



Original article

The Villafranchian perissodactyls of Italy: knowledge of the fossil record and future research perspectives[☆]



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ARTICLE INFO

Article history:

Received 28 March 2020

Accepted 17 September 2020

Available online 18 November 2020

Keywords:

Tapirus

Stephanorhinus

Hipparion

Equus

Perissodactyls

Villafranchian

Italy

ABSTRACT

The Villafranchian fossil record of Perissodactyla is of a great interest because the appearance of the genus *Equus* and disappearance of the genus *Tapirus* mark important faunal turnovers. Here, we provide new data on Italian Villafranchian Tapiridae, Rhinocerotidae, and Equidae with updates from the last comprehensive review; most relevant are those of the Rhinocerotidae and Equidae. At present only two Villafranchian rhinoceros' species are documented in Italy: *Stephanorhinus jeanvireti* and *Stephanorhinus etruscus*. The two species can be distinguished by several morphological features and by the dimensions of their bones. *Stephanorhinus etruscus* occurred throughout the Villafranchian; despite the numerous records, its remains are not enough to investigate morphometric trends. The Equidae include seven species including new occurrences of Hipparionine horses and of the genus *Equus*. The statistical analyses performed on the *Equus* species show two different evolutionary trends, namely the stenonine lineage "*Equus livenzovensis* - *Equus stenonis*" and the small-to-medium-sized lineage "*Equus senenensis* - *Equus stehlini*", suggesting a different evolution of these species. Moreover, the analyses show close relationships between the Italian *Equus stenonis* samples and three European *Equus stenonis* subspecies (*E. stenonis vireti*, *E. stenonis guthi*, and *E. stenonis pueblensis*). We begin to reconsider the validity of *E. stenonis* subspecies identification in order to provide new perspectives on the taxonomy of this species.

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1. Introduction

The Villafranchian is a key informal Mammal Age which roughly spans the late Pliocene–late Early Pleistocene interval (ca. 3.5 Ma to ca. 1.0 Ma) and it is defined by several faunal turnovers. As reported in the last overview on the Villafranchian (Rook and Martínez-Navarro, 2010; Alberdi et al., 2016), this unit includes the Pliocene–Pleistocene transition with remarkable faunal changes recorded at the global level. The fossil record of Perissodactyla is of great significance because the disappearance of *Tapirus* and the first occurrence of *Equus* reflects important environmental changes, from Pliocene warm forest ecosystems to Pleistocene cool-arid conditions (Rook and Martínez-Navarro, 2010; Petronio et al., 2011; Szabó et al., 2017).

The term Villafranchian was initially proposed by Pareto (1865) as a continental stage referred to the fluvio-lacustrine sediments near Villafranca d'Asti (Piedmont, northern Italy), which contained a rich fossil mammal fauna. During the 1960s and 1970s, Professor Augusto Azzaroli significantly advanced our knowledge about the Villafranchian (Rook, 2015). Azzaroli subdivided the Villafranchian into early, middle and late intervals and, in addition, established seven Faunal Units (FU) within the Villafranchian: Triversa, Montopoli, Coste San Giacomo, Olivola, Tasso, Farneta, and Pirro Nord. As such, the Italian peninsula is unique in the Eurasian Pliocene–Pleistocene mammal fossil record for its abundance of fossil sites and richness of their faunas. Rook and Martínez-Navarro (2010) have provided a comprehensive review of faunal turnover during the Villafranchian and the history of this interval. Herein, we provide an overview of the current knowledge on Italian Villafranchian perissodactyls, pointing out new research perspectives.

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2. Material and methods

The revised Quaternary time scale of [Gibbard et al. \(2010\)](#) is used for chronological references in this text; the Pliocene spans from 5.33 Ma up to 2.58 Ma. We present our observations on perissodactyl fossil collections housed in several academic institutions that have been recovered from various Villafranchian localities on the Italian Peninsula. Most remains come from the Piedmont, Tuscany, Umbria, Latium, and Apulia ([Fig. 1](#); [Table S1](#), [Appendix A](#)). These specimens are morphologically and morphometrically compared with those belonging to evolutionarily-related European Villafranchian species.

Morphometric and morphological descriptions on Tapiridae mainly follow [Rustioni \(1992\)](#). Concerning rhinoceroses, we follow the morphometric methodology of [Guérin \(1980\)](#) with the anatomical descriptions mainly following [Antoine \(2002\)](#). Comparative data were collected from specimens housed in several museums ([Appendix A](#)) and from data reported by [Guérin and Heintz \(1971\)](#), [Ruiz Bustos \(1973\)](#), [Santafé-Llopis and Casanovas-Cladellas \(1987\)](#), [Cerdeño \(1989\)](#), [Fortelius et al. \(1993\)](#), [Campanino et al. \(1994\)](#), [Lacombat \(2005\)](#), [Guérin \(2004\)](#), [Guérin and Tsoukala \(2013\)](#), [Pandolfi et al. \(2017a\)](#), and [Pandolfi et al. \(2019\)](#), [Pandolfi et al. \(2020\)](#). In Equidae, we follow [Eisenmann et al. \(1988\)](#) and [Bernor et al. \(1997\)](#) for anatomical nomenclature, osteological landmarks, and morphological measurements.

Anatomical abbreviations: **DP1**: upper deciduous first premolar; **P2**: upper second premolar; **P3**: upper third premolar; **P4**: upper fourth premolar; **LP**: length of the premolar row; **LM**: length of the molar row; **M1**: upper first molar; **M2**: upper second molar; **M3**: upper third molar; **p2**: lower second premolar; **MCIII**: third metacarpal; **MCIV**: fourth metacarpal; **MTIII**: third metatarsal; **MTIV**: fourth metatarsal; **AST**: astragalus; **CALC**: calcaneus;

A1PHIII: first anterior phalanx of the central digit; **2PHIII**: second phalanx of the central digit.

Institutional abbreviations: **IGF**: Museo di Storia Naturale dell'Università degli Studi di Firenze, Sezione di Geologia e Paleontologia; **POMK**: Ethnographic Museum Collection, Livnizovka, Rostov; **IQM**: Institut für Geowissenschaften Bereich Quartärpaläontologie, Weimar (Germany); **MGC**: Museo di Geologia "Giovanni Capellini" di Bologna; **MNCN**: Museo Nacional de Ciencias Naturales Madrid; **MPLBP**: Museo Paleontológico "Luigi Boldrini" Pietrafitta, Perugia; **MPUR**: Museo di Paleontologia, Università di Roma Sapienza; **MSNAF**: Museo di Storia Naturale di Siena, Accademia dei Fisiocritici; **NHMW**: Natural History Museum Wien; **NMB**: Natural History Museum, Basel; **OMNSC**: Oltenia Museum Natural Sciences Department, Craiova.

Acronyms: **MN**: Mammal Neogene Unit; **MNQ**: Mammal Quaternary Unit; **FU**: Faunal Unit; **CSG**: Coste San Giacomo; **FAD**: First Appearance Datum; **ICZN**: International Commission on Zoological Nomenclature.

3. Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Perissodactyla Owen, 1848

Family Tapiridae Burnett, 1830

Genus *Tapirus* Brisson, 1762

Tapirus arvernensis [Croizet and Jobert, 1828](#)

[Fig. 2](#)

Type material: mandibles and isolated teeth, figured in [Croizet and Jobert \(1828: 161–165, 167; pl. II, figs. 1, 3–5, pl. XII, figs. 4–6\)](#).

