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Equus stenonis (Equidae, Mammalia) from the Early Pleistocene of Pantalla (Italy) and the dispersion of stenonine horses in Europe

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ABSTRACT - Stenonine horses roamed across Eurasia for a long-time interval between the Early Pleistocene and the early Middle Pleistocene. These forms probably derived from North American Equus simplicidens *and recent research suggests that they can be at the basis of the radiation of the extant African zebras.* Equus stenonis *is the most widespread stenonine horse in the Early Pleistocene of Europe. Here we describe the* Equus *record from Pantalla (Italy) and we refer it to* E. stenonis *based on a combination of morphometric analyses of metapodials and tibia. In particular, our comparisons show remarkable similarities between the Pantalla horse and* E. stenonis *from Saint Vallier (France). The studied sample allows suggesting an age close to the beginning of the late Villafranchian (~2 Ma) for the Pantalla assemblage, thus representing one of the earliest records of* E. stenonis *in Italy. Furthermore, our analyses highlight a substantial morphometric homogeneity in European* E. stenonis *samples, supporting that they may represent intraspecific variation of a single long-lasting widespread species.*

INTRODUCTION

Equidae are the most widely distributed group of extant odd-toed ungulate mammals in Eurasia. They are characterised by slender legs, long heads, relatively long necks, manes (erect in most subspecies), and long tails. All equids are herbivorous and mostly grazers (MacFadden, 1994). The family includes several extant species of horses and relatives (asses, donkeys, and zebras), which are all included within the genus *Equus*. The fossil record suggests that *Equus simplicidens* Cope, 1892 from Idaho, USA (~3.3 Ma) may represent the common ancestor of all Old World non-caballine *Equus* species (Azzaroli & Voorhies, 1993; Bernor et al., 2019). During the Plio-Pleistocene, *Equus* quickly dispersed across Eurasia, and became abundant and common elements of Quaternary European local faunal assemblages (LFAs) with various species and subspecies, whose taxonomic status, phylogenetic relationships, and chronological ranges are still matter of debate (Palombo & Alberdi, 2017 and references therein). The first appearance of *Equus* in Eurasia is correlated with the beginning of the Pleistocene and the base of the Matuyama magnetic chron (~2.6 Ma, following Gibbard et al., 2010), and in Europe it is represented by the occurrence of the species *Equus livenzovensis* Bajgusheva, 1978 from Montopoli (Italy), El Rincón and Huélago (Spain), Roca-Neyra (France) and Liventsovka (southwestern Russia) (Bajgusheva, 1978; Azzaroli, 1982; Alberdi et al., 1997, 2001; Bernor et al., 2018; Cirilli et al., 2020a). This biochronological event, termed the *Equus* Datum (Berggren & van Couvering, 1974; Rook et al., 2019), is related to important climate changes driven by a major glaciation pulse in the northern hemisphere (Lindsay et al., 1980; Azzaroli, 1983). In fact, the Plio-Pleistocene boundary is characterised by a dramatic floral and faunal turnover in Europe (Azzaroli, 1983; Gliozzi et al., 1997; Bertini, 2010; Rook & Martinez-Navarro, 2010; Magri et al., 2017), correlative with the European mammalian middle-late Villafranchian transition.

The most common horses occurring in the middle-late Villafranchian (Gelasian and pre-Jaramillo Calabrian ages of the Early Pleistocene) belong to the "*Equus stenonis* group", which includes relatively large-sized and stout forms recorded in several European and Asian localities. Fossils attributed to this group have been recovered from different localities, sometimes differing in size and proportions, probably depending both on ecogeographical and chronological factors. This led in the last decades to the establishment of a number of different subspecies of *E. stenonis* Cocchi, 1867, whose validity is still debated (Forsten, 1999; Palombo & Alberdi, 2017; Bernor et al., 2019). Furthermore, some scholars proposed to elevate at species rank some of these subspecies to better differentiate the European Early Pleistocene *Equus* (for a complete summary see Eisenmann, 2004). The earliest occurrence of *E. stenonis* in Europe is from the French paleontological locality of Saint Vallier (Eisenmann, 2004; Palombo & Valli, 2004), dated shortly after the Plio-Pleistocene boundary (~2.5 Ma; Nomade et al., 2014). According to several authors (e.g., Azzaroli, 1995, 2003; Alberdi et al., 1998), stenonine horses are likely derived from the middle Villafranchian large-sized species *E. livenzovensis*. In particular, during the Early

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Pleistocene, *E. livenzovensis* gave rise to two different lineages, one of smaller and the other of larger-sized species. Alberdi et al. (1998) identified relatively smaller forms as including *E. stenonis*, *Equus senezensis* Prat, 1964, *Equus stehlini* Azzaroli, 1964, and eventually *Equus altidens* von Reichenau, 1915, even if the origin of the latter is still matter of debate by several authors (Guerrero-Alba & Palmqvist, 1997; Alberdi et al., 1998; Alberdi & Palombo, 2013a, b; Palombo & Alberdi, 2017). The larger-sized species-group includes *Equus major* Depéret in Delafond & Depéret, 1893 ex Boule and *Equus suessenbornensis* Wüst, 1900. Among these various species, *E. stehlini* from Italy is considered to be a species distinct from *E. senezensis* from France (e.g., Azzaroli, 1990; Palombo & Alberdi, 2017), or alternatively as a subspecies of the latter (e.g., Alberdi et al., 1998; Palombo et al., 2017). *Equus stenonis* is reported in most European sites, occurring in an interval of at least one million years spanning from ~2.6 to ~1.6 Ma (Alberdi & Palombo, 2013a). Italian records of *E. stenonis* are numerous, but few of them (e.g., Azzaroli, 1964; De Giuli, 1972) have been systematically studied.

Here we report on the *Equus* remains from the Early Pleistocene site of Pantalla (central Italy) and we compare them by morphometric methods to a large sample of horses from several New and Old World LFAs, in order to ascertain their taxonomic attribution and to offer new insight on the geographical and chronological ranges of middle-late Villafranchian horses.

GEOLOGICAL AND PALEONTOLOGICAL SETTING

The Pantalla paleontological site (42°52'46.79''N, 12°24'23.26''E) was discovered in 1994 during construction work on a silty-sandy hill, just outside the northern part of the homonymous town, about 30 km South to Perugia (Italy; Fig. 1). The area is located near the western margin of the Apennine Chain, in the southwestern branch of the Tiber Basin, a wide extensional continental basin with a characteristic "upside-down Y" shape (Basilici, 1997). Pantalla was excavated systematically in 1995 and represents one of the most interesting late Villafranchian sites in Europe from a number of standpoints. Although not abundant (the excavation inventory counts for little more than 80 specimens collected), it stands out for the exceptional state of preservation of a majority of the remains. These include some complete skulls of large mammals, including the holotype of a new genus and species of otter (see below). At the time of the discovery, the exposed stratigraphic succession was about 15 m thick, but vertebrate fossils were unearthed only from the uppermost part of the section (Gentili et al., 1997). Based on field reports, the lower part of the succession was mainly composed by fine sands of probable fluvial origin, while the upper part was more heterogeneous, with alternations of layers no thicker than one meter of fine silty sands and clays, sometimes in the form of paleosols (Gentili et al., 1997). The same authors referred the succession to the Early Pleistocene Santa Maria di Ciciliano Unit (Basilici, 1997), currently classified as a subsyntheme of the Todi Syntheme in

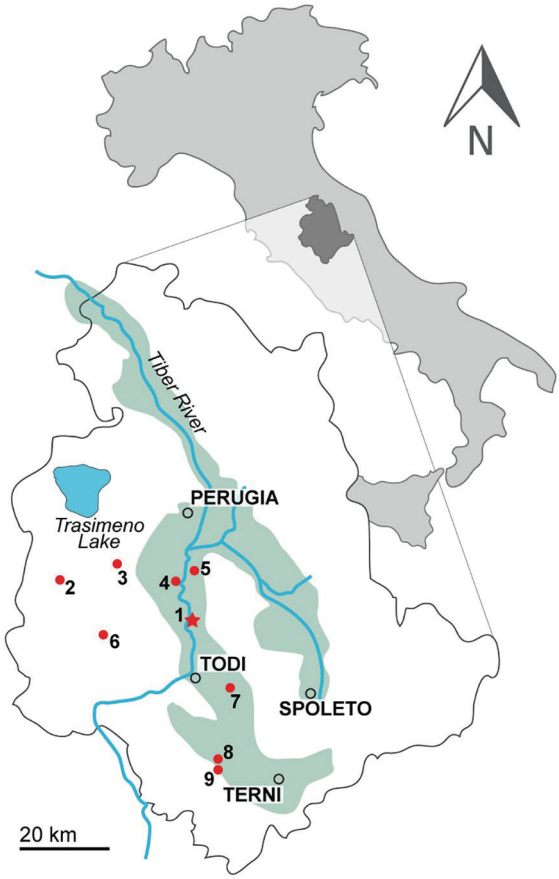

Fig. 1 - (color online) Geographical location of the study area. The Tiber Basin is highlighted in light green along the middle part of Umbria Region. 1, Pantalla, is marked by a red star. Red points refer to other Umbrian paleontological sites mentioned in the text in which the occurrence of *Equus stenonis* or Early Pleistocene undetermined equid remains is reported (Sardella et al., 1995; Petronio et al., 2002; Girotti et al., 2003; Argenti, 2004; Cherin et al., 2019a): 2, Vigna Nuova (unpublished material of *Equus* sp.); 3, Pietrafitta (unpublished material of *Equus* sp.); 4, Papiano (?*E. stenonis*); 5, Podere San Lorenzo (*E. stenonis*); 6, Parrano-Frattaguida (?*E. stenonis*); 7, Villa San Faustino (*E. stenonis*); 8, Torre Picchio (*E.* cf. *stenonis*); 9, Colle Lame (?*E. stenonis*).

recent geological maps (Regione Umbria, 2013; Cherin et al., 2019a). A new project aimed at the sedimentologic, stratigraphic, taphonomic, paleoenvironmental, and chronological characterisation of Pantalla is still ongoing, but the general description on the upper part of the succession (i.e., the fossiliferous part) is essentially confirmed.

