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New insights on the Early Pleistocene equids from Roca-Neyra (France, central Europe): implications for the *Hipparion* LAD and the *Equus* FAD in Europe

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Abstract.—We undertake a redescription of the equid sample from the Early Pleistocene of Roca-Neyra, France. This locality has been recently calibrated at the Pliocene/Pleistocene boundary (2.6 ± 0.2 Ma) and therefore it is of interest for the first appearance of the genus *Equus* and last appearance of hipparionine horses. The Roca-Neyra equid sample, reanalyzed herein using morphological, morphometrical, and statistical analyses, has revealed the co-occurrence of *Plesiohipparion* cf. ?*P. rocinantis* and *Equus* cf. *E. livenzovensis*. The analysis undertaken on several European, African, and Asian "*Hipparion*" sensu lato species from late Miocene to Early Pleistocene has revealed different remnant *Hipparion* lineages in the Plio-Pleistocene of Europe: *Plesiohipparion*, *Proboscidippaion*, and likely *Cremohipparion*. The discovery of the first European monodactyl horse, *Equus* cf. *E. livenzovensis* correlates Roca-Neyra with other 2.6 Ma European localities in Italy, Spain, and in the Khapry area (Azov Sea region). The morphological description of the *Equus* cf. *E. livenzovensis* lower cheek teeth has highlighted intermediate features between the North American Pliocene species *Equus simplicidens* and Early Pleistocene European *Equus stenonis*. Our study supports the hypothesis that *E. livenzovensis* is a plausible evolutionary predecessor for the *Equus stenonis* group. These observations underscore the importance of Roca-Neyra as an important locality for the last European hipparions and the first *Equus* in the Early Pleistocene of Europe.

Introduction

Roca-Neyra is an important Early Pleistocene locality located within the Perrier Plateau area, France (Fig. 1). The Perrier Plateau area contains a continental fluvial sequence and, due to the proximity of the Mont-Dore stratovolcano, includes several volcanic ash and pumice layers interbedded within the sedimentary sequence (Pastre, 2004; Nomade et al., 2014). Its geological record spans the late Pliocene to the Early Pleistocene and has provided an important fossil assemblage since its initial discovery in the second half of the 19th century. Within the context of their review of late Pliocene and Early Pleistocene sites of France, Nomade et al. (2014) have reassessed the chronological calibration for the most important localities included in the Perrier Plateau area, Les Etouaires, Roca-Neyra, La Loubière de Pardines, and Le Creux de Peyrolles, chronologically constrained by ^{40}Ar/^{39}Ar analysis. Roca-Neyra's age has been calibrated as being 2.6 ± 0.2 Ma (Nomade et al., 2014) and correlates with the Italian Early Pleistocene locality of Montopoli (lower Valdarno basin, Italy; Rook et al., 2017). Together these two localities mark the lowermost limit of the Pleistocene at the Gauss/Matuyama polarity transition and in turn correlate to the lower limit of Mammal Zone MNQ 16b of the European Land Mammal Age biochronologic scheme (Guérin, 1990; Mein, 1999).

As reported above, four main fossiliferous localities have been identified in the Perrier plateau area: Les-Etouaires (2.77 ± 0.02 Ma), Roca-Neyra (2.6 ± 0.2 Ma), La Loubière de Pardines (slightly younger than Roca-Neyra but older than Saint Vallier) and Le Creux de Peyrolles (1.49 ± 0.01Ma), (Nomade et al., 2014). The locality of Roca-Neyra was discovered in 1872–1873. Site excavations were led at the end of the 19th and at the beginning of the 20th century, and the collection housed in the Natural History Museum of Basel, at the Faculté des Sciences de Clermont and at the Université Claude Bernard-1, Lyon. The fossiliferous levels are considered penecontemporaneous with the debris avalanches that fossilized the sedimentary sequence of the Perrier Plateau (Nomade et al., 2014) and the Roca-Neyra fossil locality is constrained within the first two debris avalanches of the Perrier Plateau area. The Roca-Neyra equid assemblage was previously reported by Stehlin (1904), who highlighted the presence of an "*Hipparion*" (not demonstrably of the genus *Hipparion* s.s., Woodburne and

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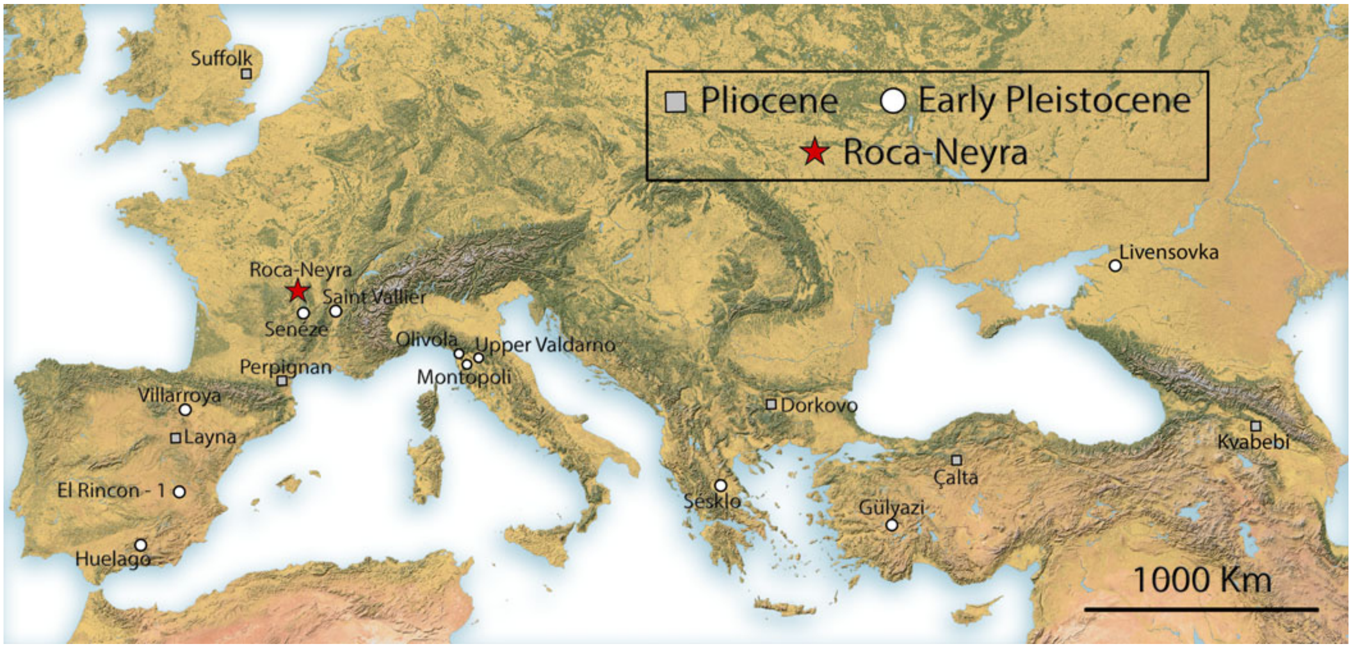

Figure 1. Geographical map showing the locality of Roca-Neyra with the European Plio-Pleistocene localities mentioned in the text. Base map from QGis (https://qgis.org/).

Bernor, 1980; Bernor et al., 1996, 2016) in the faunal assemblage. Later, the equid assemblage was discussed by several authors, many of whom challenged the presence of "*Hipparion*" and *Equus* (Schaub, 1944; Bout, 1960; Kurten, 1963; Radulescu and Samson, 1967). Finally, the co-occurrence of both genera has been clarified by Eisenmann and Brunet (1973), who confirmed the occurrence of "*Hipparion*" sp. and *Equus* cf. *E. stenonis*. The faunal assemblage of Roca-Neyra is consistent with the local stratigraphy and includes the following faunal assemblage: *Nyctereutes megamastoide* Pomel, 1842, *Chasmaporthetes lunensis* Del Campana, 1914, *Lynx issiodorensis* Croizet and Jobert, 1828, *Anancus* cf. *A. arvernensis* Croizet and Jobert, 1828, "*Hipparion*" *rocinantis* Hernández-Pacheco, 1921, *Equus stenonis* Cocchi, 1867, *Eucladoceros ctenoides vireti* Heintz, 1970, *Leptobos elatus* Pomel, 1853, *Gazellospira torticornis* Aymard, 1854, ?*Procamptoceras brivatense* Schaub, 1923, and *Gazella borbonica* Depéret, 1884 (see Palombo and Valli, 2004).

The base of the Pleistocene is an event marked by the global environmental change from warm-humid ecosystems to cool-arid conditions. In the fossil record, this event is documented by the inter-continental dispersal of the genus *Equus* (Lindsay et al., 1980; Azzaroli, 1983; Bernor et al., 2019; Rook et al., 2019). In the Mediterranean region, this faunal turnover is recorded in the Early Pleistocene (MNQ16b) sites of Montopoli (Italy) and El Rincón-1 (Spain), where the occurrence of the large stenonine horse *Equus livenzovensis* Bajgusheva, 1978 is reported (Alberdi et al., 1997; Azzaroli, 2000; Bernor et al., 2018b). In Eastern Europe, the *Equus* event is documented by the occurrence of *Equus livenzovensis* at Khapry (Azov Sea area, Russia) and Livensovka (Rostov, Russia) localities (Bajgusheva, 1978; Azzaroli, 2000; Bernor et al., 2018b; Bernor et al., 2019). In Western-Central Europe, this biochronologic event is represented by the locality of Roca-Neyra, where the occurrence of the genus *Equus* is associated with the three-toed horse "*Hipparion*." The species reported in the literature are *Equus* cf. *E. stenonis* and "*Hipparion*" *rocinantis* (Stehlin, 1904; Eisenmann and Brunet, 1973; Palombo and Valli, 2004).

Here, we revise, describe, and analyze the Roca-Neyra equid sample housed in the Université Claude Bernard-1 in Lyon, with new considerations on the last occurrence of the European "*Hipparion*" lineages and the *Equus* dispersal event.

Materials and methods

Part of the Roca-Neyra equid sample is housed in the paleontological collection at the Université Claude Bernard-1 in Lyon, and it is represented by a right calcaneum (UCBL-FSL 211232), a second phalanx of the central digit (UCBL-FSL 211733), a third phalanx of the central digit (UCBL-FSL 211733) of "*Hipparion*," and three isolated teeth, probably belonging to the same individual (left p4, m1, and m2; UCBL-FSL 211735) of *Equus*. Moreover, Eisenmann and Brunet (1973) reported two "*Hipparion*" third metatarsals from Roca-Neyra (MNHN 1948-13-11, and NHMB RN 98; table 2, p. 114). Stehlin (1904) preliminarily reported the Roca-Neyra collection housed at the Facultés des Science de Clermont, but unfortunately no data or additional information on this collection have been reported since 1904.

We review the Roca-Neyra equid sample housed in the paleontological collection at the Université Claude Bernard-1, Lyon and compare it to a suite of European, African, and Asian Miocene, Pliocene, and Pleistocene "*Hipparion*" species, with the North America and Eurasian Plio-Pleistocene *Equus* species, and with extant *Equus grevyi* Oustalet, 1882. The late Miocene–Early Pleistocene "*Hipparion*" species included in our analyses are: *Hippotherium primigenium* von Meyer, 1829 (Höwenegg, Germany; data from Bernor et al., 1997), "*Cormohipparion*" *africanum* Arambourg, 1959 (Bou Hanifia, Algeria; data from Bernor and White, 2009), *Cormohipparion sinapensis* Bernor et al. in Fortelius et al., 2003 (Sinap, Turkey; data from Bernor et al., 2003), *Eurygnathohippus feibeli* Bernor and Harris, 2003 (Sahabi, Libya; data from Bernor et al., 2012, 2020), *Sivalhippus turkanensis* Hooijer and Maglio, 1974 (Lothagam, Kenya; data from Bernor and Harris, 2003), *Sivalhippus perimensis* Pilgrim, 1910 (Siwalik, Pakistan; data from Wolf et al., 2013), *Cremohipparion mediterraneum* Roth and Wagner, 1855 (Pikermi, Greece; data from Koufos, 1986), *Cremohipparion matthewi* Abel, 1926 (Samos, Greece; data from Bernor et al., 1996), *Plesiohipparion longipes* Gromova, 1952 (Pavlodar, Kazakhstan; data from Eisenmann, 2019, https://vera-eisenmann.com), "*Hipparion*" *elegans* Gromova, 1952 (Pavlodar, Kazakhstan; data from Eisenmann, 2019, https://vera-eisenmann.com), *Plesiohipparion longipes* (Akkaşdağı and Çalta, Turkey; data from Koufos and Vlachou, 2005), *Plesiohipparion houfenense* Teilhard de Chardin and Young, 1931 (Houfeng, China; Qiu et al., 1987; data from Bernor et al., 2015), *Plesiohipparion rocinantis* Hernández-Pacheco, 1921 (Villarroya, Spain; Zhegallo, 1978; Pueyo et al., 2016; Rook et al., 2017; data from Eisenmann, 2019, https://vera-eisenmann.com), *Proboscidipparion heintzi* Eisenmann and Sondaar, 1998 (Çalta, Turkey; Eisenmann and Sondaar, 1998; data from Bernor and Sen, 2017), "*Hipparion*" *fissurae* Crusafont and Sondaar, 1971 (Layna, Spain; data from Alberdi and Alcalà, 1999), "*Hipparion*" *crassum* Gervais, 1859 (Perpignan, France; data from Eisenmann, 2019, https://vera-eisenmann.com) and "*Hipparion*" *rocinantis* from the Georgian locality of Kvabebi (Vekua, 1972; data from Eisenmann, 2019, https://vera-eisenmann.com). We utilize this broad range of "*Hipparion*" lineages in order to isolate those "*Hipparion*" lineages to be the most likely source of the Roca-Neyra "*Hipparion*" species.