Type locality and horizon: Les Etouaries (France), around the Pliocene-Pleistocene transition.



Fig. 1. Location map of the main Italian Villafranchian localities. See [Table S1 \(Appendix A\)](#) for an extensive list of the Italian localities not indicated in this figure.

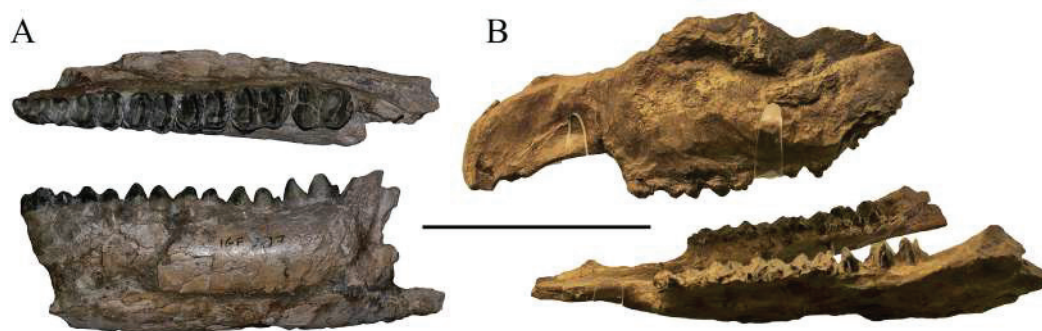


Fig. 2. Villafranchian *Tapirus arvernensis* remains from Italy. **A.** Mandible from Pieve a Fosciana (Garfagnana, IGF 971), in occlusal (top) and lateral (bottom) views. **B.** Skull and mandible from Santa Barbara (Upper Valdarno Arezzo; IGF 975), lateral view. Scale bar: 10 cm.

Remarks: The oldest reference to the presence of tapirs in Italy is dated back to the 19th century: among others, the manuscripts by Gaudin (1857), Meneghini (1880), Capellini (1881) are considered to be milestones. *Tapirus arvernensis* was established by Croizet and Jobert (1828) on some remains collected at Les Etouaires (France). The species is smaller and slenderer than *T. priscus* from the late Miocene of central Europe and the extant *T. indicus*. The long bones of *T. arvernensis* resemble those of *T. terrestris* but with relatively robust diaphyses (Rustioni, 1992). The lengths of femur, tibia and third metatarsal of *T. arvernensis* fall within the dimensional range of *T. terrestris* reported by Rustioni (1992); the lengths of the lower tooth series (minimal and maximal values LP = 52–63.3 mm; minimal and maximal values LM = 56–69.3 mm; Rustioni, 1992) are instead slightly smaller if compared with those of *T. terrestris* (minimal and maximal values LP = 55.9–67.1 mm; minimal and maximal values LM = 63–74.8 mm; Hulbert, 2010). The skull of *T. arvernensis* resembles *T. indicus* with a few differences in the development of the tubera frontalis (more prominent), the temporal fossae (narrower) and the zygomatic arches (stronger and lower) (Rustioni, 1992). The first upper premolars of *T. arvernensis* are characterized by the presence of an antero-lingual cuspule (Rustioni, 1992). The horizontal ramus of the mandible is slender, with relatively convex or slightly convex ventral border (Fig. 2). Several characters of this taxon have been discussed by Rustioni (1992), Guérin and Eisenmann (1994), and Guérin and Tsoukala (2013).

A scanty collection of specimens from Sarzanello (Pliocene, Val di Magra, La Spezia; Liguria) were ascribed to *Tapirus capellini* by Del Campana (1910) and *Tapirus* sp. by Rustioni (1992). The measurements reported by Capellini (1881) on the teeth collected at Sarzanello fall within the metric ranges given by Eisenmann and Guérin (1992: table 4) for *T. arvernensis*. Sarzanello has been listed within the localities that yielded remains of *T. arvernensis* by Guérin and Tsoukala (2013). The specimens are here referred to *T. cf. arvernensis* pending observation of the original material (not available at this time).

Family Rhinocerotidae Gray, 1821

Tribe Rhinocerotini Gray, 1821

Genus *Stephanorhinus* Kretzoi, 1942

Remarks: The debate on the taxonomic status of the European Pleistocene fossil rhinoceroses has been recently summarized by Pandolfi and Tagliacozzo (2015). Nevertheless, some issues concerning the paraphyly of the genus have been previously raised (Geraads, 1988; Heissig, 1999; Antoine and Saraç, 2005; Kirillova et al., 2017; Cappellini et al., 2019; Pandolfi et al., 2020). The name *Stephanorhinus* is maintained here at the generic level and includes all the Pliocene-Pleistocene species as defined by Pandolfi and Tagliacozzo (2015).

Stephanorhinus jeanvireti (Guérin, 1972)

Fig. 3(A)

Type material: Skull and mandible (NMB Vt 627), stored at Natural History Museum Basel and figured in Guérin (1972: pp. 133–136, pl. I).

Type locality and horizon: Viallette (Haute-Loire, France), upper Pliocene.

Remarks: Ballatore and Breda (2016) suggested that *S. elatus* is a valid species name and *S. jeanvireti* is its younger synonym. Apparently, these conclusions follow the suggestion of a former president of ICZN. Pandolfi et al. (2019), however, reported that the name *Rhinoceros elatus* is regarded as a *nomen dubium*. We follow Pandolfi et al. (2019), while the issue needs a full argumentation beyond the scope of the present article.

Stephanorhinus jeanvireti (Fig. 3(A)) has been usually confused with the latest Miocene-early Pliocene ‘*Dihoplus*’ *megarhinus* (Guérin, 1972, 1980; Pandolfi, 2013a; Pandolfi et al., 2015a, 2019). The two species differ mainly in the shape of the skull. In *S. jeanvireti* the skull is characterized by: (i) the presence of a nasal septum; (ii) thinner nasal bones; (iii) shorter occipital surface; and (iv) a nuchal crest extended more posteriorly (Guérin, 1972, 1980; Guérin and Tsoukala, 2013; Pandolfi et al., 2015a). The morphological differences between the mandibles of ‘*D.*’ *megarhinus* and *S. jeanvireti* are less conspicuous and are represented by the orientation of the anterior border of the vertical ramus (straighter in *S. jeanvireti*), partially in the morphology of the ventral border of the horizontal ramus, and in the morphology of the incisive corpus (which however is usually poorly preserved in fossil specimens). The presence of incisors has been used in the past as a distinctive difference between *S. jeanvireti* and ‘*D.*’ *megarhinus*. Nevertheless, poorly-developed incisors have been documented in a skull and mandible of *S. jeanvireti* from Greece (Guérin and Tsoukala, 2013), suggesting their presence as a potentially-retained plesiomorphic feature within some *Stephanorhinus* representatives. The postcranial remains of *S. jeanvireti* are generally slightly smaller than those of ‘*D.*’ *megarhinus* and larger than those of *S. etruscus*. The morphological differences between the postcranial remains of *S. jeanvireti* and other Pliocene and Early Pleistocene rhinoceroses were summarized by Guérin (1972), Guérin (1980), Lacombe and Mörs (2008), Guérin and Tsoukala (2013), Pandolfi (2013a), Pandolfi et al. (2016), Pandolfi et al. (2017a), Pandolfi et al. (2019), Pandolfi et al. (2020), Pandolfi and Rook (2017), and Tsoukala (2018).

