Rivista Italiana di Paleontologia e Stratigrafia
(*Research in Paleontology and Stratigraphy*)
vol. 128(1): 241-265. **March 2022**

EQUUS STEHLINI AZZAROLI, 1964 (PERISSODACTYLA, EQUIDAE). A REVISION OF THE MOST ENIGMATIC HORSE FROM THE EARLY PLEISTOCENE OF EUROPE, WITH NEW INSIGHTS ON THE EVOLUTIONARY HISTORY OF EUROPEAN MEDIUM- AND SMALL-SIZED HORSES

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Associate Editor: David M. Alba.

To cite this article: Cirilli O. (2022) - *Equus stehlini* Azzaroli, 1964 (Perissodactyla, Equidae). a revision of the most enigmatic horse from the Early Pleistocene of Europe, with new insights on the evolutionary history of European medium- and small-sized horses. *Riv. It. Paleontol. Strat.*, 128(1): 241-265.

Keywords: *Equus stehlini*; *Equus stenonis*; Early Pleistocene; Villafranchian; Europe.

Abstract. The present work provides a revision of the complete fossil collection of *Equus stehlini* from the Italian Early Pleistocene (late Villafranchian) of the Upper Valdarno Basin (Tuscany, Italy). The species was originally described in the second half of the last century, even if recent studies questioned its distinct species status, considering it a subspecies of *Equus senezensis* (i.e., *E. senezensis stehlini*). Over the succeeding decades the debate about the taxonomic status of *E. stehlini* extended to its possible evolutionary origin from two different *Equus* species from the European Early Pleistocene, *Equus stenonis* or *E. senezensis*. The revision undertaken here of *E. stehlini*, by means of morphological, morphometric and statistical comparisons, provides new insights into the taxonomic status and the evolutionary history of this enigmatic species. It is concluded that *E. stehlini* is a distinct species derived from the medium-sized *E. senezensis*. This work further highlights new insights and perspectives in the evolutionary framework and in the paleoecological understanding of the medium to small-sized *Equus* species from the early to middle Early Pleistocene of Europe.

INTRODUCTION

Equus stehlini represents one of the most enigmatic European Early Pleistocene horse species. It was described by Azzaroli (1964) based on the holotype cranium IGF563, retrieved from the surroundings of Terranuova in the Upper Valdarno Basin (Italy, Early Pleistocene). Azzaroli (1964) included in the *E. stehlini* hypodigm an incomplete mandibular symphysis from the locality of Fornacelle (Upper Valdarno Basin), housed in the Basel Naturhistorisches Museum, which had been previously published as *Equus* cf. *hydruntinus* (Stehlin & Graziosi 1935; p. 56, fig.13; pl. 6, figs. 1-2; pl. 7, figs. 20a-b). Furthermore, *E. stehlini* has been identified as an important taxon characterizing the faunal assemblage of the Casa Frata site (Upper Valdarno Basin), correlative of the Tasso Faunal Unit, ca. 1.8 Ma (De Giuli & Masini 1986; Rook & Martìnez-Navarro 2010; Bernor et al. 2019; Cirilli et al. 2020a). Indeed, the locality of Casa Frata yielded an important homogeneous equid fossil assemblage represented by teeth and postcranial elements, which has been considered as the *E. stehlini* reference sample (De

Received: June 7, 2021; accepted: September 22, 2021

Giuli & Masini 1986). Interestingly, no remains of *Equus stenonis* have been found from Casa Frata (De Giuli & Masini 1986; Bernor et al. 2019; Cirilli et al. 2020a).

In the last twenty years, new discoveries, especially from the Early Pleistocene (Middle Villafranchian) localities of Senèze (Haute Loire, France), Coste San Giacomo (Anagni Basin, Italy) and Montecarlo (Upper Valdarno Basin), have shed further light on *E. stehlini*. Recent excavations carried out at Senèze (2.2-2.0 Ma, Nomade et al. 2014) yielded an almost complete skeleton, preliminarily referred to *E. stehlini*, figured in Delson et al. (2006: fig. 9) albeit still unpublished in detail and not available to be included within this revision. Furthermore, a new middle to small-sized horse has been reported from Coste San Giacomo (ca. 2.2 Ma, Bellucci et al. 2012, 2014; Florindo et al. 2021), identified as *Equus senezensis* aff. *stehlini* (Palombo et al. 2017). Finally, Bernor et al. (2019) reported a complete third metatarsal of *E. stehlini* from Montecarlo, (ca. 2.2 Ma; Ghinassi et al. 2005; Fidolini et al. 2013), which based on size and shape shows strong affinities with the medium to small-sized horse from Coste San Giacomo and *E. stehlini*.

Besides the limited occurrence in Italy and France, the systematic position and evolutionary relationships of *E. stehlini* have been matter of debate since its discovery, with two main hypotheses. Azzaroli (1964, 1982, 1990, 2003) considered *E. stehlini* a distinct species, closely related to *E. stenonis* and originated from the latter by a cladogenetic process.

An alternative hypothesis was proposed by Alberdi et al. (1998). The authors assessed the species versus subspecies rank for European Early Pleistocene horses using multivariate morphometric analyses based on postcranial elements, including third metacarpals, third metatarsals, calcanea, astragali and proximal phalanges of the central digit. This analysis led these authors to recognize three different subspecies of *E. stenonis* (*E. stenonis vireti*, *E. stenonis guthi*, and *E. stenonis stenonis*) and two subspecies of *E. altidens* (*E. altidens altidens* and *E. altidens granatensis*). Moreover, Alberdi et al. (1998) proposed to elevate to species rank the subspecies *E. stenonis senezensis* Prat, 1964, recognizing two subspecies: *E. senezensis senezensis* from the type locality of Senèze, and *E. senezensis stehlini* from Upper Valdarno Basin. Furthermore, it has been proposed (Alberdi et al. 1998; Alberdi & Palombo 2013a, 2013b; Palombo et al. 2017; Palombo & Alberdi 2017) that *E. senezensis* originated from *E. stenonis*, and that *E. stehlini* would include populations originating from *E. senezensis*.

Recently, Cirilli et al. (2021a) reviewed the European Early Pleistocene *E. stenonis*, providing new insights on the European Early Pleistocene *Equus* species and subspecies. The analyses reported by Cirilli et al. (2021a) indicate that *E. stenonis* is better recognized as a monotypic species, and that its purported subspecies *E. stenonis vireti*, *E. stenonis guthi*, *E. stenonis pueblensis*, *E. stenonis olivolanus* and *E. stenonis stenonis* do not warrant taxonomic distinction at the subspecies rank, merely representing local ecomorphotypes. In contrast, Cirilli et al. (2021a) concluded that *E. stenonis senezensis* should be considered a distinct species (*E. senezensis*), thereby endorsing the Alberdi et al.'s (1998) opinion in this regard. An analogous taxonomic opinion has been held by Bernor et al. (2021) for *E. altidens*, considering that *E. altidens altidens* and *E. altidens granatensis* do not warrant distinction at the subspecies rank and should be merely considered ecomorphotypes of a single monotypic species, *E. altidens*. Furthermore, Cirilli et al., (2021a) and Bernor et al. (2021) concluded that *E. stenonis mygdoniensis* Koufos, 1992 is a junior subjective synonym of *E. altidens*, thus endorsing the preliminary work of Gkeme et al. (2017) and the most recent reappraisal of Koufos et al. (2021) on the Early Pleistocene horses from Libakos and Polylakkos (Wester Macedonia, ca. 1.8 Ma).

The present work provides a revision of the entire *E. stehlini* sample from the Upper Valdarno Basin, with the purpose of clarifying its taxonomy and its possible evolutionary interpretation within the framework of the European Old World *Equus* evolutionary history.

GEOLOGICAL AND PALEONTOLOGICAL FRAMEWORK

The Upper Valdarno Basin is located in the Northern Apennine mountain range and is Plio-Pleistocene in age. It is located 35 km southeast of Florence between the Chianti Mountains and the Pratomagno Ridge (Fig. 1A-C), and it is celebrated since the Renaissance for its outstanding vertebrate fossil record (Fidolini et al. 2013; Rook et al. 2013; Bartolini Lucenti & Rook 2016). Following the lat-

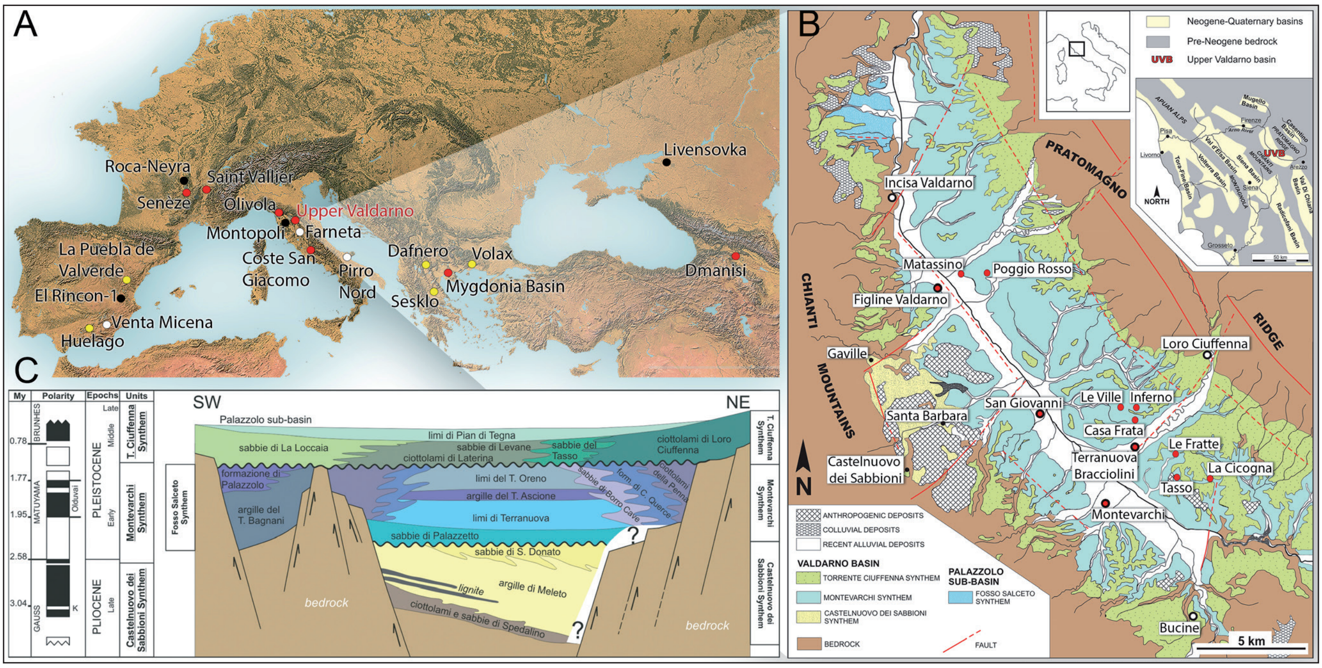

Fig. 1 - Map of the European Early Pleistocene localities (A) with the geological map of the Upper Valdarno Basin (B - C, edited from Fidolini et al. 2013). In fig. 1A, colors refers to the Mammal Neogene - Quaternary Zones (black, MNQ16b; yellow, MNQ17; red, MNQ18; white, MNQ19). In Fig. 1B, red points indicate the fossil localities of the Montevarchi Synthem of the Upper Valdarno Basin, 1.9 - 1.77 Ma. See Supplementary Table 1 for the *Equus stehlini* fossil localities. Figure 1C shows the stratigraphy of the three synthems filling the Upper Valdarno Basin. Figure 1B - C are edited from Fidolini et al. (2013).

est geological reconstruction proposed by Fidolini et al. (2013), the basin is filled by three major synthems, named Castelnuovo dei Sabbioni Synthem, the Montevarchi Synthem and Torrente Ciuffenna Synthem (Fig. 1B and 1C).

The Castelnuovo dei Sabbioni Synthem (CSB, ca. 3.3-2.6 Ma) records the first depositional phases of the basin, characterized by warm to subtropical climate and woodland areas (Fidolini et al. 2013; Bertini 2010, 2013). It is composed of alluvial gravels (Ciottolami di Spedalino, CSBa), lacustrine deposits with lignitiferous levels (Argille di Meleto, CSBb) and fluvio deltaic deposits (Sabbie di San Donato, CSBc).

The Montevarchi Synthem (VRC, ca. 2.6-1.7 Ma) consists of two cycles separated by a minor unconformity surface. The lower portion is characterized by an alluvial setting, including the Ciottolami e sabbie di Caposelvi (VRCa), Sabbie di Palazzetto (VRCb) and Sabbie and limi di Montecarlo (VRCc). In the latter, a tephra layer found at the top of the succession has a reported age of 2.21 ± 0.09 Ma (Ghinassi et al. 2005; Fidolini et al. 2013). The second portion of the Montevarchi Synthem is a fluvial succession deposited in the central portion of the basin (Ghinassi et al. 2013; Fidolini et al. 2013). It is composed of Limi di Terranuova (VRCd), Argille del Torrente Ascione (VRCe) and Limi e Sabbie del Torrente Oreno (VRCf). It records important regional environmental changes driven by the maximum expansion of the northern latitude Eurasian Ice Sheet, reflected in the increase of steppe vegetation and the glacial/interglacial cycles recorded by the pollen record (Bertini 2013).

