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The fossil horses from the Farneta Faunal Unit (Early Pleistocene, central Italy): a review with new remarks on the paleobiogeography and biochronology of the Late Villafranchian equids in Western Eurasia

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ABSTRACT

The dispersal of the genus *Equus* in Western Eurasia at the onset of the Quaternary is an important biochronological event for the evolution of mammal communities. The Farneta Faual Unit (ca. 1.6–1.4 Ma) is one of the latest in the Villafranchian Mammal Age, and its importance is also marked by the first occurrences of the species *Praemegaceros obscurus*, *Pseudodama farnetensis* and *Bison* (*Eobison*) *degiulii*. Since it was first described in 1977 by Augusto Azzaroli, the equid material of the Farneta FU has been recognized as belonging to different species by as many authors. In this work, we analyze material referred to the genus *Equus* from different localities of the Farneta FU (Farneta, Selvella and Pietrafitta). Our analyses identify one middle sized equid, *Equusaltidens,* and a large sized species, *Equus stenonis*. Our results have remarkable implications for the Early and early Middle Pleistocene European framework, as they anticipate the first appearance in Western Eurasia of the former species and postpones it for the latter.

1. Introduction

1.1. A state of the art on the Early Pleistocene record of European equids

The fossil record of European Early Pleistocene equids has been well deciphered during the last decades. Since the early works of the last Century (Azzaroli, 1964, 1982, 1990, 2000, 2003; De Giuli, 1972, De Giuli, 1986; De Giuli and Masini, 1986, De Giuli et al., 1986; Eisenmann, 1980, 2004; Alberdi and Ruiz Bustos, 1985, Alberdi and Ruiz–Bustos, 1989; Koufos, 1992; Koufos and Kostopoulos, 1993; Alberdi et al., 1997, 1998; Koufos and Vlachou, 1997; Koufos et al., 1997; Forsten, 1999), their biochronology and paleobiogeography have been constantly updated and revised, allowing to obtain a well-represented scenario through space and time (Petronio et al., 2011; Alberdi and Palombo, 2013a, 2013b; Palombo and Alberdi, 2017; Palombo et al., 2017; Bernor et al., 2018, 2019, 2021; Boulbes and Van Asperen, 2019; Rook et al., 2019; Cherin et al., 2021; Cirilli et al., 2020a, 2020b, 2021a, 2021b, 2021c, 2022, 2023a, 2024a; Cirilli, 2022; Eisenmann, 2022a, 2022b; Eisenmann and Boulbes, 2020; Gkeme et al., 2021; Koufos et al., 2022).

The earliest representatives of *Equus* appeared in Eurasia at the onset of the Quaternary, following the dispersal wave from North America of the genus (Azzaroli, 1982, 2000, 2003; Azzaroli and Voorhies, 1993; Bernor et al., 2019; Cirilli et al., 2021a, 2022, 2024b). These newcomers in Western Eurasia (from the Caucasus to the Iberian Peninsula) are represented by the species *Equus livenzovensis*, a large equid with an estimated body mass of 400–600 kg (Cirilli et al., 2022, 2024a), found at Liventsovka (2.58–2.1 Ma, Russia; Tesakov et al., 2007a; 2007b; Titov, 2008), Roca-Neyra (2.6 ± 0.02 Ma, France; Nomade et al., 2014), Montopoli (2.58 Ma Italy; Bartolini-Lucenti et al., 2022), El-Rincòn 1 (2.6 Ma, Spain; Alberdi et al., 1997) and Fonelas P-1 (Spain) (Alberdi et al., 1997, 1998, 2001; Bernor et al., 2018, 2019, 2021; Cirilli et al., 2021a, 2021b, 2021c, 2022, 2024a). In Roca-Neyra, *E. livenzoveonsis*

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shared the paleoenvironment with one of the last representatives of the three-toed equids which roamed Eurasia and Africa since the Late Miocene, namely *Plesiohipparion rocinantis* (Cirilli et al., 2023b).

Slightly later, *Equus major*, a much larger species about 600–800 kg in body mass (Cirilli et al., 2022, 2024a) with browse-to-mixed feeders habits, appeared in Central and Eastern Europe (Cirilli et al., 2024a), with records (from East to West) in the Middle and early Late Villafranchian localities of Liventsovka (Russia), Schernfeld and Erpfinger Hole (Germany), Tegelen (The Netherlands), Pardines, Chagny, and Senèze (France), East Runton and Norwich (England) (Cirilli et al., 2024a).

Equus stenonis is a medium-to large-sized species (ca. 350–500 kg, Cirilli et al., 2024a), first recorded in Western Eurasia at ca. 2.5–2.4 Ma, and it represents the most widespread species during the Middle and early Late Villafranchian (Cirilli et al., 2021b). From East to West, the species has been found in the localities of Dmanisi (Georgia), Guliazy and Sarikol Tepe (Turkey), Sesklo, Dafnero, Volax, Vatera, and Krimni (Greece), Olivola, Pantalla, and Upper Valdarno (Italy), Saint-Vallier and Chilhac (France) and La Puebla de Valverde (Spain) (Azzaroli, 1964, 1982; De Giuli, 1972, De Giuli, 1986; De Giuli et al., 1986; Eisenmann, 2004; Bernor et al., 2018, 2019, 2021; Cherin et al., 2021; Cirilli et al., 2020a, 2020b, 2022; Koufos et al., 2022). Late occurrences of *E. stenonis* have been recorded in the late Late Villafranchian sites of Pirro Nord, Italy (Arzarello et al., 2009; De Giuli, 1986; De Giuli et al., 1986), and Ceyssaguet, France (Aouadi, 1999; Aouadi and Bonifay, 2008), but unfortunately these occurrences remain hypothetical pending a revision of the entire collections from these localities (Cirilli et al., 2021b).

Equus senezensis is a medium-sized equid (ca. 300–400 kg, Cirilli et al., 2024a) occurring at the Middle Villafranchian localities of Senèze (France), Coste San Giacomo and Vigna Nuova (Italy) (Palombo et al., 2017; Cirilli et al., 2021c, 2022; Azzarà et al., 2022).

Equus stehlini is the smallest Early Pleistocene equid (ca. 250–350 kg, Cirilli et al., 2024a), at the present time recovered only in the early Late Villafranchian Italian localities of Upper Valdarno (Cirilli, 2022) and Frattaguida (Petronio and Salari, 2021).

Equus altidens is medium-sized equid (250–400 kg, Cirilli et al., 2024a) widespread in Western Eurasia in the late Early and Middle Pleistocene (Cirilli et al., 2022). The oldest presence of the species was first recognized in the paleoanthropological site of Dmanisi (Georgia, Bernor et al., 2021), and reported also in the localities of Libakos and Gerakarou (Greece; Gkeme et al., 2017; Koufos et al., 2022), Venta Micena, Fuente Nueva-3 and Barranco Léon, Atapuerca TD6, Sima de Elefante TE17, Quibas, Cullar de Baza 1, Vallparadís, Cueva Victoria, Huescar-1, (Spain; Alberdi, 2010; Alberdi and Palombo, 2013a, 2013b; Alberdi and Piñero, 2015; Alberdi et al., 1988; Bellucci et al., 2021; Madurell-Malapeira et al., 2010; Piñero and Alberdi, 2015; Van der Made, 1999), Sainzelles, Soleilhac, Bois-de-Riquet (France; Palombo and Valli, 2004; Bourguignon et al., 2016), Pirro Nord, Slivia, Venosa-Loreto (Italy; Alberdi and Palombo, 2013a; 2013b; Alberdi et al., 1988), and Süssenborn (Germany; Alberdi and Palombo, 2013a; 2013b; Cirilli et al., 2022). As for *E. stenonis* in previous times, *E. altidens* was the most widespread equid species in the Late Villafranchian - Early Galerian of Western Eurasia. Nevertheless, its systematics is debated and not all the authors recognize its validity (for a summary see Eisenmann, 2022b).

Equus suessenbornensis is a large-sized equid (ca. 550–750 kg, Cirilli et al., 2024a) closely related to *E. major* (Cirilli et al., 2023a), present in Western Eurasia during the latest Villafranchian, Epivillafranchian, and Early Galerian (Cirilli et al., 2023a). From East to West, it was recovered from the localities of Akhalkalaki (Georgia), Apollonia-1 (Greece), Stranska Skala (Czech Republic), Pirro Nord, Slivia, Il Castello, Soave, Monte Tenda, Bucine, Venosa-Loreto (Italy), Voigtstedt, Süssenborn, Dorn-Dürkheim 3 (Germany), West Runton and Pakefield (England), Barranco León, Fuente Nueva-3, Cueva-Victoria, Quibas, Huescar-1 and Cullar de Baza-1 (Spain) and possibly at Bois-de-Riquet (France) (Alberdi, 2010; Alberdi and Piñero, 2015; Piñero and Alberdi, 2015; Cirilli et al., 2023a).

Equus apolloniensis was recovered only from the latest Villafranchian type locality of Apollonia-1 (Greece; Gkeme et al., 2021) and *Equus wuesti* only from the Epivillafranchian type locality of Untermassfeld (Germany; Eisenmann and Boulbes, 2020; Eisenmann, 2022b).

1.2. The Farneta Faunal Unit and its position in the Villafranchian European Land Mammal Age

Italian continental deposits and fossil assemblages that date back to 3.5–1.2 Ma are frequently referred to as part of the Villafranchian European Land Mammal Age (ELMA; Pareto, 1865; Rook and Martínez-Navarro, 2010), to which also faunas from numerous European localities are referred (Cherin et al., 2023). This time span was subsequently divided into Faunal Units (FUs), which serve as chronological markers of defined faunal assemblages through time, as a result of peculiar bioevents that follow the evolution of climate, environments, and ultimately species eco-morphotypes. From their first introduction (Azzaroli, 1977, 1983), to the formal designation of the 17 Italian FUs made by Gliozzi et al. (1997), several revisions and further studies have been made. As a result, some FUs have been extensively and thoroughly studied, while some others are still temporally framed only by relative dating, without considering any independent proxy such as magnetostratigraphy, micropaleontology, or absolute dating of any sort (Cherin et al., 2023).

The Farneta FU lies between the older Tasso FU (ca. 1.8 Ma) and the younger Pirro Nord FU (ca. 1.5–1.2 Ma), with an estimated age range of 1.6–1.4 Ma. The Farneta, Selvella, and Pietrafitta Local Faunal Assemblages (LFAs) have been referred to the Farneta FU (Azzaroli, 1977; Gliozzi et al., 1997; Rook and Martínez-Navarro, 2010; Petronio et al., 2011; Martinetto et al., 2014). The fossil assemblages from the different localities included in the Farneta FU have been studied by several authors. Initially, Azzaroli and Ambrosetti (1970) and Ambrosetti et al. (1972) reported the occurrences of two different faunas from the northern part of the hills around the Farneta Abbey: a Late Villafranchian and a Galerian one. The Late Villafranchian deposit was used by Azzaroli (1977) to establish the Farneta FU. Azzaroli (1977) and Azzaroli and Ambrosetti (1970) reported the following taxa from the Farneta LFA: *Archidiskodon* (=*Mammuthus*) *meridionalis vestinus*, *Equus stehlini*, *Dicerorhinus* (=*Stephanorhinus*) *etruscus*, *Leptobos etruscus*, "*Leptobos*" *vallisarni*, *Dama nestii* (?), *Eucladoceros* sp. (?), *Homotherium* sp. In addition to these taxa, the faunal list of the Farneta FU published by Azzaroli (1977) included also *Macaca florentina* (?), *Ursus etruscus* (?), Bovid indet., *Sus strozzii*, *Hippopotamus major* (=*antiquus*), and *Libralces* (=*Cervalces*) *gallicus*. De Giuli, 1986 described the Selvella LFA, including Elephantidae indet., *Sus* sp., *Lynx issiodorensis*, *Canis etruscus*, *Leptobos* sp., *Eucladoceros* cf. *dicranios*, *Dama* cf. *nestii*, and *Equus* cf. *stenonis*. Eventually, the mammal faunal list of the Pietrafitta LFA includes *Bison* (*Eobison*) *degiulii*, *Castor fiber plicidens*, *Equus* sp., *Eucladoceros* sp., *Macaca sylvana florentina*, *Mammuthus meridionalis*, *Praemegaceros obscurus*, *Microtus* (*Allophaiomys*) cf. *chalinei*, *Microtus* (*Allophaiomys*) cf. *ruffoi*, *Mimomys pusillus*, *Oryctolagus* cf. *lacosti*, *Pannonictis nestii*, *Pseudodama farnetensis*, *Sciurus* sp., *Sorex* cf. *minutus*, *Stephanorhinus etruscus*, *Talpa* sp., and *Ursus etruscus* (modified after Sorbelli et al., 2021; 2023).

In the last decades, the fossil remains from the Farneta FU were revised multiple times. Azzaroli (1983), in addition to the previously published Farneta faunal list (Azzaroli, 1977), reported *Equus stenonis*, *Leptobos* sp., and possibly *Panthera toscana* and *Pachycrocuta brevirostris*. Azzaroli (1992) reviewed the Villafranchian cervids of Tuscany and erected the new genus *Pseudodama* and the new species *Pseudodama farnetensis* for the previously assigned "*Dama*" *nestii* from Farneta (from the fossil pits of La Villa, Cava Liberatori, and Casa Palazzi) and from Selvella (Azzaroli, 1992). In this regard, it is worth noting that the taxonomy of Plio-Pleistocene European medium-sized cervids is highly

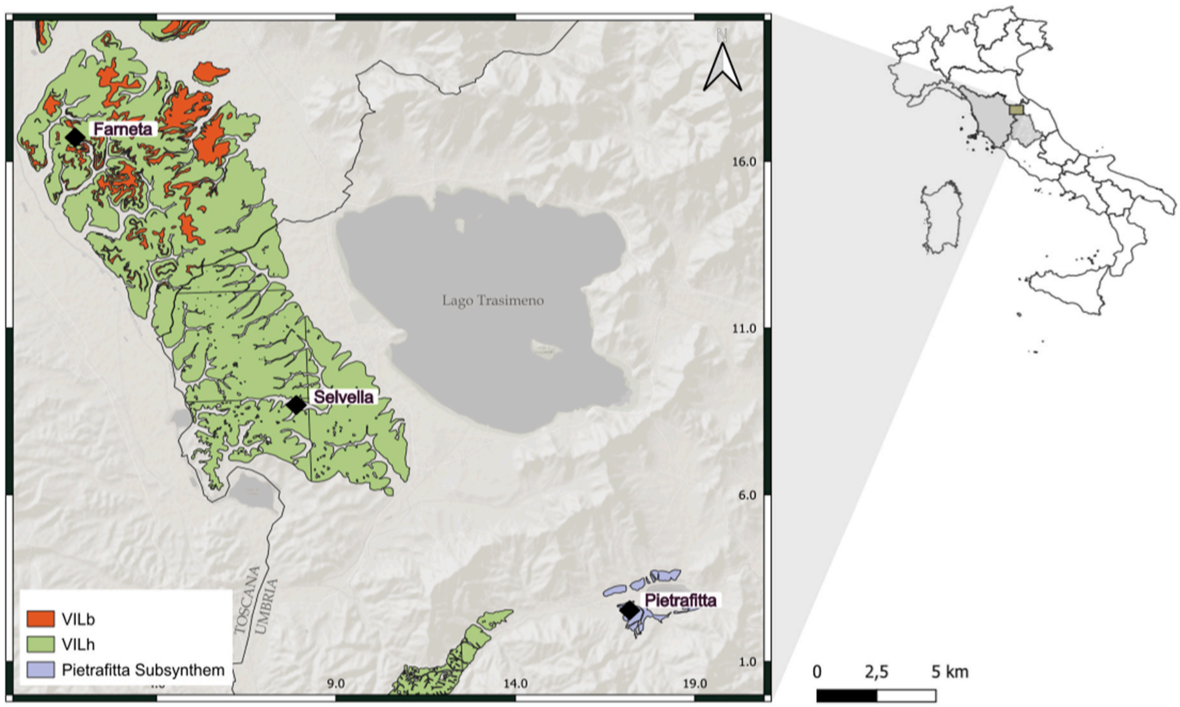

Fig. 1. Geographical distribution of the Farneta Faunal Unit areas of interest with associated geological formations. Highlighted lithologies are Vilb in orange = Villafranchian b; in green, Vilh: Villafranchian h; in purple, Pietrafitta subsynthem. The map was made using QGis software and geological data from the Geoportal of the Tuscany Region. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

debated in the literature. In this manuscript, following the most widespread view in recent bibliography (Bona and Sala, 2016; Breda et al., 2020; Cherin et al., 2022; Konidaris and Kostopoulos, 2024), we include all species of so-called *Dama*-like deer in the genus *Pseudodama* (Azzaroli, 1992). Readers may find in the literature the same samples mentioned in this present paper as assigned to a plethora of different genera and species [e.g., see "*Axis eurygonos*" as a synonym of *Ps. farnetensis* in Petronio et al. (2011) and references therein]. Returning to the characteristic taxa of the Farneta FU, Abbazzi (1995, 2004) identified *Praemegaceros obscurus* from Val di Chiana (Cava Liberatori, Farneta) and Pietrafitta. Palombo and Ferretti (2005) questioned the subspecies *M. meridionalis vestinus* Azzaroli(in Ambrosetti et al., 1972) and suggested including the remains assigned to this species to *M. meridionalis*, without any subspecific designation. They also identified the proboscidean remains from Pietrafitta as *M. meridionalis.* Following Abbazzi (2004), Rook and Martínez-Navarro (2010) reported the first appearance of *Pr. obscurus* and of the rhinoceros *Stephanorhinus* cf. *hundsheimensis* (Alberdi et al., 1998) in the Farneta FU. However, according to the recent publications by Pandolfi et al. (2017), Pandolfi and Erten (2017) and Cirilli et al. (2020a), the earliest presence of *S. hundsheimensis* in the Italian Peninsula is from the locality of Leffe (Jaramillo subchron; Vialli, 1956; Pandolfi and Erten, 2017), and the rhinos of the locality included in the Farneta FU (including Pietrafitta) are better ascribed to *Stephanorhinus etruscus*, pending a revision of these collections. Masini et al. (2013) reported the presence of *Leptobos vallisarni* from Selvella, Casa Palazzi, and Pietrafitta, although more recently the bovid sample from Pietrafitta has been identified as *Bison* (*Eobison*) *degiulii* (Sorbelli et al., 2023). Eventually, Alberdi and Palombo (2013a) recognized the presence of *Equus suessenbornensis* and *Equus altidens* in Selvella.

1.3. Previous identifications of the fossil equids from the Farneta FU and aims of the paper

The identification of the fossil equid remains from the Farneta FU (including Farneta, Selvella, and Pietrafitta LFAs) is controversial, as resulted in past publications by different authors. Azzaroli and Ambrosetti (1970) and Azzaroli (1977) reported the presence of *E. stehlini* whereas, later, Azzaroli (1983, 1992, 1998) identified both *E. stenonis* and *E. stehlini* in the Farneta LFA. De Giuli (1986) reported *E.* cf. *stenonis* from the Selvella LFA, whereas the same sample was reinterpreted as *E. stenonis* by Forsten (1999). Caloi and Palombo (1987) reported *E. stenonis* ssp. (i.e., a not identifiable subspecies) in Selvella, whereas Caloi (1995) ascribed the same sample to *E.* aff. *altidens*. Palombo et al. (2003) reported ?*E. stehlini* from Val di Chiana (=Farneta LFA) and *E. altidens* from Selvella, whereas in the last revision of the Selvella equid sample, Alberdi and Palombo (2013a) recognized the co-occurrence of *E. altidens* and *E. suessenbornensis*.