Stephanorhinus etruscus (Falconer, 1868)

Fig. 3(B–F)

Type material: Skull (IGF 756) stored at Museo di Storia Naturale, sezione di Geologia e Paleontologia, Florence, Italy. Figured in Falconer (1868: pp. 355–358, pl. XXVI, figs. 1–3, pl. XXVII, figs. 1 and 5).

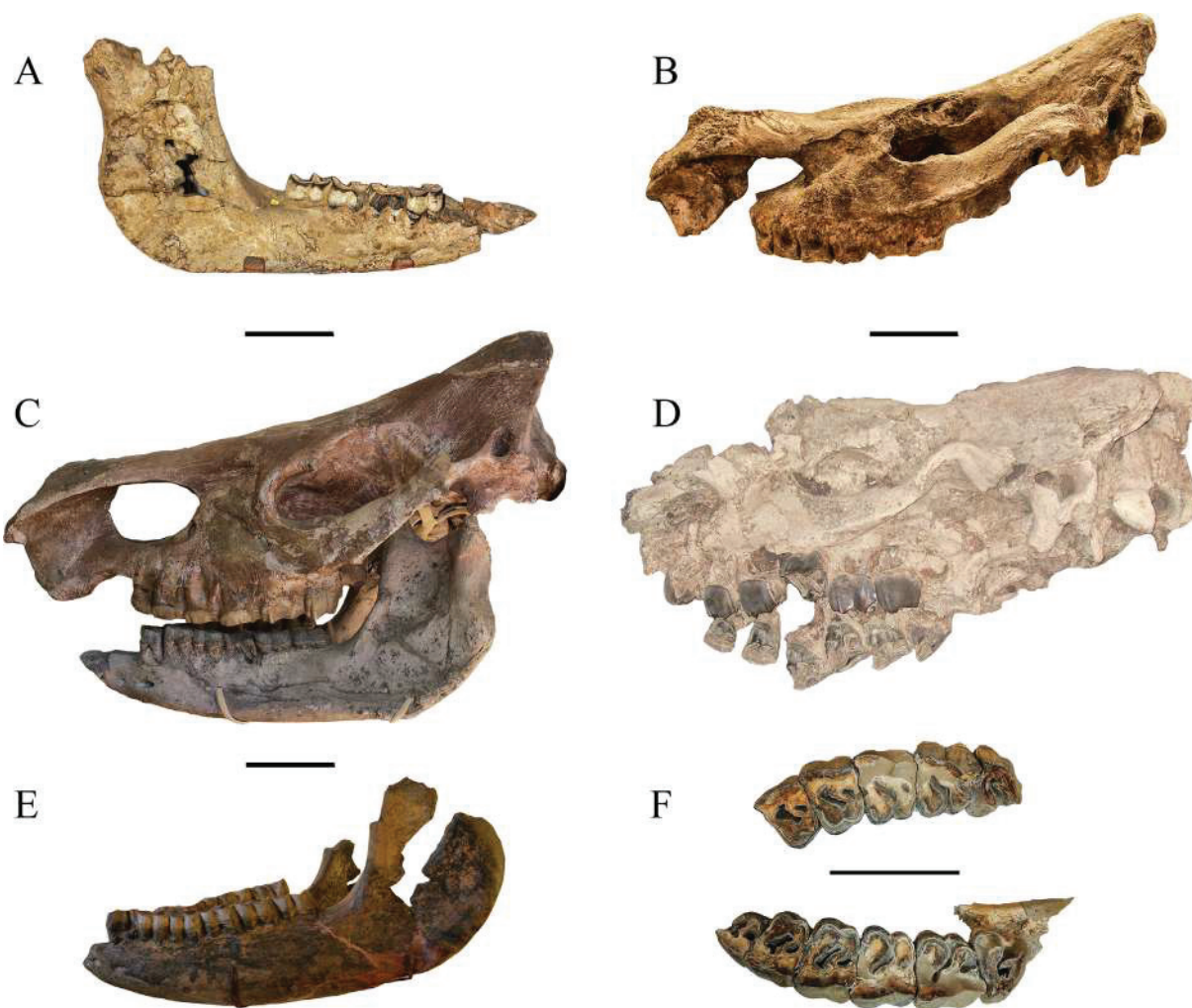


Fig. 3. Villafranchian Rhinocerotidae from Italy. **A.** *Stephanorhinus jeanvireti* mandible from Monte San Pietro (MGC 9354), lateral view. **B.** Skull of *Stephanorhinus etruscus* from Upper Valdarno (IGF 756), lateral view. **C.** Skull (IGF 3098) and mandible (IGF 2293V) of *S. etruscus* from Upper Valdarno. **D.** Crushed skull of *S. etruscus* from Pietrafitta (MPLB n585), lateral view. **E.** Mandible of *S. etruscus* from Upper Valdarno (IGF 755), lateral view. **F.** Upper tooth series of *S. etruscus* from Upper Valdarno (NMB VA453), occlusal view. Scale bars: 10 cm.

Type locality and horizon: Upper Valdarno Basin (Tuscany, Italy), Lower Pleistocene.

Remarks: *Stephanorhinus etruscus* (Falconer, 1868) is one of the most abundant Early Pleistocene rhinoceroses (Falconer, 1868; Guérin, 1980; Mazza, 1988; Cerdeño, 1992, 1993; Fortelius et al., 1993; Lacombe, 2005; Pandolfi and Petronio, 2011a; Pandolfi and Erten, 2017; Pandolfi et al., 2017a). The taxon is well known in the Upper Valdarno Basin (Tuscany, Italy), specimens of which were used by Falconer (1868) to establish the species. The species is also abundant at the French locality of Senèze (Haute-Loire) (Guérin, 1980), but an extensive systematic study of the material collected from Senèze is still needed. The cranial and postcranial material from the type area were described by Mazza (1988). The species is generally smaller than other Pliocene and Early Pleistocene Western Eurasian rhinoceroses (namely '*D.*' *megarhinus* and *S. jeanvireti*): the nasal septum is partially ossified, the nasal bones are relatively wide, the occipital surface is subtrapezoidal, the teeth are low-crowned with simple internal folds and relatively simple ectoloph profile (not wavy or with several folds). According to Heissig (1996), the Etruscan rhino is likely related to *Dihoplus pikermiensis* but this hypothesis would benefit from the support of a formal phylogenetic analysis. The taxon is unknown in Eastern

Eurasia (e.g., China) and the first occurrences are from Western Europe and date back to the late Pliocene (Pandolfi et al., 2017a).

Family Equidae Gray, 1821

Subfamily Equinae Steinmann and Doderlein, 1890

Tribe Hipparionini Quinn, 1955

Genus *Hipparion* Christol, 1832

'*Hipparion*' sp.

Fig. 4

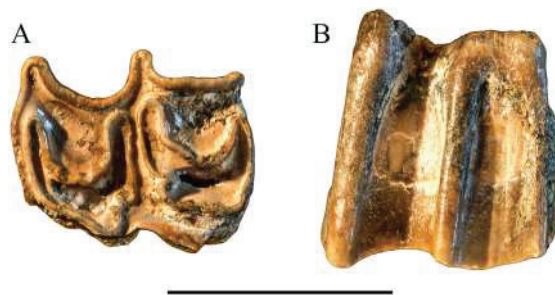


Fig. 4. *Hipparion* sp. from Montopoli, IGF 15315. **A.** Occlusal view. **B.** Labial view. Scale bar: 2 cm.