The Torrente Ciuffenna Synthem (UFF, ca. 0.9-0.5 Ma) is represented by fluvial deposits interdigitated with alluvial fan deposits, composed of Ciottolami di Laterina and Sabbie di Levane (UFFa), and Ciottolami di Loro and Sabbie del Tasso (UFFb). Although not continuous, the magnetostratigraphic record in the Torrente Ciuffenna Synthem apparently documents the Matuyama-Brunhes boundary, indicating an age of the synthem spanning from the late Early Pleistocene to the early Middle Pleistocene (Napoleone et al. 2003; Fidolini et al. 2013).

The *E. stehlini* specimens housed in the Natural History Museum of Florence come from the VRCd, VRCe and VRCf units of the Montevarchi Synthem, in a temporal interval ranging between ca. 1.9 and 1.77 Ma, which can be correlated with the Olivola and Tasso Faunal Units of the Early Pleistocene (late Villafranchian). The fossil locality

Tab. 1 - Plio-Pleistocene and extant *Equus* species from North America, Asia, Europe and Africa used in the comparative analyses.

North America			
Equus simplicidens	Hagerman Horse Quarry, Idaho	3.3 Ma	Own; V. Eisenmann website.
China			
Equus eisenmannae	Longdan	2.55 Ma	Bernor Database
Equus sanmeniensis	Nihewan	Early Pleistocene	V. Eisenmann website
Equus huanghoensis	Nihewan	Early Pleistocene	Li et al. 2016
Europe			
Equus livenzovensis	Livensovka, Russia	2.6 Ma	Forsten 1997; V. Eisenmann website
Equus livenzovensis	El Rincon - 1, Spain	2.58 Ma	Alberdi et al. 1997
Equus major	Livensovka, Russia	2.6 Ma	Forsten 1997; V. Eisenmann website
Equus major	Senèze, France	2.2 - 2.0 Ma	Own
Equus stenonis vireti	Saint Vallier, France	2.45 Ma	Own
Equus stenonis	Olivola, Italy	1.9 Ma	Own
Equus stenonis	Matassino, Italy	1.9 - 1.8 Ma	Own
Equus stenonis mygdoniensis	Gerakarou, Greece	MNQ18	Koufos 1992
Equus stenonis	Upper Valdarno Basin, Italy	1.8 Ma	Own; Cirilli et al. 2020b
Equus senezensis	Senèze, France	2.2 - 2.0 Ma	Own; V. Eisenmann website
Equus altidens	Dmanisi	1.85 - 1.77	Own
Equus altidens	Farneta, Italy	1.6 Ma	Own; Alberdi and Palombo 2013a, b
Equus altidens	Pirro Nord, Italy	1.5 Ma	Own; Alberdi and Palombo 2013a, b
Africa			
Equus koobiforensis	Koobi Fora, Kenya	1.9 Ma	Bernor Database
Equus grevyi	East Africa	0.0 Ma	Own; V. Eisenmann website
Equus quagga spp.	East Africa	0.0 Ma	Own; V. Eisenmann website

of Casa Frata, from which the *E. stehlini* reference sample originates, is located in the surroundings of Terranuova Bracciolini, like the other historical fossil localities of Le Ville, Inferno, Le Fratte, Il Tasso, and La Cicogna where *E. stehlini* is recorded (Supplementary Table 1). Moreover, other fossils of *E. stehlini* have been reported from the surroundings of Montevarchi and Figline Vadarno (Supplementary Table 1; Fig. 1B). The *E. stehlini* specimens from old collections labeled as "Upper Valdarno", without further specification, are confidently referred to the same stratigraphical units VRCd-VRCf, even if an exact locality is not available. Thus far, no *E. stehlini* occurrences have been reported from Matassino and Poggio Rosso. Nevertheless, the incomplete third metatarsal from Montecarlo reported by Bernor et al. (2019) belongs to unit VRCc, dated to 2.21 ± 0.09 Ma (Ghinassi et al. 2005; Fidolini et al. 2013).

MATERIALS AND METHODS

The equid species discussed in the present paper are included in the genus *Equus*, following the most recent cladistic results of Cirilli et al. (2021b), in which *Equus simplicidens* from North America is considered the oldest and most primitive species of the genus.

The *E. stehlini* sample analyzed herein originates from the Early Pleistocene localities from the Upper Valdarno Basin (UVB) (Supplementary Table 1 and Fig. 1). It includes 301 specimens comprising crania, mandibles, teeth and postcranial elements (Supplementary Table 1). The *E. stehini* sample is compared herein with a suite of Late Pliocene-Early Pleistocene fossil horses from North America, Europe, Asia and Africa, and with extant *Equus grevyi* and *Equus quagga*. The list of the species included in the comparative sample is given in Table 1. The *Equus* sample from the Early Pleistocene locality of Senèze is referred here to *E. senezensis*, following Alberdi et al. (1998) and Cirilli et al. (2021a).

Bivariate plots, boxplots, Log10 ratio diagrams and principal component analysis (PCA) are used to analyze the UVB *E. stehlini* sample and compare it with other Early Pleistocene species. Bivariate plots, boxplots and PCA were performed in R Environment v. 1.4.1103 (R Core Team 2013), using the packages *prcomp()* v. 3.6.2 (Venables & Ripley 2008) and *ggplot2()* v. 3.3.3 (Wickham 2016).

PCA were performed on crania, third metacarpal, third metatarsal and anterior proximal phalanges of the central digit, using the parameter scale = T to have a unit variance before starting the analyses in R. Therefore, a permutational multivariate analysis of variance (PERMANOVA) on the PC values of third metacarpals and third metatarsals was performed, using the *pairwiseAdonis()* package v. 0.4 (Martinez-Arbizu 2020) in R, which includes the Bonferroni adjustment method (p.adjust in Supplementary Tables). Third metapodials were chosen because they represent the most discriminant postcranial elements to evaluate similarities or differences in morphology among *Equus* species, so as to identify and quantify the inter- and intraspecific variability shown by extant and fossil species. The PERMANOVA results enable the detection of significant differences in morphology among *Equus* species and samples.

The Log10 Ratio diagrams on third metapodials are based on the log-transformed mean values of the Höwenegg *Hippotherium primigenium* (Bernor et al. 1997). The Höwenegg *H. primigenium* sample represents a well-studied, homogeneous quarry sample of a single species of Equinae, for which the full range of descriptive statistics (mean, standard deviation, confidence limits, and minimum, maximum, and median values) are available for each bone, including the cranium, the mandible, and teeth.

Measurements were taken to the nearest 0.1 mm using a digital caliper, following the international equid measurement guidelines (Eisenmann et al. 1988; Bernor et al. 1997). PCA on crania include the following measurements: M1 (basal length of the muzzle); M2 (palatal length); M3 (vomerine length); M4 (post vomerine length: from the middle of the vomerine notch to basion); M5 (post palatal length, from the base of the palatal spur up to basion); M6 (total basal length of the cranium); M7 (upper premolar row length, P2-P4); M8 (upper molar row length, M1-

M3); M9 (upper cheek tooth row length, P2-M3); M23 (anterior ocular line: from the prosthion to the most external point of the orbital process); M30 (length of the naso-incisival notch: from the prosthion to the back of the narial opening); M31 (cheek length: from the back of the narial opening to the most anterior point of the orbit). Due the incompleteness and fragmentary record of the *E. stehlini* crania from UVB, an average value of most complete crania (IGF563 and IGF582) was used in the PCA, in order to be compared with the entire cranial sample of the Plio-Pleistocene and extant *Equus* species.

The bivariate plot on upper dentition includes M7 and M8 (cranium measurements), whereas the bivariate plot on lower dentition includes M3 (length of premolars) and M4 (length of molars). Boxplots show variability lengths for M9 (upper cheek tooth row length, P2-M3) and M5 (lower cheek tooth row length, p2-m3).

Log10 Ratio diagrams on metapodials include the following measurements: M1 (maximum length); M3 (midshaft width); M4 (depth of the diaphysis at level of M3); M5 (proximal articular width); M6 (proximal articular depth); M7 maximum diameter of the articular facet for the third carpal/tarsal); M8 (diameter for the anterior facet for the fourth carpal/tarsal); M10 (distal maximum supra-articular width); M11 (distal maximum articular width); M12 (distal maximum keel depth); M13 (distal maximum depth of the lateral condyle); M14 (distal maximum depth of the medial condyle).

PCA measurements on metapodials include M1, M3, M4, M5, M6, M10, M11, M12, M14. Measurements 7 and 8 have not been included because of their not significant contribution to the PCAs, whereas M13 has not been considered due its missing data in *Equus eisenmannae* (see Wang & Deng 2011).

The bivariate plot on astragali includes M1 (maximum length) versus M4 (maximum width). PCA on anterior first phalanges of the central digit includes: M1 (maximum length); M3 (minimal width); M4 (proximal maximum width); M5 (proximal maximum depth); M6 (distal articular maximum width).

Anatomical nomenclature and osteological landmarks follow Bernor et al. (1997).

Institutional and Collection Abbreviations

IGF, Museo di Storia Naturale, Sezione di Geologia e Paleontologia, Università di Firenze (Italy); **IVPP**, Institute of Vertebrate Paleontology and Palaeoanthropology, Beijing, (China); **KNM - ER**, Kenyan Natural History Museum, East Rudolf, Nairobi (Kenya); **NHML**, Natural History Museum, Musée des Confluènces, Lyon (France); **NMB**, Naturhistorisches Museum, Basel (Switzerland); **NWUV**, Institute of Cenozoic Geology and Environment, North - West University, (China); **UCBL - FSL**, Université Claude Bernard - 1, Faculté des Science, Lyon (France); **USNM**, United States National Museum of Natural History, Washington D.C., (USA).

Anatomical abbreviations

POF: preorbital fossa; **UTR**: upper cheek tooth row; **LTR**: lower cheek tooth row; **P**: protocone; **I1**: premaxillary first incisor; **I2**: premaxillary second incisor; **I3**: premaxillary third incisor; **P2**: maxillary second premolar; **P3:** maxillary third premolar; **P4**: maxillary fourth premolar; **M1**: maxillary first molar; **M2**: maxillary second molar; **M3**: maxillary third molar; **i1**: mandibular first incisor; **i2**: mandibular second incisor; **i3**: mandibular third incisor; **p2**: mandibular second premolar; **p3**: mandibular third premolar; **p4**: mandibular fourth premolar; **m1**: mandibular first molar; **m2**: mandibular second molar; **m3**: mandibular third molar; **mc3**: third metacarpal; **a1ph3**: anterior first phalanx of the central digit; **2ph3**: second phalanx of the third digit; **3ph3**: third phalanx of the third digit; **ast**: astragalus; **mt3**: third metatarsal; **rt**: right; **lt**: left.

SYSTEMATIC PALEONTOLOGY

Class **MAMMALIA** Linnaeus, 1758
Order **Perissodactyla** Owen, 1848
Family Equidae Gray, 1821
Subfamily Equinae Gray, 1821
Genus *Equus* Linnaeus, 1758

Equus stehlini Azzaroli, 1964

Figs. 2-5

1998 *Equus senezensis stehlini* Alberdi et al., p. 377 ("new rank").
2004 *Allohippus stehlini* Eisenmann, p. S282 (new combination).

Holotype: IGF 563, an incomplete cranium housed at Museo di Storia Naturale, sezione di Geologia e Paleontologia, Florence, Italy (Figs. 2A, B). Previously figured in Azzaroli (1964; pl. II, figs. 2, 2a; pl. III, figs. 2, 2a; pl. IV, fig. 3; pl. V, figs. 4), Palombo & Alberdi (2017; Fig. 4), Bernor et al. (2019; Fig. 5), and Cirilli et al. (2020a; Fig. 6).

Paratype: IGF 582, an almost complete even damaged cranium kept in the Museo di Storia Naturale, sezione di Geologia e Paleontologia, Florence, Italy (Figs. 2C, D). Figured in Azzaroli (1964; pl. III, figs. 3).

Emended Diagnosis: Small-sized monodactyl horse; the smallest one from the Early Pleistocene of Europe in cranial, mandibular, dental, metapodial and phalangeal dimensions. Cranium small and slender, with a deep incision of the nasal notch extending caudally above the maxillary P3 mesostyle; braincase small and flexed downward; faintly delimited POF located high on the maxilla and placed posteriorly, close to the lacrimal bone; facial maxillary crest up to the level of P4 mesostyle. Maxillary cheek teeth with a typically stenonian triangular and short protocone, which becomes longer serially from M1 to M3. Pre- and post-fossettes poorly developed with reduced and square mesostyles. Mandibular cheek teeth with the typically stenonian V-shaped linguaflexid separating the rounded metaconid from the distolingually pointed metastylid; well-developed ectoflexid, deeper in molars than in premolars; elongated anterior border of the preflexid in p3-m3. Short and robust metapodials. Proximal central phalanges short and massive, with a deep and well-developed caudal V-scar for the attachment of the ligamentum sesamoideum obliquum.

Referred material: See Supplementary Table 1.

Type locality: Terranuova, Upper Valdarno Basin (Italy), 1.9–1.77 Ma.

Occurrence: Early Pleistocene (1.9–1.77 Ma, late Villafranchian) of the Upper Valdarno Basin (various localities: Terranuova, Casa Frata, Le Ville, Inferno, Il Tasso, La Cicogna, Figline). Possibly also present at Senèze (2.2-2.0 Ma, France; Delson et al., 2006).