The best preserved Pantalla fossils originate from a relatively small (~2 m^2) bone accumulation found within a silty-sand yellowish layer. The completeness of many of the remains even in the most delicate anatomical parts, suggests that they accumulated over a very short time. Very few specimens are articulated. Other fossils were found instead in greyish clayey layers interpreted as paleosols (Gentili et al., 1997), as demonstrated by the greater degree of fragmentation and by evident surface cracks related to prolonged subaerial exposure.

In addition to the equid remains described herein, the Pantalla mammal assemblage includes *Apodemus*

dominans Kretzoi, 1959, *Canis etruscus* Forsyth Major, 1877, *Vulpes* sp., *Lynx issiodorensis valdarnensis* Werdelin, 1981, *Acinonyx pardinensis* (Croizet & Jobert, 1828), *Lutraeximia umbra* Cherin et al., 2016, *Leptobos merlai* De Giuli, 1987, "*Pseudodama*" *nestii* (Azzaroli, 1947), *Sus strozzii* Forsyth Major, 1881, and *Mammuthus* cf. *meridionalis* (Nesti, 1825) (Gentili et al., 1997; Petronio et al., 2002; Cherin et al., 2013a, b, 2014a, b, 2016, 2018, 2019b). This LFA is referable to the early late Villafranchian (~2.1-1.7 Ma; Napoleone et al., 2003) correlative with the Olivola-Tasso Faunal Units (FUs; Gliozzi et al., 1997; Masini & Sala, 2007) and MNQ 18 in the "Mammal Neogene/Quaternary Zones" system (Mein, 1975; Guérin, 1982). However, as discussed by Cherin et al. (2019b) based on the occurrence of *L. merlai*, it is highly probable that the actual age of the LFA is closer to the lower limit of the aforementioned chronological interval, that is, ~2.0 Ma.

MATERIALS AND METHODS

The *Equus* remains from Pantalla are housed in the Soprintendenza Archeologia, Belle Arti e Paesaggio dell'Umbria (SABAP_UMB) in Perugia. The sample is represented by the postcranial elements shown in Fig. 2 and listed under Referred material below.

Before the present study, fossils were prepared in the Vertebrate Paleontology Lab of the Dipartimento di Fisica e Geologia of the Università di Perugia. For gluing and consolidation, we used solutions of Paraloid™ B-72 in acetone following Davidson & Brown (2012).

In order to determine the species identity of the Pantalla material we compare it with a large dataset of measurements of North American and Eurasian Plio-Pleistocene *Equus* species and with the extant zebra *Equus grevyi* Oustalet, 1882, using bivariate plots, boxplots, and Log10 ratio diagrams. In particular, based on the available sample from Pantalla and following the literature, we focus on the third metacarpal and third metatarsal, using the Höwenegg *Hippotherium primigenium* von Meyer, 1829 standard (Bernor et al., 1997) in Log10 ratios. Bivariate plots and boxplots have been developed using the package ggplot2 in the Software R. Several authors including Eisenmann (1995), Bernor & Harris (2003), Bernor et al. (2003, 2005, 2016), Bernor & Sen (2017), and Cirilli et al. (2020b), have used Log10 ratio diagrams on postcranial elements in order to evaluate differences and evolutionary trends in *Hipparion*. The same method has been extended to Plio-Pleistocene *Equus* by other scholars (e.g., Eisenmann, 1979; Bernor et al., 2018, 2019). Here we follow Bernor et al. (2018, 2019) in our analyses on third metapodials.

Anatomical nomenclature and osteological landmarks follow Bernor et al. (1997). Morphometric measurements are taken according to the international equid measurement guidelines of Eisenmann et al. (1988) and Bernor et al. (1997). In particular, the following measurements of third metacarpal/metatarsal are considered in this work: M1, maximum length; M3, minimum width of the diaphysis; M4, depth of the diaphysis at level of M3; M5, proximal articular width; M6, proximal articular depth; M7, diameter of the articular facet for the third carpal/tarsal; M8, maximum diameter for the anterior facet for the fourth carpal/tarsal; M10, distal maximum supra-articular width; M11, distal maximum articular width; M12, distal maximum depth of the crista sagittalis; M13, distal maximum depth of the lateral condyle; M14, distal maximum depth of the medial condyle. Bivariate plots are built comparing M11 against M1, whereas boxplots describe the variation of M1 and M11 in the examined samples.

Although the tibia is not normally used as a diagnostic skeletal element for the study of fossil horses, we carry out a quantitative comparative analysis of the distal epiphysis measurements (maximum width and maximum depth), in order to provide additional information to that offered by the study of metapodials.

The Plio-Pleistocene *Equus* samples included in the comparative analysis are as follows (where we did not use our personal data, the bibliographic source is indicated in parentheses): *E. simplicidens* from Hagerman Horse Quarry (Idaho, USA); *Equus eisenmannae* Qiu et al., 2004 from Longdan (China); *E. livenzovensis* from El Rincón-1 (Spain; Alberdi et al., 1997); *E. major* from Senèze (France); *E.* cf. *major* from Fonelas P-1 (Spain; Garrido, 2008); *E. stenonis vireti* from Saint Vallier (France); *E. stenonis guthi* from Chilhac (France; Boeuf, 1986); *E. stenonis pueblensis* from La Puebla de Valverde (Spain; V. Eisenmann's website, https://vera-eisenmann.com); *E. stenonis* from Olivola (Italy), Matassino (Upper Valdarno Basin; Italy), Dafneró (Greece; Koufos & Kostopoulos, 1993), Vólax (Greece; Koufos & Vlachou, 1997), Sésklo (Greece; Athanassiou, 2001); *E. stenonis mygdoniensis* from the Mygdonia Basin (Greece; Koufos, 1992); *Equus* sp. from Senèze (France), *E. senezensis* aff. *E. senezensis stehlini* from Coste San Giacomo (Italy; Palombo et al., 2017), *E. stehlini* from Casa Frata (Upper Valdarno Basin, Italy); *E. altidens* from Selvella (Italy; Alberdi & Palombo, 2013a); *E. altidens* from Pirro Nord (Italy; Alberdi & Palombo, 2013b); *E. altidens granatensis* from Venta Micena (Spain; V. Eisenmann's website, https://vera-eisenmann.com); *E. suessenbornensis* from Akhalkalaki (Georgia); and extant *E. grevyi* from Kenya.

The medium-sized *Equus* from the Early Pleistocene of Senèze, referred to multiple species/subspecies from different authors (Alberdi et al., 1998; Delson et al., 2006; Palombo & Alberdi, 2017; Palombo et al., 2017; V. Eisenmann's website, https://vera-eisenmann.com/the-seneze-equids-text), is here referred to as *Equus* sp.

Institutional abbreviations

SABAP_UMB: Soprintendenza Archeologia, Belle Arti e Paesaggio dell'Umbria (Perugia, Italy); IGF: Museo di Storia Naturale, Sezione di Geologia e Paleontologia, Università di Firenze (Italy); NHML: Natural History Museum, Musée des Confluences, Lyon (France); UCBL-FSL: Universitè Claude Bernard-1, Facultè des Science, Lyon (France).

Anatomical abbreviations

1PH3, proximal phalanx of the third digit; 2PH3, middle phalanx of the third digit; 3PH3, distal phalanx of the third digit; MC3, third metacarpal; MT2, second metatarsal; MT3, third metatarsal; MT4, fourth metatarsal.

Fig. 2 - (color online) *Equus stenonis* from Pantalla (Italy). a-d) Articulated right forelimb SABAP_UMB 167353 in dorsal (a), palmar (b), lateral (c), and medial (d) views; the proximal lateral sesamoid is in anatomical position in (b) and (c). e-f) Right third metacarpal SABAP_UMB 177987 in dorsal (e) and palmar (f) views. g-i) Right third metatarsal SABAP_UMB 337626 in proximal (g), dorsal (h), and plantar (i) views. j-l) Right tibia SABAP_UMB 167354bis in cranial (j), caudal (k), and distal (l) views. m-o) Left tibia SABAP_UMB 167364 in cranial (m), caudal (n), and distal (o) views. Scale bar: 5 cm.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Subfamily Equinae Gray, 1821
Tribe Equini Gray, 1821

Genus *Equus* Linnaeus, 1758

Equus stenonis Cocchi, 1867
(Fig. 2)

Taxonomic remarks - Starting from the twentieth century, different interpretations have been proposed on the taxonomy of stenonine horses, which can be summarised in their attribution to *Equus* or *Allohippus*. The latter was introduced by Kretzoi (1938) without description, and later formally defined by Gromova (1949). In both cases, *Allohippus* was considered as a subgenus of *Equus* (Samson, 1975). Kretzoi (1938) and Gromova (1949) considered the skull of *E. stenonis* and/or *E. livenzovensis* as representative of the typical morphology of the subgenus. Since then, *Allohippus* was elevated to genus rank by some authors to allocate *E. stenonis* and related species (Eisenmann & Baylac, 2000; Eisenmann, 2004, 2006; Eisenmann & Deng, 2006; Barrón-Ortiz et al., 2019; Boulbes & van Asperen, 2019 among others). Nevertheless, other scholars questioned the validity of *Allohippus*, suggesting that this name should be avoided in equid systematics (Azzaroli, 1992, 2003) or used with caution only at subgenus level (Palombo & Alberdi, 2017). Since the debate on the formal validity of *Allohippus* is far from resolved and outside the scope of this article, we prefer to refer stenonine horses to the genus *Equus*, in agreement with many other authors (Azzaroli, 1964, 1990, 1992, 2003; Azzaroli & Voorhies, 1993; Alberdi et al., 1998; Alberdi & Palombo, 2013a; Palombo & Alberdi, 2017; Bernor et al., 2018, 2019 among others).

Referred material - SABAP_UMB 167353, juvenile articulated partial distal right forelimb; SABAP_UMB 177987, distal right MC3; SABAP_UMB 337626, right MT3; SABAP_UMB 167354bis, distal right tibia; SABAP_UMB 167364, distal left tibia.

Description - The *Equus* sample from Pantalla is shown in Fig. 2. Measurements of each specimen are reported in Tab. 1.