Remarks: An incomplete M1 from the site of Montopoli Val d'Arno (MNQ16b, following Guérin, 1982) has been identified as 'Hipparion' sp. by Rook et al. (2017), albeit the identification of the specimen was informally made by Prof. Claudio De Giuli (University of Florence, Italy), as evidenced by his unpublished notes. The tooth, missing its entire lingual side (Fig. 4(A)), exhibits a smaller size and a different occlusal morphology from the other large monodactyl horse reported from the same site, *Equus* cf. *livenzovensis* (Azzaroli, 2000; Bernor et al., 2018). The morphology of the occlusal surface, even if characterized by a relatively advanced stage of wear, shows a small number of plications of pre- and postfossettes, different from *Equus* representatives.

Genus *Equus* Linnaeus, 1758

Equus livenzovensis Bajgusheva, 1978

Type material: A fragmentary skull, L-4, stored in the Ethnographic Museum Collection (POMK), Livensovka, Rostov. Figured in Bajgusheva (1978: fig. 1, p. 98).

Type horizon: Lower Pleistocene.

Type locality: Livenzovka, Southern Russia.

Remarks: *Equus* cf. *livenzovensis* Bajgusheva, 1978, occurs at Montopoli, Italy in the so-called Montopoli FU (MNQ16b; 2.58 Ma). Even if its presence was reported in several papers (Azzaroli, 1982, 2000, 2003; De Giuli, 1972; Alberdi et al., 1998; Alberdi and Palombo, 2013b; Palombo and Alberdi, 2017), the first detailed description was given in Bernor et al. (2018), wherein a complement of anterior and posterior first and second phalanges of the central digit (IGF11224, IGF11225, IGF11074) were described and compared to other extant and fossil horses. Montopoli *Equus* cf. *livenzovensis* is characterized by its very large size compared to all other European stenonine horses. Bernor et al. (2018) demonstrated that the Montopoli sample shares large size and morphological proportions comparable with *Equus livenzovensis* from Khapry, near the Azov Sea, and the locality of Livensovka, Rostov on Don (Bajgusheva, 1971; Bajgusheva, 1978). The statistical analyses have revealed that the anterior and posterior 1PHIII and 2PHIII are the largest of an extensive comparative sample which included the very large *Equus eisenmannae* from Londgan (Linxia Basin, China; 2.55–1.85 Ma; Qiu et al., 2004; Wang and Deng, 2011). The holotype skull of *E. livenzovensis* has a morphology and size comparable with the 3.3 myr-old Hagerman Horse fauna *E. simplicidens* (Idaho, USA), even though the limb bones are larger. The *E. livenzovensis* skull exhibits a well-developed preorbital fossa with accompanying medial nasal groove while the dentition's occlusal morphology exhibits the typical stenonine pattern, with a short protocone in the upper teeth and deep ectoflexid in the lower teeth (Alberdi et al., 1998). Remains ascribed to *E. cf. livenzovensis* are also cited at Cava Toppetti, an Early Pleistocene locality in the Tiber basin (Umbria), correlated with Montopoli FU (Sardella et al., 1996).

Equus senezensis aff. *Equus senezensis stehlini*

Remarks: Palombo et al. (2017) report a slender medium-sized horse from the site of Coste San Giacomo (CSG, central Italy, Anagni Basin), smaller than the "*Equus stenonis* group" and comparable to the medium-sized horse *Equus senezensis* from the locality of Senèze (France). The attribution to *Equus senezensis* aff. *E. senezensis stehlini* is supported by dental and postcranial specimens. Even though the sample is "scanty and poorly preserved" (Palombo et al., 2017), it is important because it represents the first occurrence of *E. senezensis* outside the locality of Senèze. Morphologically, *E. senezensis* exhibits the following characters: relatively long and narrow skull with a short muzzle; the occlusal pattern of the mandibular cheek teeth is typically stenonine, but smaller in size; the postcrania show a slender morphology, and its range of variability is between that of the larger *E. stenonis* and the smaller *E. altidens* (Alberdi et al.,

1998). Recently, a new finding reported in Bernor et al. (2019) of an incomplete third metatarsal from the locality of Montecarlo (Upper Valdarno Basin; 2.4–2.2 Ma; Ghinassi et al., 2005) exhibits a morphology and dimensions equivalent to the sample from CSG and to the sample of *Equus stehlini* Azzaroli, 1964 from Casa Frata (1.8 Ma). These new findings could provide new insights on this small Villafranchian *Equus*, allowing its recognition elsewhere at this time.

Equus stenonis Cocchi, 1867

Fig. 5

Type material: skull and mandible, IGF 560, stored at Museo di Storia Naturale dell'Università degli Studi di Firenze, Sezione di Geologia e Paleontologia, Florence, Italy. Figured in Azzaroli, 1964 (pl. I, fig. 3; pl. II, figs. 1, 1a; pl. IV, figs. 1, 1a; pl. V, figs. 1, 1a).

Type horizon: Lower Pleistocene.

Type locality: Terranuova, Upper Valdarno Basin.

Remarks: *Equus stenonis* Cocchi, 1867 (Fig. 5) is a large fossil species, recorded in several Italian Villafranchian localities, mainly belonging to Olivola and Tasso FUs (2.0–1.8 Ma). The holotype (IGF 560) was discovered near Terranova (Arezzo, Tuscany), a 1.8 Ma fossil locality in the Upper Valdarno basin in central Italy; it is housed in the Natural History Museum in Florence. Cocchi (1867) named the species and the holotype was described by Forsyth Major (1885) and then in more details by Azzaroli (1964). This species is characterized by heavy proportions, bigger than *E. senezensis* but slenderer than *E. livenzovensis*, which probably gave origin to the European ancestral stock for the radiation of the "*E. stenonis* group". Indeed, *E. stenonis* shares some morphological features close to the holotype of *E. livenzovensis* Bajgusheva, 1978, but it is smaller in size. The holotype of *E. stenonis* consists of a complete skull with associated mandible, even if the skull is distorted in lateral view. The skull has an elongated snout with a large canine, indicative of an adult male. The nasal bones are retracted to the level of P3 mesostyle. The preorbital fossa is faintly delimited as a depression on the postero-superior aspect of the maxilla, and the facial maxillary crest is strongly developed. The snout is elongate with an arcuate incisor arcade. The maxillary cheek teeth include dP1–M3 with M3 in wear and have the following salient features: dP1 is small and rounded; P2 has a short anterostyle; all cheek teeth have protocone short with linkage to the protoloph; pli-caballins are single on all cheek teeth; fossettes are well developed on P2–P4 and M2, lesser developed on M1 and M3; hypoglyph is moderately deep on P2–M2 and not expressed on M3. The original mandible is missing and has been replaced with a cast complete on the right side. The enamel morphology of the mandibular dentition exhibits the following salient characters: p2 with short anterostyle, metaconids rounded and metastylids with some distal squaring; linguaflexids are uniformly V-shaped as diagnostic of stenonine horses (modified from Alberdi et al., 1998; Bernor et al., 2019; Cirilli et al., 2020). Postcranial bones are heavily built; dimensions are smaller than *E. livenzovensis* but larger than *E. senezensis* and *E. altidens*.