Description

Cranium. The best preserved crania from the Upper Valdarno localities (Supplementary Table 1) are shown in Figure 2. The holotype (IGF563; Figs. 2A-B) has a short and wide snout, with an anteriorly squared incisor arcade and incisors without infindibula due to the high worn degree. The palate is short and wide, and the occlusal morphology of the

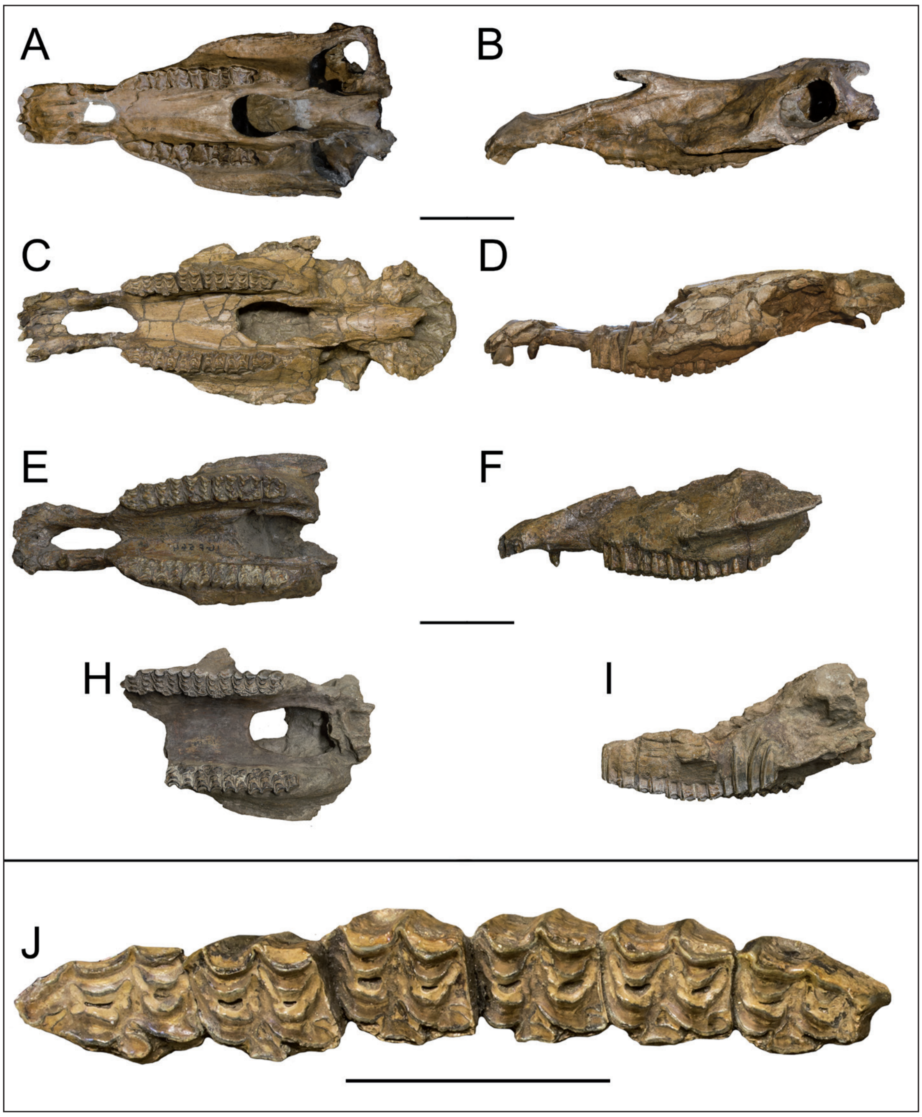

Fig. 2 - *Equus stehlini* crania in ventral and lateral view. A - B) IGF563, *E. stehlini* holotype; C - D) IGF582, *E. stehlini* paratype; E - F) IGF564; G - H) IGF536. Scale bar 10 cm. Figure 2J shows the occlusal morphology of the of the upper cheek teeth in IGF582 (*E. stehlini* paratype.) Scale bar 5 cm.

upper tooth rows is completely obliterated by the high degree of wear, except in M2 and M3, which show simple fossettes ornamentation. The choanae are square and are well preserved; the vomer is placed behind the pterygoid bones and at the medial level of the fossae temporalis, while the basisphenoid is missing. The cranium preserves the complete snout and orbits, while the maxillary bones are crushed, and the posterior braincase is missing. The nasal bones retracted to the level of P3 mesostyle. The preorbital fossa is faintly delimited as a shallow depression at the posterosuperior maxilla level, extending from a inferior-lateral extension of the nasal bone. The facial maxillary crest extends from the P4/M1 level posteriorly to the inferior orbit. The orbit is placed well posterior to M3. The complete upper tooth row is very worn, and the cups are blunt because of the high level of wear.

IGF582 (Fig. 2C-D) is the most complete cranium. It preserves the palate, the upper tooth rows, the choanae and the vomer, whereas the snout, the incisor arcade and the basisphenoid are very damaged (Fig. 2C). The incisor arcade preserves the right I3, showing a closed infundibulum. The palate is short and large, even if medio-laterally deformed. The choanae are round, although deformed on the left side. The vomer is placed behind the pterygoid bones and at the medial level of the fossae temporalis, whereas the basisphenoid is partially preserved, even if the foramen magnum is missing. The ventral occipital bones and the paracondylar processes are heavily damaged, while the occipital condyles are missing. The dorsal aspect of the snout is completely absent from the rostral portion of the maxilla (Fig. 2D). The frontal bones are preserved dorsally, while the orbits are dorso-ventrally deformed. The two

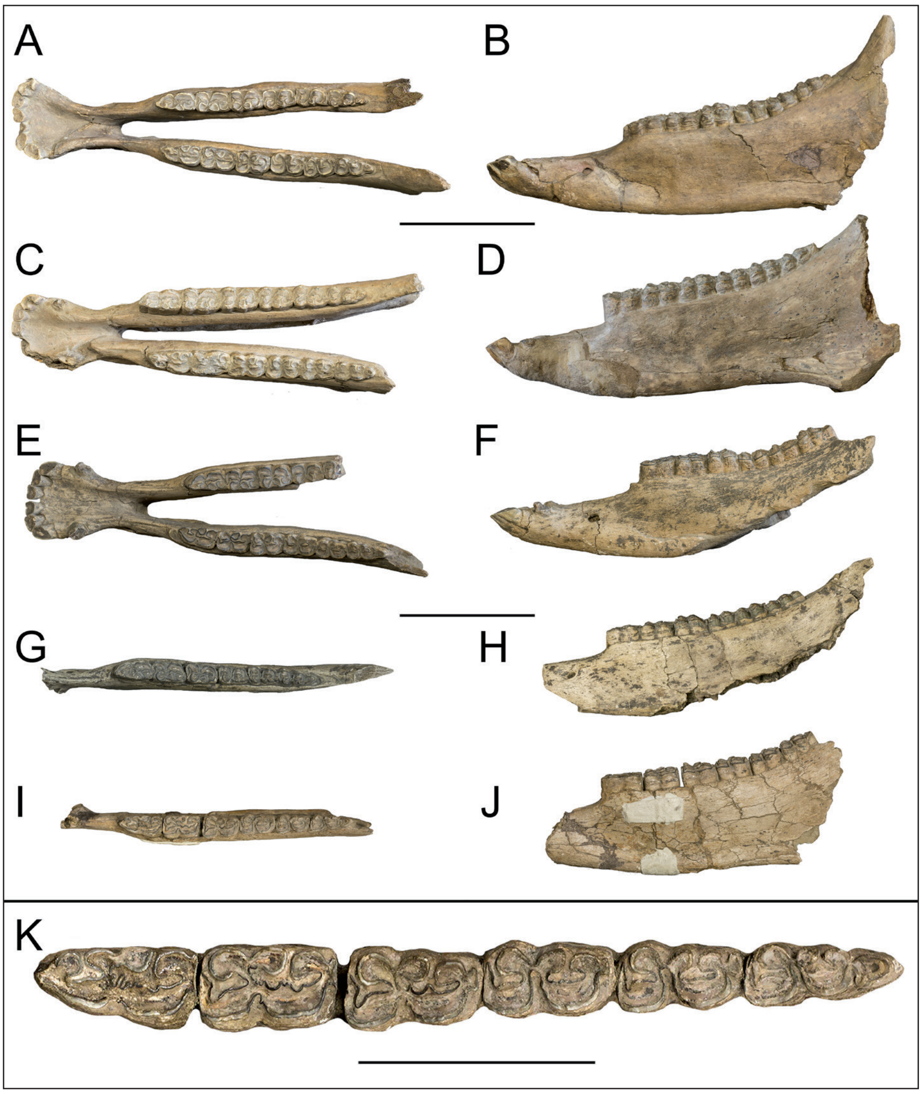

Fig. 3 - *Equus stehlini* mandibles in occlusal and lateral view. A - B) IGF520; C - D) IGF511; E - F) IGF507; G - H) IGF524; I - J) IGF508. Scale bar 10 cm. Figure 2K shows the occlusal morphology of the of the lower cheek teeth in IGF508. Scale bar 5 cm.

zygomatic bones are missing. The braincase is partially preserved, even though the parietal bones are heavily damaged and distorted. The facial maxillary crest is well developed at the P4 level. P2, P3, and P4 are preserved in their anatomical position, with the roots exposed.

IGF564 is an undeformed partial cranium (Fig. 2E-F) preserving the muzzle and the palate. The snout is short and large, as in the holotype, and has an arcuate incisor arcade; no incisors are preserved (Fig. 2E). The palate is short and large (M2 - M13), and the anteriormost borders of the choanae are damaged. Both maxillary tooth rows are preserved, displaying an early stage of wear. The cranium preserves the most rostral portion of the muzzle and the maxillary facial crest, which is strongly developed at the P4 mesostyle level (Fig. 2F). On the right side the complete canine is present.

IGF536 (Fig. 2H-I) is an incomplete and poorly preserved cranium that shows bilateral deformation. It preserves part of the palate, the two upper tooth rows (except for lacking the right P2), and the choanae (Fig. 2H). Maxillary cheek tooth enamel ornamentation exhibits a middle stage of wear. The most anterior fragment of the maxillary facial crest is located at the P4 mesostyle level; P4-M2 have high and rounded parastyle cusps (Fig. 2I).

Maxillary tooth row. The most complete UTR is represented by IGF582 (Fig. 2J). The salient features of P2-M3 are the following. The P2 has a short and blunt anterostyle. All cheek teeth have a reduced and pointed mesostyle. Protocones have the typical stenonian morphology, short and lingually flattened in P2-M3, with the protocone becoming longer from P4 to M3. The protocone is always confluent with the protoloph, being minimal in M3. The pli

Fig. 4 - *Equus stehlini* third metacarpals in cranial and caudal view. A) IGF605V; B) IGF606V; C) IGF609V; D) IGF691; E) IGF11048; F) IGF11047; G) IGF11065; H) IGF11046. Scale bar 10 cm.

caballins are single on all cheek teeth, well developed in the premolars and reduced in the molars. The fossettes are well developed on P2-P4 and M2, while less so on M1 and M3. The hypocone is large and extensive, being distally pointed in premolars and round in molars.

Mandible. The most complete mandibles from the UVB are depicted in Figure 3. They uniformly exhibit the following salient features. The incisor arcade is large and square, with a narrow symphysis (Figs. 3A, C, and E), which in lateral view is elongate and slender (Figs. 3B, F, H, and J). The mental foramen is placed midway between the i3 and the p2. The lower cheek tooth rows are long and slightly curved from p2 to m3; the molar series is short, while the premolars are shorter than in *E. senezensis* and *E. stenonis*. The mandibular ramus, the masseteric fossa and the posterior border of the mandible within the posterior angle are not preserved in any specimen. The mandibular corpus is generally slender, although IGF511 (Fig. 3D) exhibits a massive morphology compared with the rest of the sample.

Mandibular cheek tooth row. The best preserved LTR is represented by IGF508 (Fig. 3K). The mandibular cheek teeth exhibit a morphology similar to that of *E. stenonis*, being characterized by the following features. The p2 has a short, blunt anterostylid; the metaconid is rounded and the metastylid is pointed distally; the linguaflexids are uniformly V-shaped, a feature diagnostic of stenonian horses. The ectoflexid is very shallow in the p2, reduced in the p3 and p4, and deeper in the molars, invading the preflexid-postflexid isthmus. The preflexid is reduced in the p2 and larger in p3-m3, with an anteriorly elongate and labially extensive margin. The postflexid is longer in p2-p4, with a complex ornamented morphology, whereas it is more regular and shallower in the molars. The m3 hypoconulid is round, large, and well separated from the hypoconid.

Third metacarpal. The mc3 has a short, massive morphology as compared with *E. stenonis,* with a reduced maximal length and a cranio-caudally flat morphology, due to the large proximal and distal epiphyses and diaphysis (Fig. 4). However, its general aspect resembles a typical stenonian mc3 morphology, being even narrower. The proximal end has large articular facets for the second and fourth metacarpal, and a flat articular surface for the magnum; the distal epiphysis has a large medial and lateral protuberance, with a wide medial and lateral trochlea and a well-developed crista sagittalis in between. The *E. stehlini* mc3s have minimum range of variation, as shown in Fig. 4. Nevertheless, some individuals (IGF 11047, Fig. 4F) appear more gracile than the record from the Upper Valdarno Basin.

Fig. 5 - *Equus stehlini* third metatarsals in cranial and caudal view. A) IGF611V; B) IGF612V; C) IGF613V; D) IGF617V; E) IGF1608V; F) IGF10992; G) IGF11012; H) IGF11032. Scale bar 10 cm.

Third metatarsal. The mt3 is short and robust, due the large proximal and distal epiphyses and the wide circular diaphysis. The proximal end is round, flattened on the caudal side, with large articular facets for the second and fourth metatarsal. The distal epiphysis has small medial and lateral protuberances, which are not larger than the medial and lateral trochleae. The latter are round, with a well developed crista sagittalis in between. As for mc3s, the mt3s resemble *E. stenonis* in general morphology, being even narrower (Fig. 5). Furthermore, the *E. stehlini* mt3s from Upper Valdarno Basin show a homogeneous range of variation, even if some appear to be more gracile (Figs. 5 G-H).

