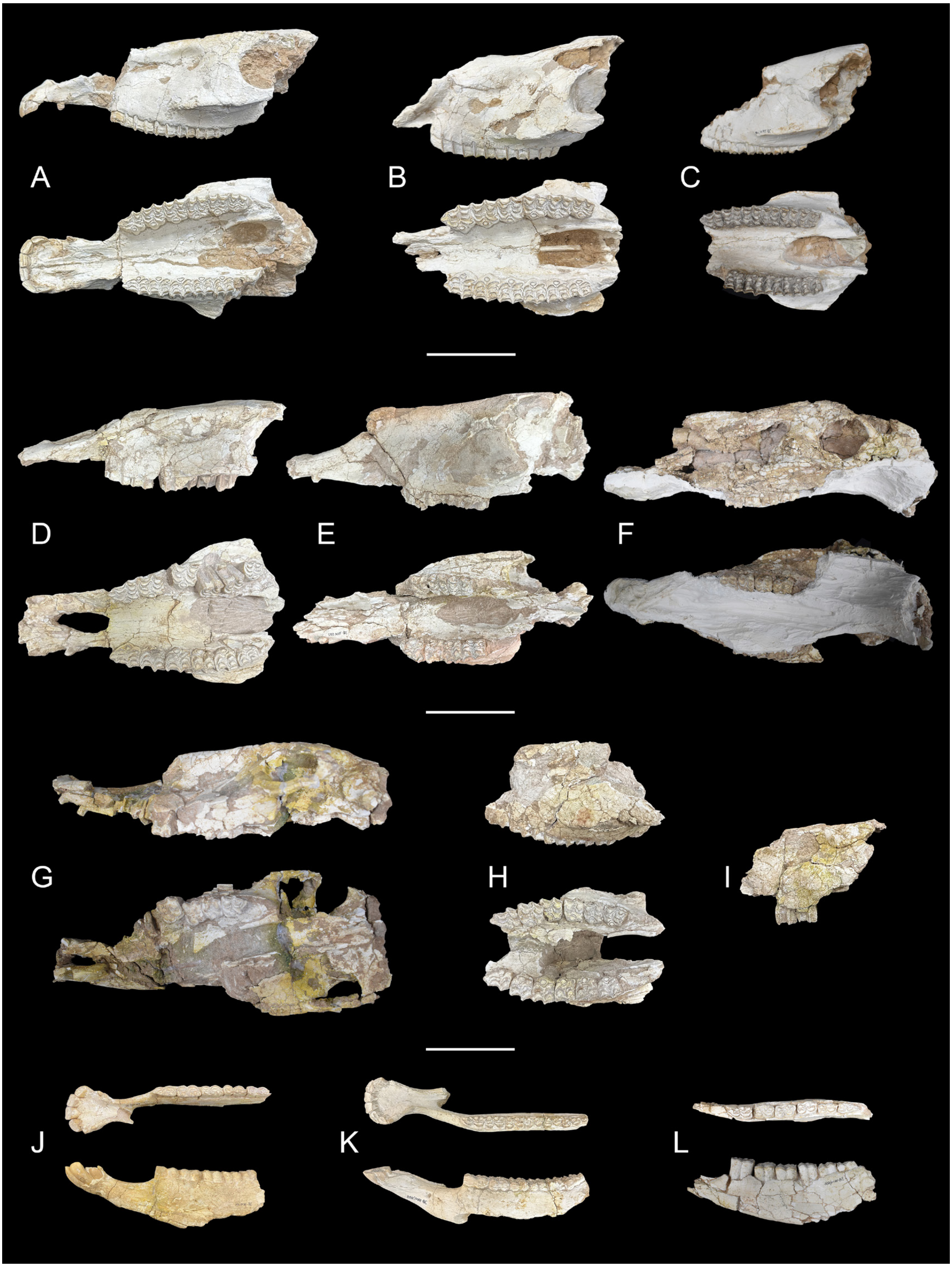

Fig. 3

Fig. 4 - Third metacarpals (A-E) and third metatarsals (F-J) of the Kayseri *Hipparion dietrichi*. A) 38-YAM/500, mc3 in dorsal and palmar view; B) 38-YAM/360, mc3 in dorsal and palmar view; C) 38-YAM/573, mc3 in dorsal and palmar view; D) 38-YAM/593, mc3 in dorsal and palmar view; E) 38-YAM/119, mc3 in dorsal and palmar view; F) 38-YAM/210, mt3 in dorsal and plantar view; G) 38-YAM/412, mt3 in dorsal and plantar view; H) 38-YAM/554, mt3 in dorsal and plantar view; I) 38-YAM/575, mt3 in dorsal and plantar view; J) 38-YAM/73, mt3 in dorsal and plantar view. Scale bar 10 cm.

Remarks. On Samos, *Hipparion dietrichi* is reported from Q4 and Ql (Sondaar 1971; Forsten 1980; Vlachou & Koufos 2009). Apart from Samos, *Hipparion dietrichi* was also recognized from the Greek localities Ravin des Zouaves 5 (RZO), Prochoma 1 (PXM), Vathylakkos 2 (VTK), Nikiti 2 (NIK) and Perivolaki (PER) (Koufos 1987c, 1987d, 1988, 2024; Vlachou & Koufos 2002, 2004, 2006), as well as from of North Macedonia and Türkiye (Forsten & Garevski 1989; Koufos & Kostopoulos 1994; Koufos & Vlachou 2005) all dated from MN11 to MN12. *Hipparion dietrichi* from Q4 is represented by a single skull and few postcranial elements, while the sample from Ql includes numerous cranial and postcranial remains. The sample from Ql shares the same morphology with that from Q4 (Sondaar 1971). The skull morphology has the typical characteristics of *Hipparion dietrichi,* without significant differences among the specimens, and furthermore, it seems comparable to the advanced morphology of the medium sized species from Middle Maragheh (*Hipparion* aff. *prostylum* in Bernor 1985; *Hipparion* "*prostylum*" in Vlachou & Koufos 2006; and *Hipparion* cf. *dietrichi* herein). As reported in the morphometric analyses herein, the metapodials assigned to *Hipparion dietrichi* are similar to *Hipparion prostylum,* but more elongated and less slender than the latter. Forsten & Garevski (1989) also stressed the morphological affinities between *Hipparion prostylum* and *Hipparion dietrichi*, and described a set of cranial and postcranial remains from Titov Veles (North Macedonia) under the name *Hipparion prostylum* / *Hipparion dietrichi*. Bernor (1985) suggested that *Hipparion dietrichi* was derived from *Hipparion prostylum*, and all remarks included herein in the morphometric analyses reinforce his conclusion. Our analysis of the crania, mc3s and mt3s suggests a broader recognition of *Hipparion dietrichi* from Samos, Maragheh, Akkaşdağı and the Kayseri localities.

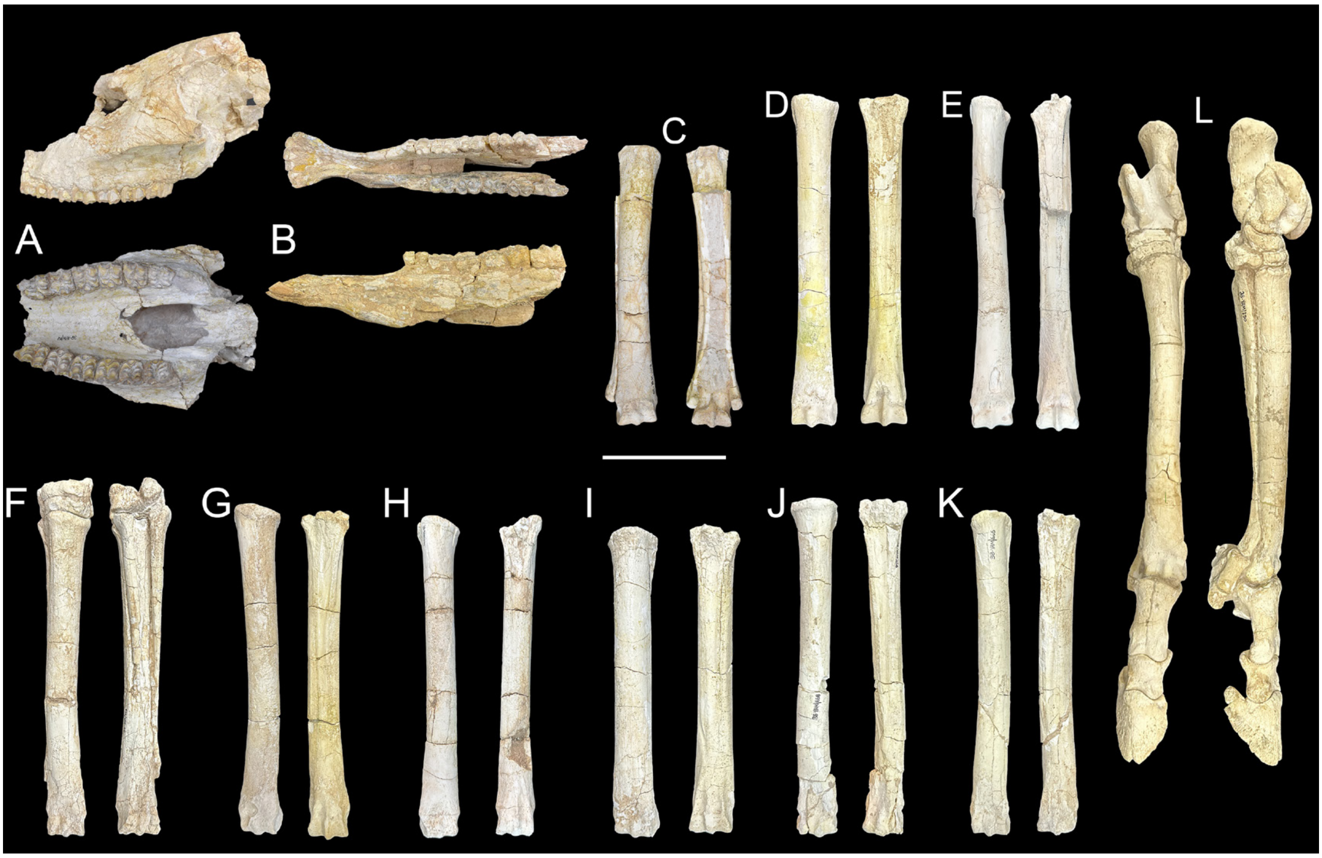

Fig. 5 - Cranial, mandibular and postcranial remains of the Kayseri *Cremohipparion moldavicum*. A) 38-YAM/115, incomplete cranium in lateral and ventral view; B) 38-YAM/103, incomplete mandible in occlusal and lateral view; C) 38-YAM/209, mc3 in dorsal and palmar view; D) 38-YAM/274, mt3 in dorsal and plantar view; E) 38-YAM/553, mt3 in dorsal and plantar view; F) 38-YAM/559, mt3 in dorsal and plantar view; G) 38-YAM/565, mt3 in dorsal and plantar view; H) 38-YAM/577, mt3 in dorsal and plantar view; I) 38-YAM/650, mt3 in dorsal and plantar view; J) 38-YAM/658, mt3 in dorsal and plantar view; K) 38-YAM/665, mt3 in dorsal and plantar view; L) 38-YAM/290 articulated hindlimb with calcaneum, astragalus, tarsals, mt2-4, 1ph2-4, 2ph2-4 and 3ph3 in dorsal and lateral view. Scale bar 10 cm.

