

The Hipparionini horses (Equidae, Perissodactyla, Mammalia) from the Late Pliocene of Jradzor (Armenia)

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Abstract

Three fossiliferous horizons of the Late Pliocene (MN15–early MN16) locality of Jradzor in Armenia have yielded numerous well-preserved dental and postcranial remains of Hipparionini. Based on anatomical comparisons and allometric analyses, all described specimens are attributed to “*Hipparion*” *longipes*. The systematics of this species remains unclear. Following detailed morphological observations and morphometric analyses of Pliocene Hipparionini, this study suggests a re-assignment of both “*Hipparion*” *longipes* and “*H.*” *fissurae* to the genus *Cremohipparion* (comb. nov.). Furthermore, the large, slender-limbed *Cremohipparion* sp. from Ruscinian localities on the Iberian Peninsula (La Gloria 4, La Calera, Orrios-1 and Villalba Alta Rio 1) is, as suggested in recent literature, morphologically distinct from *Cremohipparion fissurae* from its type locality in Layna and is likely endemic to Spain during MN14. The tentative revision of “*H.*” cf. *longipes* from Akkaşdağı (MN13, Turkey) into *Cr.* cf. *fissurae*, in addition to the confirmed record of *Cr. fissurae* in Layna (MN15, Spain), leads a reconsideration of both the palaeobiogeographic distribution and biostratigraphic range of this species.

Keywords

Armenia, *Cremohipparion*, Equidae, Hipparionini, Late Pliocene, morphometry, *Plesiohipparion*, systematics

Introduction

As described originally by De Christol (1832), the genus *Hipparion* (Equidae, Perissodactyla, Mammalia), meaning “pony” or “small horse”, included all fossil horses with an ovoid to circular-shaped and isolated protocone on upper cheek teeth as well as tridactyl feet. However, the numerous works that followed the description of De Christol (1832) have revealed that the nomen *Hipparion* refers indisputably to more than a single genus (see Bernor et al. (2021)). Even today, the systematics of hipparionine horses remains unclear. This is due to the low variability in their anatomical and dental characters, the excessive number of species that have been described and the fact that the most realistic

taxonomic frameworks should be based primarily on cranial morphology (Zouhri and Bensalmia 2005; Bernor et al. 2010). Indeed, in previous studies, up to 300 fossil Middle Miocene – Pliocene forms of the tribe Hipparionini have been described by Woodburne (1989). The earliest occurrences of the Old World Hipparionini *Hippotherium* sp. are recorded in the lowermost Late Miocene of Atzeldorf, Marethal and Gaiselberg in the Vienna Basin (ca. 11.2 Ma, earliest Mammal Neogene Unit MN9; Woodburne (2009); Hilgen et al. (2012); Bernor et al. (2017)). This is the starting point of a single immigration event of Hipparionini from North America to Eurasia, the “*Hippotherium* Datum”, replacing the “*Hipparion* Datum” (*sensu* Bernor and Sen (2017), following Berggren and Van Couvering (1974)).

Since then, these three-toed horses rapidly diversified across Eurasia and evolved into several genus-level lineages (Woodburne 1989, 2009; Bernor et al. 1990b, 1996, 2003, 2010; Scott et al. 2003; Cantalapiedra et al. 2017). However, Bernor et al. (2003) recognised *Cormohipparion sinapensis* from Sinap, Turkey at 10.8 Ma, leading Bernor and Sen (2017) and Bernor et al. (2021) to suggest *Cormohipparion* as the appropriate genus to identify the immigration event of Hipparionini from North America to Eurasia, thus calling this event the “*Cormohipparion* Datum”. Additionally, Cirilli et al. (2023) hypothesised that a mass extinction of Eurasian Hipparionini lineages occurred at the end of the Miocene, with the exception of China. This time interval (MN13) notably recorded the last appearance of *Hippotherium*, with *H. malpassii* in the V3 assemblages of the Baccinello-Cinigiano Basin (Tuscany, Italy; Bernor et al. (2011)) and at the Monticino Quarry (Brisighella, Italy; Rook and Bernor (2013)). Following Bernor et al. (2021) and Cirilli et al. (2023), five following genera *Cremohipparion*, *Proboscideipparion*, *Plesiohipparion*, *Eurygnathohippus* and *Baryhipparion* are recorded from Eurasia in the Pliocene (MN14–MN16). However, the generic assignments of the species identified are still not completely resolved.

In this paper, we report dental and postcranial remains referable to Hipparionini horses and originating from the late Pliocene Jradzor section, Armenia, located in an actively exploited diatomite-mine (Fig. 1). The section represents a 57-m-thick succession and comprises 19 fossiliferous horizons with at least 48 identified vertebrate taxa (excluding birds – which remain so far unidentified). Multiproxy dating places the studied section between 4.3 and 3.03 Ma and the mammalian fauna correlates to the MN15 – early MN16 (Lazarev et al. 2023). The studied specimens of hipparionines come nearly exclusively from a single fossil horizon (JZ–7, early MN16), corresponding to lahar deposits (Lazarev et al. 2023). Only two additional isolated specimens from pyroclastic flow deposits (JZ–3v, MN15 and JZ–9, early MN16) complete the studied material. All specimens are described and tentatively referred to *Cremohipparion longipes*, providing new considerations of the taxonomy and distribution of this species. This species was referred to the genus *Plesiohipparion* in the most recent papers, almost exclusively on the basis of the gracility and the dimensions of its elongate metapods (see Bernor and Sen (2017); Bernor et al. (2021); Cirilli et al. (2021, 2022, 2023)). However, another important result of our study is that this species should rather be referred to the genus *Cremohipparion*.

Brief history of Late Miocene – Pleistocene Hipparionini

Hipparionines were especially diverse during the Late Miocene in the Holarctic realm (Woodburne 1989; Bernor et al. 1996). However, in the Old World, they

reached their highest taxonomic and ecological diversity and abundance during the Turolian (European Land Mammal Age, 8.9–5.3 Ma, Hilgen et al. (2012)), with a diversity peak in MN12 unit (Bernor et al. 1990b, 1996; Scott and Maga 2005; Hilgen et al. 2012; Cirilli et al. 2021). This diversification is marked by an increase of the body sizes ranges, especially towards smaller sizes (Bernor et al. 1996; Ortiz-Jaureguizar and Alberdi 2003). By the end of MN13 (Mio-Pliocene boundary; Hilgen et al. (2012)), a sharp decline in diversity resulting in the extinction of several hipparionine genera has been recorded (Cirilli et al. 2023), which becomes especially evident in South and West Eurasia (India, Caucasus, Anatolia, Balkans, Eastern and Central Europe, Italian and Iberian Peninsulas and England). According to Bernor et al. (2021), in the Pliocene (MN14–MN16), 12 valid species can be identified in Eurasia. “*Hipparion*” *longipes* Gromova, 1952, originally described from Pavlodar 1A (= Gusiniy Perelet, Kazakhstan, MN12 [see details in the section Stratigraphy], Gromova (1952); Vislobokova et al. (2001); Bernor and Sen (2017); Bernor et al. (2021)), is included in the genus *Plesiohipparion* by Bernor and Sen (2017). Eisenmann and Sondaar (1998) reported “*Hipparion*” cf. *longipes* from Çalta (Turkey, Pliocene, MN15), reassessed as *Plesiohipparion* cf. *longipes* by Bernor and Sen (2017) and as *Plesiohipparion longipes* by Cirilli et al. (2023). In the circum-Mediterranean area, the following forms have also been reported: “*Hipparion*” *longipes* from the Ruscinian (MN15) of Megalo Emvolon, Greece (Koufos 2006; Koufos et al. 2021), “*Hipparion*” cf. *longipes* from the Late Miocene (MN13) of Akkaşdağ, Turkey (Koufos and Vlachou 2005; Vlachou and Koufos 2009), as well as “*Plesiohipparion*” cf. *longipes* from Baynunah (MN13), United Arab Emirates (Bernor et al. 2022). Additionally, Pesquero et al. (2011) described a cf. “*Hipparion*” *longipes* from Puente Minero (Turolian), Teruel Basin, Spain. During the Gaozhuangian age (rough equivalent of MN14–15 *sensu* Deng (2006)), the hipparionine fossil record of China apparently stays not affected by the latest Miocene Eurasian hipparionine extinction. It continues to have a diverse community of hipparion lineages, with the persistent *Plesiohipparion houfense* (Teilhard de Chardin & Young, 1931) and the first occurrence of the less derived form *Proboscideipparion pater* (Matsumoto, 1927) and a highly derived *Cremohipparion licenti* Qiu, Huang & Guo, 1987 in the Yushe Basin. This extends the stratigraphic occurrence of the group into MN15 (Bernor et al. 2021; Cirilli et al. 2023). “*Hipparion*” *crassum* Gervais, 1859, included in *Proboscideipparion* Sefve, 1927 by Cirilli et al. (2021, 2023), has been originally discovered in the Roussillon Basin and in several localities close to Perpignan (southern France). Later, this species has also been discovered in many other Ruscinian (MN14–MN15) localities of France, Spain, Greece, Bulgaria, Moldavia and Ukraine, demonstrating a much broader geographic and chronostratigraphic distribution. Moreover,

Hipparionini remains from Mălușteni, Berești and Iarăș-Cariera Nouă (Roumania) previously referred to “*H.*” *malustenense* by Rădulescu and Samson (1967) and Samson (1975), as well as that from Kisláng (Hungary) previously referred to “*H.*” *moriturum* by Kretzoi (1954), could be assigned to this species (see Cirilli et al. (2023)). “*Hipparion*” *rocinantis* Hernandez-Pacheco (1921) has been referred by Bernor et al. (1996) to the genus *Plesiohipparion* and considered by Cirilli et al. (2023) as a senior synonym of “*Hipparion*” *crusafonti*

Villalta, 1948; it is reported from the early and middle Villafranchian localities (MN16–MN17) of La Puebla de Almoradier, Las Higuieruelas, Villarroya (Spain), Rocaneyra (France), Red Crag (England), Ercsi (Hungary), Sèsklo (Greece) and Kvabebi (Georgia). In Villarroya (MN16/17), besides *Plesiohipparion rocinantis* (Hernández-Pacheco, 1921), Cirilli et al. (2023) also reports the occurrence of a poorly-represented small-sized *Cremohipparion* sp. Additionally, “*Hipparion*” *moriturum* Kretzoi, 1954, in part considered as a junior

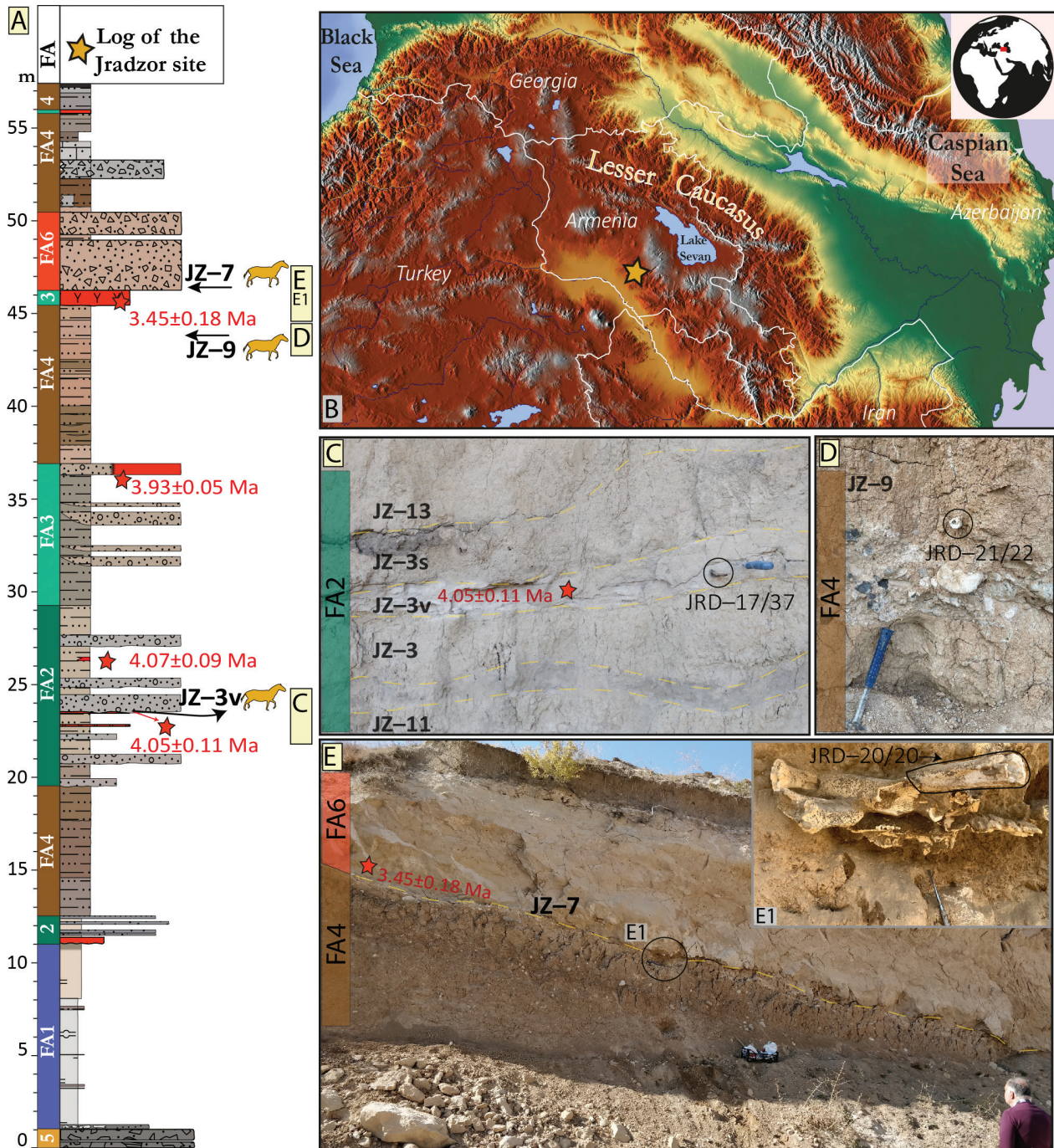


Figure 1. Log of the Jradzor section, with stratigraphic locations of three fossiliferous horizons (JZ-3v, JR-7, JR-9) and ages of the dated ashes (A). Geographical position of Jradzor locality (Late Pliocene, Armenia) in topographic map of the South Caucasus (B). Photographs of the outcrops of JZ-3v (C), JZ-9 (D) and JZ-7 (E) fossiliferous horizons and corresponding collection numbers of the selected fossil remains.

synonym of “*Hipparion*” *rocinantis* (e.g. Cirilli et al. (2023)), is also reported in Ruscinian localities of Romania (Koenigswald 1970; Forsten 2002; Zouhri and Bensalmia 2005). Recently, Cirilli et al. (2023) referred *Pl. cf. shanxiense* of Sèsklo (Greece, MN16; Athanassiou (2018)) and in part *Proboscideipparion* sp. of the Red Crag (England, MN16; Forsten (2001)) to *Pl. rocinantis*. *Plesiohipparion huangheense* Qiu, Huang & Guo, 1987 is first recorded in Inner Mongolia (MN15). The species has also been reported from the Late Pliocene (MN16) of northern China and the Indian Siwaliks (Jukar et al. 2018). “*Hipparion*” *heintzi* Eisenmann & Sondaar, 1998 has been described from the Pliocene of Çalta (Turkey, MN15) and referred to *Proboscideipparion* by Bernor and Sen (2017). “*Hipparion*” *fissurae* Crusafont & Sondaar, 1971 is reported from Ruscinian localities of the Iberian Peninsula. After Cirilli et al. (2023), the holotype (a left Mt3, LAY-TIPO, Alberdi and Alcalá (1999)) from Layna should rather be referred to the genus *Plesiohipparion*, whereas all other specimens of the Iberian localities belong to the larger, slender-limbed *Cremohipparion* sp. The genus *Eurygnathohippus*, first recorded from the latest Miocene of Africa, has been for long time considered as an endemic African lineage (Bernor et al. 2010). However, Jukar et al. (2019) reports evidence for specimens of *Eurygnathohippus* sp. from the Upper Siwaliks of Pakistan, late Pliocene, MN16. The endemic Inner Asia (Mongolia, southern Siberia, north-western China) lineage of *Baryhipparion* Qiu, Huang & Guo, 1987, is represented by the species: *Baryhipparion insperatum* Qiu, Huang & Guo, 1987 and *Baryhipparion tchicoicum* (Ivanjev, 1966). In fossil record, they occur from Late Miocene to Early Pleistocene (roughly correlated to MN12 to MN17; Bernor et al. (2021); Kalmykov (2023)).