Astragalus. The astragalus is massive and displays small medial and lateral trochleae and a large medial tuberculum tali for the attachment of the ligamentum collaterale. The trochlear groove is large; the articular facet for the navicular is faintly curved and wide, with a reduced fossa synovialis (Figs. 6A-D).

Proximal phalanx of the central digit. The proximal phalanx of the central digit is short and wide, with a large diaphysis. It has a typical stenonian shape. The proximal epiphysis is large and in dorsal view it shows a sinuous profile of the proximal end, whereas in caudal view it has a wide posterior border for the attachment for the ligamentum collaterale, being connected with the deep V-scar for the attachments of the ligamentum sesamoideum obliquum. The distal end is large, with well developed supra-articular lateral protuberances (Figs. 6E-H).

RESULTS

Morphometrical comparison

The PCA results comparing the mean of the *E. stehlini* crania from UVB with a suite of Pliocene, Pleistocene and extant *Equus* crania from Eurasia and Africa are reported in Figure 7. PC1 accounts the 78% of the total variance and clusters species by maximum cranial lengths (M6) from negative to positive values (less to more elongate), whereas PC2 represents 8.2% of the total variance and separates species mostly for M4 and M5 from positive to negative values (less to more elongate) (Figure 7A; the loadings are reported in Supplementary

Fig. 6 - *Equus stehlini* astragali in cranial and caudal view. A) IGF688V; B) IGF11352; C) IGF IGF11354; D) IGF IGF11362. *Equus stehlini* anterior first phalanges of the central digit in cranial and caudal view. E) IGF688V; F) IGF11320; G) IGF IGF11325; H) IGF IGF11332.

Table 2). These results have relevant implications for the Early Pleistocene horses from Eurasia. In particular, *E. stehlini* is well clustered compared to any other fossil species, being distinct from the medium-sized species *E. senezensis*, *E. altidens* from Dmanisi and *E. stenonis mygdoniensis* (Gerakarou-1, Mygdonia Basin, Greece). The European *E. stenonis* sample plots close to *E. koobiforensis* and the large *E. grevyi*, whereas *E. simplicidens* is clustered away from the European and African samples due to its small M4 values. *Equus senezensis* shows an intermediate variability range between *E. simplicidens*, *E. stenonis* and *E. grevyi* due to its reduced size. The species *E. huanghoensis* from the Early Pleistocene of China plots close to the *E. simplicidens* range of variation, whereas *E. sanmeniensis* falls close to *E. eiesenmannae*. In turn, PC3 accounts the 5.1% of the total variance and separates species for M30 (length of the naso-incisival notch) from positive to negative values (more to less elongate) and M31 from positive to negative values (less to more elongate) (Figure 7B; loadings are reported in Supplementary Table 2). These results agree with those based on PC2 and PC1 (Fig. 7A), where *E. stehlini* is well clustered away from any other Early Pleistocene species, and it remains well separated from the medium sized horses *E. senezensis*, *E. altidens* (Dmanisi) and *E. stenonis mygdoniensis*. Interestingly, in both diagrams, *E. stehlini* plots close to but outside ranges of variation of *E. quagga* and *E. quagga boehmi* .

Bivariate plots and boxplots of the upper and lower dentition are reported in Figure 8. In particular, Figure 8A compares the length of P2-P4 (M7) versus that of M1-M3 (M8). *Equus stehlini* exhibits the shortest dimensions among the entire sample, and the largest specimens do not overlap the smallest *E. senezensis* specimens. The *E. stehlini* holotype (IGF563) has the smallest dimensions due its advanced stage of wear. Two *E. altidens* specimens from Pirro Nord show intermediate dimensions between *E. stehlini* and *E. senezensis*. *Equus senezensis* mainly exhibits intermediate dimensions between the *E. stenonis* from Upper Valdarno Basin and the smaller *E. altidens* and *E. stehlini*, and overlaps the small to medium-sized *E. grevyi* specimens. The *E. stenonis vireti* range of variation includes the *E. stenonis* samples form Olivola, Matassino and Upper Valdarno Basin (inclusive of the *E. stenonis* holotype), and it is plotted between the *E. simplicidens* range of variation and the largest specimens of *E. grevyi*. Two specimens from Senèze (UCBL-FSL210993 and NMB336) fall within the *E. stenonis* range of variation. *Equus stenonis mygdoniensis* is the smallest sample among *E. stenonis* subspecies and falls within the *E. senezensis* variation range. *Equus livenzovensis* plots within the largest specimens of *E. simplicidens*, whereas the Chinese species *E. eisenmannae* shows the greatest M7 and M8 measurements.

Figure 8B, in turn, plots mandibular maximum length of premolars (M3) versus maximum length of molars (M4). As in Figure 8A, *E. stehlini* is the smallest species. Its largest individuals plot close to the smallest specimens of *E. senezensis*, including *E. stenonis mygdoniensis* and *E. altidens* from Pirro Nord. *Equus stenonis vireti* plots between *E. simplicidens* and the largest specimens of *E. grevyi*, and overlaps the

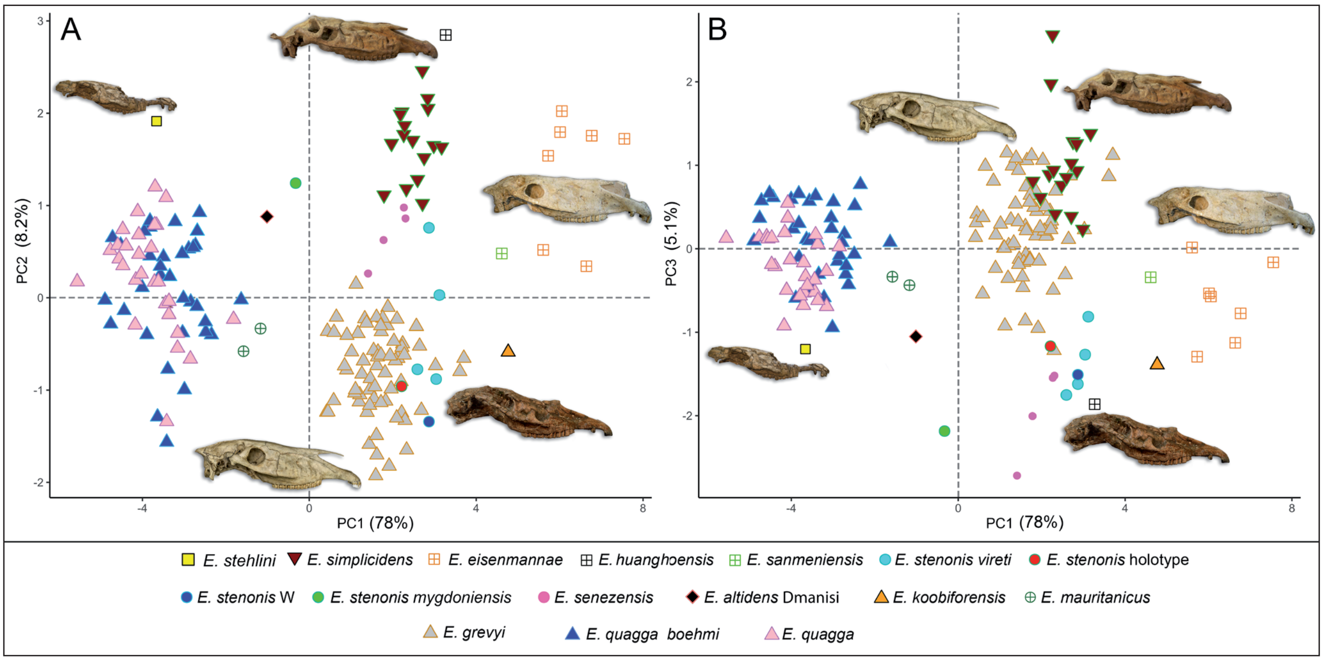

Fig. 7 - Principal component analysis comparing *Equus stehlini* with a suite of fossil Pliocene, Pleistocene and extant crania. Due the incompleteness of the *Equus stehlini* crania from the Upper Valdarno Basin, the values plotted represent the mean of the total cranial specimens studied and reported in Supplementary Table 1. The PC components and the loadings distribution are reported in Supplementary Table 2.

E. stenonis samples from Olivola and Upper Valdarno Basin. *Equus senezensis* is intermediate between the European *E. stenonis* and the smallest *E. stehlini* and overlaps the *E. grevyi* specimens. *Equus livenzovensis* is larger than *E. stenonis vireti*, and overlaps with the lower measurement range of *E. eisenmannae*.

Finally, Figures 8C-D provide boxplots of the maximum lengths for maxillary and mandibular cheek teeth rows, respectively. In both graphs, *E. stehlini* is the smallest species, with its largest specimens close to the smallest ones of *E. altidens* (Fig. 8C). In lower dentition (Fig. 8D), *E. stehlini* is likewise smaller than *E. senezensis* and *E. altidens*, and even more distinct from the larger European *E. stenonis* and *E. grevyi*.

The results for Log10 ratio diagrams on mc3 for the European Early Pleistocene horses are depicted in Figure 9A-D. In particular, Figure 9A shows the *E. stehlini* sample with maximum, mean and minimum values compared with the Italian *E. stenonis* mean of Matassino and Olivola. Interestingly, the *E. stehlini* trajectory is almost identical to that of *E. stenonis*, even if consistently smaller across all dimensions (maximum, mean and minimum measurements). Both species have a robust general morphology, marked by the M1-M3 pattern, and large proximal and distal widths (M5-M6 and M10-M12, respectively). As previously reported for cranial elements (Fig. 8), a slight size overlap between the larger *E. stehlini* specimens and the smallest *E. senezensis* is found also in the mc3, being *E. senezensis* intermediate between *E. stenonis* and *E. stehlini* (Figs. 9A-B). Compared with the European middle Villafranchian record (Fig. 9C), *E. senezensis* aff. *stehlini* shows similar features to *E. stehlini* and *E. senezensis*. Albeit short in its maximum length, the medium-sized horse from Coste San Giacomo has a robust morphology similar to that of *E. senezensis*, due to the dimensions and morphology of the mid-shaft diaphysis, of the proximal end and distal epiphyses (M3-M4, M5-M6 and M10-M12). Finally, compared to the Georgian and Italian *E. altidens*, *E. stehlini* presents a remarkably different morphology, mostly due to its reduced maximal length (M1) and the overall slenderness shown by the *E. altidens* samples (M1-M3, Fig. 9D).

Figure 10A-D displays results for Log10 ratio diagrams on mt3 for the European Early Pleistocene horses. The results are similar to those for the mc3s, with *E. stehlini* showing a pattern close to that of *E. stenonis*, albeit smaller and with relatively smaller depth of the distal epiphysis (M13-M14, Fig. 10A). Compared with *E. senezensis*, the largest *E. stehlini* specimens overlap the horse from Senèze, although *E. senezensis* is overall intermediate between *E. sten-*

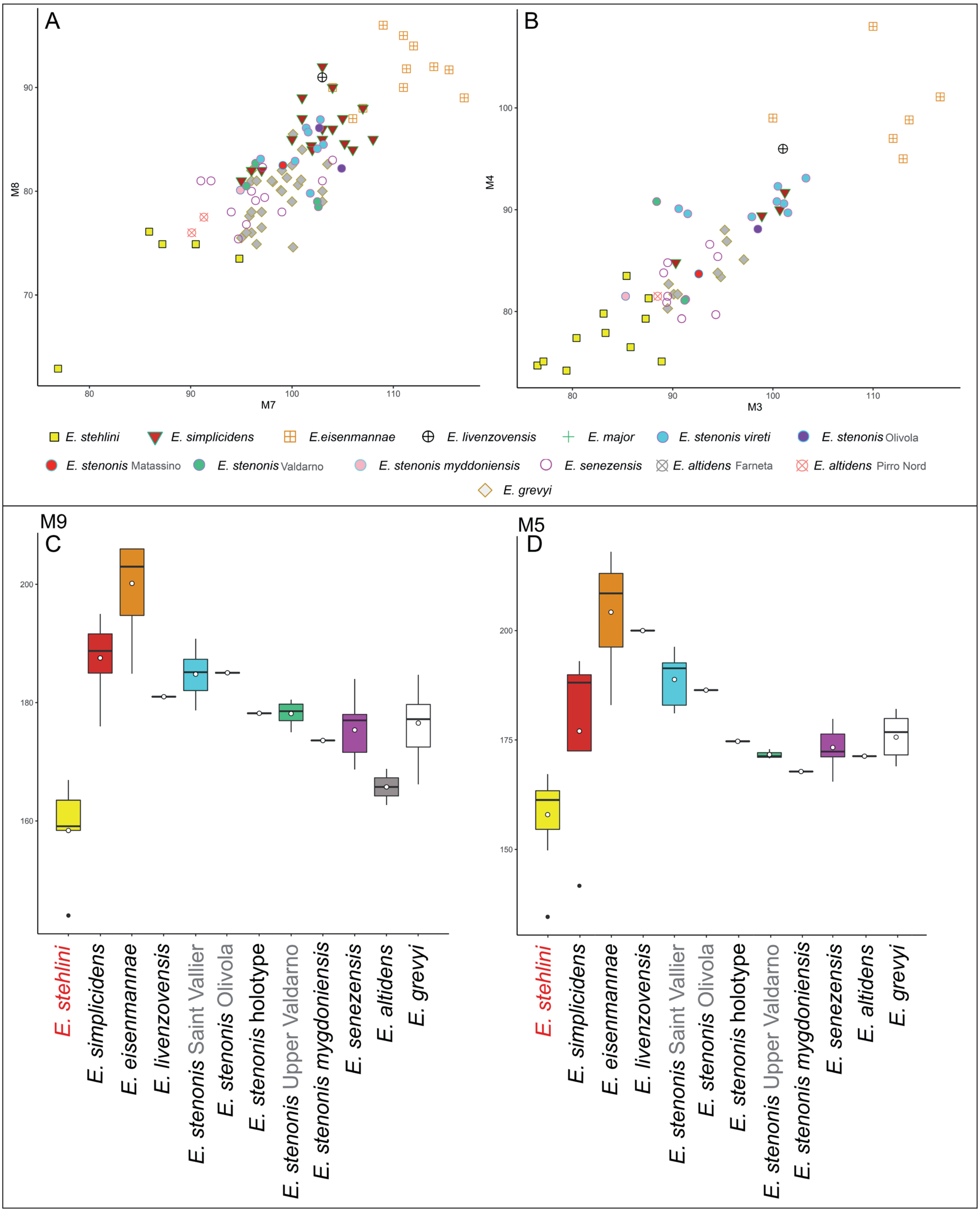

Fig. 8 - Bivariate plots comparing the *Equus stehlini* premolar and molar rows length in upper (A) and lower (B) dentition with a suite of fossil Pliocene and Pleistocene, and extant species. Boxplots comparing the *Equus stehlini* upper (C) and lower (D) cheek tooth row length the with a suite of fossil Pliocene and Pleistocene North America, Chinese and European species and with the extant *Equus grevyi*. Boxplots include minimum, median, mean, and maximum values with 25th and 75th percentile of each sample.