The Pliocene and Pleistocene *Equus* species considered are: *Equus simplicidens* Cope, 1892 (Hagerman Horse Quarry, Idaho; authors' unpublished data), *Equus stenonis vireti* Prat, 1964 (Saint Vallier, France; authors' unpublished data), *Equus* sp. (Senèze; authors' unpublished data), *Equus stenonis* Cocchi, 1867 (from both Olivola and Upper Valdarno Basin, Italy; authors' unpublished data) *Equus stehlini* Azzaroli, 1964 (Upper Valdarno Basin, Italy; authors' unpublished data), *Equus suessenbornensis* Wüst, 1900 (Süssenborn, Germany; authors' unpublished data) and *Equus grevyi* (Kenya, Africa; authors' unpublished data). The *Equus* sample from the Early Pleistocene of Senèze is here retained at the genus level (*Equus* sp.), due to the conflicting opinions about which and how many species are in the fossil locality (for a comprehensive review see Alberdi et al., 1998; Delson et al., 2006; Palombo and Alberdi, 2017; Palombo et al., 2017; and Eisenmann, 2019).

Anatomical nomenclature and osteological landmarks are according to Bernor et al. (1997). Morphometric measurements follow Eisenmann et al. (1988) and Bernor et al. (1997). We undertake morphometric and statistical analyses using bivariate plots, Log10 ratio diagrams (Höwenegg *Hippotherium primigenium* means used as the Log10 standards; Bernor et al., 1997) and Principal Components Analysis (PCA).

Eisenmann (1995), Bernor and Harris (2003), Bernor et al. (2003, 2005, 2016, 2018a, b, 2019), Bernor and Sen (2017), Sun et al. (2018), and Cirilli et al. (2020, in press) have used Log10 ratio diagrams on postcranial elements to evaluate differences between selected species of "*Hipparion*" and *Equus* species and their evolutionary trends. We follow these authors in our analyses of third metapodials and for lower dentitions in the *Equus* sample. Furthermore, we have extended the statistical analyses also using PCA, using R software through the function *prcomp()* (R Core Team, 2013).

"*Hipparion*" bivariate plots have been selected for the following anatomical elements (including the following measurements): third metacarpal and metatarsal (M1 = maximal length; M11 = distal maximal articular width), second phalanx of the central digit (M1 = maximal length; M6 = distal maximal width). "*Hipparion*" third metacarpal and third metatarsal Log10 ratio diagrams include M1 = maximum length; M3 = minimal width; M4 = depth of the diaphysis at level of M3; M5 = proximal articular breadth; M6 = proximal articular width; M7 = maximal diameter of the articular facet for the third carpal/tarsal; M8 = diameter for the anterior facet for the fourth carpal/tarsal; M10 = distal maximal supra articular width; M11 = distal maximal articular width; M12 = distal maximal keel depth; M13 = distal maximal depth of the lateral condyle; M14 = distal maximal depth of the medial condyle. "*Hipparion*" third metacarpal and metatarsal PCAs include the following measurements: M1, M3, M4, M5, M6, M10, M11, M12, M13, M14 (same measurements used in Log10 ratio diagrams).

Equus mandibular cheek tooth (tmp4–tmm2) bivariate plots include M1 (maximal length at the occlusal level) and M6 (maximal width at the occlusal level). Our PCA analyses include the previous bivariate plot measurements in addition to M3 (maximal metaconid-metastylid length, the double knot), M4 (maximum length of the preflexid), and M5 (maximum length of the postflexid).

Anatomical elements.—**dtxP1**: deciduous upper first premolar; **dtxP2**: deciduous upper second premolar; **dtxP3**: deciduous upper third premolar; **dtxP4**: deciduous upper fourth premolar; **dtxM1**: deciduous upper first molar; **dtmp1**: deciduous lower first premolar; **dtmp2**: deciduous lower second premolar; **dtmp3**: deciduous lower third premolar; **dtmp4**: deciduous lower fourth premolar; **dtmm1**: deciduous lower first molar; **txI1**: upper first incisive; **txI2**: upper second incisive; **txP2**: upper second premolar; **txP3**: upper third premolar; **txP4**: upper fourth premolar; **txM1**: upper first molar; **tmi1**: lower first incisor; **tmi2**: lower second incisor; **tmp2**: lower second premolar; **tmp3**: lower third premolar; **tmp4**: lower fourth premolar; **tmm1**: lower first molar; **tmm2**: lower second molar; **tmm3**: lower third molar; **mc3**: third metacarpal; **calc**: calcaneum **mt3**: third metatarsal; **1ph3**: first phalanx of the central digit; **2ph3**: second phalanx of the central digit; **3ph3**: third phalanx of the central digit; **lt.**: left; **rt.**: right.

Repositories and institutional abbreviations.—IGF: Sezione Geologia e Paleontologia, Museo di Storia Naturale, Università di Firenze, Italy; L: Livensovka, Russia; MNHN: Muséum National d'Histoire Naturelle, Paris, France; NHMB: Naturhistorisches Museum, Basel, Switzerland; NHML: Natural History Museum, Lyon, France; RN: Roca-Neyra; UCBL-FSL: Université Claude Bernard-1, Paleontological Collection, Lyon, France; USNM: National Museum of Natural History, Washington D.C, USA.

Figure 2. *Plesiohipparion* cf. *P. rocinantis* from Roca-Neyra. UCBL-FSL 211232, right calcaneum in cranial and lateral views (**1, 2**); UCBL-FSL 211733, articulated left second and third phalanges, in cranial and lateral view (**3, 4**). Scale bars = 5 cm.

Systematic paleontology

Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Subfamily Equinae Gray, 1821
Tribe Hipparionini Quinn, 1955
Genus *Plesiohipparion* Qiu, Huang, and Guo, 1987

Type species.—*Hipparion rocinantis* Hernández-Pacheco, 1921.

Plesiohipparion cf. ?*P. rocinantis* (Hernández-Pacheco, 1921)
Figure 2

1973 *Hipparion* sp. Eisenmann and Brunet (not figured).
2004 *Hipparion rocinantis*; Palombo and Valli (not figured).

Holotype.—Unknown.

Lectotype.—A lower third/fourth premolar, described in Hernández-Pacheco (1921) and Alberdi (1974), figured in Alberdi (1974, fig. 6.4), from La Puebla de Almoradier, Early Pleistocene, Spain.

Description.—Figure 2.1, 2.2 illustrates the right calcaneum in cranial and lateral views of UCBL-FSL 211232. This element has a slender morphology with tuber calcaneum being well developed, although it is damaged in the lateral and cranial sides. The tuber calcaneum may not have been completely fused, and therefore this individual may have been a subadult. The central body is narrow, and the distal portion is elongated, whereas the sustentaculum tali for articulation with the astragalus connection is developed antero-posteriorly. In lateral view, the processus coracoideus is well developed.

Figure 2.3 and 2.4 shows the articulated second and third phalanges UCBL-FSL 211733, in cranial and lateral view. The second and third phalanges are articulated with an artificial support. The 2ph3 is a short bone, expanded medio-laterally proximally. The proximal articular surface is inclined from the palmar to dorsal aspect, with the attachment of the ligamentum sesamoideum rectum of the flexor tuberosity being strongly developed. The proximal articular surface has robust swellings for the medial and lateral scar for the ligamentum collaterale of third digit for 1ph3 and 2ph3 articulation. In cranial view (Fig. 2.3), the distal aspect presents the medial and lateral hollowed scars for attachment of the ligamentum collaterale, which binds the second and third phalanges of the central digit. The distal articular facet presents a gentle sinuous curve in dorsal view, angular in lateral view.

The 3ph3 proximal articular surface presents a sinuous curve, as in 2ph3, for the 2ph3 articulation; the processus palmaris and medialis are not elongated. The medial and lateral grooves for attachment of the ligamentum collaterale are placed below the lateral margin of the proximal articulation. The margin of the foot's sole is curled.

Material.—Right calcaneum (UCBL-FSL 211232); left second phalanx of the central digit (UCBL-FSL 211733); left third phalanx of the central digit (UCBL-FSL 211733); two third metatarsals MNHN 1948-13-11 and NHMB RN 98, (Eisenmann and Brunet, 1973; table 2, p. 114).

Remarks.—*Plesiohipparion rocinantis* (following Alberdi, 1974; Bernor et al., 1996, 2015; Pueyo et al., 2016) was initially described by Hernández-Pacheco (1921) from the Early Pleistocene of La Puebla de Almoradier (Spain), based on a few isolated remains (see Zouhri and Bensalmia, 2005). Villalta (1948) described a new species from the locality of Villarroya, *Hipparion crusafonti* Villalta, 1948. Pirlot (1956) and Forsten (1968) were the earliest authors to remark about the morphological similarities between *H. rocinantis* and *H. crusafonti*. Alberdi (1974) considered *H. rocinantis* Hernández-Pacheco, 1921 to be a valid species, recognizing Villalta's species at the subspecies level, *H. rocinantis crusafonti*. Alberdi (1986), followed by Bernor et al. (1996, 2015) and Azanza et al. (2016), included *H. rocinantis crusafonti* in *H. rocinantis* Hernández-Pacheco, 1921, considering the latter to be the formal name of the species. Qiu et al. (1987), followed by Bernor et al. (1996, 2015) and Bernor and Sun (2015),

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recognized this species as being a member of the *Plesiohipparion* clade. As such, its biogeographic range extends across the Plio-Pleistocene boundary, reported from La Puebla de Almoradier, Las Higueruelas, Villarroya (Alberdi, 1974, 1986), Roca-Neyra (France; Alberdi, 1986; Palombo and Valli, 2004; present paper), and Kvabebi (Georgia; Vekua, 1972; Alberdi, 1986).

As reported in the previous description and in the results shown in various morphometrical analyses (Figs. 5.1, 5.2, 7.4, our data, and Eisenmann and Brunet, 1973) we ascribe this sample to ?*Plesiohipparion* cf. *P. rocinantis*. Our results suggest close morphological and morphometric similarities of the Roca-Neyra sample with the species from Villarroya and Kvabebi, and more broadly with the *Plesiohipparion* clade (see bivariate plots and Log10 ratio diagrams).

Tribe Equini Gray, 1821
Genus *Equus* Linnaeus, 1758

Type species.—*Equus caballus* Linnaeus, 1758.

Equus cf. *E. livenzovensis* Bajgusheva, 1978
Figure 3

1973 *Equus* cf. *E. stenonis*; Eisenmann and Brunet, p. 106, fig. 1.
2004 *Equus* cf. *E. stenonis*; Palombo and Valli.

Holotype.—An incomplete skull (L-4) stored in the Ethnographic Museum at Livensovka, Rostov, Russia (Bajgusheva, 1978, p. 98, fig. 1).

Description.—Figure 3 includes the Roca-Neyra *Equus* sample, UCBL-FSL 211735 left tmp4 (Fig. 3.1), tmm1 (Fig. 3.2), and tmm2 (Fig. 3.3), probably belonging to the same individual. The left tmp4 is well preserved; the metaconid-metastylid (double knot) are round, separated by a shallow V-shaped linguaflexid; the preflexid is large, and its mesial margin has a long buccally projecting pli; the postflexid is antero-posteriorly elongated, with its mesiolabial margin extending into the isthmus separating metaconid and metastylid. The protoconid and the hypoconid are large, with a small pli caballinid on the mesial margin of the hypoconid. The entoconid is broad. The posterior root is broken.

The left tmm1 (Fig. 3.2) has a damaged labial margin of the protoconid; the metaconid-metastylid (double knot) has a round shape, separated by a V-shaped linguaflexid; the preflexid is

Figure 3. *Equus* cf. *E. livenzovensis* from Roca-Neyra. UCBL-FSL 211735, left lower fourth premolar (**1**); UCBL-FSL 211735, left lower first molar (**2**); UCBL-FSL 211735, left lower second molar (**3**). The specimens, probably belonging to the same individual, are represented in occlusal and lingual view. Scale bar = 5 cm.

narrow, constricted labio-lingually, with a prominent mesio-labial pli; the postflexid is antero-posteriorly elongated, with a worn lingual margin projecting into the isthmus between metaconid and metastylid; the hypoconid is large, with a worn pli caballinid on the anterior margin; the entoconid is broad, with a worn pointed cusp on the postflexid labial margin. Both roots are preserved.

The left tmm2 (Fig. 3.3) is broken on the lingual margin of the double knot, but the rounded shape of metaconid and metastylid are apparent; the metaconid and metastylid are separated by the V-shaped linguaflexid; the preflexid is elongated mesiodistally and constricted labial-lingually; the postflexid is antero-posteriorly elongated, with its mesial margin projecting into the isthmus separating metaconid-metastylid; the protoconid and hypoconid are large, with a diminuitive pli caballinid on the hypoconid mesial margin. The entoconid is broad, with a worn pointed cusp on the postflexid labial margin. The distal root is broken.