The record of hipparionines along the Plio-Pleistocene transition becomes very rare. The co-occurrence of hipparionines with the genus *Equus* in the earliest Pleistocene is known from Roca-Neyra, France (*Plesiohipparion rocinantis*, late MN16; Cirilli et al. (2021, 2023)) and from Gülyazı, Turkey (*Plesiohipparion* aff. *huangheense*, MN17; Bernor and Lipscomb (1991)). A small “*Hipparion*” sp. reported from Montopoli (Italy, MN17) by Rook et al. (2017) is referred to *Cremohipparion* by Cirilli et al. (2023), potentially similar to that of Villarroya (MN16/17). Finally, the genera *Plesiohipparion*, *Baryhipparion* and *Proboscideipparion* persist in the fossil record of China until MN17 and *Proboscideipparion* – until MN18 (Bernor et al. 2021).

Materials and methods

The hipparionine referred material, including 61 dental and postcranial specimens from Jradzor locality. The specimens are stored in the collections of the Institute of Geological Sciences (IGS), the National Academy of Sciences of the Republic of Armenia, Yerevan, Armenia.

Abbreviations

C/c = Upper/lower canine; **DP/dp** = Upper/lower milk tooth; **I/i** = Upper/lower incisor; **M/m** = Upper/lower molar; **P/p** = Upper/lower premolar.

Ast = Astragalus; **Cal** = Calcaneus; **Dia** = Diaphysis; **Hum** = Humerus; **Mc** = Metacarpal; **Mt** = Metatarsal; **Phx** = Phalanx; **Rad** = Radius; **Tib** = Tibia; **Uln** = Ulna.

l. = left; **r.** = right.

ant = Anterior; **APD** = Antero-posterior diameter; **art** = Articular; **dist** = Distal; **H** = Height; **L** = Length; **max** = Maximum; **min** = Minimum; **post** = Posterior; **prox** = Proximal; **TD** = Transverse diameter; **W** = Width.

M = Measurement; **GI** = Gracility index; **HI** = Hypsodonty index.

Stratigraphy

The stratigraphic framework is based on the Geological Time Scale and European Land Mammal Ages (ELMA) for the Neogene (Steininger 1999; Hilgen et al. 2012; Raffi et al. 2020). The Regional stages of Eastern Paratethys and of Black Sea Basin are after Lazarev et al. (2023) for Miocene and Krijgsman et al. (2019) for Plio-Pleistocene. Successions of European Mammal Neogene units (MN) follow the age limits of Hilgen et al. (2012) and the Mammal stages of China refer to Deng (2006). Pavlodar 1A, known also as Gusiniy Perelet (Kazakhstan), is the type locality of “*Hipparion*” *longipes*. In the *Hipparion*-dedicated literature, the correlation of the site to MN units is very variable, ranging from MN12–14 (e.g. Gromova (1952); Eisenmann and Sondaar (1998); Vislobokova (2001); Bernor et al. (2021); Cirilli et al. (2023); Vasilyan et al. (2017)). However, the fossiliferous horizon can be correlated to the MN12 based, notably, on the presence of *Rhinocerosodon pauli* and *Lophocricetus vinogradovi* to MN12 (Vasilyan et al. 2017). Puente Minero site from the Teruel Basin contains three different hipparion species (Pesquero et al. 2011), which appears exceptionally diverse. The Puente Minero section contains seven fossiliferous horizons (van Dam et al. 2001). The hipparion material published in Pesquero et al. (2011) is reported to come from the Puente Minero site, without referring to a certain horizon. Given the uncertain provenance of the material and the difficulty in establishing an age for these hipparions based on literature, a broader age range is considered more appropriate; accordingly, a Turolian age is provisionally retained for the site.

Anatomical description

Hipparionine dental terminology (Fig. 2) follows that of Eisenmann et al. (1988) reviewed by Evander (2004). Dental features mainly correspond to characters used and listed by Bernor et al. (1990a, 1990b, 1997, 1999), Bernor and Lipscomb (1991) and Sun et al. (2025). The

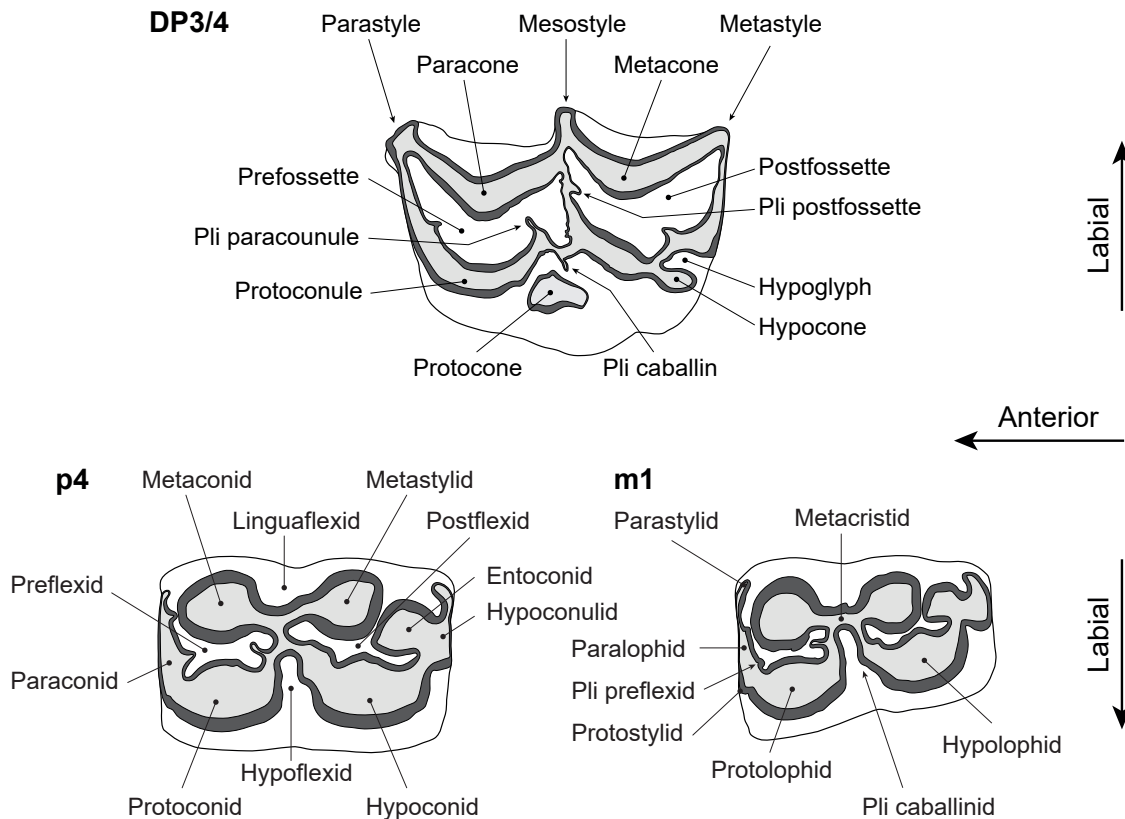


Figure 2. Dental terminology of Hipparionini cheek teeth in occlusal view (modified after Eisenmann (1981) and Evander (2004)). Right DP3/4; right p4; right m1.

description of the postcranial specimens is partly based on the anatomical features described by Antoine (2002) for the Rhinocerotidae, but broadly applicable to Perissodactyla.

Measurements

Measurements are taken at the precision of 0.1 mm using digital calipers. Dental and postcranial dimensions are based on the protocol of Eisenmann et al. (1988), with the exception of angle measurements, which were not considered in this study. Additionally, following Bernor et al. (1997), the length and width of the cheek teeth are taken at the occlusal level and 10 mm above the neck, while the protocone dimensions of the upper cheek teeth include the length and width. Incisor dimensions follow the protocol established by Heriech-Briki (2003). Measurements done in this study are all given in mm and detailed below. The complete set of measurements is provided in Table 1.

Anterior teeth – M1 (TD), M2 (APD).

Upper cheek teeth – M1 (H), M2 (occlusal L), M2' (10 mm above the neck), M3 (protocone occlusal L), M4 (occlusal W), M4' (10 mm above the neck), M5 (protocone occlusal W).

Lower cheek teeth – M1 (H), M2 (occlusal L), M2' (10 mm above the neck), M3 (occlusal preflexid L), M4 (occlusal double knot L), M5 (occlusal postflexid L), M6 (occlusal W), M6' (10 mm above the neck).

Hum – M3 (TDdia min), M4 (APDdia at the level of M3), M7 (TDmax of the trochlea), M10 (Hmin in the middle of the trochlea), M11 (lateral H of the trochlea).

Rad-Uln – M3 (TDdia min), M4 (APDdia at the level of M3), M5 (TDart prox), M6 (APDart prox), M7 (TDmax prox), M8 (TDart dist), M9 (APDart dist), M10 (TDmax dist), M11 (TD of the radial condyle).

Mc3 – M1 (Lmax), M2 (medial L), M3 (TDdia min), M4 (APDdia at the level of M3), M5 (TDart prox), M6 (APDart prox), M7 (maximal diameter of the articular facet for the third carpal), M8 (diameter of the anterior facet for the fourth carpal), M9 (diameter of the anterior facet for the second carpal), M10 (TDmax dist supra-art), M11 (TDmax dist art), M12 (APDmax dist), M13 (APDmin dist of the lateral condyle), M14 (APDmax dist of the medial condyle).

Tib – M3 (TDdia min), M4 (APDdia min), M7 (TDmax dist), M8 (APDmax dist).

Cal – M1 (Lmax), M2 (L of the proximal part), M3 (TDmin), M6 (TDmax dist), M7 (APDmax dist).

Ast – M1 (Hmax), M2 (maximal diameter of the medial condyle), M3 (TD of the trochlea, at the apex of each condyle), M4 (TDmax), M5 (TDart dist), M6 (APDart dist), M7 (medial APDmax).

Mt3 – M1 (Lmax), M2 (Lmedial), M3 (TDdia min), M4 (APDdia at the level of M3), M5 (TDart prox), M6 (APDart prox), M7 (maximal diameter of the articular facet for the third tarsal), M8 (diameter of the anterior facet for the fourth tarsal), M9 (diameter of the anterior

Table 1. Dental and postcranial dimensions (in mm) of *Cremohipparion longipes* (Gromova, 1952), comb. nov. from the Late Pliocene of Jradzor (Armenia). See Materials and Methods section for details of measurements.

Specimen	Species	Locality	Fossil horizon	Bone	Side	M1	M2	M2'	M3	M4	M4'	M5	M6	M6'	M7	M8	M9	M10	M11	M12	M13	M14
JRD-20/24	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	DP3/4	r	37.1	33.5	32.8	7.2	19.2	23.8	4.4										
JRD-19/97	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	p2	l		29.3			16.1			14.5									
JRD-19/97	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	p3	l		26.9						16.5									
JRD-19/97	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	p4	l					17.5			16.6									
JRD-19/97	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	i1	r	9.4	13.2															
JRD-19/97	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	i2	r		12.3															
JRD-19/97	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	i3	r	11.2	10.7															
JRD-19/97	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	i1	l	8.7	13.2															
JRD-19/97	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	i2	l	12.2	12.5															
JRD-20/27	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	p4	r	54.3	28.4		9.2	20.2		13.5	16.3									
JRD-20/27	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	m1	r	50.3	25.7		7.3	17.0		9.2	14.3									
JRD-20/27	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	m1	l	48.2	25.4	23.2	7.4	17.1		9.0	14.2	15.2								
JRD-20/27	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	m2	l	53.8	26.3		7.5	16.5		9.9	13.8									
JRD-17/38	<i>Cremohipparion longipes</i>	Jradzor	JZ-3s	m3	r	69.2	28.2	23.5	8.3	13.2	14.3	9.8	13.8	12.8								
JRD-17/24	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	hum	l				29.0	36.7												
JRD-19/88	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	hum	r				31.3	37.0												
JRD-20/51	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	hum	r										69.7		42.4	33.5	40.6			
JRD-20/60	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	hum	l				32.2	36.5												
JRD-20/168	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	hum	r				31.0	36.1												
JRD-20/191	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	hum	l										66.0		43.4	32.5				
JRD-20/192	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	hum	r												42.5					
JRD-21/24	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	hum	l				30.1	35.9												
JRD-19/06	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	rad	r												35.7		24.7			
JRD-19/82	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	rad-uln	r				33.8	26.2		66.1	35.5		67.5							
JRD-18/31	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	uln	l					40.5		52.1										
JRD-17/12	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	Mc3	r	248.7	244.5		29.2	24.4		44.0	30.1		37.7	12.8		39.4	37.8	31.9	25.7	27.6
JRD-19/87	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	Mc3	r				28.2	25.2												
JRD-19/96	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	Mc3	r	247.7	243.7		30.5	27.5		43.2	30.5		36.5	12.0		38.7	39.1	33.1	27.4	30.0
JRD-20/02	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	Mc3	r	261.5	257.5		27.6	24.4		41.1	30.1		36.1	11.1		38.2	39.2	34.0	27.3	28.9
JRD-20/33	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	Mc3	l	261.3	257.3		28.2	24.3		42.5	31.5		37.1	12.4		38.1	38.8	33.7	27.5	28.9
JRD-20/43	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	Mc3	l				31.2	23.1								39.9				
JRD-20/55	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	Mc3	r				28.0	24.0										30.8	25.5	27.2
JRD-20/59	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	Mc3	l				29.3	23.7								38.0		30.8	14.9	
JRD-20/90	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	Mc3	l				28.3	25.5												
JRD-20/175	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	Mc3					29.3	25.6												
JRD-20/184	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	Mc3	l													37.2	36.8	32.5	26.2	28.7
JRD-20/193	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	Mc3	r															31.0	25.7	
JRD-20/183	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	fem	r				32.0	41.2												
JRD-17/11	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	tib	l				35.3	26.9												
JRD-17/29+95	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	tib	l				39.2	29.1					65.5	46.5						
JRD-20/161	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	tib	l											46.4						
JRD-20/188	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	tib	r				39.5	30.2												
JRD-17/28	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	ast	l	58.2	57.8		27.5	55.5		45.5	34.4		49.1							
JRD-19/12	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	ast	l	55.8	51.5		25.0	51.2		43.4	32.1									
JRD-20/31	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	ast	r	56.1	53.5		27.3	55.5		45.2	34.2		48.5							
JRD-20/26	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	ast	l	60.7	59.1		30.4	58.0		47.0	34.8		52.3							
JDR-20/35	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	ast	l	58.9	55.4		29.5			44.8	32.7									
JRD-20/44	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	ast	r	61.8	61.0		29.3	57.3		48.3			53.5							
JRD-20/32	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	ast	r				26.5	51.1		43.2	34.1									
JRD-17/19	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	cal	l				18.1			48.5			50.8							
JRD-19/11	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	cal	l				17.2			44.5			45.1							
JRD-20/25	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	cal	l				19.0													
JRD-20/28	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	cal	l				18.1			47.0			49.2							
JRD-20/68	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	cal	r				18.0			46.9			48.1							
JRD-24/02	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	cal	r				17.8						50.6							
JRD-17/25	<i>Cremohipparion longipes</i>	Jradzor	JZ-7	Mt3	l				24.9	27.4												
JRD-20/67	<i>Cremohipparion longipes</i>	Jradzor	JZ-9	Mt3	r							41.9	35.6		39.6		8.3					