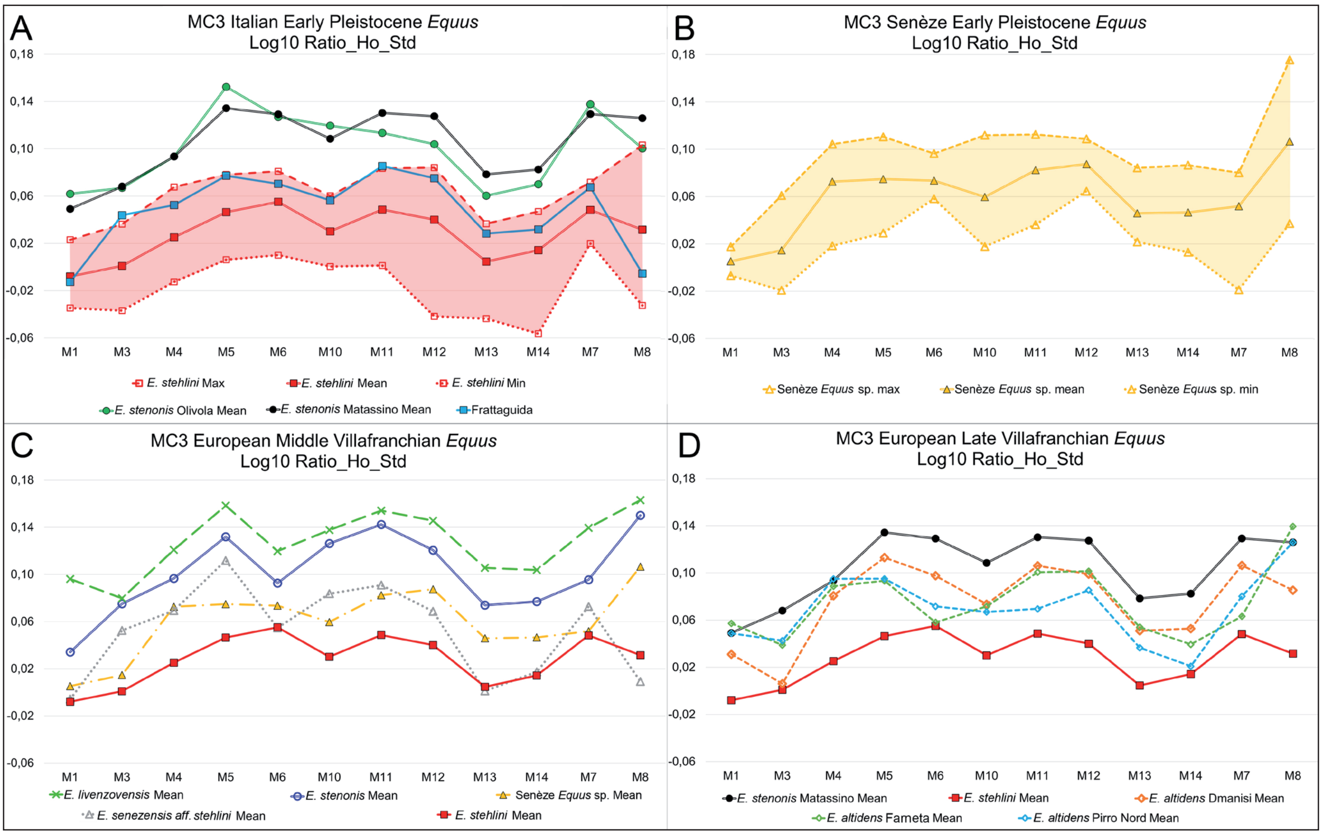

Fig. 9 - Log10 ratio diagrams in third metacarpal based on the Log10 transformed mean of the *Hippotherium primigenium* sample from Höwenegg (Germany, Late Miocene). A) *Equus stehlini* variability from Uppper Valdarno Basin reported in maximum, mean and minimum values, compared with the *E. stenonis* mean samples of Olivola and Matassino (Upper Valdarno Basin). B) *Equus senezensis* variability from the Early Pleistocene of Senèze (France) reported in maximum, mean and minimum values. C) *Equus stehlini* mean compared with a suite of middle Villafranchian *Equus* species, including *E. livenzovensis* (Liventsovka), *E. stenonis* (Saint Vallier), *E. senezensis* (Senèze) and *E. senezensis* aff. *E. senezensis stehlini* (Coste San Giacomo). D) *Equus stehlini* mean compared with a suite of late Villafranchian *Equus* species, including *E. stenonis* (Matassino), *E. altidens* (Dmanisi), *E. altidens* (Farneta) *and E. altidens* (Pirro Nord).

onis and *E. stehlini* (Figs. 10A-B). Compared with the middle Villafranchian equid record, *E. stehlini* is the smallest species, even close to *E. senezensis*. However, the incomplete specimen from Montecarlo is plotted between *E. senezensis* and *E. stehlini*, even if its incomplete pattern more closely resembles that of *E. senezensis* than the typical one of *E. stehlini*. (M3-M6, M7-M8, Fig. 10C). *Equus major* (Senèze) is the largest species, even larger than *E. livenzovensis*, and displays an overall heavy-built morphology and dimensions (Fig. 10C). As reported for the mc3s, the Georgian and Italian *E. altidens* are more slender and show overall larger dimensions than *E. stehlini* (Fig. 10D).

The PCA results for mc3 and mt3 are reported in Figure 11. In the case of mc3, PC1 and PC2 account for 83.5% of the total variance (PC1 = 74.2%; PC2 = 7.3%; Figure 11). The loading distribution is reported as an inset in Fig. 11A and in Supplementary Table 2 within the variance components. PC1 separates species by maximum length from negative to positive values (more to less elongate), whereas PC2 denotes a more slender morphology from negative to positive values. *Equus stehlini* is well separated from the rest of the sample due to its a short and flat mc3 morphology. As reported in the Log10 Ratio diagrams (Figs. 9A-B and 10A-B), the largest specimens of *E. stehlini* overlap the smallest ones of *E. senezensis*. The latter species falls between *E. stenonis* and *E. stehlini*, suggesting a possibly different cluster from the European *E. stenonis* variability. Interestingly, the Coste San Giacomo horse plots close to the *E. senezensis* range of variation. The slender *E. altidens* in part overlaps *E. senezensis*, *E. stenonis mygdoniensis* and *E. grevyi*, well separated from *E. stehlini*. The European *E. stenonis* samples (Saint Vallier, Olivola, Matassino and Upper Valdarno Basin) overlap with one another, showing a remarkable intra- and interspecific variability among the large samples analyzed. Compared with *E. stenonis*, the Hagerman *E. simplicidens* sample displays similar length dimensions but

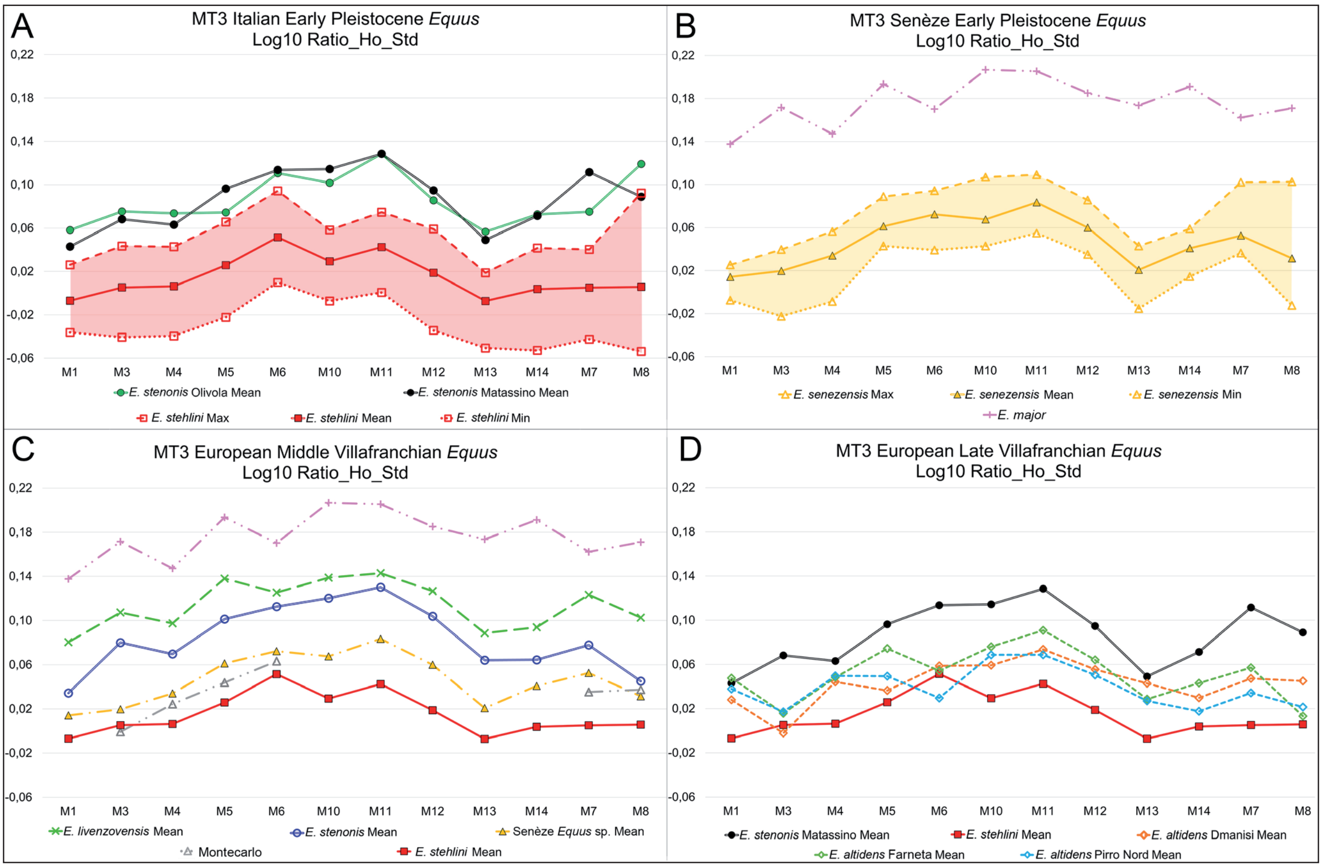

Fig. 10 - Log10 ratio diagrams in third metatarsal based on the Log10 transformed mean of the *Hippotherium primigenium* sample from Höwenegg (Germany, Late Miocene). A) *Equus stehlini* variability from Upper Valdarno Basin reported in maximum, mean and minimum values, compared with the *E. stenonis* mean samples of Olivola and Matassino (Upper Valdarno Basin). B) *Equus senezensis* variability reported in maximum, mean and minimum values with the single *Equus major* mt3 from the Early Pleistocene of Senèze (France). C) *Equus stehlini* mean compared with a suite of middle Villafranchian *Equus* species, including *E. livenzovensis* (Liventsovka), *E. stenonis* (Saint Vallier), *E. senezensis* (Senèze), *E. major* (Senèze), and Montecarlo (Upper Valdarno Basin). D) *Equus stehlini* mean compared with a suite of late Villafranchian *Equus* species, including *E. stenonis* (Matassino), *E. altidens* (Dmanisi)*, E. altidens* (Farneta) *and E. altidens* (Pirro Nord).

it is slightly more slender and overlaps the *E. grevyi* sample. *Equus eisenmannae* and *E. livenzovensis* exhibit longer dimensions when compared with *E. simplicidens* and *E. stenonis*, whereas *Equus major* is the largest species.