Currently, a project led by the Dipartimento di Scienze della Terra and the Museo di Storia Naturale, Sezione di Geologia e Paleontologia of the Università di Firenze aims to valorize the fossil collection of the Farneta LFA and to shed a better knowledge of the fossil species defining the Farneta FU. As the first outcome of this project, here we provide the review of the fossil equid remains from the Farneta, Selvella, and Pietrafitta LFAs, the latter published here for the first time. The fossil samples are compared with all known Early and early Middle Pleistocene fossil *Equus* species, in order to assess their systematics and discuss their position and relevance for the evolution of the Villafranchian faunas in Western Eurasia.

2. Geological context

2.1. Val di Chiana

Plio-Pleistocene continental deposits (Val di Chiana synthem) covers a wide area of the Val di Chiana (i.e., Chiana Valley) basin extending from the Farneta Abbey (South of Arezzo) to the Selvella farmhouse (East of Gioiella), up to westernmost Umbria and East to the Trasimeno Lake (Azzaroli, 1992), although there may be some discrepancies in the nomenclature of the stratigraphic units between different regions (Tuscany and Umbria) due to different local geological mapping projects (e.g., Azzarà et al., 2022). These deposits are largely buried under the

Table 1
Complete list of the Plio-Pleistocene and extant *Equus* species used for comparative analyses in the present work listed by age, from older to younger.

Species	Locality	Age (Ma)	Data source
Equus simplicidens	Hagerman Horse Quarry, Idaho	3.3–3.1; Cirilli et al. (2024b)	Own
Equus livenzovensis	Roca-Neyra, France	2.6 ± 0.02; Nomade et al. (2014)	Own
Equus livenzovensis	Liventsovka, Russia	2.58–2.2; Titov, 2008	Forsten (1999); Eisenmann (2022b)
Equus livenzovensis	El Rincon - 1, Spain	2.6; Alberdi et al. (1997)	Alberdi et al. (1997)
Equus major	Liventsovka, Russia	2.58–2.2; Titov, 2008	Forsten (1999); Eisenmann (2022b)
Equus livenzovensis	Montopoli, Italy	2.58; Bartolini-Lucenti et al. (2022)	Bernor et al. (2018)
Equus major	Pardines, France	ca. 2.5; Nomade et al. (2014)	Cirilli et al. (2024b)
Equus major	Chagny, France	ca. 2.5; Palombo and Valli (2004)	Cirilli et al. (2024b)
Equus stenonis	Saint-Vallier, France	ca. 2.45; Nomade et al. (2014)	Own; Cirilli et al. (2021a)
Equus senezensis	Senèze, France	2.2–2.0; Nomade et al. (2014)	Own
Equus major	Senèze, France	2.2–2.0; Nomade et al. (2014)	Own; Cirilli et al. (2024a)
Equus senezensis	Vigna Nuova, Italy	2.2–2.1; Azzarà et al. (2022)	Azzarà et al. (2022)
Equus major	Schernfeld, Germany	2.1–1.9; Mayhew (2012)	Musil (1992); Cirilli et al. (2024b)
Equus livenzovensis	Fonelas P-1, Spain	2.0; Arribas et al. (2009)	Garrido (2008)
Equus stenonis	Pantalla, Italy	ca. 2.2; Cherin et al. (2023)	Cherin et al. (2021)
Equus stenonis	Olivola, Italy	2.0–1.9; Rook and Martínez-Navarro, 2010	Own; Cirilli et al., 2021a
Equus stenonis	Upper Valdarno Basin, Italy	1.9–1.77; Fidolini et al. (2013)	Own; Cirilli et al., 2021a
Equus stehlini	Upper Valdarno Basin, Italy	1.9–1.77; Fidolini et al. (2013)	Own; Cirilli (2022)
Equus 'stenonis mygdoniensis'	Gerakarou, Greece	ca. 1.8 Ma; Konidaris and Kostopoulos, 2024	Koufos (1992)
Equus stenonis	Dmanisi, Georgia	1.85–1.77; Ferring et al., (2011)	Own; Bernor et al. (2021)
Equus altidens	Dmanisi, Georgia	1.85–1.77; Ferring et al., (2011)	Own; Bernor et al., 2021
Equus altidens	Venta Micena, Spain	1.6–1.4; Rook and Martínez-Navarro, 2010	Guerrero-Alba and Palmqvist (1997)
Equus altidens	Pirro Nord, Italy	1.5–1.2; Rook and Martínez-Navarro, 2010	Own; Alberdi and Palombo (2013a), 2013b
Equus suessenbornensis	Pirro Nord, Italy	1.5–1.2; Rook and Martínez-Navarro, 2010	Own; Alberdi and Palombo (2013a), 2013b
Equus apolloniensis	Apollonia-1, Greece	1.5–1.2;Konidaris and Kostopoulos, 2024	Gkeme et al. (2021)
Equus altidens	Quibas, Spain	1.1–1.0; Piñero et al. (2020), 2022	Piñero and Alberdi (2015)
Equus suessenbornensis	Akhalkalaki, Georgia	0.98–0.78; Tappen et al. (2002)	Cirilli et al. (2023b)
Equus suessenbornensis	Cueva Victoria, Spain	0.9–0.8; Gilbert and Scott (2015)	Alberdi and Piñero (2015)
Equus suessenbornensis	Süssenborn, Germany	0.64–0.62; Kahlke (2014)	Own; Musil (1969); V. Eisenmann website
Equus altidens	Süssenborn, Germany	0.64–0.62; Kahlke (2014)	Own; V. Eisenmann website
Equus grevyi	East Africa	0.0	Own; V. Eisenmann website

actual ground surface, yet the seismic profiles suggest that their thickness ranges from some hundred to more than one thousand meters (Aruta et al., 2007). Two different units are recognized as part of the Val di Chiana synthem. The older subsynthem is represented by yellow fine sands (De Giuli, 1986) deposited in alluvial plain, palustrine environment, and alluvial channels up to the Early Pleistocene. Conversely, fluvial and alluvial fan facies prevail in the overlying subsynthem (Aruta et al., 2007). Two different faunal assemblages were recovered in these units: the older is Early Pleistocene in age and is formed by the core taxa defining the Farneta FU (Azzaroli, 1977); the younger was recovered in small, pebbly lenses at the cemetery of Borgonovo, 2 km North-East of Farneta and in scattered outcrops to the South of Val di Chiana (Azzaroli, 1977, 1998) and it is believed to be of Galerian age (Azzaroli, 1977, 1998; De Giuli, 1986; Petronio et al., 2011). However, a preliminary survey carried out on the Borgonuovo remains suggests that a separate review of this locality is needed to clarify its faunal composition and age (Azzaroli, 1977, 1998; De Giuli, 1986). Therefore, the Borgonuovo equid sample is not included in this work.

The locality of Farneta was extensively excavated in the late 1900's for the construction of a highway (Fig. 1). A few quarries were temporarily opened in the surroundings of the Farneta village, such as Cava Liberatori, Cava La Rota, Cava Oppiello and further South, near Vaiano, Casa Palazzi (De Giuli, 1986). Excavation yielded numerous specimens of fossil taxa somewhat different from the older Tasso FU, but typical of the Villafranchian ELMA (Azzaroli, 1977; Gliozzi et al., 1997). Noteworthy is the co-occurrence of Epivillafranchian-Galerian genus *Praemegaceros* (with the oldest record of *Pr. obscurus* in the Italian Peninsula) and other typical Villafranchian taxa, like *Leptobos* and possibly *Eucladoceros* (Azzaroli and Mazza, 1993).

The Selvella locality (IGF n.87, Fig. 1) was a small sand quarry opened in 1969 close to a farm with the same name and a few kilometers East of Gioiella (De Giuli, 1986). Before the quarry opened, only a few meters of outcrops were present, and they were formed by yellow coarse-grained sands. Fossils were found in small lenses just below the top of the sandy layer and presented a certain level of sorting (De Giuli, 1986). The fauna recovered is now stored in the Natural History Museum of the University of Florence and though it was referred to the Tasso FU at first, it was later placed between the Olivola and Pirro FUs (De Giuli, 1986), based on the recovered taxa. *Equus* and *Dama*-like specimens are by far the most abundant remains, but fossils of Elephantidae indet., *Eucladoceros dicranios*, *Canis etruscus* (Cherin et al., 2014), *Lynx issiodorensis* (Cherin et al., 2013), and *Sus* sp. were also collected.

2.2. Pietrafitta

The Pietrafitta fossil locality is named after the homonymous village nearby, and it is found in the Tavernelle-Pietrafitta Basin, South of Lake Trasimeno, in the Umbria region (Fig. 1). The locality is an old lignite quarry, active in the mid to late 1900's, and is famous for its rich and well-preserved fossil specimens (Martinetto et al., 2014). Like many others in central Italy, the Tavernelle-Pietrafitta Basin is approximately NE-SW oriented and originated during the Apennine uplift (Ambrosetti et al., 1995). At least in some phases of the Early Pleistocene, the basin became part of a lateral branch of the wider Tiberino Basin and was alternatively characterized by stages of lacustrine/palustrine and alluvial plain deposition (Gentili et al., 1998; Cherin et al., 2012; Pazzaglia et al., 2013; Martinetto et al., 2014; Petronio et al., 2020; Sorbelli et al., 2021). The lignite layers, which are 5–8.5 m in total thickness, are the result of organic matter and secondarily clay deposition during stagnant water phases in perilacustrine environments ca. 1.5 Ma, before the uplift of the basin and progressive transition towards a river basin as it is currently (Ambrosetti et al., 1989; Martinetto et al., 2014). The swampy area in which these layers deposited was surrounded by a humid deciduous broad-leaved forest under a warm-temperate climate, as suggested by paleobotanical data (Martinetto et al., 2014) and

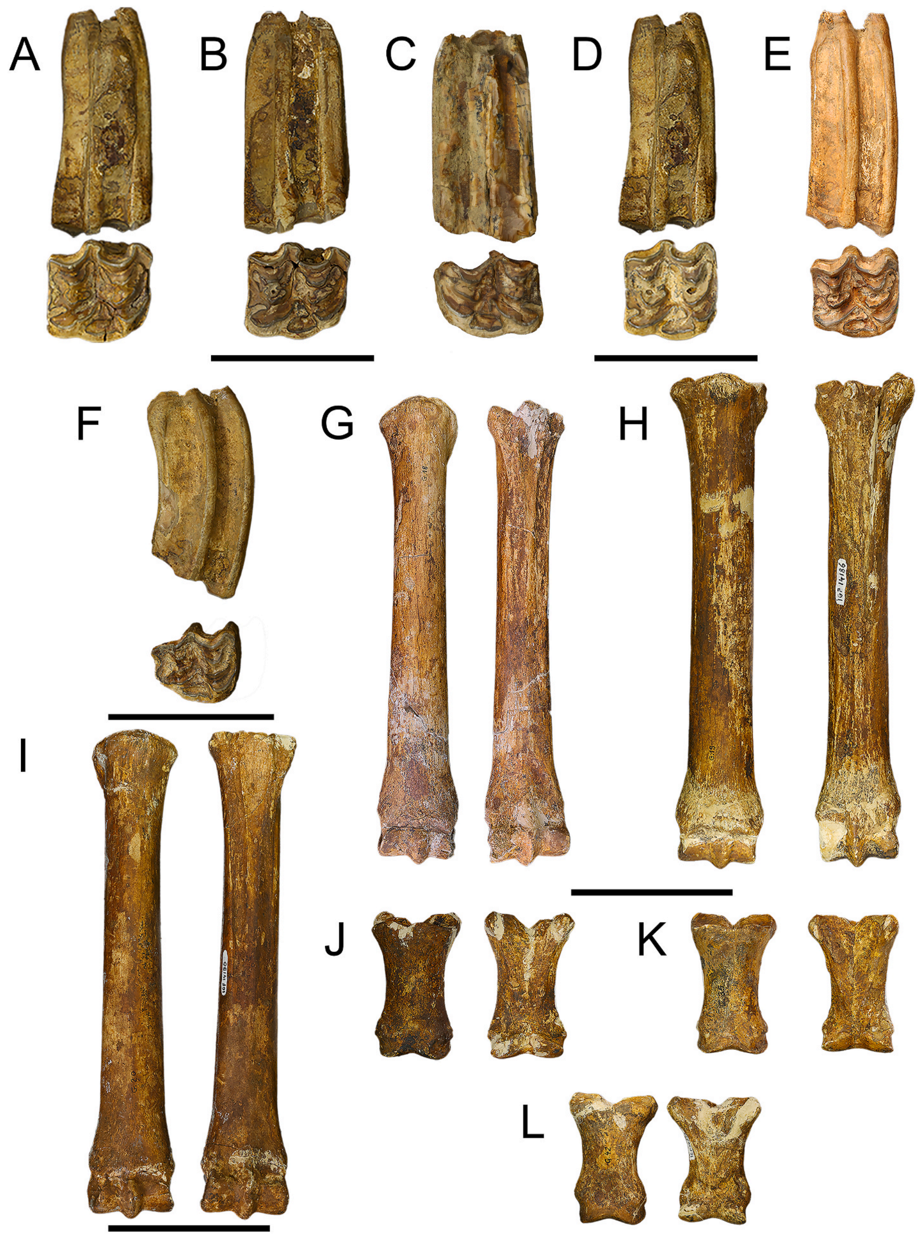

Fig. 2. *Equus stenonis* isolated maxillary teeth (A–F), third metatarsals (G–I), first anterior (J–K) and posterior (L) phalanges of the central digit in dorsal and palmar view. A) IGF14337, B) IGF14338, C) IGF14343, D) IGF14339, E) IGF14340, F) IGF14341, G) IGF14185, H) IGF14186, I) IGF14190, J) IGF14171, K) IGF14324, L) IGF14325. Scale bar 5 cm for cranial elements, 10 cm for postcranial elements.

paleoenvironmental information retrieved from the very diversified vertebrate assemblage (Martinetto et al., 2014; Cherin et al., 2018; Sorbelli et al., 2021; 2023).

3. Materials and methods

3.1. Morphometric and statistical analyses

The fossil equids from Farneta, Selvella, and Pietrafitta are housed at the Museo di Storia Naturale, Sezione di Geologia e Paleontologia, Università di Firenze (IGF; Farneta and Selvella localities), at the Mostra Paleontologica Permanente (Mo.Pa., Farneta locality) and at the Museo Paleontologico "Luigi Boldrini" of Pietrafitta (Pietrafitta locality). A complete list of the material studied herein is provided in Supplementary Table 1. The assemblages have been compared with a large dataset of Plio-Pleistocene fossil (*E. simplicidens*, *E. livenzovensis*, *E. major*, *E. stenonis*, *E. senezensis*, *E. stehlini*, *E. altidens*, *E. suessenbornensis*, and *E. apolloniensis*) and extant (*E. grevyi*) stenonid *Equus* species from North America, Eurasia, and Africa (Table 1) following Cirilli et al. (2023a, 2024a). The Plio-Pleistocene monodactyl equid species are included in the genus *Equus* following the latest cladistic results of Cirilli et al. (2021a), not recognizing *Plesippus* and *Allohippus* as distinct genera or subgenera.

Upper and lower cheek teeth and postcranial elements (third metacarpals, third metatarsals, anterior and posterior first phalanges of the central digit) are described and compared with the species mentioned above. No complete crania are available in the studied collections. The measurements and anatomical nomenclature follow the international standards for studying fossil equids by Eisenmann et al. (1988) for postcranial elements and Bernor et al. (1997) for upper and lower teeth. Morphometric and statistical analyses implemented herein include: bivariate plots, principal component analysis (PCA), Log10 ratio diagrams, and a permutational multivariate analysis of variance (PERMANOVA). In upper and lower cheek teeth, the bivariate plots compare the

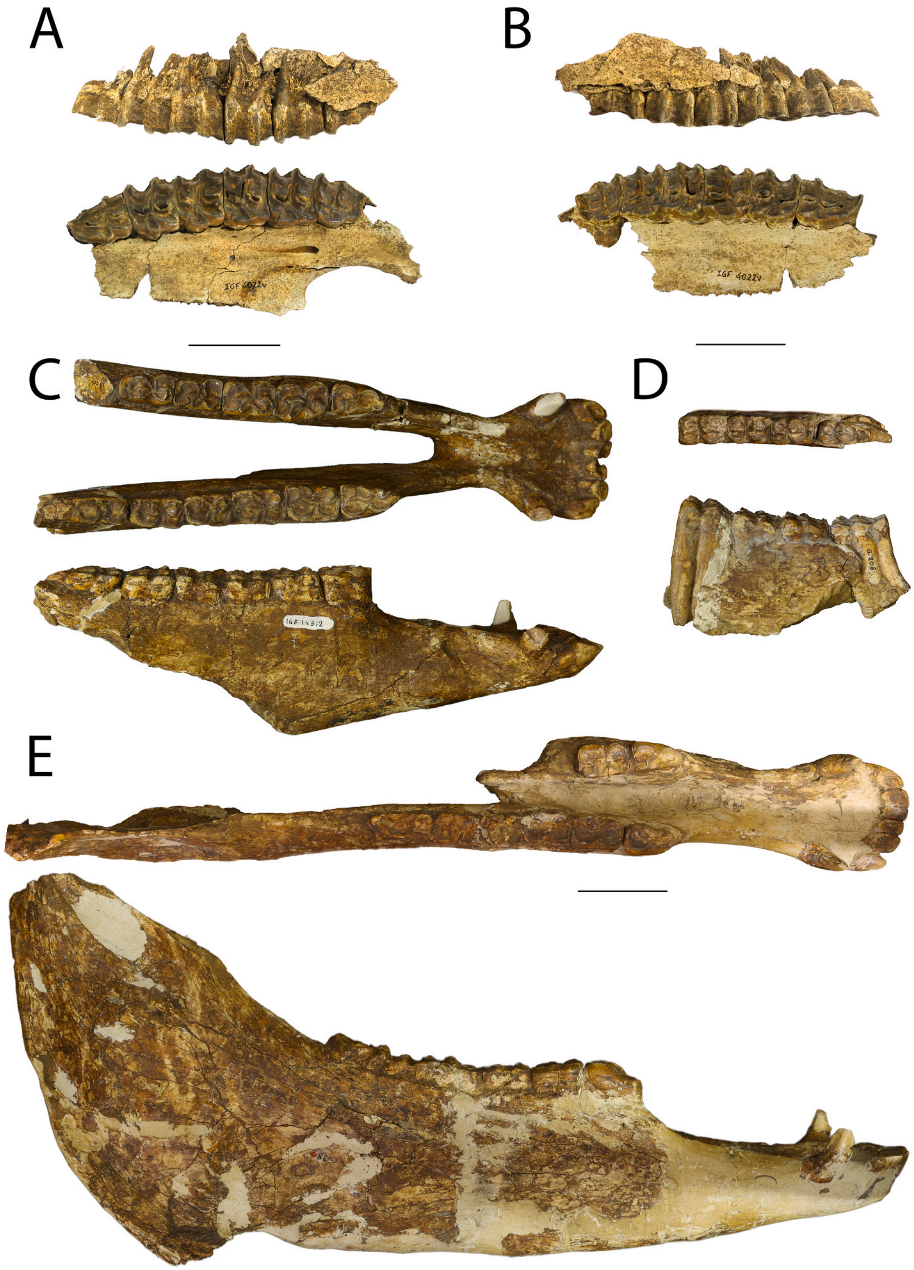

Fig. 3. *Equus altidens* upper and lower cheek tooth rows in labial and occlusal view. A) right IGF 4022v, B) left IGF4022v, C) IGF14312, D) IGF14314a, E) 14313. Scale bar 5 cm.

maximum length (M1) and maximum width (M3 in upper dentition, M6 in the lower) at the occlusal level. On postcranial elements, the bivariate plots include the maximum length (M1) versus the distal maximum articular width (M11 in third metapodials and M6 in the anterior first phalanges of the central digit). PCAs were computed on third metacarpals, third metatarsals, and first phalanges of the central digit. The variables used to build the PCAs on third metapodials include maximum length (M1), minimum width of the diaphysis (M3), depth of the diaphysis at level of M3 (M4), proximal articular width (M5), proximal articular depth (M6), distal maximum supra-articular width (M10), distal maximum articular width (M11), distal maximum depth of the crista sagittalis (M12), and the distal maximum depth of the medial condyle (M14), whereas those used to build the PCA on the first phalanges of the central digit include maximum length (M1), minimal breadth (M3), proximal breadth (M4), proximal depth (M5), and distal breadth at the tuberosities (M6).