Specimen	Species	Locality	Fossil horizon	Bone	Side	M1	M2	M2'	M3	M4	M4'	M5	M6	M6'	M7	M8	M9	M10	M11	M12	M13	M14
JRD–20/85+87	<i>Cremohipparion longipes</i>	Jradzor	JZ–7	Mt3	r	312.5			29.9	28.5								41.9	39.2	32.5	25.6	27.9
JRD–20/176	<i>Cremohipparion longipes</i>	Jradzor	JZ–7	Mt3	r				30.3	28.7		45.2	34.0		41.9	12.2	9.0					
JRD–20/180+181	<i>Cremohipparion longipes</i>	Jradzor	JZ–7	Mt3	r				28.5	28.3								40.8	38.7	31.7	26.8	28.0
JRD20/182	<i>Cremohipparion longipes</i>	Jradzor	JZ–7	Mt3	r				27.8	30.9								41.9	38.4	36	28.4	28
JRD–21/22	<i>Cremohipparion longipes</i>	Jradzor	JZ–7	Mt3	r				27.8	28.0								37.0	36.9	31.5	24.1	27.2
JRD–20/36	<i>Cremohipparion longipes</i>	Jradzor	JZ–7	dist phx3	r	45.9			46.4	34.7		22.1	34.0									
JRD–20/179	<i>Cremohipparion longipes</i>	Jradzor	JZ–7	dist phx3								24.1										

facet for the second tarsal), M10 (TDmax dist supra-art), M11 (TDmax dist art), M12 (APDmax dist), M13 (APDmin dist of the lateral condyle), M14 (APDmax dist of the medial condyle).

Phx3 – M4 (TDart), M5 (APDart), M6 (Hmax).

Palaeobiology

The anatomical type of Jradzor hipparionine is defined on the basis of the gracility index (GI) of the metapods (calculated: $100 \times \text{TDdia} / L$; *sensu* Lepetz and Hanot (2012)) and classified according to Brauner's indices to the following categories (see Spassov et al. (2018)). According to this classification, all specimens studied herein belong to a “very slender” form ($\text{GI} < 13.5$), hence the GI is used to compare the gracility levels within this category.

Following Eisenmann (2004), the body weights have been estimated from two distal dimensions of the metapodials (Mc3 and Mt3), the distal supra-articular width (M10) and the distal minimal depth of medial condyle (M13), applied to the following equations: $\text{Ln Body weight (Mc3)} = -4,525 + 1,434 (\text{Ln (M10} \times \text{M13)})$ and $\text{Ln Body weight (Mt3)} = -4,585 + 1,443 (\text{Ln (M10} \times \text{M13)})$. According to Eisenmann (1988), the shoulder height corresponds to the length of the Mc3 ($\text{M1} \times 6.41$) or to the length of the Mt3 ($\text{M1} \times 5.51$) (coefficients applied to Hipparionini).

The diet is partly discussed from the hypsodonty index (HI) of the m3 (*sensu* Janis (1986) and Muhlbachler et al. (2011): H / W). According to Muhlbachler et al. (2011), brachyodont teeth have a $\text{HI} < 1$, mesodont HI is in the range of 1–2 and hypsodont $\text{HI} > 2$.

Preliminary analysis

Allometric analyses and comparisons have been based on measurements of the hipparionine specimens from Jradzor (Table 1) and literature (Suppl. materials 1–3), including the following hipparionine species: “*Hipparion*” *longipes* from Pavlodar 1A (= Gusiniy Perelet, MN12, Kazakhstan; Gromova (1952); Eisenmann and Sondaar (1998); Vislobokova et al. (2001); Cirilli et al. (2023)); “*Hipparion*” cf. *longipes* from Akkaşdağı (MN13, Turkey; Koufos and Vlachou (2005); Scott and Maga (2005); Vlachou and

Koufos (2009)) and from Çalta (MN15, Turkey; Eisenmann and Sondaar (1998); Bernor and Sen (2017); Cirilli et al. (2023)); “*Hipparion*” *fissurae* from Layna (MN15, Spain; Crusafont and Sondaar (1971); Alberdi and Alcalá (1999)) and from La Calera, La Gloria 4, Orrios-1 and Villalba Alta Rio 1 (MN14, Spain; Alberdi and Alcalá (1999); Minwer-Barakat et al. (2012)); *Cremohipparion matthewi* from Samos and Pikermi (MN12, Greece; Bernor and Tobien (1989); Cirilli et al. (2023)); “*Hipparion*” *macedonicum* from Ravin de Pluie (MN10, Greece; Bernor and Tobien (1989); Koufos (2006)); “*Hipparion*” *elegans* from Pavlodar 1A (MN12, Kazakhstan; Gromova (1952); Eisenmann and Sondaar (1998); Vislobokova (2001); Cirilli et al. (2023)); *Plesiohipparion rocinantis* from Villaroya (MN16, Spain; Minwer-Barakat et al. (2012); Cirilli et al. (2023)) and Kvabebi (MN16, Georgia; Cirilli et al. (2023)); *Plesiohipparion rocinantis/houfenense* from Shamar (MN16, China; Zhegalov (1978); Eisenmann and Sondaar (1989); Vislobokova et al. (2001); Eisenmann (2025)); *Plesiohipparion houfenense* from Yushe (MN14, China; Bernor et al. (2015)); *Plesiohipparion shanxiense* from Shanxi (MN17, China; Bernor et al. (2015)); *Proboscoidipparion heintzi* from Çalta (MN15, Turkey; Eisenmann and Sondaar (1998); Bernor and Sen (2017); Cirilli et al. (2023)); “*Hipparion*” *crassum* from Serrat, Lassus, Perpignan and Cavaillé (MN15, France; Eisenmann and Sondaar (1989); Alberdi and Aymar (1995); Eisenmann (2025)).

Firstly, the potential correlations between the measurements within the datasets (Table 1, Suppl. material 1) have been tested to identify the associations presenting the best discriminating potential (Fig. 3). For allometric relationships to be tested, the non-parametric Spearman's rank correlation coefficient (ρ) is provided and the non-parametric test of Mantel is performed to test the significance (P ; based on 9,999 permutations). All correlation tests have been performed with the software PAST version 5.3 (Hammer et al. 2001). This does not exclude that one measurement alone could be discriminating. Measurements of the metacarpals (Fig. 3A–C) are not significantly correlated when the M1 vs. M11 and M1 vs. M3 are considered, giving these two pairs of datasets a good discriminating systematic value. In contrast, the M3 vs. M11 is highly significantly and strongly correlated. M1, M3 and M11 measurements on

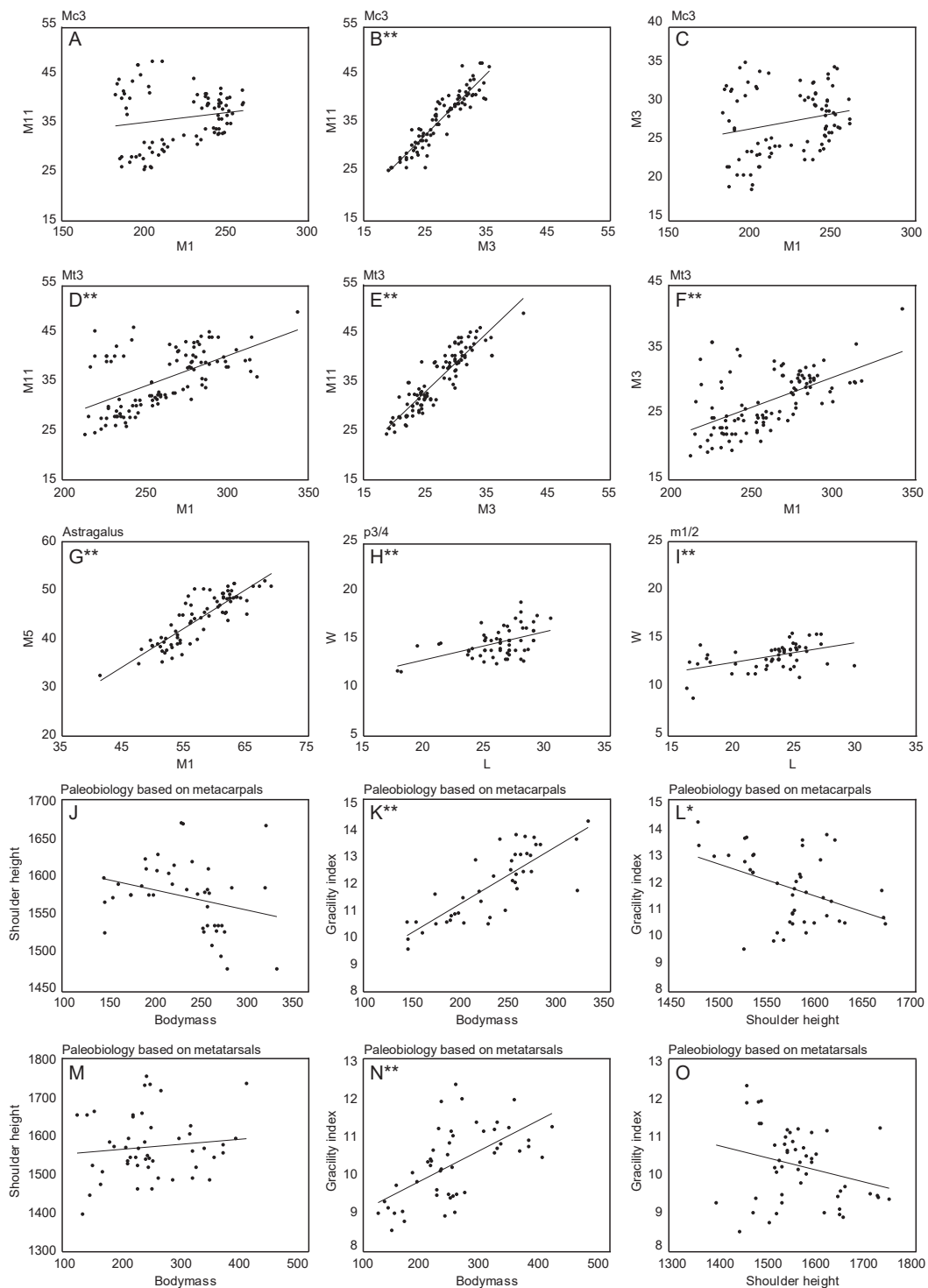


Figure 3. Allometric relationships between: **A.** M1 and M11 measurements on Mc3 ($r^2 = 0.03$; Spearman $\rho = 0.121$, $P = 0.262$); **B.** M3 and M11 measurements on Mc3 ($r^2 = 0.86$; Spearman $\rho = 0.933$, $P < 0.001$); **C.** M1 and M3 measurements on Mc3 ($r^2 = 0.05$; Spearman $\rho = 0.214$, $P = 0.045$); **D.** M1 and M11 measurements on Mt3 ($r^2 = 0.33$; Spearman $\rho = 0.552$, $P < 0.001$); **E.** M3 and M11 measurements on Mt3 ($r^2 = 0.82$; Spearman $\rho = 0.907$, $P < 0.001$); **F.** M1 and M3 measurements on Mt3 ($r^2 = 0.32$; Spearman $\rho = 0.553$, $P < 0.001$); **G.** M1 and M5 measurements on astragalus ($r^2 = 0.74$; Spearman $\rho = 0.847$, $P < 0.001$); **H.** Length (L) and width (W) of p3/4 ($r^2 = 0.24$; Spearman $\rho = 0.448$, $P < 0.001$); **I.** Length (L) and width (w) of m1/2 ($r^2 = 0.23$; Spearman $\rho = 0.493$, $P < 0.001$); **J.** Shoulder height and body weight estimated, based on Mc3 mensuration ($r^2 = 0.08$; Spearman $\rho = -0.278$, $P = 0.075$); **K.** Body weight and GI estimated, based on Mc3 mensuration ($r^2 = 0.67$; Spearman $\rho = 0.818$, $P < 0.001$); **L.** Shoulder height and GI estimated, based on Mc3 mensuration ($r^2 = 0.02$; Spearman $\rho = -0.316$, $P = 0.036$); **M.** Shoulder height and body weight estimated, based on Mt3 mensuration ($r^2 = 0.01$; Spearman $\rho = -0.077$, $P = 0.598$); **N.** Body weight and GI estimated, based on Mt3 mensuration ($r^2 = 0.36$; Spearman $\rho = 0.637$, $P < 0.001$); **O.** Shoulder height and GI estimated, based on Mt3 mensuration ($r^2 = 0.07$; Spearman $\rho = -0.213$, $P = 0.132$). * indicates correlation that are significant with $P < 0.05$ and ** indicates correlation that are highly significant with $P < 0.001$. See Table 1 and Suppl. material 1 for references and measurements used.

metatarsals are all significantly correlated, making them less powerful in discriminating taxa. Nevertheless, in both cases (M1 vs. M11 and M1 vs. M3), the coefficient of correlation indicates that less than 35% of the variation of the independent variable explains the variation of the dependent variable, making the comparison of these datasets still possible, but with caution. Measurements of the M1 vs. M5 of the astragalus are both highly significantly and strongly correlated making their comparison useless. For both p3/4 and m1/2, (Fig. 3H, I), the comparison of the L vs. W is always highly significantly correlated with a coefficient of correlation slightly under 0.5, indicating that almost 50% of the variability of one variable is explained by the other one. This makes the comparison between the length and width of the cheek teeth weakly discriminating and needs to be used with caution. Palaeobiological estimates (body weight, shoulder height and gracility index) can be based on the metacarpals or metatarsals measurements. The comparison of the body weight vs. the shoulder height is, in both cases, not correlating with each other, whereas the comparison of the shoulder height vs. gracility index is significantly correlated, mainly based on the metacarpals. The comparison of the body weight vs. gracility index (GI) is, in both cases, highly significantly correlated, with the coefficients of correlations indicating that at least 35%, and up to 70% of gracility index is explained by the variability of the body weight. Based on Spearman ρ results, the comparisons of the body weight vs. shoulder height, based on the metatarsals measurements appears to be the most discriminating one.