In the mt3 PCA, PC1 and PC2 account for 83.5% of the total variance (PC1 = 77.6%; PC2 = 5.9%; Figure 11B). The loading distribution is reported as an inset in Fig. 11B and in Supplementary Table 2 within the variance components. PC1 separates species by maximal length from negative to positive values (less to more elongate), whereas PC2 denoted a more slender morphology from negative to positive values. As in the mc3 PCA (Figure 11A), *E. stehlini* is well separated from the rest of the sample and shows a narrow and massive mt3 morphology. Herein, the largest *E. stehlini* specimens overlap the smallest *E. senezensis* and the *E. altidens* samples. *Equus senezensis* still falls in an intermediate position between *E. stenonis* and *E. stehlini*, whereas *E. stenonis mygdoniensis* shows a more slender morphology. The European *E. stenonis* samples (Saint Vallier, Olivola, Matassino and Upper Valdarno Basin) overlap in their range of variation (Fig. 11A). Interestingly, the Hagerman *E. simplicidens* and the extant *E. grevyi* completely overlap, showing no morphometric differences. *Equus eisenmannae* and *E. livenzovensis* exhibit again longer dimensions when compared with *E. simplicidens* and *E. stenonis*, whereas *E. major* remains the largest equid species from the European Early Pleistocene.

A bivariate plot of M1 (maximum length) versus M4 (maximum width) for the astragalus is reported in Figure 12A. These results support the previous interpretations based on cranial and other postcranial elements. *Equus stehlini* is the smallest species analyzed, albeit with a remarkable overlay with *E. stenonis mygdoniensis* and the Italian *E. altidens* (Pirro Nord).

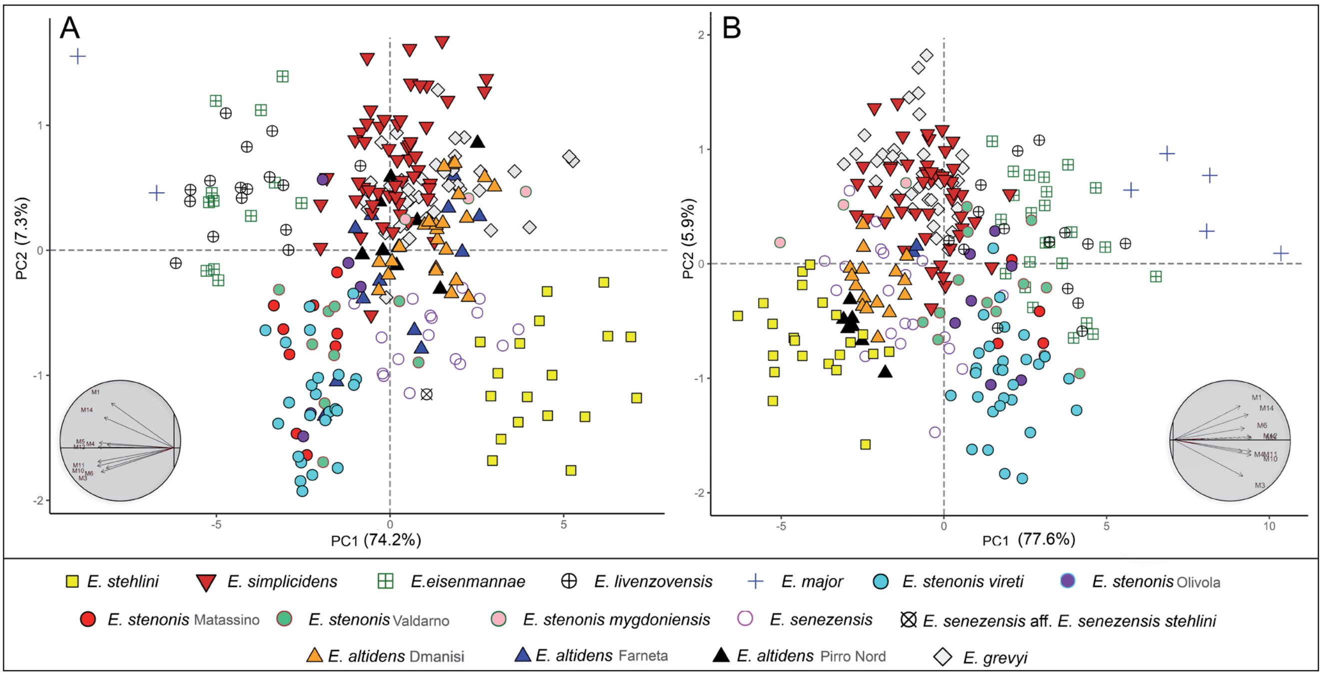

Fig. 11 - Principal component analysis on third metacarpal (A) and third metatarsal (B), comparing *Equus stehlini* with a suite of fossil Pliocene, Pleistocene, and extant species. The loadings distribution are shown as an inset in both diagrams and reported in Supplementary Table 2, whereas the complete PC components are given in Supplementary Table 2.

Furthermore, the largest specimens of *E. stehlini* show similar dimensions to the smallest ones of *E. senezensis*, while the horse sample from Coste San Giacomo shows intermediate dimensions between *E. stehlini* and *E. senezensis*. *Equus stehlini* is well separated from the larger European *E. stenonis*, while *E. senezensis* overlaps the smallest *E. stenonis*, *E. simplicidens*, and the smallest extant *E. grevyi*. The largest *E. stenonis* specimens from Saint Vallier and Upper Valdarno Basin show morphometric affinities to *E. livenzovensis* and *E. eisenmannae*, whereas *E. major* is the largest species.

The PCA results for anterior the anterior 1ph3s (see Material and methods for the dimensions included in the analysis) are depicted in Figure 12B. PC1 and PC2 account for the 89.8% of the total variance (PC1 = 81.7%; PC2 = 8.0%). The loadings' distribution is reported as an inset in Fig. 12B and in Supplementary Table 2 within the variance components. PC1 separates species by maximum length from negative to positive values (less to most elongate), whereas PC2 is indicative of relative slenderness from negative to positive values. The results are consistent with those for mc3 and mt3, with *E. stehlini* being clustered separately from all the Early Pleistocene species due to its small and wide dimensions. *Equus senezensis* is placed between *E. stehlini* and the European *E. stenonis*, while *E. altidens* shows a more slender morphology, clustering with *E. simplicidens* and the extant *E. grevyi*. *Equus eisenmannae* and *E. livenzovensis* display a more elongate and larger morphology when compared with *E. simplicidens* and *E. stenonis*, whereas *E. major* remains the largest of the European Early Pleistocene species.

Analysis of variance in *Equus stehlini* and other European species of *Equus* from the Early Pleistocene

To test for significant differences between *E. stehlini* and other European Early Pleistocene *Equus* species (*E. stenonis*, *E. senezensis* and *E. altidens*), a permutational multivariate analysis of variance (PERMANOVA) was undertaken on the PC values on mc3s and mt3s (Table 2 and Supplementary Table 3). For both mc3s and mt3s, the PERMANOVA results indicate significant differences between *E. stehlini* and the European *E. stenonis* samples from Saint Vallier, Olivola, Matassino and Upper Valdarno ($p < 0.05$), as well as relative to *E. senezensis* ($p < 0.05$) and the Italian *E. altidens* samples (Table 2). Significant differences are also found in the mt3s ($p < 0.05$) between *E. stehlini* and *E. altidens* (Dmanisi), as well as between *E. stehlini* and *E. senezensis,* whereas no significant differences are found between *E. stehlini* and Italian *E. altidens*.

Third Metacarpal

pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted
E. stehlini vs *E. altidens* Dmanisi	1	116,686954	80,1410804	0,6670581	9,999E-05	0,0119988
E. stehlini vs *E. altidens* Pirro Nord	1	132,277639	55,5554046	0,66489301	9,999E-05	0,0119988
E. stehlini vs *E. altidens* Farneta	1	109,210151	58,4351076	0,70036594	9,999E-05	0,0119988
E. stehlini vs *E. senezensis*	1	94,6593184	46,6718648	0,58580108	9,999E-05	0,0119988
E. stehlini vs *E. stenonis*	1	284,64953	164,957731	0,86839177	9,999E-05	0,0119988
E. stehlini vs *E. stenonis mygdoniensis*	1	18,9346021	8,28246729	0,30358205	0,00619938	0,74392561
E. stehlini vs *E. stenonis* Olivola	1	197,966151	104,183537	0,81915898	0,00019998	0,0239976
E. stehlini vs *E. stenonis* Upper Valdarno	1	215,247196	104,827308	0,80743651	9,999E-05	0,0119988
E. stehlini vs *E. stenonis vireti*	1	457,577439	346,908458	0,89661637	9,999E-05	0,0119988

Third Metatarsal

pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted
E. stehlini vs *E. altidens* Dmanisi	1	39,7217693	35,6775799	0,45346565	9,999E-05	0,01049895
E. stehlini vs *E. altidens* Pirro Nord	1	9,16507185	7,13370613	0,1777485	0,00979902	1
E. stehlini vs *E. altidens* Farneta	1	18,8272713	12,8397418	0,31439332	0,00209979	0,22047795
E. stehlini vs *E. senezensis*	1	79,7288844	44,5637487	0,4920705	9,999E-05	0,01049895
E. stehlini vs *E. stenonis*	1	143,689145	100,804998	0,77065097	9,999E-05	0,01049895
E. stehlini vs *E. stenonis mygdoniensis*	1	5,43818827	3,23929756	0,10047668	0,07079292	1
E. stehlini vs *E. stenonis* Olivola	1	213,711906	160,44895	0,81674628	9,999E-05	0,01049895
E. stehlini vs *E. stenonis* Upper Valdarno	1	266,419947	147,257962	0,79061298	9,999E-05	0,01049895
E. stehlini vs *E. stenonis vireti*	1	493,618364	403,924547	0,8782409	9,999E-05	0,01049895

Tab. 2 - PERMANOVA results performed on third metacarpal and third metatarsal PC values comparing *Equus stehlini* with the European Early Pleistocene *Equus* species. The complete results of the analysis is reported in Supplementary Table 3 (SOM Tab. S3).

These results support the PCA results based on postcranial elements, by distinguishing *E. stehlini* from *E. stenonis*, *E. senezensis* and *E. altidens*. However, the statistical results for the mt3s indicate no significant differences in the shape of the third metatarsal among medium- to small-sized equids. Indeed, in the mt3 PCA (Fig.11B), the Italian *E. altidens* sample overlaps with the largest *E. stehlini*, whereas these species are well separated in mc3 PCA (Fig. 11A). A similar result can be observed also for *E. simplicidens* and *E. grevyi*. Although they slightly overlap in their mc3 range of variation, no morphological differences can be found for the mt3s (Fig. 11B and Supplementary Table 3). These results suggest that mt3s are less diagnostic than mc3s, with the latter being more promising for taxonomic purposes based on postcranial morphometric analyses.

DISCUSSION

The present revision on the complete *E. stehlini* sample from the UVB provide new insights on the middle to small horse of the European pre-Olduvai local faunas assemblages (LFAs).

Equus stehlini taxonomy and systematics

Since its original description by Azzaroli (1964), the systematic and evolutionary history of *E. stehlini* has been extensively debated (Azzaroli 1964, 1982, 1990, 1992, 2003; Alberdi et al. 1998; Alberdi & Palombo 2013a, b; Palombo et al. 2017; Palombo & Alberdi 2017; Bernor et al. 2019; Cirilli et al. 2020a; Cirilli et al. 2021c), not only regarding its taxonomic rank (species or subspecies) but also to its evolutionary origin. Two hypotheses have been proposed:

i) Azzaroli (1964, 1982, 1990, 1992, 2003) considered *E. stehlini* to be a distinct species from other Early Pleistocene *Equus*, being directly derived from *E. stenonis* by a cladogenetic process. However, Azzaroli (1990) noted that *E. stehlini* shares some morphological features with *E. senezensis* (the medium size horse from Senèze), such as the deep narial notch, the shape of the diastema, the presence of shallow preorbital pit in the lateral morphology of the cranium and the tooth morphology. These characters represent typically stenonian plesiomorphies.

ii) Alberdi et al. (1998) considered *E. stehlini* a subspecies of *E. senezensis* (*E. senezensis stehlini*), proposing that *E. senezensis* originated from *E. stenon-*

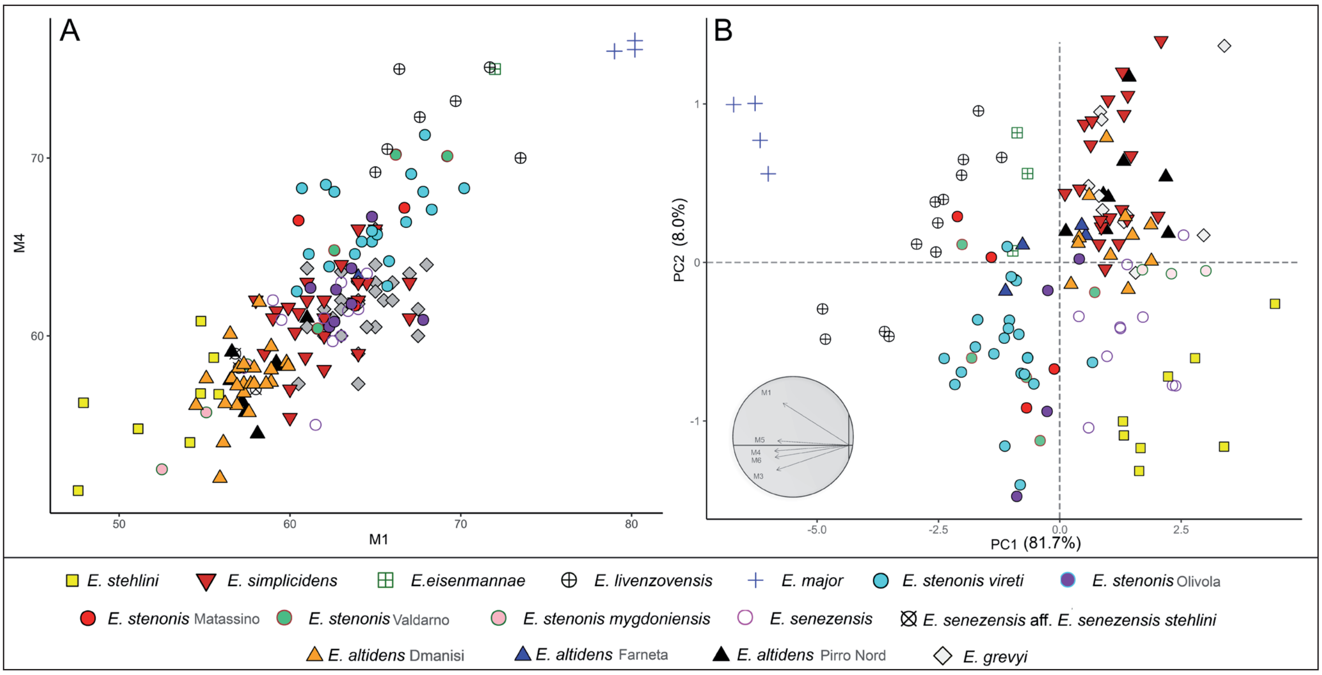

Fig. 12 - Bivariate plots for astragalus (A) comparing maximum length (M1) versus maximum width (M4) and principal component analysis on anterior first phalanx of the central digit (B). The *Equus stehlini* sample is compared with a suite of fossil Pliocene, Pleistocene, and extant species. The loadings distribution of the PCA on the anterior first phalanx of the central digit are shown as an inset in Fig. 12B and reported in Supplementary Table 2, whereas the complete PC components are given in Supplementary Table 2.

is, and that *E. senezensis stehlini* may have originated from local population of *E. senezensis* (Alberdi et al. 1998; Palombo et al. 2017).