The juvenile articulated distal right fragmentary forelimb SABAP_UMB 167353 (Fig. 2a-d) consists of the distal half of the MC3 with the anterior 1PH3 and 2PH3 in anatomical connection. The proximal lateral sesamoid is also preserved (it is shown in its anatomical position in Fig. 2b-c). The MC3 exhibits a slender shape, damaged in proximity of the midshaft width, with the distal epiphysis

Tibia SABAP_UMB 167354bis	
M3. Minimum width	57.7
M7. Distal maximum width	83.7
M8. Distal maximum depth	51.2
Tibia SABAP_UMB 167364	
M3. Minimum width	46.2
M4. Minimum depth of the diaphysis at level of M3	31.1
M7. Distal maximum width	83.5
M8. Distal maximum depth	48.7
Third metatarsal SABAP_UMB 337626	
M1. Maximum length	254.5
M2. Medial length	240.9
M3. Minimum width	39.1
M4. Depth of the diaphysis at level of M3	33.5
M5. Proximal articular width	*53.5*
M10. Distal maximum supra-articular width	56.0
M11. Distal maximum articular width	52.6
M12. Distal maximum depth of the crista sagittalis	*38.5*
M13. Distal maximum depth of the lateral condyle	29.6
M14. Distal maximum depth of the medial condyle	30.1
Third metacarpal SABAP_UMB 177987	
M10. Distal maximum supra-articular width	52.1
M11. Distal maximum articular width	48.4
M12. Distal maximum depth of the crista sagittalis	36.2
M13. Distal maximum depth of the lateral condyle	27.5
M14. Distal maximum depth of the medial condyle	29.7
Juvenile articulated forelimb SABAP_UMB 167353	
Third metacarpal	
M3. Minimum width	29.5
M4. Depth of the diaphysis at level of M3	21.3
M10. Distal maximum supra-articular width	48.3
M11. Distal maximum articular width	47.3
M12. Distal maximum depth of the crista sagittalis	34.8
M13. Distal maximum depth of the lateral condyle	26.3
M14. Distal maximum depth of the medial condyle	27.7
Proximal phalanx of the third digit	
M1. Maximum length	73.1
M2. Dorsal length	52.0
M3. Minimum width	12.8
M4. Proximal width	29.6
M5. Proximal depth	33.4
M6. Distal width at the tuberosities	41.9
M7. Distal articular width	44.1
M8. Distal articular depth	23.9
M9. Minimum length of the trigonum phalangis	45.9
M10. Medial supratuberosital length	61.4
M11. Lateral supratuberosital length	61.2
M12. Medial infratuberosital length	14.5
M13. Lateral infratuberosital length	14.8
Middle phalanx of the third digit	
M1. Maximum length	*43.0*
M2. Dorsal length	33.7
M3. Minimum width	40.2
M4. Proximal maximum width	46.4
M5. Proximal maximum depth	30.3
M6. Distal maximum articular width	*42.0*
Proximal lateral sesamoid	
Maximum length	30.4
Maximum width	19.0
Maximum depth	15.6

Tab. 1 - Measurements (mm) of *Equus stenonis* postcranial bones from Pantalla (Italy). Measurement guidelines and abbreviations follow Eisenmann et al. (1988) and Bernor et al. (1997) (see Materials and methods). Values in italics are estimated.

still not completely fused. The latter is damaged in the external borders of the medial and lateral trochleae. The crista sagittalis is well preserved in dorsal view, worn in palmar view. The lateral and medial protuberances are not preserved, but this could be due to the incomplete ossification of the distal epiphysis. In palmar view, the right and left supracondylar depressions are present. The anterior 1PH3 is complete in all its anatomical elements, although the proximal and distal epiphyses are still not completely fused with the diaphysis. Distally, the suture line corresponds with a postdepositional fracture. Even as a juvenile, the 1PH3 shows the typical stenonine morphology (Eisenmann & De Giuli, 1974), with: 1) a sinuous profile of the proximal end in dorsal view, in proximity of the attachment for the articular cartilage, and 2) a slender midshaft width. It also exhibits expanded distal articular tubercles for the attachment of the medial and lateral collateral ligaments. The supra-articular and articular dimensions are not significantly different. The palmar surface is dominated by a very long, deeply depressed "V-shaped" scar for the attachment of the ligamentum sesamoideum obliquum. The 2PH3 is a short bone, fragmented at the distolateral corner, in proximity of the lateral scar of the ligamentum collaterale for the articulation with the 3PH3.

The right MC3 SABAP_UMB 177987 (Fig. 2e-f) shows a well-preserved distal epiphysis, while the distal part of the diaphysis is heavily fractured. In spite of the overall smoothing of the external surface of the bone, the supra-articular medial and lateral protuberances are visible, and their maximum supra-articular width (M10) is very similar to the maximum articular width (M11). The medial and lateral condyles are well preserved and a prominent crista sagittalis rises between them. In palmar view, the right and left supracondylar depressions are well developed, although the distal epiphysis appears overall flat. The medial and lateral depressions for the ligamentum sesamoideum collaterale have a rounded morphology.

The right MT3 SABAP_UMB 337626 (Fig. 2g-i) is the best-preserved specimen in the collection. It is nearly complete, being damaged by taphonomic factors only in the proximal palmar extremity, where it lacks the caudal rugose surface for ligamentous attachments, the medial and articular facets for the MT2 and MT4 splints, and the facet for the cuboid. The specimen is heavily built, appearing overall robust and little elongated. In proximal view, the preserved part of the proximal epiphysis exhibits the typical stenonine circular section with wide borders. The diaphysis is relatively wide and tends to widen towards the distal epiphysis. The latter shows prominent supra-articular medial and lateral protuberances and a rounded shape of the medial and lateral condyles. The crista sagittalis is better preserved on the palmar than on the dorsal side and is associated with deep caudal supracondylar grooves. In palmar view, the long lines for the attachment of the interosseus ligaments connecting the MT2 and MT4 are preserved and well developed.

The right tibia SABAP_UMB 167354bis (Fig. 2j-l) has only its distal part preserved. The bone surface is rough and partially covered by a hard rust-colored patina. In distal view, the tibia shows a large and rounded medial malleolus and a less developed lateral malleolus, which is damaged at the anterodistal corner. The trochlear grooves for articulation with the astragalus are deep and arranged at an oblique angle to the sagittal plane of the diaphysis. The articular ridge between the two grooves is thick.

The left tibia SABAP_UMB 167364 (Fig. 2m-o) preserves a longer portion of the diaphysis than SABAP_UMB 167354bis, but is still quite damaged and fractured. The diaphysis has a massive morphology, with a wide minimum width. The distal epiphysis shows a large and rounded medial malleolus and a relatively smaller lateral malleolus, which is crossed in the middle by a wide sulcus malleolaris, visible in distal view. The trochlear grooves for the astragalus are deep and the lateral one is relatively wider than the medial. The articular ridge between the two grooves is well preserved and shaped like a curved crest.

MORPHOMETRIC ANALYSES

The results of morphometric analyses between the two most diagnostic specimens from Pantalla, MT3 SABAP_UMB 337626 and MC3 SABAP_UMB 177987, and homologous skeletal elements from our comparative dataset, are given below.

Bivariate analyses of MT3 distal maximum articular width (M11) versus maximum length (M1) are shown in Fig. 3. The two graphs offer similar results. In the first plot (Fig. 3a), European Early Pleistocene *Equus* species are compared with the Plio-Pleistocene North American *E. simplicidens* and the Early Pleistocene Chinese *E. eisenmannae*, whereas the second plot (Fig. 3b) illustrates the European record, including *E. altidens* samples from the Italian localities of Selvella and Pirro Nord, and the Spanish site of Venta Micena. SABAP_UMB 337626 plots very close to the range of *E. stenonis vireti* from Saint Vallier and its length is similar to that of the shortest MT3s from there. More broadly, all samples of *E. stenonis* show a close bivariate clustering. The only recognisable exception is represented by *E. stenonis mygdoniensis*, which has a relatively slender MT3 compared to that of the other samples of *E. stenonis* and plots together with *E. altidens* (Fig. 3b). SABAP_UMB 337626 is also well separated from the large-sized Chinese *E. eisenmannae* (whose range of variation encompasses that of *E. livenzovensis*; Fig. 3a), as well as from the European Early Pleistocene medium-sized *Equus* sp. from Senèze and *E. stehlini* from Italy. The latter results as the smallest among the considered species. *Equus major* and *E. suessenbornensis* are clearly separated from the rest of the taxa, with values even higher than those of the largest stenonine horses *E. eisenmannae* and *E. livenzovensis*. *Equus simplicidens* compares closely in length with the "*E. stenonis* group", but it is overall slenderer (Fig. 3a). Interestingly, the range of *E.* cf. *major* from Fonelas P-1 is almost completely overlapped with that of *E. eisenmannae* and *E. livenzovensis*, while it is clearly separated from the only available complete specimen of *E. major* from Senèze (Fig. 3a-b).

