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Dance of the Cave Bear: Honouring the Scientific Legacy of Björn Kurtén

Cormohipparion cappadocium, a new species from the Late Miocene of Yeniyaylacık, Türkiye, and the emergence of western Eurasian hipparion bioprovinciality

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We studied the Vallesian records from Türkiye and Iran, and uncovered a diverse record of *Cormohipparion* species from Yeniyaylacık and Sinap, Türkiye, and their apparent descendant, *Hipparion gettyi* from Maragheh, Iran. This prompted us to examine the early evolutionary diversification, biogeography and paleoclimatology of western Eurasian hipparions. Our study also included the early hipparion records from Austria, Germany and the Iberian Peninsula. Whereas the Vienna Basin, Austria, has the oldest recorded occurrence of *Hippotherium* sp. at 11.4–11.0 Ma, our investigation revealed that the most primitive Old World hipparions belonged to the North American genus *Cormohipparion*. We integrated the data on crania, dentitions, 3rd metacarpals and 3rd metatarsals to further evaluate the systematics of Vallesian hipparions (11.2–9.6 Ma). Sinap, Türkiye, has the most primitive *Cormohipparion* in Eurasia, *Co. sinapensis*, but based on postcranial anatomy, we found that also *Co.*

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kecigibi is a second *Cormohipparion* species of Sinap's early Vallesian. The locality of Yeniyaylacık, Türkiye, dated ca. 9.1 Ma, has the latest occurrence of Eurasian *Cormohipparion*, *Co. cappadocium*. Our analyses also revealed that the genus *Hipparion sensu stricto* was probably directly derived from Subparatethyan (including Türkiye) *Cormohipparion*, with the most primitive taxa being *Hipparion gettyi* and *Hipparion prostylum. Hipparion gettyi* first occurred at Maragheh, Iran, ca. 9.0 Ma at the end of MN 10. *Hipparion sensu stricto* includes *H. gettyi*, *H. prostylum*, *H. dietrichi* and *H. hippidiodus* and had a range that extended from France through Greece and Türkiye to China.

Introduction

Following Schlosser (1903), Kurtén (1952) published a landmark quantitative study on faunal provinciality and paleoecology of Chinese *Hipparion* faunas wherein he demonstrated that in the Late Miocene there were two Chinese faunal provinces, based on his assessment of occurrences of two gazelles, *Gazella gaudryi* and *Gazella dorcadoides.* Kurtén's (1952) work was distinctly quantitative and transformative. Neogene faunal provinciality was a theme of Bernor's investigations of Eurasian and African mammalian faunas (1983, 1984), and Bernor *et al.* (1996). Bernor *et al.* (1980, 1996, 2021) further advanced investigations of hipparionine superspecific group taxonomy, evolution and biogeography. Eronen *et al.* (2009) supported Old World large mammal provinciality, while Kaya *et al.* (2018) supported expansion of Late Miocene mammalian "savanna chronofaunas" across Eurasia and Africa.

Herein, we revise the understanding of Subparatethyan *Cormohipparion* and its relationship to early members of the genus *Hipparion* based on assemblages from central Anatolia and northwestern Iran, and present proof for the early differentiation of these generic-level clades in Türkiye. We describe a new, late Vallesian species, *Cormohipparion cappadocium* from Yeniyaylacık (Cappadocia, Türkiye), and emend descriptions of two species from Sinap, *Co. sinapensis* and *Co. kecigibi*. We compare these *Cormohipparion* species with closely related *Hippotherium primigenium* from the Vienna Basin (Pannonian C, D–E) and Höwenegg, Germany (MN 9, 10.3 Ma), and an early member of the *Hipparion sensu stricto* group, *Hipparion gettyi* from lower Maragheh, Iran (for localities *see* Fig. 1A).

Material and methods

Systematics

Abbreviations: POB = preorbital bar, POF = preorbital fossa, UTR = upper cheek tooth row, LTR = lower cheek tooth row, P = protocone, 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, dp3 = deciduous mandibular third premolar, 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 = 3rd metacarpal, Mt3 = 3rd metatarsal, rt = right, lt = left.

Herein, we use descriptions and definitions of hipparionine horses provided in Bernor *et al.* (1996, 1997, 2021). As the taxon *Hipparion* has been applied in a variety of ways, we interpret it as follows:

Hipparionini: A taxonomic 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*, *Sivalhippus*, *Eurygnathohippus* (senior synonym of *Stylohipparion*), *Shanxihippus*, *Baryhipparion*, *Proboscidipparion* and *Plesiohipparion*. These lineages are reviewed by Qiu *et al.* (1987), Bernor and White (2009), Bernor *et al.* (2010, 2013, 2015, 2020,

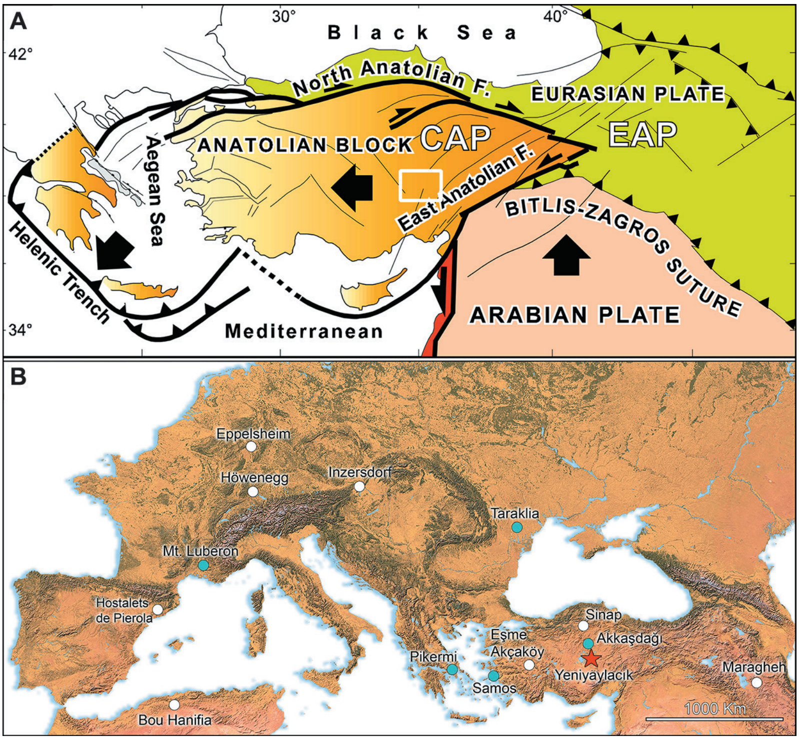

Fig. 1. — **A**: Geodynamic map of the Eastern Mediterranean and location of Cappadocia (modified from Kaya & Kaymakçı 2013: fig. 1.1). — **B**: Localities in this study; red star = Yeniyaylacık, white dots = Vallesian localities; blue dots = Turolian localities.

2021), Armour-Chelu and Bernor (2011), Wolf *et al.* (2013), Bernor and Sun (2015), Koufos (2016), Koufos and Vlachou (2005), and 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) 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) proposed *Cormohipparion occidentale* as the source for the Eurasian *Cormohipparion* radiation. *Cormohipparion* occurred in Türkiye (*Co. sinapensis*; Bernor *et al.* 2003), Pakistan (*Cormohipparion* sp.; Bernor *et al.* 2021), Algeria ("*Cormohipparion*" *africanum*; Bernor & White 2009, recognized herein at the generic rank) and arguably Ethiopia (Bernor & White, 2009, Bernor *et al.* 2010, 2021). *Cormohipparion* is a medium-sized hipparion with long preorbital bar (POB), lacrimal extending approximately half-way to preorbital fossa (POF) distal rim; well-developed POF, pocketed posteriorly with well-developed peripheral rim; maxillary cheek teeth with moderate complexity occasionally having opposing borders of pre- and postfossettes linked, particularly in P2; mandibular cheek tooth metaconids and metastylids rounded; 3rd metapodials moderately elongate and slender with midshaft cranial–caudal dimension modestly expanded (for summary *see* 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 include *Hi. primigenium*, *Hi. catalaunicum*, *Hi. intrans*, *Hi. microdon*, *Hi. kammerschmittae*, *Hi. brachypus*, *Hi. malpassii*, perhaps *Hi. giganteum* and *Hi. weihoense* (Bernor *et al.* 2011, 2021). It is a large hipparion with a long POB with lacrimal extending less 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; in the most primitive forms ectostylids appear with moderate frequency; 3rd metapodials are more robustly built than in *Cormohipparion*, *Hipparion sensu stricto* and *Cremohipparion* (for summary *see* Bernor *et al.* 2021).

Hipparion sensu stricto: This 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, 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). Comparative analysis of this genus was found to be more complex in our current analysis of the Cappadocia hipparions in that there has, to date, been insufficient information on the genotype species (*Hipparion prostylum*) postcranial size and proportions. Bernor's definition departs from that of some investigators in not recognizing North American species of *Hipparion sensu stricto*. Bernor (1985) and Bernor *et al.* (1990) argued that any morphologic similarity between North American "*Hipparion*" and Old World *Hipparion sensu stricto* is due to homoplasy. *Hipparion sensu stricto* is characterized by a long POB, lacrimal extending no more than half-way to the POF posterior rim, POF prominent, medially deep with deep to shallow posterior pocket, peripheral rim moderately well developed; maxillary cheek teeth with moderate complexity of pre- and postfossettes; mandibular adult cheek teeth lacking ectostylids; elongate and slender 3rd metapodials. The genus includes *H. gettyi*, *H. prostylum*, *H. dietrichi*, *H. campbelli* and *H. hippidiodus* ranging from France, through Greece and Iran to China (for a complete summary *see* Bernor *et al.* 2021).

Cremohipparion: Representatives of this genus are medium- to small-sized, and the genus is 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*, *Cr. proboscideum*, *Cr. forstenae* and *Cr. licenti* usually express a caninus (= intermediate) fossa between the POF and buccinator fossae, other members of the group do not; cheek teeth with moderately complex enamel plications; mandibular cheek tooth metaconids and metastylids are rounded; 3rd metapodials are elongate and slender. The genus includes *Cr. macedonicum*, *Cr. moldavicum*, *Cr. mediterraneum*, *Cr. proboscideum*, *Cr. matthewi*, *Cr. nikosi*, *Cr. periafricanum*, *Cr. antelopinum*, *Cr. forstenae* and *Cr. licenti* (for complete summary *see* Bernor *et al.* 2021).

Sivalhippus: The genus is recognized in the Indian subcontinent, China and Africa (Bernor *et al.* 2021). Its cranial morphology is characterized by a very long POB, a variable POF (large in *S. nagriensis* and *S. theobaldi* and reduced in *S. perimensis*), large maxillary cheek teeth with complex plications and frequent flattening of the lingual margin of the protocone; mandibular cheek teeth frequently have rounded metaconids and metastylids that are pointed disto-lingually, and 3rd metapodials are robustly built. The genus includes *S. nagriensis*, *S. theobaldi*, *S. anwari*, *S. macrodon*, *S. perimensis*, *S. turkanensis*, *S. platyodus* and *S. ptychodus* (for 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* but currently without a specific genus allocation. We emphasize the need to avoid confusion of well-defined hipparionine lineages with poorly characterized taxa of "*Hipparion*" *sensu lato*.

Comparative samples

The *Co. cappadocium sp. nov.* collection from Yeniyaylacık is housed at the Cappadocia Natural History Research and Application Center of the Nevşehir Hacı Bektaş Veli University. The Yeniyaylacık sample includes 117 specimens including crania, mandibles, teeth and postcranial elements (*see* Supplementary Table 1 at https://doi.org/10.5281/zenodo.10818700). We compared *Co. cappadocium* specimens (crania, 3rd metacarpals and 3rd metatarsals) with those of several Late Miocene North American, Eurasian and African hipparionine species of the genera *Cormohipparion*, *Hippotherium*, *Hipparion sensu stricto*, *Cremohipparion* and *Sivalhippus* (*see* Table 1). We integrated the discrete characters of the crania, mandible and dentition following Bernor *et al.* (2022). The scoring values are reported in Supplementary Table 2 (https://doi.org/10.5281/zenodo.10818700).

Morphometric and statistical analyses

All measurements are in millimeters to the nearest 0.1 mm. Measurement numbers (M1, M2, M3, etc.) refer to those in Eisenmann *et al.* (1988) and Bernor *et al.* (1997) for the crania and postcrania. Tooth measurement numbers refer to those in Bernor *et al.* (1997). PCA (principal component analysis) and $\log_{10}$ ratios were used to analyse the Yeniyaylacık samples and compare them with those of other Late Miocene fossil equid species. PCA was calculated using the R ver. 1.4.1103 (http://www.R-project.org/) function *prcomp* ver. 3.6.2 (https://www.rdocumentation.org/packages/stats/versions/3.6.2/topics/prcomp; Venables & Ripley 2008) and package *ggplot2* ver. 3.3.3 (https://cran.r-project.org/web/packages/ggplot2/index.html; Wickham 2016). Eisenmann (for summary *see* Eisenmann 1995) used $\log_{10}$ ratios to evaluate differences in hipparion metapodial proportions as a basis for recognizing taxa and their evolutionary relationships. This methodology was later used in many studies (Bernor & Armour-Chelu 1999, Bernor & Harris 2003, Bernor & Scott 2003, Bernor *et al.* 2003, 2005, 2010, 2013, 2015, 2020, 2022, Koufos & Vlachou 2005, Gilbert & Bernor 2008, Bernor & Haile Selassie 2009, Bernor & White 2009, Koufos *et al.* 2016, Cirilli *et al.* 2020, 2021, 2023), providing a well-resolved context for Late Miocene, Pliocene and Pleistocene Eurasian and African hipparion assemblages. More recently, Cirilli *et al.* (2021, 2023) applied PCA to 3rd metapodials to unravel the evolutionary relationships between genera and species of hipparions.