Equus stehlini Azzaroli, 1964

Fig. 6

Type material: skull IGF 563, stored at Museo di Storia Naturale dell'Università degli Studi di Firenze, Sezione di Geologia e Paleontologia, Florence, Italy. Figured in Azzaroli, 1964 (pl. II, figs. 2, 2a; pl. III, figs. 2, 2a; pl. IV, fig. 3; pl. V, fig. 4).

Type horizon: Lower Pleistocene.

Type locality: Terranuova, Upper Valdarno Basin.

Remarks: *Equus stehlini* Azzaroli, 1964 (Fig. 6), also known with the synonym *Equus senezensis stehlini* (Alberdi et al., 1988; Palombo et al., 2017), is the second Villafranchian horse discovered in the Upper Valdarno Basin (Tuscany). The holotype is the skull,

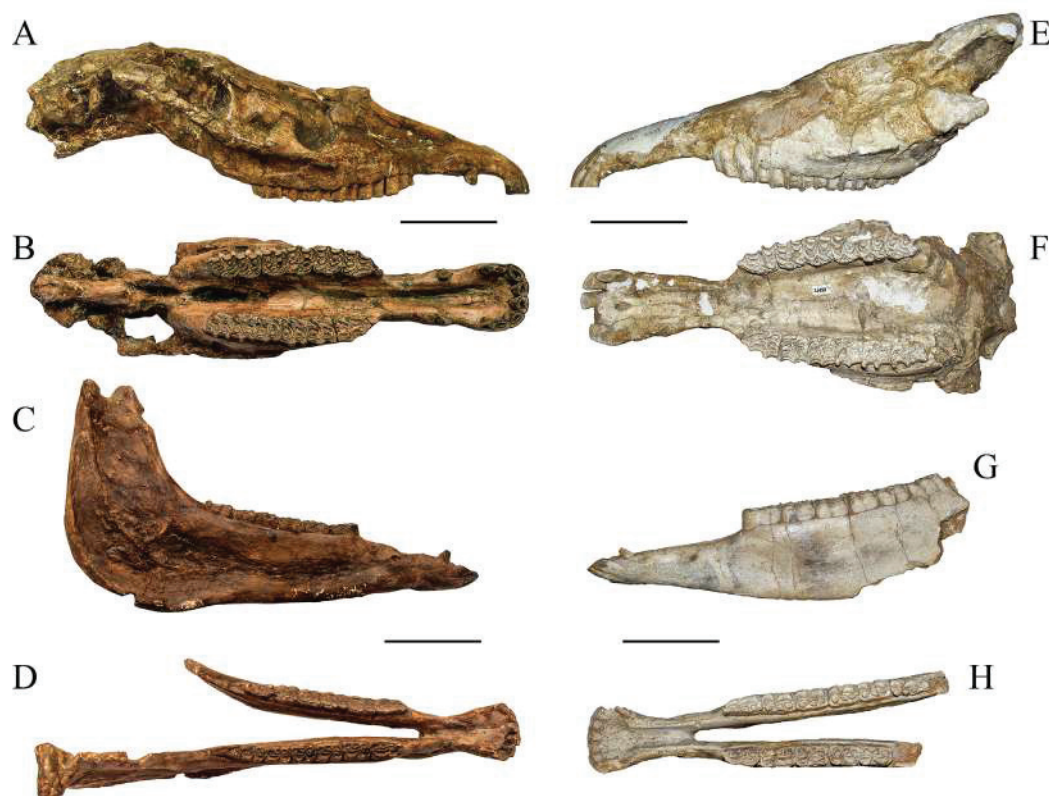


Fig. 5. *Equus stenonis*. **A–D.** *E. stenonis* Cocchi, 1867, IGF 560, holotype, Terranuova, Upper Valdarno Basin. **A:** skull, lateral view; **B:** skull, occlusal view; **C:** mandible, lateral view; **D:** mandible, occlusal view. **E–H.** *E. stenonis*, Olivola. **E, F:** skull IGF 11023 in lateral (**E**) and occlusal (**F**) views; **G, H:** mandible IGF 11024 in lateral (**G**) and occlusal (**H**) views. Scale bars: 10 cm.



Fig. 6. *Equus stehlini* Azzaroli, 1964, IGF 563, holotype; Terranuova, Upper Valdarno Basin. **A.** skull, lateral view. **B.** Skull, occlusal view. Scale bar: 10 cm.

IGF 563, is an old male with overall smaller dimensions than *E. stenonis*. It was recognized for the first time by Stehlin and Graziosi (1935) from a mandible housed in the NMB collection, and identified as *Equus* cf. *hydruntinus*. Later, Azzaroli (1964) formally recognized *E. stehlini* as a valid species name based on the holotype and several postcranial specimens. The holotype skull of *E. stehlini* has a complete snout and orbit but the posterior braincase is missing. The nasal notch extends to P3 mesostyle, as in *E. stenonis*. The max-

illa is crushed and may have had a faintly-developed preorbital fossa high and posteriorly placed on the maxilla. The cheek teeth are very worn and the cusps are heavily worn. In ventral view, the snout is relatively short and broad. The incisor arcade is arcuate and incisors are heavily worn, not preserving infundibula. On both the right and left sides, the cheek tooth occlusal surfaces are so worn that they do not preserve any meaningful morphological details except on M2 and M3, showing simple fossette ornamentation (modified from Alberdi et al., 1998; Bernor et al., 2019). The forelimb bones have shorter and slenderer dimensions than most of the entire European stenonine group.

While *Equus stehlini* is less common than *Equus stenonis* in the Upper Valdarno Basin and other middle Villafranchian localities, it is identified from the locality of Casa Frata, which is correlative with the Tasso Faunal Unit, 1.8 Ma (De Giuli and Masini, 1986; Rook and Martínez-Navarro, 2010). Nevertheless, its origin and phylogenetic relationships with other Villafranchian *Equus* is not yet fully understood. Azzaroli (1964) recognized some asinine and stenonine features on the type skull and interpreted this species as being derived from *Equus stenonis*. Later, Azzaroli (1982), Azzaroli (1989) noted that *E. stehlini* could share many cranial specializations with *Equus senezensis* from the type locality of Senèze. Alberdi et al. (1998) considered this horse as a subspecies of *E. senezensis*. De Giuli (1972) and Delson et al. (2006) both reported the presence of *E. stehlini* from Senèze in association with *E. senezensis*. Even if a close relationship with *E. senezensis* is noticeable (see below, Morphometry and evolutionary trends), which could suggest to consider *E. stehlini* as a small population or a subspecies of *E. senezensis*, based on present knowledge we prefer to maintain the species level for *E. stehlini*, despite more extensive studies are needed to resolve this topic.

Equus suessenbornensis Wust, 1900

Type material: left maxilla with P2–M3, IQM 1964/1177, stored at Institut für Geowissenschaften Bereich Quartärpaleontologie, Weimar (Germany). Figured in Musil (1969: p. 645, fig. 11).

Type horizon: Lower and Middle Pleistocene.

Type locality: Süssenborn, Germany.