To compare the single incomplete metacarpal from Pietrafitta, Log10 ratio diagrams were performed on the Log-transformed mean values of the Höwenegg *Hippotherium primigenium* (Bernor et al., 1997). Considering the present work on the genus *Equus*, the Höwenegg *H. primigenium* represents an ideal fossil sample from a single fossil equine species from a well-studied, homogeneous stratigraphic context, 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, mandible, dentition, and postcranial elements. Furthermore, the method has the advantage of being referred to a different genus and tribe (Hipparionini, not Equini) allowing an analysis of all species of the genus *Equus*. In addition to the same measurements used in the PCAs, the Log10 ratio diagrams include the diameter of the articular facet for the third carpal/tarsal (M7), maximum diameter for the anterior facet for the fourth carpal/tarsal (M8), and distal maximum depth of the lateral condyle (M13).

Bivariate plots and PCAs were computed in the R Environment v. 4.5.1 (R Core Team, 2025) using packages "stats" v. 3.6.2 (Venables and Ripley, 2008) and "ggplot2" v. 3.5.1 (Wickham, 2016). PCAs have been built using the parameter scale = T to have a unit variance before starting the analyses in R.

The PERMANOVA analyses were performed on the PC values of third metapodials using the '*pairwiseAdonis*' package v. 0.4 (Martínez-Arbizu, 2020) in R, which includes the Bonferroni adjustment method (p. adjust). Third metapodials were chosen because they represent the most discriminant postcranial elements to evaluate similarities or differences in morphology among *Equus* species. These analyses are aimed at quantifying and identifying the intra- and interspecific variability in extant and fossil (sub)species and calculating body mass (Bernor et al., 2021; Cirilli et al., 2021c, 2022, 2023a, 2024a; Cirilli, 2022; Saarinen et al., 2021).

3.2. Anatomical abbreviations

UTR, upper cheek tooth row; **LTR**, lower cheek tooth row; **P2**, maxillary second premolar; **P3**, maxillary third premolar; **P4**, maxillary fourth premolar; **M1**, maxillary first molar; **M2**, maxillary second molar; **M3**, maxillary third molar; **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; **mt3**, third metatarsal; **p1ph3**, posterior first phalanx of the central digit.

3.3. Institutional abbreviations

IGF, Museo di Storia Naturale, Sezione di Geologia e Paleontologia, Università degli Studi di Firenze (Italy); **MPLBP**, Museo Paleontologico "Luigi Boldrini" di Pietrafitta (Italy).

4. Systematic Paleontology

Class Mammalia Linnaeus, 1758.
Order Perissodactyla Owen, 1848.
Family Equidae Gray, 1821.
Subfamily Equinae Gray, 1821.
Genus *Equus* Linnaeus, 1758.
Equus stenonis Cocchi, 1867.

Holotype. The skull, IGF560, is housed in the Museo di Storia Naturale, Sezione di Geologia e Paleontologia, Florence, Italy. Originally described by Cocchi (1867) and figured in Azzaroli (1964: Pl. I fig. 3, Pl. II fig.1 and a, Pl. IV fig.1 and a, Pl. V fig.1).

Type locality. Terranuova Bracciolini, Upper Valdarno Basin (Italy), ca. 1.9–1.77 Ma (Cirilli et al., 2021c).

Age range ca. 2.5–1.3 Ma (Cirilli et al., 2021b, 2022).

Geographic range. From East to West: Georgia, Turkey, Greece, Italy, France, and Spain (Cirilli et al., 2021b, 2022).

Referred material. See Supplementary Table 1.

Description.

Cranium - No complete *E. stenonis* crania were recovered from Farneta, Selvella, or Pietrafitta. Therefore, our description of the cranial features will comprise characteristics of the maxillary teeth, retrieved only in the first two localities.

Maxillary teeth - Fig. 2A–F shows five isolated upper teeth ascribed to *E. stenonis*. All teeth show a high crown and a medium stage of wear except for IGF14343 (Fig. 2C) that has a lower, partially broken crown in labial view, but preserves all morphological features in occlusal view. In occlusal view, all teeth show a squared mesostyle, which is thicker in premolars and compressed mesio-distally in molars. Similarly, the labial ridge of the mesostyle shows a slight depression which is more pronounced in P3-P4 than in M1-M3. The protocone differs slightly in shape between the specimens: compressed labio-lingually in IGF14337 (Fig. 2A), IGF14343 (Fig. 2C), IGF14339 (Fig. 2D) and IGF14340 (Fig. 2E), while more rounded in IGF14338 (Fig. 2B). The lingual margin of the protocone shows a slight concavity in all specimens except for IGF14341(Fig. 2B). The protocone is always connected to the protoloph by a sharp, single-pointed isthmus. The pli caballin is visible in all teeth except in IGF14337 (Fig. 2A) and IGF14341 (Fig. 2E). When present, it is single and well developed. The hypocone is well developed except in M3 (Fig. 2E) and distally pointed. The fossettes have ornamentation in all teeth but show a higher complexity in the premolars (Fig. 2A–B).

Third metatarsal – Fig. 2G–I illustrates third metatarsals IGF14185, IGF14186, and IGF14190 from Selvella. The mt3s are characterized by an elongated morphology with a circular section diaphysis and by wide proximal and distal epiphyses. The supra-articular tuberosities (M10) are more developed than the distal articular processes (M11) in all three specimens. The lateral condyle (M13) is less developed than the medial condyle (M14). The mt3s have a well-developed crista sagittalis.

First anterior phalanx of the central digit – Fig. 2J and K illustrates IGF14171 and IGF14324 from Selvella, two anterior first phalanges. The a1ph3s are large and elongated with the proximal epiphysis being more laterally developed than the distal epiphysis. In dorsal view, the proximal epiphysis shows a light concavity in the midline towards the sagittal plane. In palmar view, the midline concavity is deep and well developed, and it is connected to the V-shaped, proximal-distally deep surface of the trigonum phalangis proximalis. The lateral glenoid cavity is more pronounced than the medial one. The distal supra-articular protuberances are as laterally developed as the medial and lateral trochleae.

First posterior phalanx of the central digit - Fig. 2L illustrates IGF14325 from Selvella. It shows the same morphologies of the anterior phalanges (Fig. 2J and K), but the distal supra-articular protuberances are wider than the medial and lateral trochleae.

Equus altidens von Reichenau, 1915.

Lectotype. Right P2, housed at the Universitat Halle a.d. Saale Collection, Germany. Figured in von Reichenau (1915: Pl. 6,fig. 17) and designated by Schwarz (1928).

Type locality. Süssenborn, Germany; ca. 0.64–0.62 Ma (Kahlke, 2014).

Age range. ca. 1.85–0.60 Ma (Alberdi and Palombo, 2013a; Bernor et al., 2021; Cirilli et al., 2022).

Geographic range. From West to East: Georgia, Greece, Italy, Germany, France, England, and Spain (Alberdi and Palombo, 2013a; Cirilli et al., 2022).

Referred material. See Supplementary Table 1.

Description.

Cranium - No complete *E. altidens* crania were recovered from Farneta, Selvella, and Pietrafitta. Therefore, our description of the cranial features is limited to characteristics of the maxillary teeth.

Maxillary tooth row - Fig. 3A and B illustrates the right and left complete UTRs of IGF4022v. The UTRs are low crowned suggesting a late stage of wear and the anatomical features of the occlusal morphology are faintly preserved. The anterostyle on P2 is short and subtriangular. The mesostyle is mesio-distally narrow on all teeth, with a labial tip pointed distally. The protocone is always connected to the protoloph. From P2 to M3, the shape of the protocone gradually shifts from rounded to labio-lingually flattened, with a progressive ornamentation development on the lingual ridge. The pli caballin is absent in all teeth of the UTRs. Pre- and post-fossettes are similar in size and appearance, resembling a U shape and bearing little to no ornamentation.

Isolated teeth are shown in Supplementary Fig. 1A-C.

Mandible and mandibular cheek tooth row - Fig. 3C–E shows three LTRs of *E. altidens* from Selvella. IGF14312 (Fig. 3C) is an almost complete mandible with right and left side completely preserved, with the only exception of left m3 which is missing. All incisors are preserved; the right canine is broken; the left canine has been restored but is still incomplete. In occlusal view, the teeth show the following features: in

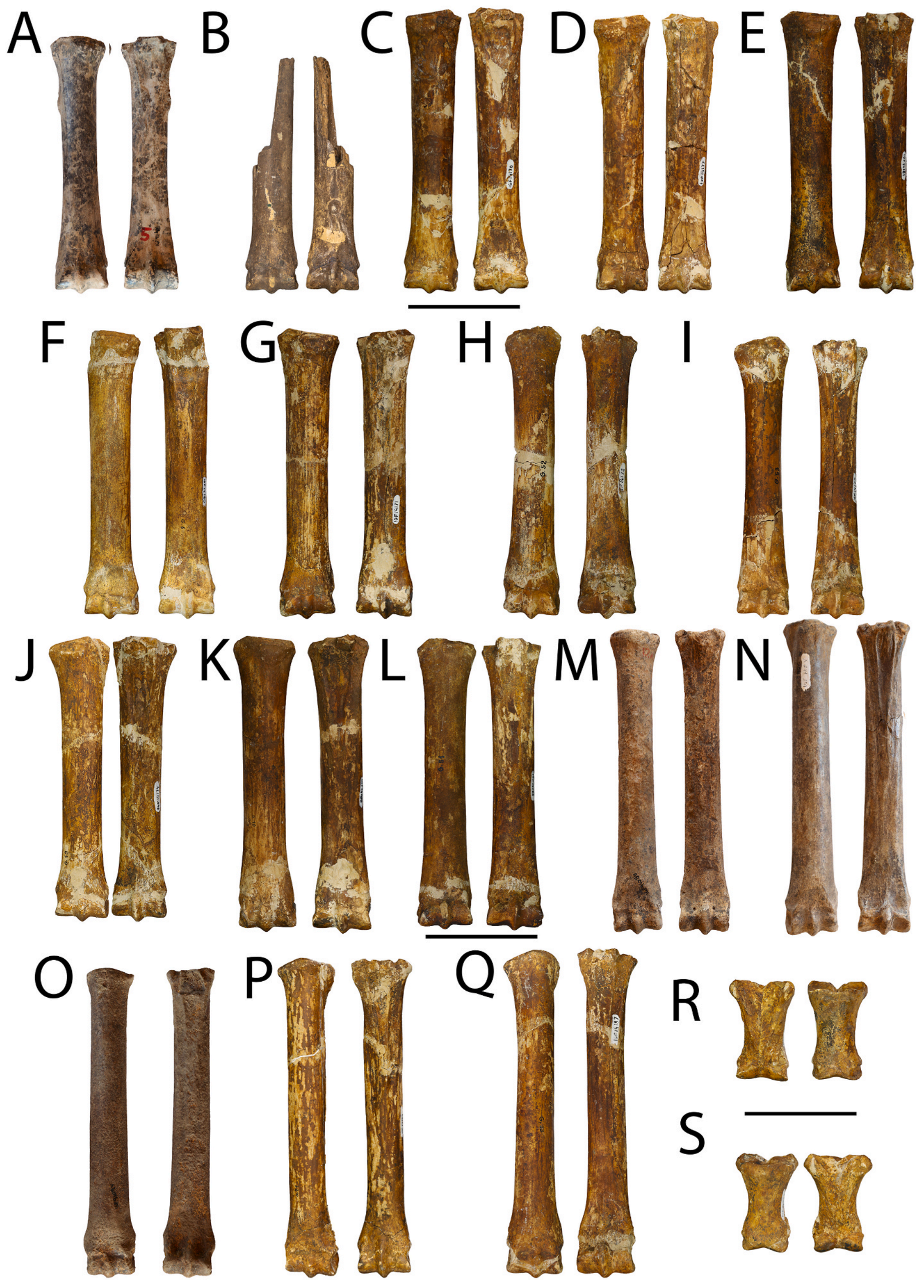

Fig. 4. *Equus altidens* third metacarpals (A–L), third metatarsals (M–Q) and first anterior phalanges of the central digit in dorsal and palmar view (R–S) from Farneta, Pietrafitta and Selvella. A) IGF9114v, B) MPLBP EQ_0001, C) IGF14171, D) IGF14172, E) IGF14173, F) IGF14174, G) IGF14175, H) IGF14176, I) IGF14177, J) IGF14180, K) IGF14181, L) IGF14182, M) IGF9108v, N) IGF785v, O) IGF9019v, P) IGF14184, Q) IGF14187, R) IGF14323, S) IGF14326. Scale bar 10 cm.

p2 the anterostylid is wide and rounded; the metaconid is rounded in all teeth, and thicker than the metastylid, which is narrow and flattened labio-lingually; the metaconid is always connected to the preflexid, which is faintly developed in left p4 and nearly absent in left p2, p3, m1, m2; on the right side, the preflexid is not always visible due to the late stage of wear; the metastylid is pointed lingually in all teeth, but thicker in left and right p2 than in p3-m3; the linguaflexid is V-shaped in all teeth, deeper and wider in p3-m3 than in p2; the ectoflexid is short in p2, and progressively more developed in premolars and molars; the preflexid is poorly developed to nearly absent, while the postflexid is flat and mesio-distally elongated in premolars, less developed in molars, with little to no ornamentation; the pli caballinid is absent.

IGF14314a (Fig. 3D) is a partially preserved left LTR. In labial view, it shows high crowns and in occlusal view the dental morphology is well preserved, suggesting an early-adult stage of wear. The morphological features slightly differ from those of IGF14312. The metastylid is still less developed than the metaconid, but it is rounded rather than flattened. The preflexid is visible in p4-m3, though poorly developed.

IGF14313 (Fig. 3E) is a mandible with the right ramus completely preserved, and the left ramus bearing only p2 and p3. The canines are preserved as well as the incisor arcade which is curved rather than horizontal. All teeth show an advanced stage of wear that hides the majority of morphological features. The anterostylid is wide and round in p2. The metaconid is slightly larger than the metasylid, which is lingually pointed. The linguaflexid is V-shaped and wider in p3-p4 than p2.

Isolated lower teeth are shown in Supplementary Fig. 1D-L.

Third metacarpal - Fig. 4 illustrates the *E. altidens* mc3 from Farneta (Fig. 4A), Pietrafitta (Fig. 4B), and Selvella (Gioiella) (Fig. 4C–L). All third metacarpals are complete except for MPLBP EQ_0001 (Fig. 4B) which lacks the proximal end and the proximal half of the medial side of diaphysis. All specimens show an elongated, massive morphology with well-developed proximal and distal epiphyses which are wider than the diaphysis. On the distal epiphysis, the supra-articular tuberosities are well developed, with the medial side being more pronounced than the lateral side. The same symmetry can be observed for the medial and lateral trochleae, which are separated by a marked crista sagittalis.

Third metatarsal - Fig. 4 shows the *E. altidens* mt3s IGF9108v, IGF785v and IGF 9019v from Farneta (Fig. 4M–O) and Selvella (Gioiella) (Fig. 4P and Q). The mt3s are characterized by elongated and slender morphology, with long, circular section diaphysis and by large proximal and distal epiphyses. The supra-articular tuberosities are as laterally prominent as the distal articular processes in all specimens, with the exception of IGF9109v where the tuberosities are more pronounced than the lateral and medial trochleae. The mt3s have a well-developed crista sagittalis.

First anterior phalanx of the central digit **-** Fig. 4R and S shows two a1ph3s (IGF14323 and IGF14326) of *E. altidens* from Selvella. The proximal end is broad and wide, the diaphysis is elongated and slightly asymmetrical, with the medial side more developed than the lateral one. In palmar view, the V-shaped *trigonum phalangis proximalis* is well developed and deep, reaching the distal end of the diaphysis. The distal end is slenderer than the proximal end, with the supra-articular protuberances being the same size as the trochleae, which are symmetrical.

5. Morphometric and statistical analyses

5.1. Morphometric analyses of the Farneta FU equids compared with the European Early and early Middle Pleistocene stenonidEquus

The morphometric comparisons of the Farneta equids with the European Early and early Middle Pleistocene *Equus* species are shown in Figs. 5–10 for cranial and selected postcranial elements. Due to the absence of complete crania, the morphometric comparisons on cranial elements are limited to upper and lower cheek teeth. In Fig. 5, the P3/4, M1/2, p3/4, and m1/2 are analyzed together due to their similar morphology and morphometrics, to increase the comparative sample size.

Fig. 5A–C illustrates bivariate plots comparing the maximum length vs maximum width at the occlusal level of upper dentitions (M1 vs M3 of Bernor et al., 1997). The Farneta and Selvella samples are included in the variability of *E. altidens* and *E. stenonis*. In Fig. 5A, the two specimens IGF4022V (right and left P2 of the same individual) are plotted close to the smallest *E. altidens* individuals from Süssenborn, Dmanisi, Pirro Nord, and Venta Micena. This result is an effect of the late stage of wear of IGF4022V, as shown in Fig. 3. Fig. 5B shows the comparisons of the P3/4. Here, the sample from Farneta is included in the *E. altidens* range of variability, larger than *E. stehlini* from Upper Valdarno (Cirilli, 2022), whereas three specimens from Selvella (IGF14337, IGF14338, and IGF14343) are plotted in the range of variability of *E. stenonis* from Saint-Vallier and Upper Valdarno Basin. In Fig. 5C (M1/2), the sample from Farneta is included in the range of variability of European *E. altidens*, whereas two specimens from Selvella (IGF14339 and IGF14340) show larger dimensions, comparable with those of *E. stenonis*.