Cremohipparion Qiu et al., 1987

Cremohipparion moldavicum Gromova, 1952

Holotype: P.I.N. 1256-3639, cranium. Figured in Gromova, 1952, Pl. 1, figs. 1–3

Type locality: Taraklia, Republic of Moldavia.

Age: Turolian, MN 11-12.

Geographic range: Moldavia, Ukraine, Türkiye and Iran.

Diagnosis: Medium-sized hipparion horse with an elongate snout. POF single, subtriangular shaped, anteroposteriorly oriented and elongate, dorsoventrally and medially deep, with slight posterior pocketing, a distinct anterior rim and strongly expressed peripheral outline. POB short with the lacrimal bone contacting or invading the posterior aspect of the POF. The nasal notch is incised at a level either just above the mesial border of P2, or slightly mesial to it. Middle wear adult cheek teeth have moderately complex plications of the pre- and postfossettes; protocones are round to oval with lingual flattening in some individuals. The P2 anterostyle is usually elongate but also shorter and rounded in some individuals. Elongate and slender mc3s and mt3s.

Description

Cranium. 38-YAM/115 (Fig. 5A) is an eroded skull from Çevril 1. The skull includes the anterior 2/3rds of the right orbit, POB, POF, right and left P2–M3; the skull lacks the premaxilla and cranium. P2–M3 length is 137.2 mm. (M9) and POB length is 33.5 mm (M32). POF measurements are: M33 = 52.3 mm; M35 = 42.0 mm; M36 = 28.0 mm. Salient morphological features include: lacrimal reduced in size, slightly invades or touches posterior border of preorbital fossa; POF subtriangular shaped and anteroventrally oriented; POF dorsoventrally extensive, pocketing reduced, moderate to slight depth, less than 15 mm; POF peripheral outline slightly delineated around entire periphery; anterior rim not preserved; nasal notch missing; crown height 40–60 mm; cheek teeth moderately complex with fewer, more shortly amplified, thinly banded plications; protocone rounded or lingually flattened and labially rounded; protocone connected to protoloph in P2; protocone spur absent; P2 anterostyle elongate.

Mandible. 38-YAM/103 (Fig. 5B) is a mandible of an old individual with an elongate, narrow symphysis, right and left i1–i3, very worn right p2–m2 and left p2 roots, p3–m3 from Cervil 1. The length of the mandibular symphysis is 109.5 mm. The cheek teeth are in advanced wear and have the following salient characteristics: p2 anterostylid is elongate; premolar and molar metaconids and metastylids are rounded; there are no premolar or molar metastylid spurs; premolar ectostylids do not separate metaconid and metastylid except in m2; pli caballinids and ectostylids are absent.

Metapodials. *Cremohipparion moldavicum* is represented 1 mc3 from Hırka 1 (38-YAM/209) and by 7 mt3s from Çevril 1 (38-YAM/553, 38-YAM/559, 38-YAM/565, 38-YAM/577, 38-YAM/650, 38-YAM/658 and 38-YAM/665) and 2 mt3s from Hırka 1 (38-YAM/274, 38-YAM/290). The mc3 is short and slender, with a reduced diaphysis, proximal and distal width. The mt3s are relatively longer and remain very slender. A representative sample of the metapodials from these localities is shown in Fig. 5C–L.

Remarks. Gromova (1952) nominated *"Hipparion" moldavicum* based on the material from Taraklia (Moldova). She characterized the species as being a medium-sized hipparion with a long muzzle, high frontal and short tooth row, single elongated and deep POF situated close to the orbit, moderately developed nasal opening; protocone oval; cheek tooth enamel plications moderately complex; lower cheek teeth with deep ectoflexid; metapodials of moderate length and slender (Koufos & Vlachou 2005). Forsten (1978) synonymized *H. moldavicum* with *H. mediterraneum* and indeed they are closely comparable but differ in facial fossa features (Bernor 1985; Bernor et al. 2016). Moreover, Bernor (1985) and Bernor et al. (2016) recognized *Cremohipparion moldavicum* as a member of this genus from the Turolian localities of Maragheh, Iran. The crania, dentitions and third metapodials the Maragheh sample are closely similar to the material described by Koufos & Vlachou (2005) from the 7.1 Ma Türkiye locality of Akkaşdağı. However, the Maragheh sample is mostly ~8 Ma, and possibly older.

Cremohipparion aff. *proboscideum*

Locality: Çevril 1
Referred specimens: 38-YAM/564, cranium.

Description

Cranium. 38-YAM/564 (Fig. 6A-B) is a crushed cranium from Çevril 1. While weathered, the skull is of a virtually complete male with a large, dorsoventrally and anteroposteriorly extensive POF, measurements are: M32 = 19.1 mm; M33 = 64.7 mm; M35 = 41.3 mm; M36 = 38.4 mm; M39 = 55.5 mm. The maxilla has right and left I2–I3, canines and P2-M3. P2–M3 length is estimated as being 150 mm; POB length is short; the long snout that narrows disto-mesially with a very tight, arcuate incisor arcade. Salient morphological features include: POF with lacrimal reduced in size, slightly invading or touching the posterior border of preorbital fossa; POF is subtriangular shaped and anteroventrally oriented; POF has reduced posterior pocketing; POF medial depth is deep, greater than 15 mm in deepest place; POF outline is moderately delineated around periphery; anterior rim is present; nasal notch cannot be certainly determined but appears to be posterior to P2; maximum crown height 40–60 mm; cheek tooth ornamentation is moderate; there is no linkage of adjacent fossettes; protocones are oval and isolated from the protoloph; there are no protocone spurs; P2 anterostyle is short and rounded. The apparent strongly retracted nasals combined with the elongate narrow snout suggests the referral to *Cremohipparion* aff. *proboscideum*.

Fig. 6 - 38-YAM/564, cranium of the Kayseri *Cremohipparion* aff. *proboscideum* in lateral (A) and ventral (B) view. Scale bar 10 cm.

Plesiohipparion Qiu et al., 1987

Plesiohipparion longipes Gromova, 1952

Holotype: PIN no 2413/5030, mt3. Figured in Gromova, 1952, Pl. 10, figs. 3-3a
Type Locality: Pavlodar, Kazakhstan.
Age: Late Miocene, MN12.

Fig. 7 - Cranial and postcranial remains of the Kayseri *Plesiohipparion longipes*. A) 38-YAM/20, incomplete cranium in lateral and ventral view; B) 38-YAM/507, mc3 in dorsal and palmar view; C) 38-YAM/443, mc3 in dorsal and palmar view; D) 38-YAM/491, mc3 in dorsal and palmar view; E) 38-YAM/438, mt3 in dorsal and plantar view; F) 38-YAM/118, mt3 in dorsal and plantar view; G) 38-YAM/597, mt3 in dorsal and plantar view; H) 38-YAM/657, mt3 in dorsal and plantar view; I) 38-YAM/286 articulated forelimb with partial humerus, radius, carpals, mc2-4, 1ph2-4, 2ph2-4 and 3ph2-4 in lateral view. Scale bar 10 cm.

Diagnosis. Large sized; elongated anterostyle, moderate enamel plications in the upper cheek teeth, large mesostyle with deep plication, elongated and wide protocone, and large hypoconal groove; very long and slender extremities, and long metapodials.

Description

Cranium. 38-YAM/20 (Fig. 7A) is an adult palate with P2-M3 present and in wear and has a length of 159.2 mm (M9) from Taşhan 2. The facial region is not preserved. There is no dP1 preserved. Maximum crown height would have been between 40 and 60 mm or possibly more. Fossette plications are complex, with several deeply amplified plications. Fossette borders are not linked. Protocone shape is oval-elongate and compressed and there is no protconal spur on any of the cheek teeth. P2 anterostyle is elongate.

Metapodials. *Plesiohipparion longipes* is represented by 4 mc3s from Hırka 1 (38-YAM/286, 38-YAM/443, 38-YAM/491 and 38-YAM/507), 3 mt3s from Çevril 1 (38-YAM/118, 38-YAM/597, 38-YAM/657) and 1 mt3 from Hırka 1 (38-YAM/438) (Supplementary Table 1; Fig. 7B–I). The mc3s and the mt3s are elongated and robust, with a well-developed diaphysis, proximal and distal width. A representative sample of the metapodials from these localities is shown in Fig. 7B–I.

Remarks: Eisenmann & Sondaar (1998) recognized "*Hipparion*" *longipes* Gromova (1952) from the Pliocene locality of Çalta, Türkiye citing the long mt3 and 1ph3. Koufos & Vlachou (2005) reported two "*Hipparion*" cf. *longipes* cranial fragments from Akkaşdağı, Türkiye (7.1 Ma). The Akkaşdağı maxillae had P2-M3 dimensions of 162.5 and 169.9 mm and were greater than Pikermi *Hippotherium brachypus* dimensions that range from 147.0-154.9 mm. Akkaşdağı "*Hipparion*" cf. *longipes* is remarkable for its very elongate third metapodials: mc3 length mean = 249.04 mm, with a range of 246.4–253.1 mm (n=11) and mt3 with length mean of 284.4 mm., minimum length of 275.5 mm, maximum length of 302.0 mm (n=15). Vlachou & Koufos (2005) remarked that few things are known about the typical morphology of "*H.*" *longipes*. The maxillary cheek teeth of "*H.*" *longipes* from Pavlodar are characterized by a large size, a short and wide protocone and moderate enamel plication. The metapodials are extremely elongated and quite slender (Gromova, 1952). Bernor & Sen (2017) reevaluated the Çalta hipparions recognizing a larger, more robust limbed form *Proboscidipparion heintzi* for a juvenile partial skull with highly retracted nasals and short, robustly built metapodials, and re-assigned the "*Hipparion*" *longipes* attribution of Eisenmann & Sondaar (1988) to *Plesiohipparion longipes*, having very elongate mt3 and 1ph3s (Bernor & Sen 2017). The age of the Çalta *Plesiohipparion* is correlative with the medial Ruscinian, ~4.0 Ma. Bernor et al. (2022) identified *Plesiohipparion* cf. *longipes* from Baynunah, UAE based on an almost complete mt3 and estimated its age as 7.1 Ma following the age of Akkaşdağı, Türkiye (Vlachou & Koufos, 2009).

MORPHOMETRIC AND STATISTICAL ANALYSES

Principal Component Analyses

Figure 8 illustrates the results of the PCA on the crania. PC1 accounts for 48.8% of the entire variability, whereas PC2 for 31.1%. The summary of the variance components and the loadings distribution are reported in Supplementary Table 3. PC1 separates specimens with longer upper cheek tooth rows from positive (smaller) to negative (larger) values. Positive PC2 values cluster specimens with longer POF (M33) and taller POF (M35), whereas negative PC2 values cluster specimens with more elongated POB (M32) and reduced POF (higher values of M36). The PCA defines 3 morphospaces: one for *Cremohipparion*, characterized by positive values of PC1 and negative-to-positive PC2 values; one comprising *Hippotherium* species, characterized by negative values of PC1 and positive PC2; one comprising *Cormohipparion* and *Hipparion* s.s., characterized by lower-positive to negative values of PC1 and PC2.