Figure 4 provides occlusal profiles of the Roca-Neyra *Equus* sample UCBL-FSL 211735 tmp4, tmm1, and tmm2, compared to North American *E. simplicidens* (Hagerman), European *E. livenzovensis* (Kapry), *E. stenonis vireti* (Saint Vallier), *E. stenonis* (Olivola), and extant African *E. grevyi* (Kenya) complete lower tooth rows. UCBL-FSL 211735 exhibits a mixture of occlusal features, shared with *E. simplicidens* and *E. stenonis*. The round shape of metaconid-metastylid is comparable to *E. simplicidens* and *E. livenzovensis* and, on the lingual side, does not exhibit the typical stenonine squared-pointed metastylid shape seen in the samples from Saint Vallier, Olivola, and Kenyan *Equus* spp. Noteworthy is the presence of a pointed metastylid on the lingual side of *E. stenonis vireti*, *E. stenonis*, and *E. grevyi*. Therefore, due to these morphological features, but in particular the metaconid-metastylid morphology, we ascribe the UCBL-FSL 211735 sample to *Equus* cf. *E. livenzovensis*.

Material.—Apparently associated left mandibular fourth premolar, first molar, and second molar (UCBL-FSL 211735), figured in Eisenmann and Brunet (1973, p. 106, fig. 1).

Remarks.—*Equus livenzovensis* Bajgusheva, 1978, is the oldest *Equus* species in Europe and it is recorded in the type locality of the Khapry area, in the Italian locality of Montopoli, and in the Spanish localities of El Rincón-1 and Huèlago (Alberdi et al., 1997; Palombo and Alberdi, 2017). All of these localities have been correlated to the Plio-Pleistocene boundary, 2.6 Ma. The species was erected by Bajgusheva in 1978, based on the *Equus* sample for the Khapry area, and its validity has been confirmed by Azzaroli (2000). *Equus livenzovensis* occurs in the Villafranchian Montopoli Faunal Unit (MNQ16b) at the beginning of the Pleistocene. The faunal turnover recorded in the Montopoli Faunal Unit is marked by the disappearance of warm-forest species such as *Tapirus arvernensis* Croizet and Jobert, 1828, *Mammut borsoni* Hays, 1834, *Sus arvernensis* Depéret, 1890, *Ursus minimus* Devèze de Chabrioland and Bouillet, 1827, and *Stephanorhinus jeanvireti* Guérin, 1972, and the first occurrence in the Villafranchian record of *Puma pardoides* Owen, 1846, *Mammuthus gromovi* Alexeeva and Garutt, 1965, *Stephanorhinus etruscus* Falconer, 1868, *Eucladoceros falconeri* Dawkins, 1868, *Gazella borbonica*, and *Equus livenzovensis* (Rook and Martìnez-Navarro, 2010; Cherin et al., 2013; Pandolfi, 2013; Bartolini Lucenti, 2017; Pandolfi et al., 2017, 2019; Rook et al., 2017; Bernor et al., 2018a, b; Cirilli et al., in press).

Statistical analysis

"Hipparion".—In order to better determine the taxonomic identity of the Roca-Neyra "*Hipparion*" sample we compared it to the Plio-Pleistocene European "*Hipparion*" samples from Layna, Perpignan, Kvabebi and Villarroya. We have utilized the following morphometrical and statistical methodologies: bivariate plots, Log10 ratio diagrams and PCA.

Figure 5 includes bivariate plots for "*Hipparion*" third metatarsal (5.1) and second phalanx of the central digit (5.2). Figure 5.1 is mt3 maximum length (M1) versus distal articular width (M11). The Roca-Neyra specimens, MNHN 1948-13-11 and NHMB RN 98, plot close to *P. rocinantis* from Villarroya and "*H.*" *rocinantis* from Kvabebi (Georgia, Vekua, 1972), and they also plot close to *P. longipes* from Pavlodar, Akkaşdağı (Koufos and Vlachou, 2005) and Çalta (Bernor and Sen, 2017). *Plesiohipparion houfenense* (data from Bernor et al., 2015) is the largest species considered in the plots (Fig. 5.1). A central group includes the primitive late Miocene species *H. primigenium*, *C. sinapensis*, and *C. africanum*. *Eurygnathohippus feibeli* is included in this sample, whereas *Cremohipparion mediterraneum* specimens are slightly longer than those of *C. sinapensis*, and *C. matthewi* is the smallest and most slender species, plotting close to *C. mediterraneum*. A second group includes the robust species *Sivalhippus perimensis*, *S. turkanensis*, and *Proboscidipparion heintzi*. It is remarkable that "*H.*" *crassum* plots in this group, close to *Proboscidipparion heintzi* and *Sivalhippus turkanensis*.

Figure 5.2 shows maximal length (M1) versus distal width (M6) of the second phalanx of the central digit. Two separate groups can be observed in this plot. The first one, which includes the medium- to small-size species *H. primigenium*, *C. africanum*, *E. feibeli*, *C. matthewi*, "*Hipparion crassum*," and "*Hipparion fissurae*," and the second with the larger species *S. turkanensis*, *P. heintzi*, and *P. rocinantis*. In this plot, UCBL-FSL 211733 is located within the larger forms, close to the Kvabebi sample, *P. rocinantis* and *S. turkanensis*. Moreover, *P. rocinantis* from Villarroya is slightly narrower than *P. heintzi* from Çalta. *Hipparion fissurae* and *H. crassum* are included in the medium- to small-size species (*H. primigenium*, *C. africanum*, and *E. feibeli*) with *C. matthewi*, which remains the narrowest individual of the entire sample.

Figure 6 is the mc3 Log10 ratio diagrams using the Höwenegg *Hippotherium* sample as standard (Bernor et al., 1997). Figure 6.1 compares species of *Cormohipparion*, *Eurygnathohippus*, and *Cremohipparion*. As previously discussed in Bernor et al. (2020), the primitive *C. sinapensis* and *C. africanum* are likely ancestral to *E. feibeli* and *C. mediterraneum*. *Eurygnathohippus feibeli* and *C. mediterraneum* follow the *C. sinapensis* and *C. africanum* Log10 line trajectories, even when the morphology is clearly more slender (M3-M10 in *E. feibeli* and M3, M10, M11 in *C. mediterraneum*). *Cremohipparion matthewi* is the smallest and most slender species considered in the analysis, and its trend reflects a plausible origin from *C. moldavicum,* the sister-taxon of *C. mediterraneum* (Bernor et al., 2016).

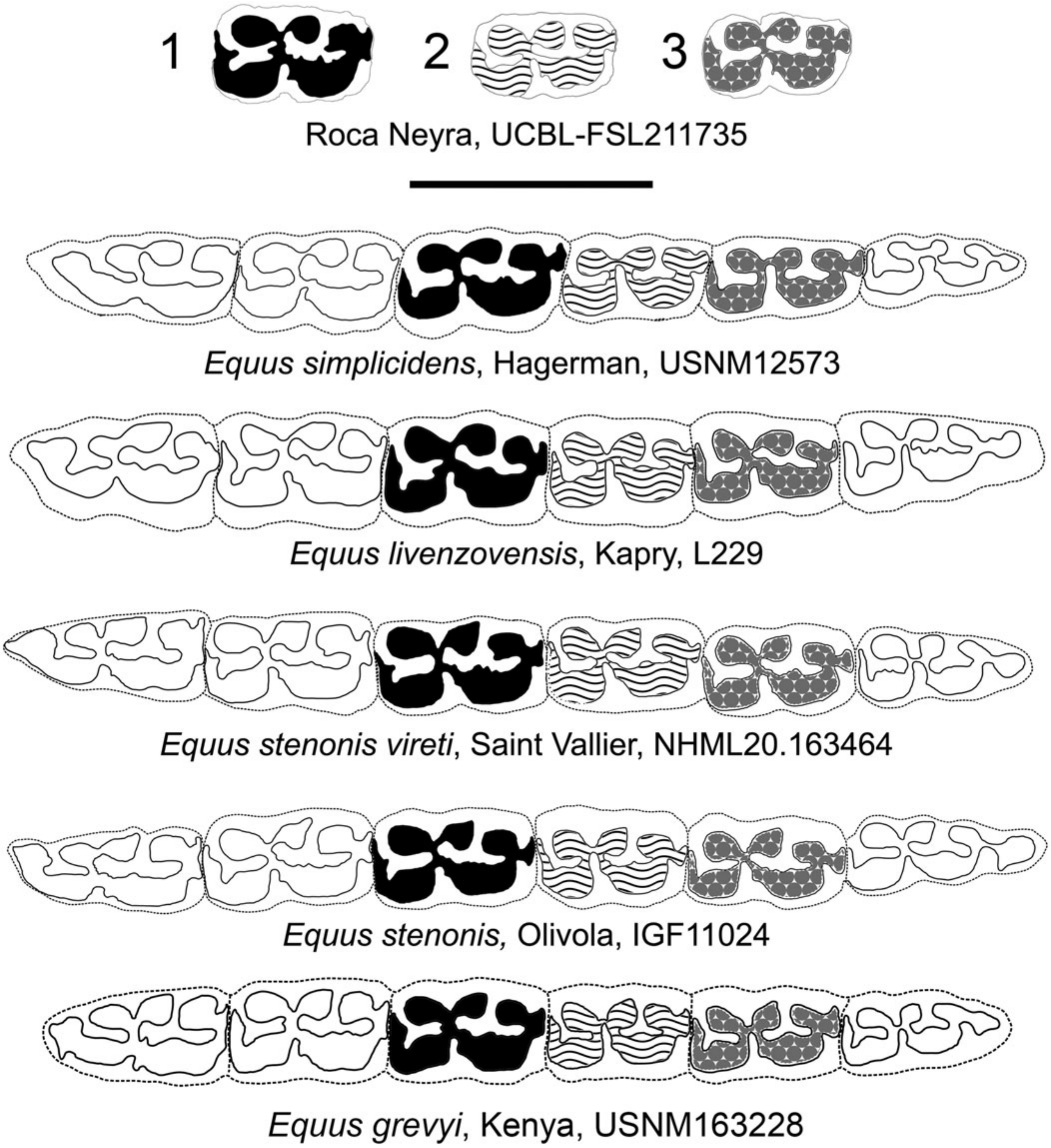

Figure 4. Anatomical comparison of the occlusal morphology of *Equus* cf. *E. livenzovensis* from Roca Neyra (**1–3**) with *Equus simplicidens*, *Equus livenzovensis*, *Equus stenonis vireti*, *Equus stenonis* from Olivola, and the extant *Equus grevyi*. Black = tmp4, undulating black lines = tmm1, gray circles = tmm2. Scale bar = 5 cm.

Figure 6.2 plots species of *Cormohipparion*, *Sivalhippus*, and *Proboscidipparion*. Compared to *C*. *sinapensis* and the *Eurygnathohippus*-*Cremohipparion* species, a different pattern is shown by *Sivalhippus* and *Proboscidipparion*. They have a wider, more robust midshaft width (M3) and a relatively shallow midshaft depth (M4), larger values in M5-M10 and M8. Çalta *Proboscidipparion heintzi* has a robust pattern similar to the *Sivalhippus* lineage: M1, M3, M10, and M8 are narrower, but the other measurements are included between the *S*. *turkanensis* and *S*. *perimensis* deviation. We cannot rule out that this similarity is due to convergent evolution within the "*Sivalhippus* Complex" (Bernor et al., 1996). "*Hipparion*" *crassum* from Perpignan displays a similar morphological pattern to *Proboscidipparion heintzi*, albeit with a reduced length and overall size.