Boxplots for MT3 measurements M1 (Fig. 4a) and M11 (Fig. 4b) are included herein. These plots agree with the bivariate plots. The maximum length (M1) of SABAP_UMB 337626 is comparable to those of the shortest specimens of *E. stenonis vireti* and *E. stenonis guthi*, while *E. stenonis* from Olivola and Matassino has

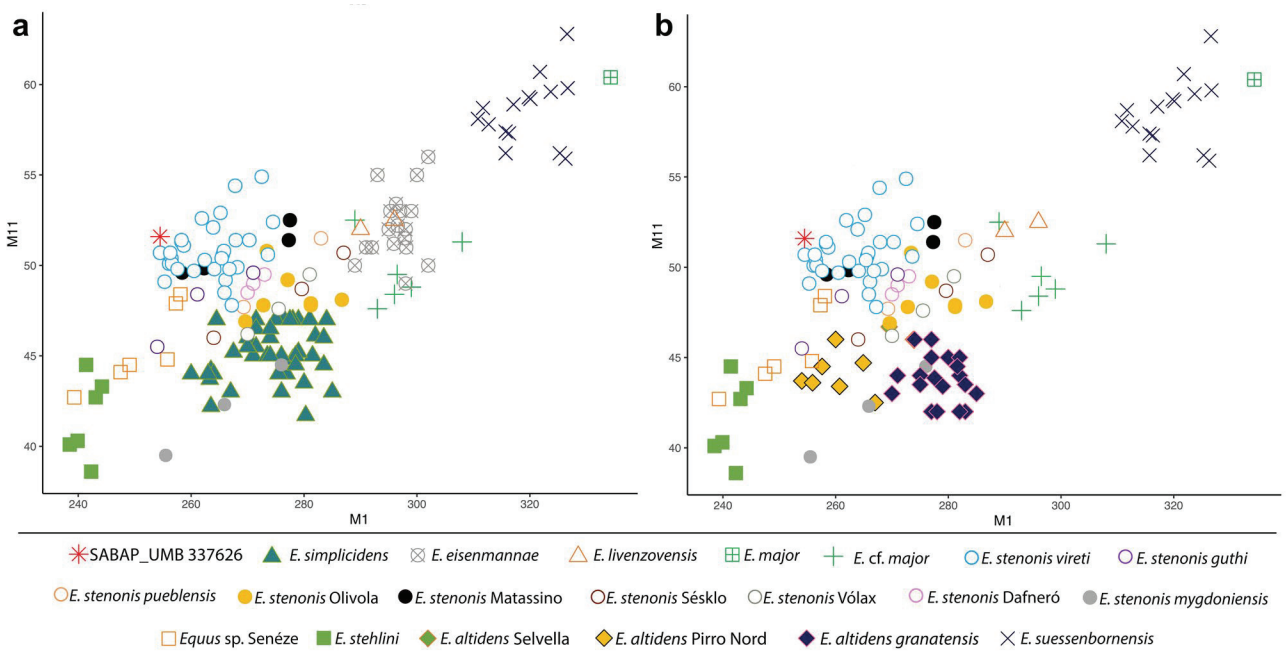

Fig. 3 - (color online) Bivariate plots comparing MT3 distal maximum articular width (M11) against maximum length (M1). a) European Early Pleistocene *Equus* spp. compared with North American *E. simplicidens* and the Chinese *E. eisenmannae*. b) European Early Pleistocene *Equus* spp. compared with the "*E. altidens* group" (i.e., *E. altidens* and *E. altidens granatensis*).

slightly more elongated MT3 (Fig. 4a). With regards to the distal maximum articular width (M11), the specimen from Pantalla plots at the upper part of the ranges of *E. stenonis vireti*, *E. stenonis pueblensis*, and *E. stenonis* from Matassino (Fig. 4b). Comparing the two graphs, MT3 length variation (Fig. 4a) is greater than distal articular width (Fig. 4b) of the "*E. stenonis* group". For *Equus* sp. from Senèze and *E. stehlini* on one side and *E. major* and *E. suessenbornensis* on the other, it is confirmed that the MT3 dimensions are significantly smaller and larger,

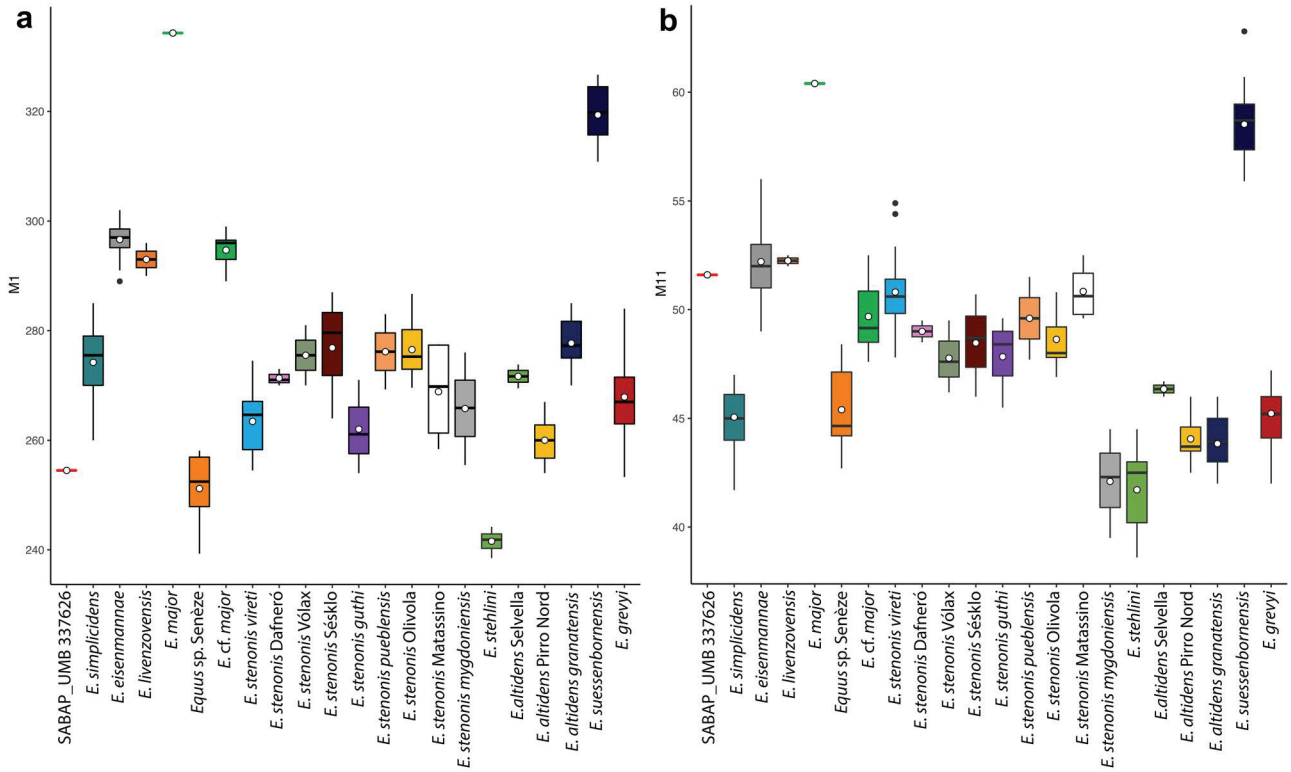

Fig. 4 - (color online) Boxplots (including minimum, median, mean, and maximum values with 25th and 75th percentile of each sample) of MT3 measurements M1 (a) and M11 (b). The sample includes European Early Pleistocene (~2.6-1.0 Ma) *Equus* spp., North American *E. simplicidens*, Chinese *E. eisenmannae*, and extant *E. grevyi*. Color code is the same as in Fig. 3.

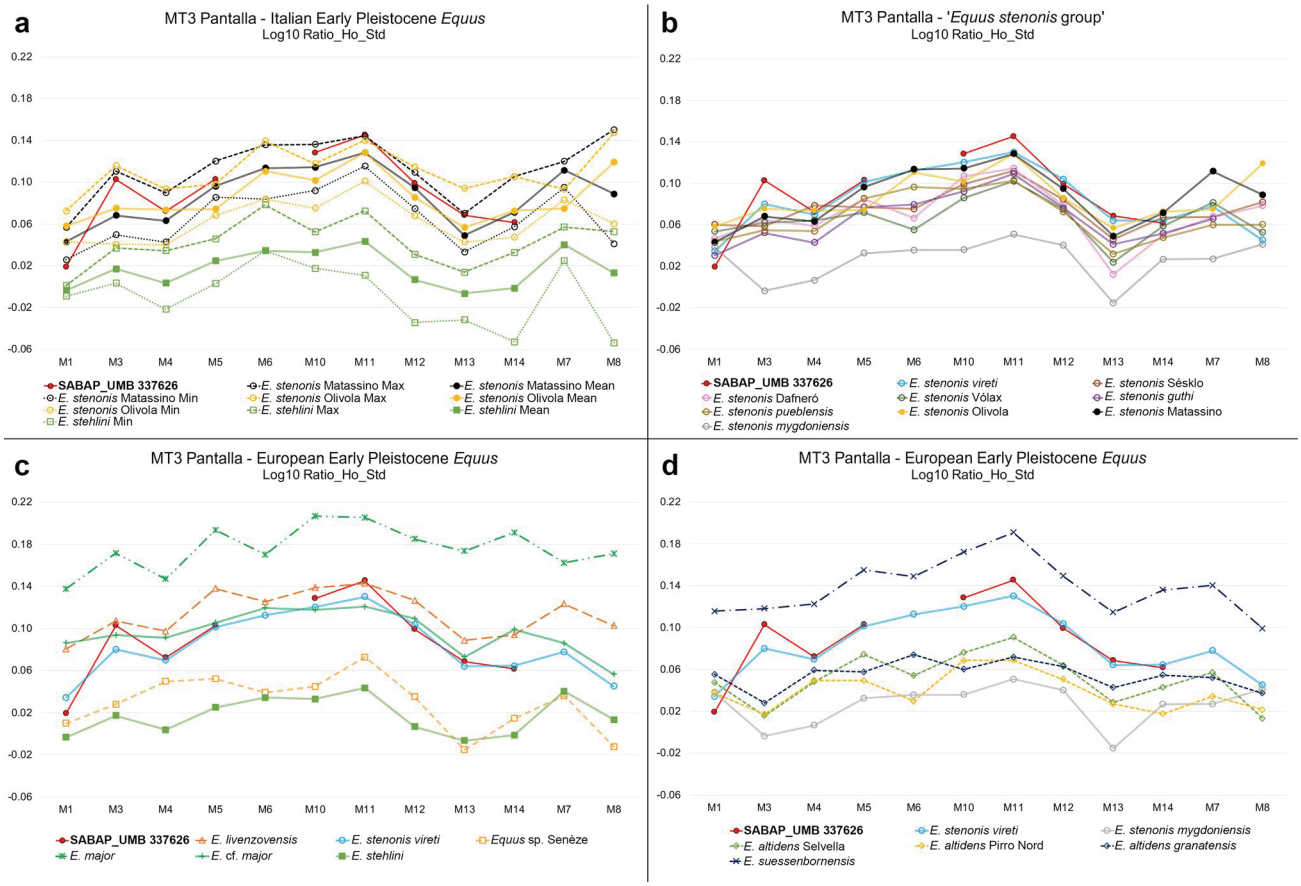

Fig. 5 - (color online) MT3 Log10 ratio diagrams. *Hippotherium primigenium* from Höwenegg is used as standard. a) SABAP_UMB 337626 compared with *E. stenonis* from Olivola and Matassino and *E. stehlini* from Casa Frata. b) SABAP_UMB 337626 compared with the European *E. stenonis* "subspecies"/samples. c) SABAP_UMB 337626 compared with European *E. livenzovensis*, *E. major*, *E.* cf. *major* (Fonelas P-1), *E. suessenbornensis*, *E. stenonis vireti* (Saint Vallier), *Equus* sp. (Senèze), and *E. stehlini*. d) SABAP_UMB 337626 compared with *E. suessenbornensis*, *E. stenonis vireti* (Saint Vallier), *E. stenonis mygdoniensis* (Mygdonia Basin), *E. altidens* (Selvella), *E. altidens* (Pirro Nord), and *E. altidens granatensis* (Venta Micena). Color code is the same as in Fig. 3.

respectively, than those of *E. stenonis* (although some large-sized specimens from Senèze partially overlap with the lower ranges of the latter species).