Fig. 6A–C shows bivariate plots comparing the maximum length vs maximum width at the occlusal level of upper dentitions (M1 vs M6 of Bernor et al., 1997). In Fig. 6A (p2), one specimen from Farneta (IGF105313) and the Selvella sample (IGF14312 [right and left], IGF14313 [right and left], IGF14348) are included in the range of variability of *E. altidens*. In Fig. 6B, the Selvella sample of p3/4 (IGF105129, IGF14312 [right and left], IGF14313 [right and left], IGF14314, IGF14349) is plotted between the range of variability of *E. altidens* and that of *E. stehlini*, whereas three specimens from Farneta (IGF105129, IGF105314, IGF105316) fall close to the range of variability of *E. altidens*. In Fig. 6C (m1/2) the sample from Farneta (IGF14282, IGF2842V) and from Selvella (IGF14312 [right and left], IGF14313 [right and left], IGF14314 [right and left], IGF14350) are plotted within the variability of *E. altidens* from Süssenborn, Dmanisi, Pirro Nord, and Venta Micena.

Overall, these plots on upper and lower cheek teeth reflect the previous reports by Cirilli et al. (2023a, 2024a), where *E. major* shows similar dimensions than *E. suessenbornensis*, representing the largest species in the European Early Pleistocene equid record. *Equus livenzovensis* from Liventsovka and Fonelas P-1 are included in the *E. stenonis* populations from Saint-Vallier and Upper Valdarno Basin, being smaller than *E. major* and *E. suessenbornensis*. *Equus senezensis*, *E. altidens*, and *E. stehlini* are the smallest of the Early Pleistocene species, with the latter being the smallest of them. All these species show a remarkable overlap in their range of variability, reflecting the different stages of wear of the specimens considered in the analyses. The same output might be recognized also with some specimens of *E. suessenbornensis* from Akhalkalaki and Süssenborn, plotted close to the *E. stenonis* variability, although preserving the different occlusal enamel morphology (Cirilli et al., 2023a). This confirms the importance of recognizing morphology over morphometry in analyzing the upper and lower cheek teeth of the fossil equids, as previously reported (Cirilli et al., 2023a, 2024a).

Fig. 7 illustrates the PCA results and bivariate plots for mc3s and mt3s. The summary of the variance components and the loadings' distribution are reported in Supplementary Table 2. In the PCA of the mc3s (Fig. 7A), PC1 and PC2 account for 88.1% of the total variance (PC1 = 82.9%; PC2 = 5.2%). PC1 separates species by size from negative to positive values (smaller to larger). Negative PC2 values indicate a shorter morphology and more robust shape, whereas positive PC2 values indicate a more elongated shape. Here, the samples from Farneta and Selvella are included in the range of variability shown by *E. altidens* from Süssenborn, Dmanisi, Pirro Nord, Venta Micena and Quibas, being well distinct from the other two small species *E. senezensis* (Senèze) and *E. stehlini* (Upper Valdarno Basin). The range of variability of *E. altidens* includes *E.* '*stenonis mygdoniensis*' from Gerakarou-1, as well as the North American *E. simplicidens* and the living *E. grevyi*. The mc3s from Farneta and Selvella are slenderer than those of *E. stenonis* from Upper Valdarno Basin and Saint-Vallier, and overall smaller than those of *E. livenzovensis*, *E. major*, and *E. suessenbornensis* which show a larger and massive morphology. Analogous results are depicted in Fig. 7B. The equids from Farneta and Selvella are included in the range of variability of *E. altidens*, larger than *E. senezensis* and *E. stehlini*, less robust than *E. stenonis*, and much smaller than *E. livenzovensis*, *E. major*, and *E. suessenbornensis*.

In Fig. 7C (mt3 PCA), PC1 and PC2 account for 86.1% of the variance (PC1 = 80.7%; PC2 = 5.3%). PC1 separates species by size from negative to positive values (smaller to larger). Positive PC2 values indicate a more elongated morphology, whereas negative PC2 values show a shorter and more robust shape. The results confirm the previous outcomes on mc3s with new insights about the Selvella sample. The Farneta sample (IGF785v, IGF9108v, IGF9109v) and the specimens from Selvella (IGF14184, IGF14187, IGF14191) are included in the range of variability of *E. altidens* from Süssenborn, Dmanisi, Pirro Nord, Venta Micena and Quibas, more elongated and larger than the mt3s of *E. senezensis* (Senèze and Vigna Nuova) and *E. stehlini* (Upper Valdarno Basin). However, three specimens from Selvella (IGF14185, IGF14186, IGF14190), previously identified as *Equus* cf. *stenonis* by De Giuli, 1986 and later as *E. suessenbornensis* (Alberdi and Palombo, 2013a) are plotted close to the *E. stenonis* samples from Upper Valdarno Basin, Saint-Vallier, Pantalla and Olivola, being different from the larger *E. livenzovensis*, *E. major*, and *E. suessenbornensis*. *Equus* '*stenonis mygdoniensis*' from Gerakarou-1 is still included in the *E. altidens* range of variability, whereas *E. apolloniensis* from Apollonia-1 shows a larger and more elongated shape than *E. altidens*. More insights come also from the comparison of the Pirro Nord *E. suessenbornensis* mt3s reported in Alberdi and Palombo (2013a, 2013b). In our analysis, these specimens are distributed over the ranges of variability of *E. altidens* and *E. stenonis*, showing a different shape and size compared to those of

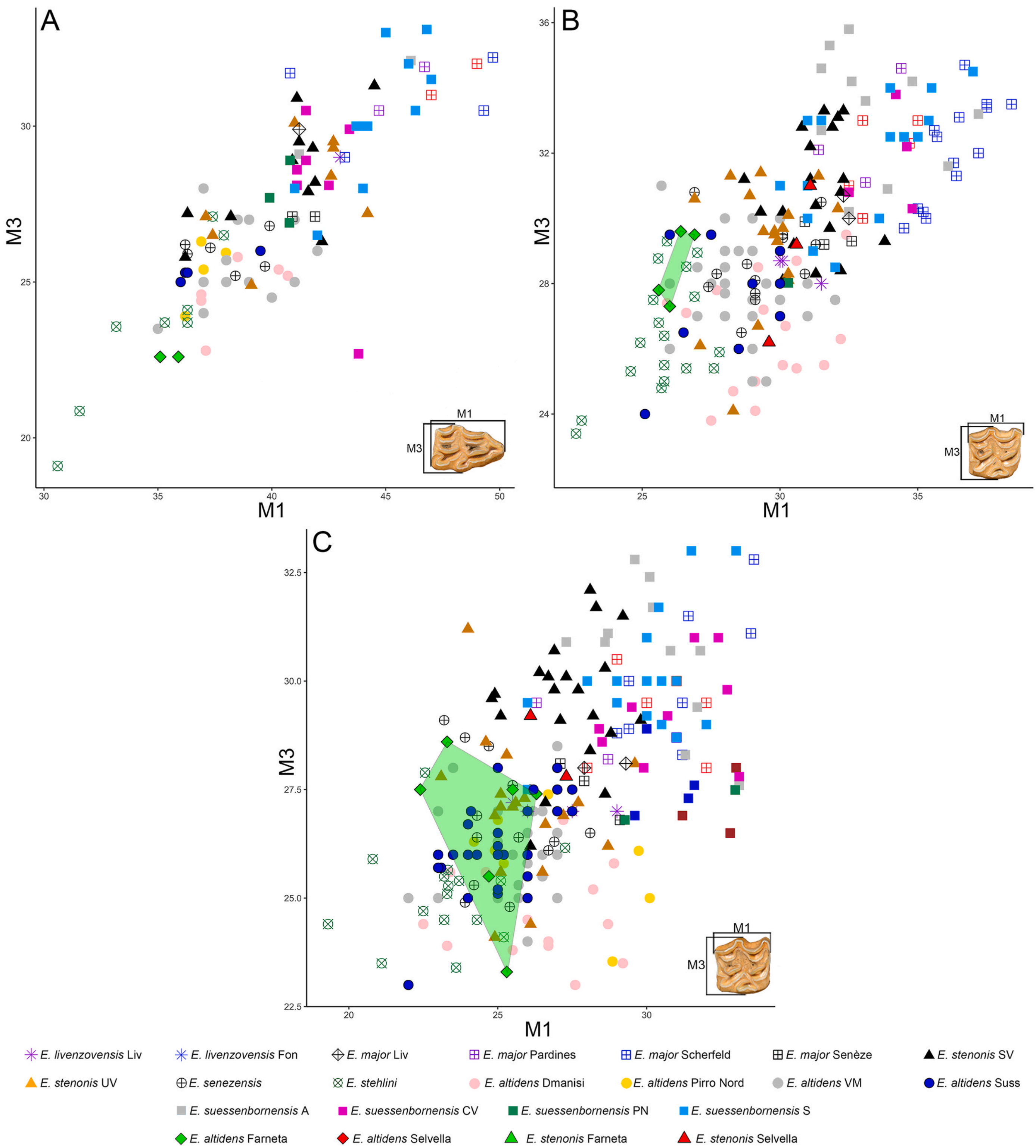

Fig. 5. Bivariate plots comparing the *E. stenonis* and *E. altidens* upper cheek teeth with the European Early Pleistocene *Equus* species in maximal length versus maximal width. A) P2; B) P3 and P4; C) M1 and M2. Abbreviations: A: Akhalkalaki; CV: Cueva Victoria; Fon: Fonelas P-1; Liv: Liventsovka; UV: Upper Valdarno; PR: Pirro Nord; SV: Saint-Vallier; S: Süssenborn; VM: Venta Micena.

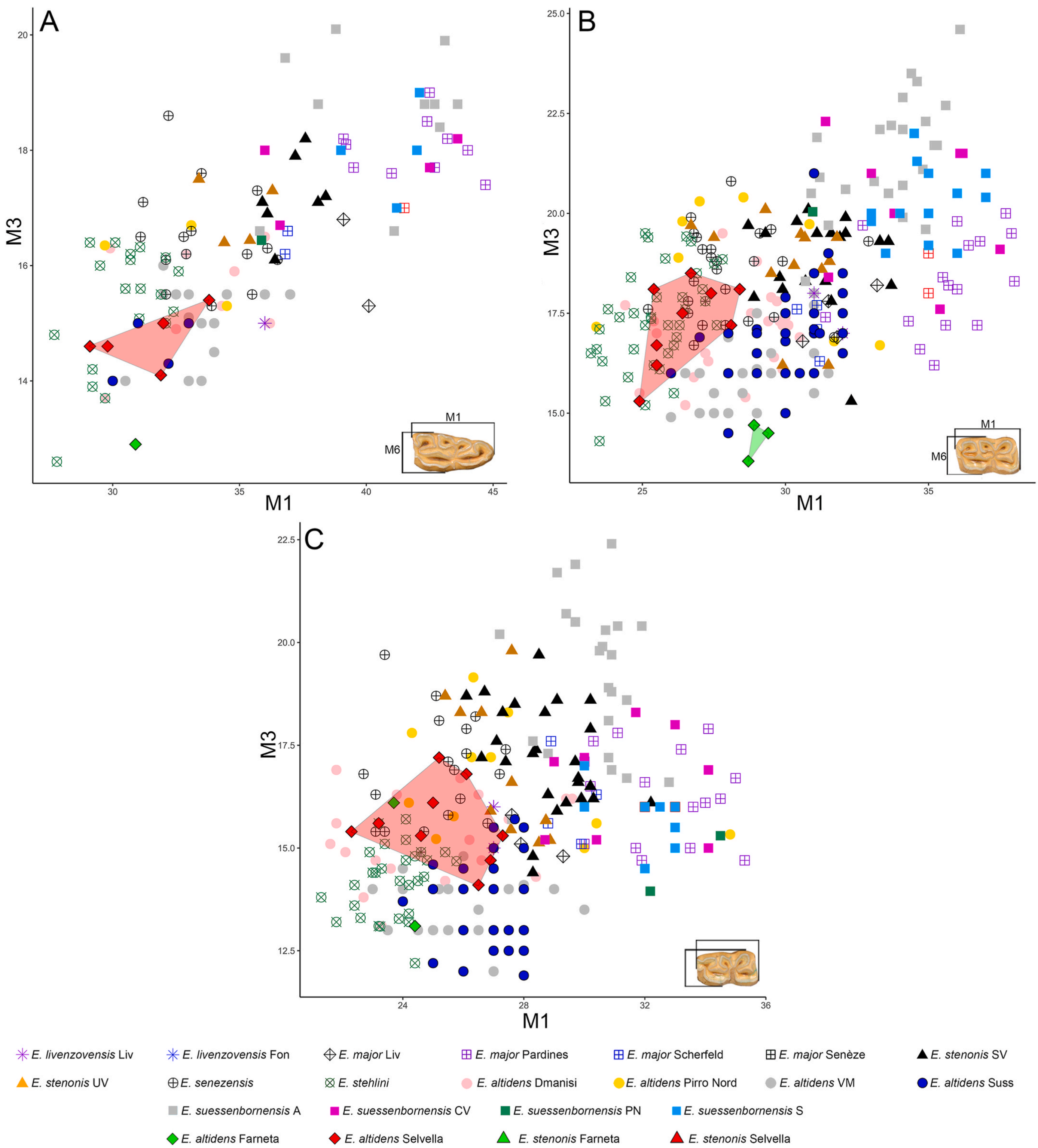

Fig. 6. Bivariate plots comparing the *E. stenonis* and *E. altidens* lower cheek teeth with the European Early Pleistocene *Equus* species in maximal length versus maximal width. D) p2; E) p3 and p4; F) m1 and m2. Measurements are referred to Bernor et al. (1997). Abbreviations: A: Akhalkalaki; CV: Cueva Victoria; Fon: Fonelas P-1; Liv: Liventsovka; UV: Upper Valdarno; PR: Pirro Nord; SV: Saint-Vallier; S: Süssenborn; VM: Venta Micena.

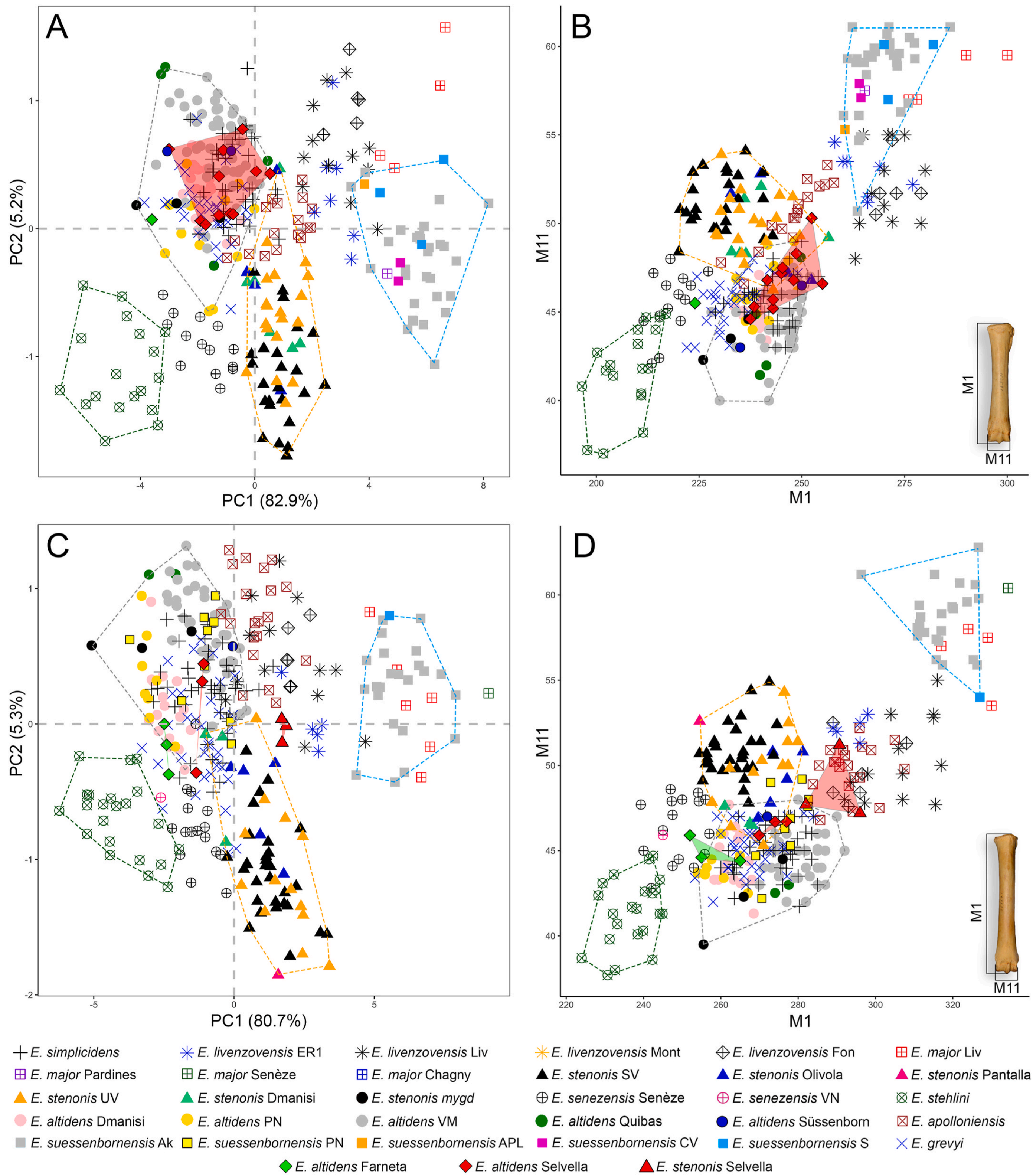

Fig. 7. Principal component analysis (A, C) and bivariate plots (B, D) on third metacarpals and third metatarsals respectively, comparing *E. altidens* and *E. stenonis* from Farneta and Selvella with a wide sample of fossil Pliocene, Pleistocene and extant *Equus* species. For each PCA, the loadings distribution is shown as an inset in the diagrams. Complete PC components are reported in Supplementary Table 2. Measurements are referred to Eisenmann et al. (1988) and Bernor et al. (1997). Abbreviations: Ak: Akhalkalaki; APL: Apollonia; CV: Cueva Victoria; ER1: El-Rincon 1; Fon: Fonelas; Liv: Liventsovka; *mygd*: *mygdoniensis*; Mont: Montopoli; PN: Pirro Nord; S: Süssenborn; SV: Saint-Vallier; UV: Upper Valdarno; VM: Venta Micena; VN: Vigna Nuova.