The results provided here, based on the analysis of both cranial and postcranial elements, give further insight to evaluate further these two competing hypotheses. Both cranial and postcranial analyses (Figs. 7-12), despite using different comparative samples, provide congruent results supporting that *E. stehlini* is distinct from the other European Early Pleistocene species of the pre-Olduvai LFAs, being also well separated from the post-Olduvai medium-size and slender species *E. altidens*. This conclusion is further supported by the PERMANOVA results, which indicate the presence of significant differences between *E. stehlini* and other European Early Pleistocene species (Table 2 and Supplementary Table 3).

Nevertheless, in all plots given here *E. stehlini* appears closest to *E. senezensis*, instead of *E. stenonis* or *E. altidens*. Albeit the large size of some anatomical elements that place some individuals of *E. altidens* within the *E. stehlini* variability (metatarsals), the Log10 Ratio diagrams and the PCA show a stout and robust postcranial morphology in the *E. stehlini*, even if small in dimensions, which indicate remarkable similarities to *E. senezensis*. Interestingly, in both mc3 and mt3 Log10 Ratio diagrams, the *E. stehlini* pattern is the typical of *E. stenonis*, and different from the slender morphologies shown by the *E. altidens* samples. This is also reflected in the PCAs, wherein the *E. stehlini* sample is closest to that of *E. senezensis*. Furthermore, similar result have previously been found using multivariate analyses of dental features (Cirilli et al. 2021c: figs. 9-11), leading to the conclusion that *E. stehlini* is most closely related to *E. senezensis*.

These results support Azzaroli's (1964) original recognition of *E. stehlini* as a distinct species instead of a subspecies of *E. senezensis*. At the same time, the results given herein also support Alberdi et al.'s (1998) evolutionary hypothesis that *E. stehlini* originated from populations of *E. senezensis* instead of the larger *E. stenonis*.

Evolution and paleobiogeography of medium-sized horses in the European Early Pleistocene

The evolutionary history of monodactyl horses in Europe is characterized by the dispersal of the genus *Equus* from North America, represented by the large species *E. livenzovensis*. The species dispersed from Eastern to Western Europe, occurring at the base of the Pleistocene (ca. 2.6 Ma) in the localities of Liventsovka (Russia), Montopoli (Italy), Roca-Neyra (France) and El-Rincón 1 (Spain) (Alberdi et al. 1997, 1998; Azzaroli 2000; Bernor et al. 2018, 2019; Rook et al. 2019; Cirilli et al. 2021a, 2021b, 2021c). The first occurrence of *E. stenonis* corresponds to the middle Villafranchian of Saint-Vallier in France (2.45 Ma, Nomade et al. 2014). This species dispersed and diversified into different populations/ecomorphotypes in the circum Mediterranean area (Palombo & Alberdi, 2017; Cirilli et al. 2020a, 2021a; Cherin et al. 2021). During the middle and late Villafranchian, throughout its geographic range, *E. stenonis* co-occurs with other species of different size, such as *E. major* (the largest species of the genus from the Early Pleistocene of Europe; Saarinen et al. 2021) and *E. senezensis*, which is characterized by a medium size and a typical stenonian morphology but smaller than *E. stenonis*.

The medium to small-sized horses from the time span comprised between 2.5 and 1.8 Ma deserve further discussion from a paleobiogeographic viewpoint. Recent studies on the middle Villafranchian localities of Senèze (France) and Coste San Giacomo (Italy) have shown the presence of a medium-sized horse (Delson et al. 2006; Palombo et al. 2017). The new discovery of a horse in Coste San Giacomo (2.2 Ma, Bellucci et al. 2012, 2014; Florindo et al. 2021), referred to *E. senezensis* aff. *stehlini* by Palombo et al. (2017), has re-opened the discussion on the dispersal of European medium-sized horses before 2.0 Ma. In particular, it has demonstrated for the first time the occurrence of a close relative of *E. senezensis* outside the type locality of Senèze. Recent geochronological analyses on the Anagni Basin have provided an age of 2.23 ± 0.032 Ma for Coste San Giacomo (Florindo et al. 2021), which is almost identical to the age of the oldest stratigraphical levels from Senèze (2.21 ± 0.02 Ma, Nomade et al. 2014). Bernor et al. (2019) further reported the occurrence of a horse close in morphology and dimensions to *E. stehlini* from the locality of Montecarlo in the Upper Valdarno Basin, biochronologically and radiometrically dated between 2.4 and 2.2 Ma (Ghinassi et al. 2005; Fidolini et al. 2013). Although poorly represented, the Log10 Ratio diagrams reported in Figs. 9-10 indicate that these horses from Italy are slightly larger than average *E. stehlini* from the Upper Valdarno Basin, and may be considered more related to *E. senezensis* than to *E. stehlini*. Nevertheless, this observation should be regarded as tentative, pending the discovery and the study of additional material form these localities. If the occurrence of *E. stehlini* at Senèze (as provisionally reported by Delson et al. 2006) is confirmed, it would extend its biochronologic range at least up to 2.0 Ma.

At present, the record of *E. stehlini* is restricted to the Upper Valdarno Basin, during a time span constrained between 1.9-1.77 Ma. As reported in Cirilli et al. (2020a), some localities in the Upper Valdarno Basin show the co-occurrence of *E. stehlini* and *E. stenonis*. Both species have been reported from the fossil localities of Terranuova, Il Tasso, Le Ville and Figline, which are included in the late Villafranchian stratigraphical units VRCd, VRCe and VRCf of the Upper Valdarno Basin (Azzaroli 1982; Cirilli et al. 2020a, 2021a). The co-occurrence of these species at some fossil localities of the UVB was already observed by Azzaroli (1982), who postulated that, even if both species might have shared the same habitat, they did not occur sympatrically. Nevertheless, the new results reported here support the hypothesis that *E. stenonis* and *E. stehlini* might have overlapped in their habitat ranges. A pattern of co-occurrence of a large and a small-sized species has also been documented from other Early Pleistocene fossil localities, such as Senèze, Dmanisi, Mygdonia Basin and Pirro Nord (Koufos 1992; Delson et al. 2006; Alberdi 2010; Alberdi & Palombo 2013a, b; Bernor et al. 2019; Saarinen et al. 2021; Bernor et al. 2021; Cirilli et al. 2021a).

The possible occurrence of *E. stehlini* in younger deposits of central Italy was discussed by Forsten (1999), who referred the middle to small-sized horses from the Italian localities of Farneta and Pirro Nord to *E. stehlini*, thereby suggesting a longer biochronologic range for this species in the late Early Pleistocene. However, Alberdi & Palombo (2013a, b) referred these occurrences to *E. altidens*, which is supported by the analyses provided herein.

The European medium-sized horses of the late Early Pleistocene underwent a turnover circa 1.8 Ma. Bernor et al. (2021) recognized the first occurrence of *E. altidens* in the paleoanthropological site of Dmanisi (1.85-1.76 Ma), predating the first *E. altidens* occurrences of Farneta and Pirro

Nord. *Equus altidens* would appear to be the most geographically widespread species in the late Early Pleistocene, sharing its habitat with the last representatives of *E. stenonis* and the earliest representatives of *E. suessenbornensis* (Alberdi & Palombo 2013a, b; Palombo & Alberdi 2017; Cirilli et al. 2020a; Bernor et al. 2021; Cirilli et al. 2021a).

Paleoecology of middle-sized horses from the European pre-Olduvai Local Faunal Assemblages

Traditionally, medium-sized horses have been associated with open environments, while medium-sized and slender horses have been related to open and arid landscapes (Eisenmann 1985; Alberdi et al. 1998; Palombo et al. 2017; Palombo & Alberdi 2017; Saarinen et al. 2021; Bernor et al. 2021). The presence of the medium-sized horse *E. senezensis* in southern France and possibly Italy by 2.2-2.0 Ma has been related to the geographic expansion of open country environments with the association of some wooded environments (Palombo et al. 2017). This hypothesis is further supported a by palynological data from Senèze (Delson et al. 2006) and from the Upper Valdarno Basin (Bertini 2010, 2013). The progressive reduction in size along the evolutionary lineage *E. stenonis*–*E. senezensis*–*E. stehlini* may be interpreted as an adaptive response to changing ecological conditions, due to the emergence of open environments across the circum-Mediterranean area between the Gelasian and Calabrian stages (Suc & Popescu 2005; Bertini 2010, 2013; Bellucci et al. 2014; Magri et al. 2017; Palombo et al. 2017). *Equus senezensis* and *E. stehlini* preserve the typically stenonian morphology of the maxilla, mandible and third metapodial, the latter having a massive and stout shape even if reduced in their dimensions. On the other hand, the third metapodial morphology of the aforementioned species differs from that of *E. altidens*, which has overall more slender metapodials compared with *E. stenonis, E. senezensis* and *E. stehlini.* A similar morphology can be recognized also in proximal phalanges. The postcranial evidence for *E. senezensis* and *E. stehlini* suggests an adaptation to increasingly open landscapes, even if not arid, as those recognized in the post Olduvai LFAs of Dmanisi, Pirro Nord and Venta Micena, where *E. altidens* occurs (Arribas & Palmqvist 1999; Messager et al. 2010; Kahlke et al. 2011; Alberdi & Palombo 2013a, b; Bernor et al. 2021; Koufos et al. 2021).

Recent meso- and microwear analyses on herbivorous communities from the middle Villafranchian of Europe corroborate the interpretations above. Strani (2020) has shown that heterogeneous feeding behaviors among the middle Villafranchian ungulates support the idea of different landscapes, with a mosaic of biomes spanning from wetlands to woodlands to open habitats. Paleoenvironmental reconstructions also indicate more humid environmental conditions in the central Italian regions than in Southeastern Europe (Strani et al. 2018, 2019; Strani 2020), and may have been more similar to those of Central Europe during the middle Villafranchian. The herbivorous guild from the Greek locality of Sésklo supports this reconstruction, showing a diverse community of grazers and mixed feeders with a prevalence of grazing behavior (Rivals & Athanassiou 2008; Strani 2020). At present, no equid remains similar to *E. senezensis* or *E. stehlini* have been found in Greece, whereas the possible occurrence in some localities of the Mygdonia Basin (ca. 1.8 Ma) of the medium-sized horse *E. altidens*, well adapted to open and arid environments, has been suggested (Koufos 1992; Forsten 1999; Gkeme et al. 2017; Cirilli et al. 2020a, 2021a; Bernor et al. in 2021; Koufos et al. 2021).

No occurrence of fossil remains similar to *E. senezensis* or attributable to *E. stehlini* have been reported from the Iberian Peninsula, where the last European occurrence of hipparionin horses is possibly recorded by *Plesiohipparion rocinantis* from Villarroya (ca. 2.2 - 2.0 Ma; Pueyo et al. 2015), although this interpretation is not shared by other scholars, which have challenged this correlation based on faunal evidence, correlating Villarroya to Mammal Zone MNQ16 (Azanza et al. 2016; Cirilli et al. 2021c). Also in the Iberian Peninsula is recorded the last occurrence of *E. livenzovensis* (Huelago, MNQ 17) and possibly Fonelas P-1 (ca. 2.0 Ma; Alberdi et al. 1997, 1998; Arribas et al. 2009; Palombo & Alberdi 2017; Cherin et al. 2020; Cirilli et al. 2021a, 2021c). In turn, *E. stenonis* is reported from La Puebla de Valverde (ca. 2.1 Ma, Madurell-Malapeira et al. 2014), whereas Venta Micena marks the first occurrence of *E. altidens* in the Iberian Peninsula (ca. 1.6-1.4 Ma; Madurell-Malapeira et al. 2014; Palombo & Alberdi 2017).

The evidence summarized above may support a paleobiogeographic connection between the Italian and Central European middle Villafranchian localities, where the medium-sized *E. senezensis* occurs.