Most of the crania from the Kayseri localities plot close to the *Hipparion dietrichi* (38-YAM/367 from Hırka 1, 38-YAM/423 from Hırka 1 and 38-YAM/579 from Çevril 1), whereas two specimens are separated from them. 38-YAM/115 from Çevril 1 is placed between the range of variability defined by *Hipparion prostylum – Hipparion dietrichi* and the *Cremohipparion* spp. However, given its extension of the POF we ascribe it to *Cremohipparion moldavicum*, even if it shows a longer POB than the *Cremohipparion moldavicum* average. 38-YAM/564 from Çevril 1 is plotted between the range of *Cremohipparion*, *Hipparion* and *Hippotherium*. The cranium exhibits a short POB similar to *Cremohipparion*, and a large POF, larger than in *Cremohipparion mediterraneum – Cremohipparion moldavicum* but smaller than in *Cremohipparion proboscideum*. Moreover, the position of the nasals is more retracted than in the skulls of *Cremohipparion mediterraneum – Cremohipparion moldavicum*, but still not as elongated as in *Cremohipparion proboscideum*. For these anatomical features, and for its position in the plot in Figure 7, we refer this specimen to *Cremohipparion* aff. *proboscideum*, suggesting an affinity with *Cremohipparion proboscideum* from Samos although not having the same derived morphology.

Concerning the other taxa, the other two Turkish species *Cormohipparion cappadocium* and *Cormohipparion sinapensis* are included in the range of variability defined by the North American *Cormohipparion fricki* Woodburne, 2007 (MacAdams Quarry), *Cormohipparion occidentale* (Xmas Quarry) and *Cormohipparion matthewi* Woodburne, 2007 (Xmas Quarry), whereas *Cormohipparion sofularensis* is still the largest *Cormohipparion* species, placed close to *Cormohipparion africanum* from Bou Hanifia and close to the *Hippotherium* variability. *Cormohipparion sinapensis* likewise occupies a space very close to *Hipparion* s.s. (*Hipparion dietrichi, Hipparion gettyi* and *Hipparion prostylum*).

The range of variability of *Hipparion dietrichi* from Samos Quarry 1 includes specimens referred to *Hipparion dietrichi* from Samos Quarry 4 (AMNH22860) and *Hipparion* sp. from Quarry 6 (AMNH22990) and they collectively show a great range of variability for PC1. The type cranium of *Hipparion gettyi* from Lower Maragheh is included in this range of variability, whereas *Hipparion prostylum* from Mt. Luberon, France (NHMUKPVM26617, NHMUKPVM 33603, UCBL-FSL 590001, MNHNL156), plots close to the smallest *Hipparion dietrichi* from Samos (AMNH20626, AMNH20692, AMNH94905) and has all positive values for PC1. The

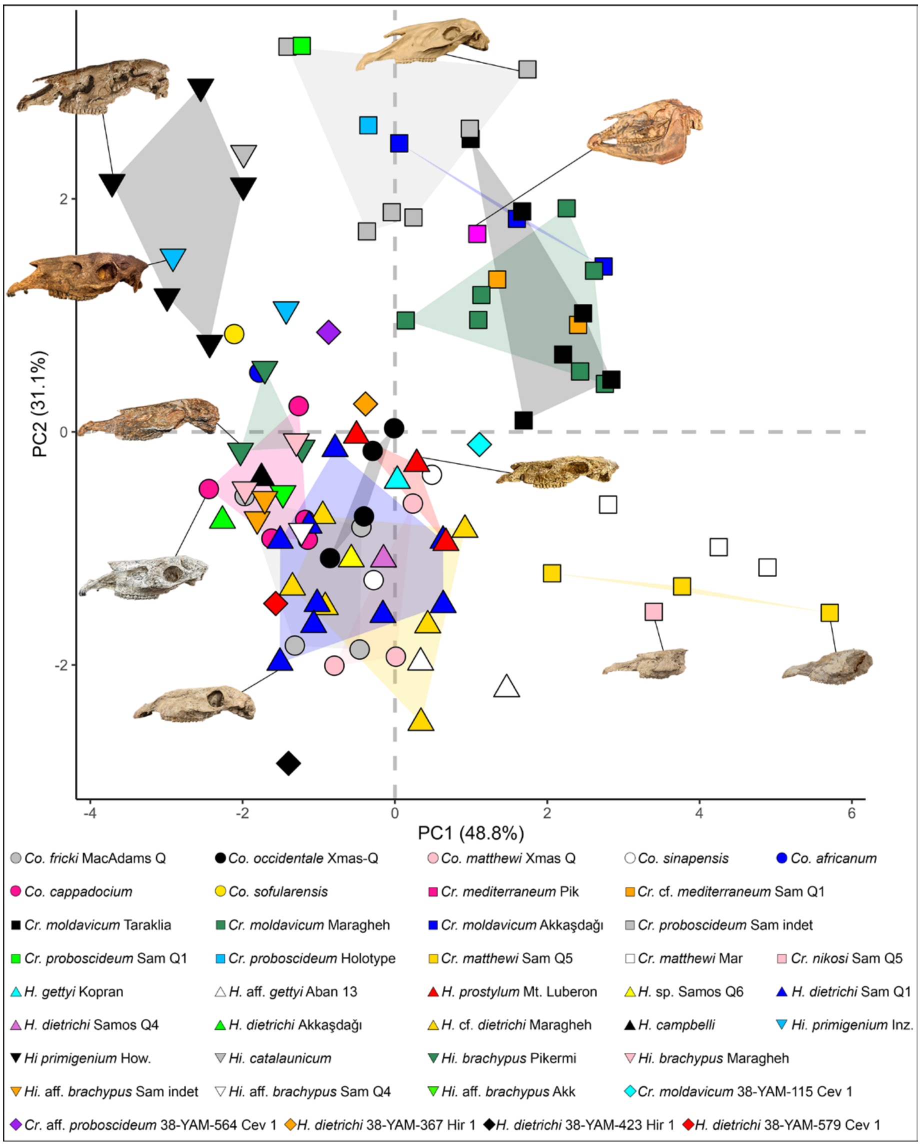

Fig. 8 - Results of the Principal Component Analysis (PCA) on crania. Abbreviations: Q: Quarry; Pik: Pikermi; Sam Q1; Samos Q1; Sam indet; Samos indeteminate; Sam Q5: Samos Q5; Mar: Maragheh; Mt. Luberon: Mount Luberon; Inz; Inzersdorf; How: Höwenegg; Cev 1: Çevril 1; Hir 1: Hırka 1; *Co.*: *Cormohipparion*; *Cr.*: *Cremohipparion*; *H.*; *Hipparion*; *Hi.*: *Hippotherium*.

range of variability of *Hipparion dietrichi* and *Hipparion prostylum* includes also six incomplete crania from Middle Maragheh (JGUMMB102, JGUMMB67, MNHN18, MNHNMar1171, MNHNMar1474, MNHNMAR1475), here referred to *Hipparion* cf. *dietrichi*. This identification is based on the results on cranial and postcranial elements (Figs. 9-12). Crania from Aban 13, Lower Maragheh (Bernor et al. 2024: PRCI-M1014 and PRCI-M1015) referred to *Hipparion* aff. *gettyi* plot close to *Hipparion prostylum*, and they are included in the morphospace defined by the genera *Cormohipparion* and *Hipparion* s.s.

Hippotherium primigenium from Inzersdorf and *Hippotherium catalaunicum* plot within the range of variability of *Hippotherium primigenium* from Höwenegg. *Hippotherium catalaunicum* overlaps with Höwenegg *Hippotherium primigenium*, supporting their close evolutionary relationship. *Hippotherium brachypus* from Pikermi (NHMUKM11178, NHMUKM11179, NHMUKM11191) and *Hippotherium* aff. *brachypus* from Samos Q4 (AMNH22838), non-specified quarries in Samos (AMNH10732, NHMWA4740) and from Akkaşdağı (Koufos & Vlachou 2005) are separated from the range of variability of *Hippotherium primigenium*, due the reduction of the POF (M33, M35). This range of variability includes also two incomplete crania from Middle Maragheh.

The range of variability of *Cremohipparion moldavicum* from Taraklia (PIN 1256-2878, PIN 1256-3639, PIN 1256-3648, PIN 1256-2882, PIN 1256-6854) includes *Cremohipparion moldavicum* from Maragheh (NHMUK3924, KNHM8402, MNHN7915, MNHN8402, MNHN8403, MNHNMar3428, MNHNMar466) and *Cremohipparion moldavicum* from Akkaşdağı (Koufos & Vlachou 2005), *Cremohipparion mediterraneum* from Pikermi (MNHNP259) and

Cremohipparion cf. *mediterraneum* from Samos Q1 (AMNH20628, AMNH94906). *Cremohipparion matthewi* from Samos Q5 and Maragheh and *Cremohipparion nikosi* from Samos Q5 are the smallest of the entire sample, separated from the cluster of *Cremohipparion moldavicum – Cremohipparion mediterraneum*. *Cremohipparion proboscideum,* including the holotype (Bern46), a suite of crania from non-specified quarries in Samos (SENK7878, SENK7883, SENKM4706, SENKM4708, SENKM4709, SMNSFAKrupp1895) and a cranium from Samos Q1 (AMNH20594), is separated from *Cremohipparion moldavicum – Cremohipparion mediterraneum*, characterized by its larger size and larger POF.

Figure 9 illustrates the PCA results on mc3s. These results are illustrated for the selected genera: A, *Hippotherium*; B, *Hipparion* s.s.; C, *Cremohipparion*, D, *Plesiohipparion*. PC1 accounts for 73.6% of the variance, and PC2 for 10.1%. The summary of the variance components and the loadings' distribution are reported in Supplementary Table 3. PC1 clusters specimens by size from smaller (positive values) to larger ones (negative values), whereas PC2 separates the specimens by their elongation, from shorter specimens in positive values to more elongated ones in negative values. *Hippotherium brachypus* from Hırka 1 (38-YAM/362) is plotted close to the range of variability shown by *Hippotherium brachypus* from Pikermi, which includes also the samples from Maragheh and Sofular. *Hippotherium brachypus* strongly overlaps with *Hippotherium primigenium* from Höwenegg and Eppelsheim, whereas the sample from Inzersdorf shows narrower dimensions. The *Hippotherium* populations from Samos (Q1 and Q4) and from Akkaşdağı shows a stouter morphology, and they are well separated from the other populations of *Hippotherium brachypus*. For this reason, we refer them to *Hippotherium* aff. *brachypus* (Fig. 9A).