Remarks: *Equus suessenbornensis* Wust, 1900, is a large horse, mainly reported from the Italian Galerian localities of Slivia and Venosa Loreto, Middle Pleistocene (Alberdi and Palombo, 2013b). It differs from *E. stenonis* and *E. livenzovenis* in having more complex enamel plications in the upper and lower teeth. Moreover, the morphology of its dentition shows a mixture of stenonine and caballine features. Caballine features are the asymmetrical long and large protocone and the large mesostyle in the upper dentition; stenonine characters are the elevated number of plications in pre- and postfossette in upper teeth, and the V-shape linguaeflexid between the metaconid–metastylid (double knot) in the lower teeth (see Musil, 1969, p. 646, fig. 11, *E. suessenbornensis* lectotype). The *E. suessenbornensis* postcranial bones are long and massive, larger than those of *E. livenzovenis* and *E. stenonis*, and slightly narrower than *E. major* Delafond and Depéret, 1893. The phylogenetic relationships of *E. suessenbornensis* with other Villafranchian stenonine horses are still not completely resolved. Musil (1969) did not recognize any morphological similarities with *E. stenonis*. Nobis (1971), Samson (1975) and Azzaroli (1984), Azzaroli (2003) consider this species derived from *E. stenonis*, due to the size similarity and the complicated occlusal morphology of the cheek teeth. Gromova (1949) considered this species to be a caballoid horse. Alberdi et al. (1998) ascribed it to a secondary lineage *E. major*–*E. suessenbornensis* derived from the ancestral European population of *E. livenzovenis*, evolutionarily separated from the *E. stenonis* clade. Although some dental features could link *E. suessenbornensis* to primitive caballine horses, this species shares many morphological characteristics with the most advanced stenonine horses. Alberdi et al. (1998) argued that *E. suessenbornensis* should be considered to be a true stenonine horse.

Equus altidens von Reichenau, 1915

Fig. 7

Type material: right p2, stored at the Universität Halle a.d. Saale Collection. Figured in von Reichenau (1915: pl. 6, fig. 17) and designated in Schwarz (1928: p. 437).

Type horizon: Lower and Middle Pleistocene.

Type locality: Süssenborn, Germany.

Remarks: *Equus altidens* von Reichenau, 1915 (Fig. 7) is a slender stenonine horse well documented from Middle Pleistocene European localities. In Italy, it is recorded from the Galerian localities of Slivia, Ponte Galeria and Venosa-Loreto (Alberdi and Palombo, 2013b). *Equus altidens* exhibits a close morphological similarity to *E. stenonis*, even though it is smaller in size. The enamel morphology exhibits the typical stenonine pattern, with triangular and flattened protocone on the lingual side of the upper cheek teeth and V-shaped linguaeflexid between the metaconid and metastylid in the lower cheek teeth. The post-protoconal groove is somewhat deep and the pli-caballin is sometimes obliterated in worn maxillary cheek teeth. The morphology of the protocone generally extends more distally than in *E. stenonis*. MCIII and MTIII are slenderer than in other stenonine species, including *E. senecensis*. Researchers disagree about the origin of this species. Most authors believe it to be a small stenonine horse (Alberdi et al., 1998). Others consider *E. altidens* to be part of the “non-stenonine” group, and probably related to *E. numidicus* from the Early Pleistocene of Africa (Guerrero-Alba and Palmqvist, 1997; Alberdi and Palombo, 2013b).

4. Biochronology

4.1. Tapiridae

So far, *Tapirus arvernensis* has been reported in France, Spain, Netherlands, Slovakia, Hungary, Romania and Greece (Fejfar, 1964; Heintz et al., 1974; Jánosy and Krolopp, 1981; Rustioni, 1992; Radulescu et al., 2003; Made and Stefanovic, 2006; Gómez

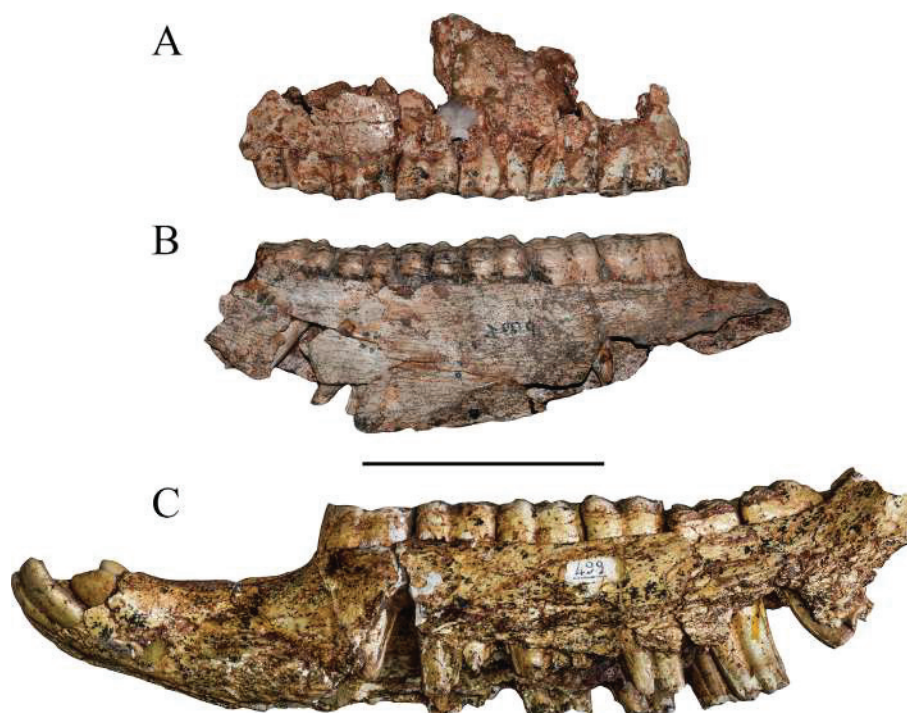


Fig. 7. *Equus altidens*, Pirro Nord. A. Right maxilla, SN6, labial view. B. Mandible P771, labial view. C. Mandible PN499, labial view. Scale bar: 10 cm.

de Soler et al., 2012; Guérin and Tsoukala, 2013). Tapir remains tentatively referred to *T. arvernensis* are recorded in Italy from a few latest Miocene localities: at Il Casino (Siena) and Baccinello V3 (Grosseto), both assigned to MN13 (Pantanelli, 1879; Del Campana, 1910; Hürzeler and Engesser, 1976; Rook and Rustioni, 1991; Rustioni, 1992). Almost all the specimens of Pliocene tapir collected in Italy were attributed to *T. arvernensis* (Meneghini, 1880; Del Campana, 1910; Sala et al., 1990; Rustioni, 1992; Dominici et al., 1995; Rustioni and Mazza, 2001; Petronio et al., 2011; Pandolfi and Kotsakis, 2016). In Piedmont, *T. arvernensis* has been reported at Villafranca d'Asti (Asti). In Liguria it is found at Ponzano di Magra (La Spezia). In Emilia Romagna it is found at Livergnana and Sasso di Glosina (Bologna) and Vignola (Modena). In Tuscany, it is found at Castelnuovo Garfagnana (Lucca), Pieve Fosciana (Lucca), Barga (Lucca), Casenuove (Empoli), Gaville (Florence), Santa Barbara (Arezzo), Monticchiello (Siena) and in Umbria at Spoleto-Santa Croce (Spoleto) (Table S1, Appendix A). The presence of a tapir at Poggio Mirteto/Castel San Pietro (Rieti, Latium) or Nera Montoro (Terni, Umbria) has been recently discussed by Pandolfi and Kotsakis (2016) and Pandolfi et al. (2017b). The tapir has never been recorded South of the Spoleto lignite deposits in Umbria.