Following this preliminary analysis and literature data (e.g. Pesquero (2011); Bernor et al. (2016); Bernor and Sen (2017); Cirilli et al. (2021, 2023)), bivariate plot diagrams have been used to discriminate taxa at different systematic levels. Mainly, two bivariate plot diagrams are performed, based on the Mc3 and Mt3 measurements. One plot juxtaposes the maximum length (M1) versus the distal articular transverse diameter (M11). The second compares maximum length (M1) versus minimal transverse diameter of the diaphysis (M3), corresponding to the GI. Likewise, bivariate plots, based on measurements of the lower cheek teeth, complete the analyses and provide further support in identifying taxa. Palaeobiological estimates are illustrated by a series of box plots and a specific trivariate plot diagram including the body weight, shoulder height and gracility index (see section Discussion for figures).

Commonly, principal component analysis (PCA), based on measurements of the metacarpals and metatarsals, is used for the purpose of discriminating taxa (e.g. Bernor et al. (2003); Koufos (2016); Koufos and Vlachou (2016, 2019); Cirilli et al. (2021, 2023)). As discussed above, a number of the measurements employed as variables in the aforementioned analyses are found to be significantly correlated, albeit to differing extents. PCA is predicated on the assumption that the variables under analysis are independent of each other. In fact, the descriptive ability of PCA may be significantly influenced by autocorrelation,

particularly when the variables exhibit varying degrees of autocorrelation (Vanhatalo and Kulahci 2016), as is evident in this instance. The utilisation of autocorrelated variables has been demonstrated to result in an overestimation of variance, thereby causing the first principal component (PC) to predominantly capture variability (Zamprogno et al. 2020). Consequently, variables should ideally be filtered according to their level of correlation prior to any PCA (Zamprogno et al. 2020). However, in order to facilitate comparison with previously published results (e.g. Koufos (2016); Cirilli et al. (2021, 2023)), a comparable dataset (with an extensive scope, including several taxa not considered in the present study; see Suppl. materials 1–3) has been compiled and a PCA analysis has been performed, despite the possible autocorrelation amongst variables. PCA analysis has been performed with the software PAST version 5.3 (Hammer et al. 2001).

Systematics

In agreement with the consensual vision of many authors (e.g. Bernor et al. (2010, 2011, 2012); Bernor and Sen (2017); Rook et al. (2017); Cirilli et al. (2020)), the tribe Hipparionini (Equidae) corresponds to taxa with an isolated protocone on the upper jugals and tridactyl limbs, including all species of the following genera: *Cormohipparion*, *Neohipparion*, *Nannippus*, *Pseudohipparion*, *Hippotherium*, *Cremohipparion*, *Hipparion*, “*Sivalhippus*”, *Eurygnathohippus* (= senior synonym of “*Stylohipparion*”), *Proboscoidipparion* and *Plesiohipparion*.

Class Mammalia Linnaeus, 1758
Order Perissodactyla Owen, 1848
Famille Equidae Gray, 1821
Tribe Hipparionini Quinn, 1955

Genus *Cremohipparion* Qiu, Huang & Guo, 1987

Diagnosis. See Qiu et al. (1987) and Bernor and Tobien (1989).

Type species. *Cremohipparion licenti* Qiu, Huang & Guo, 1987.

Other species. (following Bernor et al. (2021) and Cirilli et al. (2022, 2023)): *Cremohipparion antelopinum* (Falconer & Cautley, 1849), *Cremohipparion mediterraneum* (Roth & Wagner, 1855), *Cremohipparion proboscideum* (Studer, 1911), *Cremohipparion matthewi* (Abel, 1926), *Cremohipparion elegans* (Gromova 1952), *Cremohipparion moldavicum* (Gromova, 1952), *Cremohipparion gromovae* (Villalta & Crusafont, 1957), *Cremohipparion periafricanum* (Villalta & Crusafont, 1957), *Cremohipparion forstenae* (Zhegallo, 1971), *Cremohipparion fissurae* (Crusafont & Sondaar, 1971), *Cremohipparion macedonicum* (Koufos, 1984), *Cremohipparion nikosi* Bernor & Tobien, 1989.

***Cremohipparion longipes* (Gromova, 1952), comb. nov.**

Figs 4–8, Table 1

- * 1952 *Hipparion longipes*, Gromova
 1975 *Hipparion longipes*, Heintz et al.
 1987 *Plesiohipparion longipes*, Qui et al.
 1989 *Hipparion longipes*, Eisenmann and Sondaar
 1996 “*Plesiohipparion*” *longipes*, Bernor et al.
 1998 *Hipparion* cf. *longipes*, Eisenmann and Sondaar
 1999 *Hipparion longipes*, Alberdi and Alcalá
 2000 *Hipparion* cf. *longipes*, Zouhri and Ben Moussa
 non 2005 *Hipparion* cf. *longipes*, Koufos and Vlachou
 non 2005 *Hipparion longipes*, Scott and Maga
 2011 cf. *Hipparion longipes*, Pesquero et al.
 p.p. 2017 *Plesiohipparion longipes*, Bernor and Sen (*sine Akkaşdağı*)
 p.p. 2021 *Plesiohipparion* cf. *longipes*, Bernor et al. (*sine Akkaşdağı*)
 2021 *Plesiohipparion longipes*, Bernor et al.
 p.p. 2021 *Plesiohipparion longipes*, Cirilli et al. (*sine Akkaşdağı*)
 p.p. 2022 “*Plesiohipparion*” cf. *longipes*, Bernor et al. (*sine Akkaşdağı*)
 p.p. 2022 *Plesiohipparion longipes*, Cirilli et al. (*sine Akkaşdağı*)
 p.p. 2023 *Plesiohipparion longipes*, Cirilli et al. (*sine Akkaşdağı*)

Emended diagnosis. Large-sized and very slender *Cremohipparion* species with an average GI on Mc3 of 11.2 and on Mt3 of 9.5 and an average TDmax dist art/L index on Mc3 of 15.1 and on Mt3 of 12.4. Differs from all small-sized *Cremohipparion* species by dimensions 25% larger. Differs from *Cremohipparion fissurae* and large slender-limbed *Cr.* sp. from Ruscinian localities of the Iberian Peninsula (La Gloria 4, La Calera, Orrios-1 and Villalba Alta Rio 1) in being slightly larger and more gracile.

Distribution. Late Miocene to Pliocene (MN11 – early MN16) Eurasia; Puente Minero (Teruel Basin, Spain, Turolian), originally described as cf. “*Hipparion*” *longipes* (Pesquero et al. 2011), Pavlodar 1A (Kazakhstan, MN12), originally described as “*Hipparion*” *longipes* (Gromova 1952; Vislobokova et al. 2001; Bernor and Sen 2017; Bernor et al. 2021), Baynunah (United Arab Emirates, MN13), originally described as “*Plesiohipparion*” cf. *longipes* (Bernor et al. 2022), Çalta (Turkey, MN15), originally described as “*Hipparion*” cf. *longipes* (Eisenmann and Sondaar 1998), Megalo Emolon (Greece, MN15), originally described as “*Hipparion*” *longipes* (Koufos 2006; Koufos et al. 2021) and Jradzor (Armenia, MN15 – early MN16, this study).

Referred material. From level JZ–3v (MN15) – r. m3 (JRD–17/37).

From level JZ–9 (early MN16) – l. distal ends Mt3 (JRD–21/22).

From level JZ–7 (early MN16) – r. DP3/4 (JRD–20/24); fragmented symphysis and left mandibular corpus with r. c and l. p2–4 associated to separate fragmented l. c and l. and r. i1–3 (JRD–19/97); associated r. p4–m1 and l. m1–2 (JRD–20/27); incomplete atlas (JRD–20/189); cervical vertebra 3/4/5 (JRD–20/17); cervical vertebra 6 (JRD–17/18); l. humerus diaphysis (JRD–17/24; JRD–20/60); r. humerus diaphysis (JRD–19/88; JRD–20/168); r. incomplete distal end of humerus

(JRD–21/24; JRD–20/51; JRD–20/192); l. incomplete distal end of humerus (JRD–20/191); r. proximal end of radius–ulna (JRD–19/82); r. proximal end of radius (JRD–19/06); l. incomplete trochlear incisure of ulna (JRD–18/31); r. proximal end of Mc3 (JRD–19/87); r. Mc3 with incomplete Mc2 and 4 (JRD–19/96); l. Mc3 and Mc4 (JRD–20/33); r. Mc2 and Mc3 (JRD–17/12); r. Mc3 (JRD–20/02); r. fragmented diaphysis of Mc2–3–4 (JRD–20/90); l. distal ends of Mc3 (JRD–20/43; JRD–20/184); r. distal ends of Mc3 (JRD–20/193); associated l. and r. distal ends of Mc3 (JRD–20/59; JRD–20/55); fragmented diaphysis Mc3 (JRD–20/175); r. femur diaphysis (JRD–20/183); l. juvenile tibia diaphysis (JRD–19/95) associated to l. distal end of tibia (JRD–17/29), l. astragalus (JRD–17/28) and l. calcaneus (JRD–17/19); r. incomplete proximal end of tibia (JRD–19/91); r. tibia diaphysis (JRD–20/188); l. juvenile tibia diaphysis (JRD–17/11); r. juvenile tibia diaphysis (JRD–17/21); l. juvenile distal end of tibia (JRD–20/161); l. juvenile astragalus (JRD–19/12) associated with l. calcaneus (JRD–19/11); l. juvenile astragalus (JRD–20/26) associated with incomplete l. calcaneus (JRD–20/25); r. astragali (JRD–20/31; JRD–20/44; JRD–20/32); l. astragalus (JRD–20/35); l. calcaneus (JRD–20/28); r. calcanei (JRD–20/68; JRD–24/02); l. small cuneiform (JRD–20/194); r. Mt3 (JRD–20/87+85); r. proximal end of Mt3 (JRD–20/176; JRD–20/67); l. proximal end of Mt3 (JRD–17/25); r. distal ends Mt3 (JRD–20/180; JRD–20/181; JRD–20/182); r. anterior distal phalanx 3 (JRD–20/36); incomplete distal phalanx 3 (JRD–20/61; JRD–20/186; JRD–20/187).

Description. Mandible and lower dentition. Specimen JRD–19/97 is an incomplete mandible, including the symphysis bearing a fragmented right canine and the anterior part of the left horizontal branch bearing the first three premolars. The separate left and right i3 and incomplete left c are associated with this specimen. A significant tooth wear and the presence of canines suggest the specimen to be a male individual of advanced age. Specimen JRD–20/27 corresponds to a set of four lower cheek teeth (right p4–m1 and left m1–2) of moderate wear belonging to the same adult individual. The medium-worn specimen JRD–17/38 is typical of an adult equid m3, characterised by an elongated occlusal outline, a posteriorly reduced width and a well-developed and isolated hypoconulid, forming a third crescent (lobe) at the back of the tooth.

The symphyseal region of JRD–19/97 is nearly horizontal, spindly, and middle-sized (W min of the symphysis = 42.72, H symphysis = 40.9) with a relatively weak constriction in dorsal view. The morphology of the lower incisors and canines is not observable due to the incompleteness and the very advanced wear of the specimens. In occlusal view, the outline of the incisors is biangular (isosceles triangle) in shape, indicating an age of over 20 years (Nicks et al. 2007). The canines are divergent and roughly anteriorly orientated. On the horizontal branch, there is no evidence of the presence of the dp1. The series p2–3 measure 80.2 mm in length.