PCA was carried out for crania, 3rd metacarpals and 3rd metatarsals (*see* Supple-

Table 1. Late Miocene hipparions used for comparative analyses in this study listed by age, from older to younger.

Species	Locality	Source
Cormohipparion fricki	MacAdams Quarry, Texas, USA; X-Mas Quarry Nebraska, USA	Woodburne 2007, and first author's data
Cormohipparion occidentale	X-Mas Quarry, Nebraska, USA	Woodburne 2007, and first author's data
Cormohipparion matthewi	X-Mas Quarry, Nebraska, USA	Woodburne 2007, and first author's data
Cormohipparion africanum	Bou Hanifia, Algeria	Bernor & White 2009
Cormohipparion sinapensis	Sinap, Türkiye	Bernor *et al.* 2003
Cormohipparion kecigibi	Sinap, Türkiye	Bernor *et al.* 2003
Cormohipparion aff. *sinapensis*	Esme Acakoy, Türkiye	first author's data
Hippotherium primigenium	Inzersdorf, Austria	first author's data
Hippotherium primigenium	Hoewenegg, Germany	Bernor *et al.* 1997, 2022
Hippotherium primigenium	Eppelsheim, Germany	first author's data
Hippotherium catalaunicum	Hostalets de Pierola, Spain	first author's data
Hipparion gettyi	Kopran Maragheh, Iran	Bernor *et al.* 2016
Hipparion aff. *gettyi*	Alban 13 Maragheh, Iran	this study
Hipparion prostylum	Luberon, France	first author's data
Hipparion dietrichi	Samos, Greece	first author's data
Hipparion cf. *dietrichi*	Akkasdagi, Türkiye	Koufos & Vlachou 2006, and first author's data
Eurygnathohippus feibeli	Sahabi, Libya	Bernor *et al.* 2012, 2020, Cirilli *et al.* 2020
Sivalhippus perimensis	Siwalik, Pakistan	Wolf *et al.* 2013
Cremohipparion moldavicum	Taraklia, Moldavia	https://vera-eisenmann.com
Cremohipparion mediterraneum	Pikermi, Greece	first author's data
Cremohipparion matthewi	Samos, Greece	Bernor *et al.* 1996

mentary Table 3 at https://doi.org/10.5281/zenodo.10818700). Third metapodial measurements included in PCA were: 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), and M14 (distal maximum depth of the medial condyle). We extended the application of PCA to crania to characterize the facial morphologies of the genera and species. Two data sets were constructed to carry out PCA on crania. The first included M7 (premolar row length), M8 (molar row length), M9 (upper cheek tooth series teeth length), M30 (length of the naso-incisival notch), M32 (distance between the orbit and the POF), M33 (length of the POF), M35 (height of the POF) and M36 (distance between the POF). The second included the same measurements except M30 (length of the naso-incisival notch). Due to fragmentation of hipparion remains, to include more specimens we created a second data set including lateral facial morphology but excluding length of snout.

In the $\log_{10}$-ratio analysis of 3rd metapodials, we included the same measurements as in PCA, with addition of M7 (maximum diameter of the articular facet for the third carpal/tarsal) and M8 (diameter for the anterior facet for the fourth carpal/tarsal), even though they tend to be variable. The ratios were calculated using the $\log_{10}$-transformed mean values for the Höwenegg *Hippotherium* (= *Hi.*) *primigenium* sample (Bernor *et al.* 1997) as standard, as it 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, mandible, teeth and postcranial elements (Bernor *et al.* 1997, 2022).

Mean ordinated hypsodonty maps

We retrieved the data on large herbivorous mammals (Artiodactyla, Perissodactyla, Proboscidea and Primates) from the NOW database (NOW — Database of fossil mammals, https://doi.org/10.5281/zenodo.4268068, Žliobaite *et al.* 2023) and calculated the mean ordinated crown height for each locality from MN 9 and MN 10 following Fortelius *et al.* (2002) for localities with at least two species with a hypsodonty value. All NOW localities between 11.2 Ma and 8.9 Ma from western Eurasia and North Africa were included. Mean ordinated crown height is a robust proxy for humidity and productivity of the environment 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 them 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 grid borders. The interpolation method employed an inverse distance-weighted algorithm (IDW).

Institutional abbreviations

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); BMNH = British Museum of Natural History, London, UK; MNHNL = Natural History Museum, Musée des Confluénces, 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; PRCI = Paleontological Research Center of Iran, Maragheh, Iran; MNHN = Museum National de Histoire Naturelle, Paris, France; UCBL-FSL = Université Claude Bernard Lyon 1, Paleontological Collection, Lyon, France; YYA = Yeniyaylacık, Cappadocia, Türkiye.

Geology

Türkiye is located at the crossroads of Europe, Asia and Africa. Due to its unique location at this tectonically very active zone, the Anatolian

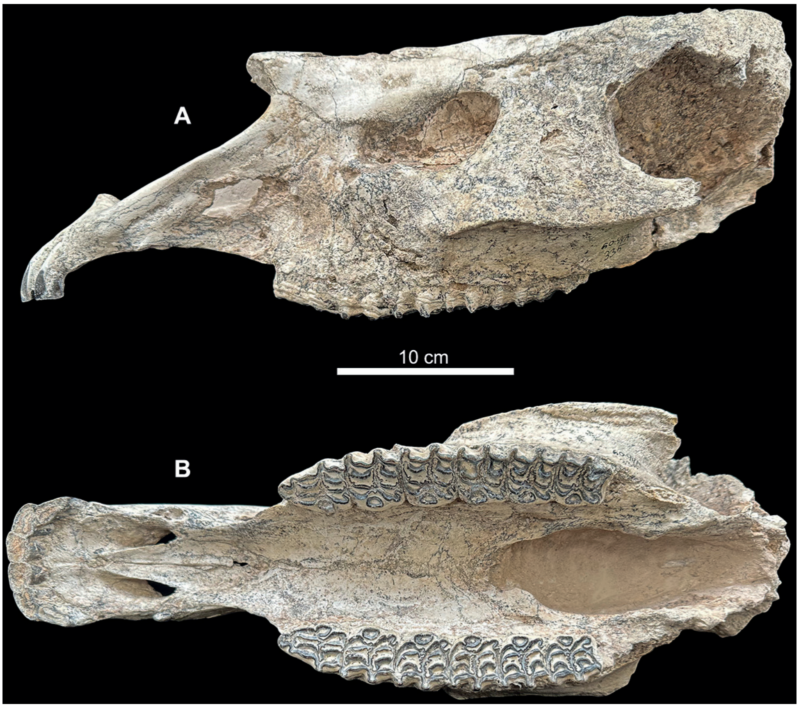

Fig. 2. *Cormohipparion cappadocium* ***sp. nov.*** holotype cranium (50-YYA-335). — **A**: Lateral view. — **B**: Ventral view.

Plateau is divided into two adjacent plateaus. The higher Eastern Anatolian Plateau (EAP) lies in a zone of convergence between the Arabian and Eurasian plates, whereas the Central Anatolian Plateau (CAP) lies on the westward-shifting Anatolian microplate (Fig. 1).

These plateaus are surrounded by geographically diverse terrains with high elevation and low relief topography of the Pontide mountains to the north, the Anatolide–Tauride mountains to the south, and high Eastern Anatolian mountains to the east. The Cappadocia region is located closer to the central part of the CAP and is characterized by the presence of volcanic rocks (lavas, ignimbrites, and pyroclastic deposits) that alternate with fluvio-lacustrine Late Miocene, Pliocene and Quaternary deposits (Aydar *et al.* 2012, Çiner *et al.* 2015). These deposits constitute a unique landscape that characterizes the Cappadocia region. Etymologically, Cappadocia means “the land of beautiful horses”. The Late Miocene and Pliocene ignimbrites cover 20 000 km^2 (Le Pennec *et al.* 1994) and include fossiliferous lenses. The Kızılırmak River, the longest river in Türkiye, and its drainage system has been actively incising the CAP and the Cappadocia region since approx. the last 5.5 Ma (Doğan & Şenkul 2020).

The stratigraphic relations of the CAP ignimbrites have been controversial due to their complex topography, tectonics and geochronology (Aydar *et al.* 2012). Here, we follow the most updated understanding about the geology and geochronology of the CAP (*see* Aydar *et al.* (2012). The CAP is divided into 10 ignimbrite members, and the Yeniyaylacık site is positioned in the Zelve ignimbrite, one of the most spectacular ignimbrites of the CAP (Aydar *et al.* 2012). The Yeniyaylacık mammal fossil-bearing level consists of grey fine sandstone of reworked tuff components including poorly consolidated glass-rich elements. This late Miocene fluvial sequence unconformably overlies the Zelve ingnimbrites and is gradually replaced by lacustrine environments towards the top of the section. The Zelve ignimbrite is mostly beige to pink, and consists of multiple flow units with pumice-ash-rich and lithic-poor horizons. Aydar *et al.* (2012) determined the age of the Zelve ignimbrite to be 9.1 ± 0.1 Ma for based on uranium/lead dating, while according to Lepetit *et al.* (2014) the age range is 10.1–9.8 Ma based on ^{40}Ar/^{39}Ar isoch-

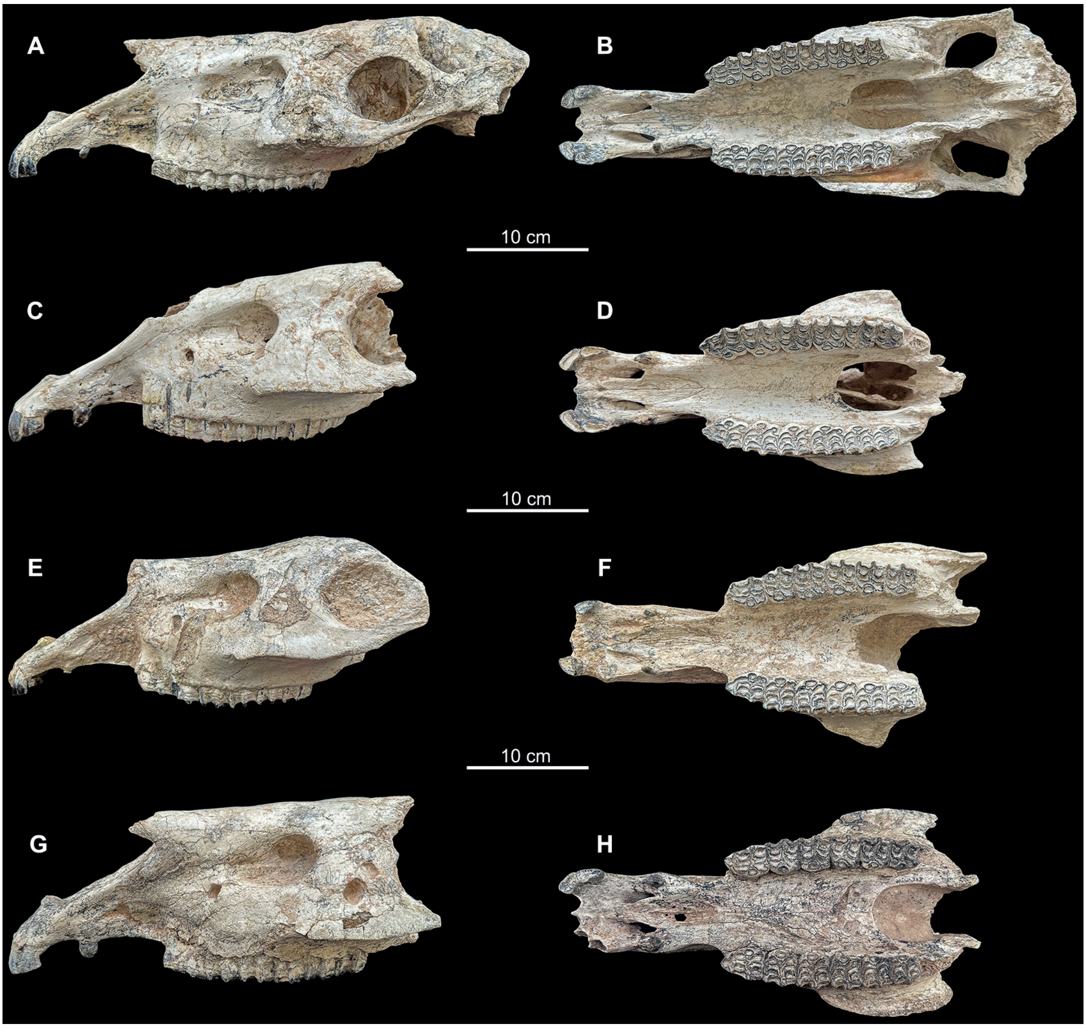

Fig. 3. *Cormohipparion cappadocium* ***sp. nov.*** crania in lateral and ventral view. — **A–B**: 50-YYA-900. — **C–D**: 50-YYA-13. — **E–F**: 50-YYA-102. — **G–H**: 50-YYA-373.

ron. A paleomagnetic age reported by Piper *et al.* (2013) supports the age range given by Aydar *et al.* (2012) of 9.1 ± 0.1 Ma for the Yeniyaylacık mammal fossil bearing level. Currently, the Berkeley Geochronology Center is re-evaluating these ages.