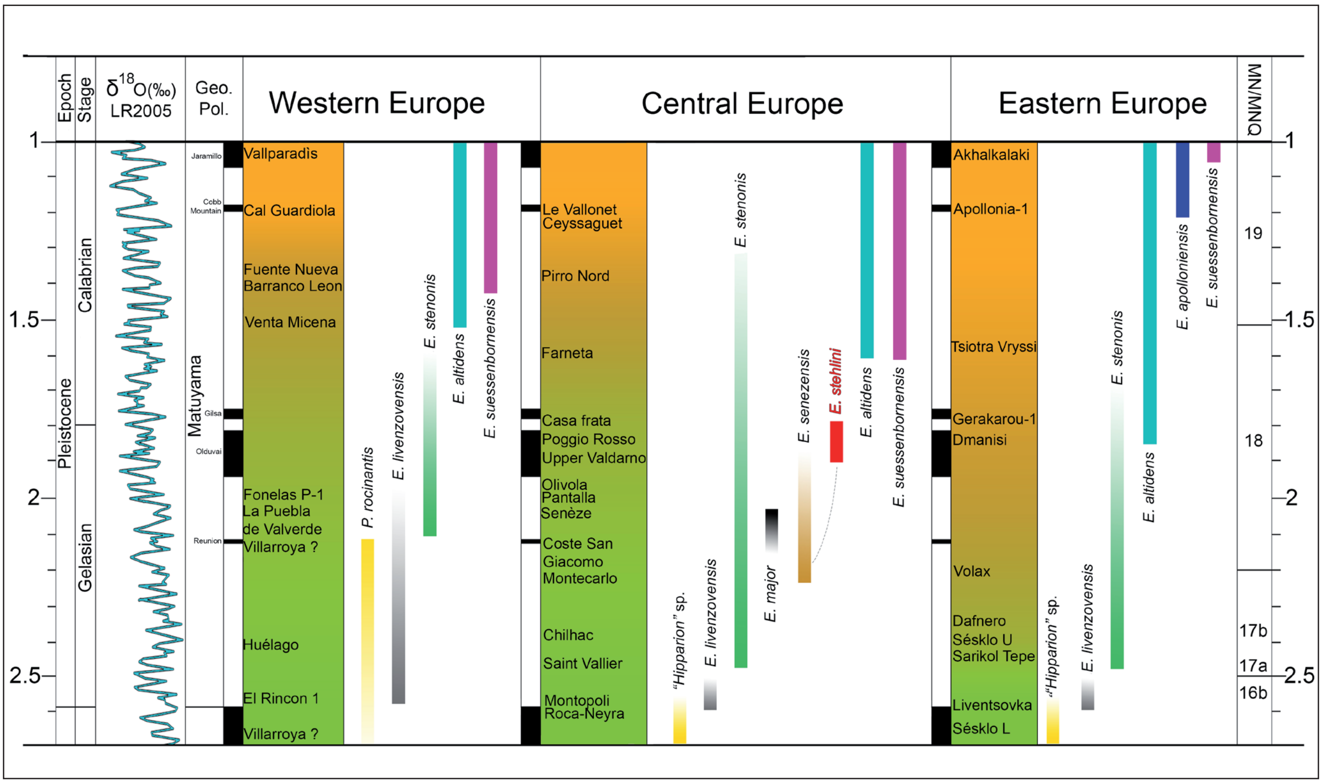

Fig. 13 - New biochronology scheme of the Early Pleistocene *Equus* in Eastern, Central and Western Europe. Eastern Europe includes localities from the Caucasus, Turkey and Greece, Central Europe includes localities from France and Italy, and Western Europe includes localities of the Iberian Peninsula. Localities are included in a green to orange columns, representing the increasing of aridity in each regional area during the Early Pleistocene. Paleoenvironmental interpretations are based on reconstructions of several published papers as Suc and Popescu (2005), Rivals & Athanassiou (2008), Rook & Martínez-Navarro (2010), Messager et al. (2010), Bertini (2010, 2013), Kahlke et al. (2011), Nomade et al. (2014), Magri et al. (2017), Strani et al. (2018, 2019, 2020), Saarinen et al. (2021), Florindo et al. (2021), Bernor et al. (2021).

This result is also supported by the new dates for these European middle Villafranchian localities, ca. 2.2 Ma. From this perspective, *E. stehlini* may have originated from populations of *E. senezensis* by a progressive size reduction and habitat overlap with the widespread *E. stenonis*. A complete overview of the *Equus* species from the European Early Pleistocene is depicted in Figure 13.

E. stenonis, E. senezensis and *E. stehlini*. A progressive speciation process?

The *E. stenonis*–*E. senezensis*–*E. stehlini* evolutionary lineage provides some interesting insights into the speciation process of these taxa. As recently demonstrated by Cirilli et al. (2021a), the European *E. stenonis* subspecies (*E. stenonis vireti*, *E. stenonis guthi*, *E. stenonis pueblensis*, *E. stenonis olivolanus* and *E. stenonis stenonis*) are better recognized as different ecomorphotypes of a single species, considering *E. stenonis* as a monotypic but polymorphic species (i.e., with different ecomorphotypes but not distinct subspecies), supporting the preliminary hypotheses by Alberdi & Palombo (2013a) and Palombo & Alberdi (2017). Indeed, these authors highlighted the high inter- and intraspecific variability among them. These purported subspecies were based largely on size and on dimensions of the postcranial elements, while the most recent morphometric analyses (Cirilli et al. 2021a) on cranial and postcranial elements have shown a homogeneous range of inter- and intraspecific variability among the *E. stenonis* populations separated in time and space (e.g. the *E. stenonis* sample from Saint Vallier, dated to 2.45 Ma, and the UVB sample, dated to 1.9–1.77 Ma, which overlap in their metric ranges of variability), thus failing to validate the discrimination of different subspecies based upon morphometric traits. Furthermore, similar conclusions are reached based on estimated body masses, according to which all the European *E. stenonis* populations are constrained within a restricted range of variation, indicating a smaller size than in *E. livenzovensis*, *E. major* and *E. suessenbornensis*, but larger than observed in *E. senezensis*, *E. stehlini* and

E. altidens (Cirilli et al. 2021a). Indeed, the statistical tests performed here on both the multivariate morphometric analyses and the body mass estimates failed to show significant differences among these alleged *E. stenonis* subspecies (Cirilli et al. 2021a). When considering morphometric traits, Cirilli et al. (2021a) concluded that the European *E. stenonis* is better recognized as a monotypic species (without distinguishable subspecies but multiple ecomorphotypes), in which different populations show a large variability. The differences in mean body mass of *E. stenonis* broadly correspond to the net primary production estimates (NPP), with larger sizes concentrated in the Western European sites that have higher NPP values, and smaller sizes found in Southeastern European sites where open and savanna-like paleoenvironments are found, with herbivorous taxa being predominantly grazers and mixed-feeders.

In contrast, *E. senezensis* and *E. stehlini* cannot be synonymized with *E. stenonis*. In particular, the morphometric results provided herein and in Cirilli et al. (2021a) support the distinction of *E. senezensis* from *E. stenonis* populations at the species rank, both on the basis of cranial and postcranial elements, even though it preserves a distinctly stenonian morphology. The same conclusions have been reached in the present study regarding the *E. stehlini* sample from the UVB, which is distinct from any other Early Pleistocene *Equus* sample on morphometric grounds.

Mayr (1951, 1963) developed the peripatric speciation model, whereby marginal peripheral isolated populations undergo character displacement that lead to speciation. Peripatric speciation is a distinct component of the allopatric speciation model, together with the vicariance model (Harrison 2012). The vicariance definition was formulated by Croizat (1958) and today is recognized as the most common model of speciation, and the primary model in allopatric speciation (Howard 2003; Harrison 2012). The vicariance model applies when populations of geographically broadly distributed species are isolated by geographic or environmental barriers which impede gene flow, leading to speciation (Crips et al. 2011; Harrison 2012). Vicariant barriers can influence the distribution of species populations (Lieberman 2000; Coyne & Allen Horr 2004; Harrison 2012; Lawson et al. 2015). Contrary to the vicariance model, the peripatric model refers to new species that originate from a peripheral population of a more broadly distributed species (Coyne & Allen Horr 2004; Lawson et al. 2015). Mayr (1951, 1963) postulated that the most distinct isolated species are always found along its marginal range and that new species should often still be either allopatric to the species from which they have diverged, or just barely overlapping in their range (Mayr 1963, p. 496).

The *E. stenonis*–*E. senezensis*–*E. stehlini* lineage agrees well with this speciation model. The initial vicariant speciation event may have involved some peripheral isolated populations of the broadly distributed *E. stenonis*, which would have given rise to *E. senezensis* in Central Europe. As discussed above, while retaining a stenonian morphology, *E. senezensis* is characterized by its smaller size and slender postcranial elements, plausibly an adaptation following the geographic expansion of open country environments with the association of some wooded environments. Although it is probable that environmental change played a relevant role in this process, where this speciation event occurred is not known. Indeed, although the oldest *E. senezensis* occurrence has traditionally been considered to be the type locality of Senèze, the new studies on coeval Italian localities of Coste San Giacomo and Montecarlo have shown the existence of a similar medium-sized horse referrable to *E. senezensis* around 2.2–2.0 Ma both in France and Italy. The possible origin of *E. stehlini* from *E. stenonis* would have implied sympatric speciation, given the coexistence of both species in the UVB, and the well documented occurrence of *E. stenonis* in the Early Pleistocene localities of Pantalla and Olivola (Cherin et al. 2021; Cirilli et al. 2021a). However, *E. stenonis* is much larger than *E. stehlini*, so that speciation from the former to the latter must have involved strong selective pressures toward size reduction. Based on currently available cranial and postcranial evidence, it seems more likely that *E. stehlini* is closer to *E. senezensis* , having originated by means of peripatric speciation from a peripheral population of the latter. According to Mayr (1963, p. 502), the invasion of the geographic range of a parental (or sister) species by a newly emerged species is conclusive evidence that speciation has occurred. The occurrences of *E. stenonis*, *E. senezensis* and *E. stehlini* are consistent with such an evolutionary scenario implying peripatric speciation. For example, *E. stenon-*

is co-occurs with *E. stehlini* in the Upper Valdarno Basin, but not with *E. senezensis* at Senèze. Moreover, *E. stenonis* is found in the Italian localities of Pantalla and Olivola, whereas *E. senezensis* occurs at Coste San Giacomo and possibly in Montecarlo (UVB) without co-occurrence. Finally, the possible occurrence of *E. stehlini* at Senèze may be regarded as a geographic marginal overlap of a descendant species with its parental species.

CONCLUSIONS

The present analysis of the complete *E. stehlini* collection from the Upper Valdarno Basin has led to several important conclusions on this enigmatic Early Pleistocene European horse. The morphometric analyses based on a large comparative sample indicate that *E. stehlini* differs from other *Equus* species in multiple cranial and postcranial features. Therefore, it is concluded that as originally proposed by Azzaroli (1964), *E. stehlini* must be considered a taxonomically valid species.

Furthermore, the results of the analyses support a close relationship between *E. stehlini* and *E. senezensis*, leading to the conclusion that *E. stehlini* might have originated from *E. senezensis* instead of *E. stenonis*. Furthermore, *E. senezensis* appears taxonomically distinct from any *E. stenonis* ecomorphotype, being intermediate in size between *E. stenonis* and *E. stehlini*. These conclusions agree with the evolutionary hypothesis proposed by Alberdi et al. (1998) and, more recently, by Cirilli et al. (2021a) for European stenonian horses.

Equus stehlini can be confidently considered a typical species from the Italian Early Pleistocene, being recorded from several localities of the Upper Valdarno Basin. Due to the great research effort devoted to the stratigraphy of this basin (Fidolini et al. 2013; Ghinassi et al. 2013; Bertini 2013), the stratigraphic range of *E. stehlini* there is well constrained to the time span comprised between 1.9 and 1.77 Ma, corresponding to the late Villafranchian Tasso Faunal Unit. However, this chronological range does not include the new collection from the Early Pleistocene locality of Senèze in France, which might record an older occurrence of *E. stehlini* outside of Italy. Further detailed research on the horse sample from Coste San Giacomo may provide new insights on the dispersal of *E. senezensis* in Europe before 2.0 Ma. In any case, the stenonian morphology of both cranial and postcranial elements, coupled with its small size, suggests that *E. stehlini* was endemic to the Early Pleistocene of southern central Europe (at least central Italy and, possibly, southern France).

Acknowledgements: This study is framed within the complete PhD project of the present author on the evolution of the Old World *Equus* species in Europe and the origin of extant zebras. I wish to acknowledge Elisabetta Cioppi and Luca Bellucci (Museo di Storia Naturale dell'Univerisità degli Studi di Firenze, Sezione di Geologia e Paleontologia), Emanuel Robert (Université Claude Bernard - 1, Lyon), Didier Berthet (Museé des Confluences, Lyon), Maia Bukhsianidze (Georgian National Museum, Tbilisi), Amanda Millhouse and John Ososky (Museum Support Centre, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA) for providing access to study the fossil *Equus* collections. I also thank Vera Eisenmann for her generosity to share data on fossil and extant horses in her public web database, and any other authors who have included available research data. I wish to acknowledge the Editor David Alba and two anonymous reviewers for their comments, suggestions and advices which have improved the quality of the present manuscript. Furthermore, I am grateful to Prof. Lorenzo Rook (University of Florence) and to Prof. Raymond Louis Bernor (Howard University) for their support in this research and in the whole PhD project of the present author, providing constant advice, discussing ideas and results in the studying of fossil equids. This study is funded by the University of Pisa PhD program and by the University of Florence (Fondi di Ateneo). This work is part of the "Augusto Azzaroli (1921-2015) centennial papers" by the Vertebrate Paleontology Group at the Earth Sciences Department, University of Florence. This is the FuTRES publication number 25.

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