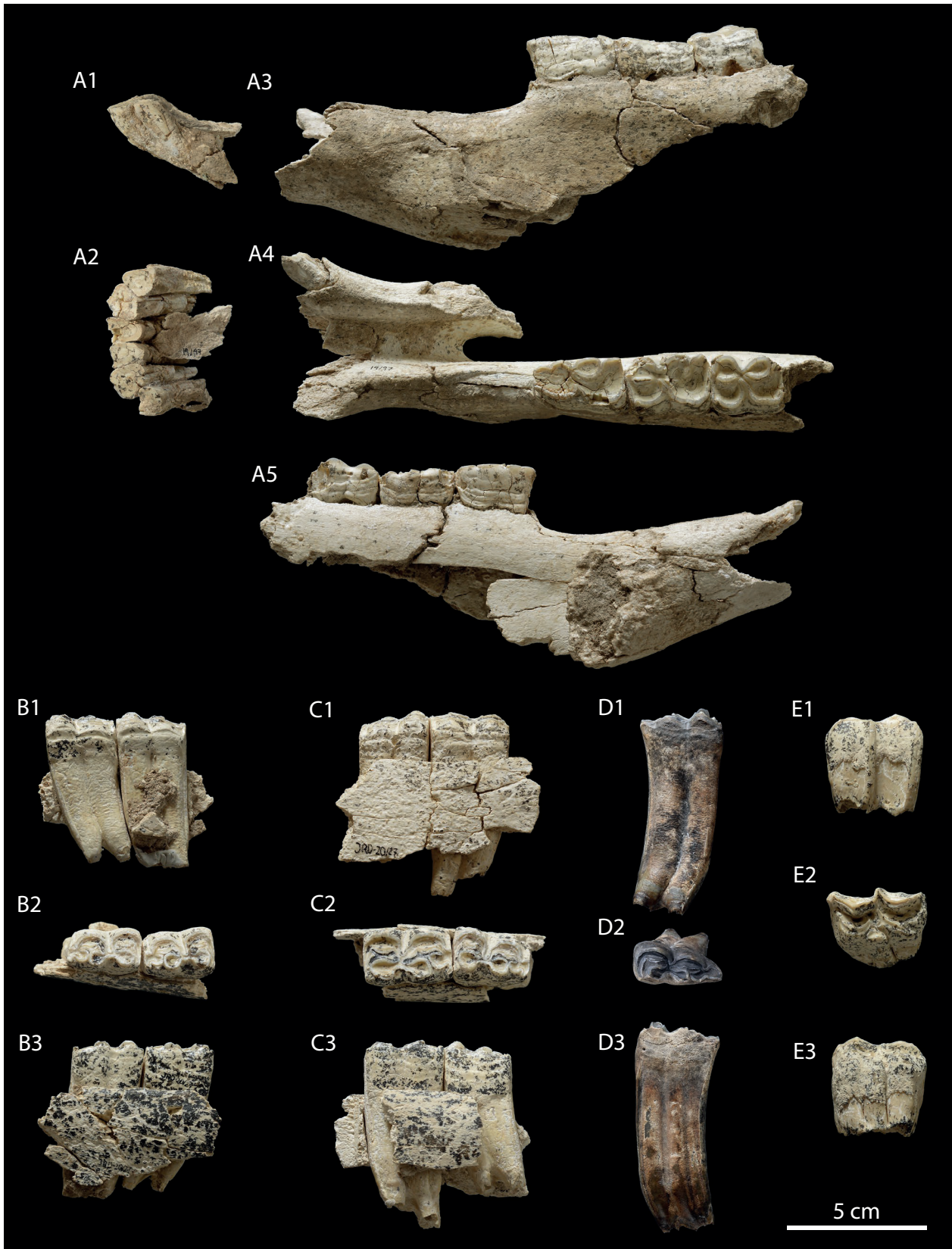


Figure 4. *Cremohipparion longipes* (Gromova, 1952), comb. nov. (Perissodactyla, Equidae) from Jradzor locality, Armenia (MN15 – early MN16, Late Pliocene). Incomplete and fragmented mandible (JRD–19/97), anterior dentition in lateral (A1) and occlusal (A2) views, left mandibular corpus in lateral (A3) and medial (A5) views, canines and left p2–4 in occlusal view (A4); associated l. m1–2 in labial (B1), occlusal (B2) and lingual (B3) views and r. p4–m1 (JRD–20/27) in in labial (C1), occlusal (C2) and lingual (C3) views; r. m3 (JRD–17/37) in labial (D1), occlusal (D2) and lingual (D3) views; r. DP3/4 (JRD–20/24) in labial (E1), occlusal (E2) and lingual (E3) views. Scale bar: 5 cm.

The cement is well developed on all of the lower cheek teeth and the crown is high, with a HI > 5 in the m3 (JRD–17/38). The metaconid and metastylid are always rounded. The protoconid and hypoconid form two labially rounded to slightly flattened bands of enamel. The lower premolars are completely molarised. On p2, the linguaflexid has a shallow and open V-shape. The hypoflexid (= ectoflexid *sensu* Eisenmann et al. (1988)) is thin and shallow, not reaching the labial margin of the metacristid (= isthmus *sensu* Eisenmann et al. (1988)). The prefixid is difficult to observe due to tooth wear. Only a lingual notch remains, isolating an elongate and anteriorly projecting paraconid. The postflexid has a large anterolingual extension, almost isolating the metastylid from the metacristid. The pli caballinid is absent, as are the protostylid, ectostylid and hypostylid. The p3–4 have shallow open V-shaped (JRD–19/97) to U-shaped (JRD–20/27) linguaflexid. The hypoflexid extends anterolingually to the level of the metacristid. The prefixid is reduced to a narrow anteroposteriorly orientated prefossette on the very worn p3–4 (JRD–19/97), whereas it shows a simple morphology with two slightly asymmetrical labially orientated “horns” and anterior and posterior plicids on the p4 (JRD–20/27). The postflexid, which cannot be observed on the p3 (JRD–19/97), invades the metacristid anterolingually on the p4s. Labially, the protoconid and hypoconid have a rounded and flattened band of enamel, respectively. From the labial folds, only the poorly-developed protostylid is present on the p3–4 (JRD–19/97) and a reduced pli caballinid on the p4 (JRD–20/27). The m1–2 (JRD–20/27) can mainly be distinguished from lower premolars by a deeper hypoflexid reaching the labial margin of the metacristid. In addition, these lower molars display a shallow U-shaped linguaflexid, a prefixid with two symmetrical labially orientated “horns” and a distinct posterior plicid. The postflexid is complex with a wavy labial margin and does not reach the metacristid. The pli caballinid is incipient to missing. The hypoconulid is distinguished by a posterior constriction of the entoconid. The m3 (JRD–17/38) has a shallow open V-shaped linguaflexid. The hypoflexid is narrow and has an intermediate depth, reaching the labial margin of the metacristid without penetrating it. The prefixid has two symmetrical labially-orientated “horns” and a posterior plicid. The postflexid is narrow, with an undulating labial margin reaching the posterior margin of the metacristid. The protoconid and hypoconid form two labially rounded bands of enamel. The pli caballinid, protostylid, ectostylid and hypostylid are absent.

Upper cheek teeth. The single referred specimen of upper cheek teeth is an unworn DP3/4 (JRD–20/24). The upper half of the crown is covered by cement. In occlusal view, the dental pattern is typical plagiolophodont. However, compared to adult cheek teeth, the tooth is longer than narrow, forming a slender rectangle. The pli caballin is simple, developed and anterolingually orientated. The protocone is isolated, elongated, triangular in shape and flattened lingually, typical for an unworn upper cheek tooth. The parastyle, mesostyle and parastyle are well developed and labially orientated. A modest

anterostyle is visible. The pre- and post-fossette are barely separated by a discreet enamel ridge joining the lingual side of the mesostyle to the anterolabial extremity of the crescent of the paraconule. The folds of these fossettes are not visible due to the earlier wear of the tooth and the cement cover. The pli protoconule is marked, its labial extension creates a distinct median fossette. The hypoconal groove is deeply incised and thin.

Postcranial bones. Most of postcranial elements are fragmented and belong mostly to juvenile individuals. For instance, all available tibia and calcaneus have unfused distal epiphysis and tuber calcanei, respectively. Additionally, different sets of bones can be articulated together and belong to the same individual, such as the partial complete left posterior limb of a juvenile individual included the tibia diaphysis (JRD–19/95) and its distal end (JRD–17/29), as well as the astragalus (JRD–17/28) and calcaneus (JRD–17/19).

From the atlas (JRD–20/189), only the anteroventral side is preserved. The condyle facets are kidney-shaped and ventrally almost in contact. The ventral tubercle is prominent. The referred cervical vertebra JRD–20/17 is incomplete. The body is relatively long and bears a developed ventral crest, characteristic of cervical vertebrae 3–5. In anterior view, the head of the body is convex, prominent and sagittally oval in shape with a dorsal incisure, whereas the vertebral foramen is transversally oval. In posterior view, the vertebral fossa is deep and oblique anteroposteriorly. The cervical vertebra 6 (JRD–17/18) is characterised by a strongly reduced ventral crest and well-defined transverse fossa.

The referred humeri are too incomplete for an accurate anatomical description. A rare notable character is the presence of a deep and distinct accessory fossa for the extensor muscle of the digit located laterally to the fossa radialis (shallow in *Equus*, observation by Bernor et al. (1997)). This character is visible in anterior view of the distal ends of JRD–20/24 and JRD–20/51. Additionally, in distal view (JRD–20/51), a medioposteriorly oriented groove for the ligamentous attachment is well marked on the medial trochlea (weak in *Equus*, observation by Bernor et al. (1997)). In medial view, the nutrient foramen is visible in JRD–17/24 and JRD–19/88 and, in lateral view, the lateral supracondylar in JRD–21/24 is well distinct, but rounded.

The radius-ulna (JRD–19/82) is prominently developed (poorly developed in *Equus*, observation by Bernor et al. (1997)). The trochlear incisure of the ulna is strongly developed and, in proximal view, the radius head is stout, relatively short and deep compared to extant Equidae. From the proximal articulation of the radius, the fossa synovialis and incisure on the posterior border of the fovea capitis radialis (like in *Equus* after Bernor et al. (1997)) are present. In anterior view, the lateral and middle ridges of the proximal articulation are marked; and the radial tuberosity is poorly developed (unlike in *Equus* after Bernor et al. (1997)). The corpus of the ulna is fused with the shaft of the radius and slightly reduced, reaching almost the distal end of the radius. In distal view,



Figure 5. *Cremohipparion longipes* (Gromova, 1952), comb. nov. (Perissodactyla, Equidae) from Iradzor locality, Armenia (MN15 – early MN16, Late Pliocene). r. Mc3–2 (JRD–17/12) in anterior (A1), lateral (A2), posterior (A3) and medial (A4) views; r. Mc3–2 (JRD–19/96) in anterior (B1) and lateral (B2) views; r. Mc3 (JRD–20/02) in anterior (C1) and lateral (C2) views; r. proximal end Mc3 (JRD–19/87) in anterior (D1) and lateral (D2) views; l. distal end Mc3 (JRD–20/43) in anterior (E1) and lateral (E2) views; l. Mc3 (JRD–20/33) in anterior (F1), lateral (F2), posterior (F3) and medial (F4) views; r. anterior distal phalanx 3 (JRD–20/36) in dorsal (G1), distal (G2), lateral (G3), solar (G4), proximal (G5) and medial (G6) views. Scale bar: 5 cm.



Figure 6. *Cremohipparion longipes* (Gromova, 1952), comb. nov. (Perissodactyla, Equidae) from Jradzor locality, Armenia (MN15 – early MN16, Late Pliocene). r. Mt3 (JRD–20/87+85) in anterior (A1–2), lateral (A3–4), posterior (A5–6) and medial (A7–8) views; r. proximal end Mt3 (JRD–20/176) in anterior (B1), lateral (B2), posterior (B3) and medial (B4) views; r. proximal end Mt3 (JRD–20/67) in anterior (C1), lateral (C2), posterior (C3) and medial (C4) views; l. proximal end Mt3 (JRD–17/25) in anterior (D1), lateral (D2), posterior (D3) and medial (D4) views; l. distal end Mt3 (JRD–21/22) in anterior (E1), lateral (E2), posterior (E3) and medial (E4) views. Scale bar: 5 cm.



Figure 7. *Cremohipparion longipes* (Gromova, 1952), comb. nov. (Perissodactyla, Equidae) from Jradzor locality, Armenia (MN15 – early MN16, Late Pliocene). l. calcaneus (JRD–17/19) in anterior (A1) and lateral (A2) views; l. calcaneus (JRD–19/11) in anterior (B1) and lateral (B2) views; l. juvenile calcaneus (JRD–20/28) in anterior (C1) and lateral (C2) views; l. juvenile astragalus (JRD–17/28) in anterior (D1) and lateral (D2) views; l. astragalus (JRD–19/12) in anterior (E1) and lateral (E2) views; l. astragalus (JRD–20/35) in anterior (F1) and lateral (F2) views; l. astragalus (JRD–20/26) in anterior (G1) and lateral (G2) views; r. calcaneus (JRD–24/02) in anterior (H1) and lateral (H2) views; r. calcaneus (JRD–20/68) in anterior (I1) and lateral (I2) views; r. astragalus (JRD–20/44) in anterior (J1) and lateral (J2) views; r. astragalus (JRD–20/31) in anterior (K1) and lateral (K2) views; l. small cuneiform (JRD–20/194) in proximal (L1), anterior (L2), lateral (L3), distal (L4), posterior (L5) and medial (L6) views. Scale bar: 5 cm.



Figure 8. *Cremohipparion longipes* (Gromova, 1952), comb. nov. (Perissodactyla, Equidae) from Jradzor locality, Armenia (MN15 – early MN16, Late Pliocene). Cervical vertebra 6 (JRD–17/18) in anterior (A1), lateral (A2), dorsal (A3) and ventral (A4) views; r. distal end humerus (JRD–21/24) in anterior (B1) and lateral (B2) views; l. distal end humerus (JRD–20/191) in anterior (C1) and lateral (C2) views; r. proximal end radius-ulna (JRD–19/82) in anterior (D1) and lateral (D2) views; r. distal end radius (JRD–19/06) in anterior (E1), lateral (E2), distal (E3) and posterior (E4) views; r. proximal end tibia (JRD–19/91) in anterior (F1) and lateral (F2) views; l. juvenile diaphysis tibia (JRD–17/11) in anterior (G1) and lateral (G2) views; l. juvenile end tibia (JRD–20/161) in anterior (H1) and lateral (H2) views; l. articulated juvenile tibia, calcaneus and astragalus (JRD–19/95, JRD–17/29, JRD–17/19, JRD–17/28) in anterior (I1), lateral (I2), posterior (I3) and medial (I4) views.

the isolated and unfused distal articulation (JRD–19/06) possesses the poorly-developed middle tendon groove for the extensor muscle of the digit, while the lateral one is developed. The medial margin of the distal articular trochlea is shortened (like in *Equus*, while it is enlarged in *Hippotherium* after Bernor et al. (1997, fig. 6.3.1.2d)).

The referred Mc3 are very slender with $GI < 13.5$ (between 10.53 and 12.40) and semi-cylindrical in cross-section. In anterior view, the diaphysis is smooth. The angle between the proximal edge of the lateral facet for the magnum and the medial one for the unciform is ca. 150° , whereas in *Hippotherium*, this angle is ca. 130° and in extant *Equus* ca. 160° (after Bernor et al. (1997)). Just proximal to the crista sagittalis of the distal trochlea, the supratrochlear fossa is shallow and transverse with a rounded proximal limit (triangular in *Hippotherium*, vestigial in extant *Equus*, after Bernor et al. (1997)). The lateral and medial protuberances above the trochlea are strongly developed (poorly developed in *Equus*, observation by Bernor et al. (1997)). In posterior view, the diaphysis has a rather depressed aspect intermediate between two parasagittally disposed long rugose ridges for the joints with the functional Mc2 and Mc4. These ridges are close to the trochlea, but do not reach it, leaving free distal ends of the Mc2 and Mc4 for independent articulation with phalanges. In extant *Equus*, these ridges are only developed on the proximal half of the length of the Mc3 and represent the articular contacts with the atrophied and non-functional Mc2 and Mc4 (Bernor et al. 1997). In distal view, the crista sagittalis is rounded anteriorly and sharp posteriorly and is positioned obliquely so that its anterior part is slightly shifted laterally.