Systematic paleontology

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

Cormohipparion cappadocium sp. nov.

Holotype: cranium 50-YYA-335 (Fig. 2).

Type locality: Yeniyaylacık, Cappadocia, Türkiye.

Age: Vallesian, ca. 9.1 Ma (Aydar *et al.* 2012).

Etymology: Named after Cappadocia, the region in Türkiye where has been discovered.

Referred specimens: crania: 50-YYA-900, 50-YYA-13, 50-YYA-102, 50-YYA-373 (Fig. 3); mandibles: 50-YYA-853, 50-YYA-231, 50-YYA-849, 50-YYA-338, 50-YYA-90, 50-YYA-163 (Fig. 4); 3rd metacarpals: 50-YYA-206,

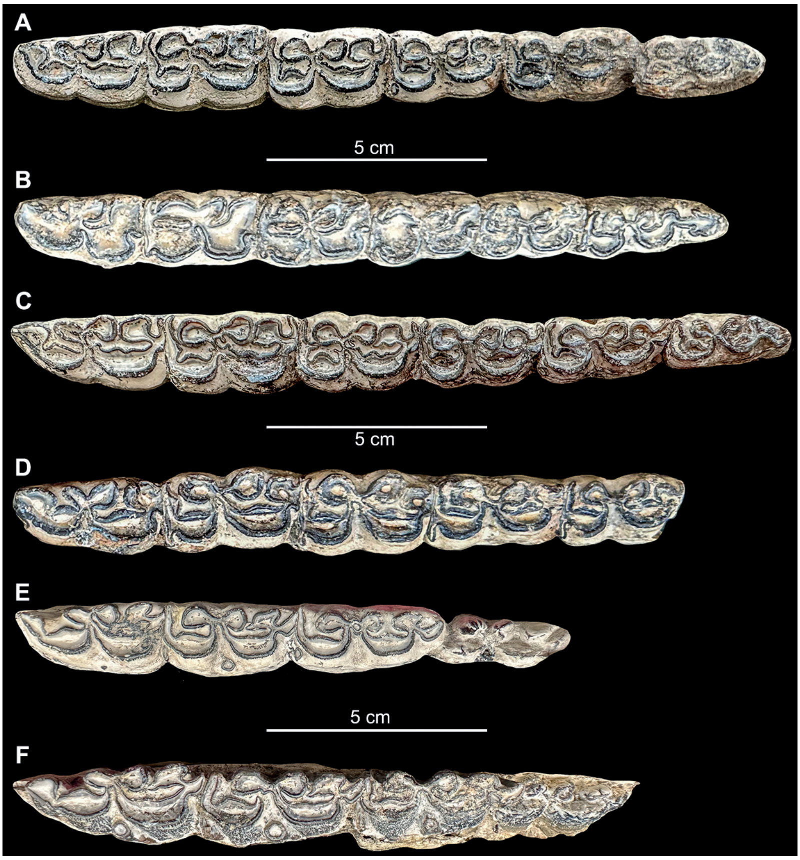

Fig. 4. *Cormohipparion cappadocium* ***sp. nov.*** lower cheek tooth rows in occlusal view. — **A**: 50-YYA-853. — **B**: 50-YYA-231. — **C**: 50-YYA-849. — **D**: 50-YYA-338. — **E**: 50-YYA-90. — **F**: 50YYA-163.

50-YYA-527, 50-YYA-23, 50-YYA-236, 50-YYA-98 (Fig. 5); 3rd metatarsals: 50-YYA-73, 50-YYA-506, 50-YYA-414, 50-YYA-14, 50-YYA-777, 50-YYA-272 (Fig. 6); radii: 50-YYA-203, 50-YYA-122.

Geographic range: Central Anatolia, Türkiye.

Diagnosis. Cranium with long POB having the lacrimal bone placed more than half the distance from the anterior orbital rim to the posterior rim of the fossa; POF is subtriangular shaped and antero-ventrally oriented; POF is deeply pocketed posteriorly, medially very deep, peripheral border very strongly delineated around the entire periphery, anterior rim is present and deeply set; nasal notch is near the anterior border of the P2; maximum molar crown height is 55–60 mm; upper cheek tooth plication frequency is mostly moderately complex; protocone is mostly oval being variously also elongate oval, flattened lingually or rounded; protocone occasionally connected to the protoloph; protoconal spur occasionally present; P2 anterostyle mostly elongate. Mandibular cheek teeth with rounded to elongated premolar metaconids; rounded molar metaconids; premolar metastylids rounded to square-shaped or pointed; premolar metastylid spurs vary from present to absent; molar metastylids rounded to square-shaped; premolar ectoflexid varies from separating to not separating metaconid and metastylid; pli caballinids mostly absent; ectostylids absent on adult but present and rounded in juvenile premolars.

Description. Five following crania from Yeniyaylacık: 50-YYA-335, 50-YYA-900, 50-YYA-13, 50-YYA-102 and 50-YYA-373.

50-YYA-335, type specimen, is a well-preserved adult female cranium with right and left I1–3, small canine and P2–M3 past middle wear

Fig. 5. *Cormohipparion cappadocium* ***sp. nov.*** 3rd metacarpals in cranial and caudal view. — **A**: 50-YYA-23. — **B**: 50-YYA-98. — **C**: 50-YYA-206. — **D**: 50-YYA-236. — **E**: 50-YYA-527.

Fig. 6. *Cormohipparion cappadocium* ***sp. nov.*** 3rd metatarsals in cranial and caudal view. — **A**: 50-YYA-114. — **B**: 50-YYA-73. — **C**: 50-YYA-272. — **D**: 50-YYA-414. — **E**: 50-YYA-506. — **F**: 50-YYA-777.

(Fig. 2). 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); it is deeply pocketed posteriorly (C5A); its medial depth is greater than 15 mm in its deepest place (C6A); POF is strongly expressed around the entire periphery (C8A); its anterior rim 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 (C18B); maxillary cheek tooth plication is moderately complex with shortly amplified plications (in part may be due to advanced age) (C19B). There are no detectable linkages of the opposing margins of the pre- and post-fossettes for any of the cheek teeth (FLink = No); protocone is oval and lingually flattened (C23CE); P2 and M1 have protocone linked to protoloph due to later wear (C24A, P2 and M1); P2 and M1 have reduced, but present, protoconal spurs (seen as linkage in 24; C25 B, P2 and M1); P2 anterostyle is elongate (C28).

50-YYA-900 (Fig. 3A and B) is an adult female cranium with dentition well-worn and past middle wear. Dentition includes right and left I2–I3, small canine, and P2–M3. The cranium is virtually identical to 50-YYA-335 in facial morphology (C1C, C4D, C5A, C6A, C8A, C9A+, C15C). Maximum crown height is estimated as being the same as in 50-YYA-335 (C18C). Dental morphology is likewise similar differing in the reduced plication complexity due to advanced age (C19B–); there is no linkage of the pre- and post-fossettes on any of the cheek teeth (FLink = No); protocone shape is oval/rounded (C23CG); protocone is connected to protoloph in P2, M1, and M2 (C24A); protoconal spur is reduced in P3 and M2 (C25B); P2 anterostyle is less elongate than in 50-YYA-900 (C28B+).

50-YYA-13 (Fig. 3C and D) is an adult male cranium in an earlier stage-of-wear than the two crania described above. This cranium is virtually identical to 50-YYA-335 and 50-YYA-900 in facial morphology (C1C, C4D, C5A, C6A, C8A, C9A+, C15C). Maximum crown height is estimated as being the same as in YYA-335 (C18C). Dental morphology is similar to those of 50-YYA-335 and 50-YYA-900 except cheek teeth are more complex due to an earlier adult stage of wear (C19A); protocone is mostly oval, becoming elongate in the early stage-of-wear M3 (C23CD); protocone has a reduced protoconal spur only on P2 (C25B); P2 anterostyle is elongate (C28A).

50-YYA-102 (Fig. 3E and F) is an adult female cranium in an advanced stage-of-wear. The cranium is virtually identical to 50-YYA-335, 50-YYA-900 and 50-YYA-13 in facial morphology (C1C, C4D, C5A, C6A, C8A, C9A+, C15C). Cheek teeth are very similar to the other advanced cheek tooth worn specimens. Maximum crown height (C18C) and maxillary cheek tooth ornamentation (C19B) are as in 50-YYA-335 and 50-YYA-900; there is no linkage of the cheek tooth pre- and post-fossettes (FLink = No); protocone is round to oval (C23CG); protocone is linked to protoloph in P2, M1 and M2 and incipient in P3 (C24A); protoconal spur is small but apparent in P3 (C25B); P2 anterostyle is elongate (C28A).

50-YYA-373 (Fig. 3G and H) is an adult male cranium with right and left I1–3, C and P2–M3. The cranium is virtually identical to 50-YYA-335, 50-YYA-900 and 50-YYA-13 in facial morphology (C1C, C4D, C5A, C6A, C8A, C9A+, C15C). The maxillary cheek tooth morphology is similar to other specimens with maximum crown height being between 40 and 60 mm (C18A); maxillary cheek tooth ornamentation being moderately complex (C19B); P2 has pre- and post-fossettes closely opposed but not linking (FLink = No); protocone shape is oval but lingually flattened (C23CE); only P2 shows protocone-protoloph linkage (C24A for P2 only); there are no protoconal spurs apparent (C25C); P2 anterostyle is elongate (C28A).

The mandible 50-YYA-853 (Fig. 4A) has premolar metaconid rounded (C32A), molar metaconid square shaped (C33E), premolar metastylid square shaped (C34E), premolar metastylid spur absent (C35B), molar metastylid rounded/square shaped (C36A/E), molar metastylid spur absent (C37B), premolar ectoflexid not separating metaconid and metastylid (C38A), pli caballinid absent (C40C) and ectostylids absent (C43B).

50-YYA-231 (Fig. 4B) is a very worn adult mandibular dentition with right and left p2–m3 that does not preserve characters C32–C37. However, premolar ectoflexid does not separate metaconid and metastylid (C38A), pli caballinids are absent (C40C), and ectostylids are absent (C43B).

50-YYA-849 (Fig. 4C) is a left adult mandibular dentition with p2–m3. Premolar metaconid is rounded to elongate (C32AB), molar metaconid is rounded (C33A), premolar metastylid is rounded (C34A), premolar metastylid spur is variably present/absent (C35A–), molar metastylid is rounded to square-shaped (C36AE), molar metastylid spur is absent (C37B), premolar ectoflexid separates metaconid and metastylid (C38B–), pli caballinid is rudimentary to absent (C40BC) and ectostylids are absent (C43B).

50-YYA-338 (Fig. 4D) is a partial adult female mandible with all incisors, left canine, and p2–m2. The premolars are rounded to elongate (C32AB), molar metaconids are rounded (C33A), premolar metastylid is rounded to pointed except where it is missing (C34AF), premolar metastylid spur is absent C35B), molar metastylids are rounded (C36A), molar metastylid spurs are absent (C37B), premolar ectoflexid separates metaconid and metastylid on p2 and p3 (C38B), pli caballinid is absent (C40C) and ectostylids are absent (C43B).

50-YYA-90 (Fig. 4E) is a right juvenile mandible with dp2–4 and m1 just emerging in its crypt. Deciduous premolars have rounded to elongate metaconids (C32AB); metastylids are rounded (C34A); ectoflexids separate metaconid and metastylid (C38B); pli caballinids are absent (C40C); ectostylid is tiny on dp2; large and rounded on dp3 and missing on dp4 (C43AB).

50-YYA-163 (Fig. 4F) is a left juvenile mandible with dp2–m1 (emerging). The premolar metaconids are rounded to elongate (C32AB); metastylids are rounded (C34A), metastylid spurs are absent (C35B); pli caballinids are absent (C40C); ectostylids are present and round on all deciduous premolars (C43A). The m1 is not yet fully erupted and worn.

Third metacarpal: The Yeniyaylacık mc3s (Fig. 5) are not very elongated and the proximal end has medium-sized articular facets for the second and fourth metacarpals, as well as a flat articular surface for the magnum and a deep articulation for the unciform and the Mc4. At the distal extent of the Mc3, the width of the epiphysis (M11), the supra-articular protuberances (M10) have almost the same dimensions as the medial and lateral condyles (M13, M14), with well-developed crista sagittalis in between (M12) (*see* Supplementary Table 1 at https://doi.org/10.5281/zenodo.10818700).

Third metatarsal: The Yeniyaylacık mt3s (Fig. 6) are elongated and slender. The proximal end has medium-sized articular facets for the second and fourth metatarsal, a flat articular surface for the cuneiform, and a deep articulation for the cuboid and the mt4. At the distal extent of the Mt3, the supra-articular protuberances (M10) are almost of the same size as the condyles (M11) (*see* Supplementary Table 1 at https://doi.org/10.5281/zenodo.10818700), with a prominent crista sagittalis between the medial and lateral condyles.

Cormohipparion sinapensis Bernor *et al.*, 2003

Holotype: AS 93/826 (Fig. 7A).

Type locality: Sinap Loc. 108.

Age: Late Miocene, early Vallesian (MN 9), 10.8–10.1 Ma.

Referred specimens: cranium: SEN 1 (Fig. 7B); p4: AS 92/618; 3rd metacarpal: AS 92/228, AS 93/604A, AS 92/238; 3rd metatarsal: AS 93/9, AS 92/240, AS 93/1213, AS 93/332.