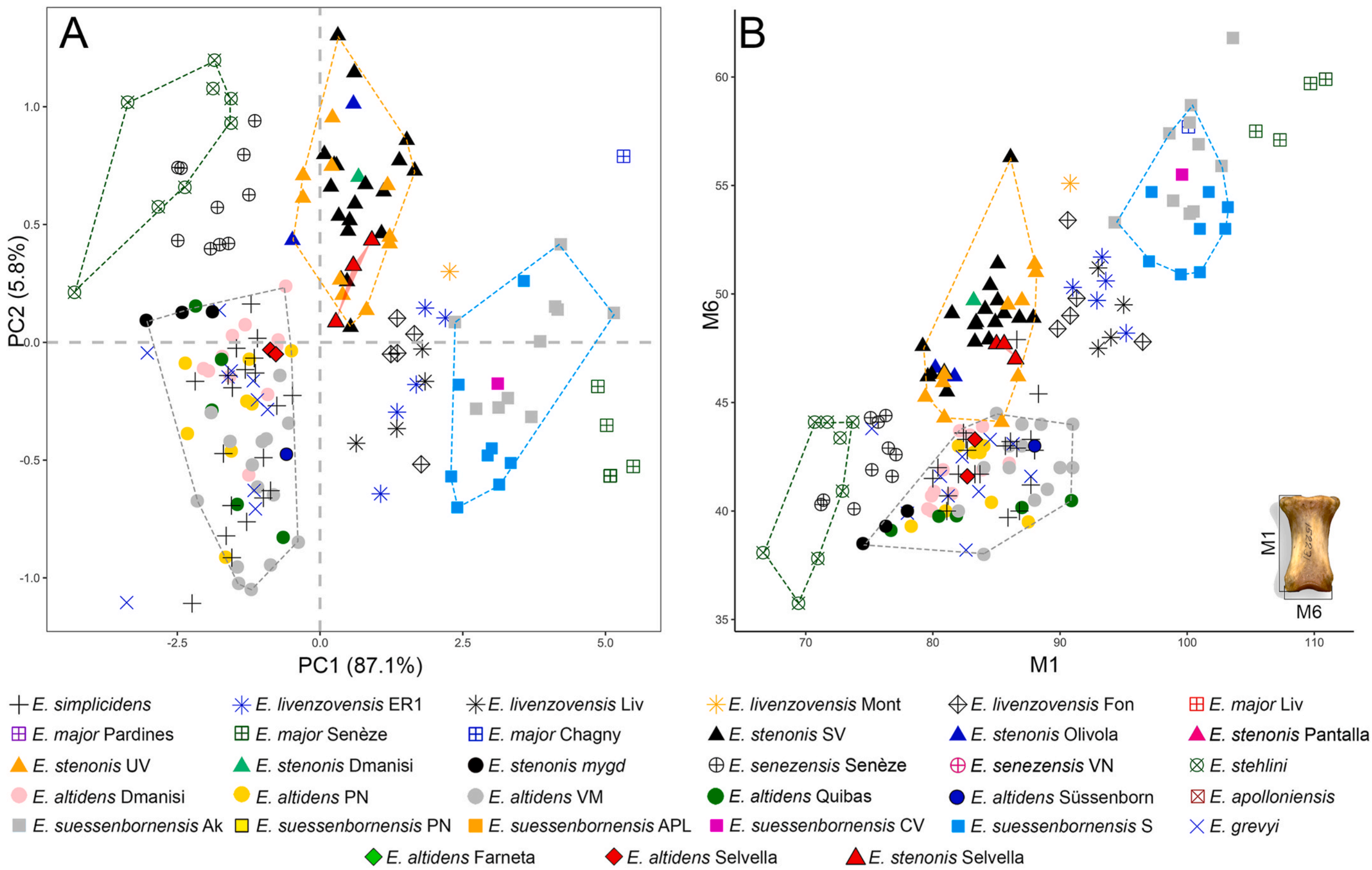

Fig. 8. Principal component analysis (A) and bivariate plot (B) on first anterior phalanges of the central digit, comparing *E. altidens* and *E. stenonis* from Farneta and Selvella with a wide sample of fossil Pliocene, Pleistocene and extant *Equus* species. For the PCA, loadings distribution is shown as an inset in the diagrams. Complete PC components are reported in Supplementary Table 2. Measurements are referred to Eisenmann et al. (1988) and Bernor et al. (1997). Abbreviations: Ak: Akhalkalaki; APL: Apollonia; CV: Cueva Victoria; ER1: El-Rincon 1; Fon: Fonelas; Liv: Liventsovka; *mygd*: *mygdoniensis*; Mont: Montopoli; PN: Pirro Nord; S: Süssenborn; SV: Saint-Vallier; UV: Upper Valdarno; VM: Venta Micena; VN: Vigna Nuova.

E. suessenbornensis from Akhalkalaki and Sussenborn. These results support the preliminary insights reported by Cirilli et al. (2023a) about the questionable presence of *E. suessenbornensis* in the Italian Farneta and Pirro Nord FUs based on postcranial elements. Similar results are shown in Fig. 7D. The medium-sized equids from Farneta and Selvella are plotted with the European *E. altidens* samples, distinct from *E. senezensis* and *E. stehlini*, less robust than *E. stenonis* and much smaller than *E. livenzovensis*, *E. major*, and *E. suessenbornensis*. The *E. stenonis* remains from Selvella are plotted close to those of *E. stenonis* from Olivola, being slightly more elongated than the those from Upper Valdarno and Saint-Vallier, but with the M11 values fitting into the variability of *E. stenonis* from Upper Valdarno. However, they are much smaller than the typical *E. suessenbornensis* from Akhalkalaki and Süssenborn. Furthermore, the Pirro Nord *E. suessenbornensis* reported in Alberdi and Palombo (2013a, 2013b) is plotted over the range of variability of the European *E. altidens* and *E. stenonis*, being in fact, distinct from *E. suessenbornensis*.

Fig. 8A plots the results for the a1ph3 PCA with PC1 and PC2 accounting for 92.9% of the total variance (PC1 = 87.1%; PC2 = 5.8%). Summary of the variance components and the loadings' distribution are reported in Supplementary Table 2. PC1 separates species by size from negative to positive values (smaller to larger), whereas PC2 is indicative of relative slenderness from negative to positive values (more to less slender). The results of the a1ph3 concur with the previous outcomes on mc3s and mt3s. The Selvella equids are included in the range of variability of *E. altidens* (IGF14323, IGF14326) and *E. stenonis* (IGF14171, IGF14324, IGF14325). The *E. altidens* samples of Süssenborn, Dmanisi, Pirro Nord, Venta Micena and Quibas overlap extensively and show a slenderer morphology than those of *E. senezensis* and *E. stehlini*. Overall, the Selvella equids are well separated from the large-sized species, namely *E. livenzovensis*, *E. major*, and *E. suessenbornensis*. Fig. 8B plots the maximal length (M1) versus the maximal distal width (M6) of the a1ph3. The results concur with those of Fig. 8A, with the Selvella equid sample included in the *E. altidens* and *E. stenonis* range of variability, well separated from the smaller *E. senezensis* and *E. stehlini* on one side, and from the larger *E. livenzovensis*, *E. major*, and *E. suessenbornensis* on the other.

The Log10 ratio diagrams on mc3s and mt3s provide additional information about the equid assemblage from the Farneta FU compared to the other European Early and Middle Pleistocene stenonid *Equus*. Fig. 9A (mc3) illustrates the range of variability with maximum, mean, and minimum values for the Selvella *E. altidens* with the *E. altidens* specimens from Farneta (IGF9114v) and with the incomplete mc3 from Pietrafitta (MPLBP EQ_0001). As shown in the diagram, the Selvella sample includes the Farneta and Pietrafitta ones, characterized by a slender morphology represented by an elongated M1 and medium-sized M3, larger than *E. senezensis* and *E. stehlini* (Fig. 9B), and with a pattern similar to the other *E. altidens* samples from Dmanisi, Gerakarou (*E. 'stenonis mygdoniensis'*), Pirro Nord, Venta Micena, and Quibas (Fig. 9C). The specimen from Pietrafitta plots closely with the mean of the Selvella sample, supporting its attribution to *E. altidens*.

Fig. 10A (mt3) shows the Log10 patterns for the Farneta and Selvella *E. altidens* samples and for the Selvella *E. stenonis* sample, with maximum, mean, and minimum values. As for the mc3s, the Farneta and Selvella *E. altidens* have a pattern similar to the other *E. altidens* samples from Dmanisi, Gerakarou (*E. 'stenonis mygdoniensis'*), Pirro Nord, Venta

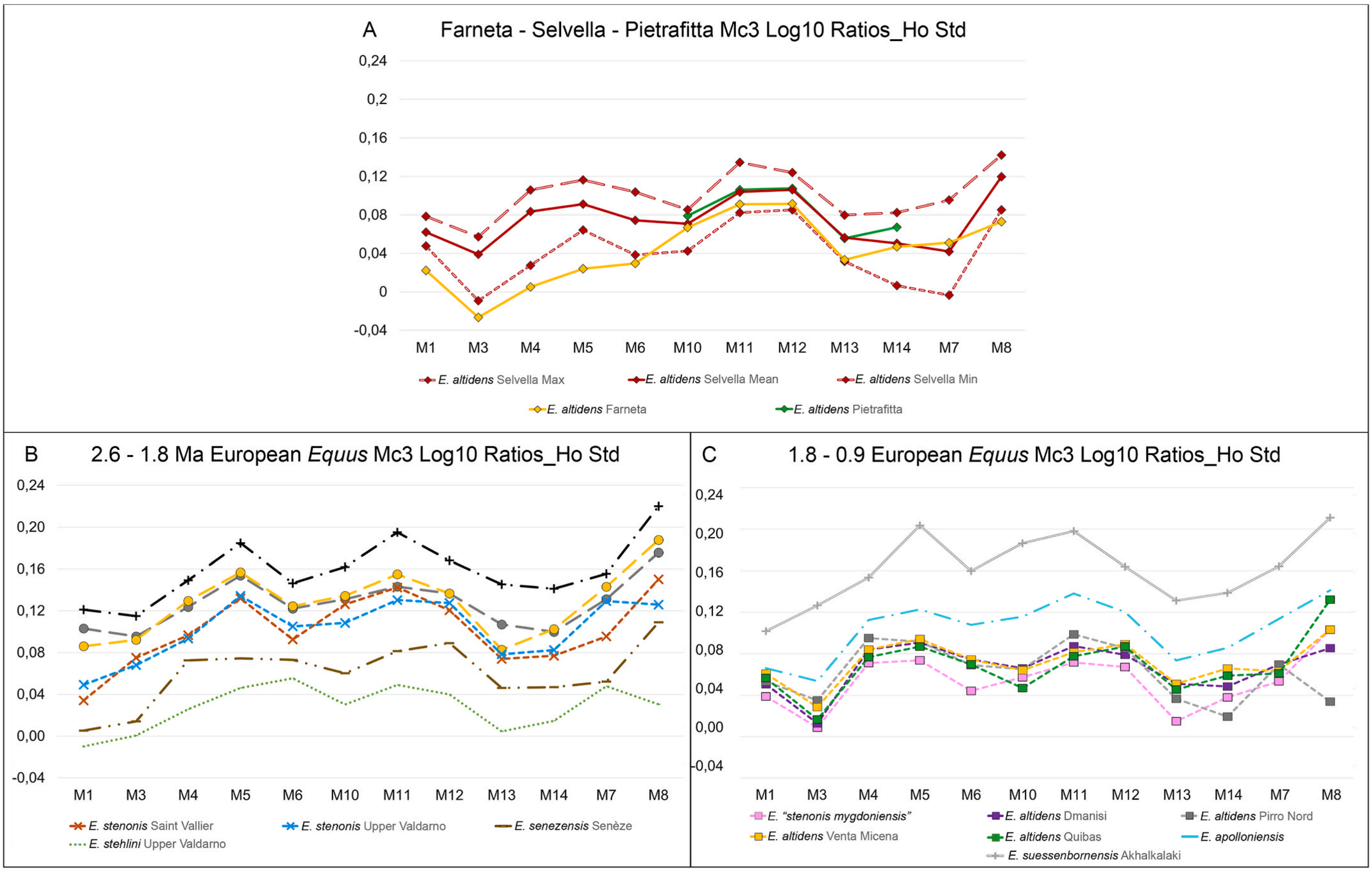

Fig. 9. Log10 ratio diagrams in third metacarpal based on the Log10 transformed mean of the *Hippotherium primigenium* sample from Höwenegg (Germany, Late Miocene). A) *Equus altidens* mc3 variability from Selvella (maximum, mean and minimum values) compared with the mean values of *E. altidens* from Farneta and Pietrafitta. B) Mean values of mc3 variability of *Equus* fossil species from 2.6 to 1.8 Ma. C) Mean values of mc3 variability of *Equus* fossil species from 1.8 to 0.9 Ma. Measurements are referred to Eisenmann et al. (1988) and Bernor et al. (1997).

Micena, and Quibas (Fig. 10C), with slender proportions (M1-M3), and medium-sized diaphysis, proximal, and distal epiphysis (M3-M4, M5-M6, and M10-M14, respectively). As in Fig. 9, the Farneta and Selvella *E. altidens* populations differ from *E. senezensis* and *E. stehlini* (Fig. 10B) for a more elongated M1 and general larger size of their extremities. On the other hand, the range of variability of *E. stenonis* from Selvella is more similar to the mean values of the *E. stenonis* samples from Saint-Vallier and Upper Valdarno (Matassino, Poggio Rosso; Fig. 10B), rather than *E. suessenbornensis* (Fig. 10C). Despite having a longer M1, the Selvella *E. stenonis* has a smaller diaphysis (M3-M4), and less robust proximal (M5-M6) and distal epiphyses (M10-M14) if compared to *E. suessenbornensis* (Fig. 10C).

Overall, these results concur with the previous comparison of the upper and lower dentition and with the PCAs on postcranial elements, supporting the attribution to *E. stenonis* and *E. altidens* for the fossil equids of the Farneta FU.

5.2. Analysis of the variance of the Farneta FU equids compared with the European Early and early Middle Pleistocene stenonid Equus

To test for significant differences between the fossil equids from the Farneta FU and other European *Equus* species, a PERMANOVA was undertaken on the PC values on mc3s and mt3s (Supplementary Table 3). Unfortunately, given the reduced sample in the mt3s (three mt3s from each sample), the best results were obtained for mc3s for the Selvella sample, which includes 10 specimens. These results are reported in Table 2. The PERMANOVA results indicate significant differences between *E. altidens* from Selvella from *E. livenzovensis* (El-Rincon 1, Liventsovka), *E. stenonis* (Saint-Vallier, Upper Valdarno), *E. stehlini*, *E. apolloniensis*, and *E. suessenbornensis* (Akhalkalaki) (p. = 0.0297), as well as with *E. senezensis* (p. = 0.0594). On the other hand, the Selvella *E. altidens* does not show any significant differences with the other *E. altidens* samples (Dmanisi, Pirro Nord, Venta Micena, and Quibas), thus far supporting the results of the PCAs and of the Log10 Ratio Diagrams mentioned above. These results are better supported between pairwise large sample comparison (with at least 10 specimens), which helps to better evaluate their range of variability. The not significant results obtained with *E. major* (Liventsovka, Pardines), *E. stenonis* (Dmanisi, Olivola), and *E. suessenbornensis* (Cueva Victoria, Süssenborn) are related to the limited complete specimens retrieved in these samples used for the PCA. Nevertheless, the results shown in Fig. 7 help to distinguish these samples from the Selvella *E. altidens*.

6. Discussion

6.1. Equus stenonis and Equus altidens from the Farneta FU: new results compared to previous findings

This review of the samples from Farneta, Selvella, and Pietrafitta LFAs provides a new perspective on the large- and middle-sized horses occurring in the Farneta FU. Our results partially agree with previous interpretations, and do not support others. Specifically, the presence of *E. stenonis* in Selvella agrees with the previous identifications by De Giuli, 1986, Forsten (1999), and partially Caloi and Palombo (1987). As preliminary suggested in Cirilli et al. (2023a), the large-sized equids from Selvella are not comparable with the typical *E. suessenbornensis*

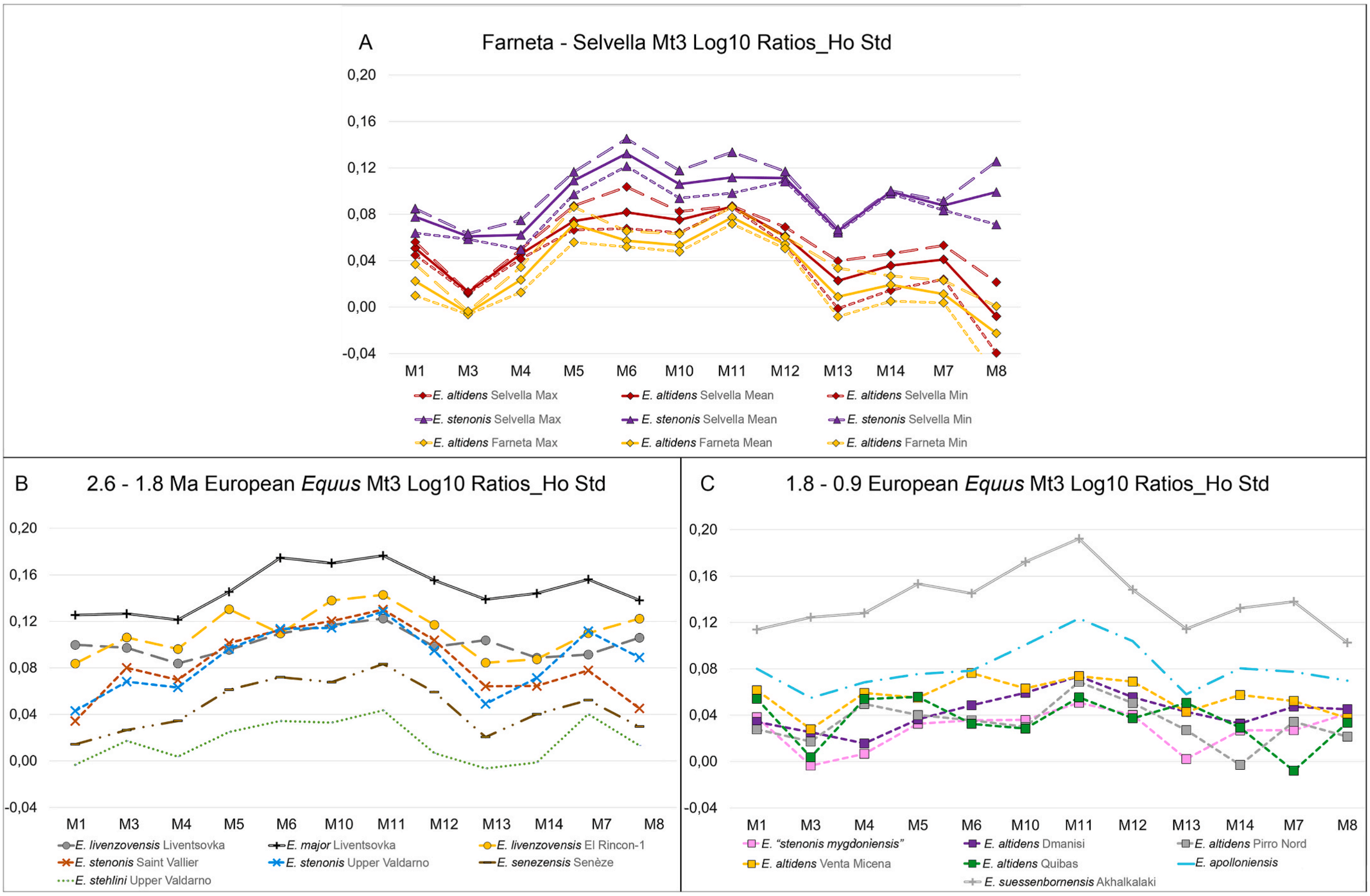

Fig. 10. Log10 ratio diagrams in third metatarsal based on the Log10 transformed mean of the *Hippotherium primigenium* sample from Höwenegg (Germany, Late Miocene). A) *Equus altidens* and *Equus stenonis* mt3 variability from Selvella and Farneta in maximum, mean and minimum values compared. B) Mean values of mt3 variability of *Equus* fossil species from 2.6 to 1.8 Ma. C) Mean values of mt3 variability of *Equus* fossil species from 1.8 to 0.9 Ma. Measurements are referred to Eisenmann et al. (1988) and Bernor et al. (1997).

from Akhalkalaki and Süssenborn, characterized by a larger size of the cranial and postcranial elements (Figs. 5–10), and by a much more complex occlusal enamel morphology of the upper and lower cheek (Cirilli et al., 2023a: figs. 2, 3 and 10). For the medium-to small-sized equids, our results agree with the previous identifications of *E. altidens* (Alberdi and Palombo, 2013a, 2013b), and do not support the presence

Table 2
PERMANOVA results performed on third metacarpal PC values comparing the Selvella *Equus altidens* with the European Early and early Middle Pleistocene *Equus* species.