In solar view, the distal phalanx 3 (JRD–20/36) displays a parabolic U-shaped outline typical for an Equidae anterior digit (Barone 1999). The other distal phalanx remains are too fragmented for a description and even to identify their anatomical position.

The femur is represented by a single distal fragment of diaphysis (JRD–183). The only visible features are the oval cross-section and the deep and large supracondylar fossa.

The referred tibias are very incomplete. The main observable characters are: the soft rugose surfaces of the medial and lateral malleolus in anterior view; the very shallow and slightly marked mediodistal gutter (way for the tendon of the posterior tibial muscle) in medial view and the lack of the fossa synovialis on the articular ridge between the articular grooves for the astragalus in distal view.

All studied astragals have similar morphologies, but differ in size. These size differences are interpreted as individuals of different ages in accordance with the incomplete ossification observed on some calcanei and tibias. In anterior view, the bone is systematically higher than broad ($H > TD$, while $H < TD$ in *Equus* after Bernor et al. (1997)). The lateral trochlear lip is more robust than the medial one, but both have the same proximal extension (medial trochlear lip higher in *Equus*, observation by Bernor et al. (1997)). The ovoid cavity is moderately deep and has a smooth outline. The medial tubercle is high and well developed. In posterior view, the posterior

part of the lateral trochlear lip is sharp, whereas it is rounded in *Equus* (Bernor et al. 1997). The tongue-like distal extension of the proximolateral facet for the calcaneus is narrow and low. It can be fused (JRD–20/31) or independent (JRD–20/26), while it is wide, low and fused in *Equus* (Bernor et al. 1997). In distal view, the navicular facet has a shortened and flattened medial border. The cuboid facet is strongly developed (poorly developed in *Equus*, observation by Bernor et al. (1997)) and triangular. The synovial fossa is U-shaped, widely incised from the lateral edge of the navicular facet and potentially extending to its centre.

From the referred calcanei, none has preserved the tuber calcanei. In lateral view, the processus coracoideus is short (developed in *Equus*, observation by Bernor et al. (1997)) and the anterior border of the processus calcanei is almost straight (concave in *Equus*, observation by Bernor et al. (1997)), except in the juvenile specimen (JRD–19/12) where it is more concave. Consistent with the referred astragals, the tongue-like distal extension of the proximolateral facet for the astragalus is narrow and low, especially visible on the articulated astragalus-calcaneus (JRD–19/12 and JRD–19/11) of a juvenile individual. However, the tongue-like extension is always fused with the proximolateral facet of the astragalus in all available calcanei.

The small cuneiform (cuneiform 1+2, JRD–20/194) is complete ($TD_{ant} = 14.5$ mm, $APD = 34.0$ mm; $H = 22.4$ mm). In proximal view, the facet for the navicular is large and concave and has an irregular-ovoid outline. It comprises more than the half of the proximal side of the bone. The furrow defining the fused borders of the cuneiforms 1 (entocuneiform = cuneiform mediale) and 2 (mesocuneiforme = cuneiform intermedium) is faintly marked. In distal view, the Mt2 facet is double, a strong furrow delimiting an oval-shaped facet on cuneiform 1 from a square facet on the fused cuneiform 2. The Mt3 facet is the largest. It is in contact with the lateral Mt2 facet and delimited by a right angle with the latter. In *Equus*, these three facets are in contact and roughly delimited by obtuse angles. The lateral Mt2 facet is the largest (observation by Bernor et al. (1997)).

From the studied Mt3, the diaphysis has a smooth surface at its anterior side and a circular cross-section. In anterior view, the proximal border is sigmoidal and the tuberositas metatarsi are well developed. Above the crista sagittalis, the supratrochlear fossa is transverse, proximally rounded and deeper. It is more developed than in the Mc3 (unlike in *Equus* after Bernor et al. (1997)). The crista sagittalis has a form of a sharp keel. The medial trochlea is larger than the lateral one. In posterior view, the lateral and medial flat rugose depressions for the joints with the Mt2 and Mt4 fade distally above the trochlea, leaving free the distal ends of the Mt2 and Mt4. In distal view, the posterior profile of the crista sagittalis is sharp and narrow. Its anterior aspect is relatively flattened (unlike in *Equus* after Bernor et al. (1997)). The prominent proximal border of the fossa supratrochlearis and the medial protuberance are visible.

Discussion

Numerous dental and postcranial features observed in Jradzor specimens point to modern Equidae, such as molarised premolars, hypsodonty (m3, JRD-17/38; $IH > 5$), plagiolophodont upper cheek teeth with a well-developed mesostyle, slender metapodials of cursorial type and reduced lateral digits compared to the central one (e.g. Eisenmann et al. (1988); Bernor et al. (1997); Barone (1999)). However, the referred specimens differ from the genus *Equus* in having an isolated protocone on the DP3/4 (JRD-20/24) and central metapodials with long lateroposterior rough ridges for the articulations of the lateral metapodials. The latter extend close to the trochlea of the former, leaving the distal ends free for independent articulations with functional digits. According to Bernor and Tobien (1989), these features correspond to the diagnostic characters of Hipparionini. Additionally, the deep and transversally developed supratrochlear fossa of Mt3 is also considered as a character of Hipparionini.

The genera *Hipparion* and *Hippotherium* differ from Jradzor specimens by a set of dental and postcranial morphological characters. The lower premolars from Jradzor differ from those of the type species of *Hipparion*, *Hipparion prostylum*, by the absence of a protostylid, a developed pli caballinid and a linguaflexid with a marked lingual plicid (see online data on *H. prostylum* from Mont Luberon in Eisenmann (2025)). The type species of *Hippotherium*, *Hippotherium primigenium*, differs by a narrower and deeper V-shaped linguaflexid in lower premolars (see Bernor et al. (1997, fig. 4.1.3.b); supplementary data in Sun et al. (2025)). From Mc3, the angle between the proximal edge of the lateral facet for the magnum and the medial one for the unciform is more acute (ca. 130° vs. ca. 150° in specimens from Jradzor) and the supratrochlear fossa is triangular (after Bernor et al. (1997)). Furthermore, the use of PCA analyses as processed by Cirilli et al. (2023) on metapodials confirm this discrimination, highlighting a well-individualised morphological space of *Hipparion* and *Hippotherium* from that of Jradzor specimens (see Fig. 9).

At a generic level, additional diagnostic features allow us to differentiate the specimens from Jradzor from the following Eurasian Pliocene Hipparionini. *Baryhipparion* differs from the studied Hipparionini remains of Jradzor by a rounded protocone in upper cheek teeth and a hypoflexid extending deeply into the metacristid of the metaconid-metastylid on all lower cheek teeth, including p2–4 (Pang 2011; Bernor et al. 2021). Likewise, *Eurygnathohippus* differs by its very narrow and blade-like mesostyle in upper cheek teeth and elongate metaconid and square-shaped metastylid in lower cheek teeth (Bernor et al. 2020). Moreover, lower cheek teeth display generally pointed metaconid and metastylid, a usually persistent pli caballinid and the presence of an ectostylid (Jukar et al. 2019). In general, *Proboscideipparion* differs by smaller dimensions and more robust central metapodials (Cirilli et al. 2023). The metapodial bivariate

plots (Fig. 10) show *Pr. crassum* and *Pr. heintzi* being well separated from other Hipparionini (*Cremohipparion*, *Plesiohipparion*, “*H. fissurae*”, “*H. longipes*”, “*H.*” cf. *longipes* and Jradzor specimens), basically highlighting shorter and stouter metapodials. According to the diagnoses and descriptions of *Plesiohipparion* species, significant characters of lower cheek teeth differ from Jradzor specimens, such as the U-shaped linguaflexid associated with linguallly pointed metaconid and metastylid, the so-called derived “double knot” and the presence of a single to bifid pli caballinid (Qiu et al. 1987; Bernor et al. 2015; Cirilli et al. 2023). Additionally, although the central metapodials of *Plesiohipparion* are also elongated, they exhibit a more robust construction (see dataset in Suppl. material 1). In bivariate plots of metapodials (Fig. 10), the contrast is apparent, but remains weakly expressed. *Plesiohipparion* representatives, including *Pl. rocinantis* from Villaroya and Kvabebi, as well as the Chinese *Pl. houfenense* and *Pl. shanxiense*, appear basically slightly less gracile than *Cremohipparion* species and the Jradzor specimens. Incidentally, the Hipparionini from Shamar, very close to *Pl. rocinantis* of Villaroya while displaying stockier metapodials, should be referred to *Pl. cf. rocinantis* rather than *Pl. rocinantis/houfenense* or *Pl. houfenense* as suggested by Vislobokova et al. (2001) and Zhegallo (1978), respectively.

Indeed, the Jradzor Hipparionini specimens display strong similarities to the combination of morphological features that characterise the generic diagnosis of *Cremohipparion* (see Qiu et al. (1987) and Bernor and Tobien (1989)), including: an i3 not atrophied, an unworn protocone of DP3/4 isolated, linguallly placed relative to the hypocone and showing a lingual flattening, a p2 with an elongate paraconid; lower cheek teeth with rounded metaconid and metastylid, V- to shallow U-shaped linguaflexids, hypoflexid separating metaconid and metastylid on lower molars, but not on lower premolars, a pli caballinid being generally absent, a protostylid occasionally present and a ectostylid missing, as well as elongate and slender metapodials.

However, the morphometric comparison of the central metapodials from the Eurasian Hipparionini species and Jradzor (Fig. 10) does not fit with any known species of *Cremohipparion*, but instead indicate very similar morphometric spaces between elongate and slender Mc3 and Mt3 of “*Hipparion*” *longipes* from Pavlodar 1A (type locality; Gromova (1952)) and Çalta (Eisenmann and Sondaar 1998; Bernor and Sen 2017; Cirilli et al. 2023). “*Hipparion*” *longipes* is regularly included in the genus *Plesiohipparion* in recent literature (e.g. Bernor and Sen (2017); Cirilli et al. (2021, 2023)) on the basis of morphometric analysis of only postcranial specimens, especially the metapodials. Regrettably, the dental remains attributed to “*H. longipes*” are scarce, poorly described and illustrated and almost never used for taxonomic identification of this species. However, as abovementioned, *Plesiohipparion* species significantly differ from Jradzor specimens by the “double knot” and the presence of a single to bifid pli caballinid (Qiu et al. 1987; Bernor et al. 2015; Cirilli et al.

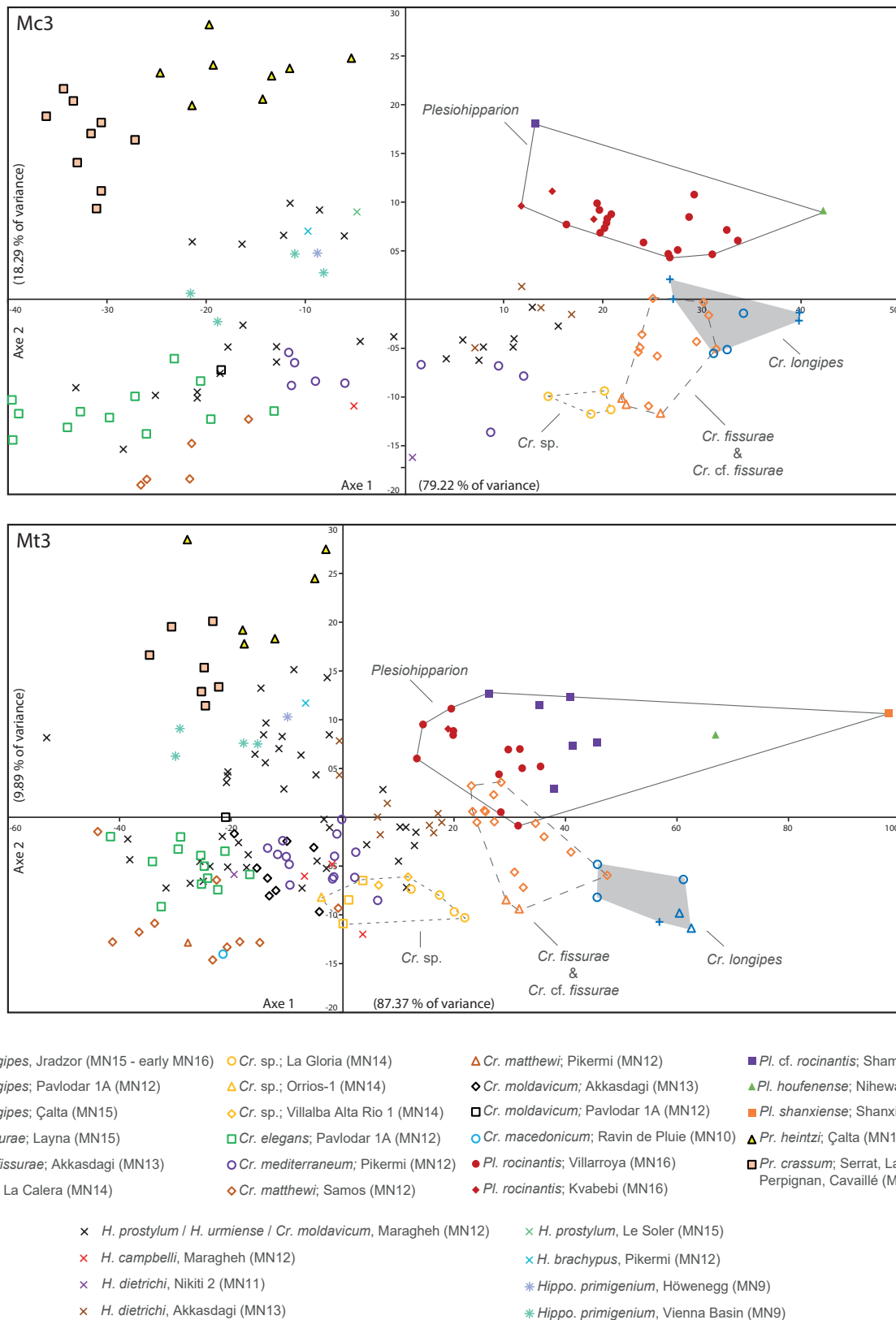


Figure 9. Principal component analyses on Mc3 and Mt3 of Hipparionini. Only the two first axes are illustrated for Mc3 (97.81% of the total variance) and Mt3 (97.26% of the total variance). The specimens are represented by shapes and colours. The types of different shapes represent different genera: empty shapes = *Cremohipparion*; full shapes = *Plesiohipparion*; full shapes with black outlines = *Proboscoidipparion*; cross = *Hipparion*; stars = *Hippotherium*; Jradzor specimens are illustrated by a blue '+'. See Table 1 and Suppl. materials 1–3 for references, measurements used and PCA results.

