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CORMOHIPPARION SOFULARENSIS N. SP., A NEW HIPPARION SPECIES FROM THE LATE MIOCENE OF SOFULAR (TÜRKİYE, EARLY TUROLIAN)

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Abstract. In this contribution, we study the hipparion remains from the Early Turolian locality of Sofular, Türkiye. We identify the presence of a new species, *Cormohipparion sofularensis*, with three other taxa which we refer to *Hippotherium brachypus*, *Hipparion dietrichi* and *Cremohipparion moldavicum*. We compare these taxa with other Late Miocene hipparions from Iran, Türkiye, Greece, Moldova, Austria, Germany, France, Spain, Algeria and Libya, by morphologic and morphometric comparisons of crania, mandibles, maxillary and mandibular dentitions, third metacarpals and third metatarsals to further evaluate the morphological and systematic comparisons. Recently, the Sofular locality has been dated radioisotopically to 8.422±0.34 Ma, correlative with early MN11 (Early Turolian) faunas in our comparisons. The Sofular hipparions record the early evolutionary radiation of hipparion lineages in the Subparatethyan Province. Our analyses further reveal that Sofular *Cormohipparion sofularensis* is the youngest member of the genus *Cormohipparion* reported from Eurasia and Africa and is found to be derived in skull morphology compared to the Late Vallesian *Cormohipparion cappadocium* from Yeniyaylacık, Türkiye.

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Introduction

The Sofular fossil vertebrate localities are situated in the Central Anatolian Volcanic Complex (CAVP), close to the Sofular village, part of the Ürgüp town in Nevşehir (Fig. 1A,B and C). These localities are located on the eastern slope of the Kışlacık Stream, approximately 3 kilometers from the village, which flows into the Kızılırmak River Valley. The area lies at an elevation of about 930 meters above sea level. The fossil localities were first discovered in 2011 by our research team within the framework of the "Nevşehir Province Miocene Vertebrate Fossil Research" project (Başoğlu 2017). The fossil-bearing layer extends horizontally over an area of approximately 4 square kilometres and has an average thickness of 1 to 1.5 meters. The fossils are found in situ in Late Miocene fluvial deposits, suggesting a low flow velocity fluvial depositional environment. This also indicates that the fossils were transported only short distances.

Systematic excavations at Sofular have been ongoing since 2014. These excavations have revealed a remarkably rich and diverse vertebrate fauna (Başoğlu 2017). The fossil assemblage includes representatives of Artiodactyla, Perissodactyla, Proboscidea, Carnivora, Primates, Testudines, Aves, and Tubulidentata. The diversity is particularly notable amongst the Bovidae and Equidae. Notably, species such as *Gazella* sp., *Miotragocerus* sp. and *Nisidorcas* sp. from the Bovidae family highlight this diversity. In addition to these, other significant artiodactyls and perissodactyls include *Samotherium* sp., *Hippopotamadon* sp., *Miodiceros* sp., *Acerorhinus* sp., *Chilotherium* sp., the proboscidean species *Choerolophodon pentelici*, the large carnivore *Amphimachairodus* sp. and various hyenas also occur at Sofular. Turtles belong to the reptilian group, while members of the family Ciconiidae represent the avian fauna.

Geological setting

Türkiye, situated at the tectonically active crossroads of continents, hosts several major fault zones, including the North Anatolian, East Anatolian, Central Anatolian, and Bitlis-Zagros Suture zones, all formed as a result of the Arabia-Eurasia collision (Fig. 1A). This dynamic tectonic activity has shaped adjacent plateaus within the Anatolian landscape (Fig. 1A) (Bernor et al. 2024). These plateaus are bordered by varied geographical features, such as the high-elevation, low-relief Pontide Mountains to the north, the Anatolide-Tauride Mountains to the south, and the towering Eastern Anatolian Mountains to the east. Located near the central part of the Central Anatolian Plateau (CAP), the Cappadocia region is distinguished by widespread volcanic formations from the Late Miocene, Pliocene, and Quaternary periods (Aydar et al. 2012; Ciner et al. 2015). Together, these deposits form the unique landscape of the Central Anatolian Volcanic Province, which encompasses a region of exceptional topographical beauty.

The geology of CAVP is well known, although there are still geochronological issues regarding the identification of ignimbrite layers and dating of fossil mammal localities (Aydar et al. 2012; Tholt et al. 2025). One of these is the lack of a common discourse about the Sofular Ignimbrite in the Ürgüp Formation (Aydar et al. 2012; Piper et al. 2013; Lepetit et al. 2014). The Sofular Ignimbrite, first described by Pasqueré (1968), takes its name from the Sofular Village of Ürgüp. This ignimbrite, defined as a local unit, consists of a 1 m thick pumice deposit formed by pyroclastic precipitation at the base and an ignimbrite with a thickness of up to 25 m formed by a single flow on top of it (Aydar et al. 2012). The Sofular fossil area is located within the fluvial deposits called the Aksalur conglomerate member between the Topuzdağı Lava and the Sofular Ignimbrite (Piper et al. 2013; Lepetit et al. 2014; Mouralis & Aydar 2019; Doğan & Şenkul 2020). In the $^{40}Ar/^{39}Ar$ dating analysis, it is correlated as being 8.17 ± 0.16 million years (Aydar et al. 2012). In the K/Ar dating method evaluated by Innocenti et al. (1975), the correlation was 6.8 ± 1.4 million years. A total of 83 samples were taken from this approximately 51 m thick section consisting of thin-bedded and laminated siltstones, laminated siliceous claystones and occasionally sandstone levels. Figure 1B presents the localities referred to in our text while Figure 1C provides views of the excavation.

The stratigraphic sequence of the Sofular localities consists of numerous volcanic layers interbedded with sedimentary depositions and exceeds 100 meters in total thickness. Here, we present a simplified stratigraphic section illustrating the fossiliferous and radioisotopically dated levels, which include sedimentary rocks as well as volcanic and

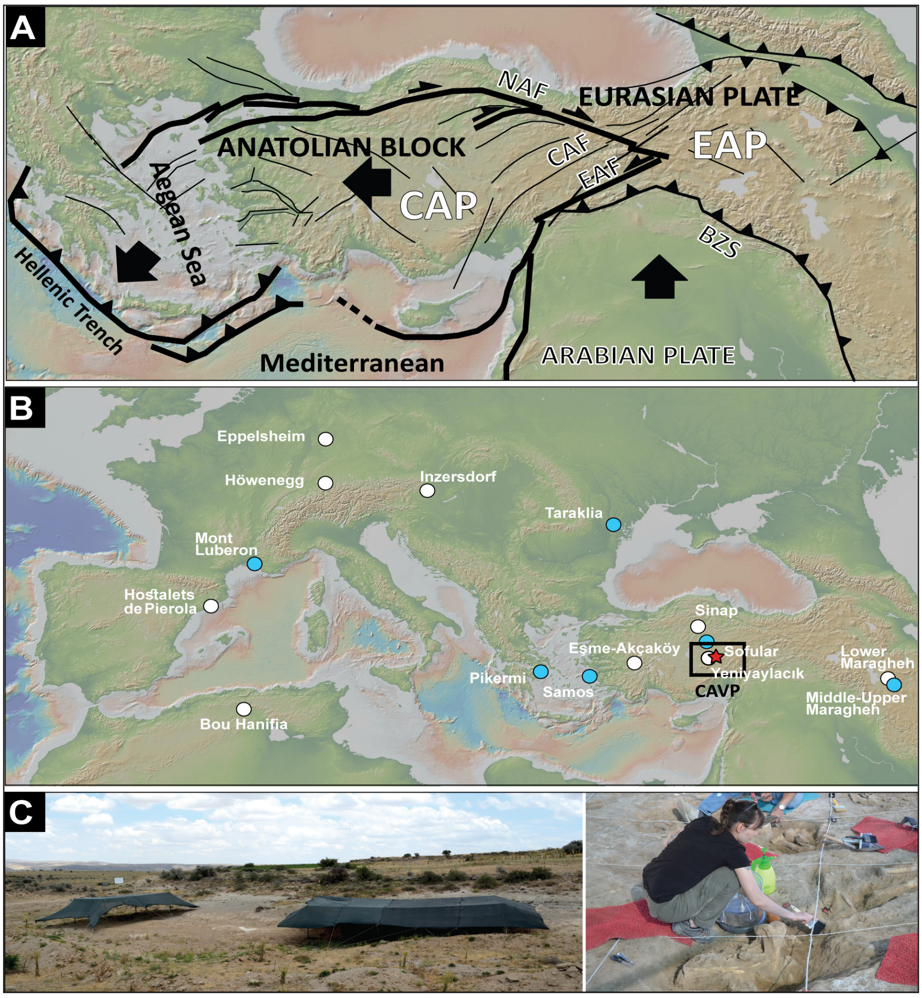


Fig. 1 - A) Topographic map of Anatolian landscape showing major geological structures: BZS—Bitlis-Zagros suture; CAF—Central Anatolian fault; NAFZ—North Anatolian fault; EAF—East Anatolian fault zone; CAP—Central Anatolian Plateau; EAP—East Anatolian Plateau. Black arrows show global system velocities relative to Eurasia. B) Location map of the Western Eurasian localities analyzed in this study. Red star: Sofular-2; white circles: Vallesian localities; blue circles: Turolian localities.

reworked volcanic horizons (Fig. 2). The bone bed, characterized by the silica-cemented sandstone and dated airfall pumice deposits, lays below it. New Ar/Ar radioisotopic age determinations have recently been published with an age of 8.422 ±0.34 Ma (Tholt et al. 2025). We take this as the age of the Sofular hipparions and recognize that this is correlated with early MN11 (Bernor et al. 2021).