Pairs	Df	SumsOfSqs	F.Model	R2	*p.value*	*p.adjusted*
E. simplicidens vs *E. altidens* Selvella	1	0.899183699	1.302690507	0.025392245	0.257574243	1.0000
E. livenzovensis Liventsovka vs *E. altidens* Selvella	1	90.85630012	90.82315467	0.812203474	9.999E-05	0.0297
E. livenzovensis Fonelas P1 vs *E. altidens* Selvella	1	67.25493345	83.00158081	0.855672455	0.00019998	0.0594
E. livenzovensis El Rincon-1 vs *E. altidens* Selvella	1	64.35461799	81.5433042	0.835970289	9.999E-05	0.0297
E. major Liventsovka vs *E. altidens* Selvella	1	131.9336846	116.5601835	0.899660531	0.00119988	0.3564
E. major Pardines vs *E. altidens* Selvella	1	30.31998957	30.30389755	0.751885038	0.079492051	1.0000
E. stenonis Saint-Vallier vs *E. altidens* Selvella	1	45.59070431	64.65555143	0.662077583	9.999E-05	0.0297
E. stenonis Upper Valdarno vs *E. altidens* Selvella	1	32.7806055	49.73345852	0.648132633	9.999E-05	0.0297
E. stenonis Dmanisi vs *E. altidens* Selvella	1	14.48411432	15.44021559	0.507230822	0.00069993	0.2079
E. stenonis Olivola vs *E. altidens* Selvella	1	12.57350515	13.45671332	0.456830101	0.00039996	0.1188
E. stenonis mygdoniensis vs *E. altidens* Selvella	1	6.376269243	5.342979889	0.308077385	0.0409959	1.0000
E. senezensis vs *E. altidens* Selvella	1	12.94702315	14.57340458	0.387864894	0.00019998	0.0594
E. stehlini vs *E. altidens* Selvella	1	101.785171	84.57230213	0.758004456	9.999E-05	0.0297
E. apolloniensis vs *E. altidens* Selvella	1	26.84970606	28.83399849	0.525841618	9.999E-05	0.0297
E. altidens Dmanisi vs *E. altidens* Selvella	1	3.256489659	6.355537904	0.161490307	0.01259874	1.0000
E. altidens Pirro Nord vs *E. altidens* Selvella	1	2.530867097	2.24329179	0.092532475	0.135786421	1.0000
E. altidens Venta Micena vs *E. altidens* Selvella	1	1.475583307	1.903267482	0.03344742	0.163983602	1.0000
E. altidens Quibas vs *E. altidens* Selvella	1	2.137735024	1.342449757	0.093599753	0.258174182	1.0000
E. altidens Selvella vs *E. altidens* Sussenborn	1	1.447218439	1.272130435	0.103660114	0.312468753	1.0000
E. suessenbornensis Akhalkalaki vs *E. altidens* Selvella	1	379.2931519	353.7136596	0.902990363	9.999E-05	0.0297
E. suessenbornensis Cueva Victoria vs *E. altidens* Selvella	1	64.49076392	70.80228697	0.865529432	0.01239876	1.0000
E. suessenbornensis Sussenborn vs *E. altidens* Selvella	1	105.3566546	98.68140903	0.891580708	0.00219978	0.6533
E. grevyi vs *E. altidens* Selvella	1	3.135131716	3.831931834	0.08011242	0.04979502	1.0000

of *E. stehlini* in Farneta, Selvella, and Pietrafitta. Although in the comparisons of the upper and lower teeth a certain overlap with *E. stehlini* from Upper Valdarno can be observed, the results on the postcranial elements show a remarkable difference with that sample and, on the other hand, exhibit a striking similarity with the early *E. altidens* samples from Dmanisi, Pirro Nord, Venta Micena and Quibas. Our results are also in agreement with the hypothesis of Gkeme et al. (2017), Bernor et al. (2021), Cirilli et al. (2021b) and Koufos et al. (2022) in considering also the sample from Gerakarou as comparable with these early *E. altidens* samples, although a detailed study on the collection is missing since Koufos (1992). We show that *E. altidens* from Süssenborn (type locality of the species) is included in the range of variability defined by the samples from Dmanisi, Farneta, Selvella, Pietrafitta, Pirro Nord, and Venta Micena.

Our study highlights the presence of two equid species in the Selvella LFA: *E. stenonis* and *E. altidens*, with the latter more abundant by number of specimens retrieved. The greater abundance of the latter species over the former could explain its failure to be recognized in the almost coeval sites of Farneta and Pietrafitta, where a relatively smaller number of horse remains were recovered (especially in the second; Supplementary Table 1).

6.2. Implications for the biochronology of Early Pleistocene Equus species in Western Eurasia

Our review of the Farneta FU equids allows us to shed new insights on the biochronology of the Early Pleistocene *Equus* species in Western Eurasia, especially for the latest occurrence of *E. stenonis* and the earliest of *E. altidens*. As reported by Cirilli et al. (2021b), *E. stenonis* is the most widespread species in the Middle and early Late Villafranchian in Western Eurasia. The species has been reported in several fossil localities dated between ca. 2.5–1.8 Ma (Cirilli et al., 2021b), but its last occurrences are still controversial and not well defined. De Giuli and Torre (1984) reported the occurrence of *E.* ex gr. *stenonis* from Pirro Nord, later changed in *E.* cf. *altidens* (De Giuli et al., 1986). More recently, the fossil equids from Pirro Nord have been ascribed to *E. altidens* and *E. suessenbornensis* (Alberdi and Palombo, 2013a, 2013b), although this identification has been partially challenged by Cirilli et al. (2023a). As shown in Fig. 8C and D, and in Cirilli et al. (2023a), the mt3s from Pirro Nord previously ascribed to *E. suessenbornensis* from Alberdi and Palombo (2013a, 2013b) extensively overlap the range of variability shown by the *E. altidens* and *E. stenonis* samples, remarkably different from the large-sized *E. suessenbornensis* from Akhalkalaki and Süssenborn. On the other hand, *E. suessenbornensis* from Pirro Nord is better reported by isolated teeth (Cirilli et al., 2023a: fig. 10), which show an identical morphology with the Akhalkalaki and Süssenborn fossils. Moreover, Aouadi (1999) and Aouadi and Bonifay (2008) reported *E. stenonis* from Ceyssaguet (France). The measurements provided by these authors (including only maximal, mean, and minimal values) for the species identified in Ceyssaguet, *E. stenonis* and *E. bressanus* (=*E. major*), show a great range of variability, making it difficult to use them for comparative analyses with other Early and early Middle Pleistocene European *Equus* species as provided herein. In Eastern Europe, the best-known record of *E. stenonis* is from Greece. Koufos (1992) and Koufos et al. (2022) reported *E. stenonis* latest known record come from the localities of Krimni 1 and Riza-1, ca. 1.8–1.6 Ma (Konidaris and Kostopoulos, 2024). *Equus stenonis* is not reported from Tsiotra Vryssi, where at the present time *Equus* ex gr. *apolloniensis* has been identified (Konidaris et al., 2015; Konidaris and Kostopoulos, 2024), or from Apollonia-1, where *E. apolloniensis* and *E. suessenbornensis* have been reported (Gkeme et al., 2021; Cirilli et al., 2023a; Konidaris and Kostopoulos, 2024). On the other hand, the latest record of *E. stenonis* in the Iberian Peninsula is known from La Puebla de Valverde (Cirilli et al., 2021b), ca. 2.1–1.95 Ma (Sinusía et al., 2004), while *E. stenonis* is not reported from the locality of Venta Micena (ca. 1.5 Ma), where only *E. altidens* is known (Alberdi and Ruiz Bustos, 1985, 1989; Guerrero-Alba and Palmqvist, 1997; Alberdi and Palombo, 2013a). The results reported in the present work allow to extend the biochronologic range of *E. stenonis* into the Farneta FU (i.e., until ca. 1.6–1.5 Ma), pending the revision of the equid collections from Pirro Nord, Ceyssaguet, and the aforementioned Greek localities.

The taxonomy and biochronology of *E. altidens* are highly debated by different scholars. The species was erected for the Middle Pleistocene sample of Süssenborn, but in the last decades it has been reported in several sites from the late Early and early Middle Pleistocene. Most of the controversy regards its taxonomic status. Some scholars (Alberdi et al., 1998; Alberdi and Palombo, 2013a, 2013b; Palombo et al., 2017; Gkeme et al., 2017; Bernor et al., 2021; Cirilli et al., 2020a, 2021b, 2023a, 2024a; Koufos et al., 2022; Konidaris and Kostopoulos, 2024) recognize the validity of the species, whereas others (Eisenmann and Boulbes, 2020; Eisenmann, 2022b) question it, suggesting to split the middle-sized equid samples ascribed to *E. altidens* in a variety of species as *Equus vekuae* (Dmanisi), *Equus mygdoniensis* (Gerakarou), *Equus granatensis* (Venta Micena), and *Equus* aff. *granatensis* (Pirro Nord), and to restrict *E. altidens* for the only sample of Süssenborn or even questioning its validity as a distinct taxon. Here, we add some pieces of evidence to this discussion which could help to clarify this complicated framework. Our analyses on multiple skeletal elements have shown no morphological, morphometric, or even statistical differences between the samples ascribed to *E. altidens* (Figs. 5–10, Table 2). Moreover, the specimens from the type sample of Süssenborn are always included within the range of variability shown by the other samples here analyzed, making it unlikely to refer these samples to separate taxa. Furthermore, the range of variability shown by the samples from Dmanisi, Gerakarou, central Italy (including Farneta, Selvella, and Pietrafitta), Pirro Nord, Venta Micena, Quibas and Süssenborn is similar to the one shown by the European samples of *E. stenonis* (see Cirilli et al., 2021b), *E. suessenbornensis* (Cirilli et al., 2023a), *E. livenzovensis*, and *E. major* (Cirilli et al., 2024a). The range of variability shown by the studied samples is similar to that shown by *E. stehlini* from Upper Valdarno Basin, which include specimens from different localities of a single basin with a well-constrained age (Cirilli, 2022). These results indicate a remarkable similarity between the populations of these middle-sized equids, not providing compelling evidence to support the hypothesis of splitting them into different species or subspecies. In this regard, the most parsimonious hypothesis is to consider *E. altidens* as a monotypic and polymorphic species and, as *E. stenonis*, the purported species/subspecies proposed in the past years do not warrant taxonomic distinction at the species or subspecies rank and could represent local eco-morphotypes of a single widespread species. Nevertheless, this hypothesis needs to be tested with large samples from other Western Eurasian sites not included here, where these middle-sized equids have been reported. At the present time, this hypothesis needs to be considered preliminary rather than conclusive, not disregarding the chance that local speciation events could have occurred leading to the origin of different species (e.g., *E. wuesti* from Untermassfeld).

Our study supports the identification of a middle-sized equid from the Farneta FU different from *E. stehlini* which we refer to *E. altidens*, supporting the previous identification of Alberdi and Palombo (2013a, 2013b). This is in agreement also with the hypothesis provided by Gkeme et al. (2017), Bernor et al. (2021), Cirilli et al. (2022), and Koufos et al. (2022), to consider the first occurrence of *E. altidens* in the Caucasus and Greece at ca. 1.8 Ma (Dmanisi, Gerakarou), with a subsequent dispersal of the species toward Central and Western Europe during the Farneta FU (cf. central Italian sites studied herein, Venta Micena). An updated biochronological scheme of Early Pleistocene *Equus* species is reported in Fig. 11.

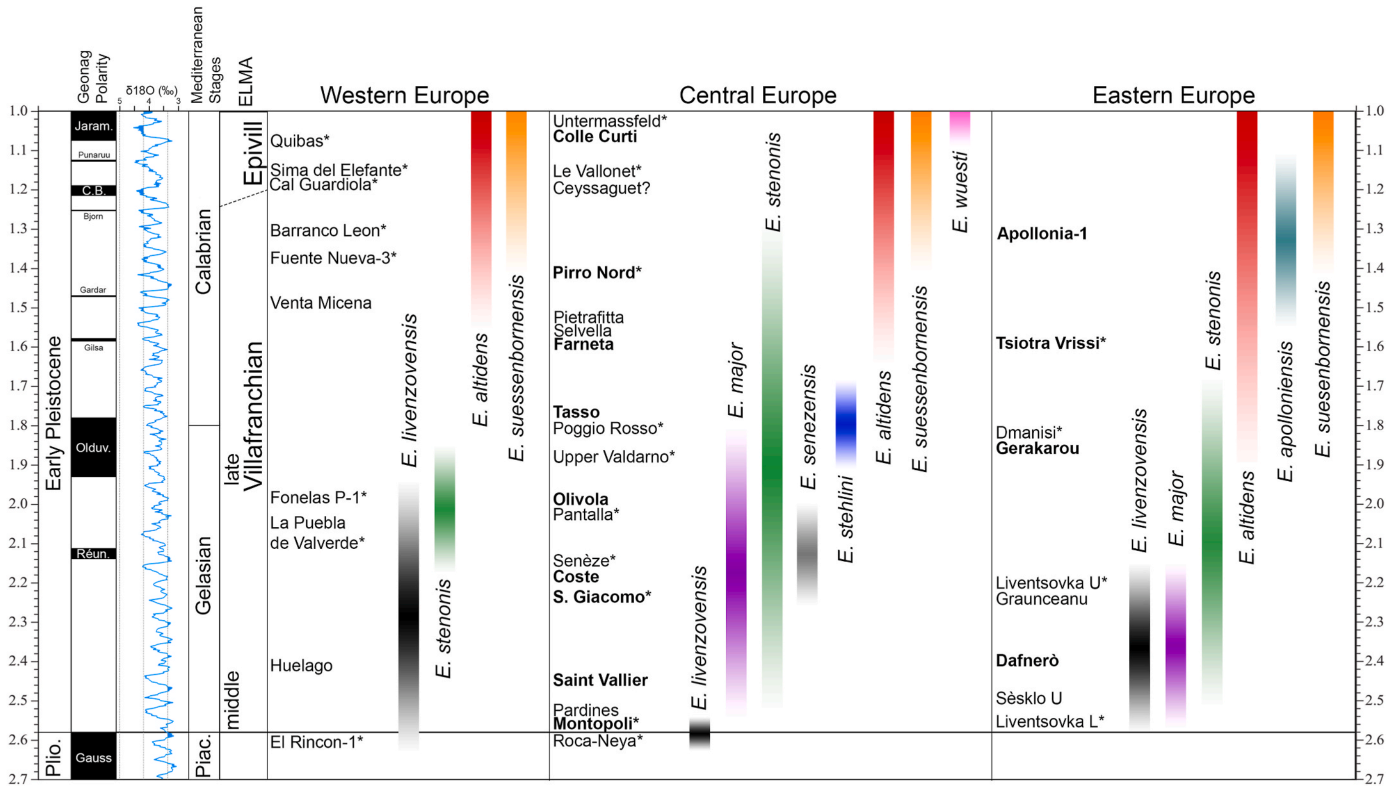

Fig. 11. Updated biochronological scheme of European *Equus* fossils species of the Late Pliocene and Early Pleistocene. Each *Equus* species' occurrence is represented in each locality with its age range. The Quaternary chronology on the left refers to Gibbard and Head (2020). Asterisks indicate those localities with well supported geochronology, by means of magnetostratigraphic, radiometric, or other absolute dating. Liventsovka: Tesakov et al. (2007a, 2007b); Titov (2008). Dmanisi: Ferring et al. (2011). Tsiotra Vrissi: Konidaris et al. (2021). Montopoli: Lindsay et al. (1980). Roca-Neyra and Senèze: Nomade et al. (2014). Coste San Giacomo: Bellucci et al. (2014). Pantalla: Cherin et al. (2023). Upper Valdarno and Poggio Rosso: Fidolini et al. (2013). Pirro Nord: Pavia et al. (2012); Bertok et al. (2013). Untermassfeld: Kahlke (2022); El Rincon-1: Alberdi et al. (1997). La Puebla de Valverde: Sinusía et al. (2004). Fonelas P-1: Arribas et al. (2009). Fuente Nueva-3: Duval et al. (2012). Barranco Leon: Toro-Moyano et al. (2013). Cal Guardiola: Madurell-Malapeira et al. (2010). Sima del Elefante: Carbonell et al. (2008). Quibas: Piñero et al. (2020, 2022).

Fig. 12. Visual representation of the Early Pleistocene locality of Farneta with the presence of two *Equus* fossil species. On the left: *Equus stenonis*, on the right: *Equus altidens*. Artwork by Isacco Alberti.

7. Conclusions

Our review of the fossil equids from the Farneta FU has allowed us to better clarify their taxonomy and has provided new insights on the paleobiogeography and biochronology of *Equus* species of Western Eurasia. The presence of *E. stenonis* remarks a continuity with the Tasso FU, and it allows to better frame the occurrence of this species to date. Moreover, these results support the oldest occurrence of *E. suessenbornensis* in the locality of Pirro Nord in the Italian fossil record, as recently reported (Arzarello et al., 2009; Cirilli et al., 2023a). On the other hand, the recognition of *E. altidens* marks a renewal in the Italian fossil record of the latest Villafranchian. This, combined with the first occurrences of *Ps. farnetensis*, *Pr. obscurus*, and *B.* (*Eobison*) *degiulii*, highlight the importance of the Farneta FU in the Italian (and Western Eurasian) biochronological record, being placed in a timeframe (ca. 1.6–1.5) where few localities have been reported in Western Eurasia (Rook and Martínez-Navarro, 2010; Kahlke et al., 2011). Ultimately, this work provides a new contribution in the definition of *E. altidens* and related forms, allowing at better clarifying its systematics. An artistic representation of the co-occurrence of *E. stenonis* and *E. altidens* in Selvella is given in Fig. 12.

Autor contribution

F.B, O.C., L.B., M.C. and M.B. conceived the paper. F.B, O.C. and M.C. collected the data. F.B. and O.C. wrote the preliminary draft of the manuscript, designed and produced the figures. O.C. performed the morphometric analyses. I.A. made the final illustration. All authors discussed and interpreted the results and equally contributed to finalize the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix B. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.quascirev.2025.109593.

Data availability

All data and/or code is contained within the submission.

References

Abbazzi, L., 1995. *Megaceroides obscurus* from the Val di Chiana (Cava Liberatori, Tuscany, Central Italy, Farneta f.u., Early Pleistocene). Remarks on the early evolution and systematics of *Megaceroides*. Boll. Soc. Paleont. Ital. 34 (2), 223–234.

Abbazzi, L., 2004. Remarks on the validity of the generic name *Praemegaceros* Portis 1920, and an overview on *Praemegaceros* species in Italy. Rendiconti Lincei 9 (15), 115–132.