Referred localities: Sinap Locs. 94, 108, 108/8 (between Locs. 108 and 8), and 91.

Geographic range: Central Anatolia, Türkiye.

Emended diagnosis. A medium-sized hipparionine; POB long with anterior limit of the lacrimal being placed more than one-half the distance from the anterior orbital rim to the posterior rim of the POF; POF subtriangular shaped and anteroventrally oriented, deeply pocketed posteriorly, deep medially, with well-delineated peripheral border outline and prominent anterior rim; dP1 persistent and functional; maxillary cheek teeth strongly curved mediolaterally, moderately high-crowned having a maximum crown height estimated to be between 40 and 50 mm; P2 with linked pre- and post-fossettes; fossette ornamentation moderately complex; posterior wall of postfossette variably distinct or confluent with posterior enamel wall, pli caballinid varies from complex to double, hypoglyph frequently encircled in earlier wear becoming moderately incised later in wear; protocone shape variably oval to lingually flattened-labially rounded; protocone isolated until later wear frequently becoming connected to the protoloph, protoconal spur absent; P2 anterostyle variably elongate to short and rounded; mandibular cheek teeth lacking metastylid spur; premolar ectoflexid not separating metaconid/metastylid; pli caballinid absent; protostylid absent on occlusal surface but vertically placed lying flush with protoconid enamel band; ectostylids absent in adult cheek teeth; premolar linguaflexid with deep V-shaped, preflexid and postflexid with simple margins; limbs elongate and slightly built compared to *Hi. primigenium.*

Remarks. Bernor *et al.* (2003) reported *Co. sinapensis* from the lowest Sinap stratigraphic units with hipparion, Loc. 94 (formerly 10.551 Ma adjusted to 10.8 Ma). *Cormohipparion sinapensis* is known from an adult and unworn p4, AS 92/618. This individual has a very low crown height (maximum height ca. 40–45 mm), which is remarkably low crowned for an Old World hipparion. Loc. 108, approximately 25 m higher in the section (ca. 10.3 Ma), has produced a partial hipparion skeleton (AS 93/826), including a fragmentary cranium, which was assigned as the type specimen for *Co. sinapensis.* This taxon is further recognized by a cranium collected by Şenyürek at a locality stratigraphically intermediate between Locs. 108 and 8 designated as Loc. 108/8. A metatarsal, AS 93/9 (Loc. 91) was also identified as *Co. sinapensis* by Bernor *et al.* (2003).

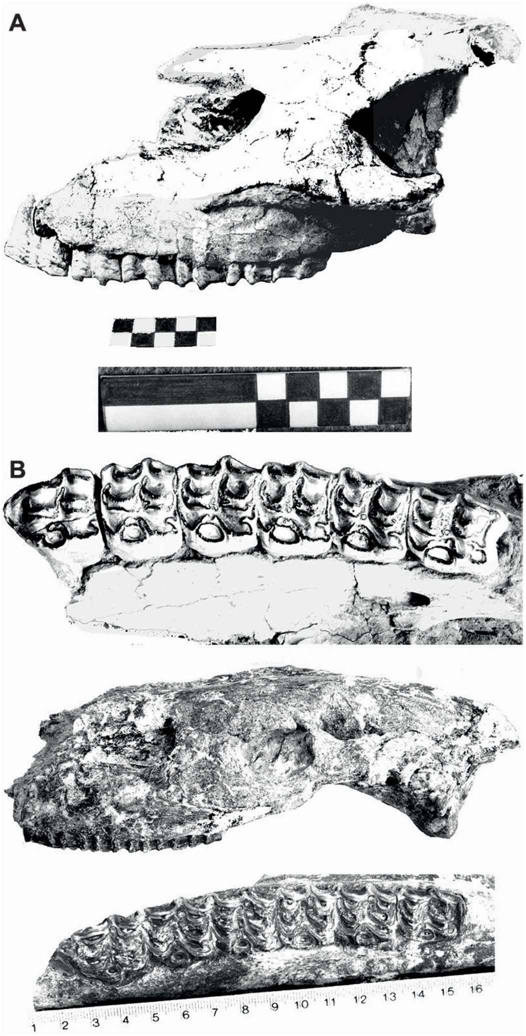

Fig. 7. *Cormohipparion sinapensis* from Sinap, Türkiye (modified from Bernor *et al.* 2003: fig. 11.15). — **A**: cranium (AS 93/826) in lateral and occlusal view. — **B**: SEN 1 in lateral and occlusal view.

Cormohipparion sinapensis is smaller than *Hi. primigenium* from Höwenegg, Eppelsheim and Inzersdorf, and exhibits some primitive characters compared with that species. *Cormohipparion sinapensis* mostly shares primitive cranial characters with *Hi. primigenium* and North American *Co. occidentale* (Bernor *et al.* 2003, 2021). Woodburne (1996) reported that the dP1 is large and functional in the more primitive *Cormohipparion* species, *Co. quinni.* In fact, *Co. sinapensis* and the Eppelsheim and Höwenegg hipparions all have dP1 morphologies that compare closely with *Co. quinni* (Bernor *et al.* 1997 2022, Woodburne 1996: 17, fig. 9, type specimen F:AM 71888 from Devil's Gulch Member, Valentine Formation, late Barstovian, Brown County, north central Nebraska, ca. 13–12.5 Ma). *Cormohipparion sinapensis* differs from both *Co. occidentale* and *Hi. primigenium* in the following characters: the peripheral rim of the POF is well-delineated (but not complete anteriorly due to breakage of the cranium) and the maxillary cheek teeth are lower crowned (a primitive feature). As is with North American *Co. occidentale*, *Co. sinapensis* exhibits linkage of P2 fossettes, less complex fossette plications than *Hippotherium*, shorter P2 anterostyle and has a tendency to link protocone with the protoloph in later wear more frequently than *Hippotherium.* Bernor *et al.* (2003, 2021) argued that *Co. sinapensis* is distinct from central and western European *Hi. primigenium* and may well be derived from an earlier member of the *Co. occidentale* group (*sensu* Woodburne 1996) than is represented from the X-Mas Quarry, Hans Johnson Quarry, and MacAdams Quarry sam-

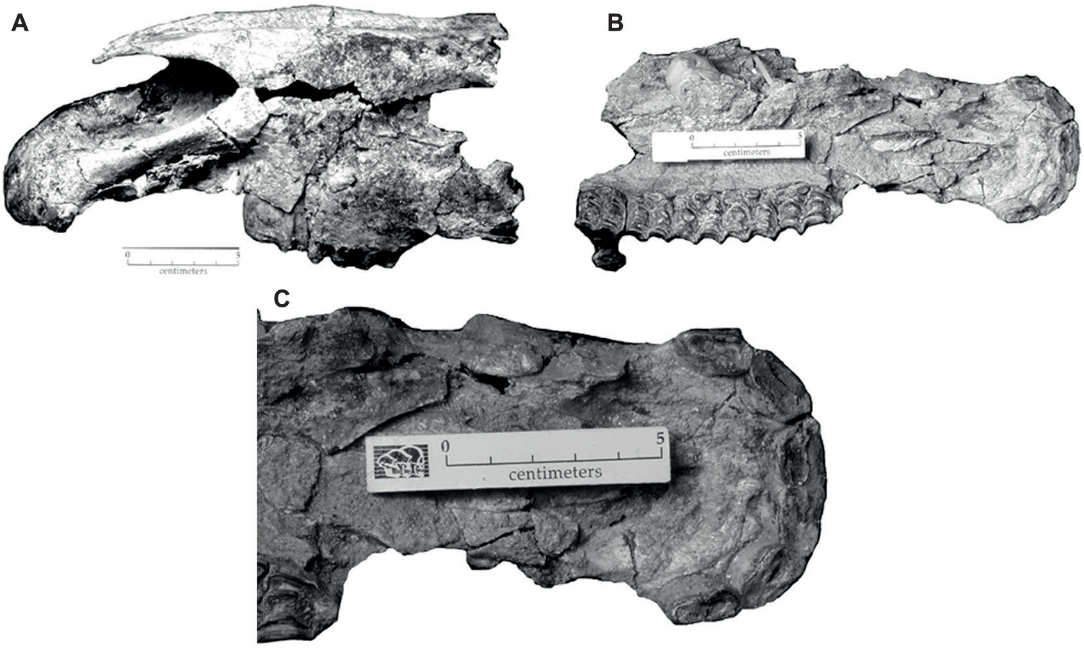

Fig. 8. *Cormohipparion kecigibi* cranium (MNHN-TRQ 9001) from Sinap, Türkiye (from Bernor *et al.* 2003: 11.18).

ples, but similar to *Co. occidentale* type 1 from X-Mas Quarry (*see* Woodburne 1996: 47).

Cormohipparion kecigibi Bernor *et al.*, 2003

"*Hipparion*" *kecigibi* Bernor *et al.*, 2003; Bernor *et al.* 2003: 269, fig. 11.18.

Holotype: MNHN-TRQ 9001 (Bernor *et al.* 2003: fig. 11.18A–C; *see* also Fig. 8).

TYPE locality: Sinap Loc. S01.

AGE: Late Miocene, early Vallesian (MN 9), 9.683 Ma.

REFERRED SPECIMENS: cranium: MNHN-TRQ 9002; 3rd metacarpasl: AS 93/840, MNHN-TRQ 1125, MNHN-TRQ 1127, MNHN-TRQ 1129; 3rd metatarsals: AS 92/251, MNHN-TRQ 1160, MNHN-TRQ 1163, MNHN-TRQ 1164, MNHN-TRQ 1168.

GEOGRAPHIC RANGE: Central Anatolia, Türkiye.

EMENDED DIAGNOSIS. A medium-sized hipparion with a short, wide snout; POF subtriangular shaped and anteroposteriorly oriented, deeply pocketed posteriorly, medially deep, with moderately delineated peripheral border outline and no anterior rim; nasal notch retracted nearly to P2; maxillary cheek teeth strongly curved mediolaterally, moderately high-crowned, having an estimated mesostyle height 45 mm, fossette ornamentation moderately complex, posterior wall of postfossette distinct, pli caballinid double, hypoglyph deeply incised, protocone oval and isolated from the protoloph; protoconal spur occurs as weakly formed on P2 but absent on other cheek teeth except early wear M3; premolar and molar protocone more lingually placed than hypocone except in early wear M3.

REMARKS. The type specimen (MNHN-TRQ 9001) is a well-preserved cranium and it is conservative, resembling both *Hi. primigenium* and *Co. occidentale* in most of its characters. It is like *Co. sinapensis* in its moderately prominent peripheral border outline. It differs from *Hi. primigenium*, *Co. occidentale* and *Co. sinapensis* in its POF subtriangular shape with an anteroposterior orientation. The maxillary cheek teeth of MNHN-TRQ 9001 and MNHN-TRQ 1064 are very similar and similar to *Co. occidentale* and *Co. sinapensis* in their moderately complex fossettes and isolation of the protocone. MNHN-TRQ 9001 and MNHN-TRQ 1064 are similar to *Hi. primigenium* in their occasional occurrence of a reduced protoconal spur. *Cormohipparion kecigibi* is markedly variable in pli caballinid morphology. Protocone shape is mostly oval.

Cormohipparion kecigibi is also characterized by its short snout proportions. Bernor *et*

Fig. 9. *Hipparion gettyi* cranium NHMW 2015/0238/0001 (KNHM-RLB 8401 in Bernor 1985). — **A**: lateral view. — **B**: occlusal view.

al. (2003) reported that short snout length (M1) accompanied with expanded width (M15) proportions are functionally significant, in that they reflect feeding adaptation and suggest an adaptation for short grass feeding. MNHN-TRQ 9001 has a POF depth dimension that is greater than those of the X-mas Quarry sample of *Co. occidentale*. Specimen MNHN-TRQ 9001 also has P2, M2, and M3 exposed in the maxilla, allowing mesostyle height measurements. Although this specimen is in a rather early wear stage, its crown heights are low: P2 = 29.8 mm, M2 = 32.5 mm, and M3 = 32.3 mm. In this primitive characteristic, *Co. kecigibi* is similar to *Co. sinapensis*.

Hipparion gettyi Bernor, 1985

Hipparion sp. 3 Bernor *et al.*, 1979; Bernor *et al.* 1979: 94, fig. 1.

Hipparion sp. 3 Campbell *et al.*, 1980; Campbell *et al.* 1980: 841.

Hipparion sp. Bernor *et al.*, 1980; Bernor *et al.* 1980: 723, fig. 8.

Hipparion sp. (Kopran horse) Woodburne *et al.*, 1981; Woodburne *et al.* 1981: 1343, fig. 5d.

Hipparion sp. Bernor and Hussain, 1985; Bernor and Hussain 1985: 36, fig. 3d.

HOLOTYPE: cranium NHMW 2015/0238/0001 (KNHM-RLB 8401 in Bernor 1985) (Fig. 9).

TYPE LOCALITY: Kopran, Maragheh, Iran.

AGE: Circa 9.0 Ma, late Vallesian, MN 10.