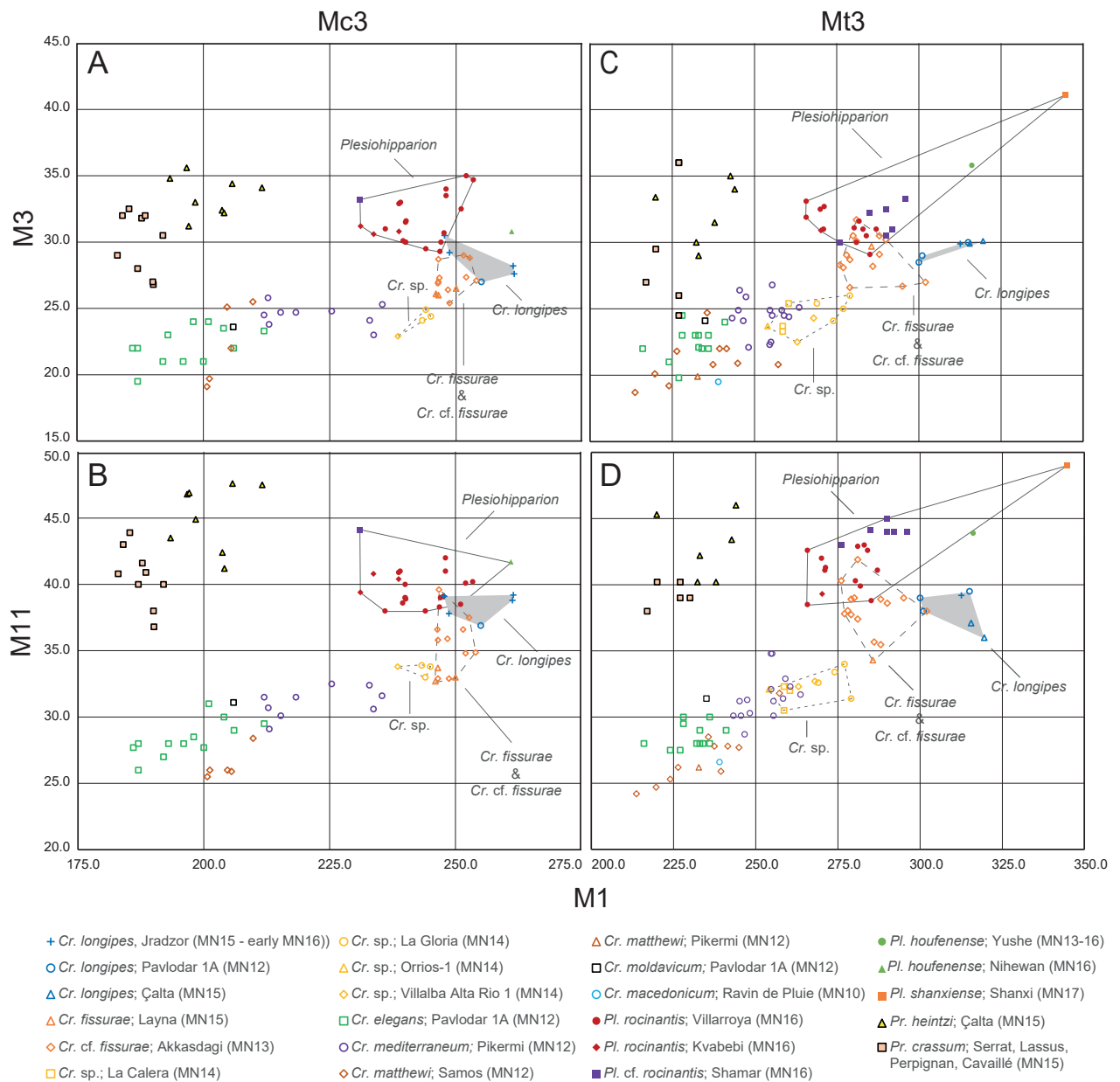


Figure 10. Bivariate plots for Hipparionini metapodials. **A.** Mc3, maximum length (M1) versus minimum transverse diameter of the diaphysis (M3); **B.** Mc3, maximum length (M1) versus distal articular width (M11); **C.** Mt3, Mc3, maximum length (M1) versus minimum transverse diameter of the diaphysis (M3); **D.** Mt3, maximum length (M1) versus distal articular width (M11). See Table 1 and Suppl. material 1 for references and measurements used.

2023). Moreover, the comparison of Jradzor specimens with the lower cheek teeth of “*H.*” *longipes* from the type locality Pavlodar 1A (r. p3 PIN-2413/3325; Gromova (1952)) display clearly common diagnostic characters of *Cremohipparion* (see Qiu et al. (1987) and Bernor and Tobien (1989)), i.e. lower cheek teeth with rounded metaconid and metastylid, shallow linguaflexid, hypoflexid separating metaconid from metastylid on lower molars (but not on lower premolars), pli caballinid and ectostylid missing. Thus, we suggest that “*H.*” *longipes* should rather be referred to the genus *Cremohipparion*. Accordingly, we refer tentatively the specimens from Jradzor to *Cremohipparion longipes* comb. nov.. Cf. “*Hipparion*” *longipes* from Puente Minero, based on

the lower cheek teeth morphology (Pesquero et al. 2011, pl. 1.4–7), exhibit the same *Cremohipparion* diagnostic characters mentioned previously, especially the outline of the “double knot” (rounded metaconid and metastylid, shallow linguaflexid). The metapodials from Puente Minero (Pesquero et al. 2011, pl. 2.1–2) display Lmax (M1), gracility index ($M3/M1 \times 100$) and TDmax distal articular/L index ($M11/M1 \times 100$) values (Pesquero et al. (2011, fig. 4; table 2)) closely comparable to those reported for Pavlodar 1A and Jradzor (Suppl. material 1). Accordingly, the Puente Minero specimens are also tentatively referred to *Cremohipparion longipes* comb. nov.

The small-sized supposed *Cremohipparion* sp. from Villarroja (MN16/17) and Montopoli (MN16/17),

although a direct comparison is not possible due to the lack of similar anatomical bones or tooth available, display a strong incompatibility in size, the Hipparionini of Jradzor being significantly larger (see Rook et al. (2017); Cirilli et al. (2021, 2023)). Other small-sized *Cremohipparion* species (*Cr. matthewi*, *Cr. elegans*, *Cr. moldavicum*, *Cr. macedonicum*) and large slender-limbed *Cr.* sp. of La Gloria 4, La Calera, Orrios-1 and Villalba Alta Río 1 are clearly distinct from *Proboscideipparion* and *Plesiohipparion* in morphometric spaces of metapodials (Fig. 10). These forms of *Cremohipparion* underline an evolutionary trend towards larger sizes of metapodials including also “*H.*” *fissurae* (Layna, type locality), “*H.*” *longipes* (Pavlodar 1A type locality, Çalta), the large-sized Hipparionini from Jradzor and also tentatively the Hipparionini of Akkaşdağı (Fig. 10). The Ruscinian large slender-limbed *Cremohipparion* sp. from Spain (La Gloria 4, La Calera, Orrios-1 and Villalba Alta Río 1), “*H.*” *fissurae* (Layna) and “*H.*” *longipes* (Pavlodar 1A, Çalta) each have distinctive metapodial morphometric spaces, essentially controlled by size distribution, but not that of slenderness (GI), which remains stable and are separate from *Plesiohipparion* species. On the other hand, “*H.*” cf. *longipes* from Akkaşdağı, although close to “*H.*” *longipes* and partly overlapping the morphometrical space of *Pl. rocinantis*, rather fits the morphometrical range of “*Hipparion*” *fissurae*. The latter shares a strong similarity with the lower premolars’ features (rounded metaconid and metastylid, V- to shallow U-shaped linguaflexids, hypoflexid not separating metaconid and metastylid) to the referred material from Jradzor (Crusafont and Sondaar 1971; Alberdi and Alcalá 1999).

However, they have significantly smaller dimensions (Fig. 11A). The same observation can be done with the astragalus, calcaneus and metapodials. However, large slender-limbed *Cremohipparion* sp. from the Iberian Peninsula (La Gloria 4, La Calera, Orrios 1, Orrios 3, Villalba Alta Río 1, Villalba Alta) seems to be distinctive from “*Hipparion*” *fissurae*, as supported especially with the morphometry (Fig. 10) and the GI (Fig. 12C, F) of metapodials. Our observations corroborate the specific discrepancy suggested by Cirilli et al. (2023). The lower cheek teeth of “*H.*” *fissurae* from Layna (type locality; Alberdi and Alcalá (1999, figs 4p, 6)), as in the Jradzor specimens, display a combination of morphological features consistent with the generic diagnosis of *Cremohipparion* (see Qiu et al. (1987); Bernor and Tobien (1989)). These include rounded metaconid and metastylid, shallow U-shaped linguaflexids, a hypoflexid separating the metaconid and metastylid on lower molars, but not on premolars and the absence of both a pli caballinid and of an ectostylid. Consequently, “*H.*” *fissurae* is also proposed to be assigned to *Cremohipparion fissurae* comb. nov. Dental measurements (Fig. 11) show no evidence to either confirm or refute these taxonomic conclusions. However, the lower premolars of *Cr. longipes* are clearly separated from those of *Cr. fissurae*.

Finally, the palaeobiological estimates (Fig. 12) strongly support most of systematic results of this study. More specifically, the shoulder height and the GI calculations cluster “*H.*” *longipes* and Jradzor Hipparionini together and refer “*H.*” *fissurae* from Layna to the *Cremohipparion* genus. However, it separates the large slender-limbed *Cremohipparion* sp. from the Ruscinian localities of

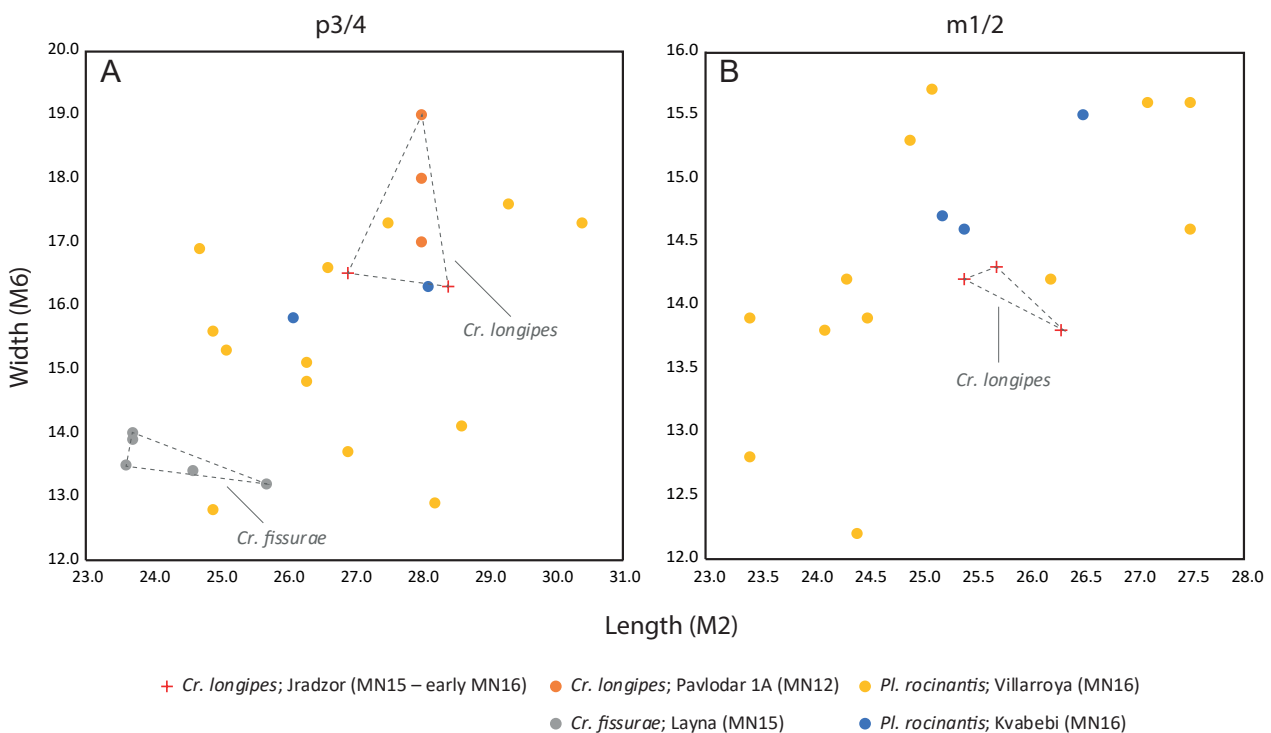
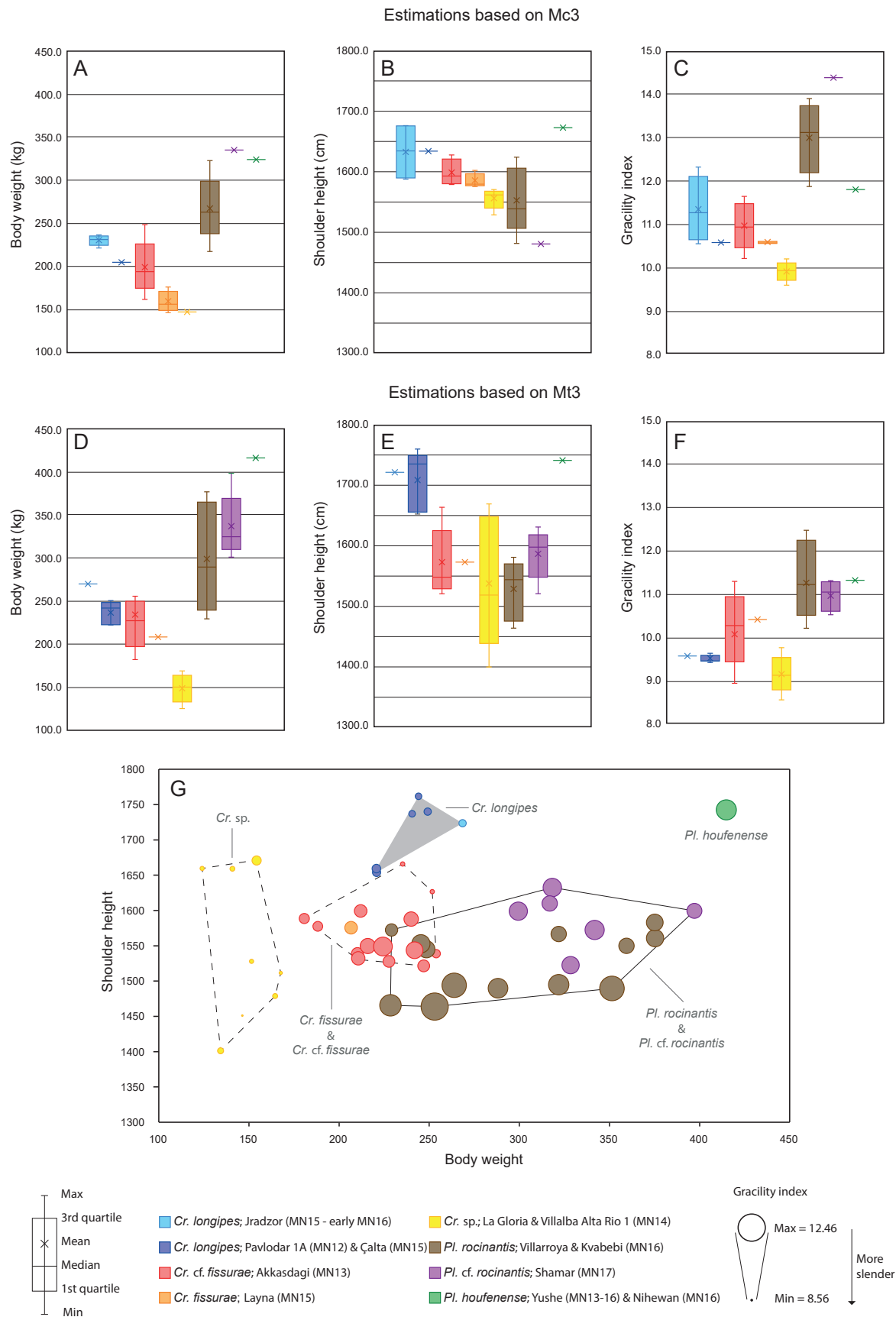


Figure 11. Bivariate plots for Hipparionini lower cheek teeth (L versus W). (A) p3/4; (B) m1/2. See Table 1 and Suppl. material 1 for references and measurements used.