Log10 ratio diagrams (Fig. 5) compare the MT3 SABAP_UMB 337626 from Pantalla with a set of North American and Eurasian Plio-Pleistocene fossil horses for all the available measurements. Only Italian samples are shown in Fig. 5a, in which SABAP_UMB 337626 is compared with *E. stenonis* from Matassino and Olivola, and with *E. stehlini* from Casa Frata (dash lines represent the maximum values, thick lines the mean values, and dot lines the minimum values). SABAP_UMB 337626 plots within the range of variation of Italian *E. stenonis* (except for the slightly lower maximum length), while none of its measurements fall within the range included between the maximum and minimum values of *E. stehlini*.

In Fig. 5b, all European *E. stenonis* samples are shown in comparison to the Pantalla specimen. Again, SABAP_UMB 337626 tracks the trends of *E. stenonis vireti*, *E. stenonis* from Sésklo and from the Italian localities of Matassino and Olivola, in M3, M4, M10, M11, M12, and M13 values, but it shows slightly lower maximum length (M1) and narrower distal maximum depth of the medial condyle (M14). As previously pointed out in the bivariate and boxplot analyses, morphometric homogeneity in European *E. stenonis* samples can be recognised. *Equus stenonis guthi* from Chilhac has the lowest maximum length (M1) and midshaft width (M3) and depth (M4); its MT3s are slender on the whole. The only noteworthy exception is *E. stenonis mygdoniensis*, whose pattern recalls the minimum values of *E. stenonis* only for measurements M1 and M8, but it is overall slenderer.

A more synthetic view is found in the other two diagrams. In particular, in Fig. 5c we compare the Pantalla MT3 with that of *E. livenzovensis*, *E. stenonis vireti*, *E.* cf. *major* from Fonelas P-1, the large-sized *E. major*, and the smaller *Equus* sp. from Senèze and *E. stehlini*. In Fig. 5d the Pantalla MT3 is compared to *E. stenonis vireti*, *E. stenonis mygdoniensis*, *E. altidens*, and *E. altidens granatensis*. These two diagrams confirm the strong affinity between SABAP_UMB 337626 and the MT3 of *E. stenonis vireti*. The fossil from Pantalla is almost completely separated from the small and slender Early Pleistocene species (*Equus* sp. from Senèze, *E. stehlini*, and *E. altidens*). Again, the similarity between *E. stenonis mygdoniensis* and *E. altidens* is remarkable (Fig. 5d). The different samples of the latter species exhibit very similar patterns to each other, which in turn roughly follow those of the larger-sized *E. stenonis* samples. However, this

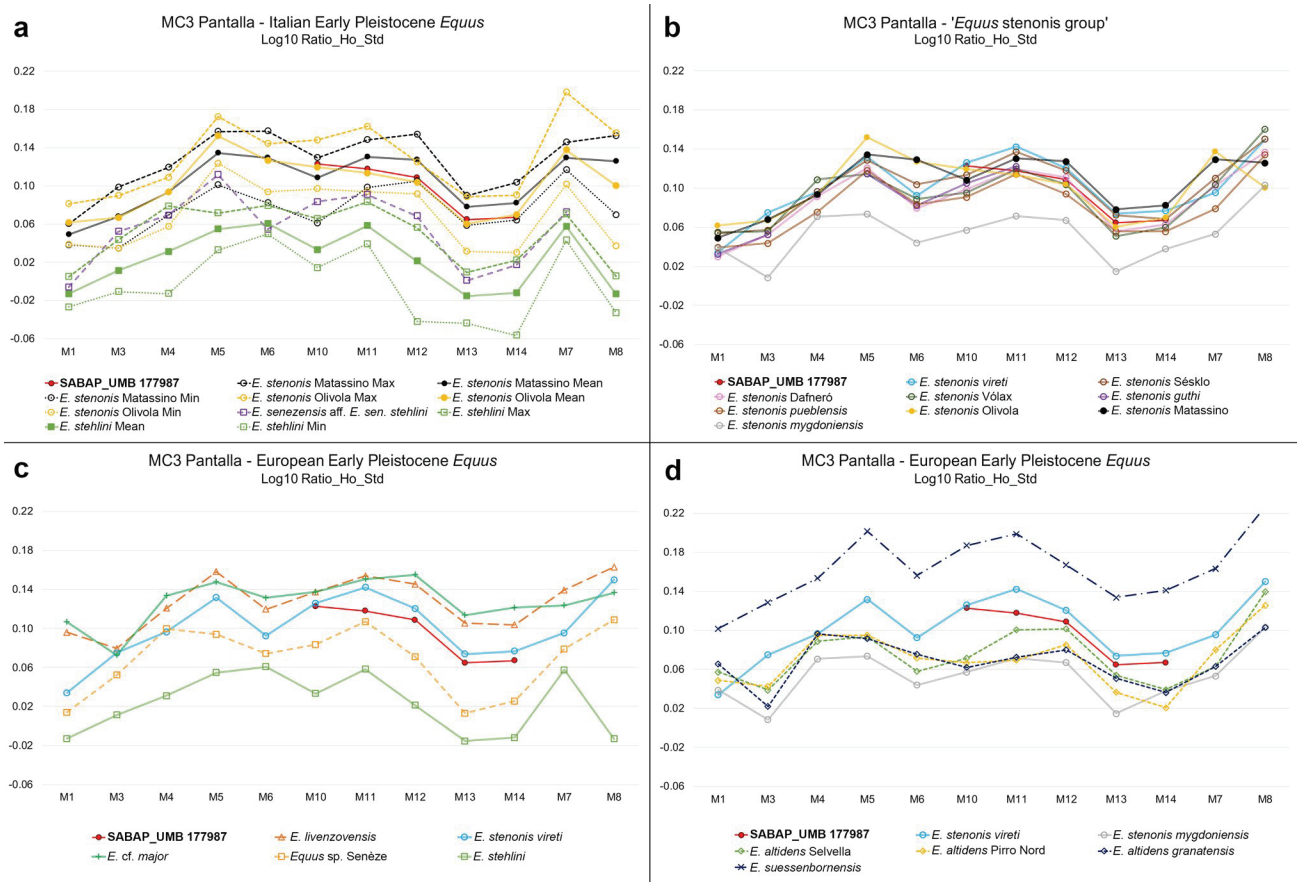

Fig. 6 - (color online) MC3 Log10 ratio diagrams. *Hippotherium primigenium* from Höwenegg is used as standard. a) SABAP_UMB 177987 compared with *E. stenonis* from Olivola and Matassino, *E. senezensis* aff. *E. senezensis* stehlini from Coste San Giacomo, and *E. stehlini* from Casa Frata. b) SABAP_UMB 177987 compared with the *E. stenonis* "subspecies"/samples. c) SABAP_UMB 177987 compared with European *E. livenzovensis*, *E.* cf. *major* (Fonelas P-1), *E. stenonis vireti* (Saint Vallier), *Equus* sp. (Senèze), and *E. stehlini*. d) SABAP_UMB 177987 compared with *E. suessenbornensis*, *E. stenonis vireti* (Saint Vallier), *E. stenonis mygdoniensis* (Mygdonia Basin), *E. altidens* (Selvella), *E. altidens* (Pirro Nord), and *E. altidens granatensis* (Venta Micena). Color code is the same as in Fig. 3.

latter evidence deserves further studies which are beyond the scope of this paper. The *E. livenzovensis* plot confirms that the MT3s are larger than those of the "*E. stenonis* group", but with a very similar trajectory (Fig. 5c); it was a more heavily built horse. A very similar pattern is recognisable for *E.* cf. *major* from Fonelas P-1, whose measurements fall between those of *E. livenzovensis* and those of the larger *E. stenonis*. Again, *E. suessenbornensis* and *E. major* are clearly separated from other stenonine species by their considerably larger dimensions, even if their patterns roughly track those of *E. livenzovensis*.

Log10 ratio diagrams for the MC3 are provided in Fig. 6, although the fragmentary nature of the Pantalla specimen SABAP_UMB 177987 allowed us to take and then compare only five measurements (M10-M14). We use here the same comparative samples as in Fig. 5, with the exclusion of *E. major* due to the absence of data, and the addition of *E. senezensis* aff. *E. senezensis stehlini* from the late middle Villafranchian of Coste San Giacomo (Palombo et al., 2017). The results obtained for the MC3 support those described above for the MT3. Even though SABAP_UMB 177987 is incomplete and damaged, its dimensions are included in the variation range of Italian *E. stenonis* (Fig. 6a). The Pantalla specimen does not exhibit morphometric values comparable to those of *E. senezensis* aff. *E. senezensis stehlini* from Coste San Giacomo, which is on the whole more similar to *E. stehlini*. By extending the comparative analysis outside of Italy (Fig. 6b), we can confirm the close affinity between the Pantalla MC3 to that of the European forms of the "*E. stenonis* group". SABAP_UMB 177987 only shows a relatively lower M11 value, but this could be the effect of an underestimation of this measurement due to the poor preservation of the distal articular area of this specimen. With the aforementioned exception of measurements M11, the line of SABAP_UMB 177987 closely follows that of *E. stenonis vireti* also in Fig. 6c-d. Also, in comparison to the MC3 dimensions, *E. senezensis* aff. *E. senezensis stehlini* and *E. stehlini* exhibit proportions comparable to those of *Equus* sp. from Senèze (Fig. 6c), while *E. stenonis mygdoniensis* and *E. altidens* have very similar patterns, mostly related to the slenderness plotted in M1-M3 (Fig. 6d). Again, *E.* cf. *major* from Fonelas P-1 exhibits a pattern similar to that of *E. livenzovensis*, and *E. suessenbornensis* stands out as the largest species in these graphs.