Material and Methods

Systematic Conventions

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. (1996, 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*, *Nannippus*, *Pseudhipparion*, *Hippotherium*, *Cremohipparion*, *Hipparion* sensu strictu, *Sivalhippus*, *Eurygnathohippus* (senior synonym of *Stylohipparion*), *Shanxihippus*, *Baryhipparion*, *Proboscidipparion* 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 (2016), Koufos & Vlachou (2005), Cirilli et al. (2020, 2021, 2023). 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) recognized *Cormohipparion* sp. from the Punchbowl Formation (California) as a suitable antecedent

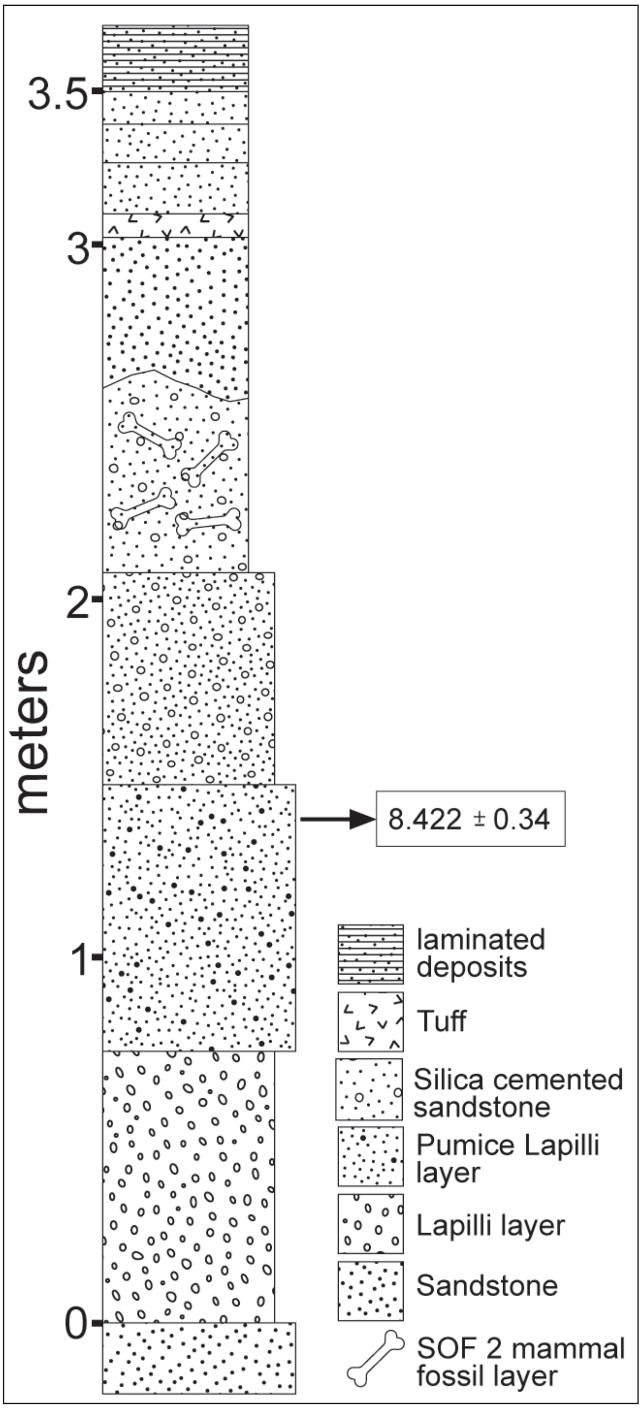


Fig. 2 - Short stratigraphical column of the Sofular bone bed with the new $^{40}Ar/^{39}Ar$ date (Tholt et al. 2025).

morphotype for the Old World hipparion ancestor, although more recently Bernor et al. (2022) have proposed *Cormohipparion occidentale* 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), Pakistan (*Cormohipparion* sp., Bernor et al. 2021, 2025), Algeria (*Cormohipparion africanum*, 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 midshaft cranial–caudal dimension modestly expanded (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, Hippotherium catalaunicum, Hippotherium intrans, Hippotherium microdon, Hippotherium kammerschmitti, Hippotherium brachypus*, *Hippotherium malpassii,* perhaps *Hippotherium giganteum* and *Hippotherium weihoense* (Bernor et al. 2011, 2021). *Hippotherium* is characterized by being 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, 1990a,b; 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* 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. 1990a,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. The genus *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, peripheral rim moderately well-developed, moderately complexly ornamented cheek teeth, rounded metaconids and metastylids in mandibular dentitions and slender third metapodials. The genus includes *Hipparion gettyi, Hipparion prostylum, Hipparion dietrichi, Hipparion campbelli* and *Hipparion hippidiodum* 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 primitively dorsoventrally and medially deep with well-developed peripheral rim. *Cremohipparion mediterraneum*, *Cremohipparion proboscideum*, *Cremohipparion forstenae* and *Cremohipparion licenti* usually express an intermediate fossa between the POF and buccinator fossae, other members of the group do not; cheek teeth have moderately complex enamel plications; mandibular cheek tooth metaconids and metastylids are rounded; third metapodials are elongate and slender. The genus includes *Cremohipparion macedonicum*, *Cremohipparion moldavicum*, *Cremohipparion mediterraneum*, *Cremohipparion proboscideum*, *Cremohipparion matthewi*, *Cremohipparion nikosi*, *Cremohipparion periafricanum*, *Cremohipparion antelopinum*, *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.

Table 1 is a complete list of hipparionine equids used in our analyses. The Sofular sample includes 144 studied specimens including crania, mandibles, teeth and postcranial elements. A complete list of specimens and their measurements is provided in Supplementary Table 1.

Comparative samples

The *Cormohipparion sofularensis* n. sp. collection studied herein originate from Sofular and are housed at the University of Ankara, Department of Anthropology. The Sofular equid sample is herein compared with a suite of Late Miocene North American, Eurasian and African hipparionine species of the genera *Cormohipparion*, *Hippotherium*, *Hipparion* sensu strictu and *Cremohipparion* (Table 1). Comparisons are undertaken on crania, third metacarpals and third metatarsals. We integrate the discrete characters of the crania, mandible and dentition for the specimens we describe, following Bernor et al. (2022, 2024). The scoring values are reported in Supplementary Tables 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 Sofular sample and compare them with other Late Miocene fossil equid species. PCAs were calculated using R v. 4.5.0 (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.

Cirilli et al. (2021, 2023) and Bernor et al. (2024) 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

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 & 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	*Hippotherium primigenium*	Inzersdorf, Austria	Bernor Database
Late Miocene	*Hippotherium primigenium*	Hoewenegg, 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* 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 & 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 & Vlachou 2005 / Bernor Database
Late Miocene	*Hipparion* cf. *dietrichi*	Middle Maragheh, Iran	Bernor et al. 2016
Late Miocene	*Hipparion campbelli*	Upper Maragheh	Bernor et al. 2016
Late Miocene	*Sivalhippus perimensis*	Siwalik, Pakistan	Wolf et al., 2013
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 & Vlachou 2005 / Bernor Database
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*	Akkaşdağı, Türkiye	Koufos & Vlachou 2005 / Bernor Database

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

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).

We extend the application of PCA to crania to characterize the facial morphologies of the genera and species. Two different datasets have been constructed to develop PCAs on crania. The first one includes M1 (ventral muzzle length), M2 (palatal length), M7 (premolar row length), M8 (molar row length), M9 (upper cheek tooth series length), M30 (length of the naso-incisive notch), M32 (distance between the anterior rim of the orbit of the distal rim of the POF), M33 (length of the POF), M35 (height of the POF) and M36 (distance between the POF and the facial maxillary crest). The second dataset includes the same measurements except M1, M2 and M30 mentioned above. Due the nature of fragmentary remains in hipparions, we created a second dataset to analyze more specimens preserving the lateral facial morphology but lacking the snout (as applied in Bernor et al. 2024).

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 (Bernor & Armour–Chelu 1999; Bernor & Harris 2003; Bernor & Scott 2003; Bernor et al. 2003, 2005, 2010, 2013, 2015, 2020, 2022, 2024; Gilbert & Bernor 2008; Bernor & Haile Selassie 2009; Bernor & White, 2009; Koufos & Vlachou 2005; Koufos et al. 2016; Cirilli et al. 2020, 2021, 2023), leading to a well-resolved context for Late Miocene, Pliocene and Pleistocene Eurasian and African hipparion assemblages. Log10 ratio diagrams of mc3 and mt3 include the same measurements considered in the metapodial 3 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* 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 2024) and calculated the mean ordinated crown height for each locality from MN10 and MN11 following Fortelius et al. (2002) for lists with at least two species with a hypsodonty value. All NOW localities between 9.9 Ma to 7.6 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; Liu et al. 2012; Kaya et al. 2018; Oksanen et al. 2019). 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; **dI1**, deciduous 1st premaxillary incisor, **dI2**, deciduous 2nd premaxillary incisor, **dI3**, deciduous 3rd premaxillary incisor, **dC**, deciduous maxillary canine, **dP1**, deciduous maxillary P1, **dP2**, deciduous maxillary P2, **dP3**, deciduous maxillary P3, **dP4**, deciduous maxillary P4; **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; **di1**, deciduous 1st mandibular incisor; **di2**, deciduous 2nd mandibular incisor; **di3**, deciduous 3rd mandibular incisor, **dc**, deciduous mandibular canine, **dp1**, deciduous mandibular p1, **dp2**, deciduous mandibular p2, **dp3**, deciduous mandibular p3, **dp4**, deciduous mandibular p4; **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); **NHMUK**, Museum of Natural History of London, England; **MDC**, Musée des Confluences, Lyon, France; **MNHN–TRQ**, Museum National de Histoire Naturelle, Paris, France, Sinap Collection; **MMTT**, Muze Melli Tankh Tabei, Tehran, Iran; **NHMW**, Natural History Museum in Wien, Austria; **PIN**, Paleontological Institut, Moskow; **PRCI**, Paleontological Research Center of Iran, Maragheh, 13Aban Locality, Lower Maragheh; **SEN MNHN**, 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.

Systematic Paleontology

Class **MAMMALIA** Linnaeus, 1758
Order **Perissodactyla** Owen, 1848
Family Equidae Gray, 1821
Tribe Hipparionini Quinn, 1955
Genus *Cormohipparion* Skinner & MacFadden, 1977

Cormohipparion sofularensis n. sp.

Zoobank Link: urn:lsid:zoobank.org:pub:261B1AF9-5B73-414D-B2A2-444E660F806C

Etymology: *Cormohipparion sofularensis,* after the locality where it was excavated (Sofular).

Holotype: SOF 50-2/194, complete skull housed at Ankara Hacı Bayram Veli University, Department of Anthropology (Fig. 3 A-C)

Referred Specimens: 50-SOF-2/278, mandible with i1-m3 50-SOF-2/613, mandible with c, i2-3, p2-m3 (Fig. 4A-B); mc3s, 50-SOF-2/28; 50-SOF-2/408; 50-SOF-2/72.

Type Locality: Sofular, Cappadocia, Türkiye.

Age: Early Turolian, 8.422±0.34 Ma, early MN11 (Tholt et al. 2025).