REFERRED SPECIMENS: Cranium: NHMW no number, an old adult palate with right P3–M3 and left P3-M3; Upper dentition: MMTT 41/2464, lt. M1; MMTT 41/2211, lt. P4; MMTT 41/2220, lt. M2; MMTT 41/2248, lt. M1; MMTT 36/2022, rt. P2; MMTT 41/2213, rt. dP3 or 4; MMTT 41/2216, rt. dP3 or 4; Mandible: NHMW A4866, young adult female mandible with i1–m3; right i1–p2; Lower dentition: MMTT 41/2224, lt. p2; MMTT 41/2519, lt. p4; MMTT 41/2234, lt. p4; MMTT 36/2027, lt. p2; 41/2225, rt. m2; 43/2489, rt. m1; 43/2484, lt. m1 (Bernor 1985).

EMENDED DIAGNOSIS. A medium-sized species of *Hipparion* with a long POB; lacrimal does not invade POF; POF is antero-posteriorly long, egg-shaped and antero-posteriorly oriented, dorsoventrally deep, with strong posterior pocketing, medially deep with a faint anterior rim and having moderately expressed peripheral outline. Nasal notch is placed above the P2 anterostyle. Adult cheek teeth have moderately complex plications of the pre- and post-fossettes; pli caballinids are persistently double; hypoglyphs are deeply incised; protocones are moderately elongate; P2 anterostyle is elongate. An uncertainly associated 3rd metapodial from Kopran is slender and elongate.

DESCRIPTION. A medium-sized species. Bernor (1985) named and described the NHMW and MMTT material referred to *H. gettyi* which we briefly summarize herein. The type specimen is a cranium, NHMW 2015/0238/0001 (Fig. 9A and B). This specimen is of a moderately-sized old female *Hipparion* with a small canine. The cranium is virtually complete except for the posterior orbits and posterior and inferior cranium. The snout is moderately long, the nasals are shallowly retracted to the P2 anterostyle. The POB is long with the distalmost lacrimal being well posterior to the POF (C1C). The POF is relatively large, subtriangular shaped and anteroventrally oriented (C4D), moderately pocketed posteriorly (C5B), medial depth is somewhat reduced from being deep (C6A/B,) peripheral outline is well defined until the anterior end where it loses its definition altogether (C8 A/B), anterior rim is lacking (C9B); nasal notch is at the anterior limit of P2 (C15C); maximum crown height is approximately 50 mm (C18C); cheek tooth fossette ornamentation is moderately complex with fewer, more shortly amplified, thinly banded plications (C19B); cheektooth fossettes are not linked (FLink = No); protocone is oval with some lingual flattening (C23CE); protocone is isolated from protoloph (C24B); only P2 expresses a very reduced protoconal spur (C25 P2 = B); anterostyle is short and rounded (C28B). The ventral view reveals that the type cranium has all teeth preserved and half of the crown is worn in at least one of them; this clearly is an older individual. The incisors have well-defined infundibula that are irregularly shaped and fill the central portion of the occlusal surface. Both canines are complete and small, indicating that this individual is a female.

Bernor (1985) described an unnumbered NHMW fragmentary maxilla of an old individual from Kopran, Maragheh, which has very worn cheek teeth that are not easily referred to any species. Also, there is a young adult female mandible in the NHMW collection from Kopran with the following salient characters: elongate anterostylid, metaconid and metastylid subequal in size and with rounded to slight angular shape, pli caballinids absent, and linguaflexids shallow on all teeth.

The Lake Rezaiyeh Expedition collected a number of maxillary and mandibular cheek teeth from Kopran. Bernor (1985) reported the following salient features for this sample which agree with the type specimen: maximum crown height is 50 mm; protocone shape in early wear is elongate, labially rounded and lingually flattened with a generally elongate-oval shape; pre- and post-fossette plications are moderately complex and the bands are thicker than in the type; hypoglyph is deeply incised. Mandibular cheek teeth have the following salient features: maximum recorded crown height is 44 mm; pli caballinid is absent; ectoflexid is generally not deep; linguaflexid is moderately deep; metaconid and metastylid vary in shape, being generally rounded to squared.

REMARKS. The type specimen of *H. gettyi* was collected by Pohlig from Kopran in the later half of the 19th century. Kopran I and II occur in the westernmost portion of the Maragheh Basin where the local exposures are currently encroached upon by the expanding town of Maragheh. The Kopran localities are the lowest fossil levels of the section (150–120 m below loose chippings of Campbell *et al.* 1980 and Mirzaie Atabaadi *et al.* 2013). Bernor (1985) referred maxillary cheek teeth to *H. gettyi*, these being collected by the Lake Rezaiyeh Expedition from the 150 to 70 m levels. Mirzaie Ataabadi *et al.* (2013) revised the biostratigraphy and chronology of the Maragheh sequence, indicating that Kopran I occurs at the –150 m level and Kopran II occurs at the –120 m level, and they have interpolated ages of 8.967 and 8.7216 Ma, respectively. These ages are correlative with European MN10, the late Vallesian.

Hipparion gettyi has approximately the same size as *Co. sinapensis*, it has a less well-developed POF than *Co. sinapensis*, and it has cheek teeth that have less elongate protocones than *Co. sinapensis.* There are a number of cranial and dental features that unite *H. gettyi* with *Cormohipparion* including a lack of deeply incised nasal bones, a long POB, a medially deep and distally deeply pocketed POF, maxillary cheek teeth with relatively complexly plicated fossettes and persistently double pli caballinids. Third metapodials are thus far unknown for *H. gettyi*, which makes comparisons to species of *Hippotherium* and *Cormohipparion* untenable. Morphologically, *H. gettyi* appears to be derived from *Cormohipparion* and a precursor to other more advanced members of *Hipparion sensu stricto* including *H. prostylum*, *H. dietrichi* and *H. campbelli* (Bernor *et al.* 2016, 2021).

Hipparion aff. *gettyi*

Locality: 13 Aban, Maragheh, Iran.

Age: ca. 9.0 Ma, late Vallesian, MN10.

Referred specimens: cranium: PRCI M1014, PRCI M1015; 3rd metacarpal: N17; 3rd metatarsals: N18, N19, N20, N21, N24.

Description. There are two crania from 13 Aban, Lower Maragheh, recently collected by the staff of MMTT from 13 Aban just outside the town of Maragheh (37°24´13.2´´N, 46°16´28.4´´E). 13 Aban is located at an elevation of 1570–1580 m, near the Jahangir village (Zahanjegh in Bernor 1986; Fig. 2). We estimate that this locality is 140 to 150 m below the Loose Chippings marker bed very close to Lower Maragheh localities MMTT 41 and 43, and therefore circa 9.0 Ma.

PRCI M1014 (Fig. 10A and B) is a partial cranium of undetermined sex with damaged snout that preserves the nasals, right orbit and POF morphology. PRCI M1015 (Fig. 11A and B) is a partial old male cranium with snout, facial region, partial orbit, left canine and P2–M3 and right canine and P4–M3 preserved.

Cranium PRCI M1014 (Fig. 10A and B) has POF as in *H. gettyi*, with a long preorbital bar and lacrimal placed more than half the distance from the anterior orbital rim to the posterior rim of the fossa (C1C). POF is subtriangular-shaped and anteroventrally oriented (C4D) with no posterior pocketing (C5C), moderate medial depth (C6B) and POF peripheral border outline being moderately delineated around its periphery (C8B) and lacking an anterior rim altogether (C9B). The nasal notch (C15C) is near the mesial border of P2. The dP1 is absent (C16C) and maximum crown height was 40–60 mm (C18C). The right maxilla preserves P3–M3 in advanced wear with fossette ornamentation being simplified by advanced wear (C19C), with non-linkage of fossettes (FLink = No); pli caballinid is poorly expressed (C19B) protocones are rounded (C23G); P3, M1, and M2 protocones exhibit linkage with the protoloph (C24AB); protoconal spur is absent (C25C). P2 morphology is not preserved (C28NA).

Cranium PRCI M1015 (Fig. 11A and B) has virtually an identical morphology to cranium PRCI M1014 (*see* Supplementary Table 2 at https://doi.org/10.5281/zenodo.10818700). Together with PRCI M1014, these two crania exhibit a POF that is relatively reduced in posterior pocketing and medial depth and as such are advanced toward the condition seen in *Hipparion* aff. *prostylum* (Bernor 1985, Bernor *et al.* 2021).

Results

Principal Component Analysis

In the case of crania with snout length included (M30 in Eisenmann *et al.* 1988 and Bernor *et al.* 1997), PC1 and PC2 accounted for 42.1% and 28.8% of the variation, respectively (Fig. 12A; for summary *see* Supplementary Table 3 at https://doi.org/10.5281/zenodo.10818700). PC1 separated specimens with longer upper cheek tooth rows (negative values) from shorter cheek tooth rows (positive values). Specimens with longer snout (M30), longer POF (M33) and dorsoventrally deeper POF (M35) grouped on the positive side of PC2, whereas specimens with more elongated POB (M32) and reduced POF dorsoventral dimension placed more distant from the maxillary crest (M36) grouped on the negative side of PC2.

PCA defined 3 morphospaces (Fig. 12A): first including the genus *Cremohipparion* (greater positive values of PC1 and PC2); second including the genus *Hippotherium* (greater negative values of PC1 and positive PC2); and third including the genera *Cormohipparion* and *Hipparion sensu stricto* (smaller positive to negative values of PC1 and PC2).

The Turkish *Co. cappadocium* was placed close to North American *Co. fricki* (MacAdams

Fig. 10. *Hipparion* aff. *gettyi* PRCI M1014. — **A**: lateral view. — **B**: occlusal view.

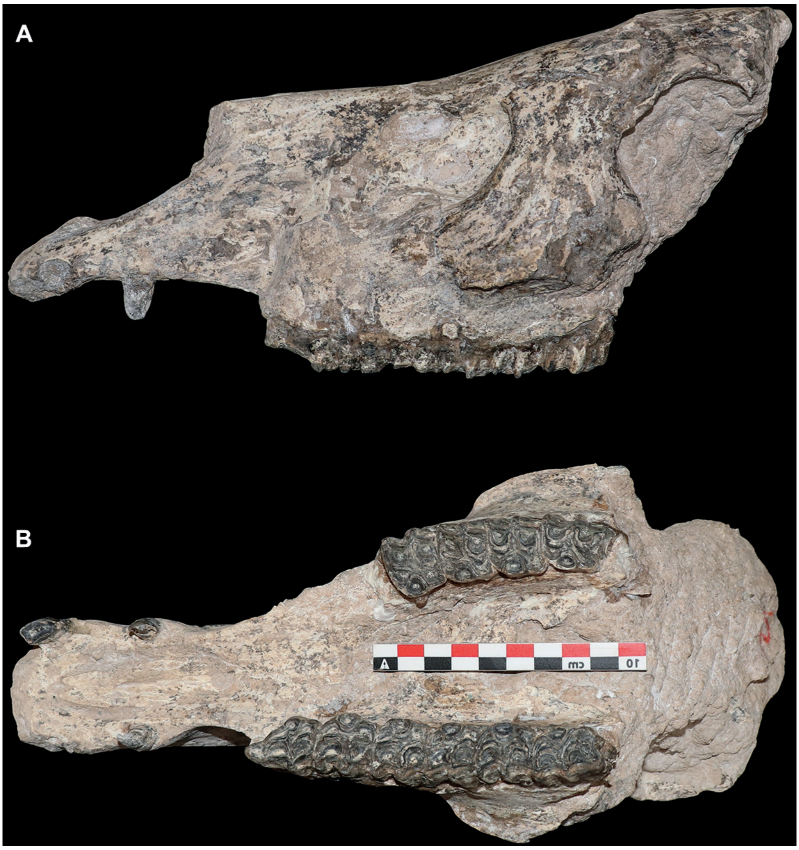

Fig. 11. *Hipparion* aff. *gettyi* PRCI M1015.— **A**: lateral view. — **B**: occlusal view.

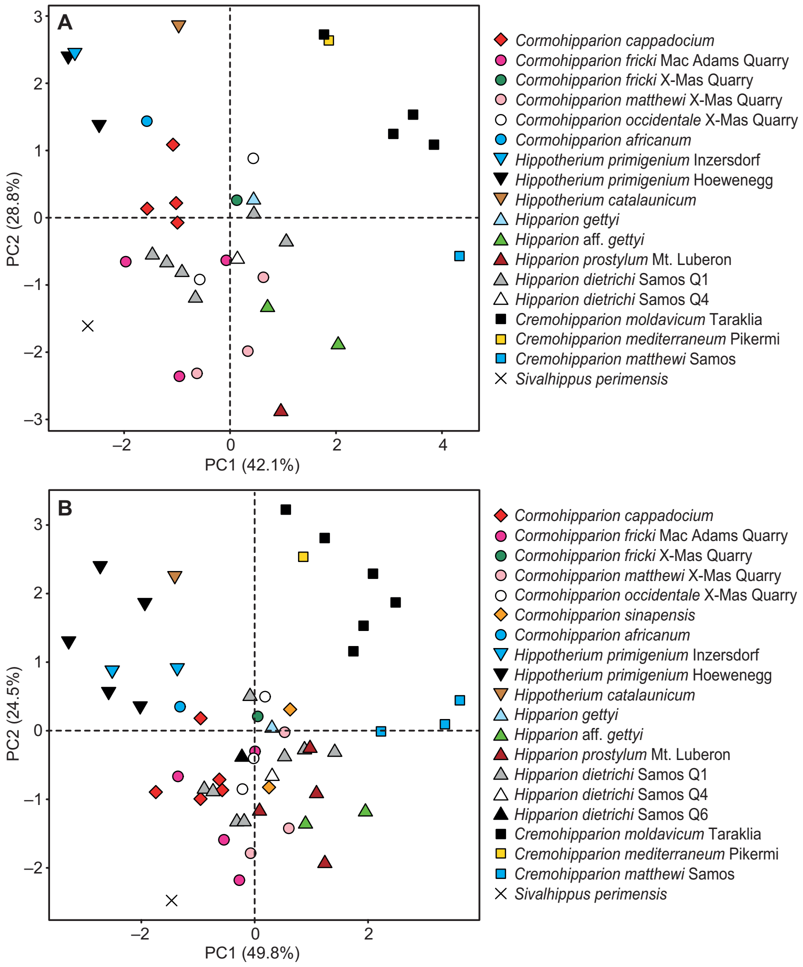

Fig. 12. Results of principal component analysis (PCA) on crania (**A**) with and (**B**) without the length of snout (M30, length of the naso-incisival notch, incl) included in calculations.

and X-Mas quarries), *Co. occidentale* (X-Mas Quarry) and *Co. matthewi* (X-Mas Quarry) (Fig. 12). This species is larger than them, as is *Co. africanum* from Bou Hanifia.