Three specimens from Çevril 1 (38-YAM/119, 38-YAM/573, 38-YAM/593) and two from Hırka 1 (38-YAM/360, 38-YAM/500) are included in the *Hipparion dietrichi* variability from Samos Q1, Middle Maragheh, Akkaşdağı and Sofular (Fig. 9B). The *Hipparion dietrichi* samples from Samos Q1 and Akkaşdağı overlap extensively and include in their variability the population from Middle Maragheh. The *Hipparion dietrichi* populations from Samos Q1, Akkaşdağı and Middle Maragheh are well separated from *Hipparion prostylum* (Mt. Luberon), which has a more slender and gracile morphology (Fig. 9B).

One specimen from Hırka 1 (38-YAM/209) is included in the *Cremohipparion moldavicum* variability. *Cremohipparion matthewi* (Maragheh and Samos Q5) and *Cremohipparion nikosi* are the smallest species of the dataset, well separated from *Cremohipparion moldavicum* and *Cremohipparion mediterraneum* (Fig. 9C).

Plesiohipparion longipes from Akkaşdağı and Pavlodar have the most elongated morphology of the entire dataset, more elongated than *Hipparion dietrichi*, and three specimens from Hırka 1 (38-YAM/443, 38-YAM/491, 38-YAM/507) are included in their ranges of variability (Fig. 9D).

Figure 10 illustrates the PCA results on mt3s for the selected genera: A, *Hippotherium*; B, *Hipparion* s.s.; C, *Cremohipparion*, D, *Plesiohipparion*. PC1 accounts for 71.4% of the variance, whereas PC2 accounts for 8.3%. The summary of the variance components and loadings distributions are reported in Supplementary Table 3. PC1 clusters specimens by size from smaller (negative values) to larger ones (positive values), whereas PC2 separates the specimens by their elongation, from shorter specimens with positive values to more elongated ones in negative values.

Hippotherium brachypus is represented by two specimens from Hırka 1 (38-YAM/432, 38-YAM/486) and one from Taşhan 2 (38-YAM/245). They are plotted within the range of variability shown by *Hippotherium brachypus* from Pikermi, which includes also the samples from Maragheh and Sofular. *Hippotherium brachypus* strongly overlaps with *Hippotherium primigenium* from Höwenegg and Eppelsheim, whereas the sample from Inzersdorf has narrower dimensions. The *Hippotherium* populations from Samos (Q1 and Q4) and from Akkaşdağı has a stouter morphology, and they are well separated from the other populations of *Hippotherium brachypus*. For this reason, we support our attribution to *Hippotherium* aff. *brachypus* (Fig. 10A).

Five specimens from Çevril 1 (38-YAM/117, 38-YAM/554, 38-YAM/575, 38-YAM/633, 38-YAM/674), eight from Hırka 1 (38-YAM/200, 38-YAM/210, 38-YAM/412, 38-YAM/455, 38-YAM/456, 38-YAM/461, 38-YAM/473, 38-YAM/517) and one from Taşhan 2 (38-YAM/73) are included in the variability for Samos Q1 *Hipparion dietrichi*, Middle Maragheh, Akkaşdağı and Sofular (Fig. 10B). The *Hipparion dietrichi* samples from Samos Q1 and Akkaşdağı overlap extensively and include in their variability the population from Middle

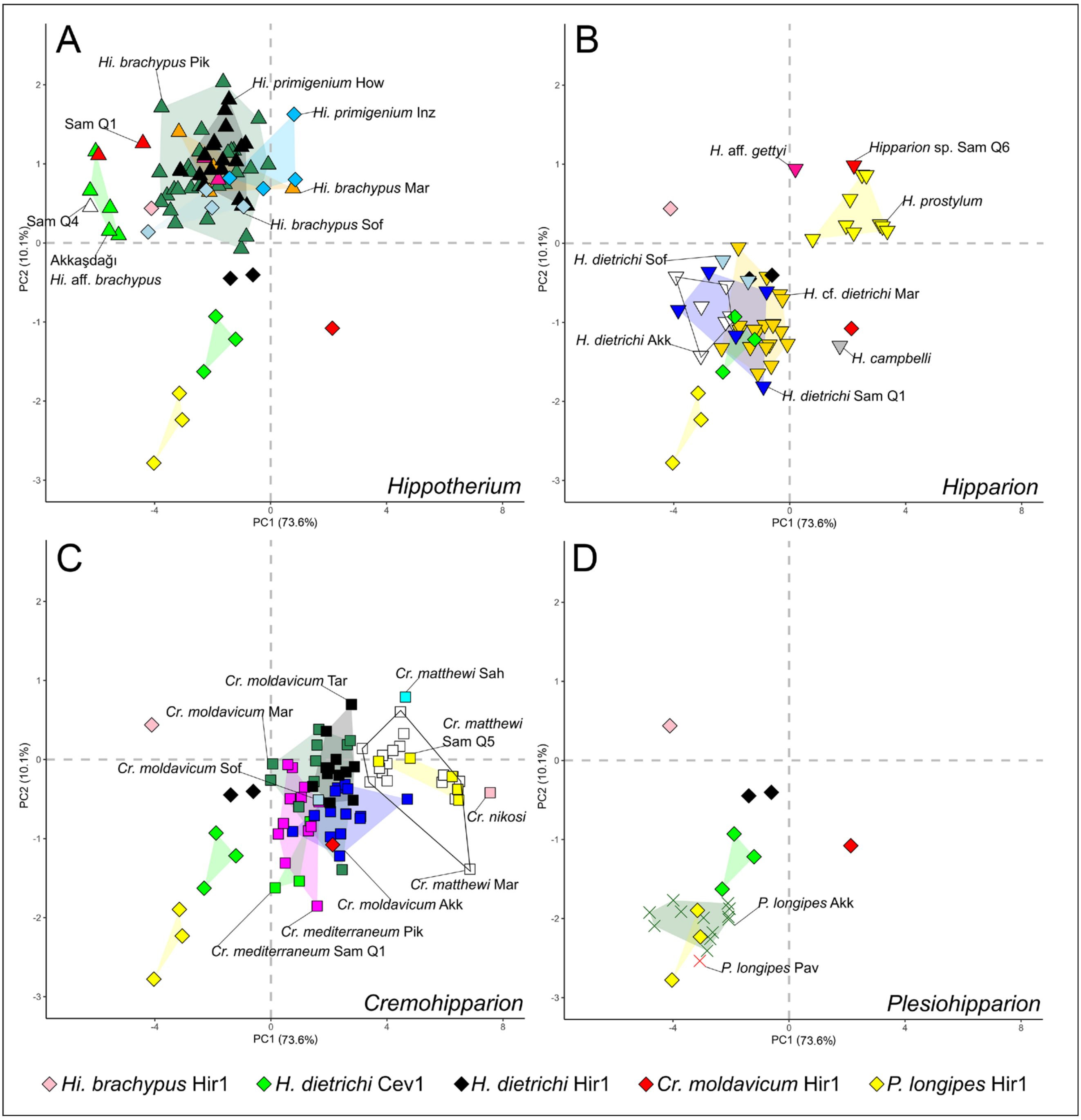

Fig. 9 - Results of the Principal Component Analysis (PCA) on third metacarpals. A) *Hippotherium*. B) *Hipparion* sensu strictu. C) *Cremohipparion*. D) *Plesiohipparion*. Abbreviations: Pik: Pikermi; Sam Q1; Samos Q1; Sam indet; Samos indeteminate; Sam Q5: Samos Q5; Mar: Maragheh; Sof: Sofular; Akk: Akkaşdağı; Sah: Sahabi; Tar: Taraklia; Pav; Pavlodar; Mt. Luberon: Mont Luberon; Inz; Inzersdorf; How: Höwenegg; Cev 1: Çevril 1; Hir 1: Hırka 1.

Maragheh. The *Hipparion dietrichi* populations from Samos Q1, Akkaşdağı and Middle Maragheh are well separated from *Hipparion prostylum* (Mt. Luberon), which has a more slender and gracile morphology (Fig. 10B).

One specimen from Hırka 1 (38-YAM/274) and seven from Çevril 1 (38-YAM/553, 38-YAM/559, 38-YAM/565, 38-YAM/577, 38-YAM/650, 38-YAM/658, 38-YAM/665) are included in the *Cremohipparion moldavicum* variability, including the populations from Taraklia, Maragheh, Sofular and Akkaşdağı. *Cremohipparion matthewi* (Maragheh and Samos Q5) and *Cremohipparion nikosi* are the smallest species of the dataset, well separated from *Cremohipparion moldavicum* and *Cremohipparion mediterraneum*. *Cremohipparion proboscideum* from