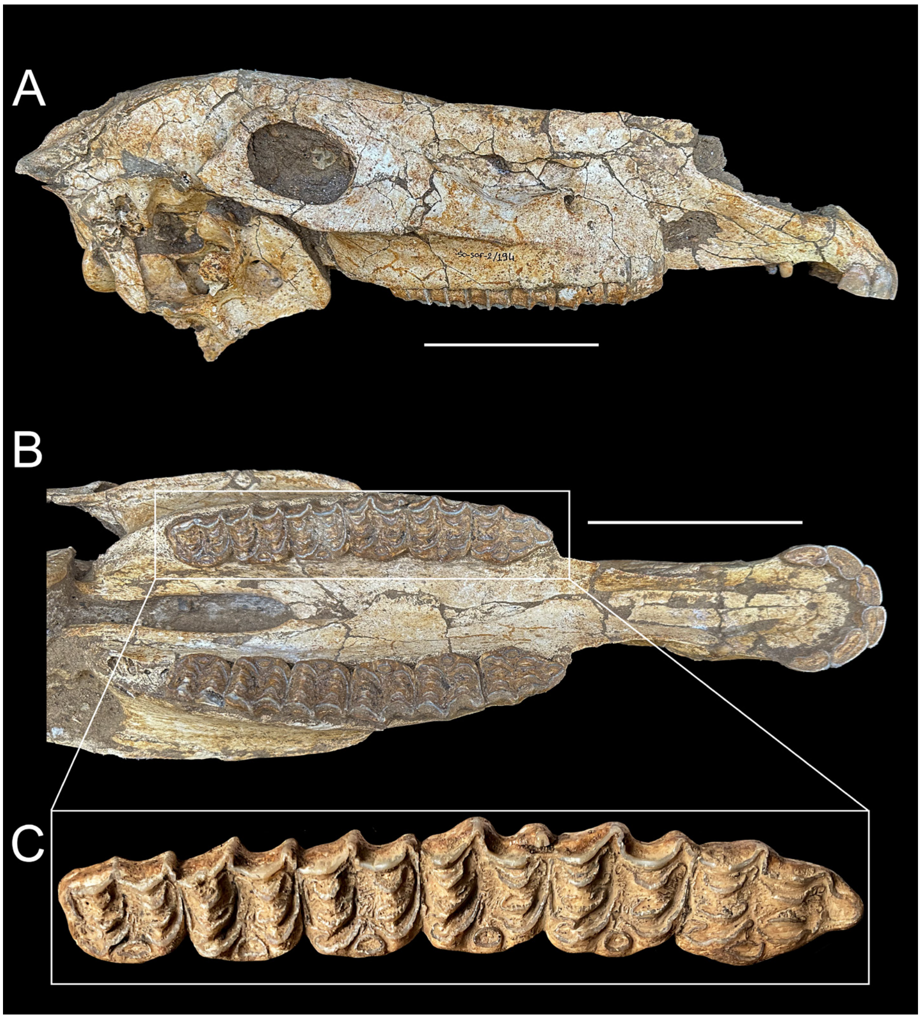


Fig. 3 - *Cormohipparion sofularensis* n. sp. Type cranium SOF 50-2/194; A) Lateral view. B) ventral view. C) close up of the upper cheek tooth row. Scale bar 10 cm.

Geographic Range: Central Anatolia, Türkiye.

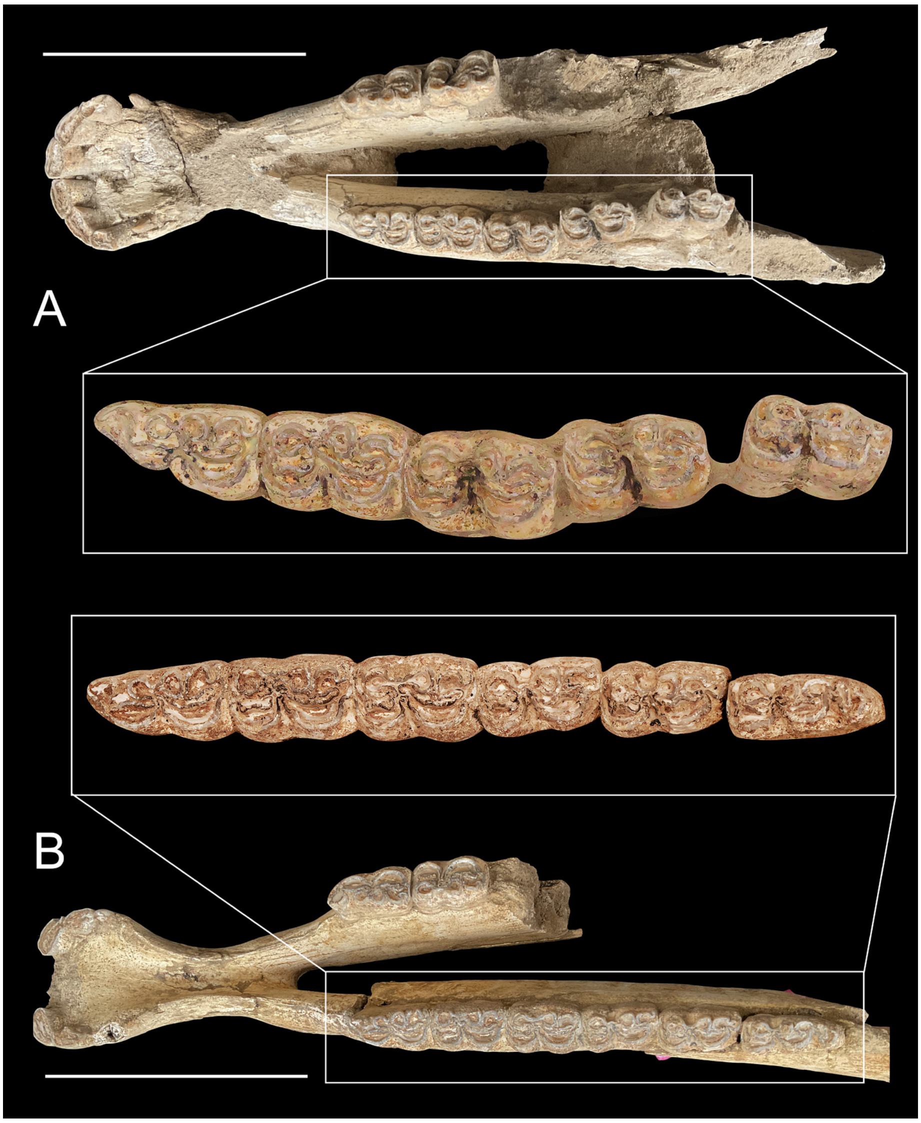
Diagnosis: Cranium with long POB having lacrimal placed more than half the distance from the anterior orbital rim to the posterior rim of the fossa but not penetrating the POF; POF subtriangular shaped and antero-ventrally oriented, slightly pocketed posteriorly, moderately deep medially, peripheral border very strongly delineated around the ventral and anterior periphery, less strongly dorsally, anterior rim deeply set; nasal notch near the mesial border of the P2; maximum crown height between 55–60 mm; P2-M3 length 157.9 mm; complex frequency of the cheek tooth plication; round to oval and lingually flattened protocone, protocone not connected to the protoloph until very late wear, protoconal spur may be present and strongly developed on P2, elongated P2 anterostyle; mandibular cheek teeth with rounded premolar metaconids, rounded molar metaconids, rounded to square-shaped premolar metastylids, premolar and molar metastylids lack spurs, molar metastylids squared-shaped, premolar ectoflexids not separating the metaconid and metastylid, pli caballinids and ectostylids absent (S. Table 2A&B).

Description

Cranium. The type specimen 50-SOF2/194 is a well-preserved adult female cranium with right and left I1–3, small canine and P2–M3 past middle wear (Fig. 3A-C). The POB is 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 POF (C1C); POF is subtriangular shaped and anteroventrally oriented (C4D); the POF is shallowly pocketed posteriorly (C5C); POF medial depth is moderately deep, (C6B); POF is strongly expressed around most of the entire periphery, except the dorsal edge (C8B+); anterior rim of POF is prominent and deeply set (C9A+); nasal notch is placed near the anterior border of P2 (C15C); maxillary maximum cheek tooth height is estimated to be between 40 and 60 mm (C18C); maxillary cheek tooth plication is complex (C19A); P2 exhibits linkage of the opposing margins of the pre- and post-fossettes at their labialmost extent (FLink, Yes); protocone varies from oval, to round to flattened lingually (C23CGE); P2 has a prominent protoconal spur (C25A); P2 anterostyle is elongate (C28A).

Mandible. We refer the mandible, 50-SOF-2-278 (Fig. 4A) to *Cormohipparion sofularensis*. This is a female specimen with right and left i1-c, left p2-m2

Fig. 4 - *Cormohipparion sofularensis* n. sp. mandibles occlusal view with a close up of the lower cheek tooth rows. A) 50-SOF-2/278. B) 50-SOF-2/613. Scale bar 10 cm.



and right p2-p3. The mandible has an arcuate incisor arcade. Premolar metaconids are rounded (C32A) as are the metastylids (C33A); premolar metastylids are rounded to square-shape (C34AE); premolar metastylid spurs are absent (C35B); molar metastylids are square-shaped (C36E); molar metastylid spurs are absent (C37B); premolar ectoflexid does not separate metaconid from metastylid (C38A); pli caballinid is absent (C40C); ectostylids are absent (C43B).

50-SOF-2/613 (Fig. 4B) is an adult male mandible with right and left i2-c, right p2-p3, left p2-m3. Character states are similar to 50-SOF-2-278 (re: Table 1), length p2-m3 is 154.1 which is very close to the type skull 50-SOF2/194 P2-M3 dimension (M9) which is 157.9.

50-SOF-2/613, *Cormohipparion sofularensis* Fig. 4B) is a female mandible with right and left i2-c, right p2-p3 and left p2-m3. Length (M5) p2-m3 is 154.1 mm. The mandibular dentition exhibits the following salient characters: premolar metaconids are rounded (C32A); molar metaconids are rounded (C33A); premolar metastylids are rounded (C34A); premolar metastylid spurs are absent (C35B); molar metastylids are rounded to square-shaped (C36AE); molar metastylid spurs are absent (C37B); premolar ectoflexids do not separate metaconid and metastylid (C38A); pli caballinids are absent (C40C); ectostylids are absent (C43B).

Third metacarpal. Our statistical analyses which follow below have revealed three *Cormohipparion sofularensis* mc3s, 50-SOF-2/28 (Fig. 5A), 50-SOF-2/408 (Fig. 5B) and 50-SOF-2/72 (Fig. 5C).

Other hipparions represented at Sofular

We do not formally nominate other new species of hipparion herein. However, based on the postcrania and mandibles, we have identified three other hipparion taxa at Sofular: *Hippotherium bra-*

Fig. 5 - *Cormohipparion sofularensis* n. sp. third metacarpals in cranial and caudal view. A) 50-SOF-2/28. B) 50-SOF-2/408. C) 50-SOF-2/72. Scale bar 10 cm.

chypus, Cremohipparion moldavicum and *Hipparion dietrichi* based on mc3s and mt3, and several specimens are not referrable to any of these four taxa. We present our identifications on third metapodials with our statistical analyses below. We recognize three mandibles of *Cremohipparion*. (Fig. 5A-D).