Hipparion dietrichi from Samos Quarry 1 included another specimen referred to *H. dietrichi* from Samos Quarry 4 (AMNH 22860); altogether Samos *H. dietrichi* was highly variable along PC1 and less so along PC2 (Fig. 12A). The type cranium of *H. gettyi* from Lower Maragheh was placed close to that of the Samos *H. dietrichi*, whereas the cranium of *H. prostylum* from Mt. Luberon (France, UCBL-FSL 590001) was separated from this cluster by its reduced snout length. The new crania from Lower Maragheh (PRCI M1014 and PRCI M1015) were referred to *Hipparion* aff. *gettyi* and placed between the Samos *H. dietrichi* and *H. prostylum*, included in the morphospace defined by the genera *Cormohipparion* and *Hipparion sensu stricto* This supports our interpretation that *Hipparion sensu stricto* is directly related to *Cormohipparion.*

Hippotherium primigenium from Inzersdorf was placed close to *Hi. primigenium* from Höwenegg, whereas the type cranium of *Hi. catalaunicum* was placed at the far end of PC2 being distinct from *Hi. primigenium* from Höwenegg but still within the range of variation of the *Hippotherium* group (Fig. 12A).

Crania of *Cremohipparion mediterraneum* from Pikermi plotted within the range of variability of *Cremohipparion moldavicum* from Taraklia, at high values for both PC1 and PC2 (Fig. 12A). *Cremohipparion matthewi* from Samos (AMNH 22908) is the smallest species and it was placed close to the *Cremohipparion* cluster at very high PC1 and modest PC2 values (Fig. 12A).

In case of crania with snout length excluded, PC1 and PC2 accounted for 49.8% and 24.5% of the variation, respectively (Fig. 12B; for summary *see* Supplementary Table 3 at https://doi.org/10.5281/zenodo.10818700). The two axes separated the same clusters as in Fig. 12A, but with a larger comparative sample. PC1 separated specimens with longer upper cheek tooth rows (negative values) from shorter cheek tooth rows (positive values). Specimens with longer POF (M33) and taller POF (M35) grouped on the positive side of PC2, whereas those with more elongated POB (M32) and reduced POF grouped on the negative side of PC2.

Also in this case PCA defined 3 morphospaces (Fig. 12B): the first one including the genus *Cremohipparion* (positive of PC1 values and negative-to-positive PC2 values); the second one including the genus *Hippotherium* (negative values of PC1 and positive PC2); and the third one including the genera *Cormohipparion* and *Hipparion sensu stricto* (smaller positive to negative values of PC1 and PC2).

Turkish *Co. cappadocium* and *Co. sinapensis* grouped together with the North American *Co. fricki* (MacAdams and X-mas quarries), *Co. occidentale* (X-mas Quarry) and *Co. matthewi* (X-mas Quarry) (Fig. 12B). *Cormohipparion cappadocium* and *Co. africanum* from Bou Hanifia are larger than the North American *Cormohipparion* species, although here *Co. africanum* was plotted closer to the range of variability of *Hippotherium*.

Like the other species of *Cormohipparion*, *Co. sinapensis* occupied a space very close to *Hipparion sensu stricto* (*H. dietrichi*, *H. gettyi* and *H. prostylum*) (Fig. 12B). The range of variability of *H. dietrichi* from Samos Quarry 1 included specimens referred to *H. dietrichi* from Samos Quarry 4 (AMNH 22860) and Quarry 6 (AMNH 22990), all varying greatly along PC1. Also the type cranium of *H. gettyi* from Lower Maragheh fitted within this range, whereas the crania of *H. prostylum* from Mt. Luberon, France (BMNH 26617, BMNH M33603, UCBL-FSL 590001, MNHNL 156), plotted close to that of the smallest *H. dietrichi* from Samos (AMNH 20626, AMNH 20692, AMNH 94905) on the positive side of PC1. Also as reported above, the new crania from Lower Maragheh (PRCI M1014 and PRCI M1015) referred to *Hipparion* aff. *gettyi* plotted close to *H. prostylum*, being included in the morphospace defined by the genera *Cormohipparion* and *Hipparion sensu stricto* (Fig. 12B).

Hippotherium primigenium from Inzersdorf and *Hi. catalaunicum* plotted within the range of variability of *Hi. primigenium* from Höwenegg (Fig. 12B). *Hippotherium catalaunicum* overlapped with *Hi. primigenium* from Höwenegg, supporting their close evolutionary relationship.

Cremohipparion mediterraneum from Pikermi (MNHN P259), plotted within the range of variation of *Cr. moldavicum* from Taraklia, whereas *Cr. matthewi* from Samos, the smallest of the entire sample, was placed close to the *Cremohipparion* cluster (Fig. 12B).

The cranium of *Sivalhippus perimensis* was separated from those of the genera *Cormohipparion* and *Hipparion sensu stricto* by its more elongated POB and reduced POF, and was placed at the lowest PC2 values (Fig. 2B).

In case of 3rd metacarpals (Mc3s), PC1 and PC2 accounted for 69.5% and 11.5% of the variation, respectively (Fig. 13A; for summary *see* Supplementary Table 3 at https://doi.org/10.5281/zenodo.10818700**)**. PC1 clustered specimens by size, from smaller (negative PC1 values) to larger (positive PC1 values), whereas PC2 separated specimens from shorter and stouter (negative values) to more elongated and more slender (positive values). Mc3 proportions clearly distinguished the two *Cormohipparion* species from the X-Mas Quarry. *Cormohipparion occidentale* is slender, and *Co. matthewi* is smaller and even more slender than *Co. occidentale* being similar in size to the smallest Eurasian *Cr. matthewi* from Samos (Fig. 13A). The X-Mas Quarry *Co. occidentale* sample overlapped with the Turkish *Co. sinapensis* and *Co. kecigibi* samples, whereas Eşme Akçaköy *Co.* aff. *sinapensis* which is slightly larger, plotted close to the larger *Co. occidentale* individuals, as well as *Co. africanum* from Bou Hanifia (Fig. 13A). The *Hi. primigenium* sample from Inzersdorf overlapped with the larger individuals of *Co. occidentale* and the smallest *Hi. primige-*

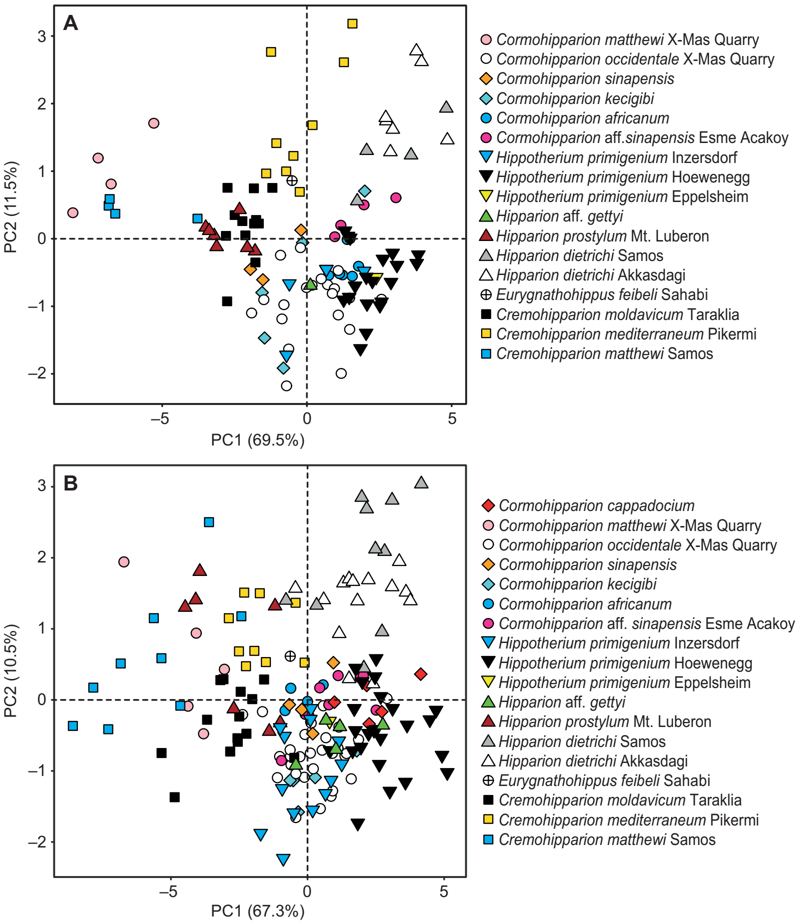

Fig. 13. Results of principal component analysis (PCA) on (**A**) 3rd metacarpals, and (**B**) 3rd metatarsals.

nium from Höwenegg, whereas the *Hi. primigenium* from Eppelsheim and Höwenegg grouped together (Fig. 13A). *Hipparion dietrichi* from Samos and Akkaşdağı overlapped, being the largest of the *Hipparion* and *Cremohipparion* species. Mt. Luberon *H. prostylum* overlapped with *Cr. moldavicum* from Taraklia (Fig. 13A). *Eurygnathohippus feibeli* from Sahabi plotted within the lower range of Pikermi *Cr. mediterraneum*. Mc3 of *Hipparion* aff. *gettyi* from 13Aban, Lower Maragheh (associated with the other 2 crania analysed earlier) was included in the range of variability of X-Mas Quarry *Co. occidentale* (Fig. 13A).

In case of 3rd metatarsals (Mt3s), PC1 and PC2 accounted for 67.3% and 10.5% of the variation, respectively (Fig. 13B; for summary *see* Supplementary Table 3 at https://doi.org/10.5281/zenodo.10818700**)**. PC1 clustered individuals by size, from smaller (negative values) to larger (positive values), whereas PC2 separated specimens from shorter and stouter (negative values) to more elongated and more slender (positive values). These results mirror the ones for Mc3s with only slight differences. *Cormohipparion occidentale* and *Co. matthewi* from X-Mas Quarry were again well discriminated, the latter being smaller and more slender than *Co. occidentale*, close in dimensions to *Cr. matthewi* from Samos (Fig. 13B). *Cormohipparion occidentale* from the X-Mas Quarry overlapped with the Turkish *Co. sinapensis* and *Co. kecigibi*, *Co.* aff. *sinapensis* from Eşme Akçaköy and *Co. cappadocium*, although *Co. cappadocium* is the largest of all *Cormohipparion* species analysed herein (Fig. 13B). *Cormohipparion africanum* grouped with *Cormohipparion*, and was well separated from *Hippotherium*.

Hippotherium primigenium from Inzersdorf and Eppelsheim overlapped with *Co. occidentale* which is smaller and more slender than the smallest *Hi. primigenium* from Höwenegg (Fig. 13B). As in the case of Mc3 (Fig. 13A), *H. dietrichi* from Samos and Akkaşdağı overlapped being the largest of the *Hipparion* and *Cremohipparion* species (Fig. 13B). On the other hand, *H. prostylum* from Mt. Luberon overlapped with *Cr. moldavicum* (Taraklia) and *Cr. mediterraneum* (Pikermi) (Fig. 13B). *Eurygnathohippus feibeli* from Sahabi plotted close to Pikermi *Cr. mediterraneum* and to *Co. africanum*. Mt3 of *Hipparion* aff. *gettyi* from 13Aban, Lower Maragheh (associated with the other 2 crania analysed earlier) were included in the ranges of variability of *Co. occidentale* and *Hi. primigenium* from Höwenegg and Inzersdorf, and plotted close to the other *Cormohipparion* species (*Co. sinapensis*, *Co. kecigibi*, *Co. cappadocium*) (Fig. 13B).

Log_{10} ratios

Comparing the *Hi. primigenium* Höwenegg Mc3 $\log_{10}$ mean values to those for *Hi. primigenium* from Inzersdorf and Eppelsheim (Fig. 14A), we found that the latter two had slightly narrower midshaft widths (M3). In the Inzersdorf specimen also the lower proximal epiphyseal width (M5) was smaller than the Höwenegg mean. The Eppelsheim specimen was quite similar to the Höwenegg one with slightly elevated values of proximal depth (M6) and distal epiphyseal width (M10) (Fig. 14A). These deviations from the Höwenegg mean were, however, minor and insufficient to distinguish them at the species level.