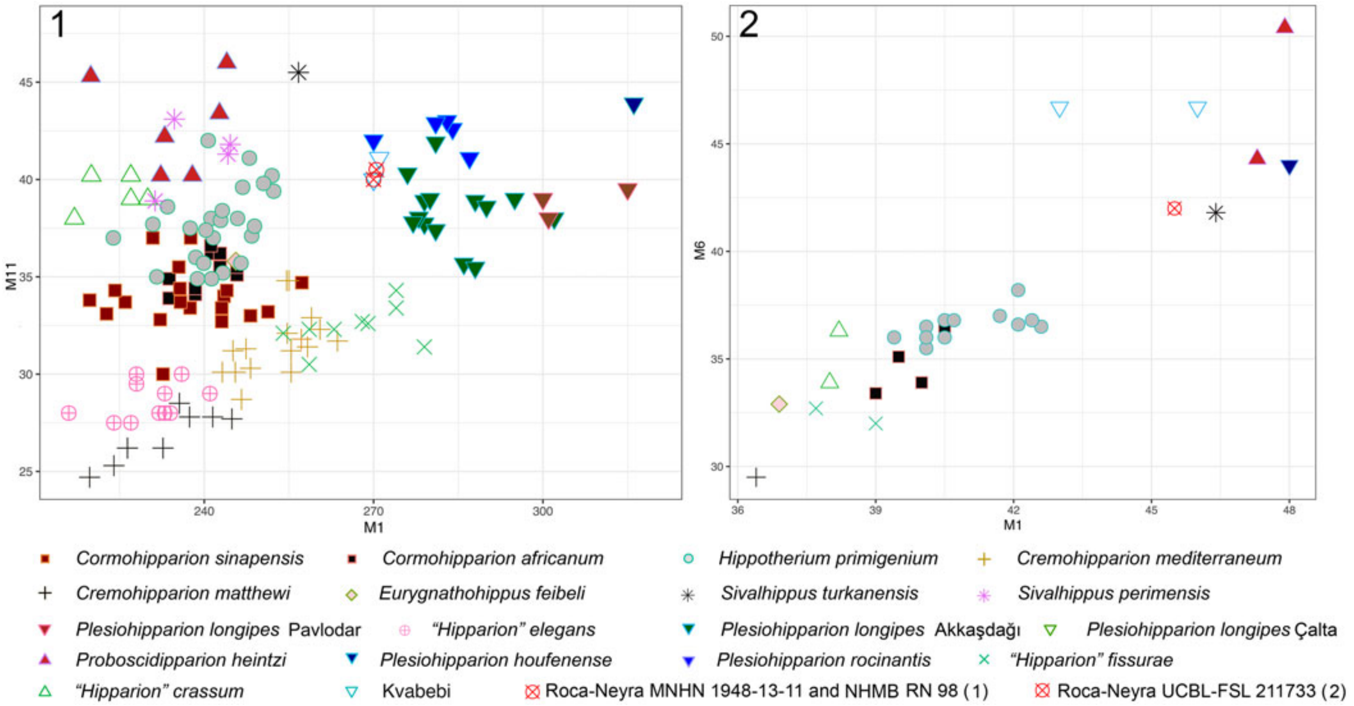

Figure 5. Bivariate plots for third metatarsal (**1**) and second phalanx of the central digit (**2**), comparing the *Plesiohipparion* cf. *P. rocinantis* from Roca-Neyra with a suite of Miocene, Pliocene and Early Pleistocene hipparions. The source of data is reported in Material and methods.

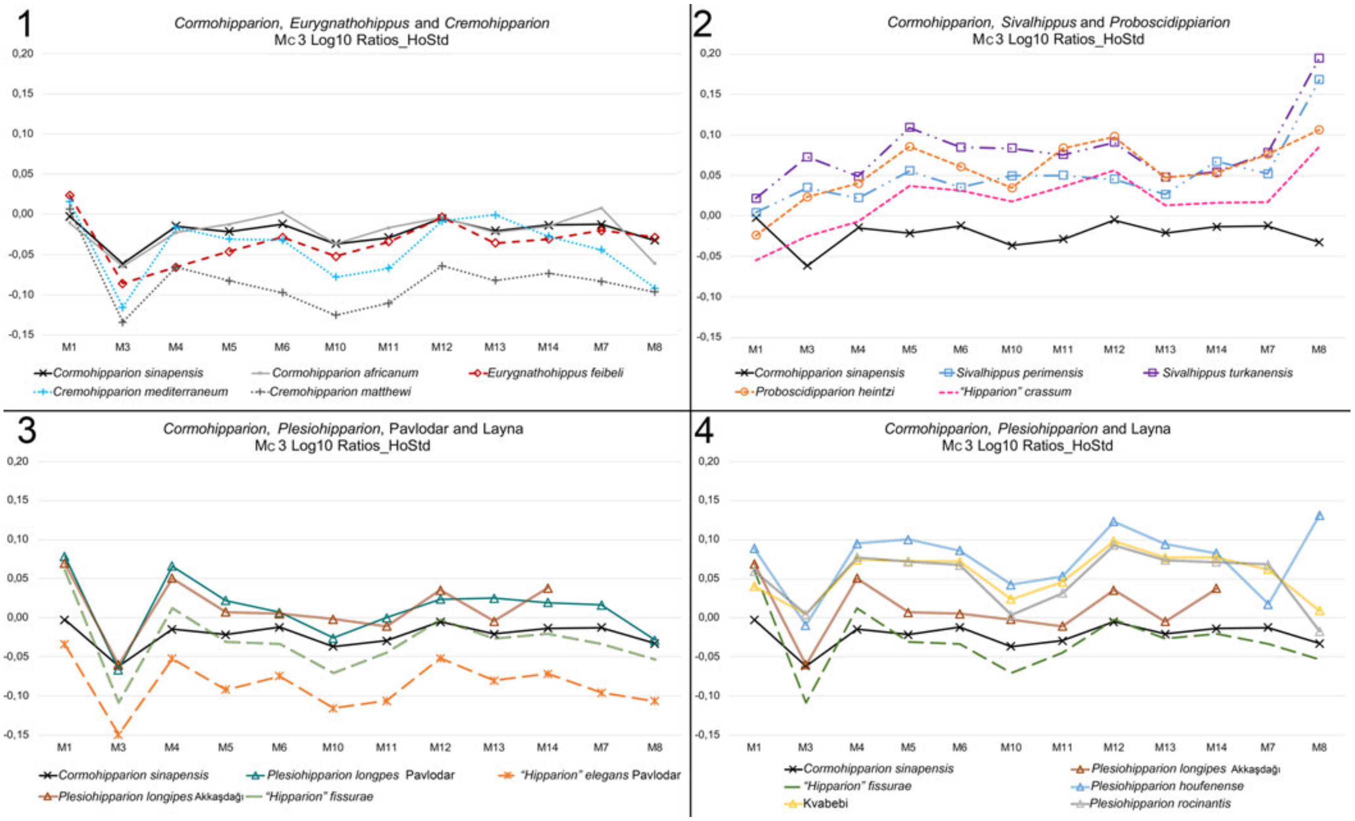

Figure 6. Log10 Ratio diagrams analysis for third metacarpal (*Hippotherium primigenium* from Höwenwgg, Germany used as standard; Bernor et al., 1997), comparing a suite of Miocene, Pliocene and Early Pleistocene hipparions (**1–4**). The source of data is reported in Material and methods.

Figure 6.3 plots *Cormohipparion sinapensis* and *Plesiohipparion longipes* from Pavlodar and Akkaşdağı, with the Pavlodar "*Hipparion*" *elegans* and Layna "*Hipparion*" *fissurae* samples. *Plesiohipparion longipes* from Pavlodar and Akkaşdağı exhibits the same pattern, with a slender morphology marked by M1-M3, and an overall similar morphology (even larger M10 in *P. longipes* form Akkaşdağı and larger M13 in *P. longipes* from Pavlodar). Noteworthy, the "*Hipparion*" *elegans* pattern shows a very similar morphology to "*Hipparion*" *fissurae*, even if the latter has generally larger dimensions and a more elongated maximum length (M1), and different morphological aspect of the proximal and distal epiphysis (Alberdi and Alcalà, 1999).

Figure 6.4 plots species of *Cormohipparion* and *Plesiohipparion* with the Layna sample. The Plio-Pleistocene *Plesiohipparion* species (*P. rocinantis* and *P. houfenense*) have generally larger dimensions when compared to the Late Miocene *P. longipes* from Akkaşdağı, even if their pattern exhibits the same slender morphology (M1-M3) and the same morphology of the distal epiphysis, with wider values in M5, M6, and M13. "*Hipparion*" *rocinantis* from Kvabebi shows an identical morphology and pattern to *P. rocinantis* from Villarroya, and together they are comparable with *P. longipes,* but with a shorter maximal length (M1), a narrower distal maximal supraarticular width (M10), and a wider distal maximal depth of the lateral condyle (M13). *Plesiohipparion houfenense* is the largest species in this plot, and its pattern is similar to *P. rocinantis*. "*Hipparion*" *fissurae* is more slender than the *Plesiohipparion* group, nevertheless its morphology remains intermediate between the *Plesiohipparion* and *Cremohipparion* groups.

Figure 7 shows the corresponding mt3 Log10 ratio diagrams using the Höwenegg *Hippotherium primigenium* mean. These plots produce results for each clade that are similar to those calculated for the mc3 Log10 ratio diagrams.

Figure 7.1 plots species of *Cormohipparion*, *Eurygnathohippus*, and *Cremohipparion*. The *Eurygnathohippus feibeli* and *C. matthewi* morphology is similar to *C. sinapensis* and *C. africanum*, even more slender. *Cremohipparion matthewi* is similar to *C. mediterraneum*, but smaller and narrower.

Figure 7.2 plots species of *Cormohipparion*, *Sivalhippus*, and *Proboscidipparion*. *Sivalhippus turkanensis* and *S. perimensis* have an almost identical pattern, even if the African species shows larger dimensions. *Proboscidipparion heintzi* exhibits a pattern comparable to *S. perimensis*. Furthermore, the "*Hipparion*" *crassum* trend is similar to *P. heintzi*, except for a small M10 and its general narrower dimensions.

Figure 7.3 plots species of *Cormohipparion* and *Plesiohipparion* with the Pavlodar and Layna samples. As reported in Figure 6.3, *P. longipes* exhibits an identical morphology to the *P. longipes* sample from Akkaşdağı and Çalta, even if the *P. longipes* from Akkaşdağı has a less elongated maximum length (M1). Furthermore, the remarkable similarities between *"Hipparion" elegans* and *"Hipparion" fissurae* can be observed, even if *"Hipparion" elegans* from Pavlodar remains larger.

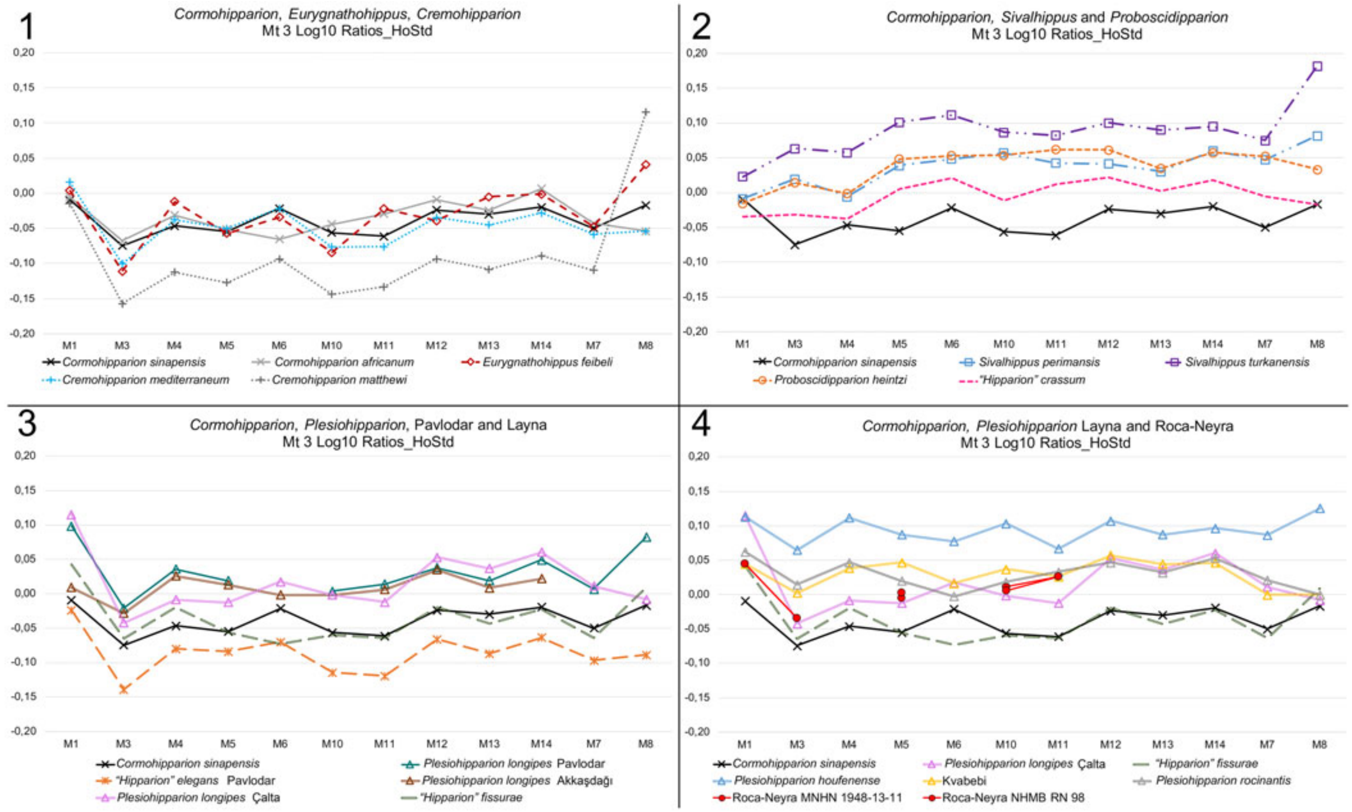

Figure 7. Log10 Ratio diagrams analysis for third metatarsal (*Hippotherium primigenium* from Höwenwgg, Germany used as standard; Bernor et al., 1997), comparing a suite of Miocene, Pliocene, and Early Pleistocene hipparions (**1–4**). The source of data is reported in Material and methods. *Plesiohipparion* cf. *P. rocinantis* from Roca-Neyra is included in (**4**).