50-SOF-2/29, *Cremohipparion* sp. (Supplementary Figure 1A) is a laterally crushed mandible, lacking incisor and canine dentition but retaining right and left p2-m3. Sex cannot be determined. Length of p2-m3 (M5) is 136.5 mm. The mandibular dentition exhibits the following salient characters (Supplementary Tables 2A,B): premolar metaconids vary from rounded to elongate (C32AB); molar metaconids vary from rounded to square-shaped (C33AE); premolar metastylids vary from rounded to square-shaped (C34AE); premolar metastylid spurs are absent (C35B); molar metastylids are rounded (C36A); molar metastylid spurs are absent (C37B); premolar ectoflexids nearly separate metaconid and metastylid on p3 and p4 (C38B-); pli caballinids are absent (C40C); ectostylids are absent (C43B).

50-SOF-2/50, *Cremohipparion* sp. (Supplementary Figure 1B) is an adult male mandible with right and left i1-c, right p2-m3 and left p2-4. Length of p2-m3 (M5) is 140.4 mm. Mandibular i1-2 are nearly horizontally arranged and the left canine is clearly large. The mandibular dentition exhibits the following salient characters: premolar metaconids are rounded (C32A); molar metaconids are rounded (C33A); premolar metastylids are rounded (C34A); premolar metastylid spurs are absent (C35B); molar metastylids are rounded (C36A); molar metastylid spurs are absent (C37B); premolar ectoflexids do not separate metaconid and metastylid (C38A); pli caballinids are mostly absent (C40BC); ectostylids are absent (C43B). The incisor arcade has horizontally alignment for i1-i2 similar to *Hipparion dietrichi* from Samos.

50-SOF-2/342, *Cremohipparion* sp. (Supplementary Figure 1C) is a female mandible with right and left i1-i3, right canine, p2-m3 and left p2. Length of p2-m3 (M5) is 137.3 mm. Mandibular i1-3 are nearly arcuately arranged and the right canine is clearly slenderly built. The mandibular dentition exhibits the following salient characters: premolar metaconids are rounded (C32A); molar metaconids are rounded (C33A); premolar metastylids are rounded (C34A); premolar metastylid spurs are absent (C35B); molar metastylids are rounded (C36A); molar metastylid spurs are absent (C37B); premolar ectoflexids do not separate metaconid and metastylid (C38A); pli caballinids are absent (C40C); ectostylids are absent (C43B).

This character state assessment of mandibular cheek teeth along with cheek tooth row length (M5) supports the existence of at least two species of hipparion at Sofular based on mandibles: *Cormohipparion solufarensis* (the mandible 50-SOF-2-278 which is believed to be associated with the type specimen SOF 50-2/194 and the mandible 50-SOF-2/613, *Cormohipparion sofularensis* M5 = 154.1 mm) and *Cremohipparion* sp. (mean of M5 = 138.1 mm [n=3]) which is similar in length and its cheek tooth morphology. Statistical analysis of mc3s and mt3s have identified these species.

Morphometric and statistical analyses

Principal Component Analyses

The PCA crania results that include the length of the snout dimension (M30 in Eisenmann et al. 1988 and Bernor et al. 1997) are illustrated in Figure 6A. PC1 accounts for 40.9% of the variance, whereas PC2 for the 24.1% of the variance. The summary of the variance components and the loadings' distribution are reported in Supplementary Table 3 and Supplementary Figure 2A. PC1 separates specimens with longer upper cheek tooth rows from positive (smaller) to negative (larger) values. Positive PC2 values include specimens with longer snout (M1, M30), longer POF (M33) and dorsoventrally deeper POF (M35), whereas negative PC2 values cluster specimens with more elongated POB (M32) and reduced POF dorsoventral dimension placed more distant from the maxillary crest (M36) (see Supplementary Figure 1A). The PCA defines 3 morphospaces: one of *Cremohipparion*, characterized by positive values of PC1 and PC2; one of *Hippotherium*, characterized by negative values of PC1 and positive PC2; one of *Cormohipparion* and *Hipparion* sensu strictu characterized by lower-positive to negative values of PC1 and PC2. *Cormohipparion sofularensis* is the largest *Cormohipparion* considered in the analysis, and plots close to *Cormohipparion africanum* from Bou Hanifia, close to *Hippotherium brachypus* from Pikermi and *Hippotherium* aff. *brachypus* from Samos Q4, having negative values of PC1 and positive PC2. *Cormohipparion sofularensis* and *Cormohipparion africanum* (Bou Hanifia) are larger than *Cormohipparion cappadocium* which, in turn, has larger dimensions than the North American *Cormohipparion fricki* (MacAdams Quarry), *Cormohipparion occidentale* (Xmas Quarry) and *Cormohipparion matthewi* (Xmas Quarry). The range of variability of *Hipparion dietrichi* from Samos Quarry 1 includes another specimen referred to *Hipparion dietrichi* from Samos Quarry 4 (AMNH22860); altogether Samos *Hipparion dietrichi* exhibits a broad range of variability for PC1 and more restricted variation for PC2. The type cranium of *Hipparion gettyi* from Lower Maragheh plots close to the Samos *Hipparion dietrichi* variability, whereas *Hipparion prostylum* from Mont Luberon (France, UCBL-FSL 590001) is separated from this cluster by its reduced snout length. The new crania from Aban 13, Lower Maragheh, described in Bernor et al. (2024: PRCI-M1014 and PRCI-M1015) plot between the Samos *H. dietrichi* and *H. prostylum*, included in the morphospace defined by the genera *Cormohipparion* and *Hipparion* s.s. This supports the interpretation that *Hipparion* s.s. is directly related to *Cormohipparion* (Bernor et al. 2024). The *Hippotherium primigenium* from Inzersdorf plots close to Höwenegg *Hippotherium primigenium*, whereas the type cranium of *Hippotherium catalaunicum* is distinct from the Höwenegg *Hippotherium primigenium* but still included within the *Hippotherium* group. The range of variability of *Cremohipparion moldavicum* from Taraklia includes the crania of *Cremohipparion mediterraneum* from Pikermi having positive values for both PC1 and PC2. *Cremohipparion matthewi* (Maragheh and Samos Q5) and *Cremohipparion nikosi* (Samos Q5) are the smallest species and are separated from the cluster of *Cremohipparion moldavicum* and *Cremohipparion mediterraneum* with very high PC1 and modest PC2 values. Ultimately, *Cremohipparion proboscideum* (SENKM4709) is separated from *Cremohipparion moldavicum* and *Cremohipparion mediterraneum*, characterized by its larger size and larger POF.

The results of the PCA on crania lacking the snout are shown in Figure 6B. PC1 accounts for the 51.9%, whereas PC2 for the 27.4% of the variability. The summary of the variance components and the loadings' distribution are reported in Supplementary Table 3 and Supplementary Figure 2B. The two axes separated the same clusters as in Fig. 6A, but with a larger comparative sample. 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 POFs with increased height (M35), whereas negative PC2 values cluster specimens with more elongated POB (M32) and reduced POF (M36) (see Supplementary Figure 1B). The PCA again defines 3 morphospaces: one of *Cremohipparion*, characterized by positive values of PC1 and negative-to-positive PC2 values; one of *Hippotherium*, characterized by negative values of PC1 and positive PC2; one of *Cormohipparion* and *Hipparion* s.s., characterized by lower-positive to negative values of PC1 and PC2. The Turkish *Cormohipparion sofularensis* is still the largest *Cormohipparion* species, placed close to *Cormohipparion africanum* from Bou Hanifia and close to the *Hippotherium* variability. This affects the size, when considering that compared to *Cormohipparion sofularensis*, *Hippotherium primigenium* has a larger POF and a reduced snout length, whereas *Hippotherium brachypus* has a more elongated snout and a reduced

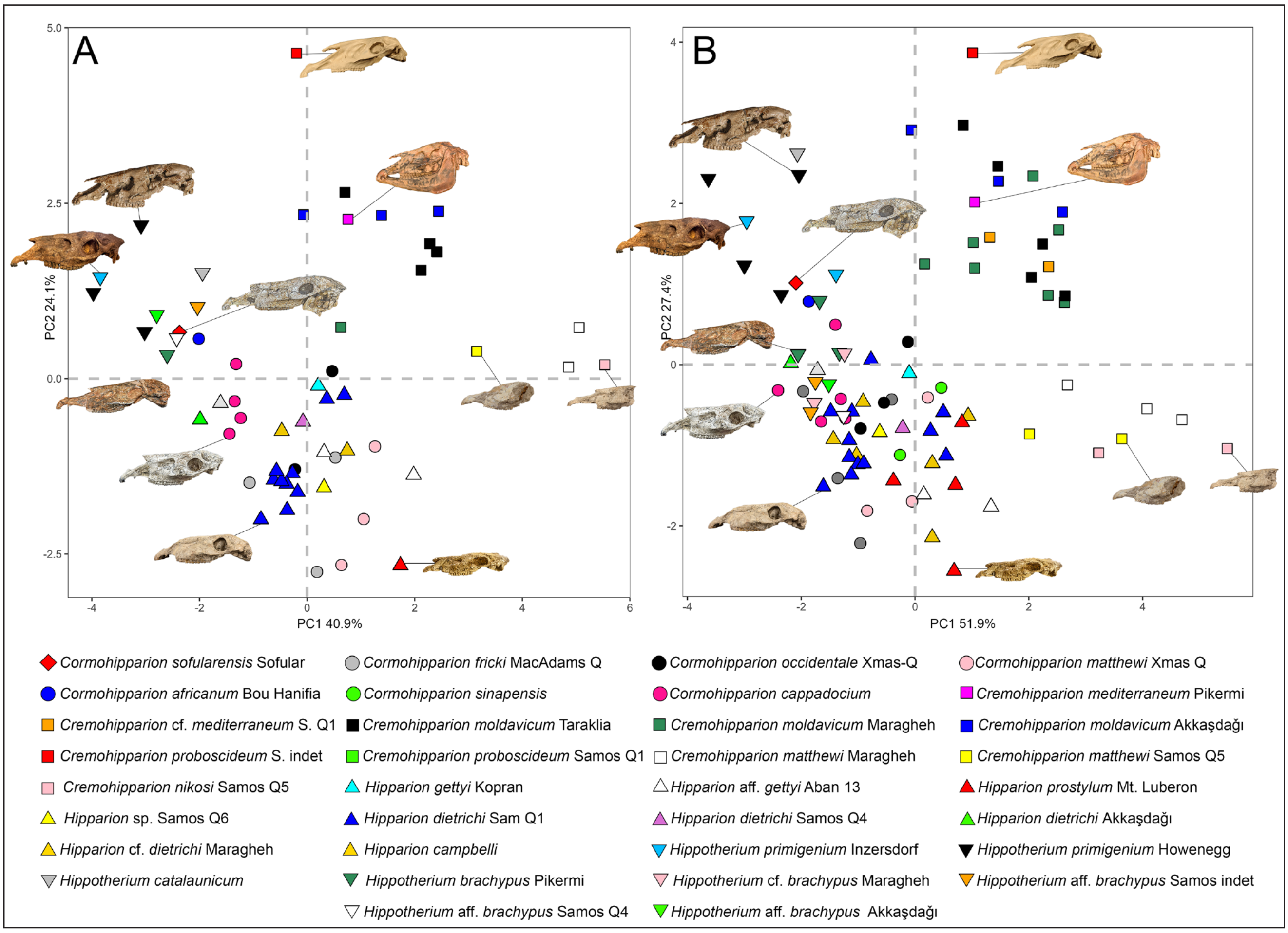


Fig. 6 - Results of principal component analysis (PCA) on crania with snout (A) and without the length of snout (B) included in calculations.