Eventually, Fig. 7 provides an evolutionary perspective. We compare the oldest European *E. stenonis* from Saint Vallier with North American *E. simplicidens*, the large European species *E. livenzovensis*, *E. major*, and *E. suessenbornensis*, and extant African *E. grevyi*. *Equus*

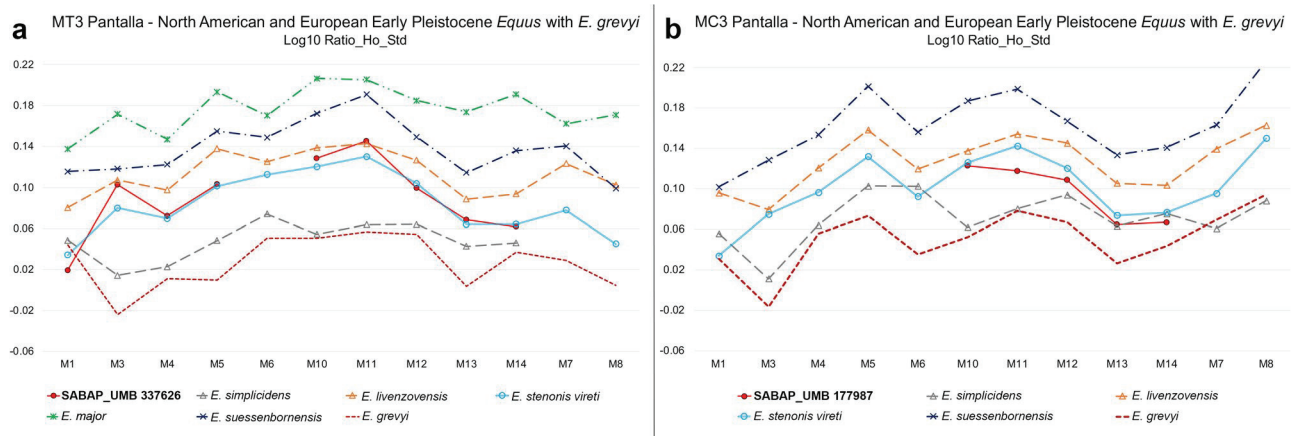

Fig. 7 - (color online) MT3 (a) and MC3 (b) Log10 ratio diagrams. *Hippotherium primigenium* from Höwenegg is used as standard. a) SABAP_UMB 337626 compared with *E. simplicidens*, *E. livenzovensis*, *E. stenonis vireti*, *E. major*, *E. suessenbornensis*, and *E. grevyi*. b) SABAP_UMB 177987 compared with *E. simplicidens*, *E. livenzovensis*, *E. stenonis vireti*, *E. suessenbornensis*, and *E. grevyi*.

simplicidens plot is overall tracked by both Eurasian stenonine horses (which only show relatively wider MT3 diaphysis; M3) and is particularly similar to extant *E. grevyi* (Fig. 7a), providing further support for the hypothesised evolutionary relationships between all these forms (Bernor et al., 2019). *Equus major* and *E. suessenbornensis* are distinctly larger than the "*E. stenonis* group", and more similar to *E. livenzovensis*. Even if more analyses are undertaken, this evidence supports the possible derivation of *E. major* and *E. suessenbornensis* from *E. livenzovensis* as reported by Alberdi et al. (1998). Finally, the horse from Pantalla is very similar with *E. stenonis* from Saint Vallier.

Comparative measurements of the distal epiphysis of the tibia are provided in Tab. 2. The maximum width and depth of the two specimens from Pantalla are similar to those recorded for *E. stenonis*. In particular, they are close to the values published for the tibia SABAP_UMB 153535 from the neighboring locality of Podere San Lorenzo (Cherin et al., 2019a; Fig. 1) and to the mean

Taxon	Locality	Distal max width			Distal max depth			Source of data
		n	min–max	mean	n	min–max	mean	
Equus stenonis	Pantalla (Italy)	2	83.5-83.7	83.6	2	48.7-51.2	50.0	a
Equus stenonis	Podere San Lorenzo (Italy)	1	-	84.0	1	-	50.0	b
Equus stenonis	Upper Valdarno (Italy)	3	74.0-76.0	75.2	3	47.5-54.0	49.8	b
Equus stenonis	Olivola (Italy)	4	80.0-83.5	81.4	4	51.0-54.5	52.4	b
Equus stenonis	Sésklo (Greece)	23	73.3-86.0	79.1	27	49.0-56.9	52.3	c
Equus stenonis guthi	Chilhac (France)	5	62.0-78.0	73.2	5	44.0-52.0	48.0	d
Equus stenonis vireti	St. Vallier (France) - old collection	22	75.0-85.0	80.5	24	47.0-55.0	52.0	e
Equus stenonis vireti	St. Vallier (France) - new collection	14	74.0-88.0	82.7	16	45.5-max	52.0	e
Equus stenonis mygdoniensis	Mygdonia Basin (Greece)	18	63.0-72.0	66.1	19	42.4-46.0	44.3	f
Equus stehlini	Upper Valdarno (Italy)	2	65.0-72.5	68.8	2	43.0-49.0	46.0	b
Equus sp.	Senèze (France)	15	60.0-80.0	71.0	10	44.0-49.0	47.6	g
Equus altidens	Pirro Nord (Italy)	2	69.4-73.4	71.4	2	47.2-48.2	47.7	a
Equus altidens granatensis	Venta Micena (Spain)	40	68.0-79.0	73.2	40	43.0-51.0	48.0	h

Tab. 2 - Measurements (mm) of the equid tibiae from Pantalla (Italy) and of the comparative material used in this study. References for morphometric data: a, this work; b, Cherin et al. (2019a); c, Athanassiou (2001); d, Boeuf (1986); e, Eisenmann (2004); f, Koufos (1992); g, V. Eisenmann's website, https://vera-eisenmann.com; h, Alberdi & Piñero (2012).

values of the specimens from Saint Vallier and Olivola. Conversely, smaller-sized stenonine horses such as *Equus* sp. from Senèze, *E. stehlini*, and *E. altidens* have tibiae with overall smaller dimensions of the distal epiphysis.

DISCUSSION

Taxonomic affinities of the Pantalla horse

In light of our morphometric comparisons, the equid sample from Pantalla can be confidently referred to *E. stenonis*. Due to the scantiness of complete cranial remains and based on minor morphometric differences in the appendicular skeleton (e.g., metapodial proportions) and teeth (e.g., relative length of the protocone in the cheek teeth), members of the "*E. stenonis* group" were split into a number of subspecies, each often restricted to a single locality. According to this approach, the material from the type locality (Upper Valdarno Basin) would be referred to the nominotypical subspecies *E. stenonis stenonis* (see De Giuli, 1972), which according to some authors, would be different from *E. stenonis vireti* from Saint Vallier (Prat, 1980), *E. stenonis senezensis* from Senèze (Prat, 1964, 1980; "*E. senezensis senezensis*" in Alberdi et al., 1998; *Equus* sp. in the present paper), *E. stenonis guthi* from Chilhac (Boeuf, 1986), *E. stenonis pueblensis* from La Puebla de Valverde (Caloi, 1997), *E. stenonis olivolanus* from Olivola (Caloi, 1997), and *E. stenonis mygdoniensis* from Gerakarou-1, Mygdonia Basin (Koufos, 1992). This paper suggests potentially important improvements of this group's taxonomy.

The most complete specimen from Pantalla, the MT3 SABAP_UMB 337626, exhibits a relatively short maximum length (M1). Although this shortness may be exaggerated by taphonomic factors (i.e., the fossil is slightly curved laterally at the distal end and the crista sagittalis is slightly depressed; Fig. 2h), it is compatible with the values measured in early *E. stenonis* samples from Saint Vallier (*E. stenonis vireti*) and Chilhac (*E. stenonis guthi*). Conversely, M1 mean values are slightly higher in late Villafranchian *E. stenonis* from Matassino (Upper Valdarno) and, especially, Olivola (Fig. 8). At the same time, the distal maximum articular width (M11) of the specimen from Pantalla is consistent with the variation expressed by the samples from Saint Vallier, La Puebla de Valverde (*E. stenonis pueblensis*), and Matassino. Similar results have been obtained for the distal MC3 SABAP_UMB 177987 (Fig. 6) and the tibiae SABAP_UMB 167354bis and SABAP_UMB 167364 (Tab. 2).

On the other hand, the sample from Pantalla is distinctly different from European smaller-sized stenonine horses, that is, *Equus* sp. from Senèze, *E. senezensis* aff. *E. senezensis stehlini* from Coste San Giacomo, and *E. stehlini* from Casa Frata (Upper Valdarno). The MT3 SABAP_UMB 337626 is markedly stouter than those from Senèze and Casa Frata (Figs 5c, 8), as confirmed by the analysis of the distal MC3 (Fig. 6a, c). In this regard, it is worth noting that the MC3 of *E. senezensis* aff. *E. senezensis stehlini* from Coste San Giacomo (Palombo et al., 2017) roughly resembles those of the larger individuals of *E. stehlini* from Casa Frata (Fig. 6a).