Figure 7.4 plots species of *Cormohipparion* and *Plesiohipparion* with the Layna sample. The *P. longipes* trajectory (Pavlodar, Akkaşdaği, and Çalta) is likewise found in the Plio-Pleistocene species *P. rocinantis* and *P. houfenense*, even if *P. longipes* from Çalta exhibits a more elongated maximal length (M1) and wider dimension of the proximal articular width (M6). *Hipparion rocinantis* from Kvabebi has an almost identical morphology to *P. rocinantis* from Villarroya, whereas *P. houfenense* is the largest *Plesiohipparion* species. "*Hipparion*" *fissurae* is the slenderest species when compared to the *Plesiohipparion* group, with a morphology intermediate between the *Plesiohipparion* and *Cremohipparion* groups (Figure 6.4). Finally, the two Roca-Neyra specimens (MNHN1948-13-11 and NHMB RN 98; data from Eisenmann and Brunet, 1973) show morphology and dimensions equivalent to *P. rocinantis* from Villarroya and Kvabebi, respectively, confirming the evidence presented in the bivariate plots. The Kvabebi material includes skull, maxillary cheek teeth, and mandibular cheek teeth that compare well with *Plesiohipparion* (see Vekua, 1972).

Figure 8.1, 8.2 provides PCAs for mc3 and mt3, respectively. In the mc3 Principal Component Analysis, PC1 and PC2 account for most of the variance with 89.5% (PC1 = 76.5%; PC2 = 13.0%). In mt3, PC1 and PC2 account for 83.7% of the cumulative variance (PC1 = 73.4%; PC2 = 10.3%) (a summary of the variance components is reported in Table 2). In Figure 8.1, 8.2, PC1 indicates a progressively more slender shape from positive to negative values, whereas PC2 indicates a more elongated morphology, from negative to positive values. The results described in the bivariate plots and Log10 Ratios analyses are here confirmed, both in Figure 8.1, 8.2. Three different areas can be described, defined by the following species. A morphologically primitive assemblage represented by the late Miocene species includes *H. primigenium*, *C. sinapensis*, and *C. africanum*, with *E. feibeli* and *C. mediterraneum* slightly separated from one another. These are the primitive "*Hipparion*" morphologies with *C. sinapensis*, *E. feibeli*, and *C. mediterraneum* (see Bernor et al., 2020). A derived *Plesiohipparion* group (with larger and more elongated metapodials compared to the primitive European and African late Miocene species), including *P. longipes*, *P. rocinantis*, *P. houfenense*, and the Kvabebi sample, which by these analyses suggests their grouping with *P. rocinantis*. Another more robustly built mc3 group includes *S. turkanensis*, *S. perimensis*, *P. heintzi*, and "*H.*" *crassum*. *Cremohipparion matthewi* is separated from the entire sample by its small size and slenderness, but shows a relationship to *Cremohipparion mediterraneum* (also, Bernor et al., 2016 related it to *C. moldavicum*). "*Hipparion*" *elegans* plots within the *Cremohipparion* group, between *C. mediterraneum* and *C. matthewi*, and "*H.*" *fissurae* plots between *C. mediterraneum* and the *Plesiohipparion* group. "*Hipparion*" *crassum* plots close to *Proboscidipparion heintzi*, and this evidence supports its referral to "*Proboscidipparion*" *crassum*.

Figure 8.2 (mt3) exhibits the same species clusters shown in Figure 8.1, but packed closer together with slight differences. The variability seen in the "*H.*" *elegans* group overlaps with the *Cremohipparion* group, whereas "*H.*" *fissurae* remains intermediate between *Cremohipparion* and *Plesiohipparion*.

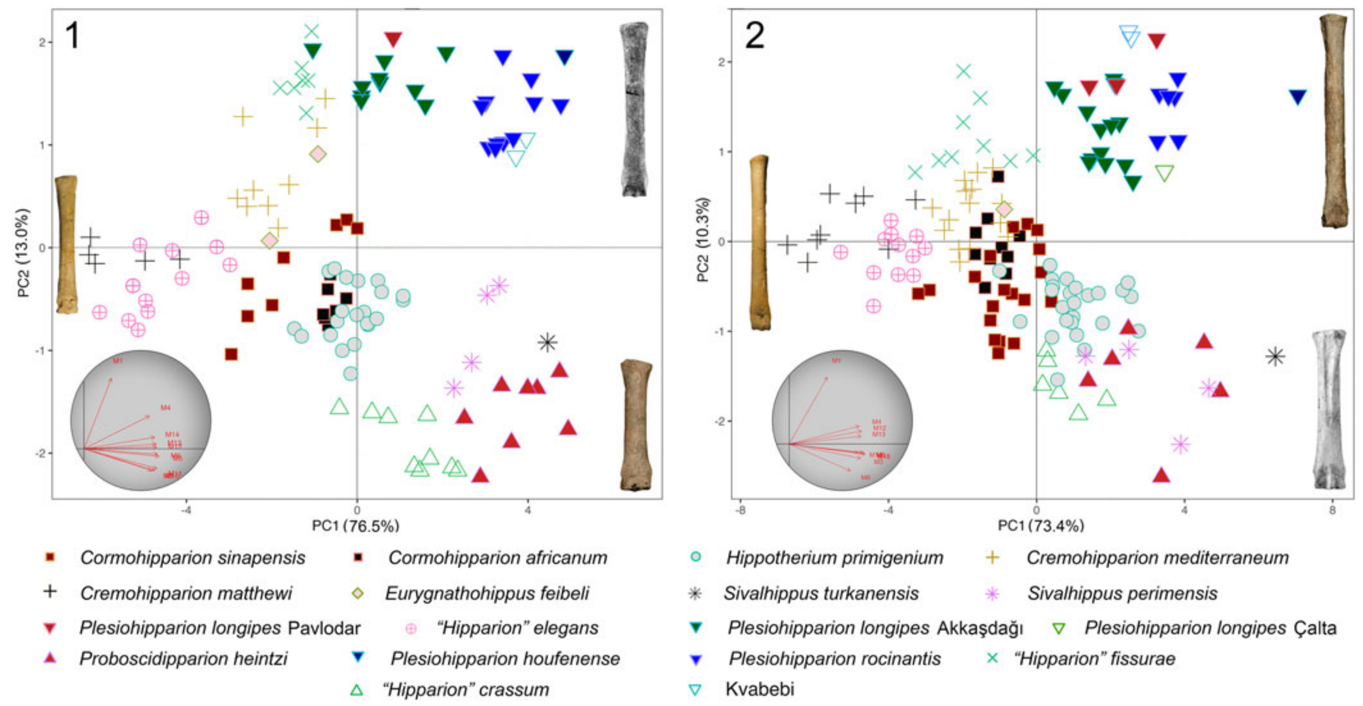

Figure 8. Principal Component Analysis for third metacarpal (**1**) and third metatarsal (**2**) on a suite of Miocene, Pliocene, and Early Pleistocene hipparions. Loadings distribution in PC1 and PC2 for third metacarpal (**1**) and third metatarsal (**2**) are shown in the biplot diagrams, left lower corner on both graphs. Mc3 images of *Cremohipparion matthewi* (Sahabi), *Plesiohipparion longipes* (Akkaşdağı, Koufos and Vlachou, 2005), and *Proboscidipparion heintzi* (Bernor and Sen, 2017). Mt3 images of *Cremohipparion matthewi* (Sahabi), *Plesiohipparion longipes* (Çalta, Bernor and Sen, 2017), and *Proboscidipparion heintzi* (Eisenmann and Sondaar, 1998). The complete sample used for this analysis is shown in supplementary table 1 for mc3 and supplementary table 2 for mt3.

Table 1. Anatomical measurements (following Eisenmann et al., 1988; Bernor et al., 1997) of the Roca-Neyra equid sample.

SPEC_ID	Species	Element	Side	Age	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10
UCBL-FSL 211232	*Plesiohipparion* cf. *P. rocinantis*	calc	rt	2.6 ± 0.02	100.2	64.9	17.8	27.4	42.9	50.3	50.3			
UCBL-FSL 211733	*Plesiohipparion* cf. *P. rocinantis*	2ph3	lt	2.6 ± 0.02	43.5	31.3	35.9	45.3	27.1	38.9				
UCBL-FSL 211733	*Plesiohipparion* cf. *P. rocinantis*	3ph3	lt	2.6 ± 0.02	61.5	58.5	63.9	22.6	39.1					
UCBL-FSL 211735	*Equus* cf. *E. livenzovensis*	tmp4	lt	2.6 ± 0.02	31.6	27.9	18.1	10.1	14.1	20.3	17.6	17.4	18.1	61.2
UCBL-FSL 211735	*Equus* cf. *E. livenzovensis*	tmm1	lt	2.6 ± 0.02	29.4	24.9	16.9	8.2	13.9	16.5	14.6		13.9	51.5
UCBL-FSL 211735	*Equus* cf. *E. livenzovensis*	tmm2	lt	2.6 ± 0.02	29.9		16.8	8.8	12.4	17.2	15.2	16.2	52.6	

"*Hipparion*" *crassum* plots close to the variability seen in the *Proboscidipparion-Sivalhippus* plots.

Equus.—In the *Equus* sample, statistical analyses are provided through bivariate plots (Figs. 9.1, 10.1, and 11.1) and PCA (Figs. 9.2, 10.2, and 11.2) in tmp4, tmm1, and tmm2. Bivariate plots and PCAs for each element are shown together, to better determine the species clusters.

Figures 9.1, 10.1, and 11.1 are bivariate plots for UCBL-FSL 211735 tmp4, tmm1, and tmm2, respectively. The measurements plotted are maximum occlusal length (M1) versus occlusal width (M6). In all the bivariate plots, UCBL-FSL 211735 is plotted close to the larger *E. stenonis vireti* specimens and *E. suessenbornensis* (Akhalkalaki, Georgia). *Equus simplicidens* shows an M1 variation comparable to the *E. stenonis vireti*, *E. stenonis* from Olivola, and *E. stenonis* from Upper Valdarno, with a narrower width. *Equus* sp. from Senèze plots between the *E. stenonis* group and *E. stehlini*. Extant *E. grevyi* overlaps with the *E. stenonis* group (*E. stenonis vireti*, *E. stenonis* Olivola, *E. stenonis* Upper Valdarno, and *Equus* sp. Senèze), and in Figures 9.1 and 10.1 overlaps with the largest *E. simplicidens* specimens.

Figures 9.2, 10.2, and 11.2 are PCAs for tmp4, tmm1, and tmm2, respectively. In tmp4 (Fig. 9.2), PC1 and PC2 account the 80.7% of the variance (PC1 = 68%; PC2 = 12.7%). In tmm1 (Fig. 10.2), PC1 and PC2 explain 85.9% of the cumulative variance (PC1 = 68.3%; PC2 = 17.6%). In tmm2 (Fig. 11.2), PC1 and PC2 amount to 83.3% of the cumulative variance (PC1 = 67.9%; PC2 = 15.4%). PC1 segregates species by maximum occlusal length (M1) from positive to negative values, from largest to smallest. PC2 differs among diagrams: in tmp4, it is mainly represented by M4 (maximum length of the preflexid) in positive values and M5 (maximum length of the postflexid) for negative, whereas in tmm1 and tmm2 it is explained by M4-M5 and M6 (maximal width at the occlusal level), which have opposite values (the variance components are reported in Table 3).

Equus simplicidens is always included within the variability of *E. stenonis*, whereas *E. stenonis vireti* overlaps the larger portion of the *E. stenonis* sample. Remarkably, a progressive clustering can be observed through *E. stenonis*, *Equus* sp. from Senèze, and *E. stehlini*, which correlates *E. stehlini* with *Equus* sp. (Senèze) instead of the typical *E. stenonis* samples from Saint Vallier, Olivola, and Upper Valdarno Basin. UCBL-FSL 211735 is plotted outside of any species variability range, and it is always placed between *E. stenonis vireti* and *Equus suessenbornensis*. *Equus suessenbornensis* is the species with the widest dimensions found in the analysis. Finally, *E. grevyi* once again plots within *E. stenonis* variability.

Evolutionary and biogeographic implications

Hipparionine lineages.—Old World Hipparionini have their earliest occurrence in the lowermost late Miocene of the Vienna Basin Pannonian C, 11.4–11.0 Ma at the base of Mammal Neogene Unit MN9, and it is termed the *Cormohipparion* Datum (Bernor et al., 2017; formerly the "*Hipparion* Datum" of Berggren and Van Couvering, 1974). Hipparions rapidly diversified across Eurasia and Africa, evolving into several genus-level lineages (Bernor et al., 1990, 1996, 2010). Their acme in terms of lineage diversity and abundance was MN12 (7.6–6.8 Ma), followed by a sharp decline by the end of MN13 (5.3 Ma) resulting in the extinction of several lineages, including *Cormohipparion*, *Hippotherium*, *Hipparion* s.s., *Sivalhippus* (Bernor et al., 1996), *Baryhipparion* (Qiu et al., 1987), *Shanxihippus* (Bernor et al., 2018a), and *Cremohipparion* (except a single species in China, *C. licenti* Qiu, Huang, and Guo, 1987). The occurrence of hipparions through the Plio-Pleistocene interval becomes progressively rarer, so that the co-occurrence of *"Hipparion*" with *Equus* in the Pleistocene is known from relatively few Eurasian localities.