POF lacking the anterior rim margin. On the other hand, the other two Turkish species *Cormohipparion cappadocium* and *Cormohipparion sinapensis* are included in the range of variability defined by the North American *Cormohipparion fricki* (MacAdams Quarry), *Cormohipparion occidentale* (Xmas Quarry) and *Cormohipparion matthewi* (Xmas Quarry). *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 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 (BMNH26617, BMNHM33603, UCBL-FSL 590001, MNHNL156), plots close to the smallest *H. dietrichi* from Samos (AMNH20626, AMNH20692, AMNH94905) and has all positive values for PC1. The 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* based on metapodial 3 metrics (see later). As reported above, the 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. Pikermi *Hippotherium brachypus* (NHMUKM11178, NHMUKM11179, NHMUKM11191) and *Hippotherium* aff. *brachypus* from Samos Q4 (AMNH22838), Samos indet (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 (AMNH27809, NHMWA4847). 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, MNHN-Mar3428, MNHNMar466), *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* (SENKM4709) is separated from *Cremohipparion moldavicum* – *Cremohipparion mediterraneum*, characterized by its larger size and larger POF.

The PCA results on mc3s are shown in Figure 7 and Supplementary Figure 3. Figure 7 shows the results on the mc3s for selected genera (A, *Cormohipparion*; B, *Hippotherium*; C, *Hipparion* s.s.; D, *Cremohipparion*), whereas Supplementary Figure 3 plots the entire dataset of comparison (A, complete dataset; B, *Cormohipparion*; C, *Hippotherium*; D, *Hipparion* s.s.; E, *Cremohipparion*; F, *Plesiohipparion*). This allows a better understanding of the analysis. PC1 accounts for 74.1% of the variance, whereas PC2 for 9.6% of the variance. The summary of the variance components are reported in Supplementary Table 3, whereas the loadings' distribution are shown in Supplementary Figure 4A. PC1 clusters specimens by size from smaller (positive values) to larger ones (negative values), whereas PC2 separates the specimens by their elongation, from shorter individuals in positive values to more elongated ones in negative values. The range of variability of the X–Mas Quarry *Cormohipparion occidentale* sample includes three specimens of *Cormohipparion sofularensis* (50-SOF-2/408, 50-SOF-2/72, 50-SOF-2/28), as well as the Turkish *Cormohipparion sinapensis* and *Cormohipparion kecigibi* samples (Fig. 7A). The Eşme Akçaköy *Cormohipparion* aff. *sinapensis* is slightly larger and plots close to the larger *Cormohipparion occidentale* individuals (Fig. 7A), as well as *Cormohipparion africanum* from Bou Hanifia. The *Hippotherium primigenium* sample from Inzersdorf overlaps the larger individuals of *Cormohipparion occidentale* and the smallest *Hippotherium primigenium* from Höwenegg, whereas the Eppelsheim *Hippotherium primigenium* is included within the Höwenegg variability (Fig. 7B). *Hippotherium brachypus* from Pikermi shows a large range of variability, including the *Hippotherium primigenium* ones (Höwenegg and Eppelsheim), *Hippotherium* cf. *brachypus* from Maragheh and three specimens from Sofular (50-SOF-2/380, 50-SOF-2/383, 50-SOF-2/487) (Fig. 7B). The *Hippotherium* populations from Samos (Q1 and Q4) and from Akkaşdağı have 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. 7B). The *Hipparion dietrichi* samples from Samos Q1 and Akkaşdağı overlap extensively and include in their variability the populations from Middle Maragheh and Samos Q5 (Fig. 7C). Moreover, two specimens from Sofular (50-SOF-2/106, 50-SOF-2/598) are included within these ranges of variability (Fig. 7C). The *Hipparion dietrichi* populations from Samos (Q1 and Q5), Akkaşdağı and Middle Maragheh are well separated from *Hipparion prostylum* (Mt. Luberon), which has a more slender and gracile morphology and plots between the *Cormohipparion* variability and *Cremohipparion moldavicum* (Maragheh, Akkaşdağı and Taraklia) (Fig. 7C). One specimen from Sofular (50-SOF-2/452) 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. 7D). *Plesiohipparion longipes* from Akkaşdağı has the most elongated morphology of the entire dataset, more elongated than *Hipparion dietrichi* (Supplementary Figure 3F).

The PCA results on mt3s are shown in Figure 8 and Supplementary Figure 5. Figure 8 shows the results on the mt3s for selected genera (A, *Cormohipparion*; B, *Hippotherium*; C, *Hipparion* s.s.; D, *Cremohipparion*), whereas Supplementary Figure 5 plots the entire dataset of comparison (A, complete dataset; B, *Cormohipparion*; C, *Hippotherium*; D, *Hipparion* s.s.; E, *Cremohipparion*; F, *Plesiohipparion*). This allows for a more complete understanding of the analysis. PC1

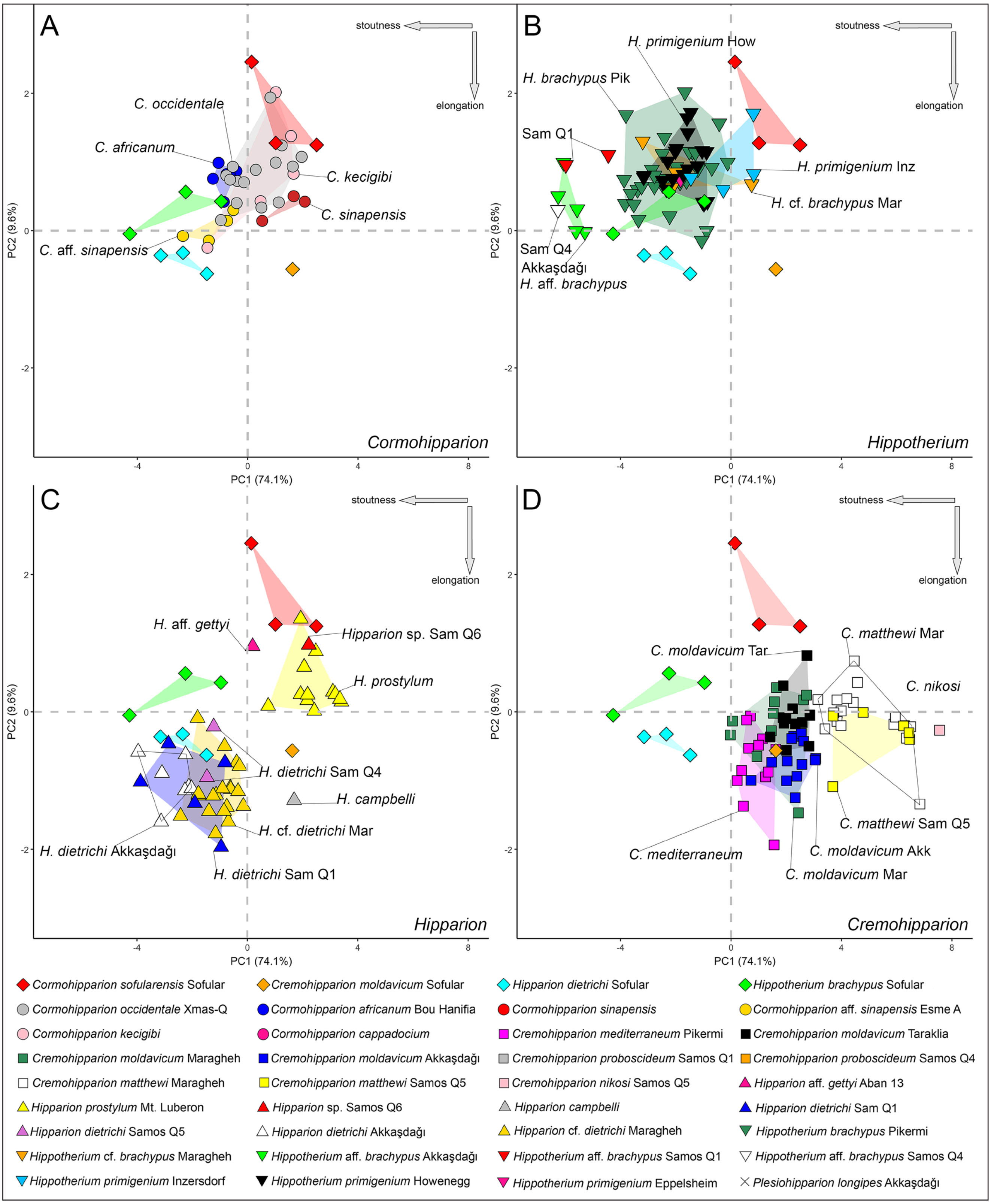


Fig. 7 - Results of selected principal component analysis (PCA) on third metacarpals. A) *Cormohipparion*. B) *Hippotherium*. C) *Hipparion* sensu strictu. D) *Cremohipparion*.