Tapirus arvernensis became extinct in Italy at the end of the Pliocene, at the transition from the Triversa FU to the Montopoli FU (Fig. 8). Accordingly, *Tapirus* can be considered an important biochronological marker that discriminates between the latest Pliocene and earliest Pleistocene faunal complexes and therefore between the early and middle Villafranchian assemblages. Due to the scarcity of remains of tapir in Italy, new data are relatively poor in respect to those published by Rustioni (1992) and the taxon has been only reported in a few localities during the past 27 years. However, we reported here a comprehensive overview of the occurrences of this species, with new ages for some localities.

4.2. Rhinocerotidae

Stephanorhinus jeanvireti is relatively poorly documented in Eurasia with respect to *S. etruscus*. The fossil record of *S. jeanvireti* has been recently summarized by Pandolfi et al. (2019) who located the western limit of the geographic distribution at the north-easternmost part of the Iberian Peninsula (Camp dels Ninots, Girona) and its eastern limit in Romania. The species has been confirmed in France (MNQ16a, MNQ16b), Spain (MNQ15–MNQ16 transition), Germany (MNQ16), Slovakia (MNQ16a, MNQ16b/17a), Bulgaria (second half of MNQ15), Hungary (early Villafranchian), Greece (MNQ16) and Romania (MNQ16a, final part of MNQ17 or the first half of MNQ18) (Guérin, 1972, 1980; Lacombat and Mörs, 2008; Vlačický et al., 2008; Guérin and Tsoukala, 2013; Pandolfi, 2013; Šujan et al., 2013; Ros-Montoya et al., 2017; Pandolfi et al., 2019).

Stephanorhinus jeanvireti is relatively scarce in Italy compared to other species of the same genus such as *S. etruscus*, *S. hundsheimensis*, *S. kirchbergensis* and *S. hemitoechus* (e.g., Guérin, 1980; Mazza, 1988; Sala and Fortelius, 1993; Mazza and Varola, 1999; Pandolfi and Petronio, 2011a, 2011b; Pandolfi, 2013b; Pandolfi and Tagliacozzo, 2013, 2015; Pandolfi and Marra, 2015; Pandolfi et al., 2015a, 2015b, 2017a, 2017b). In Piedmont, a few remains (teeth) from Incisa Belbo, Dusino San Paolo and Castello d'Annone are referred to *S. jeanvireti* by Szabó et al. (2017), whilst at Roatto the species is well-documented by an almost complete skeleton (Campanino et al., 1994). Some remains housed at NMB (a lower molar, a radius, an MCIII, an MCIV and an astragalus lacking collection number) and recovered at Villafranca d'Asti (Asti, Piedmont) are here referred to *S. jeanvireti*. At Monte Pulgnasco (Piacenza, Emilia-Romagna), a mandible (cast housed as MGC 9352 and IGF 4684) displays a high ratio between the length of p3–p4 and the length of the molars (Lp3–p4/Lmolars), which is a

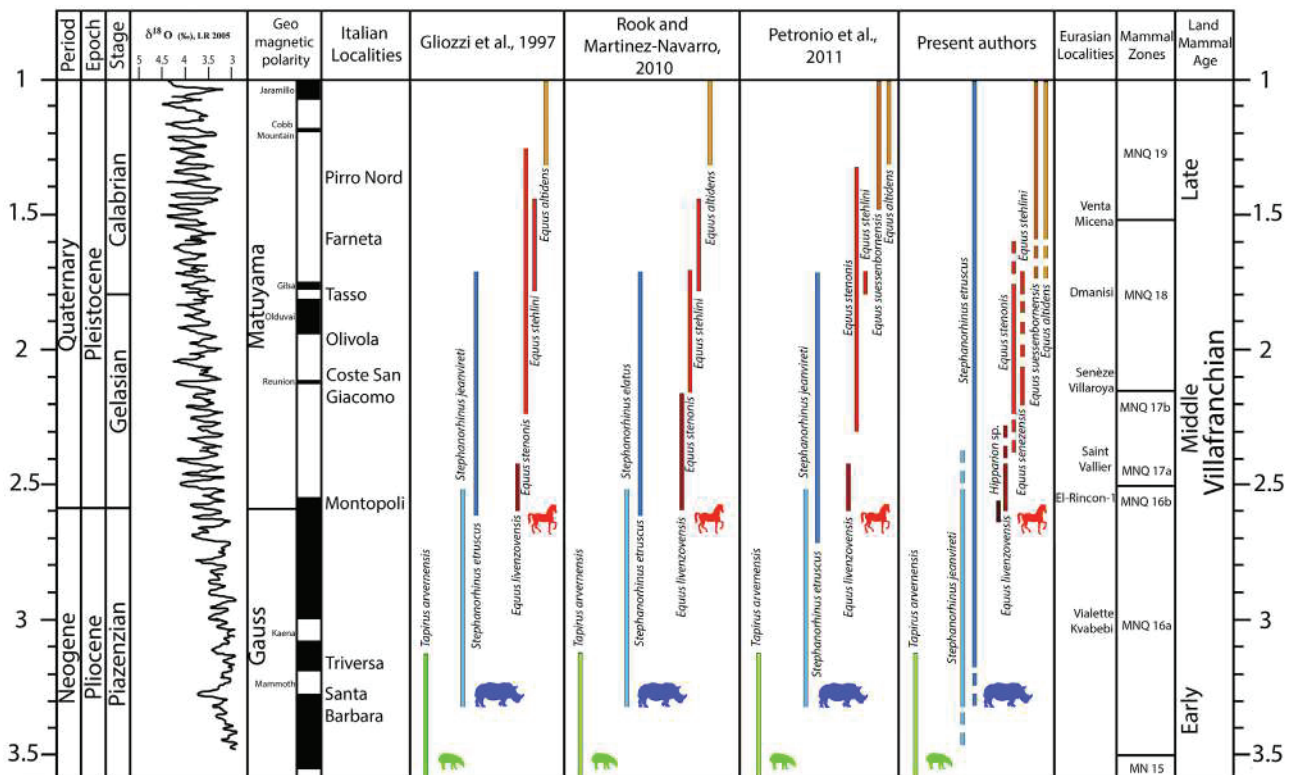


Fig. 8. Biochronology of the Villafranchian perissodactyls of Italy, with Italian localities correlated with Eurasian localities. Update of the fossil record from Gliozzi et al. (1997), Rook and Martínez-Navarro (2010) and Petronio et al. (2011).

distinctive character of *S. jeanvireti*. The species is documented by a well-preserved astragalus (MGC without specimen number) at Pradalbino (Bologna, Emilia-Romagna; Capellini, 1894) and by a distal epiphysis and a very damaged proximal epiphysis of humerus (MGC without specimen number), probably belonging to the same individual, at Monte Pastore (Bologna, Emilia-Romagna). An almost complete mandible (MGC 9354) recovered at Monte San Pietro (Bologna, Emilia-Romagna; Capellini, 1920) and a fragmentary mandible (IGF 1449v) from Capannoli (Lower Valdarno) can be referred to *S. jeanvireti*. Two almost complete forelimbs, two almost complete hindlimbs, two incomplete lower cheek teeth, and a fragmentary skull of a young individual, housed at IGF, have been collected from Montopoli (Lower Valdarno, Tuscany; Azzaroli, 1962; Guérin, 1980; Pandolfi, 2013a). The four almost complete limbs and the two cheek teeth (IGF 1075) probably belong to the same adult individual; they have been recovered during the paleontological excavations of Forsyth Major in 1877–1880. Based on the morphological characteristics of the specimens, the attribution to *S. jeanvireti* is confirmed. The fragmentary skull (IGF 14869), referred to *S. jeanvireti*, is under study by one of us (LP). The last occurrence of *S. jeanvireti* in Europe has been usually reported at the Pliocene-Pleistocene transition. Nevertheless, Pandolfi et al. (2019) recently recorded its presence in a middle Villafranchian assemblage in Romania, extending the biochronological range of this species until the first half of the Early Pleistocene.