In summary, the postcranial material from Pantalla shows greater affinity with earlier forms of *E. stenonis* from France (Saint Vallier) and Spain (La Puebla de Valverde), although falling within the range of variation

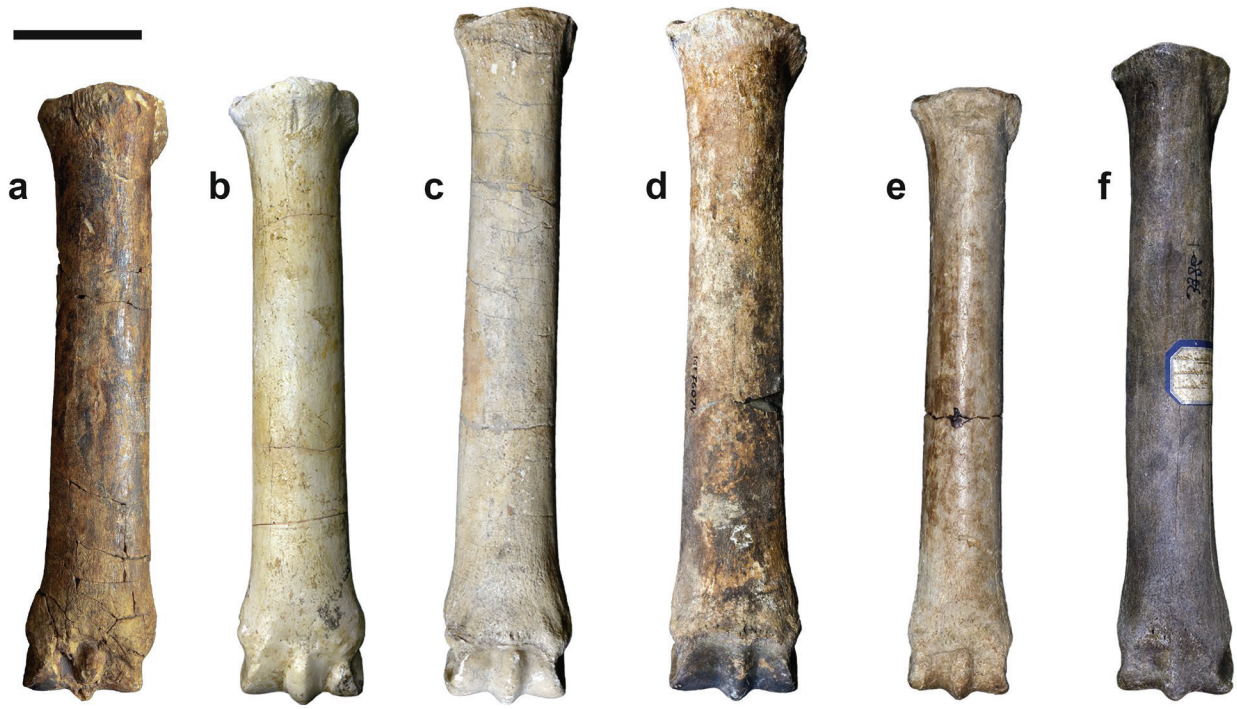

Fig. 8 - (color online) Comparative dorsal views of MT3 of selected Pleistocene equids. a) *Equus stenonis*, right MT3 SABAP_UMB 337626 from Pantalla. b) *Equus stenonis vireti*, left MT3 NHML 20.163489 (reversed) from Saint Vallier (France). c) *Equus stenonis*, right MT3 IGF 11268 from Olivola (Italy). d) *Equus stenonis*, right MT3 IGF 7607V from Matassino (Italy). e) *Equus stehlini*, right MT3 IGF 617V from Casa Frata (Italy). f) *Equus* sp., left MT3 UCBL-FSL 210882 (reversed) from Senèze (France). Scale bar: 5 cm.

of the species as a whole. Conversely, it is clearly distinct from smaller-sized middle-late Villafranchian taxa.

The results of our analysis show that most of the European *E. stenonis* samples (with the exception of *E. stenonis mygdoniensis*; see below) have homogeneous dimensions of the MC3, MT3, and tibia. The combination of these morphometric characteristics supports previous assertions by Forsten (1999) and Palombo & Alberdi (2017) that these forms exhibit intraspecific variation of a single widespread, long-lasting species, and that *E. stenonis* subspecies need to be reconsidered in their taxonomic significance and, ultimately, in their validity.

Biochronology

The age of the Pantalla LFA is currently based only on biochronological evidence. In particular, the co-occurrence of *Canis etruscus*, *Lynx issiodorensis valdarnensis*, *Sus strozzii*, and "*Pseudodama*" *nestii* indicates an early late Villafranchian (~2.1-1.7 Ma) age. The presence of the bovid *Leptobos merlai* suggests that the correlation should be at the lower limit of this time interval (Cherin et al., 2019b).

The results obtained here on the Pantalla horse record offer further confirmation of this biochronological correlation. The analysed postcranial bones from the Umbrian site show clear morphometric similarities with the middle Villafranchian *E. stenonis* records from La Puebla de Valverde (~2.2 Ma; Sinusía et al., 2004), Chilhac (~2.4 Ma), and in particular Saint Vallier (~2.5 Ma). With the exception of a couple of other fragmentary records from central Italy, Saint Vallier is the only other European site where the certain presence of *L. merlai* is reported (Viret, 1954; Cherin et al., 2019b). On the other hand, while taking into consideration the morphological homogeneity found within the "*E. stenonis* group", the Pantalla sample shows significant differences with that from Olivola (~2.0 Ma), which is characterised by its larger dimensions. Moreover, although characterised by fairly similar taxa, the Olivola LFA differs significantly from that of Pantalla in the presence of *Leptobos etruscus* (Falconer, 1868) instead of *L. merlai* (Masini et al., 2013; Cherin et al., 2019b). Therefore, pending the results of ongoing geochronological studies at the site, we suggest that the Pantalla LFA can be correlated with the very beginning of the late early Villafranchian (early MNQ 18), i.e., between the Coste San Giacomo FU (~2.1 Ma; Bellucci et al., 2014) and the Olivola FU.

Biogeography and chronology of E. stenonis *and related forms in Europe*

The transition from the middle to late Villafranchian, which follows the beginning of the Pleistocene by about 0.5 Ma, is characterised by profound changes in the structure of European ecosystems, with the appearance of several new mammalian species. Newcomers of African origin such as the bone-cracking hyena *Pachycrocuta brevirostris* (Gervais, 1850) presage the establishment of European faunal assemblages in which early *Homo* will enter in the late early Villafranchian (Rook & Martínez-Navarro, 2010; Sardella et al., 2018). Alongside these, new Asian taxa enrich the European Early Pleistocene paleodiversity, including the stenonine horses presumably derived from *E. livenzovensis*, among which *E. stenonis* is the most widespread species. During its long natural history in a wide territory (Fig. 9), *E. stenonis* diversifies into numerous populations (some corresponding to the putative "subspecies" introduced in the literature; see above) with slightly different skeletal dimensions/proportions, probably in response to geographical vicariance.

As a matter of fact, the paleontological record suggests that the range of *E. stenonis* may also have extended into Asia and North America, based on its reported occurrences in the Early Pleistocene of Tajikistan (Kuruksai; "*Equus pamirensis*" Sharapov, 1986 in Sharapov, 1986; "*E. stenonis bactrianus*" in Vangengeim et al., 1988; "*E. stenonis pamirensis*" in Forsten, 1999), Kazakhstan (Podpusk; Vangengeim, 1977), China (Fan Tsuan; Azzaroli, 1987), and USA (Glenns Ferry Formation, Idaho; "*E. stenonis anguinus*" in Azzaroli & Voorhies, 1993). However, these scanty records are debated among specialists (Forsten, 1999; Palombo & Alberdi, 2017; Sun & Deng, 2019) and must be observed with caution.

The available data support the first appearance of *E. stenonis* in Europe in the earliest Pleistocene (i.e., at the beginning of the middle Villafranchian; MNQ 16-17 transition), that is, slightly subsequent with the European records of its putative ancestor *E. livenzovensis* (Fig. 9). In particular, worth noting is the sample from Roca-Neyra in the Perrier plateau area, calibrated close to the Plio-Pleistocene boundary (2.58 ± 0.02 Ma; Nomade et al., 2014). The sample includes few lower cheek teeth previously referred to *E.* cf. *stenonis*, reported together with remains of "*Hipparion* sp." (Eisenmann & Brunet, 1973; Guérin, 1996; Palombo & Valli, 2004). Thanks to a recent reappraisal, the equid material from Roca-Neyra has been referred to *E.* cf. *livenzovensis* and *Plesiohipparion* cf. *rocinantis* (Hernández-Pacheco, 1921) (Cirilli et al., 2020a). The co-occurrence of *E.* cf. *livenzovensis* and a hipparionine horse is also reported in the nearly coeval (MNQ 16b) site of Montopoli (Italy; Rook et al., 2017), whereas two younger (MNQ 17) sites, namely Sésklo (Greece) and Gülyazı (Turkey) (Fig. 9), record the presence of *E. stenonis* together with hipparionine horses (*Plesiohipparion* cf. *shanxiense* Bernor, Sun & Chen, 2015 and *Plesiohipparion* aff. *huangheense* [Qiu, Huang & Guo, 1987], respectively). However, while this interesting co-occurrence seems confirmed in the older site of Gülyazı (Bernor & Lipscomb, 1991), Athanassiou (2018) demonstrated that in Sésklo *Plesiohipparion* is found in lower stratigraphic deposits than *Equus*.

Soon after the beginning of the middle Villafranchian, during MNQ 17a (~2.6-2.36 Ma; Nomade et al., 2014), the presence of *E. stenonis* in Europe is broadly confirmed by the abundant records from Saint Vallier (Viret, 1954; Prat, 1964; Eisenmann, 2004) and several Greek sites including Dafneró, Vólax, and the aforementioned Sésklo (Koufos & Kostopoulos, 1993; Koufos & Vlachou, 1997; Athanassiou, 2001), as well as by the slightly younger ones (MNQ 17b; ~2.36-2.13 Ma; Nomade et al., 2014) from Chilhac (Boeuf, 1986) and La Puebla de Valverde (Eisenmann, 1980; Caloi, 1997) (Fig. 9).