accounts for 71.6% of the variance, whereas PC2 accounts for 8.6% of the variance. The summary of the variance components is reported in Supplementary Table 3, whereas the loadings distribution is shown in Supplementary Figure 4B. PC1 clusters specimens by size from smaller (negative values) to larger ones (positive values), whereas PC2 separates the specimens by their elongation, from shorter individuals with positive values to more elongated ones in negative values. No mt3s of *Cormohipparion sofularensis* have been identified in our sample, but the analysis provides some insights about the presence of the other taxa recognized previously. As in the mc3s, the range of variability of the X–Mas Quarry *Cormohipparion occidentale* sample overlaps with the Sinap *Cormohipparion sinapensis* and *Cormohipparion kecigibi,* as well as *Cormohipparion africanum* from Bou Hanifia (Fig. 8A). The Eşme Akçaköy *Cormohipparion* aff. *sinapensis* is slightly larger and plots close to the larger *Cormohipparion occidentale* and *Cormohipparion cappadocium* individuals (Fig. 8A). The *Hippotherium primigenium* sample from Inzersdorf is more gracile than the Höwenegg one and overlaps with the *Cormohipparion* variability (Fig. 8B). The range of variability of *Hippotherium primigenium* from Höwenegg includes the Eppelsheim population, as well as *Hippotherium brachypus* from Pikermi and Maragheh (Fig. 8B). Here, two specimens from Sofular (50-SOF-2/275, 50-SOF-2/299) are included in the *Hippotherium brachypus* variability (Fig. 8B). As with the mc3s, the *Hippotherium* populations from Samos (Q1 and Q4) and from Akkaşdağı exhibit a stouter morphology, and they are well separated from the other populations of *Hippotherium brachypus* (Fig. 8B). The *Hipparion dietrichi* samples from Samos Q1 and Akkaşdağı overlap extensively and include in their variability the populations from Middle Maragheh and Samos Q5 (Fig. 8C). One specimen from Sofular (50-SOF-2/260) is included in these ranges of variability (Fig. 8C). *Cremohipparion proboscideum* from Samos Q1 and Samos Q4 shows an elongated morphology, close to *Hipparion dietrichi* (Fig. 8C). The *Hipparion dietrichi* populations from Samos (Q1 and Q5), Akkaşdağı and Middle Maragheh are well separated from *Hipparion prostylum* (Mont Luberon), which shows a more slender and gracile morphology and overlap extensively with *Cremohipparion moldavicum* (Maragheh, Akkaşdağı and Taraklia) and *Cremohipparion mediterraneum* (Pikermi) (Fig. 8C-D). One specimen from Sofular (50-SOF-2/574) is included in the *Cremohipparion moldavicum – mediterraneum* variability (Fig. 8D). *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. 8D). Akkaşdağı *Plesiohipparion longipes* Akkaşdağı exhibits the most elongated morphology of the entire dataset, greater than *Hipparion dietrichi* (Supplementary Figure 5F).

Log10 Ratio Diagrams

The mc3 Log10 Ratio diagrams comparing Sofular *Cormohipparion solufarensis* with a suite of *Cormohipparion*, *Hippotherium*, *Cremohipparion* and *Hipparion* s.s. species is illustrated in Figs. 9A-H. We use the Höwenegg skeletal sample as the standard Log10 mean for our mc3 and mt3 comparisons.

Figure 9A lists six species of *Cormohipparion* from North America (*Cormohipparion occidentale*), North Africa (*Cormohipparion africanum*), Sinap, Türkiye (*Cormohipparion kecigibi*, and *Cormohipparion sinapensis*), Eşme Akçaköy, Türkiye (*Cormohipparion sinapensis*), and Yeniyaylacık, Türkiye (*Cormohipparion cappadocium*). Compared to the Höwenegg Log10 mean all the comparative *Cormohipparion* taxa are approximately the same length, except *Cormohipparion kecigibi* which is shorter; all have slenderer midshaft width (M3) relative to their midshaft depth (M4) which Bernor et al. (2003) referred to as the "Eşme Akçaköy effect" wherein the midshaft is narrower than the midshaft depth. Proximal width (M5) and depth (M6) ranges from being close to the Höwenegg, with *Cormohipparion occidentale, Cormohipparion kecigibi* and *Cormohipparion sinapensis* being smaller. Distal measurements M10, M11, M12 and M14 range from being the same as Höwenegg mc3s (*Cormohipparion cappadocium*) to less. M7 and M8 vary in all hipparions. Overall, all of these *Cormohipparion* species show a similar Log10 trajectory varying in the absolute size of the species.

Figure 9B illustrates how the three Sofular mc3s range. The three mc3s (50-SOF-2/408, 50-SOF-2/28 and 50-SOF-2/72) track together except for proximal articular width (M6) for which 50-SOF-2/408 is smaller than the other two mc3s. These three mc3s are most similar in their dimensions to *Cormohipparion occidentale, Cormohipparion sinapensis, Cormohipparion kecigibi* and *Cormohipparion africanum.*

Figure 9C illustrates six species of *Hipparion* s.s. mc3 from Iran (*Hipparion campbelli* and *Hipparion* cf. *dietrichi*, formerly *Hipparion* cf. *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 mc3s than the

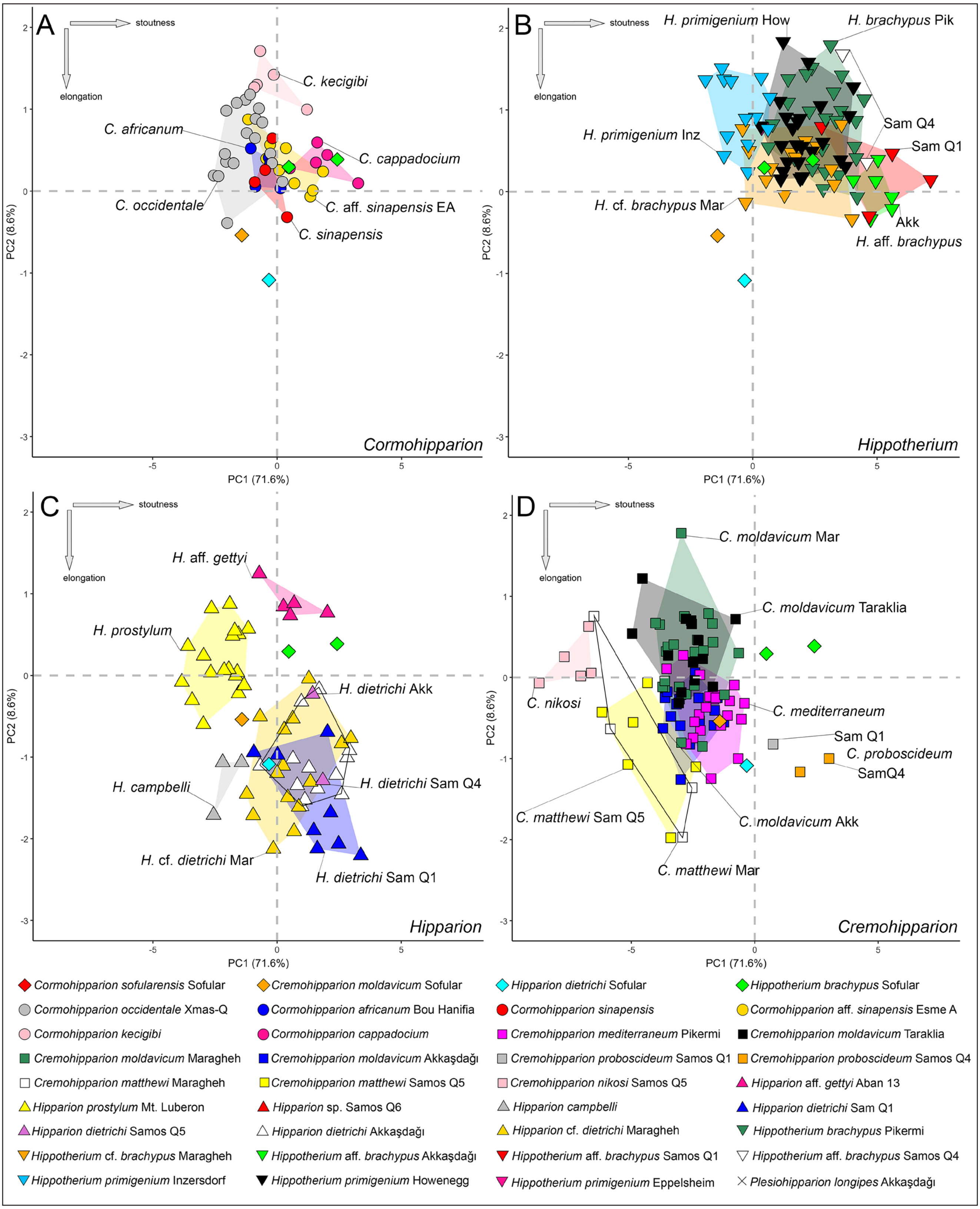


Fig. 8 - Results of selected principal component analysis (PCA) on third metatarsals. A) *Cormohipparion*. B) *Hippotherium*. C) *Hipparion* sensu strictu. D) *Cremohipparion*.

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 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 Mont Luberon *Hipparion prostylum.* Overall, the *Hipparion* s.s. sample tracks closely except for Samos Q6 *Hipparion,* Mont Luberon *Hipparion prostylum* and Upper Maragheh *Hipparion campbelli* that are consistently more slender limbed than the rest of the sample.

50-SOF-2/106 and 50-SOF-2/598 are referred herein to *Hipparion dietrichi* (Fig. 9D). They compare most closely to Samos *Hipparion dietrichi* and Maragheh *Hipparion* cf. *dietrichi.*

Figure 9E illustrates ten samples of *Cremohipparion* from Samos (*Cremohipparion* cf. *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 by 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 over the *Cormohipparion* species plots. 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* are less to substantially less depending on individual species size. 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* from Samos, Maragheh and Samos Q5.

Figure 9F plots a single complete mc3 from Sofular, 50-SOF-2-452 which we refer to *Cremohipparion moldavicum.* This specimen closely matches the *Cremohipparion moldavicum* samples from Maragheh, Taraklia and Akkaşdağı.

Figure 9G illustrates six samples of *Hippotherium* from Inzersdorf and Eppelsheim (*Hippotherium primigenium*), Pikermi and Samos (*Hippotherium brachypus* and *Hippotherium* aff. *brachypus*), Maragheh (*Hippotherium* cf. *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* cf. *brachypus* compare closely to one another and show a slight "Eşme Akçaköy" effect similar to Sinap *Cormohipparion* (Bernor et al. 2003). These three samples track each other closely across all measurements and compare closely with the Höwenegg standard.

There are three Sofular mc3 specimens that we refer to *Hippotherium brachypus,* 50-SOF2/380, 50-SOF2/383 and 50-SOF2/487 (Figure 9H). These specimens track very close to one another, only 50-SOF2/380 deviates from the Log10 plot profile the others share, particularly for M6, proximal articular depth. 50-SOF2/383 and 50-SOF2/487 compare closely with Inzersdorf and Eppelsheim *Hippotherium primigenium*, Pikermi *Hippotherium brachypus* and Maragheh *Hippotherium* cf. *brachypus,* respectively.

The mt3 Log10 Ratio diagrams comparing Sofular *Hipparion* s.s. (Figs 10A-B) *Cremohipparion* (Fig. 10C-D) and *Hippotherium* (Fig.10E-F) are summarized below. There were no *Cormohipparion* mt3 elements identified in the Sofular sample. The results of the mt3 Log10 ratio analyses closely follow those of mc3.