Alberdi, M.T., 2010. Estudio de los caballos de los yacimientos de Fuente Nueva-3 y Barranco León-5 (Granada). In: Toro, I., Martínez-Navarro, B., Agustí, J. (Eds.), Ocupaciones Humanas En El Pleistoceno Inferior Y Medio De La Cuenca De Guadix-Baza. Junta de Andalucía, Consejería de Cultura, pp. 291–306.

Alberdi, M.T., Caloi, L., Palombo, M.R., 1988. The Quaternary fauna of Venosa: equidae. Bull. Musee Anthropol. Prehist. Monaco 31, 5–39.

Alberdi, M.T., Palombo, M.R., 2013a. The late early to early middle Pleistocene stenonoid horses from Italy. Quat. Int. 288, 25–44.

Alberdi, M.T., Palombo, M.R., 2013b. The early Pleistocene Equidae from Pirro Nord (Apricena, Southern Italy). Palaeontograph. Abt. 298, 147–167.

Alberdi, M.T., Piñero, P., 2015. Estudio de los caballos del yacimiento de Cueva Victoria, Pleistoceno Inferior (Murcia). In: Gilbert, L., Ferràndez-Canadell, C. (Eds.), Geologia Y Paleoontologia De Cueva Victoria, vols. 11–13. Rivista del Museo Arquelogico Municipal de Cartagena, p. 285.

Alberdi, M.T., Ruiz Bustos, A., 1985. Descripción y significado biostratigrafico y climatico del *Equus* e *Hippopotamus*, en el yacimiento de Venta Micena. Est. Geol. 41, 251–261.

Alberdi, M.T., Ruiz–Bustos, A., 1989. “Taxonomía y Biostratigrafía de Equidae (Mammalia, Perissodactyla) en la cuenca de Guadix–Baza (Granada)” in Geología y Paleontología de la Cuenca de Guadix-Baza. In: Alberdi, M.T., Bonadonna, F.P. (Eds.), Trabajos Sobre Neógeno-Cuaternario 11, 239–271.

Alberdi, M.T., Cerdeno, E., Lopez-Martínez, Morales, J., Soria, M.D., 1997. La fauna villafranquiense de El rincon-1 (Albacete, Castilla-La mancha). Estud. Geol. (Madr.) 53, 69–93.

Alberdi, M.T., Ortiz-Jaureguizar, E., Prado, J.L., 1998. A quantitative review of European stenonoid horses. J. Paleontol. 72, 371–387.

Alberdi, M.T., Jaureguizar, E.O., Prado, J.L., 2001. Comments on “*Equus* species as stratigraphic markers. Reality or wishful thinking?” and “A review of *Equus stenonis* Cocchi (Perissodactyla, Equidae) and related forms” by A. Forsten. Quat. Sci. Rev. 20, 1149–1152.

Ambrosetti, P., Azzaroli, A., Bonadonna, F.P., Follieri, M., 1972. A scheme of Pleistocene chronostratigraphy for the Tyrrhenian side of Central Italy. Boll. Soc. Geol. Ital. 91, 169–184.

Ambrosetti, P., Cattuto, C., Gregori, L., 1989. Geomorfologia e neotettonica nel bacino di Tavernelle/Pietrafitta (Umbria). Il Quat. 2, 57–64.

Ambrosetti, P., Azzaroli, A., Bonadonna, F.P., Follieri, M., 1972. A scheme of Pleistocene chronology for the thyrrhenian side of central Italy. Bollettino della Societa Geologica Italiana 91, 169–184.

Ambrosetti, P., Basilici, G., Capasso Barbato, L., Carboni, M.G., Di Stefano, G., Esu, D., Gliozzi, E., Petronio, C., Sardella, R., Squazzini, E., 1995. Il Pleistocene inferiore nel ramo Sud-Occidentale del Bacino Tiberino (Umbria): aspetti litostratigrafici e biostratigrafici. Il Quat. 8 (1), 19–36.

Aouadi, N., 1999. Etude préliminaire des restes cranes de chevaux Villafranchiens. Bull. Musée d’Anthropol. Prehist. Monaco 40, 23–42.

Aouadi, N., Bonifay, M.F., 2008. Les métapodes des chevaux de Ceyssaguet: études morphologiques et biométriques. Bull. Musée d’Anthropol. Prehist. Monaco 48, 17–29.

Arribas, A., Garrido, G., Viseras, C., Soria, J.M., Pla, S., Solano, J.G., Garces, M., Beamud, E., Carrion, J.S., 2009. A mammalian lost world in southwest Europe during the late Pliocene. PLoS One 4, e7127.
Aruta, G., Bruni, P. Cecchi G., 2007. Stratigraphy and structural setting of the Northern Apennines in the Upper Arno's watershed. EPITOME 2, 402.
Arzarello, M., Marcolini, F., Pavia, G., Pavia, M., Petronio, C., Petrucci, M., Rook, L., Sardella, R., 2009. L'industrie lithique du site Pléistocène inférieur de Pirro Nord (Apricena, Italie du sud): une occupation humaine entre 1,3 et 1,7 Ma. l'Anthropologie 113 (1), 47–58. https://doi.org/10.1016/j.anthro.2009.01.004.
Azzarà, B., Breda, M., Cirilli, O., Madurell-Malapeira, J., Ruzza, F., Sorbelli, L., Tancredi, D., Cherin, M., 2022. Vigna Nuova: the first Middle Villafranchian mammal assemblage from the Valdichiana Basin, Perugia (Italy). Boll. Soc. Paleont. It. 61 (2), 223–247.
Azzaroli, A., 1964. The two villafranchian horses of the Upper Valdarno. Palaeontogr. Ital. 59, 1–12.
Azzaroli, A., 1977. The Villafranchian stage in Italy and the Plio-Pleistocene boundary. Giornal. Geol. 41, 61–79.
Azzaroli, A., 1982. On villafranchian palaearctic equids and their allies. Palaeontogr. Ital. 72, 74–97.
Azzaroli, A., 1983. Quaternary mammals and the "end-Villafranchian" dispersal event. A turning point in the history of Eurasia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 44, 117–139.
Azzaroli, A., 1990. The genus *Equus* in Europe. In: Lindsay, E.H., Fahlbusch, V., Mein, P. (Eds.), European Neogene Mammal Chronology. Plenum Press, New York, pp. 339–355.
Azzaroli, A., 1992. The cervid genus *Pseudodama n. g.* in the Villafranchian of Tuscany. Palaeontogr. Ital. 79, 1–41.
Azzaroli, A., 1998. Biogeography of early and Early/Mid-Pleistocene Mammalian faunas of Italy. Biogeographia, n.s. 19, 31–40.
Azzaroli, A., 2000. On *Equus livenzovensis* Baigusheva 1978 and the "stenonid" lineage of equids. Paleontogr. Ital. 87, 1–17.
Azzaroli, A., 2003. Phylogeny of the genus *Equus* L. Palaeontogr. Ital 84, 11–16.
Azzaroli, A., Ambrosetti, P., 1970. Late Villafranchian and early middle Pleistocene faunas in Italy. Palaeogeogr. Palaeoclimatol. Palaeoecol. 8, 107–111.
Azzaroli, A., Mazza, P., 1993. Large early Pleistocene deer from Pietrafitta lignite mine, central Italy. Palaeontogr. Ital. 80, 1–24.
Azzaroli, A., Voorhies, M.R., 1993. The genus *Equus* in North America. The Blancan species. Palaeontogr. Ital. 80, 175–198.
Bartolini-Lucenti, S., Cirilli, O., Pandolfi, L., Rook, L., 2022. The Montopoli site, a reference local fauna in the Pliocene and Pleistocene European large mammals biochronology, first discovered by Giovanni Capellini (1833-1922). Boll. Soc. Paleontol. Ital. 61, 207–222.
Bellucci, L., Bona, F., Corrado, P., Magri, D., Mazzini, I., Parenti, F., Scardia, G., Sardella, R., 2014. Evidence of late Gelasian dispersal of African fauna at Coste San Giacomo (Anagni Basin, central Italy): early Pleistocene environments and the background of early human occupation in Europe. Quat. Sci. Rev. 96, 72–85.
Bellucci, L., Palombo, M.R., De Miguel, D., Strani, F., Alberdi, M.T., 2021. New taxonomical, biochronological and paleoenvironmental data from the Middle Pleistocene site of Cullar de Baza 1 (Granada, Spain). Quat. Sci. Rev. 261, 106932.
Bernor, R.L., Tobien, H., Hayek, L.A.C., Mittmann, H.W., 1997. *Hippotherium primigenium* (Equidae, Mammalia) from the late Miocene of Höwenegg (Hegau, Germany). Andrias 10, 1–230.
Bernor, R.L., Cirilli, O., Wang, S.Q., Rook, L., 2018. *Equus* cf. *livenzovenzis* from Montopoli, Italy (Early Pleistocene; MN16b; ca. 2.6 Ma). Boll. Soc. Paleontol. Ital. 57, 203–216.
Bernor, R.L., Cirilli, O., Jukar, A.M., Potts, R., Buskianidze, M., Rook, L., 2019. Evolution of early *Equus* in Italy, Georgia, the Indian subcontinent, East Africa, and the origins of African zebras. Front. Ecol. Evol. 7, 166. https://doi.org/10.3389/fevo.2019.00166.
Bernor, R.L., Cirilli, O., Buskianidze, M., Lordkipanidze, D., Rook, L., 2021. The Dmanisi *Equus*: systematics, biogeography and paleoecology. J. Hum. Evol. 158, 103051. https://doi.org/10.1016/j.jhevol.2021.103051.
Bertok, C., Masini, F., Di Donato, V., Martire, L., Pavia, M., Zunino, M., Pavia, G., 2013. Stratigraphic framework of the type-locality of Pirro Nord mammal faunal unit (late villafranchian, apricena, southeastern Italy). Palaeontogr. Abt. 298, 5–17.
Bona, F., Sala, B., 2016. Villafranchian-Galerian mammal faunas transition in South-Western Europe. The case of the late early Pleistocene mammal fauna of the Frantoio locality, Arda River (Castell'Arquato, Piacenza, Northern Italy). Geobios 754, 1–19.
Boulbes, N., van Asperen, E.N., 2019. Biostratigraphy and palaeoecology of European *Equus*. Front. Ecol. Evol. 7, 301. https://doi.org/10.3389/fevo.2019.00301.
Bourguignon, L., Crochet, J.Y., Capdevila, R., Ivorra, J., Antoine, P.O., Agustí, J., Barsky, D., Blain, H.-A., Boulbes, N., Bruxelles, L., Claude, J., Cochard, D., Filoux, A., Firmat, C., Lozano-Fernandez, I., Magniez, P., Pelletier, M., Rios-Garaizar, J., Testu, A., Valensi, P., De Weyer, L., 2016. Bois-de-Riquet (Lézignan-la-Cèbe, Hérault): a late early Pleistocene archeological occurrence in southern France. Quat. Int. 393, 24–40.
Breda, M., Kahlke, R.D., Lister, A.M., 2020. New results on cervids from the early Pleistocene site of Untermassfeld. In: Kahlke, R.D. (Ed.), Das Pleistozän Von Untermassfeld Bei Meiningen (Thüringen), vol. 4. Monographien des RGZM, pp. 1197–1249.
Caloi, L., 1995. Il genere Equus nell'Italia centrale. In: Farinacci, A. (Ed.), Biostratigrafia Dell'Italia Centrale, pt. B. Studi Geologici Camerti. Vol. spec., pp. 469–486
Caloi, L., Palombo, M.R., 1987. Osservazioni sugli equidi italiani del Pleistocene Medio inferiore. Geolog. Rom. 26, 187–221.
Carbonell, E., Bermúdez de Castro, J.M., Parés, J.M., Pérez, G.A., Cuenca-Bescós, G., Ollé, A., Mosquera, M., Huguet, R., van der Made, J., Rosas, A., Sala, R., Vallverdú, J., García, N., Granger, D.E., Martinón-Torres, M., Rodríguez, X.P., Stock, G.M., Vergès, J.M., Allué, E., Burjachs, F., Cáceres, I., Canals, A., Benito, A., Díez, C., Lozano, M., Mateos, A., Navazo, M., Rodríguez, J., Rosell, J., Arsuaga, J.L., 2008. The first hominin of Europe. Nature 452, 465–469.
Cherin, M., Bizzarri, R., Buratti, N., Caponi, T., Grossi, F., Kotsakis, T., Pandolfi, L., Pazzaglia, F., Barchi, M.R., 2012. Multidisciplinary study of a new Quaternary mammal-bearing site from Ellera di Corciano (central Umbria, Italy): preliminary data. Rend. Onl. Soc. Geol. Ital. 21, 1075–1077.
Cherin, M., Iurino, D.A., Sardella, R., 2013. New well-preserved material of *Lynx issiodorensis valdarnensis* (Felidae, Mammalia) from the early Pleistocene of Pantalla (Central Italy). Boll. Soc. Paleontol. Ital. 52, 103–111.
Cherin, M., Berte, D.F., Rook, L., Sardella, R., 2014. Re-defining *Canis etruscus* (Canidae, Mammalia): a new look into the evolutionary history of early Pleistocene dogs resulting from the outstanding fossil record from Pantalla (Italy). J. Mamm. Evol. 21, 95–110.
Cherin, M., Iurino, D.A., Zanatta, M., Fernandez, V., Paciaroni, A., Petrillo, C., Rettori, R., Sardella, R., 2018. Synchrotron radiation reveals the identity of the large felid from Monte Argentario (Early Pleistocene, Italy). Sci. Rep. 8, 8338.
Cherin, M., Cirilli, O., Azzarà, B., Bernor, R.L., 2021. *Equus stenonis* (Equidae, Mammalia) from the early Pleistocene of Pantalla (Italy) and the dispersion of stenonine horses in Europe. Boll. Soc. Paleontol. Ital. 60, 1–18.
Cherin, M., Breda, M., Esattore, B., Hart, V., Turek, J., Porciello, F., Angeli, G., Holpin, S., Iurino, D.A., 2022. A Pleistocene Fight Club revealed by the palaeobiological study of the Dama-like deer record from Pantalla (Italy). Sci. Rep. 12, 13898.
Cherin, M., Basilici, G., Duval, M., Shao, Q., Sier, M., Parés, J.M., Gliozzi, E., Mazzini, I., Magri, D., Di Rita, F., Iurino, D.A., Azzarà, B., Margaritelli, G., Pazzaglia, F., 2023. The dawn of the late Villafranchian: paleoenvironment and age of the pantalla paleontological site (Italy; early Pleistocene). Quat. Sci. Rev. 316, 108279.
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. Ital. Paleontol. Strat. 128, 231–255.
Cirilli, O., Pandolfi, L., Bernor, R.L., 2020a. The Villafranchian perissodactyls of Italy: knowledge of the fossil record and future research perspectives. Geobios 63, 1–21.
Cirilli, O., Melchionna, M., Serio, C., Bernor, R.L., Bukhsianidze, M., Lordkipanidze, D., Rook, L., Profico, A., Raia, P., 2020b. Target deformation of the *Equus stenonis* holotype skull: a virtual reconstruction. Front. Earth Sci. 8, 247. https://doi.org/10.3389/feart.2020.00247.
Cirilli, O., Pandolfi, L., Rook, L., Bernor, R.L., 2021a. Evolution of Old World *Equus* and origin of the zebra-ass clade. Sci. Rep. 11, 10156. https://doi.org/10.1038/s41598-021-89440-9.
Cirilli, O., Saarinen, J., Pandolfi, L., Rook, L., Bernor, R.L., 2021b. An updated review on *Equus stenonis* (Mammalia, Equidae): new implications for the European Early Pleistocene *Equus* taxonomy and paleoecology, and remarks on the Old World *Equus* evolution. Quat. Sci. Rev. 269, 107155. https://doi.org/10.1016/j.quascirev.2021.107155.
Cirilli, O., Bernor, R.L., Rook, L., 2021c. New insights on the early Pleistocene equids from Roca-Neyra (France, central Europe): implications for the *Hipparion* LAD and the *Equus* FAD in Europe. J. Paleontol. 95, 406–425.
Cirilli, O., Machado, H., Arroyo-Cabrales, J., Barron-Ortiz, C.I., Davis, E., Jass, C.N., Jukar, A.M., Landry, Z., Marin-Leyva, A.H., Pandolfi, L., Pushkina, D., Rook, L., Saarinen, J., Scott, E., Semprebon, G., Strani, F., Villavicencio, N.A., Kaya, F., Bernor, R.L., 2022. Evolution of the family Equidae, subfamily Equinae, in North, Central and South America, Eurasia and Africa during the Plio-Pleistocene. Biology 11, 1258.
Cirilli, O., Saarinen, J., Bukhsianidze, M., Lordkipanidze, D., Bernor, R.L., 2023a. *Equus suessenbornensis* from Akhalkalaki (Georgia, Caucasus): a review with new insights on the paleoecology, paleobiogeography and evolution of the palearctic large-sized equids during the early – middle Pleistocene Transition. Quat. Sci. Rev. 314, 108188.
Cirilli, O., Pandolfi, L., Alba, D.M., Madurell-Malapeira, J., Bukhsianidze, M., Kordos, L., Lordkipanidze, D., Rook, L., Bernor, R.L., 2023b. The last Plio-Pleistocene hipparions of Western Eurasia. A review with remarks on their taxonomy, paleobiogepgraphy and evolution. Quat. Sci. Rev. 306, 107976.
Cirilli, O., Saarinen, J., Bernor, R.L., 2024a. Lost in the collections. A critical re-appraisal on *Equus major* provides a new perspective on the paleobiogeography of the Plio-Pleistocene European equids and on the *Equus* Datum. Quat. Sci. Rev. 323, 108428.
Cirilli, O., Semprebon, G., Bernor, R.L., 2024b. Paleodietary reconstruction of *Equus simplicidens* from the Hagerman Horse Quarry (Idaho, USA) highlights high abrasive habits in North American fossil equids during the Pliocene. Palaeogeogr. Palaeoclimatol. Palaeoecol. 650, 112376.
Cocchi, I., 1867. L'uomo fossile dell'Italia Centrale. Mem. Soc. Ital. Sci. Nat. 2, 1–180.
De Giuli, C., 1972. On the type form of *Equus stenonis* Cocchi. Palaeontogr. Ital. 48, 35–48.
De Giuli, C., 1986. Late villafranchian faunas of Italy: the Selvella local fauna in the Southern Chiana Valley, Umbria. Palaeontogr. Ital. 74, 11–50.
De Giuli, C., Masini, F., 1986. Late villafranchian faunas in Italy: the Casa frata local fauna (upper valdarno, tuscany). Palaeontogr. Ital. 74, 1–9.
De Giuli, C., Torre, D., 1984. A microfauna with *Allophaiomys pliocaenicus* from Gargano (Southern Italy). Paleont. Ital. 73, 116–128.
De Giuli, C., Masini, F., Torre, D., 1986. The late villafranchian faunas in Italy: the Pirro Nord fauna (Apricena, Gargano). Paleontogr. Ital. 74, 51–62.
Duval, M., Falguères, C., Bahain, J.-J., Grün, R., Shao, Q., Aubert, M., Dolo, J.-M., Agusti, J., Martínez–Navarro, B., Palmqvist, P., Toro-Moyano, I., 2012. On the limits of using combined U–series/ESR method to date fossil teeth from two early Pleistocene archaeological sites of the Orce area (Guadix–Baza basin, Spain). Quat. Res. 77, 482–491.