Cormohipparion kecigibi from Sinap (Fig. 14B) has short Mc3 maximum length (M1) and narrow midshaft width (M3) that contrasts with a greater midshaft depth (M4) relative to other measurements than the Höwenegg $\log_{10}$ mean. It compares closely to Sinap *Co. sinapensis* (Fig. 14B). *Cormohipparion* aff. *sinapensis* from Eşme Akçaköy shows a similar pattern to that of *Co. sinapensis* but is slightly larger in size. X-Mas Quarry *Co. occidentale* has a similar shape to that of Sinap *Cormohipparion* (Fig. 14B). *Cormohipparion africanum* is closely similar to Sinap *Cormohipparion* and likewise is more slender than the Höwenegg, Inzersodorf and Eppelsheim *Hi. primigenium.* X-Mas Quarry *Co. matthewi* is substantially smaller and more slender-limbed than all the other taxa shown in Fig. 14B, retaining an elongated length (M1) and reduced diaphysis, proximal and distal epiphyses (Fig. 14B).

Mc3 of Yeniyaylacık *Co. cappadocium* was not analysed using PCA because of the absence of data on the distal epiphysis (M11–M14). This species is characterized by long (M1) dimensions, narrow midshaft width (M3) and sharply contrasting large midshaft depth (M4). Proximal epiphysis width (M5) and depth (M6) as well as distal width (M10 and M11) are similar to those of the Höwenegg standard (*see* Fig. 14C).

In *Hipparion sensu stricto* (Fig. 14D), *H. prostylum* has an elongated and very slender Mc3 morphology (high relative M1 and low M3), small proximal and distal epiphyses (M5–M6 and M10–M14), and it is the smallest species in this sample. New *Hipparion* aff. *gettyi* from 13Aban is similar in length to *H. prostylum* but has less slender midshaft width dimension (M3) and tracks higher for M4–M14 (Fig. 14D). The dimensions of *H. dietrichi* from Samos and Akkaşdağı are very similar to one another, lengths (M1) being greater than those in *H. prostylum* and *H.* aff. *gettyi*, and relatively greater dimensions M5, M6, M12 and M13 (Fig. 14D).

Cremohipparion species are slender-limbed with midshaft width (M3) being particularly narrow and having very sharply contrasting midshaft depth (M4) (Fig. 14E). *Cremohipparion moldavicum* and *Cr. mediterraneum* are virtually identical in their dimensions while *Cr. matthewi* also has elongated dimensions (high relative M1) but is distinctly smaller than the other two species.

As noted by Scott *et al.* (2005) Inzersdorf *Hi. primigenium* has an overall more slender Mt3 morphology than the Höwenegg sample. The Eppelsheim sample has smaller dimensions midshaft width (M3) and depth (M4) as well as proximal epiphyseal width (M5) (Fig. 15A).

Cormohipparion kecigibi has a short Mt3 maximum length (M1) compared with that of *Co. sinapensis*, but with the same dimensions for diaphysis and proximal and distal epiphy-

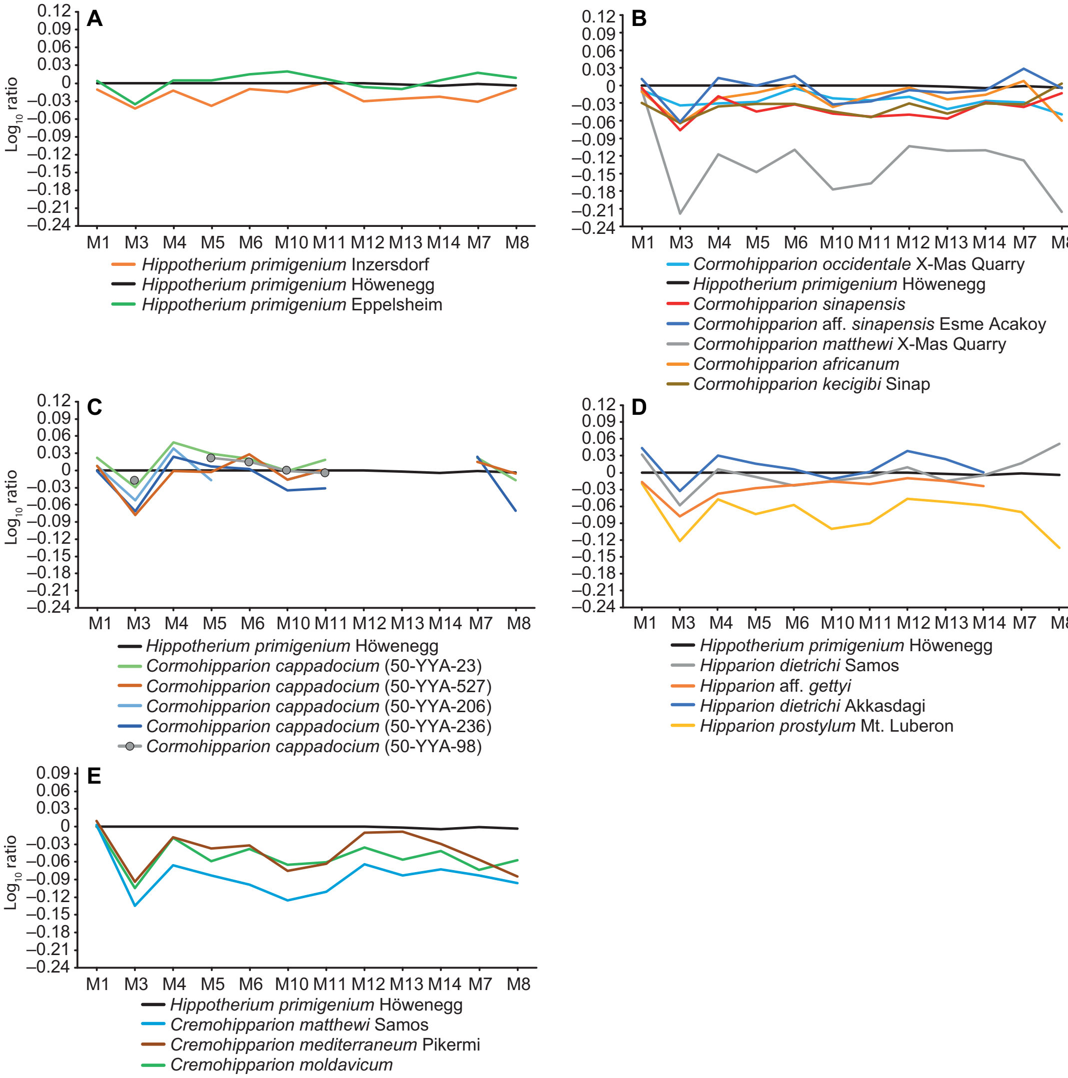

Fig. 14. Results of $\log_{10}$-ratio analysis on 3rd metacarpals of *Hippotherium*, *Cormohipparion*, and *Hipparion* using that of *Hippotherium primigenium* Höwenegg as standard. The following samples are represented by mean values: *Hippotherium primigenium* Höwenegg (n = 29), *Hi. primigenium* Inzersdorf (n = 4), *Cormohipparion occidentale* X-Mas Quarry (n = 23), *Co. matthewi* X-Mas Quarry (n = 4), *Co. africanum* (n = 11), *Co. sinapensis* (n = 3), *Co.* aff. *sinapensis* Esme Acakoy (n = 7), *Co. kecigibi* Sinap (n = 4), *Cremohipparion moldavicum* (n = 17), *Cr. matthewi* Samos (n = 8), *Cr. mediterraneum* Pikermi (n = 16), *Hipparion dietrichi* Samos (n = 5), *H. dietrichi* Akkasdagi (n = 16), *H. prostylum* Mt. Luberon (n = 24), *Hipparion* aff. *gettyi* (n = 1).

ses (Fig. 15B). *Cormohipparion sinapensis*, *Co. africanum* and *Co.* aff. *sinapensis* all compare closely to X-Mas Quarry *Co. occidentale.* X-Mas Quarry *Cormohipparion matthewi* is a tiny and very slender species, with a relatively elongated M1, and reduced diaphysis dimensions accompanied with reduced proximal and distal epiphysial dimensions (Fig. 15B).

Mt3 of Yeniyaylacık *Co. cappadocium* are similar with only 50-YYA-73 having greater dimensions of midshaft width (M4), distal epiphyseal width (M10), midsagittal keel (M12) and distal articular depth (M14) (Fig. 15C); we consider this to be normal variability. *Cormohipparon cappadocium* has dimensions similar to those of the other *Cormohipparion* species

(Fig. 15B), characterized by greater maximum length (M1), reduced midshaft width (M3) and deep midshaft depth (M4).

Among *Hipparion sensu stricto* species (Fig. 15D), *H. prostylum* is characterized by having an elongated and very slender Mt3 morphology (long M1 and narrow M3, in relative terms), and small proximal and distal epiphyses (M5–M6 and M10–M14). *Hipparion dietrichi* from Samos and Akkaşdağı have more elongated and more robust Mt3 than *H. prostylum*. *Hipparion* aff. *gettyi* from 13 Aban, Lower Maragheh have a shorter Mt3 maximum length (M1), with the dimensions of the diaphysis (M3 and M4), the proximal width (M5) and distal ends (M10 and M11) being similar to those of *H. dietrichi* (Fig. 15D). Overall, these *Hipparion sensu stricto* species are also similar to *Cormohipparion*, supporting the close evolutionary relationship between *Cormohipparion* and *Hipparion sensu stricto* in terms of the crania (Fig. 15D).

Pikermi *Cr. mediterraneum* and Taraklia *Cr. moldavicum* track each other very closely suggesting a close evolutionary relationship (Fig. 15E). *Cremohipparion matthewi* from Samos has a similar Mt3 length (M1) but it is much more slender than *Cr. mediterraneum* and *Cr. moldavicum*, making it the smallest *Cremohipparion* species in our sample. *Cremohipparion* differs from *Hipparion sensu stricto* in having an overall more slender shape. We believe that these dimensions evolved convergently because the facial morphology differs between *Hipparion sensu stricto* and *Cremohipparion*, the former having reduced and the latter relatively large POFs (Fig. 12).

Overall, the results of the $\log_{10}$-ratio analyses (Figs. 14–15) are similar to those of PCA (Fig. 13).

Hipparion Vallesian diversification: Subparatethyan Province and central Europe

The oldest documented western Eurasian hipparions originated from Pannonian C horizons of the Vienna Basin, Austria (Bernor *et al.* 2017). The localities include Gaiselberg, Atzesldorf and Mariathal being between 11.4 and 11.0 Ma, with Mariathal being the youngest. These collections are almost entirely limited to cheek teeth and in the cases of Gaiselberg and Atzelsdorf these teeth have lost their cementum diagenetically. The primitive dental features found in the Pannonian C sample include low maximum crown height (mostly around 50 mm except in Mariathal which is slightly elevated), relatively high incidences of a pli protocone, connection of the protocone to protoloph, flattening of the protocone, confluence of opposing borders of the pre- and postfossette, incidence of mandibular pli caballinids and ectostylids on the permanent cheek tooth dentition.

Ectostylids occur rarely in *Hi. primigenium* from Höwenegg and are absent from the adult dentition of other Old World hipparion lineages except Plio–Pleistocene African *Eurygnathohippus* where they are persistent and increase in length, width and height from the late Miocene to the Pleistocene (Bernor *et al.* 2021). Because the Vienna Basin Pannonian C hipparions had the derived feature of complex plications of the cheek tooth crown, Bernor *et al.* (2017) referred the taxon to *Hippotherium* sp. This result compares closely to an earlier study based on smaller data set (Woodburne 2009) in citing a potential ancestral morphotype from the California Punchbowl Formation taxon *Cormohipparion* sp. The paleodiet (based on the mesowear method) showed that Pannonian C hipparions ranged from browsers to mixed feeders and non-extreme grazers (Bernor *et al.* 2017).