By the middle-late Villafranchian transition, *E. stenonis* is found across nearly all of Europe. The greatest concentration of sites with the ascertained presence of this species occurs in the early late Villafranchian

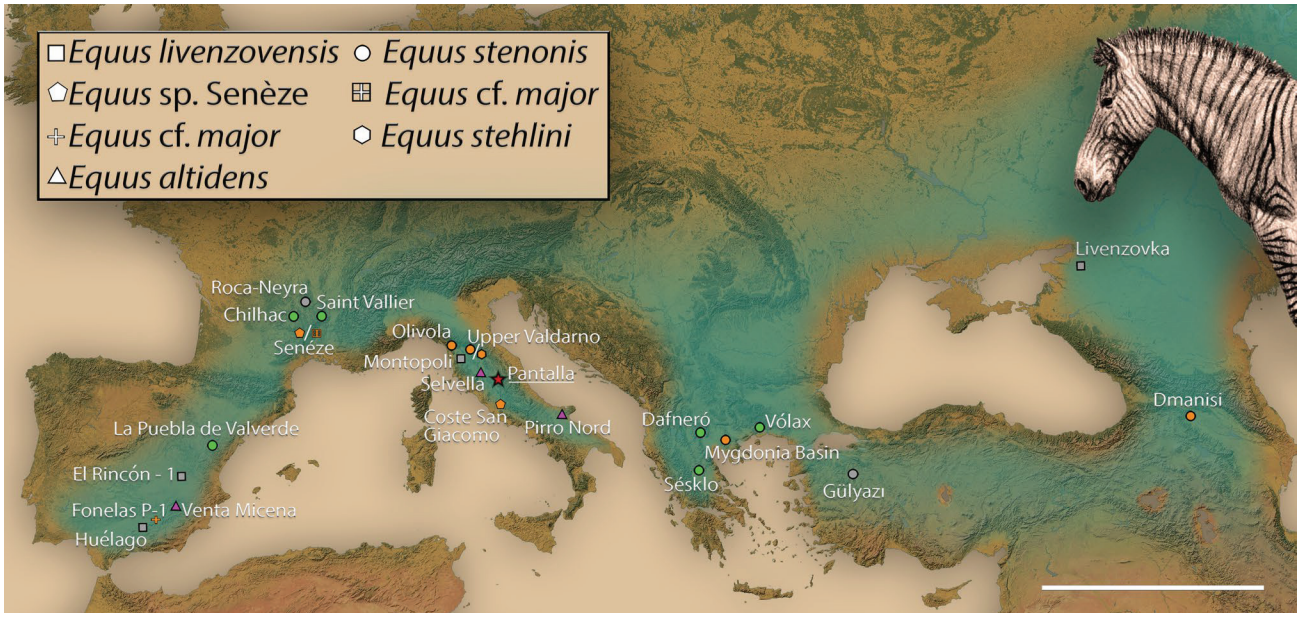

Fig. 9 - (color online) Geographic map of *Equus* dispersion in Europe in the Early Pleistocene, with location of selected paleontological sites. Symbols indicate different taxa (see legend at the top left; the same symbol was used for the middle-sized horses from Senéze and Coste San Giacomo following Alberdi et al., 1998 and Palombo et al., 2017); colors indicate biochronology: grey, early middle Villafranchian (MNQ 16-17 transition); green, middle Villafranchian (MNQ 17); orange, late middle-early late Villafranchian (MNQ 18); pink, late Villafranchian (MNQ 19). Pantalla is marked by a red star. The light blue area in the background indicates the probable geographical range of *E. stenonis* in the Early Pleistocene. At the top right, reconstruction of *E. stenonis* by Mauricio Antón. Scale bar: 1000 km.

(MNQ 18), with particularly well-preserved specimens especially in Italy (e.g., Olivola, Upper Valdarno Basin; Fig. 9). The sample from Pantalla here described is part of this group of horses, and based on biochronological information (see above), it may represent one of the earliest records of *E. stenonis* in Italy (~2.0 Ma). This species is reported in a number of neighboring localities in Umbria (Fig. 1). However, to date, with the exception of Pantalla (this work) and Podere San Lorenzo (Cherin et al., 2019a), no other samples have thus far been studied systematically.

The middle-late Villafranchian transition is also characterised by an important diversification event for stenonine horses in Europe. Parallel to the geographical dispersion of *E. stenonis*, both slenderer and more massive forms appear in the fossil record, both probably derived from a primitive stock related to *E. livenzovensis* (Alberdi et al., 1998; Azzaroli, 2003; Alberdi & Palombo, 2013a; Bernor et al., 2018, 2019). The earliest records of these forms are from the localities of Coste San Giacomo and Senèze (Fig. 9). In the first, Palombo et al. (2017) describe a middle-sized, slender horse attributed to *E. senezensis* aff. *E. senezensis stehlini*. In the second, interestingly, Alberdi et al. (1998) and Palombo & Alberdi (2017) report the co-occurrence of two taxa: the smaller *E. senezensis senezensis* (sensu Alberdi et al., 1998; here named *Equus* sp.) and the larger *E. major*. In the early late Villafranchian, the "slender" lineage is well represented in Italy by *E. stehlini* ("*E. senezensis stehlini*" sensu Alberdi et al., 1998) from the Upper Valdarno (Azzaroli, 1964; De Giuli & Masini, 1986; Bernor et al., 2019). The same species would be present also in Senèze by a nearly complete skeleton, according to Delson et al. (2006). The recent mention of a single incomplete small-sized MT3 from Montecarlo (Italy; ~2.4-2.2 Ma; Ghinassi et al., 2005) with features resembling *E. stehlini* (Bernor et al., 2019), could suggest the appearance of these "slender" forms in Europe in the middle Villafranchian. On the other hand, *E. major* continues to be reported only based on very fragmentary remains, such as those from Chagny (France; Viret, 1954) and Schernfeld (Germany; Musil, 1992). The case of Fonelas P-1 (Fig. 9) is a noteworthy exception. The very rich LFA from this Spanish site is dated at between ~2.0 and 1.8 Ma (relying on biochronological or magnetostratigraphic data, respectively; Arribas et al., 2009) and comprises some exceptionally preserved horse remains (including a complete cranium) referred to *E.* cf. *major* (Garrido, 2008). However, our analyses of postcranial bones (see Morphometric analyses) show that the Fonelas horse clearly differs from *E. major* from Senèze and is actually similar to the primitive *E. livenzovensis*. Moreover, the Fonelas LFA may be older than expected, as it clearly shows middle Villafranchian affinities. Given all this, a revision of this horse collection may account for an interesting late report of an *E. livenzovensis*-like form in southern Europe. Another critical site in this interval is Gerakarou-1 in the Mygdonia Basin (~1.8 Ma; Fig. 9), in which *E. stenonis mygdoniensis* has been described (Koufos, 1992). Our comparisons (see Morphometric analyses) illustrate consistent morphometric differences between this taxon and other samples referred to *E. stenonis*, and clear similarities with slenderer forms such as *E. stehlini* and especially *E. altidens* (already pointed out by Forsten, 1999).

The latest Villafranchian (MNQ 19) marks another important step in European horse evolution, corresponding to the extinction of *E. stenonis*. Beginning at ~1.6 Ma, *E. altidens* becomes the most common stenonine horse in Europe. This species is well represented at Selvella and Pirro Nord (Italy), Cúllar de Baza 1 and Huéscar (Spain;

"*E. altidens altidens*" sensu Alberdi et al., 1998) and at Venta Micena (Spain, "*E. altidens granatensis*" sensu Alberdi et al., 1998; Fig. 9). In Italian localities, *E. altidens* is associated with a second, larger horse, commonly attributed to *E. suessenbornensis* (Alberdi & Palombo, 2013a, b). The available fossil record suggests that both *E. altidens* and *E. suessenbornensis* occur in Europe at least until the early Middle Pleistocene, which represents the period in which the stenonine horses are reported to have become extinct in Europe and replaced by caballine horses (Palombo & Alberdi, 2017). Therefore, as far as current knowledge is concerned, the long natural history of *E. stenonis*, which succeeded *E. livenzovensis* following the earliest Pleistocene, ends in Europe in the middle of the late Villafranchian, ~1.6 Ma. The intriguing claim by Boulbes & van Asperen (2019) concerning the presence of this species in Ceyssaguet (France; ~1.2 Ma) needs further investigation.

CONCLUSIONS

We refer the horse postcranial material from Pantalla to *E. stenonis*. It may represent one of the earliest occurrences of *E. stenonis* in Italy (~2.0 Ma), as well as one of the southernmost certain records along the Peninsula. Our comprehensive morphometric analyses compared the Pantalla sample with a number of horse taxa from the Plio-Pleistocene of North America and Eurasia, as well as with the extant Grévy's zebra. In summary, our results suggest the following conclusions:

1. The derivation of Eurasian stenonine horses from North American *E. simplicidens* and, in turn, the origin of extant African zebras from Plio-Pleistocene stenonine equids (Bernor et al., 2019 and references therein), is supported.

2. Almost all members of the "*E. stenonis* group" (except "*E. stenonis mygdoniensis*") show homogeneous dimensions and Log10 proportions in third metapodials and tibia, suggesting that the detected morphometric differences may be related to normal population variability and vicariance rather than reflecting genuine subspecific taxonomic differences.

3. For some of the European samples analysed, taxonomic questions still persist. In particular, we would welcome the revision of "*E.* cf. *major*" from Fonelas P-1 (which shows clear affinities with *E. livenzovensis*) and "*E. stenonis mygdoniensis*" from the Mygdonia Basin (which seems more similar to *E. altidens*).

The combination of different morphometric analyses on third metapodials reaffirms its value in discriminating *Equus* species (see Eisenmann, 1995), and we hope that this approach can be commonly applied in the future on other fossil samples, starting from the Italian ones in which the presence of *E. stenonis* has yet to be verified.

AUTHOR CONTRIBUTIONS

M.C. and O.C. conceived the study. M.C., O.C., and B.A. collected the data and made the figures. O.C., R.L.B., and M.C. developed the methods and performed the analyses. M.C. and O.C. wrote the manuscript with input from the other authors. All authors contributed equally to develop the ideas, discussed the results, and reviewed the final version of the manuscript.

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