Hipparion s.s. includes four taxa (Fig. 10A) from Turkish, Iranian, Greek and French localities: *Hipparion campbelli* (Maragheh, Iran), *Hipparion dietrichi* (Akkaşdağı, Türkiye; Samos, Greece Q1 and Q5), *Hipparion prostylum* (Mont 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), mid-shaft depth (M4), proximal articular width (M5), proximal ar-

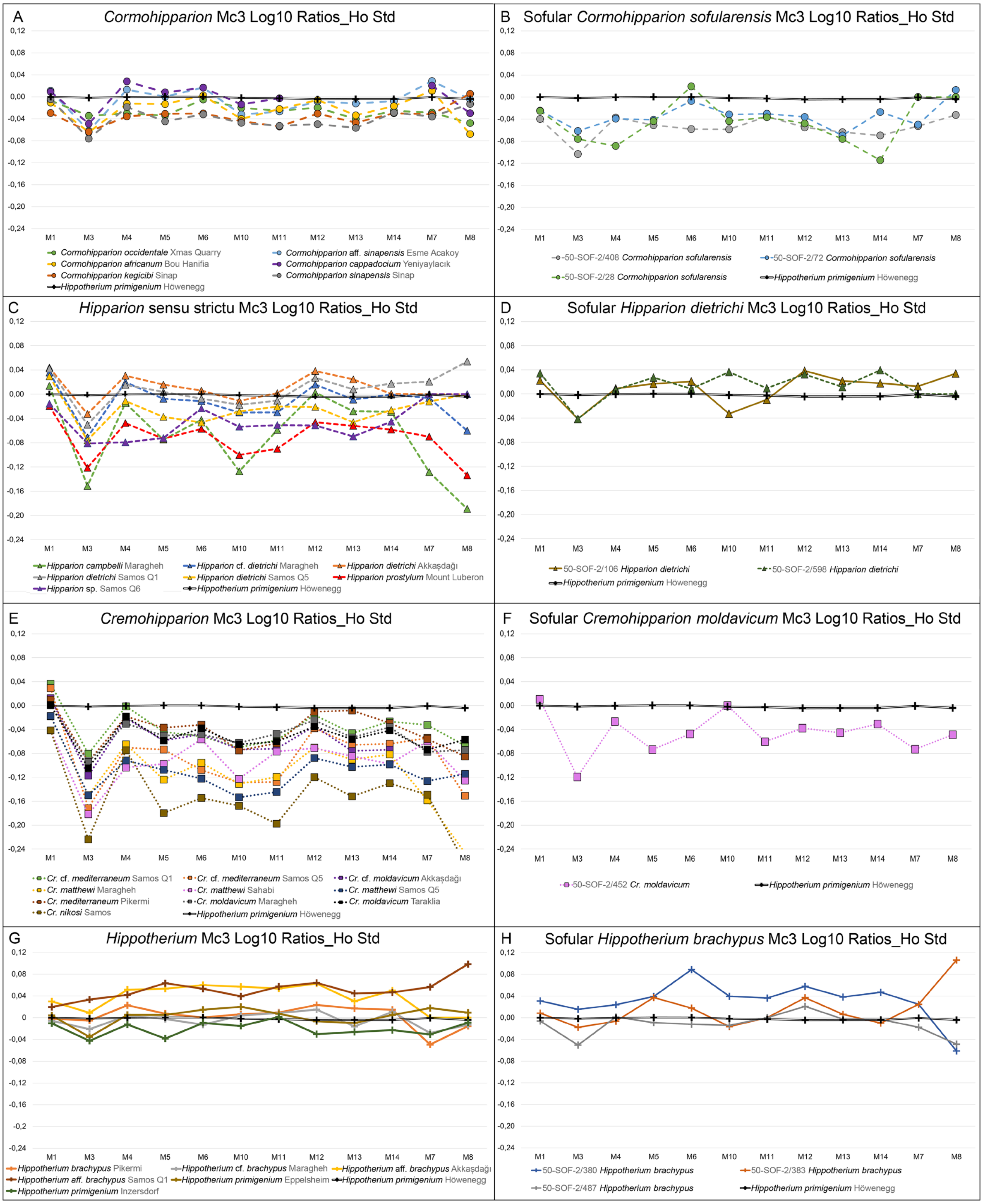


Fig. 9 - Log10 Ratio diagrams on third metacarpals. A) North American and Western Eurasian *Cormohipparion* species. B) Sofular *Cormohipparion*. C) Western Eurasian *Hipparion* sensu strictu. D) Sofular *Hipparion dietrichi*. E) Western Eurasian *Cremohipparion* species. F) Sofular *Cremohipparion moldavicum*. G) Western Eurasian *Hippotherium* species. H) Sofular *Hippotherium brachypus*.

ticular depth (M6) and distal articular dimensions (M10-M14); it clearly has a more gracile build than these other hipparions. *Hipparion prostylum* (Mont 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*.

Sofular has a single mt3 referred to *Hipparion dietrichi*, 50-SOF-2/260 (Fig. 10B). The length (M1) is similar to Samos Q1 and Q5 *Hipparion dietrichi* and Maragheh *Hipparion campbelli*. Its midshaft width (M3) and depth (M4) are less than in *Hipparion dietrichi*. Measurements M5-M14 of 50-SOF-2/260 do not deviate much from Samos Q1 and Q5 *Hipparion dietrichi* and Maragheh *Hipparion campbelli* except M13 which is less. Overall, 50-SOF-2/260 supports the presence of *Hipparion* cf. *dietrichi* at Sofular 2.

Cremohipparion includes seven taxa from seven localities (Fig. 10C): *Cremohipparion* cf. *mediterraneum* from Samos Q4, *Cremohipparion mediterraneum* from Pikermi, *Cremohipparion matthewi* from Maragheh, Samos Q5 and Sahabi; *Cremohipparion moldavicum* from Maragheh and Taraklia, *Cremohipparion* cf. *moldavicum* from Akkaşdağı, *Cremohipparion nikosi* from Samos Q5, *Cremohipparion proboscideum* from Samos Q1 and Q4. 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 (10-M14) except distal measurement M12 which is slightly higher (Samos Q1 specimen). Samos Q1 *Cremohipparion proboscideum* 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 (M10-14) are Maragheh, Samos Q5 and Sahabi *Cremohipparion matthewi* and Samos *Cremohipparion nikosi*. The remaining plots intervening between *Cremohipparion proboscideum* and *Cremohipparion matthewi*/*nikosi* include *Cremohipparion mediterraneum* and *Cremohipparion moldavicum,* two closely related species (Bernor et al. 2016).

Sofular 50-SOF-2-574 (Fig. 10D) tracks very closely with *Cremohipparion moldavicum* but is also similar to Pikermi *Cremohipparion mediterraneum* and Samos Q4 *Cremohipparion* cf. *mediterraneum*. This result provides further evidence that *Cremohipparion moldavicum* and *Cremohipparion mediterraneum* are closely related species (Bernor et al. 2016). The *Cremohipparion* species depicted herein show similarities in mt3 slenderization with the *Hipparion* s.s. specimens. Except for the largest *Cremohipparion* species, *Cremohipparion proboscideum*, most *Cremohipparion* species show advanced slenderization, in particular the exaggerated contrast in midshaft width (M3) and depth (M4) dimensions. *Cremohipparion* also includes much smaller taxa, *Cremohipparion matthewi* and *Cremohipparion nikosi* which certainly had smaller body masses (Bernor et al. 2021).

Hippotherium includes four taxa from seven localities (Fig. 10E): *Hippotherium brachypus* from Pikermi; *Hippotherium* aff. *brachypus* from Akkaşdağı, Samos Q1 and Q4; *Hippotherium* cf. *brachypus* from Maragheh, *Hippotherium primigenium* from Inzersdorf and Eppelsheim. 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 Inzerdorf 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). Eppelsheim 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 longer M4 and M5 dimensions. Overall, the *Hippotherium* sample is the most robustly built series of mt3 measurements of our sample, lacking the strongly contrasting measurements of midshaft width (M3) versus midshaft depth (M4) found in the *Cormohipparion, Hipparion* s.s. and *Cremohipparion* taxa. Sofular 50-SOF2/275 and 50-SOF2/299 (Fig. 10F) both closely track Pikermi *Hippotherium brachypus*. Both of these specimens are less robust than Akkaşdağı *Hippotherium* aff. *brachypus*. Overall, *Hippotherium* species are