China retained hipparions into the Pliocene and Pleistocene, including two Asian lineages, *Plesiohipparion* and *Proboscidipparion* (Qiu et al., 1987; Bernor et al., 1996; Bernor and Sun, 2015). *Plesiohipparion* has a substantial diversity in the late Miocene–Pleistocene of China, being represented by

Table 2. Importance of components of Principal Component Analysis for the "*Hipparion*" sensu lato sample, Figure 8.

mc3										
Importance of components:	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Standard deviation	2.7667	1.1409	0.56185	0.42459	0.38535	0.35347	0.31950	0.28554	0.22819	0.19669
Proportion of Variance	0.7655	0.1302	0.03157	0.01803	0.01485	0.01249	0.01021	0.00815	0.00521	0.00387
Cumulative Proportion	0.7655	0.8956	0.92719	0.94522	0.96007	0.97256	0.98277	0.99092	0.99613	1.00000
mt3										
Importance of components:	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Standard deviation	2.7096	1.0150	0.66053	0.5967	0.54210	0.43863	0.34197	0.30647	0.2738	0.25154
Proportion of Variance	0.7342	0.1030	0.04363	0.0356	0.02939	0.01924	0.01169	0.00939	0.0075	0.00633
Cumulative Proportion	0.7342	0.8372	0.88086	0.9165	0.94585	0.96509	0.97679	0.98618	0.9937	1.00000

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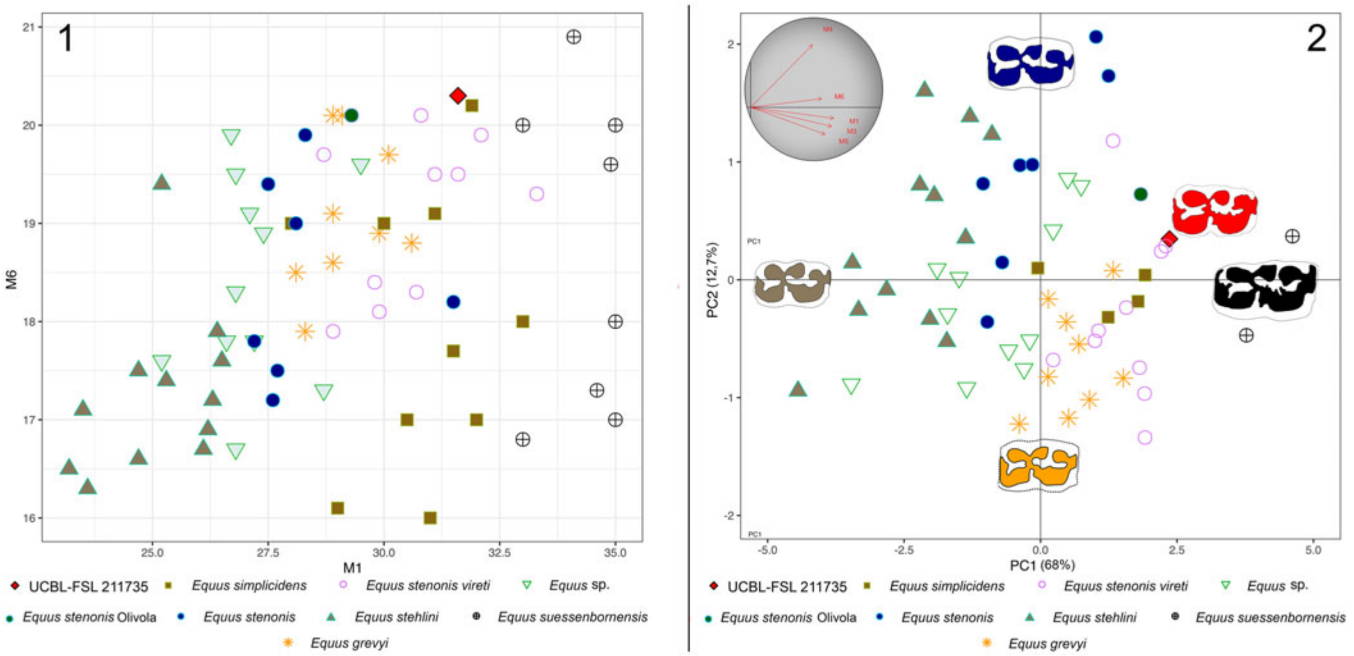

Figure 9. Lower fourth premolar bivariate plots (**1**) and Principal Component Analysis (**2**), comparing *Equus* cf. *E. livenzovensis* from Roca-Neyra with a suite of Early Pleistocene *Equus* and with the extant *Equus grevyi*. Loadings distribution in PC1 and PC2 are shown in the biplot diagram. Occlusal surface profile of *Equus suessenbornensis* (black), Roca-Neyra (red), *Equus stenonis* (blue), *Equus stehlini* (dark green), and *Equus grevyi* (orange). The complete database for Principal Component Analysis is reported in supplementary table 3.

three species, *Plesiohipparion houfenense*, *Plesiohipparion huangheense* Qiu, Huang, and Guo, 1987, and *Plesiohipparion shanxiense* Bernor, Sun, and Chen, 2015 (Qiu et al., 1987; Bernor and Sun, 2015; Bernor et al., 2015).

Plesiohipparion species have skulls lacking a preorbital fossa and the nasal bones are not retracted. Their cheek teeth are similar to *Proboscidipparion*, having protocones that are moderately elongate, flattened lingually, and sometimes having a lingual indentation. Overall, they are similar to species of *Sivalhippus* (Bernor and Hussain, 1985; Wolf et al., 2013). *Plesiohipparion* lower cheek teeth characteristically have lingually pointed metaconids and metastylids, broad linguaflexids, and

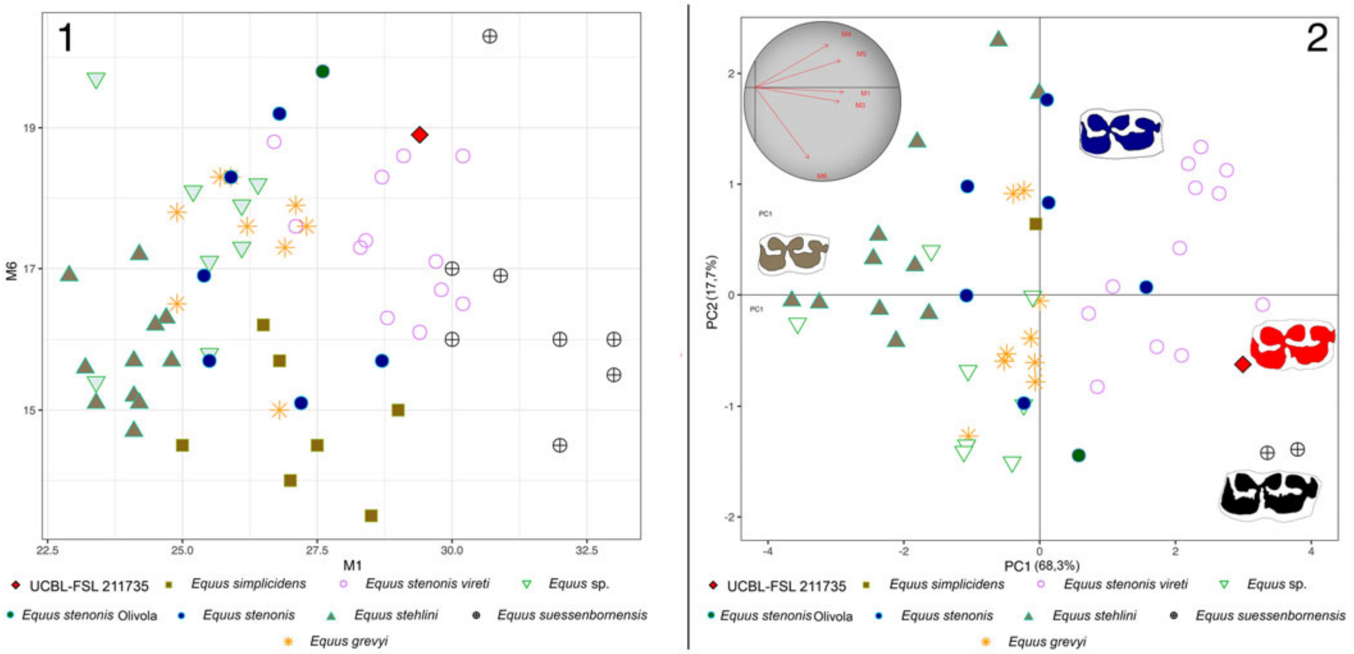

Figure 10. Lower first molar bivariate plots (**1**) and Principal Component Analysis (**2**), comparing *Equus* cf. *E. livenzovensis* from Roca-Neyra with a suite of Early Pleistocene *Equus* and with the extant *Equus grevyi*. Loadings distribution in PC1 and PC2 are shown in the biplot diagram. Occlusal surface profile of *Equus suessenbornensis* (black), Roca-Neyra (red), *Equus stenonis* (blue), and *Equus stehlini* (dark green). The complete database for Principal Component Analysis is reported in supplementary table 4.

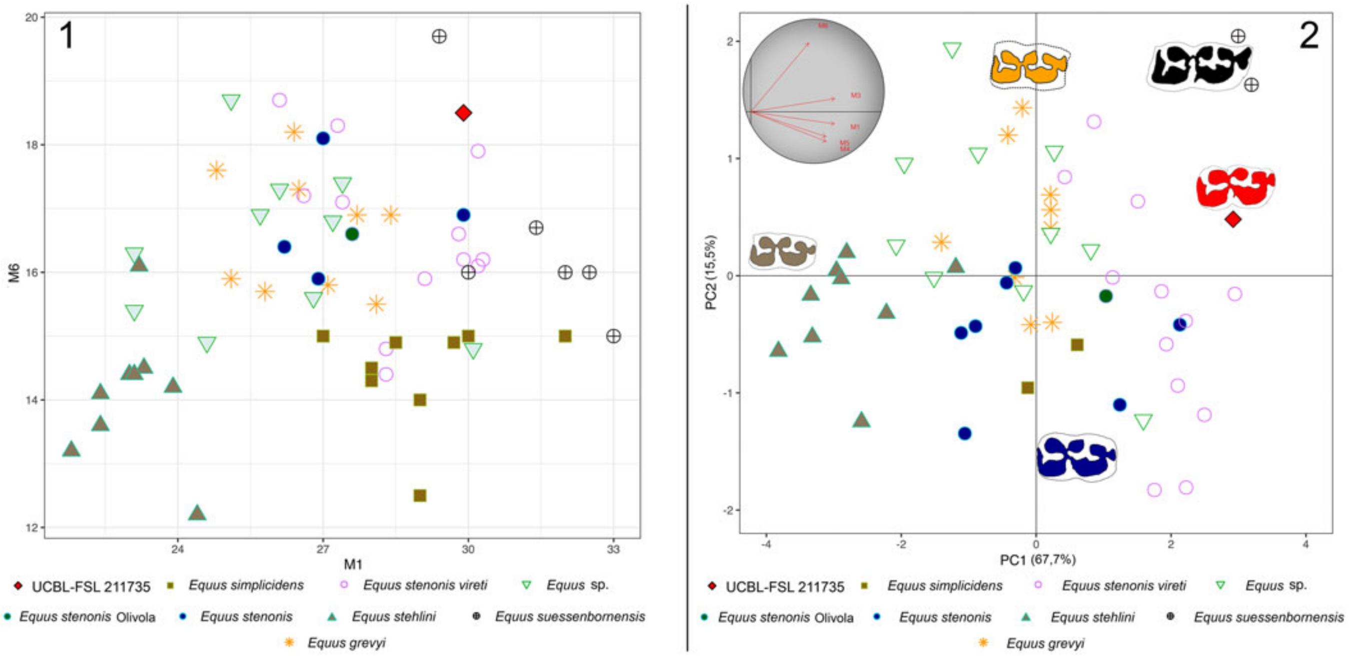

Figure 11. Lower second molar bivariate plots (**1**) and Principal Component Analysis (**2**), comparing *Equus* cf. *E. livenzovensis* from Roca-Neyra with a suite of Early Pleistocene *Equus* and with the extant *Equus grevyi*. Loadings distribution in PC1 and PC2 are shown in the biplot diagram. Occlusal surface profile of *Equus suessenbornensis* (black), Roca-Neyra (red), *Equus stenonis* (blue), *Equus stehlini* (dark green), and *Equus grevyi* (orange). The complete database for Principal Component Analysis is reported in supplementary table 5.

very broad ectoflexids penetrating deeply into the isthmus separating metaconid and metastylid of the molars. Third metatarsals are very elongated in *Plesiohipparion* species.

The *Proboscidipparion* lineage includes two successive species in China, *P. pater* Qiu, Huang, and Guo, 1987 in the latest Miocene and early Pliocene, and the very large form *Proboscidipparion sinense* Sefve, 1927 in later earliest to Late Pleistocene (Sefve, 1927; Qiu et al., 1987; Bernor et al., 1989; Bernor and Sun, 2015). *Proboscidipparion* has a large skull with an extraordinarily elongate snout that is downturned anteriorly, and strongly to very strongly retracted nasals (Bernor et al., 2018a).