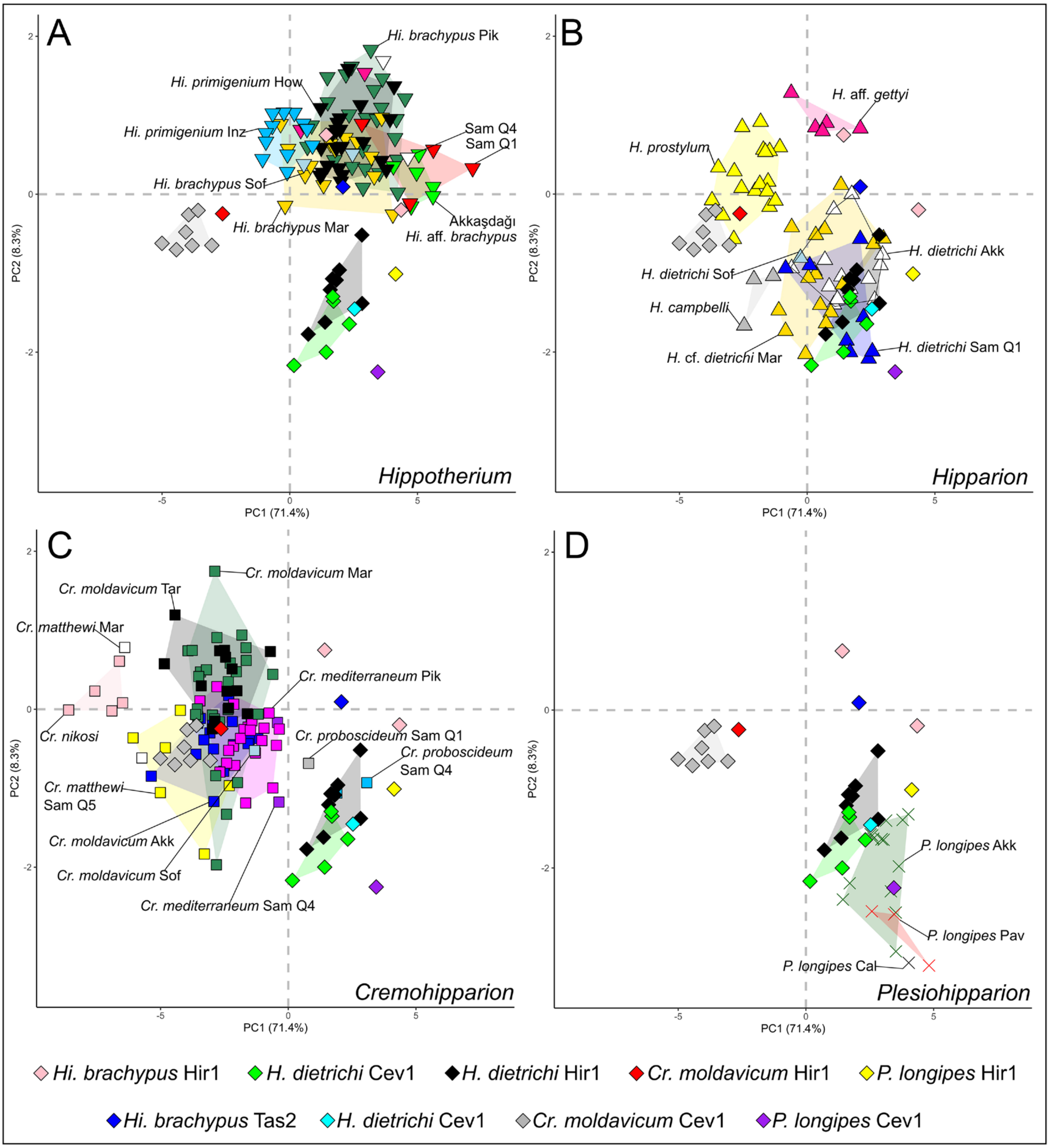

Fig. 10 - Results of the Principal Component Analysis (PCA) on third metatarsals. A) *Hippotherium*. B) *Hipparion* sensu strictu. C) *Cremohipparion*. D) *Plesiohipparion*. Abbreviations: Pik: Pikermi; Sam Q1; Samos Q1; Sam indet; Samos indeteminate; Sam Q5: Samos Q5; Mar: Maragheh; Sof: Sofular; Akk: Akkaşdağı; Sah: Sahabi; Tar: Taraklia; Pav; Pavlodar; Mt. Luberon: Mont Luberon; Inz; Inzersdorf; How: Höwenegg; Cal: Çalta; Cev 1: Çevril 1; Hir 1: Hırka 1; Tas 2: Taşhan 2.

Samos Q1 and Q4 are the largest among the *Cremohipparion* species, with dimensions similar to *Hipparion dietrichi* (Fig. 10C).

Plesiohipparion longipes from Akkaşdağı, Pavlodar and Çalta have the most elongated morphology of the entire dataset, more elongated than *Hipparion dietrichi*, and one specimen from Hırka 1 (38-YAM/435) and one from Çevril 1 (38-YAM/118) are included in their ranges of variability (Fig. 10D).

Log10 Ratio Diagrams

The mc3 Log10 Ratio diagrams comparing the Kayseri hipparion samples with a suite of *Hippotherium*, *Hipparion* s.s., *Cremohipparion* and *Ple-*

siohipparion species is illustrated in Fig. 11A–H. We use the Höwenegg skeletal sample as the standard Log10 mean for our mc3 and mt3 comparisons.

Figure 11A illustrates six samples of *Hippotherium* from Inzersdorf and Eppelsheim (*Hippotherium primigenium*) Pikermi and Samos (*Hippotherium brachypus* and *Hippotherium* aff. *brachypus*), Maragheh (*Hippotherium brachypus*) and Akkaşdağı (*Hippotherium* aff. *brachypus*). All *Hippotherium* species are similar in their large size. Mc3 length is similar or slightly larger in Samos Q1 and Akkaşdağı *Hippotherium* aff. *brachypus* and may warrant a new species designation. *Hippotherium primigenium* from Inzersdorf and Eppelsheim and *Hippotherium brachypus* compare closely to one another and show a slight "Eşme Akçaköy" effect similar to Sinap *Cormohipparion* wherein the midshaft log depth (M4) is greater than its log width (M3) (Bernor et al. 2003). This effect is more exaggerated in *Hipparion, Cremohipparion* and *Plesiohipparion* (Fig. 11C–H). These three samples track each other closely across all measurements and compare closely with the Höwenegg standard.

One mc3 from Hırka 1 (38-YAM/362) is referred to *Hippotherium brachypus* (Figure 11B). This specimen tracks very close to those in Fig. 11A.

Figure 11C illustrates six species of *Hipparion* mc3 from Iran (*Hipparion campbelli* and *Hipparion* cf. *dietrichi*, formerly *Hipparion* aff. *prostylum* Bernor, 1985), Samos Greece (*Hipparion dietrichi* Q5 and *Hipparion* sp. Q6), Akkaşdağı, Türkiye (*Hipparion dietrichi*) and Mt. Luberon, France (*Hipparion prostylum*). Much of the sample has longer mc3 than the Log10 mean except *Hipparion* sp. from Samos Q6 and the smaller and more gracile *Hipparion prostylum* from Mt. Luberon. All of these samples have narrower midshaft with dimensions (M3) than midshaft depth dimensions (M4; the "Eşme Akçaköy Effect"). Midshaft depth dimensions (M4) vary from being slightly greater (*Hipparion dietrichi* from Maragheh, Samos and Akkaşdağı) to less than these and Höwenegg. The same pattern persists, in general for proximal articular width (M5) and depth (M6). Distal supra-articular width (M10) and articular width (M11) vary from being closely similar to the Höwenegg standard to being substantially less (*Hipparion campbelli* and *Hipparion prostylum*). Distal articular measurements M12, M13 and M14 range on either side of the Höwenegg standard to substantially smaller in Samos Q6, *Hipparion prostylum* and Mt. Luberon *Hipparion prostylum.* Overall, the *Hipparion* s.s. sample tracks closely except for Samos Q6 *Hipparion,* Mt. Luberon *Hipparion prostylum* and Upper Maragheh *Hipparion campbelli* that are consistently slenderer limbed than the rest of the sample.

Four specimens from Hırka 1(38-YAM/208, 38-YAM/360, 38-YAM/490, 38-YAM/500), and three from Çevril 1 (38-YAM/119, 38-YAM/573, 38-YAM/593) are referred herein to *Hipparion dietrichi* (Fig. 11D). They compare most closely to the *Hipparion dietrichi* samples shown in Figure 11C.

Figure 11E illustrates ten samples of *Cremohipparion* from Samos (*Cremohipparion mediterraneum* Q1 and Q5, *Cremohipparion nikosi* Q5, *Cremohipparion matthewi* Q5), Pikermi (*Cremohipparion mediterraneum*), Maragheh (*Cremohipparion matthewi*), Sahabi (*Cremohipparion matthewi*), Akkaşdağı and Taraklia (*Cremohipparion moldavicum*). As a genus, *Cremohipparion* is characterized as having elongate and slender limbs. *Cremohipparion mediterraneum* (Samos Q1 and Pikermi) as well as *Cremohipparion moldavicum* (Maragheh and Tarkalia) have the longest (M1) mc3s. *Cremohipparion matthewi* and *Cremohipparion nikosi* are the smallest species with shorter M1 dimensions. Midshaft width (M3) is narrower than the depth dimensions (M4) exaggerating their "Eşme Akçaköy" effect. Proximal width (M5) and depth (M6) dimensions are small. Distal supra-articular width and distal articular width dimensions are less than the Höwenegg sample. While Pikermi *Cremohipparion mediterraneum* has distal articular dimension (M12 and M13) similar to the Höwenegg sample; all other *Cremohipparion* species have smaller size dimensions corresponding to overall smaller size of the species. Distal articular M14 dimensions are all less than the Höwenegg profile. As a genus, this plot demonstrates the elongate-slender morphology of *Cremohipparion* with *Cremohipparion mediterraneum* (Pikermi) and *Cremohipparion moldavicum* (Maragheh, Akkaşdağı and Taraklia) being larger than *Cremohipparion matthewi* and *Cremohipparion nikosi* from Samos, and *Cremohipparion matthewi* from Maragheh.

Figure 11F plots a single complete mc3 from Hırka 1, 38-YAM/209 which we refer to *Cremohipparion moldavicum.* This specimen compares closely with the *Cremohipparion moldavicum* samples from Maragheh, Taraklia and Akkaşdağı.

Figure 11G illustrates two samples of *Plesiohipparion longipes* (Akkaşdağı and Pavlodar) compared with Höwenegg *Hippotherium primigenium*. *Plesiohipparion longipes* shows an extremely elongated M1

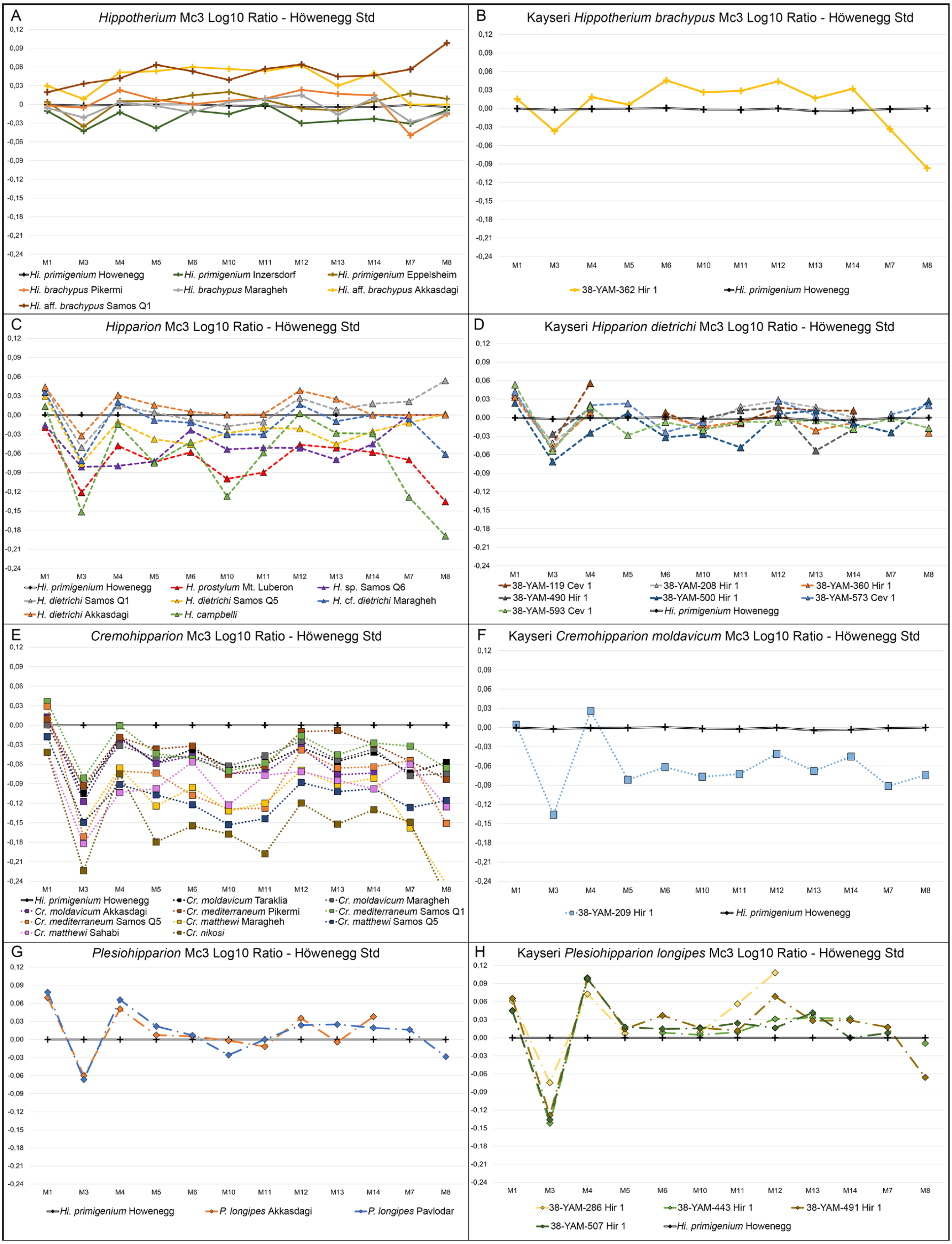

Fig. 11 - Log10 Ratio diagrams on third metacarpals. A) *Hippotherium* Mc3; B) Kayseri *Hippotherium brachypus* Mc3; C) *Hipparion*; D) Kayseri *Hipparion dietrichi* Mc3; E) *Cremohipparion* Mc3; F) Kayseri *Cremohipparion moldavicum* Mc3; G) *Plesiohipparion* Mc3; H) Kayseri *Plesiohipparion longipes* Mc3. Abbreviations: Cev 1: Çevril 1; Hir 1: Hırka 1.

dimension, and the midshaft width (M3) is narrower than the depth dimensions (M4). Proximal width (M5) and depth (M6) dimensions are slightly larger than the Höwenegg sample, whereas M10-M14 are larger than *Hippotherium primigenium*.