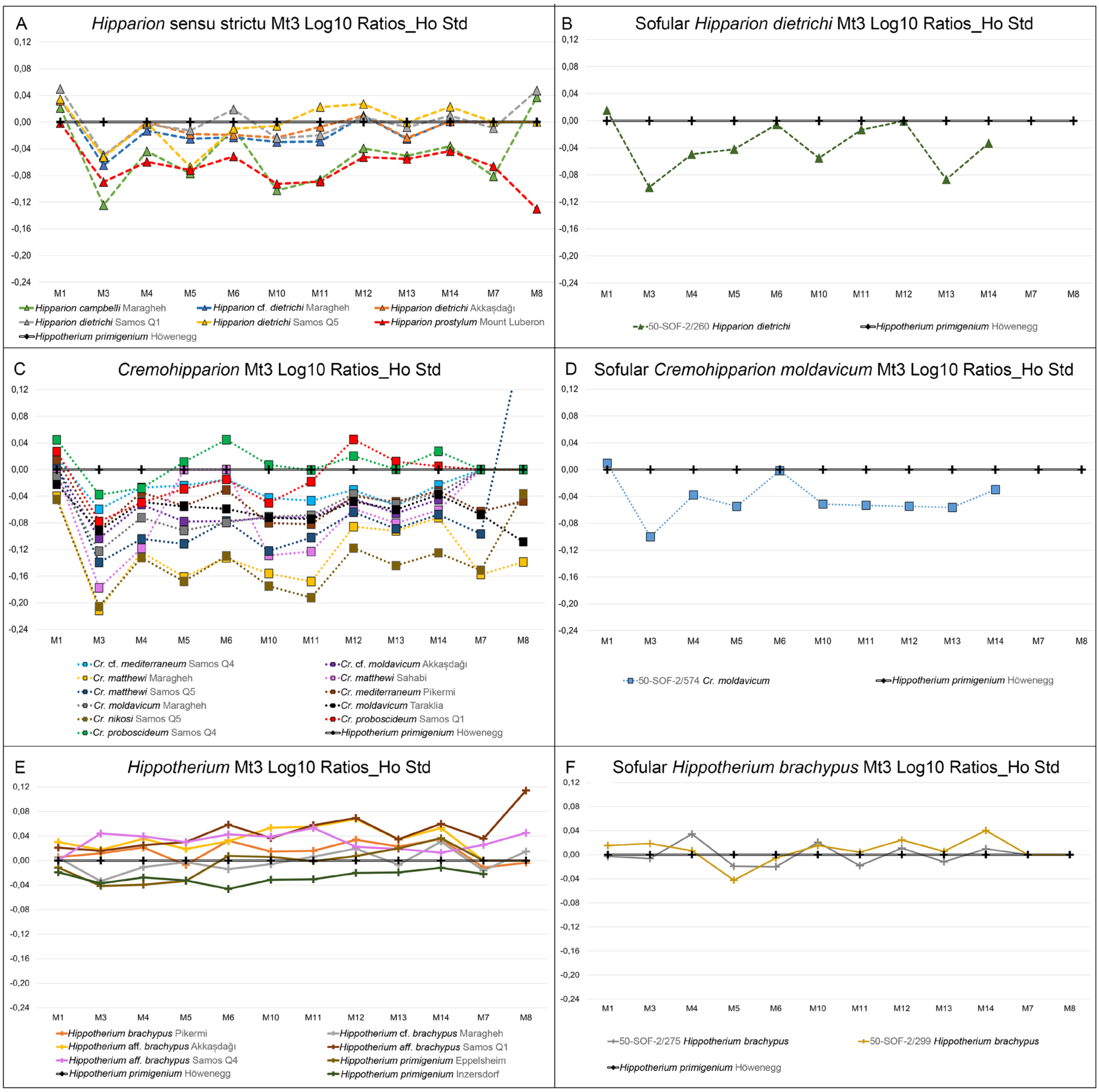


Fig. 10 - Log10 Ratio diagrams on third metatarsals. A) Western Eurasian *Hipparion* sensu strictu. B) Sofular *Hipparion dietrichi*. C) Western Eurasian *Cremohipparion* species. D) Sofular *Cremohipparion moldavicum*. E) Western Eurasian *Hippotherium*. F) Sofular *Hippotherium brachypus*.

characterized as being robustly built, not extraordinarily elongate (M1), with midshaft width (M3) and depth (M4) not strongly contrasting in their dimensions, and remaining measurements close to the Höwenegg standard.

Overall, the outcomes of the PCAs and of the Log10 Ratio diagrams are congruent, strongly supporting the four genera we recognize at Sofular: *Cormohipparion, Hippotherium, Hipparion* s.s., and *Cremohipparion*.

Discussion

We have identified four species belonging to four separate genera of hipparion from Sofular. *Cormohipparion sofularensis* n. sp. is represented by a complete skull SOF 50-2/194 (Fig. 3), two mandibles 50-SOF-2/278 and 50-SOF-2/613 and three mc3s 50-SOF-2/408, 50-SOF-2/28 and 50-SOF-2/72. *Cremohipparion moldavicum* is a smaller, more gracile species represented by three mandibles, 50-

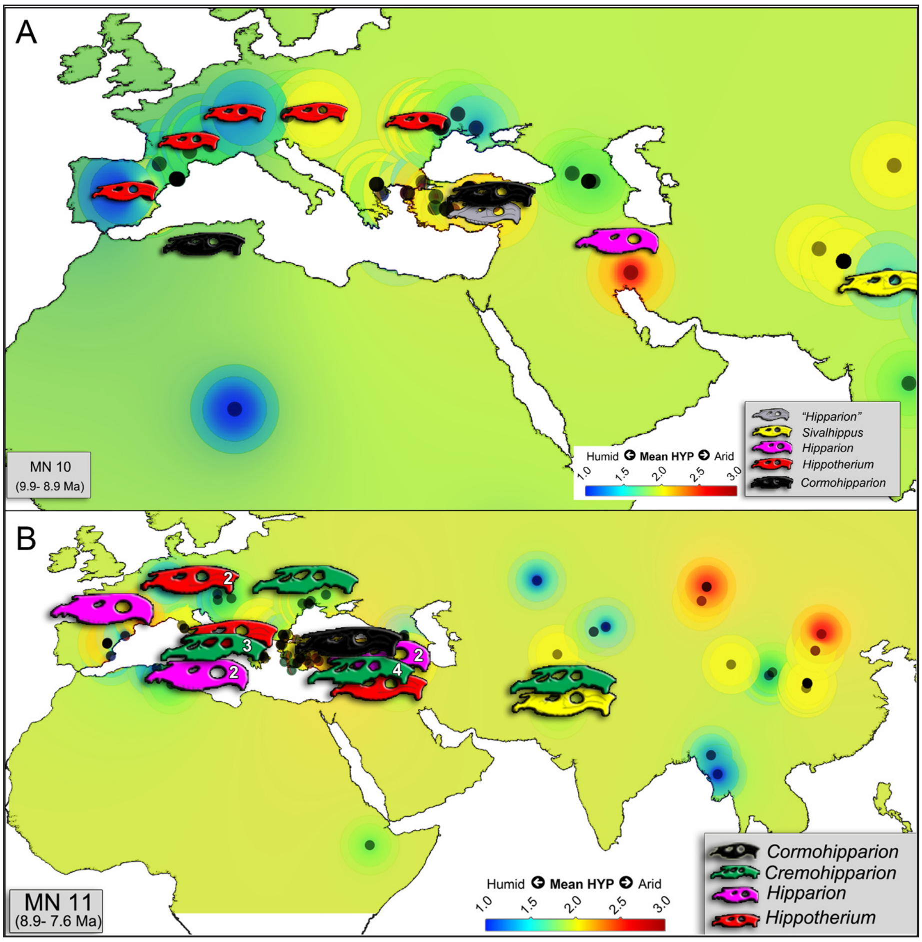


Fig. 11 - Paleogeographic, paleoclimatic and ecological maps of (A) MN10 (9.9-8.9 Ma) and (B) MN11 (8.9 – 7.6 Ma) hipparions included in this study. Note here that the cluster of diverse hipparions in the center of the image include recognized taxa from Greece, Turkey, Iran and Western Ukraine. Paleoclimatologic conditions based on mean ordinated hypsodonty (HYP) are visualized with the color gradient from blue (humid) to red (arid).

SOF-2/29, 50-SOF-2/50 and 50-SOF-2/342 and a suite of mc3s and mt3. *Hipparion dietrichi* and *Hippotherium brachypus* have been identified solely by mc3s and mt3s. *Hippotherium* is first known from MN9 whereas *Hipparion* s.s. is first reported from MN10 (Koufos et al. 2016; Bernor et al. 2021). These three taxa also occur in MN 11, but what is unique about Türkiye is that *Cormohipparion* occurs during MN9 at Sinap (Bernor et al. 2003, 2024), MN10 at Yeniyaylacık ca. 9.46 ± 0.24 Ma (Bernor et al. 2024; Tholt et al. 2025) and now also at Sofular in early MN11, ca. 8.42 ± 0.34 Ma (Tholt et al. 2025). The paleoclimatic map for MN10 exhibits mesic conditions for MN10 of Türkiye and more broadly distributed open conditions for MN11 (Fig. 11A-B).

North American *Cormohipparion* was the founding source of the *Cormohipparion* Datum in the Old World (Bernor et al. 2021, 2022, 2024). The oldest Old World hipparions are from Pannonian C, Vienna Basin dated between 11.0 and 11.4 Ma (Bernor et al. 2017). While these hipparions are referred to *Hippotherium* sp., it is clear that early Vallesian *Cormohipparion sinapensis* shows a more primitive morphology close to the North American *Cormohipparion* species. The more advanced lineages of *Cremohipparion moldavicum* (Gromova, 1952) and *Hipparion* s.s. did not appear until MN10 (Bernor et al. 1996; Bernor et al. 2021). *Hippotherium brachypus* first occurred in MN11 at Middle Maragheh, Sofular and Pikermi and had a morphology very close to Central European *Hippotherium primigenium*. *Cremohipparion moldavicum* is also found at MN11 localities of Middle Maragheh, Taraklia and Sofular, together with its sister taxon *Cremohipparion mediterraneum* in Pikermi. The early Turolian (MN11) witnessed an explosive diversification of hipparions which included multiple species of *Hippotherium, Cremohipparion, Hipparion* s.s. and *Sivalhippus* that are known to have ranged from Spain, Central and Southern Europe, the Eastern Mediterranean and Indo-Pakistan (Bernor et al. 2021; Fig. 11B here). Figure 11B illustrates the great diversity of hipparions from the Subparatethyan Province (Bernor 1983, 1984) including Western Ukraine, Balkans, Greece, Türkiye and Iran where species of *Cormohipparion, Hippotherium, Hipparion* and *Cremohipparion* occurred. The Sofular fauna documents this early phase of hipparion lineage differentiation in early MN11. The paleoclimatic map for MN10 exhibits mesic conditions for MN11 of Türkiye and more broadly distributed open conditions for MN11 (Fig. 11 A-B). This paleoclimatic and ecologic change accompanied hipparion diversification and closely agrees with the model of climatic change driving Equini evolutionary diversification observed by Cantalaipedra et al. (2017).

Conclusions

The 8.4 +/- 0.32 Ma early MN11 (Tholt et al. 2025) Sofular fauna has the youngest recorded *Cormohipparion* in Eurasia and Africa, *Cormohipparion sofularensis*. Our integrated analyses of crania, dentitions, mc3s and mt3s has led us to our conclusion that *Cormohipparion* shares an evolutionary relationship with MN10 *Cormohipparion cappadocium* from Yeniyaylacık, Türkiye, ca. 9.46 ± 0.24 Ma (Tholt et al. 2025). *Cormohipparion sofularensis* exhibits features of the skull and mandible as well as the postcrania that secure its generic allocation but also is derived compared to *Cormohipparion cappadocium*. *Cormohipparion sofularensis* was penecontemporaneous with Lower Maragheh *Hipparion gettyi*, which in turn precedes *Hipparion* aff. *gettyi* and then Mont Luberon *Hipparion prostylum* (the genotype species for *Hipparion* s.s.) and Middle Maragheh *Hipparion* aff. *prostylum* (Bernor et al. 2021) here recognized as *Hipparion* cf. *dietrichi*.

The initial explosive radiation of hipparion species in the Vallesian Sinap faunas does not appear to have any members of the *Cremohipparion* or *Hipparion* s.s. clades. These two clades first appear in MN10 and are of uncertain origin, but likely *Hipparion* s.s. originated from a population of *Cormohipparion* (Bernor et al. 2024). This aspect of our work is undergoing further research based on Turkish hipparion faunas. Early appearing Vallesian Central European and Iberian Peninsula *Hippotherium* would appear to have their evolutionary origins within the genus *Cormohipparion* (Bernor et al. 2021, 2024).

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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