Proboscidipparion pater has cheek teeth with protocones that are moderately elongated and lingually flattened, complex plications of fossettes, and mostly single pli caballins; maxillary cheek teeth are overall similar to Indian subcontinent *Sivalhippus*. The lower cheek teeth have rounded metaconids, slightly squared metastylids, and deep linguaflexids that may be V- or U-shaped (Bernor and Sen, 2017, fig. 2). *Proboscidipparion sinense* (2.6–1.0 Ma) has maxillary cheek teeth with complex fossette plications, mostly single pli caballins, and protocones that are elongate and flattened lingually, as in *P. pater*. Lower cheek teeth have elongated tmp2 and tmm3, very elongate and shallow linguaflexids, rounded to pointed metaconids, mostly pointed metastylids, and elongate-deep linguaflexids (Bernor and Sun, 2015, fig. 4). Some *Proboscidipparion sinense* maxillary cheek teeth have smaller rounded protocones (Bernor and Sun, 2015, fig. 5). While strongly divergent in their skull morphology, *Plesiohipparion* and *Proboscidipparion* would appear to be closely related and derived from the Indian subcontinent *Sivalhippus* radiation. And, in fact, Sun et al. (2018)

Table 3. Importance of components of Principal Component Analysis for the *Equus* sample, Figures 9.2, 10.2, 11.2.

tmp4					
Importance of components:	PC1	PC2	PC3	PC4	PC5
Standard deviation	1.8446	0.7991	0.7531	0.46803	0.4155
Proportion of Variance	0.6805	0.1277	0.1134	0.04381	0.03453
Cumulative Proportion	0.6805	0.8082	0.9217	0.96547	1.00000
tmm1					
Importance of components:	PC1	PC2	PC3	PC4	PC5
Standard deviation	1.8484	0.94	0.64711	0.44447	0.28924
Proportion of Variance	0.6833	0.1767	0.08375	0.03951	0.01673
Cumulative Proportion	0.6833	0.86	0.94376	0.98327	1.00000
tmm2					
Importance of components:	PC1	PC2	PC3	PC4	PC5
Standard deviation	1.8397	0.8794	0.61534	0.57512	0.36418
Proportion of Variance	0.6769	0.1547	0.07573	0.06615	0.02653
Cumulative Proportion	0.6769	0.8316	0.90732	0.97347	1.00000

identified two species of *Sivalhippus* in the late Miocene of China—*S. platyodus* (Sefve, 1927) and *S. ptychodus* (Sefve, 1927).

The *Plesiohipparion* lineage arose in Asia at the end of the Miocene, MN 13, and is known from Pavlodar, Russia (Gromova, 1952), Akkaşdağı, Turkey (Koufos and Vlachou, 2005), and Çalta, Turkey (Bernor and Sen, 2017). Bernor and Lipscomb (1991) identified an advanced *Plesiohipparion*, *P. huangheense*, occurring with *Equus* in the Early Pleistocene Turkish locality of Gülyazi (ca. 2.58 Ma). Jukar et al. (2018) identified a lower cheek tooth row of *Plesiohipparion huangheense* from 3.5–2.6 Ma Tatrot Formation horizons, India. Jukar et al. (2019) also identified a specimen of *Eurygnathohippus* sp. in these horizons, marking its first known extension of this lineage outside of Africa.

The early Pliocene locality of Çalta, Turkey includes the occurrence of two Asian *Hipparion* clades (Eisenmann and Sondaar, 1998; Bernor and Sen, 2017). Eisenmann and Sondaar (1998) recognized two species of hipparions, "*Hipparion*" *longipes* and "*Hipparion*" *heintzi*. Bernor and Sen (2017) recognized these as being referable to the Asian lineages *Proboscidipparion heintzi* and *Plesiohipparion* cf. *P. longipes*. *Proboscidipparion heintzi* is represented by a juvenile skull with strongly retracted nasals, cheek teeth (deciduous dtxP1-tx4) with short rounded protocones, and txM1 with more elongate protocone flattened lingually. The lower cheek teeth have rounded metaconids and metastylids (again, dptm2-4, tmm1), with the tmm1 having an extremely elongate linguaflexid. While still in their crypts, the permanent mandibular tmi1s are very large. The Çalta *P. heintzi* has a very short and robust mc3 and a short and massively built 1ph3 akin to Siwalik *S. perimensis* and African *S. turkanensis* (Bernor and Harris, 2003; Wolf et al., 2013). The Çalta *Plesiohipparion* cf. *P. longipes* has a very elongate and slender mt3 and elongate-slender 1ph3.

Forsten (2002) reported remains of the "*Hipparion*" *crassum* "Group" from the Pliocene of Europe. She defined the "Group" as having rounded to rounded-triangular metaconids and metastylids of the lower cheek teeth, and aligned her systematics with Alberdi (1989) who identified this "Group" as her "morphotype 4." Despite the strong divergence in skull characters of Chinese *Plesiohipparion* and *Proboscidipparion*, Forsten suggested that *Plesiohipparion* is the junior synonym of *Proboscidipparion*, which created a lasting taxonomic confusion. *Plesiohipparion* and *Proboscidipparion* are distinct lineages of generic status, differing profoundly in skull morphology and, we believe, postcranial anatomy (Qiu et al., 1987; Bernor et al., 1996, 2015; Bernor and Sun, 2015; present paper). Forsten identified "*Hipparion*" *crassum* as occurring in France, Italy, Spain, England, Hungary, Bulgaria, Romania, Ukraine, Moldova, Russia, Turkey (including Çalta), Azerbaijan, and China. Hipparions from these localities are united by their occurrence in Plio-Pleistocene horizons and have mixed cranial, dental, and postcranial morphologies.

The "*Hipparion*" *crassum* that occurs at Perpignan, France, is 4.1 Ma. (Clauzon et al., 2015). This species shows striking similarities to *Proboscidipparion heintzi* (Çalta, also ca. 4.0 Ma; Bernor and Sen, 2017) in its robustly built third metapodials. This evidence has been discussed in the morphometric and statistical analysis (Figs. 5–8). The maxillary cheek teeth have elongated second premolars, complex enamel plications, and short, rounded protocones. The mandibular cheek teeth have rounded to squared metaconids, more pointed metastylids, V-shaped to elongate linguaflexids, and elongate third metapodials. A mandible, Pp208 (Depéret, 1890; Eisenmann, 2019; https://vera-eisenmann.com) has an elongate symphysis and tmi1-tmi2 hypertrophied with distinct lingual grooving, and tmp2-tmp4 with deeply extending ectoflexids approaching the isthmus separating metaconid-metastylid. These characters, in particular the short and robust proportions of the mc3s and mt3s, are consistent with a referral to *Proboscidipparion crassum*. Alberdi and Alcalà (1999) referred also the equid sample from the early Pliocene of Dorkovo (Bulgaria), MN14 to *Hipparion* cf. *H. crassum*.

Crusafont and Sondaar (1971), Alberdi (1974), and Alberdi and Alcalà (1999) assigned the Layna Pliocene *Hipparion* to *H. fissurae*. Domingo et al. (2007, 2013) correlated Layna as being 3.91 Ma, confirming the earlier hypothesis on the age based on rodent remains made by López-Martínez (1989) and Sesé (2006). In particular, Alberdi and Alcalà (1999) described several other Spanish samples wherein "*H.*" *fissurae* was identified as occurring from the Pliocene of La Gloria, Villalba Alta Rio 1, Orrios, and La Calera, late Ruscinian MN15. The maxillary cheek teeth from Layna (Alberdi, 1974, figs. 30, 40, 41, 43; Alberdi and Alcalà, 1999, fig. 40) have moderately complex plications, weakly developed pli caballins, and protocones that are triangular and oval to lingually flattened. The mandibular cheek teeth have lingually pointed metaconids and metastylids, and mandibular lower third molar has a distally extended talonid. The La Gloria 4 MT3 is very elongate and slender. These characters could suggest a referral to *Plesiohipparion*, *P. fissurae*. The morphometric and statistical analyses provided herein have also exhibited similarities with the Pavlodar "*Hipparion*" *elegans* and, more broadly, with the *Cremohipparion* group. These results could suggest that the Layna "*Hipparion*" could either be a small Eurasian *Plesiohipparion* or one of the longest limbed *Cremohipparion* of the Old World. This issue could be resolved if a skull were recovered from any of these localities because of the distinct differences in cranial morphology between *Cremohipparion* (nasal bones retracted and multiple facial fossae) and *Plesiohipparion* (nasals not retracted and no facial fossae). However, our results support observations made by Alberdi and Alcalà (1999) considering "*H.*" *fissurae* a different and valid species, distinguished from Pavlodar "*H.*" *elegans*.

Kvabebi 1 and Kvabebi 2, Georgia (Vekua, 1972; Eisenmann, 2019; https://vera-eisenmann.com) have two cheek tooth series with elongate tmp2, and remaining cheek teeth with lingually pointed metaconids and metastylids typical of *Plesiohipparion* suggesting a referral to *Plesiohipparion crusafonti*, which we consider to be a junior synonym of *Plesiohipparion rocinantis*. Agusti et al. (2009) have suggested a correlation of 3.09 Ma. based on a paleomagnetic chronology.

The Villarroya *Hipparion* was initially described by Villalta (1948, 1952) as *Hipparion rocinantis* and was recognized as resembling North American *Neohipparion* by Zhegallo (1978) and MacFadden (1984). Qiu et al. (1987), followed by Bernor et al. (1996, 2015) and Bernor and Sun (2015), recognized this species as being a member of the *Plesiohipparion* clade. The Villarroya *Plesiohipparion rocinantis* (Alberdi,

1974) has a skull lacking a preorbital fossa, maxillary cheek teeth with moderately complex plications, small and simple pli caballins, and lingually flattened and labially rounded protocones. The mandibular cheek teeth have pointed metaconids and metastylids with deep, broadly U-shaped linguaflexids; mandibular tmm3 has an elongate talonid. The first phalanges of the central digit are elongated and slender. These are all morphological hallmarks of *Plesiohipparion*.

These lines of evidence are supported in the morphometric and statistical analyses provided herein, wherein the Villarroya sample is consistently included in the *Plesiohipparion* group (Figs. 5.1, 6.4, 7.4, 8). Pueyo et al. (2016) recently cited the Villarroya "*Hipparion*" as the last occurring European assemblage in Western Europe, correlating it with the Reunion chron (C2r.1n, 2.128–2.148 Ma). Azanza et al. (2016) have challenged this correlation based on faunal evidence, with conflicting data from the micromammal assemblage. As a result, Azanza et al. (2016) correlated the Villarroya Mammal Zone with MNQ16b. If this revised correlation is correct, Villaroya, Roca-Neyra, and Sésklo (Athanassiou, 2018) could represent the last occurrence of *Plesiohipparion* in Europe, at the Plio-Pleistocene transition.

Rook et al. (2017) described a small fragmentary left txM1 of an "*Hipparion*" sp. from Montopoli, Italy. While fragmentary, its size and simple occlusal morphology are akin to latest Miocene *Cremohipparion* sp., as found at Baccinello, Italy (Bernor et al., 2011). There is nothing in the morphology of this small *Hipparion* that would suggest an affinity either with *Plesiohipparion* or *Proboscidipparion*, but still, its generic status remains enigmatic.

The westernmost occurring hipparions come from the Red Crag deposits, Suffolk, England and are believed to be 3.8–2.8 Ma in age (Forsten, 2001). Based on a sample of ∼53 teeth from the Ipswich Borough Council Museum (IPSMG), the Natural History Museum in London (BMNH), and the Museum of Comparative Zoology (MCZ), Harvard University, Forsten (2001) identified two *Hipparion* taxa, *Hipparion* sp.-*crassum* group and *Proboscidipparion* sp., from the Red Crag. Forsten (2001, fig. 1) identified eight cheek teeth, including four mandibular and two maxillary cheek teeth, as being *Hipparion* sp., and two mandibular cheek teeth as *Proboscidipparion* sp. The two maxillary cheek teeth, a right txP2 (IPSMG R 1939.85.57.5) and a left txM1or txM2 (IPSMG R 1876 4.1) have the following salient features: very complex plications of the fossettes, bifid pli caballins, small rounded (the txP2) to lingually flattened short oval protocone (txM1-2). This morphology agrees with "*H.*" *crassum* and we believe is a *Proboscidipparion* (see Bernor and Sun, 2015). The lower cheek teeth (Forsten, 2001, figs. 1–4) include a right tmp2 (ISPMG R 1876.4.10), a left tmp3or4 (ISPMG R 1876 4.5), right tmm1or2 (ISPMG R1939.85.57.8), and left tmp3or4 (ISPMG R 1876 4.9) that have broad linguaflexids, rounded metaconids, squared metastylids, and very broad linguaflexids referable to *H. crassum*, which we believe allied with *Proboscidipparion*. The two lower cheek teeth referred by Forsten (2001) to *Proboscidipparion* sp. are a right tmp2 (ISPMG 1939 85.57.4) and right tmm3 (ISPMG R 1876 4.7). The lower second premolar is very worn, elongated, and with rounded metaconid and squared metastylid and shallow U-shaped linguaflexid. The lower third molar has a rounded metaconid, lingually pointed metastylid, and broad linguaflexid, which compare with *Proboscidipparion pater* from China (Bernor and Sun, 2015). In our opinion, the entire Red Crag sample may indeed be a species of the *Proboscidipparion* clade, and not *Plesiohipparion* or "*Hipparion*" sensu lato.