Eisenmann, V., 1980. Les Chevaux (*Equus* Sensu Lato) Fossiles Et Actuels: Crânes Et Dents Jugales Supérieures. Editions du Centre National de la Recherche Scientifique, CNRS, Paris.
Eisenmann, V., 2004. Les Équidés (Mammalia, Perissodactyla) de Saint-Vallier (Drôme, France) et les Équidés plio-pléistocènes d'Europe. Geobios 37, 279–305.
Eisenmann, V., 2022a. The equids from Liventsovka and other localities of the Khaprovskii Faunal Complex, Russia: a revision. Geobios 70, 17–33.
Eisenmann, V., 2022b. Old world fossil *Equus* (Perissodactyla, mammalia), extant wild relatives and incertae sedis forms. Quaternary 5, 38.
Eisenmann, V., Boulbes, N., 2020. New results on equids from the Early Pleistocene site of Untermassfeld. In: Kahlke, R.D. (Ed.), The Pleistocene of Untermassfeld near Meiningen (Thütingen, Germany), Part. 4. Römisch Germanischen Zentralmuseums, Weimar, pp. 1295–1321.
Eisenmann, V., Alberdi, M.T., De Giuli, C., Staesche, U., 1988. Methodology. In: Woodburne, M., Sondaar, P.Y. (Eds.), Studying Fossil Horses. EJ Brill Press, Leiden, pp. 1–71.
Ferring, R., Oms, O., Agustí, J., Berna, F., Nioradze, M., Sheila, T., Tappen, M., Vekua, A., Zhvania, D., Lordkipanidze, D., 2011. Earliest human occupations at Dmanisi (Georgian Caucasus) dated to 1.85-1.78 Ma. Proc. Natl. Acad. Sci. USA 108, 10432–10436.
Fidolini, F., Ghinassi, M., Magi, M., Papini, M., Sagri, M., 2013. The Plio-Pleistocene, fluvio-lacustrine Upper Valdarno Basin (Central Italy): Stratigraphy and Basin fill evolution. Italian Journal of Geoscience 132, 13–32.
Forsten, A., 1999. A review of *Equus stenonis* Cocchi (Perissodactyla, Equidae) and related forms. Quat. Sci. Rev. 18, 1373–1408.
Geoportal of the Tuscany Region. Available online: http://www.regione.toscana.it/-/geoscopio (accessed on Novembre 2024).
Garrido, G., 2008. The Perissodactyls (*Equus* cf. *major* Depéret, 1893 and *Stephanorhinus etruscus* Falconer, 1859) of the Late Upper Pliocene Fonelas P-1 Site (Gaudix Basin, Granada), 10. Cuadernos del Museo Geominero, pp. 553–595.
Gentili, S., Mottura, A., Rook, L., 1998. The Italian fossil primate record: recent finds and their geological context. Geobios 31, 675–686.
Gibbard, P.L., Head, M.J., 2020. The Quaternary period. In: Gradsteinm, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.), Geologic Time Scale 2020 2, 1217–1255.
Gilbert, L., Scott, G., 2015. Edad del yacimiento de Cueva Victoriay su relaciòn con otros yacimientos de la Península Ibérica. In: Gilbert, L., Ferràndez-Canadell, C. (Eds.), Geologia Y Paleoontologia De Cueva Victoria. Rivista Del Museo Arquelogico Municipal De Cartagena 11-13, pp. 85–101.
Gkeme, A.G., Koufos, G.D., Kostopoulos, D.S., 2017. The early Pleistocene stenonoid horse from Libakos (Western Macedonia, Greece): biochronological and palaeoecological implications and dispersal events. In: Drina, H., Antonarakou, A., Dermitzakis, M.D., Anastasakis, G., Kontakiotis, G., Karakitsios, V., Tsourou, T., Louvari, M. (Eds.), Proceedings of the Abstracts of 15th Congress of the Regional Committee on Mediterranean Neogene Stratigraphy: Exploring a 'Physical Laboratory: the Mediterranean Basin, p. 67.
Gkeme, A.G., Koufos, G.D., Kostopoulos, D.S., 2021. Reconsidering the equids from the early Pleistocene fauna of Apollonia 1 (Mygdonia Basin, Greece). Quaternary 4, 12. https://doi.org/10.3390/quat4020012.
Gray, H., 1821. On the natural arrangement of vertebrose animals. London Medic. Rep. Rev. 15, 296–310.
Gliozzi, E., Abbazzi, L., Argenti, P., Azzaroli, A., Caloi, L., Capasso, Barbato L., Di, Stefano G., Esu, D., Ficcarelli, G., Girotti, O., Kotsakis, T., Masini, F., Mazza, P., Mezzabotta, C., Palombo, M.R., Petronio, C., Rook, L., Sala, B., Sardella, R., Zanalda, E., Torre, D., 1997. Biochronology of selected mammals, molluscs and ostracods from the Middle Pliocene to the Late Pleistocene in Italy. The state of the art. Riv. Ital. Paleontol. Stratigr. 103, 369–388.
Guerrero-Alba, S., Palmqvist, P., 1997. Estudio morfométrico del caballo de Venta Micena (Orce, Granada) y su comparación con los equidos modernos y del Plio-Pleistoceno en el viejo mundo. Paleontol. Evol. 30–31, 93–148.
Kahlke, R.-D., 2014. The origin of Eurasian mammoth faunas (Mammuthus–Coelodonta faunal complex). Quat. Sci. Rev. 96, 32–49.
Kahlke, R.D., 2022. The Pleistocene of Untermassfeld - a synopsis of site origin, palaeobiodiversity, taphonomic characteristics, palaeoenvironment, chronostratigraphy, and significance in Western Palaearctic faunal history. In: Kahlke, R.D. (Ed.), The Pleistocene of Untermassfeld near Meiningen (Thüringen, Germany) Part 5. Monographien des Römisch-Germanischen Zuntralmuseums 40 (5), 1635–1734.
Kahlke, R.-D., García, N., Kostopoulos, D.S., Lacombat, F., Lister, A.M., Mazza, P.P.A., Spassov, N., Titov, V.V., 2011. Western Palaearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe. Quat. Sci. Rev. 30, 1368–1395.
Konidaris, G.E., Kostopoulos, D.S., 2024. The late pliocene–middle Pleistocene large mammal faunal units of Greece. Quaternary 7, 27. https://doi.org/10.3390/quat7020027.
Konidaris, G.E., Tourloukis, V., Kostopoulos, D.S., Thompson, N., Giusti, D., Michailidis, D., Koufos, G.D., Harvati, K., 2015. Two new vertebrate localities from the Early Pleistocene of Mygdonia Basin (Macedonia, Greece): preliminary results. C. R. Palevol 14, 353–362.
Konidaris, G.E., Kostopoulos, D.S., Maron, M., Schaller, M., Ehlers, T.A., Aidona, E., Marini, M., Tourloukis, V., Muttoni, G., Koufos, G.D., Harvati, K., 2021. Dating of the lower Pleistocene vertebrate site of Tsiotra Vryssi (Mygdonia Basin, Greece): biochronology, magnetostratigraphy, and cosmogenic radionuclides. Quaternary 4, 1. https://doi.org/10.3390/quat4010001.
Konidaris, G.E., Kostopoulos, D.S., 2024. The late pliocene–middle Pleistocene large mammal faunal units of Greece. Quaternary 7, 27.
Koufos, G.D., 1992. Early Pleistocene equids from Mygdonia Basin (Macedonia, Greece). Palaeontogr. Ital. 79, 167–199.
Koufos, G.D., Kostopoulos, D.S., 1993. A stenonoid horse (Equidae, Mammalia) from the Villafranchian of Western Macedonia (Greece). Bull. Geol. Soc. Greece 28, 131–143.
Koufos, G.D., Vlachou, T., 1997. *Equus stenonis* from the middle villafranchian locality of Volax (Macedonia, Greece). Geodiversitas 19, 641–653.
Koufos, G.D., Kostopoulos, D.S., Sylvestrou, I.A., 1997. *Equus apolloniensis* n. sp. (Mammalia, Equidae) from the latest Villafranchian locality of Apollonia, Macedonia, Greece. Paleontologia i Evolucio 30–31, 49–76.
Koufos, G.D., Vlachou, T., Gkeme, A., 2022. The fossil record of equids (Mammalia: perissodactyla: equidae) in Greece. In: Vlachos, E. (Ed.), Fossil Vertebrates of Greece, vol. 2. Springer, Dortrecht, pp. 351–401.
Lindsay, E.H., Opdyke, N.D., Johnson, N.M., 1980. Pliocene dispersal of the horse Equus and late Cenozoic mammal dispersal events. Nature 287, 135–138.
Linnaeus, C., 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species Cum Characteribus, Differentiis, Synonimis, Locis: Editio Decima, Reformata. Laurentii Salvii, Stockholm, p. 824.
Madurell-Malapeira, J., Minwer-Barakat, R., Alba, D.M., Garcés, M., Gómez, M., Aurell-Garrido, J., Ros-Montoya, S., Moyà-Solà, S., Berástegui, X., 2010. The Vallparadís section (Terrassa, Iberian Peninsula) and the latest Villafranchian faunas of Europe. Quat. Sci. Rev. 29, 2972–2982.
Martinetto, E., Bertini, A., Basilici, G., Baldanza, A., Bizzarri, R., Cherin, M., Gentili, S., Pontini, M.R., 2014. The plant record of the Dunarobba and Pietrafitta sites in the Plio-Pleistocene palaeoenvironmental context of central Italy. Alp. Mediterr. Quat. 27, 29–72.
Martínez-Arbizu, P., 2020. Pairwise Adonis: pairwise multilevel comparison using adonis. R. package version 0.4. https://github.com/pmartinezarbizu/pairwiseAdonis.
Masini, F., Palombo, M.R., Rozzi, R., 2013. A reappraisal of the early to middle Pleistocene Italian bovidae. Quat. Internat. 288, 45–62.
Mayhew, D.F., 2012. Revision of the fossil vole assemblage (Mammalia, rodentia, arvicolidae) from Pleistocene deposits at Kislang, Hungary. Palaeontology 55, 11–29.
Musil, R., 1969. Die Equiden–Reste aus dem Pleistoz′an von Sussenborn bei Weimar. Pal′aontolog. Abh. 3, 617–666.
Musil, R., 1992. Die Pferde aus der oberplioz′an Spaltenfüllung Schernfeld bei Eichst′att. Mitt. Bayer. Staatsslg. Pal′aont hist. Geol. 32, 115–162.
Nomade, S., Pastre, J.F., Guillou, H., Faure, M., Gué erin, C., Delson, E., Debard, E., Voinchet, P., Messager, E., 2014. 40Ar/39Ar constraints on some French landmark late Pleistocene to early Pleistocene large Mammalian paleofaunas: paleoenvironmental and paleoecological implications. Quat. Geochronol. 21, 2–15.
Owen, R., 1848. Description of the teeth and portions of jaws of two extinct anthracotheroid quadrupeds (*Hyopotamus vectianus* and *Hyopotamus bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits of the N.W. coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the classification of Pachyderms by the number of their toes. Q. J. Geol. Soc. Lond. 4, 103–141.
Palombo, M.R., Alberdi, M.T., 2017. Light and shadows in the evolution of South European stenonoid horses. Foss. Imp. 73, 115–140.
Palombo, M.R., Ferretti, M.P., 2005. Elephant fossil record from Italy: knowledge, problems, and perspectives. Quat. Internat. 126, 107–136.
Palombo, M.R., Valli, A.M.F., 2004. Remarks on the biochronology of Mammalian faunal complexes from the Pliocene to the middle Pleistocene in France. Geolog. Rom. 37, 145–163.
Palombo, M.R., Azanza, B., Alberdi, M.T., 2003. Italian mammal biochronology from latest Miocene to middle Pleistocene: a multivariate approach. Geolog. Rom. 36, 335–368.
Palombo, M.R., Alberdi, M.T., Bellucci, L., Sardella, R., 2017. An intriguing middlesized horse from Coste San Giacomo (Anagni Basin, Central Italy). Quat. Res. 87, 347–362.
Pandolfi, L., Erten, H., 2017. *Stephanorhinus hundsheimensis* (Mammalia, Rhinocerotidae) from the late early Pleistocene of the Denizli Basin (Anatolia). Geobios 50, 65–73.
Pandolfi, L., Cerdeño, E., Codrea, V., Kotsakis, T., 2017. Biogeography and chronology of the Eurasian extinct rhinoceros *Stephanorhinus etruscus* (Mammalia, Rhinocerotidae). C. R. Palevol 16, 762–773.
Pareto, L., 1865. Note sur les subdivisions que l'on pourrait établir dans les terrains tertiaires de l'Apennin septentrional. Bull. Soc. Geol. France 22, 210–277.
Pavia, M., Zunino, M., Coltorti, M., Angelone, C., Arzarello, M., Bagnus, C., Bellucci, L., Colombero, S., Marcolini, F., Peretto, C., Petronio, C., Petrucci, M., Pieruccini, P., Sardella, R., Tema, E., Villier, B., Pavia, G., 2012. Stratigraphical and palaeontological data from the early pleistocene Pirro 10 site of Pirro Nord (Puglia, south eastern Italy). Quat. Int. 267, 40–55.
Pazzaglia, F., Barchi, M.R., Buratti, N., Cherin, M., Pandolfi, L., Ricci, M., 2013. Pleistocene calcareous tufa from the Ellera basin (Umbria, central Italy) as a key for an integrated paleoenvironmental and tectonic reconstruction. Quat. Int. 292, 59–70.
Petronio, C., Bellucci, L., Martinetto, E., Pandolfi, L., Salari, L., 2011. Biochronology and palaeoenvironmental changes from the middle Pliocene to the late Pleistocene in Central Italy. Geodiversitas 33, 485–517.
Petronio, C., Angelone, C., Atzori, P., Famiani, F., Tassos, K., Salari, L., 2020. Review and new data of the fossil remains from monte Peglia (late early Pleistocene, central Italy). Riv. Ital. Paleontol. Stratigr. 126, 791–819.
Petronio, C., Salari, L., 2021. Fossil remains of Villafranchian mammals from Frattaguida (Parrano, Terni, central Italy). Revue de Paléobiologie, Genève (juin 2021) 40 (1), 199–209.
Piñero, P., Alberdi, M.T., 2015. Study of horses from the Quibas site, latest early Pleistocene (Abanilla, Murcia, Spain). Estud. Geol. 71, 34. https://doi.org/10.3989/egeol.41863.348.

Piñero, P., Agustí, J., Oms, O., Blain, H.-A., Furió, M., Laplana, C., Sevilla, P., Rosas, A., Vallverdú, J., 2020. First continuous pre-Jaramillo to Jaramillo terrestrial vertebrate succession from Europe. Sci. Rep. 10, 1–11. https://doi.org/10.1038/s41598-020-58404-w.

Piñero, P., Agustí, J., Laborda, C., Duval, M., Zhao, J.-x., Blain, H.-A., Furió, M., Laplana, C., Rosas, A., Sevilla, P., 2022. Quibas-Sima: a unique 1 Ma-old vertebrate succession in southern Iberian Peninsula. Quat. Sci. Rev. 283, 107469. https://doi.org/10.1016/j.quascirev.2022.10746.

R Core Team, 2025. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Reichenau, W. von, 1915. Beiträge zur näheren Kenntnis fossiler Pferde aus deutschem Pleistozän, insbesondere über die Entwicklung und die Abkaustadiem del Gebisses von Hochterrassenpferde. Equus mosbachensis v. R.). Abh. Gross. Hess. Geolog. Darmstadt 7, 1–55.

Rook, L., Martínez-Navarro, B., 2010. Villafranchian: the long story of a Plio-Pleistocene European large mammal biochronologic unit. Quat. Int. 219, 134–144.

Rook, L., Bernor, R.L., Avilla, L.D., Cirilli, O., Flynn, L., Jukar, A.M., Sanders, W., Scott, E., Wang, X., 2019. Mammal biochronology (land mammal ages) around the world from the late Miocene to middle Pleistocene and major events in horse evolutionary history. Front. Ecol. Evol. 7, 268.

Saarinen, J., Cirilli, O., Strani, F., Meshida, K., Bernor, R.L., 2021. Testing equid body mass estimate equations on modern zebras-with implications to understanding the relationship of body size, diet and habitats of *Equus* in the Pleistocene of Europe. Front. Ecol. Evol. 9, 622412. https://doi.org/10.3389/fevo.2021.622412.

Schwarz, E., 1928. Uberdiluviale Pferde der Equus caballus-Gruppe. J. Prenss. Geolog. Landesanstalt zu Berlin 48, 428–476.

Sinusía, C., Pueyo, E.L., Azanza, B., Pocoví, A., 2004. Datacion magnetostratigrafica del yacimiento paleontologico de la Puebla de Valverde (Teruel). Geotemas 6, 329–342.

Sorbelli, L., Villa, A., Gentili, S., Cherin, M., Carnevale, G., Tschopp, E., Delfino, M., 2021. The early Pleistocene ectothermic vertebrates of Pietrafitta (Italy) and the last Western European occurrence of *Latonia* Meyer, 1843. C. R. Palevol 20 (26), 555–583.

Sorbelli, L., Cherin, M., Kostopoulos, D.S., Sardella, R., Mecozzi, M., Plotnikov, V., Prat-Vericat, M., Azzarà, B., Bartolini-Lucenti, S., Madurell-Malapeira, J., 2023. Earliest bison dispersal in Western Palearctic: insights from the *Eobison* record from Pietrafitta (Early Pleistocene, central Italy). Quat. Sci. Rev. 301, 107923.

Tappen, M., Adler, D.S., Ferring, C.R., Gabunia, M., Vekua, A., Swisher, C.C., 2002. Akhalkalaki: the taphomony of an early pleistocene locality in the republic of Georgia. J. Archeol. Sci. 29, 1367–1391.

Tesakov, A.S., Vangengeim, E., Pevzner, M., 2007a. Arvicolid zonation of continental Pliocene deposits of east Europe. Cour. Forsch. Inst. Senckenberg 259, 227–236.

Tesakov, A.S., Dodonov, A.E., Titov, V.V., Trubikhin, V.M., 2007b. Plio-Pleistocene geological record and small mammal faunas, eastern shore of the Azov Sea, Southern European Russia. Quat. Int. 160, 67–69.

Titov, V.V., 2008. Late Pliocene large mammals from northeastern Sea of Azov region. Managing Editor Acad. SSC RAS Publishing, p. 264. , Rostov-on-Don.

Toro-Moyano, I., Martínez-Navarro, B., Agustí, J., Souday, C., Bermúdez de Castro, J.M., Martinon-Torres, M., Palmqvist, P., 2013. The oldest human fossil in Europe, from Orce (Spain). J. Hum. Evol. 65, 1–9.

Vialli, V., 1956. Sul rinoceronte e l'elefante dei livelli superiori della serie lacustre di Leffe (Bergamo). Memorie della Società Italiana di Scienze Naturali 12, 1–71.

Van der Made, J., 1999. Ungulates from atapuerca TD6. J. Hum. Evol. 37, 389–413. https://doi.org/10.1006/jhev.1998.0264.

Venables, W.N., Ripley, B.D., 2008. Modern Applied Statistics with R. Springer- Verlag, New York, p. 498.

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York, p. 213.