Spain from other species within this genus. With regard to “*Hipparion*” cf. *longipes* from Akkaşdağı (Koufos and Vlachou 2005; Vlachou and Koufos 2009), despite a partial overlap with *Pl. rocinantis*, the general trend in metapodial morphometry indicates a greater similarity with large-sized *Cremohipparion* species from Spain, Pavlodar 1A, Çalta and Jradzor, supporting an attribution to this genus (Fig. 10). However, specific identifications on the basis of metapod morphometry remains uncertain. The strong affinities of Akkaşdağı Hipparionini with *Cr. fissurae* observed in the palaeobiological data from the box plots (Fig. 12A–F) and the trivariate plot (Fig. 12G), including body weight, shoulder height and GI, tentatively lead to an assignment to *Cr. cf. fissurae*.

The analysis of the dataset in PCA (Fig. 9) does not contribute any further evidence to the discussion. As was discussed in the preliminary analysis of the data, any interpretation of a PCA based on a dataset including several autocorrelated variables can significantly bias the results giving the appearance that a few components explain most of the variance and, thus, overestimating the variance explained by the first components (Vanhatalo and Kulahci 2016; Zamprognio et al. 2020). The result of this type of bias is a significant limitation in the ability to discriminate between specimens on a systematic level. The results obtained from the analysis provide confirmation of these biases, with the first axes demonstrating a high degree of variability (79.22% for Mc3, 87.37% for Mt3) and the loadings indicating that the variable M1 contributes almost entirely to this axis (Suppl. materials 2, 3). In contrast, all other variables contribute almost exclusively to the second axis (18.29% for Mc3, 9.89% for Mt3) as a result of their autocorrelation. It is evident that the variability of PCA, Mc3 and Mt3 is negligible beyond two primary axes, thereby rendering the PCA barely more informative than the biplot diagrams (Fig. 10). Indeed, the morphometric space patterns demonstrate a high degree of similarity between the PCA and the biplot diagrams for what concerns the genera *Cremohipparion*, *Plesiohipparion* and *Proboscideipparion*.

Conclusions

Our results suggest that “*Hipparion*” *longipes* and “*H.*” *fissurae* should be referred to *Cremohipparion longipes* comb. nov. and *Cremohipparion fissurae* comb. nov. These attributions are supported by both the morphological characters and morphometric data. Large slender-limbed *Cr. sp.* from Ruscinian localities of the Iberian Peninsula (La Gloria 4, La Calera, Orrios-1 and Villalba Alta Rio 1) remain distinct from *Cr. fissurae* of the type locality Layna and are most likely endemic to Spain during the MN14. The tentative revised record of *Cr. cf. fissurae* in Akkaşdağı (MN13, Turkey), additionally to the type locality Layna (MN15, Spain), leads to reconsidering the palaeobiogeographical distribution and biochronological range of this species. With regard to the palaeobiogeography of *Cremohipparion longipes* comb.

nov. (Fig. 13), its origin is difficult to identify, being given the uncertain Turolian age of Puente Minero (van Dam et al. 2001; Pesquero et al. 2011). It could rather be traced to Central Asia, as indicated by the record from Pavlodar 1A (Kazakhstan, MN12; Gromova (1952); Vasilyan et al. (2017)). In MN13, its palaeobiogeographical distribution extends its occurrence in the Middle East in Baynunah (“*Plesiohipparion*” cf. *longipes*, United Arab Emirates, MN13; Bernor et al. (2022)). So far being absent in the MN14, they reappear in MN15–MN16 sites of Balkans in Megalo Emvolon (“*Hipparion*” *longipes*, Greece, MN15; Koufos (2006); Koufos et al. (2021)) and West Asia in Çalta (Turkey, MN15) and Jradzor (Armenia, MN15 – early MN16).

Cremohipparion longipes is a very gracile, cursorial and large-sized Hipparionini with true hypsodont cheek teeth, adapted to open and dry environment. Its first appearance in late Late Miocene and its palaeobiogeographical extension during the Pliocene could coincide with the general cooling trend of the climate during this period and expansion of *C₄* grasses in Eurasia since the Late Miocene (e.g. Zachos et al. (2001); Zhisheng et al. (2001); Liu et al. (2009); Eronen et al. (2010); Muhlbachler et al. (2011); Yao et al. (2011)). Interestingly, some of the palaeobiogeographic dispersals of *Cr. longipes* correlate with climatic/palaeoenvironmental events in Eurasia. Its appearance in Central Asia coincides with the Khersonian Drying of the Eastern Paratethys (Lazarev et al. 2025), when, due to the drier climate, the Eastern Paratethys Sea shrank, exposing waste territories of Central Eurasia (Fig. 13C, D). Further, the MN15 and early MN16 sites as Megalo Emvolon, Çalta and Jradzor correlate to the period once the Caspian Sea shrank to its smallest extent (Productive Series) (Fig. 13C). It was suggested to be a result of either climate or tectonics reorganisations or both (Vincent et al. 2010; Krijgsman et al. 2019). Interestingly, the following period in the region (Akchagylian Stage) is characterised by humid climate (Vasiliev et al. 2022) and another hipparionine form (*Plesiohipparion rocinantis*) from the Kvabebi site (Lazarev et al. 2021; Cirilli et al. 2023). Data on carbon and oxygen isotopes of tooth enamel complete this discussion of the Jradzor hipparionine (see this volume).

Finally, our study also emphasises that the method used to study hipparionines must take morphology and its variability into account. While some morphological characteristics may vary greatly, others, particularly the combination of those relating to teeth, have diagnostic value at least at the generic level (e.g. lower cheek teeth with rounded metaconid and metastylid, V- to shallow U-shaped linguaflexids, hypoflexid separating metaconid and metastylid on lower molars, but not on lower premolars, a pli caballinid being generally absent, a protostylid occasionally present and a ectostylid missing, as well as elongate and slender metapodials). When performed correctly, statistical analysis of datasets can be very interesting, but an approach based solely on measurement data—particularly if analysed using uncontrolled statistical methods—can lead to erroneous interpretations.

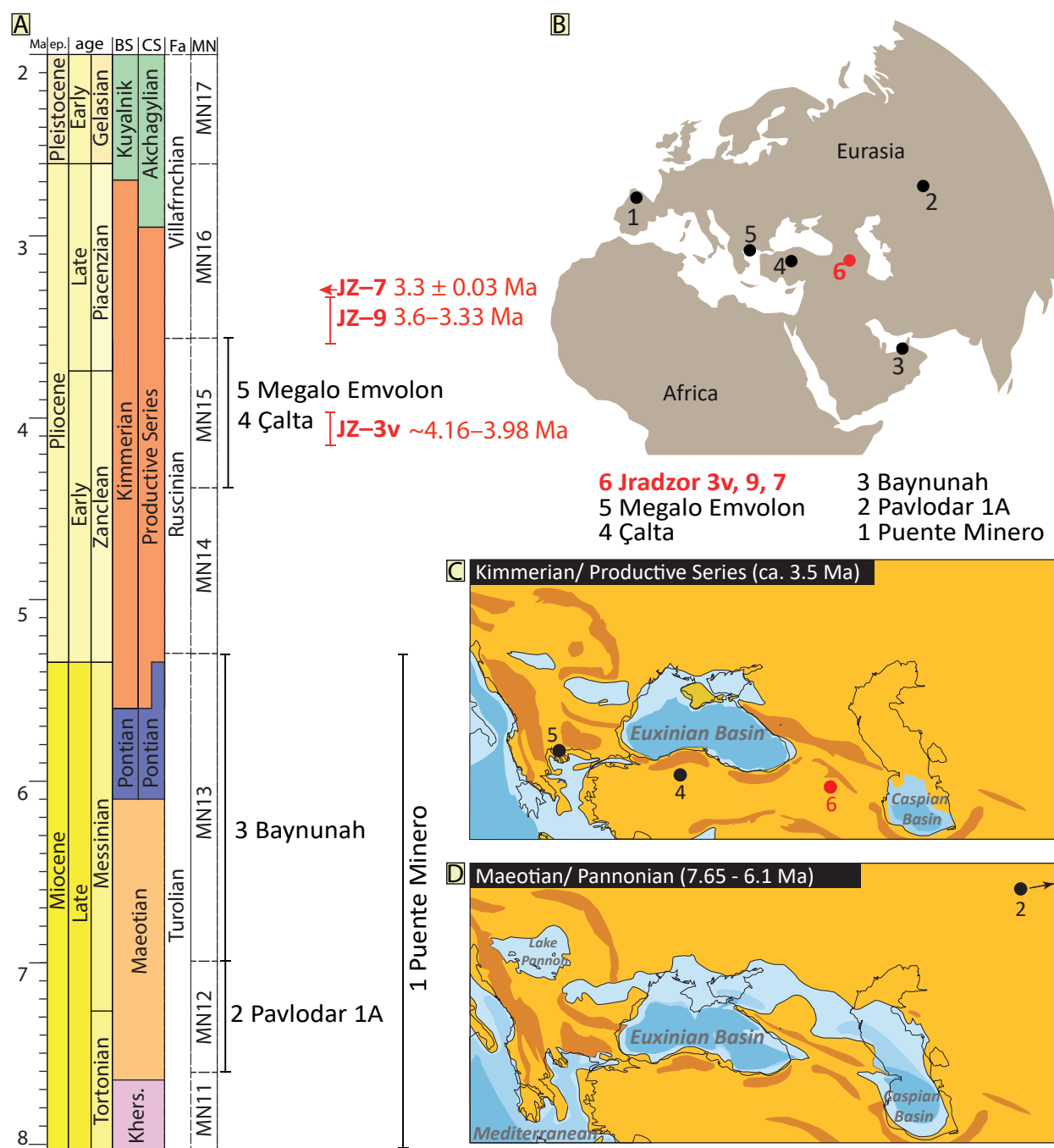


Figure 13. A. Stratigraphical and B–D. Palaeogeographical distribution of *Cremohipparion longipes* (Gromova, 1952), comb. nov. in Eurasia. A. Stratigraphic coverage of sites: 1. Puente Minero (Teruel Basin, Spain, Turolian), originally described as cf. “*Hipparion*” *longipes* (Pesquero et al. 2011); 2. Pavlodar 1A (Kazakhstan, MN12), originally described as “*Hipparion*” *longipes* (Gromova 1952; Vislobokova et al. 2001; Bernor and Sen 2017; Bernor et al. 2021); 3. Baynunah (United Arab Emirates, MN13), originally described as “*Plesiohipparion*” cf. *longipes* (Bernor et al. 2022); 4. Çalta (Turkey, MN15), originally described as “*Hipparion*” cf. *longipes* (Eisenmann and Sondaar 1998); 5. Megalo Emolon (Greece, MN15), originally described as “*Hipparion*” *longipes* (Koufos 2006; Koufos et al. 2021); 6. Jradzor (JZ–3v, –9, –7) (Armenia, MN15 – early MN16); B. Map of Eurasia and Africa with geographic location of the sites. Palaeogeographic maps of Eastern Paratethys during C. Kimmerian and D. Khersonian with location of the sites of corresponding ages.

The evolutionary history of hipparionines is not yet fully understood and a revision of the group is still necessary, but this can only be done using an integrative method that takes into account all the aspects that can be studied: measurements and statistics, but also morphology, palaeoecology, biostratigraphy and biogeography.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.

No AI tools were used in the preparation of this manuscript.

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Author contributions

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Dataset of measurements

Authors: Damien Becker, Manhon Mouhat Bourquard, Olivier Maridet, Davit Vasilyan

Data type: xlsx

Explanation note: Dataset of measurements (mm) used in this study: including dental and metacarpial, metatarsial and astragal measurements of Late Miocene-Pliocene Hipparionini from Eurasia (localities included: Akkaşdağı, Çalta, Cavaillé, Höwenegg, Jradzor, Kvabebi, La Calera, La Gloria, Lassus, Layna, Le Soler, Maragheh, Nihewan, Nikiti 2, Orrios-1, Pavlodar 1A, Perpignan, Pikermi, Ravin de Pluie, Samos, Serrat, Shamar, Vienna Basin, Villalba Alta Rio 1 and Villarroja). The estimation of body weight (kg), shoulder height (cm) and gracility index, based on this dataset are also provided with their calculation methods.

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Link: <https://doi.org/10.3897/sjp.145.189856.suppl1>

Supplementary material 2

Results of the PCA, based on metacarpal measurements

Authors: Damien Becker, Manhon Mouhat Bourquard, Olivier Maridet, Davit Vasilyan

Data type: xlsx

Explanation note: Results of the PCA, based on metacarpal measurements, including the eigenvalue and percentage of variance represented on each axis, the score of each specimen on the axes and the loading of each variable on the axes.

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Link: <https://doi.org/10.3897/sjp.145.189856.suppl2>

Supplementary material 3

Results of the PCA, based on metatarsal measurements

Authors: Damien Becker, Manhon Mouhat Bourquard, Olivier Maridet, Davit Vasilyan

Data type: xlsx

Explanation note: Results of the PCA, based on metatarsal measurements, including the eigenvalue and percentage of variance represented on each axis, the score of each specimen on the axes and the loading of each variable on the axes.

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