Whereas the North African late Miocene has recorded occurrences of *Cremohipparion*, *Sivalhippus*, and *Eurygnathohippus*, the Plio-Pleistocene only records the hipparion species *Eurygnathohippus pomeli* (Eisenmann and Geraads, 2007) (Eisenmann and Geraads, 2007; Bernor et al., 2010). In the latest Miocene, a small slender-limbed form *Eurygnathohippus feibeli* occurred in Kenya, Ethiopia, Libya, and Morocco (Bernor and Harris, 2003; Bernor et al., 2010, 2012, 2020; Cirilli et al., 2020). In East Africa, *Eurygnathohippus feibeli* became very rare and was replaced by *Eurygnathohippus woldegabrieli* Berner et al., 2013 by 4.4 Ma, except at Ekora, Kenya (ca. 4.2 Ma; Bernor et al., 2010, 2013). Between 3.8 and 2.9 Ma Ethiopia records two Hipparion species, *Eurygnathohippus hasumense* Eisenmann, 1983 and *Eurygnathohippus afarense* (Eisenmann, 1976) (Eisenmann, 1983; Bernor et al., 2010). The latest recognized species from Olduvai Bed 1, Tanzania (1.9 Ma) to the 1 Ma. levels of Daka, Ethiopia and Cornelia, South Africa is *Eurygnathohippus cornelianus* Van Hoepen, 1930, a species with hypertrophied txI1 and txI2 and tmi1 and tmi2 with very high crowns. Other than a single occurrence of *Eurygnathohippus* from the Indian Tatrot (Jukar et al., 2019), the genus was restricted to Africa. *Equus* first occurs in East Africa at 2.3 Ma (Bernor et al., 2010).

Equus dispersal.—The *Equus* dispersal into Eurasia was a major biochronologic event marking the lower Quaternary boundary, at 2.58 Ma. Associated with this immigration event was a strong paleoclimatic pulse recorded in terrestrial and marine strata, related to the initiation of a major glaciation pulse in the northern hemisphere (Lindsay et al., 1980; Azzaroli, 1983). The *Equus* Datum can be observed across Eurasia (2.58 Ma in Europe and 2.55 in China), and slightly shifted in sub Saharan Africa at 2.33 Ma (Rook et al., 2019).

Equus livenzovensis is the first appearing species in Europe and Western Asia (Caucasus), at ca. 2.58 Ma. *Equus livenzovensis* was originally recognized by Bajgusheva (1978) based on the cranial and postcranial sample from the Early Pleistocene of Livensovka and Kapry. Azzaroli (1982) first recognized the occurrence of *Equus* cf. *E. livenzovensis* in the Montopoli fauna, which has been studied in detail and confirmed by Bernor et al. (2018b). Alberdi et al. (1997) reported the occurrence of *Equus livenzovensis* from El Rincón-1 (Spain, Early Pleistocene), included in a faunal assemblage that shares many mammalian taxa with the Italian locality of Montopoli. Finally, Alberdi et al. (1998), Forsten (1998), and Azzaroli (2000) studied the type *E. livenzovensis* sample from Khapry, reaffirming its presence in the Caucasus area and validating the species.

Azzaroli (1982, 1992, 2000, 2002) provided a detailed discussion on the origin of Old World *Equus*. The genus *Equus* originated in North America, having been derived from *Dinohippus*, which had already evolved monodactyly (Barrón-Ortiz et al., 2019; Bravo-Cuevas and Jiménez-Hidalgo, 2019; Carranza-Castañeda, 2019). There is no consensus on which species is the earliest known "*Equus*," because opinions differ among authors (Eisenmann and Baylac, 2000; Eisenmann and Deng, 2005; Barrón-Ortiz et al., 2019). Bernor et al. (2019) have evaluated and supported Azzaroli and Voorhies (1993) hypothesis that North American *Equus simplicidens* is the most likely source for Old World first-occurring *Equus*. *Equus simplicidens* shares many characters with European *E. livenzovensis* and *E. stenonis* (see Bernor et al., [2019] for a comprehensive morphological review of the Early Pleistocene *Equus* species) and with the Chinese species *E. eisenmannae* Qiu, Deng, and Wang, 2004, *E. qingyangensis* Deng and Xue, 1999, and *E. sanmeniensis* Teilhard de Chardin and Piveteau, 1930 (see Sun and Deng, 2019), which represent the oldest Eurasian Early Pleistocene *Equus* species (ca. 2.6 Ma). Azzaroli (1982, 1992, 2002) and Bernor et al. (2018b, 2019) have stated that Eurasian Old World *Equus* species could be related to Kenyan *Equus koobiforensis* Eisenmann, 1983, which is the first species reported in the Early Pleistocene African fossil record.

Our results support observations by Bernor et al. (2019) that *E. grevyi* shares morphologic and morphometric dental features with the ancestral *E. simplicidens* and the Old World *Equus* stenonine species. Our analyses on the lower cheek teeth underscore an important evolutionary perspective: there is no significant morphometric difference in the *E. simplicidens*, *E. stenonis vireti*, *E. stenonis*, and *E. grevyi* lower cheek teeth, and the enamel occlusal morphology of the extant *E. grevyi* is found in the European fossil species *E. stenonis*. Furthermore, our analyses of the dental *Equus* sample from Roca-Neyra highlight the importance of *E. livenzovensis*, which exhibits mixed features with *E. simplicidens* and *E. stenonis*, and, with the support of the morphometric analysis explained in Bernor et al. (2018b), can be considered the primitive species for the radiation of the *E. stenonis* group. Following Azzaroli and Voorhies (1993) and Bernor et al. (2019), it appears that *Equus simplicidens* is plausibly ancestral to earliest occurring old World *Equus*, and the earliest *Equus* was very large (*E. livenzovensis*), and that in turn *Equus stenonis* and ultimately *Equus grevyi* are derived from early "stenonine" *Equus* spp.

Hipparion-Equus sympatry

The Roca-Neyra equid sample underscores an interesting ecological perspective in the European Plio-Pleistocene faunal turnover: the *Hipparion* (sensu lato)-*Equus* sympatric co-occurrence. In Europe, co-occurrence of *Equus* with "*Hipparion*" is rare, being represented at Montopoli in Italy (Rook et al., 2017, 2019; Bernor et al., 2018b), Roca-Neyra in France (Eisenmann and Brunet, 1973; Palombo and Valli, 2004; this paper), Gülyazi in Turkey (Bernor and Lipscomb, 1991), and possibly in the Khapry area (Eisenmann and Brunet, 1973; Bajgusheva et al., 2001). Africa has a protracted co-occurrence of *Equus* and *Eurygnathohippus* from 2.3 to <1 Ma (Bernor et al., 2010). *Proboscidipparion* co-occurs with *Equus* up to 1 Ma in China (Qiu et al., 1987). Furthermore, the possible youngest occurrence of "*Hipparion*" in Europe is recorded by the occurrence of *Plesiohipparion rocinantis* at Villarroya, which recently was estimated by Pueyo et al. (2016) to be 2.1 Ma, based on their paleomagnetic interpretation of the section. However, as previously explained, Azanza et al. (2016) questioned this age, suggesting a referral to the Mammal Zone MNQ16b. Athanassiou (2018) reported new insights from Sésklo (Greece, Early Pleistocene) with the occurrence of *Plesiohipparion* cf. *P. shanxiense* and *E.* cf. *E. stenonis* at two different stratigraphic levels, correlated with the Mammal Zones MNQ16b and MNQ17. Athanassiou (2018) has commented that the Sésklo hipparionine population did not occur sympatrically with the genus *Equus*.

The Eurasian *Hipparion* Last Appearance Datum (LAD) is more controversial, and it is unlikely to have been synchronous. Our current understanding is that the latest occurrences of *Plesiohipparion rocinantis* from Villarroya and *Plesiohipparion shanxiense* from the Shanxi Basin indicate an approximate Early Pleistocene age of 2.0 Ma.

Considering Azanza et al.'s (2016) correlation of Villarroya to Mammal Zone MNQ16b, the youngest European hipparions would now appear to have occurred at the Plio-Pleistocene boundary, ca. 2.6 Ma, and not much later in time. This assertion is supported by reported occurrences of European "*Hipparion*" sensu lato at penecontemporaneous earliest Pleistocene localities of Roca-Neyra, Villaroya, Sésklo, and Gülyazi. These localities all have species of *Plesiohipparion* recognized by us. The penecontemporaneous Italian locality of Montopoli has an "*Hipparion*" sp., which we believe is referable to ?*Cremohipparion* by its size and morphology (Rook et al., 2017; this paper). In this regard, new research on the Caucasus area could reinforce the biogeographic linkage between European and Chinese species.

Equus-Hipparion sympatry in Europe is represented by the occurrence of multiple residual lineages of three-toed equids, *Plesiohipparion*, and possibly *Cremohipparion*: *Plesiohipparion huangheense* (Gülyazi, Turkey; Bernor and Lipscomb, 1991), *Plesiohipparion* cf. *P. shanxiense* (Sésklo, Greece; Athanassiou, 2018), a possible referral *Plesiohipparion rocinantis* (Kvabebi, Roca-Neyra, and Villarroya; present paper, pending a complete review of the equid sample of these localities), and the enigmatic record from Montopoli (Italy; Rook et al., 2017; this paper), which could be referred to ?*Cremohipparion* sp. We have presented evidence that *Proboscidipparion* is restricted to the Pliocene, represented by the species *P. heintzi* from Çalta, (Turkey) (Bernor and Sen, 2017) and *P. crassum* from Perpignan (France), Dorkovo (Bulgaria), Suffolk (England) (Alberdi and Alcalà, 1999; present paper), and therefore not recorded as co-occurring with the genus *Equus* outside China.

In China, *Proboscidipparion* co-occurs with *Equus* until 1 Ma (Qiu et al., 1987). In Africa, *Eurygnathohippus* persists until sometime younger than 1 Ma (Bernor and Armour-Chelu, 1999; Bernor et al., 2010), co-occurring with the genus *Equus* since its FAD at 2.33 Ma (Eisenmann, 1983; Bernor et al., 2010, 2019; Rook et al., 2019). Clearly, the so-called "*Hipparion* Last Appearance Datum" was diachronous across Eurasia and Africa, with multiple lineages having become extinct by ca. 1 Ma.

Conclusions

Our review of the Roca-Neyra equid sample and comparisons with other Eurasian Plio-Pleistocene equid assemblages has led to new insights on the taxonomic diversity of Plio-Pleistocene "*Hipparion*" evolutionary lineages and on the *Equus* FAD in Eurasia.

As reported in our morphometric and statistical analyses, “*Hipparion*” *crassum* from Perpignan (4.1 Ma, Ruscinian, MN15) is referred to the genus *Proboscidipparion* due its close similarities with the early Pliocene *Proboscidipparion heintzi* from Çalta (ca. 4 Ma) in its cranial and postcranial morphology.

The European “*Hipparion*” samples at the Plio–Pleistocene transition (Kvabebi, Villarroya, and Roca-Neyra) have shown a remarkable resemblance to the late Miocene–Early Pleistocene *Plesiohipparion* species: *P. longipes* from Pavlodar and Çalta and *P. houfenense* from Yushe Basin. Furthermore, the Kvabebi, Villarroya, and Roca-Neyra samples may be referred to *Plesiohipparion rocinantis* due to their morphological similarity. Nevertheless, a revision of the Kvabebi and Villarroya samples would help to clarify the occurrence of multiple *Plesiohipparion* species in the Plio-Pleistocene Eurasian fossil record.

The Pliocene sample of “*Hipparion*” *fissurae* from Layna (3.91, Ruscinian, MN15) remains enigmatic. Its elongate-slender metapodial morphology could suggest a referral to either *Plesiohipparion* or *Cremohipparion*, and more information from the skull and dentition are needed in order to determinate its generic assignment. Nevertheless, this study has pointed out the possible relationship between the Layna sample and “*Hipparion elegans*” from Pavlodar, due their close morphological similarities.

The Montopoli fragmentary cheek tooth remains the most obscure “*Hipparion*.” Its size and simplicity of occlusal morphology do not match *Plesiohipparion* and *Proboscidipparion*, but, given the latest Miocene occurrence of a small *Cremohipparion* from Baccinello V3, ?*Cremohipparion* sp. is a plausible referral.

The Roca-Neyra *Equus* sample is referred to *Equus* cf. *E. livenzovensis*, supported by the occlusal morphology of the lower cheek teeth, which includes intermediate features between the North American *Equus simplicidens* and the European *Equus stenonis*. The presence of *Equus* cf. *E. livenzovensis* at Roca-Neyra confirms the dispersion of this species at the beginning of the Pleistocene in Europe, and the new age proposed of 2.6 ± 0.2 Ma (Nomade et al., 2014) correlates this locality with the 2.6 Ma sites of Livensovska, Montopoli, El Rincòn-1, and Huélago, where *Equus livenzovensis* occurs.

The occurrences of the three-toed equid, here referred to *Plesiohipparion* cf. *P. rocinantis*, and the monodactyl horse *Equus* cf. *E. livenzovensis* at Roca-Neyra, underscore the importance of this locality in Central and Western Europe, allowing us to recognize it as an important crossroad for the transition from the last European Plio-Pleistocene “*Hipparion*” sensu lato to the first occurrence of the genus *Equus*.

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Accessibility of supplemental data

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.hqbzkh1dj.

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