Figure 11H illustrates four mc3s from Hırka 1 (38-YAM/286, 38-YAM/443, 38-YAM/491, 38-YAM/507), which we refer to *Plesiohipparion longipes*. The pattern of these specimens closely tracks the *Plesiohipparion longipes* samples from Akkaşdağı and Pavlodar.

Fig. 12A–H are the mt3 Log10 Ratio diagrams comparing the Kayseri hipparion samples with a suite of *Hippotherium*, *Hipparion* s.s., *Cremohipparion* and *Plesiohipparion* species. The results of the mt3 Log10 ratio analyses closely follow those of mc3.

Hippotherium includes *Hippotherium brachypus* from Pikermi and Maragheh, *Hippotherium* aff. *brachypus* from Akkaşdağı, Samos Q1 and Q4 and *Hippotherium primigenium* from Inzersdorf and Eppelsheim (Fig. 12A). The largest species is *Hippotherium* aff. *brachypus* from Akkaşdağı, Samos Q1 and Q4; all dimensions are greater than the Höwenegg standard, but track the standard well except for elevated midshaft width, proximal articular depth and distal articular M12 measurement. *Hippotherium brachypus* from Pikermi is shorter than *Hippotherium* aff. *brachypus*, similar in midshaft width (M3) and depth (M4), shorter in proximal articular width (M5) and similar in proximal articular depth (M6) to Akkaşdağı, but smaller in dimensions M10–M14 than *Hippotherium* aff. *brachypus*. The early Vallesian sample from Inzersdorf has the most gracile build with short dimensions for M1–M14; in this regard it is closer to *Cormohipparion* than other *Hippotherium* samples (Bernor et al. 2003). The Eppelsheim sample has a shorter length (M1) has lower midshaft width (M3), depth (M4) and proximal articular width (M5) than the Höwenegg sample but the remaining measurements (M6–M14) are close to the Höwenegg sample. The Maragheh sample most closely tracks the Eppelsheim sample except for greater M4 and M5 dimensions.

Figure 12B illustrates one mt3 from Taşhan 2, (38-YAM/245) and two from Hırka 1 (38-YAM/432, 38-YAM/486) which we refer to *Hippotherium brachypus*. Their pattern closely tracks the *Hippotherium brachypus* samples illustrated in Figure 12A.

Hipparion s.s. includes three taxa (Fig. 12C) from Turkish, Iranian, Greek and French localities: *Hipparion campbelli* (Maragheh, Iran), *Hipparion dietrichi* (Akkaşdağı, Samos Q1 and Q5), *Hipparion* cf. *dietrichi* (Maragheh) and *Hipparion prostylum* (Mt. Luberon, France). *Hipparion campbelli* (Maragheh), *Hipparion* cf. *dietrichi* (Maragheh) and *Hipparion dietrichi* (Samos Q1 and Q5) essentially have the same length (M1) and have similar trajectories throughout the Log10 plot except *Hipparion campbelli* which has smaller dimensions of mid-shaft width (M3), midshaft depth (M4), proximal articular width (M5) and distal articular dimensions (M10–M14); it clearly has a more gracile build than the other hipparions. *Hipparion prostylum* (Mt. Luberon, France) has a shorter length (M1) and a more gracile build than *Hipparion dietrichi*, except for proximal articular depth (M6). *Hipparion prostylum* has M3-M6 dimensions that are smaller but that track *Hipparion dietrichi* from Akkaşdağı and Samos, while its M10-M14 dimensions are virtually identical to *Hipparion campbelli*.

Nine specimens from Hırka 1(38-YAM/299, 38-YAM/210, 38-YAM/412, 38-YAM/455, 38-YAM/456, 38-YAM/461, 38-YAM/473, 38-YAM/517, 38-YAM/73), and five from Çevril 1 (38-YAM/554, 38-YAM/575, 38-YAM/633, 38-YAM/674, 38-YAM/117) are referred herein to *Hipparion dietrichi* (Fig. 12D). They compare most closely to the *Hipparion dietrichi* samples shown in Figure 12C.

Cremohipparion includes *Cremohipparion mediterraneum* from Samos Q4 and Pikermi; *Cremohipparion matthewi* from Maragheh, Samos Q5 and Sahabi; *Cremohipparion moldavicum* from Maragheh, Taraklia and Akkaşdağı; *Cremohipparion nikosi* from Samos Q5; *Cremohipparion proboscideum* from Samos Q1 and Q4 (Fig. 12E). The largest *Cremohipparion* is *Cremohipparion proboscideum* from Samos Q1 and Q4; it has the longest mt3 (M1); it has the highest values of midshaft width (M3) and depth (M4), which are however less than the Höwenegg Log10 values. It has the same values for proximal articular width (M5), and distal articular dimensions (M10–M14) except distal measurement M12 which is slightly higher (Samos Q1 specimen). *Cremohipparion proboscideum* from Samos Q1 tracks the Q4 specimen but is smaller except for distal articular measurements M12–M14. The smallest hipparions, with the shortest length (M1), midshaft width (M3) and depth (M4) measurements as well as distal articular measurement (M10–M14) are Maragheh, Samos Q5 and Sahabi *Cremohipparion matthewi* and Samos *Cremohipparion nikosi*. The remaining

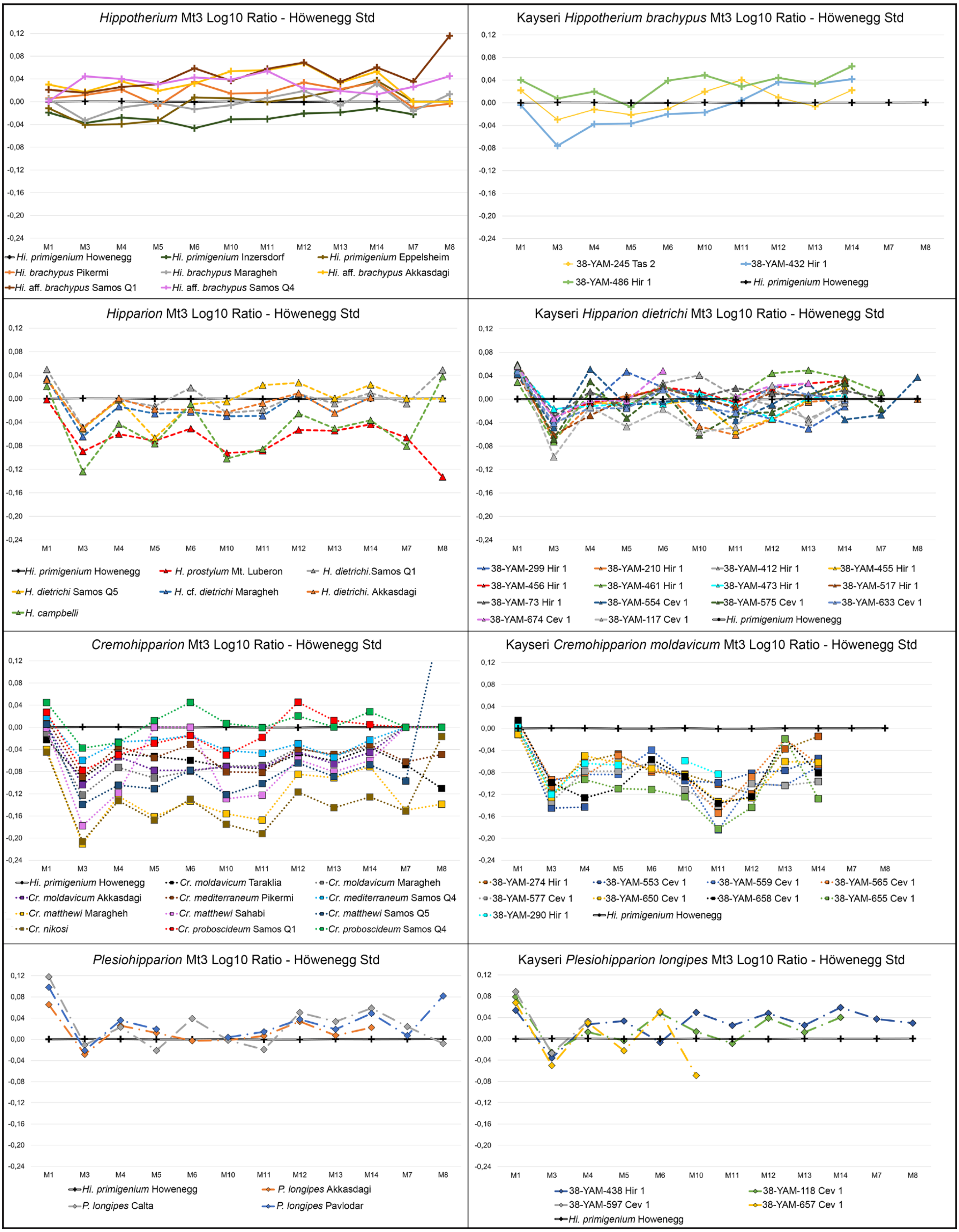

Fig. 12 - Log10 Ratio diagrams on third metatarsals. A) *Hippotherium*; B) Kayseri *Hippotherium brachypus*; C) *Hipparion* sensu strictu. D) Kayseri *Hipparion dietrichi*. E) *Cremohipparion;* F) Kayseri *Cremohipparion moldavicum*. G) *Plesiohipparion*; H) Kayseri *Plesiohipparion longipes*. Abbreviations: Cev 1: Çevril 1; Hir 1: Hırka 1; Tas 2: Taşhan 2.

plots intervening between *Cremohipparion proboscideum* and *Cremohipparion matthewi/nikosi* include *Cremohipparion mediterraneum* and *Cremohipparion moldavicum,* two closely related species (Bernor et al. 2016).