Bernor *et al.* (1988) described and analysed the Pannonian D and E hipparions from the Vienna Basin and referred them to *Hi. primigenium.* The cranium of these hipparions (as in NHMW A4229) had a lateral maxilla with a long preorbital bar and lacrimal placed half the distance between the orbit and POF; the POF was large, anteroventrally oriented, dorsoventrally extensive, medially deep and deeply posteriorly pocketed. The cheek teeth were typical for *Hippotherium* with relatively low crown height and complex plications of the pre- and post-fossettes; fossette-opposing borders were not connected; pli caballinids were multiple, protocones oval and occasionally lingually flattened. The lower cheek teeth have elongated anterostylid for p2; premolars have rounded metaconids and metastylids lacking metastylid spurs; molars have

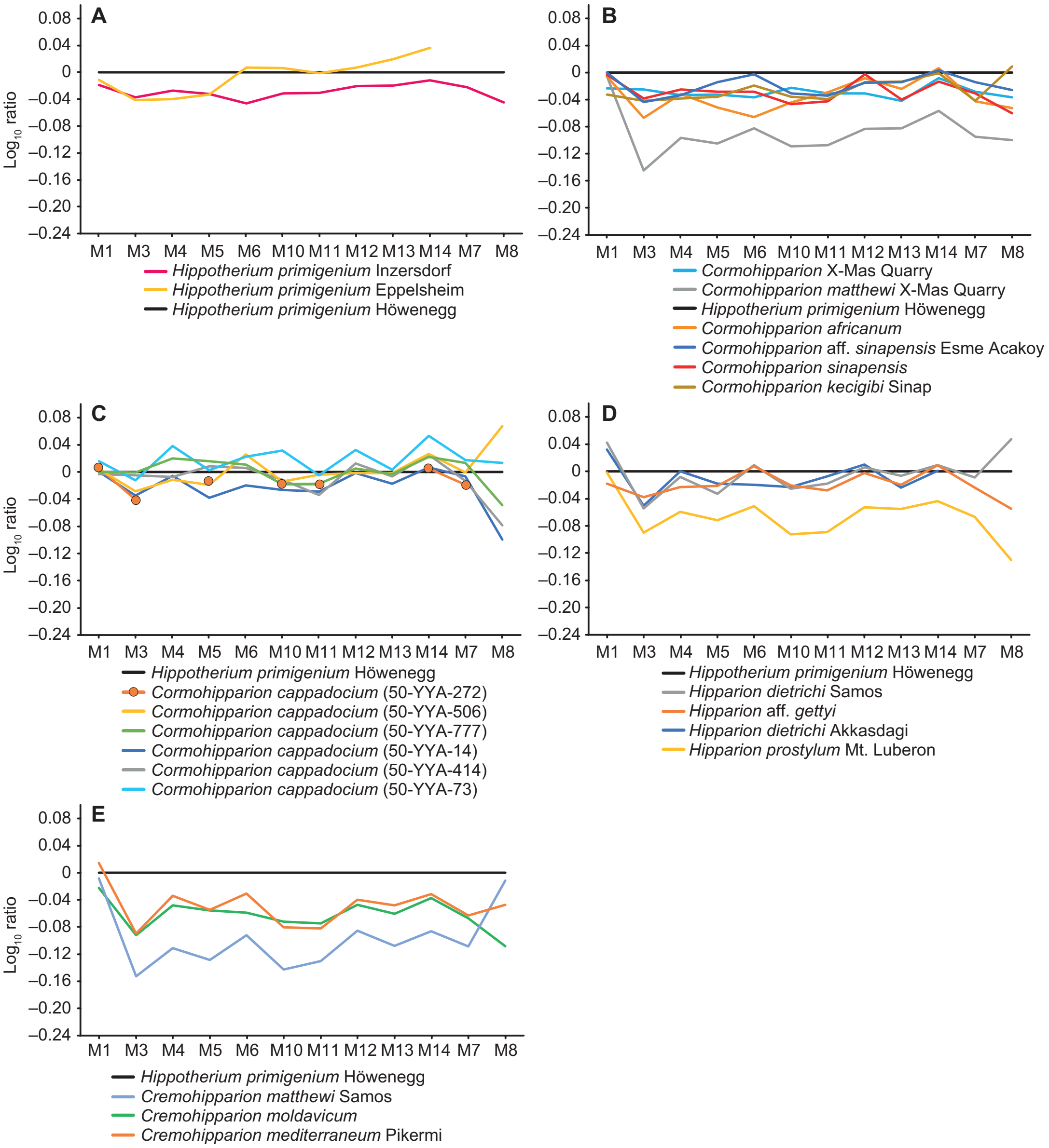

Fig. 15. Results of $\log_{10}$ ratio analysis on 3rd metatarsals of *Hippotherium*, *Cormohipparion*, and *Hipparion* using that of *Hippotherium primigenium* Höwenegg as standard. The following samples are represented by mean values: *Hippotherium primigenium* Höwenegg ($n = 37$), *Hi. primigenium* Eppelsheim ($n = 2$), *Hi. primigenium* Inzersdorf ($n = 14$), *Cormohipparion* X-Mas Quarry ($n = 36$), *Co. matthewi* X-Mas Quarry ($n = 7$), *Co. africanum* ($n = 16$), *Co. sinapensis* ($n = 4$), *Co.* aff. *sinapensis* Esme Acakoy ($n = 12$), *Co. kecigibi* Sinap ($n = 5$), *Cremohipparion moldavicum* ($n = 19$), *Cr. matthewi* Samos ($n = 10$), *Cr. mediterraneum* Pikermi ($n = 16$), *Hipparion dietrichi* Samos ($n = 12$), *H. dietrichi* Akkasdagi ($n = 35$), *H. prostylum* Mt. Luberon ($n = 33$), *Hipparion* aff. *gettyi* ($n = 5$).

rounded metaconids and squared metastlyids; linguaflexid is shallow on the premolars and separate metaconid–metastylid on the molars; there are no ectostylids apparent (*see* specimen NHMW 1985IX Sk 1357)

Scott *et al.* (2005) study of the Pannonian D–E hipparion postcrania reported that while the Inzerdorf cheek teeth were similar to those of *Hi. primigenium* from Germany, the Mc3 and Mt3 had proportions that were more similar to those

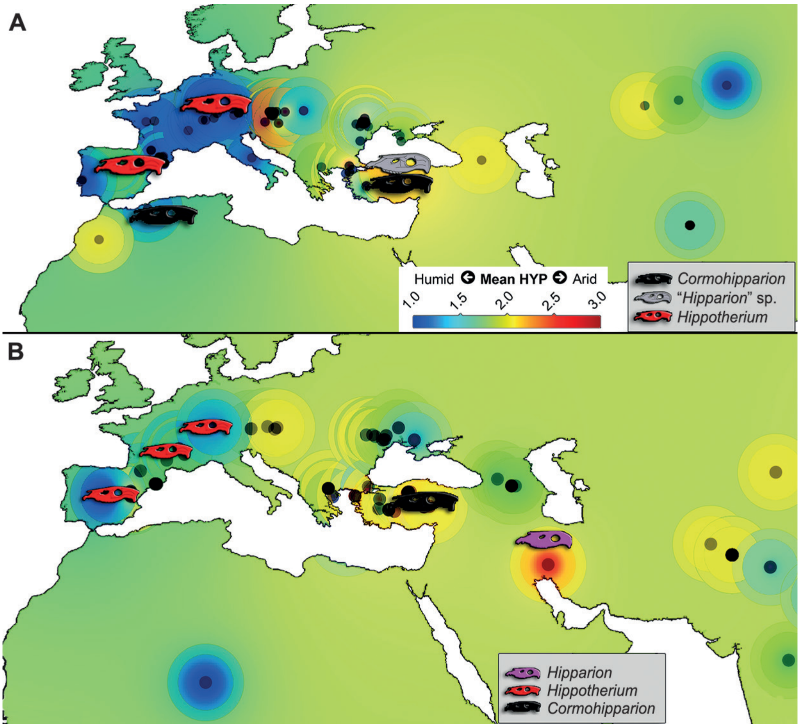

Fig. 16. Paleogeographic, paleoclimatic and ecological maps of (**A**) MN9 (11.2–9.9 Ma) and (**B**) MN10 (9.9–8.9 Ma) hipparions included in this study. Paleoclimatological conditions based on mean ordinated hypsodonty (HYP; the scale in **A** also applies to **B**) are visualised with the colour gradient from blue (humid) to red (arid).

of Sinap *Co. sinapensis* than the Höwenegg hipparion. Those observations agree with our results. The Pannonian D–E populations were found in a densely wooded habitat that offered mixed diet resources (Bernor *et al.* 1986).

Bernor *et al.* (1997) presented a detailed description of the Höwenegg hipparion based on 14 skeletons excavated by Tobien and Joerg (Tobien 1986). While this monograph included precise line drawings, Bernor *et al.* (2022) published the first digital images of crania, mandibles and dentitions. The crania exhibit considerable variability in their facial dimensions, but overall POB is long, POF length and height are great with ventral border of POF closely approaching the facial maxillary crest, more so than in North American and Turkish *Cormohipparion*, which was reconfirmed by us. Maximum cheek tooth height is slightly more than 50 mm, cheek tooth fossette linkage occurs rarely and only on the P2 (Ho C skeleton; Bernor *et al.* 2022). Cheek tooth fossette ornamentation is complex; protocone shape is mostly oval with some lingual flattening; protocone linkage to protoloph only occurs rarely in extremely worn cheek teeth, protocone spur is absent; P2 anterostyle is mostly elongated. In the mandibular cheek teeth premolar and molar metaconids are rounded, premolar metastylid is rounded and metastylid spur is present; molar metastylid is mostly square-shaped and molar metastylid spur is absent; premolar ectoflexid varies in its separation of metaconid and metastylid; ectostylids are very rare occurring only on HLMD Ho486 (*see* Bernor *et al.* 2022: fig. 7c). Höwenegg *Hi. primigenium* is advanced as compared with North American *Co. occidentale* and Turkish *Co. sinapensis*, *Co. kecigibi* and *Co. cappadocium* in the increased dorsoventral height of the POF, more complex plications of the cheek teeth and more elongate protocones. The X-Mas Quarry 3rd metapodials are more slender than the Höwenegg ones and at the same time more similar to the Turkish and Algerian *Cormohipparion* samples.

The Bou Hanifia hipparion is the oldest reported African hipparion. It occurs in the Anaseur Formation, Bou Hanifia, Algeria, which includes 300 m of sediments. There are two K/Ar dates from near the base of the Bou Hanifia section, 12.18 ± 1.03 Ma (Ameur *et al.* 1976) and 12.03 ± 0.25 Ma (Sen 1989). The Bou Hanifia mammal-bearing horizons are located 100 m above the ash levels and have been evaluated magneto-stratigraphically as 10.5 Ma for the "*Hipparion*"-bearing horizons (Bou Hanifia 1; Sen 1989; Harland *et al*. 1982). Bernor and White (2009) referred the Bou Hanifia 1 "*Hipparion*" to "*Co.*" *africanum*. The cranium and cheek tooth lengths of the Bou Hanifia hipparion are smaller, but overlap with the Höwenegg *Hi. primigenium* in POB and POF length, but POF is less dorso-ventrally extensive being placed further from the facial-maxillary crest. The Bou Hanifia cheek teeth have elongate-oval protocones; P2 anterostyle is elongate; premolar metaconid and meatastylid are rounded; premolar metastylid spur is present only on p2; molar metastylid is rounded; pli caballinids are absent; there are no ectostylids on the mandibular cheek teeth. Maximum crown height has been reported as being 60 mm. Third metacarpals and 3rd metatarsals are slenderer than in the Höwenegg horse and similar to Sinap *Co. sinapensis*. Our analysis supports our referral of this hipparion to *Co. africanum* based on our integrated cranial, dental and postcranial analysis.

Cormohipparion exhibits greater species diversity in the Vallesian age than previously reported (Fig. 16A and B). We verified that Sinap has a genuine occurrence of *Cormohipparion* in the identification of *Co. sinapensis*, based on integrated cranial and postcranial analyses. We further recognize *"H." kecigibi* as being a genuine *Cormohipparion*, *Co. kecigibi*. New discoveries from Yeniyaylacık have extended the chronologic range of *Cormohipparion* towards more recent time with our recognition of *Co. cappadocium* in the late Vallesian age, ca. 9.1 Ma. The paleogeographic and paleoclimatic mapping of these results are represented for Vallesian age biochronologic units MN9 and MN10 of western Eurasia (Figs. 16A, MN9; and 16B, MN10). MN9 *Hippotherium* sp. has been identified in the Vienna Basin, *Hi. primigenium* in Germany, *Hi. catalaunicum* in Spain, *Co. sinapensis*, *Co. kecigibi*, *Co.* aff. *sinapensis* and "*Hipparion*" sp. in Türkiye; MN10, *Hippotherium* in central Europe and Spain; *Co. cappadocium* in Türkiye; *Hipparion gettyi* and *Hipparion* aff. *gettyi* in Iran.

Our analyses of cranial and dental morphology along with morphometric analysis suggest that *H. gettyi* is an early member of the *Hipparion sensu stricto* clade (after Woodburne & Bernor 1980, Bernor *et al.* 1996, Bernor *et al.* 2021). The type specimen of *H. gettyi* is more primitive in its POF morphology than the two new specimens of *Hipparion* aff. *gettyi*, which in turn would appear to be slightly more primitive than Middle Maragheh *Hipparion* aff. *prostylum* (Bernor *et al.* 2021). A study of *H. dietrichi* cranial morphological variation is needed to determine whether or not Middle Maragheh *Hipparion sensu stricto* is better referred to *H. dietrichi* or *H. prostylum.*

Conclusions

Just as Kurtén (1952) demonstrated ecologically bound provinciality in the late Miocene of China, Bernor (1979, 1983, 1984) and Bernor *et al.* (1996, 2021) demonstrated provinciality in Late Miocene western Eurasian mammal faunas, and in particular in the evolutionary diversification and dispersion of hipparionine horses. This contribution amplifies the provincial differences between the Subparatethyan Turkish-Iranian Vallesian and central western-Eurasian Vallesian provincial hipparion faunas.

A further analysis of the Sinap Vallesian age faunas revealed that there are two species of *Cormohipparion*: *Co. sinapensis* and *Co. kecigibi.* The 9.1 Ma Yeniyaylacık fauna produced the youngest recorded *Cormohipparion* in Eurasia and Africa, *Co. cappadocium sp. nov.* Our analyses of crania, dentitions, Mc3 and Mt3 led us to conclude that *Cormohipparion* shares an evolutionary relationship with *Hipparion sensu stricto* in MN10. *Cormohipparion cappadocium sp. nov.* has a cranial and postcranial morphology that precedes Lower Maragheh *Hipparion gettyi*, which in turn precedes *Hipparion* aff. *gettyi* and then Mt. Luberon *Hipparion prostylum* (the genotype species for *Hipparion sensu* *stricto*) and Middle Maragheh *Hipparion* aff. *prostylum* (Bernor *et al.* 2021).

The initial explosive radiation of hipparion species in the Vallesian Sinap faunas (Bernor *et al.* 2003) would appear to also share phyletic relationships with the genus-level clades *Cremohipparion* and *Eurygnathohippus.* This part of our work is continuing 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).

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