Two specimens from Hırka 1 (38-YAM/274, 38-YAM/290) and seven from Çevril 1 (38-YAM/553, 38-YAM/559, 38-YAM/565, 38-YAM/577, 38-YAM/650, 38-YAM/658, 38-YAM/655) are referred herein to *Cremohipparion moldavicum* (Fig. 12F). They compare most closely to the *Cremohipparion moldavicum* samples shown in Figure 12E.

Figure 12G illustrates three samples of *Plesiohipparion longipes* (Akkaşdağı, Pavlodar and Çalta) compared with *Hippotherium primigenium* from Höwenegg. *Plesiohipparion longipes* exhibits an extremely elongated M1 dimension, and the midshaft width (M3) is narrower than the midshaft depth dimensions (M4). Proximal width (M5) and depth (M6) dimensions are on the average of the Höwenegg sample, except for M6 of the Çalta samples, which is larger. M10-M14 are generally slightly larger than in *Hippotherium primigenium*.

Figure 12H illustrates one mt3 from Hırka 1 (38-YAM/438) and three from Çevril 1 (38-YAM/118, 38-YAM/597, 38-YAM/657) which we refer to *Plesiohipparion longipes*. The pattern of these specimens closely tracks the *Plesiohipparion longipes* samples from Akkaşdaği, Pavlodar and Çalta.

Overall, the outcomes of the PCAs and of the Log10 Ratio diagrams are very similar, strongly supporting the different morphotypes between the different genera, and supporting the presence of four different lineages in the Kayseri hipparion assemblages.

Discussion

The Kayseri three-toed horses and the hipparions from Maragheh and Samos

Five hipparion species have been identified from the Kayseri localities:

Çevril 1 (older than 7.74 Ma; Tholt et al. 2025; Meijers et al. 2018) has *Hippotherium brachypus*, *Hipparion dietrichi*, *Cremohipparion moldavicum*, *Cremohipparion* aff. *proboscideum*;

Taşhan 2 (older than 7.74 Ma; Tholt et al. 2025; Meijers et al. 2018) has *Hippotherium brachypus*, *Hipparion dietrichi* and *Plesiohipparion longipes*;

Hırka 1 (7.53–7.46 Ma; Tholt et al. 2025; Meijers et al. 2018) has *Hippotherium brachypus*, *Hipparion dietrichi*, *Cremohipparion moldavicum* and *Plesiohipparion longipes*;

The single adult and deformed cranium 38-YAM/564 from Çevril 1 is referred to *Cremohipparion* aff. *proboscideum* because of its short POB, high POF dimension and retracted nasals. Although its facial anatomy is not as derived as the *Cremohipparion proboscideum* skulls from Samos Q1 and Q4, it compares most closely to it.

Overall, the taxonomic composition of the Kayseri hipparion assemblage is similar to those from Maragheh, Iran (Bernor 1985; Steininger et al. 1996; Swisher 1996; Atabaadi et al. 2013; Bernor et al. 2016), and Samos, Greece (Kostopolous et al. 2003; Vlachou & Koufos 2009; Koufos et al. 2022). Campbell et al. (1980), Bernor (1985, 1986), Steininger et al. (1996), Bernor et al. (1980, 1996b), Swisher (1996) Atabaadi et al. (2013) and Bernor et al. (2016) have published their studies on Maragheh biostratigraphy, biochronology and radioisotopically based chronology. Swisher (1996) followed by Atabaadi et al. (2013) and Bernor et al. (2016) have summarized the chronology of the three Maragheh biozones: Lower Maragheh, 9.0–8.2 Ma; Middle Maragheh 8.2–8.0 Ma; Upper Maragheh 8.0–7.6 Ma. Biostratigraphic occurrences of the Hipparion fauna (Bernor 1985, 1986; Bernor et al. 1996b, 2016, 2021; Atabaadi et al. 2013) are:

Lower Maragheh: *Hipparion gettyi*;

Middle Maragheh: *Hipparion* aff. *prostylum* (here, *Hipparion* cf. *dietrichi*), *Cremohipparion moldavicum* and *Cremohipparion* ?*matthewi*;

Upper Maragheh: *Hipparion campbelli* and *Cremohipparion matthewi*.

While the Hipparion-bearing localities are very rich at Samos, the stratigraphy is complicated by short, highly tectonically fractured sections, as well as by competing opinions on the age of some Samos localities (Bernor et al. 1996a; Koufos et al. 2009, 2022). Koufos and his collaborators have undertaken a monumental study of the Samos faunas and reported a sequence ranging in age from 8.0–6.7 Ma. An initial discrepancy occurs in the chronology of the oldest stratigraphic levels, the “Old Mill Beds” (OMB). Weidman et al. (1984) extended the chronology downward as old as 8.57–8.38 Ma for Samos Locality G, 8.26–7.8 Ma for locality Samos Q6 and 8.57–8.0 Ma for Samos Qx, respectively.

These ages were followed by Bernor et al. (1996a). Subsequently, Swisher (1996) dated the OMB 8.38–8.28 Ma. Koufos et al. (2009) correlated the OMB with the Chron C4n.2n (8.0–7.6 Ma), including the Samos Qx but not Q6, which instead was placed in the upper part of the main fossiliferous beds, with a minimum age of 7.4 Ma (Koufos et al. 2009). Acknowledging these discrepancies, the proposed ages of Swisher (1996) for the OMB (including the localities G, Q6 and Qx) are used herein.

The revised stratigraphic and chronological context of the Samos localities from Koufos et al. (2009) includes:

Basal part of the Mytilinii Formation (~8.0–7.6 Ma; late MN11 – early MN12 of Hilgen et al. 2012), including the localities Qx and Vryssoula;

Lower part of the main fossiliferous beds (~7.65–7.45 Ma; MN12 of Hilgen et al. 2012), including the localities Mytilinii-4 (MLN in Koufos et al. 2009), the old Stefano Quarry and Q2;

Upper part of the main fossiliferous beds (~7.4–7.0 Ma; MN12 of Hilgen et al. 2012), including: Q6 (contra Weidman et al. 1984; Bernor et al. 1996b; Swisher 1996), with an estimated age of ~7.4 Ma; Mytilinii-3 (MYT in Koufos et al. 2009), Q3, S2-3 (localities from Solounias 1981) and Potamies from Forsyth-Major, with an estimated age of ~7.3 Ma, whereas according to Koufos et al. (2009) Q4 should be slightly younger; Mytilinii 1A-C (MTL, MTLA, MTLB, MTLC in Koufos et al. 2009), the Adriano Ravine and Q1, with an estimated age of 7.3–7.1 Ma (MN12 of Hilgen et al. 2012);

Uppermost part of the Mytilinii Formation, including the locality Q5 with an estimated age of 6.9–6.7 Ma, early MN13 of Hilgen et al. (2012) (Koufos et al. 2009).

After this subdivision, Koufos et al. (2009) and Vlachou & Koufos (2009) reported the following hipparion species from the different Samos stratigraphic horizons:

- Primary Mammal Assemblage of Samos (PMAS in Koufos et al. 2009), including the Qx and Vryssoula localities (~8.0–7.6 Ma; late MN11 – early MN12 of Hilgen et al. 2012), with *Hipparion prostylum* and *Cremohipparion proboscideum*.
- Intermediary Mammal Assemblage of Samos (IMAS in Koufos et al. 2009), including the localities Mytilinii-4, the Stefano Quarry, Q2 and Q6 (~7.65–7.45 Ma; MN12 of Hilgen et al. 2012), with *Hipparion prostylum*, *Cremohipparion proboscideum*, *Cremohipparion* cf. *matthewi* and "*Hipparion*" cf. *forstenae*.
- Dominant Mammal Assemblage of Samos (DMAS in Koufos et al. 2009), including the localities of Mytilinii 1A-C, the Adriano Ravine and Q1, (~7.3–7.1 Ma; MN12 of Hilgen et al. 2012), with *Hippotherium brachypus, Hipparion dietrichi*, *Cremohipparion* cf. *matthewi*, *Cremohipparion mediterraneum* and "*Hipparion*" cf. *forstenae*.
- Final Mammal Assemblage of Samos (FMAS in Koufos et al. 2009), including the locality Q5 (6.9–6.7 Ma, early MN13 of Hilgen et al. 2012), with *Hipparion dietrichi*, "*Hipparion*" cf. *forstenae*, and *Cremohipparion nikosi*.

Our results can provide new insights into the complicated equid guild of the different Samos localities (AMNH Samos collection).

From Q6, the cranium AMNH22990 and the third metacarpal AMNH140292 closely resemble *Hipparion prostylum* from Mt. Luberon. Although in Figure 8 the AMNH22990 is placed within the range of variability of the Samos Q1 *Hipparion dietrichi*, the attribution to the latter is unlikely, considering the morphological differences between them. AMNH140292 is placed close to the range of variability of *Hipparion prostylum* from Mt. Luberon (Figure 9B).

Our results for Samos Q4, show the presence of *Hipparion dietrichi* (Fig. 8), *Hippotherium* aff. *brachypus* (Fig. 8, 9A, 10A), *Cremohipparion proboscideum* (Fig. 10C) and *Cremohipparion mediterraneum* (10C)

Following our analysis, Samos Q1 has *Hipparion dietrichi* (Fig. 8, 9B, 10B), *Cremohipparion* cf. *mediterraneum* (Fig. 8, 9C), *Cremohipparion proboscideum* (Fig. 8, 10C) and *Hippotherium* aff. *brachypus* (Fig. 9A, 10A)

Following our analysis, Samos Q5 has *Cremohipparion matthewi* and *Cremohipparion nikosi* (Fig. 8, 9C, 10C).

The crania originally assigned to *Cremohipparion proboscideum* from Samos Qx (Vlachou & Koufos 2009) are not included in the analyses because of their incompleteness. However, the position of the nasals in AMNH20772 (Vlachou & Koufos 2009, fig. 10A) is not retracted as in the holotype of *Cremohipparion proboscideum* (Studer 1911, fig. 1). In AMNH20772 the nasal notch lies above the P2 mesostyle, as in the holotype of *Cremohipparion med-*

iterraneum, whereas in the holotype of *Cremohipparion proboscideum* the nasals are retracted up to the P4 mesostyle or the P4/M1 boundary (Studer 1911, fig. 1). A cranium with a morphology similar to the holotype of *Cremohipparion proboscideum* has been reported from Ravin de Zouaves 5 (~ 8.2 Ma, Koufos 2024). Whereas Vlachou & Koufos (2009) believe that nasal notch incision reduced in time, we believe that it increased in its depth overtime as did lengthening and narrowing of the snout. In our analyses on the crania (Fig. 8A), the *Cremohipparion proboscideum* holotype and the skull from Q1 are included in the range of variability of other *Cremohipparion proboscideum* skulls from Samos (indeterminate localities). Moreover, the extension of its range of variability mostly approaches those of other species from a single locality, as does *Hippotherium primigenium* from Höwenegg, *Cremohipparion moldavicum* from Maragheh, and *Hipparion dietrichi* from Samos Q1.

Vlachou & Koufos (2004) initially recognized *Hipparion* (= *Cremohipparion* of Bernor, 2021) *mediterraneum* which was reassigned "*Hipparion*" cf. *forstenae* by Vlachou & Koufos (2009). Later, Koufos et al. (2022) identified "*Hipparion*" aff. *forstenae* as a questionable determination. For the moment, we retain the nomen *Cremohipparion* cf. *mediterraneum* for the crania from Samos Q1, considering also their placement in Figure 8, close to the holotype of *Cremohipparion mediterraneum* from Pikermi.

Vlachou & Koufos (2009) reported the presence of *Hippotherium brachypus* from the Samos Dominant Mammal Assemblage (DMAS), and Koufos & Vlachou (2005) reported the same species from Akkaşdağı, Türkiye. Our analyses on third metapodials show that the *Hippotherium* samples from Samos Q1, Q4 and Akkaşdağı are not included in the range of variability of *Hippotherium brachypus* from Pikermi, having overall larger (more massive) dimensions. For this reason, we assign them to *Hippotherium* aff. *brachypus*, as also preliminary reported in Kahya-Parıldar et al. (2025). On the other hand, the *Hippotherium* samples from Middle Maragheh and Sofular are included in the range of variability of the Pikermi *Hippotherium brachypus* (Figs. 9A, 10A).

Our findings on *Hipparion dietrichi*, *Cremohipparion matthewi* and *Cremohipparion nikosi* are in broad agreement with those of Vlachou & Koufos (2009) and Koufos et al. (2009). However, our results highlight a close similarity between the classic *Hipparion dietrichi* sample from Samos Q1 and those from Middle Maragheh, Sofular, Samos Q4 and Akkaşdağı, underlying the need for reconsideration of these samples to identify their evolution from *Hipparion prostylum* (Bernor 1985; Ataabadi et al. 2013; Bernor et al. 2016, 2021).

Paleoclimatic context of the Kayseri hipparion horses

Our hypsodonty-based paleoclimatic reconstruction of the Kayseri localities documents the transition from more closed to more open environments in Western Eurasia between MN10, MN11, and MN12. These assemblages reflect the provincial faunal response to progressive climate-driven aridification and the expansion of Subparatethyan open-country communities characterized by diverse equids, rhinocerotids, bovids, giraffids, hyaenids, felids, and proboscideans. In this broader framework, the Kayseri faunas show clear affinities with the early–middle Turolian "Old World Savanna Paleobiome (OWSP)" assemblages of Pikermi, Samos, and Maragheh (Bernor 1983, 1984; Eronen et al. 2009; Kaya et al. 2018; Bernor et al. 2021). Although mid-Turolian Pikermi has long been interpreted as a mixed woodland–grassland system trending toward increased aridification prior to the Messinian Salinity Crisis, hipparionines are not straightforward indicators of fully developed grass–dominated savannas. Consequently, the expansion of hypsodont equids does not necessarily imply the establishment of open grassland ecosystems. Even the more robust and hypsodont members of the *Hippotherium* complex were more gracile than modern equids and likely retained substantial browsing capacities (Bernor et al., 1999). Likewise, although C_3/C_4 isotopic proxies (Böhme et al., 2017) document shifts in vegetation composition, these may reflect changes within structurally heterogeneous open–canopy woodland systems rather than wholesale biome replacement.

Within this more nuanced framework, well-documented regional differences across the Pikermian biome suggest that the Yamula reservoir sites in Kayseri occupied a distinct ecological position. Saarinen and Liu (2024) demonstrated that Pikermi reflects slightly more humid, productive, and less grass–dominated conditions than Maragheh, consistent with earlier interpretations (e.g., Kurtén 1952), a distinction also mirrored in the absence of small grazing *Cremohipparion* at Pikermi. In Kayseri,

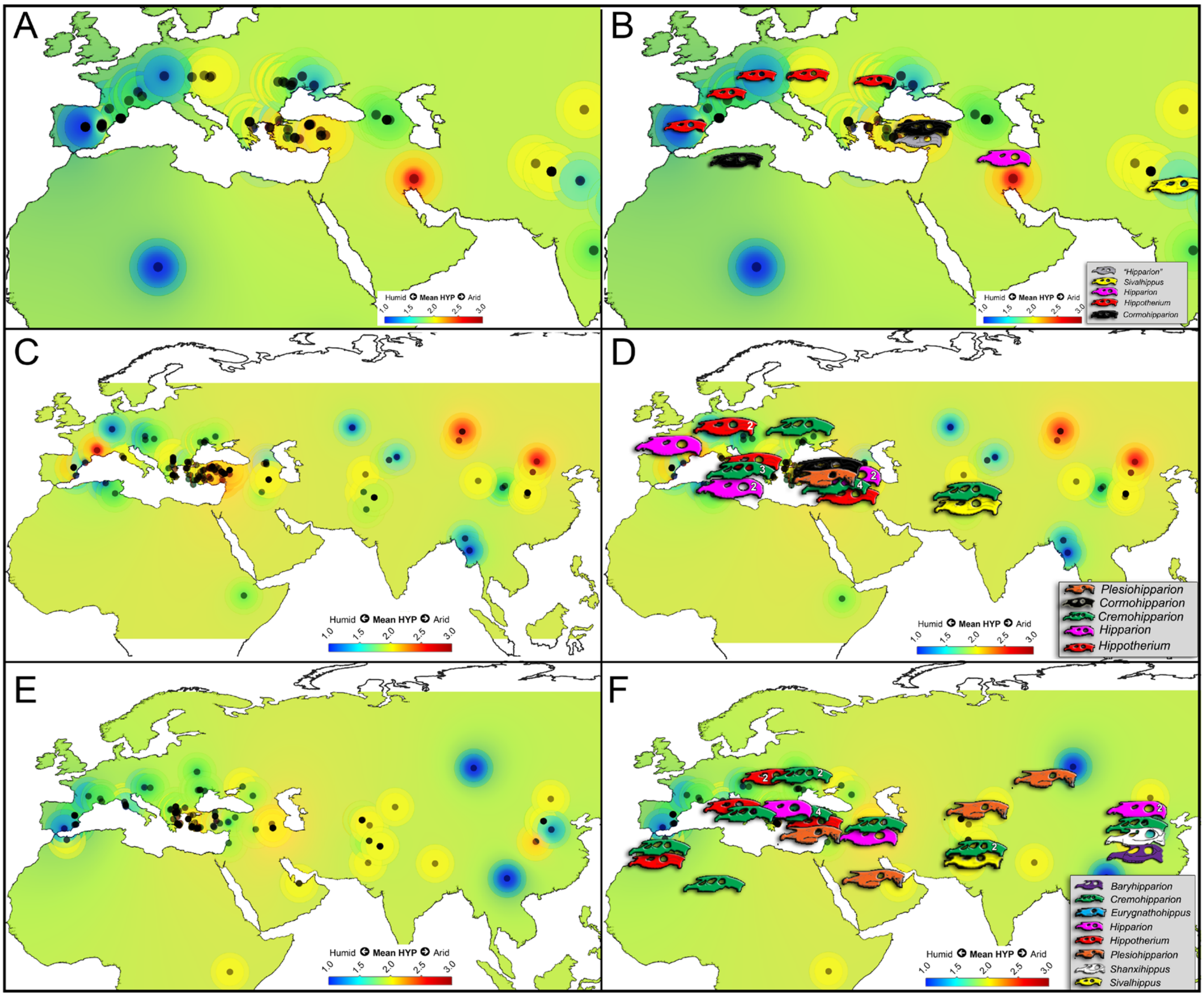

Fig. 13 - Paleoclimatic maps for MN10 (9.9–8.9 Ma, A–B), MN11 (8.9–7.6 Ma, C–D) and MN12 (7.6–6.8 Ma, E–F) Units (sensu Hilgen et al. 2012) showing the paleoenvironmental changes and the radiation of the hipparion horse lineages from the late Vallesian to the early–middle Turolian in Eurasia and in the Subparatethyan bioprovince (sensu Bernor, 1983, 1984 and Bernor et al., 2021). A: MN10 paleoclimatic maps without hipparion lineages; B: MN10 paleoclimatic maps with hipparion lineages; C: MN11 paleoclimatic maps without hipparion lineages; D: MN11 paleoclimatic maps with hipparion lineages; E: MN12 paleoclimatic maps without hipparion lineages; F: MN12 paleoclimatic maps with hipparion lineages.

the absence of small *Cremohipparion* species (e.g., *C. matthewi*), together with the dominance of more open–adapted hipparions such as *Hipparion dietrichi* and *Plesiohipparion longipes*, supports the interpretation that environmental conditions differed from both Pikermi and Maragheh. Rather than representing a simple intermediate along a gradient of grassland expansion, Kayseri likely reflects a structurally open yet ecologically complex mosaic system (less grass-dominated than Maragheh but more open than Pikermi) thereby reinforcing the view that the OWSP was heterogeneous, dynamic, and regionally differentiated.

CONCLUSIONS

The Kayseri hipparion-bearing localities are derived from radiometrically dated fluvial and lacustrine deposits along the shores of the Yamula Reservoir in Cappadocia, (Türkiye), from the localities of Çevril (1 and 2), Taşhan (1 and 2) and Hırka with an age range of ~7.74–7.48 Ma, which can be correlated to the late MN11 - early MN12 European Mammal Neogene Units (Hilgen et al. 2012). Çevril (1 and 2), Taşhan (1 and 2) and Hırka fill the gap with the older Middle Maragheh (Iran) and Sofular (Türkiye) (MN11 of Hilgen et al. 2012) localities, and with the more recent Samos Q1, Q4 and Q5 (Greece) and Akkaşdağı (Türkiye) (MN12 to early MN13 of Hilgen et al. 2012) localities. The Yamula Reservoir localities retain previously identified taxa *Hippotherium brachypus*, *Cremohipparion moldavicum*, and *Hipparion dietrichi* from Middle Maragheh and Sofular, but reveal the earliest occurrence of *Plesiohipparion longipes*, previously reported from the localities of Akkaşdağı (Koufos & Vlachou, 2005), Pavlodar (Kazakhstan; Gromova, 1952) and Baynunah, UAE (Bernor et al. 2022), Çalta (Türkiye; Bernor & Sen 2017). However, contrary to Akkaşdağı and Samos Q1, Q4 and Q5, the Kayseri localities do not include the larger *Hippotherium* (here *Hippotherium* aff. *brachypus*; Samos Q1, Q4 and Akkaşdağı) and the dwarf *Cremohipparion matthewi* and *Cremohipparion nikosi* (Samos Q5). The Kayseri assemblages capture a key phase of Late Miocene environmental change in Western Eurasia and display strong similarities to Turolian faunal communities associated with the OWSP. Nevertheless, the faunal structure marked by the prevalence of *Hipparion dietrichi, Cremohipparion moldavicum* and *Plesiohipparion longipes* and the absence of dwarf *Cremohipparion* indicates that the region likely supported a relatively open but ecologically heterogeneous landscape, underscoring that the OWSP consisted of regionally variable mosaic habitats rather than a uniform grass-dominated savanna.

Data Availability Statement: The data supporting the results of this research are available upon request. Interested researchers may contact the corresponding Author to obtain access.

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