According to Guérin (1980) and Pandolfi (2013a), *Stephanorhinus etruscus* occurred in Italy during the latest Pliocene (MN16a) in the site of Villafranca d'Asti and around the Pliocene-Pleistocene transition (MN16b) at Montopoli. The isolated remains from Villafranca d'Asti (housed at NMB) come from an undefined stratigraphic level, and an attribution to an age younger than the early Villafranchian cannot be excluded (Pandolfi et al., 2017a). The Etruscan rhino is represented only by one astragalus (IGF 1452V) and a fragmentary metatarsal (IGF 4688V) from the site of Montopoli (where *S. jeanvireti* is also present; Pandolfi, 2013a). *Stephanorhinus etruscus* is also reported in latest Pliocene deposits of Castelnuovo di Baradenga Scalo (Siena Province; Pandolfi et al., 2017a).

Papers published several years ago (e.g., Rustioni et al., 1996) denied the presence of *Stephanorhinus etruscus* in the early Villafranchian, but investigators lacked new data about fossil rhinoceroses published during the past 20 years and the new considerations about material and localities. Indeed, knowledge about fossils increased substantially after the 1990s. *Stephanorhinus etruscus* is recorded in a number of early late Villafranchian localities (assigned to the Olivola and Tasso FUs; Guérin, 1980; Mazza, 1988; Cerdeño, 1992; Pandolfi et al., 2017a), in particular from Tuscany. The latest Villafranchian Italian rhinoceroses from Pirro Nord (Foggia Province, southern Italy), Madonna della Strada (L'Aquila Province, central Italy), Imola Basin (Imola Province, northern Italy) and Pietrafitta (Perugia Province, central Italy) can be assigned to *S. etruscus* (Pandolfi and Petronio, 2011a; Pandolfi et al., 2017a). Nevertheless, Pandolfi et al. (2017a) also recognized that a mounted skeleton of one individual housed at MPLBP and collected from a clay level of Pietrafitta displays some differences with *S. etruscus*, being more similar to *S. hundsheimensis*. This would mean that both species may have been present at Pietrafitta, coming from two distinct fossiliferous levels. Further investigations are needed to clarify this point. The occurrence of *Stephanorhinus hundsheimensis* at Lefte (Bergamo Province) represents the earliest record of this species in northern Italy (Pandolfi and Erten, 2017) whereas *S. etruscus* persisted in central Italy until the end of the Early Pleistocene (e.g., Monte delle Piche, Rome; Pandolfi and Marra, 2015). Pandolfi and Marra (2015) and Pandolfi et al. (2015b), Pandolfi et al. (2017a) suggested that *Stephanorhinus etruscus* was the sole rhinoceros species in Western Europe from ca. 2.5 Ma (last occurrence of *S. jeanvireti*) to 1.5 Ma

(first occurrence of *S. hundsheimensis*; Pandolfi and Erten, 2017). Indeed, until the discovery of *S. jeanvireti* remains from Lower Pleistocene deposits of Romania, there were no other rhinos in Western Eurasia during that time span. The present knowledge of *S. jeanvireti* and *S. etruscus* in the Italian fossil record is shown in Fig. 8, with the new updates from Pandolfi (2013) and Pandolfi et al. (2017a), Pandolfi et al. (2019).

4.3. Equidae

The Italian Villafranchian fossil Equidae include the genera 'Hipparion' and *Equus*. The *Equus* Datum is represented at the site of Montopoli, which is known as the earliest occurrence of the genus in Italy (Lindsay et al., 1980; Azzaroli, 1983; Bernor et al., 2018). The occurrence of 'Hipparion' has been reported for the first time from Montopoli FU (MNQ16b; Rook et al., 2017). The fossil record of *Equus* spans from the Montopoli FU through the entire Villafranchian, Galerian, and Aurelian; the occurrence in the site of Montopoli Val d'Arno of the large monodactyl *Equus* cf. *livenzovensis* allowed Azzaroli (1983) to recognize the so-called Elephant-*Equus* event, characterizing the beginning of the Pleistocene. Even if the *Equus* Datum is recorded in many localities in the Old World and was heralded as a synchronous event (Lindsay et al., 1980), Rook et al. (2019) have shown that this extension can be verified at the genus level, but not at the species one. The "Equus Datum" reflects a regional-intercontinental event with an estimated age of 2.58 Ma in Europe, 2.55 Ma in the Linxia Basin, China, and 2.33 Ma in Ethiopia. The Villafranchian Equidae species recorded in the Italian sites have been referred to 'Hipparion' sp., *Equus* cf. *livenzovensis*, *Equus senegensis* aff. *Equus senegensis stehlini*, *Equus stenonis*, *Equus stehlini*, *Equus suessenbornensis*, and *Equus altidens*.

Hipparionine horses first occurred in Europe between 11.4 and 11.0 Ma in the Vienna Pannonian C Basin (Bernor et al., 1988, 2017; Woodburne, 2007, 2009). The primitive radiation of the hipparionine horses through the Old World from North America have been identified as the *Cormohipparion* Datum (Berggren and Van Couvering, 1974; Bernor et al., 2017). 'Hipparion' diversification reached its maximum in the late Miocene and, by a relatively brief time span, had a collapse in diversity at the end of the late Miocene (Bernor et al., 1996, 2010; Eronen et al., 2009). During the Pliocene, few lineages of Old World 'Hipparion' survived and the extension of the Chinese lineages of *Plesiohipparion* and *Proboscoidipparion* into Turkey and *Plesiohipparion* into Spain was accompanied with the extinction of the most common western Eurasian hipparionine genera, namely *Hippotherium*, *Cremohipparion*, *Sivalhippus* and *Hipparion* s.s. (Bernor and Lipscomb, 1991; Bernor and Sun, 2015; Bernor et al., 2015; Bernor and Sen, 2017).

Bernor and Lipscomb (1991) identified an hipparionine horse from Gulyazi, Turkey, as *Plesiohipparion* aff. *huangheense*, co-occurring with *Equus* at ca. 2.6 Ma. *Plesiohipparion huangheense* is also known from the early middle Villafranchian of China (MN16b, ca. 2.5 Ma), likewise co-occurring with the genus *Equus* (Qiu et al., 1988). *Plesiohipparion huangheense* has also been reported from the Tatrot Fm., India (Jukar et al., 2018). The presence of an 'Hipparion' sp. co-occurring with *Equus livenzovensis* in the Montopoli FU is correlated with fragmentary remains of *Plesiohipparion* cf. *P. rocinantis* from the French locality of Roca-Neyra (dated at 2.6 ± 0.02 Ma; Nomade et al., 2014; Cirilli et al., in press). Other Villafranchian occurrences of 'Hipparion' in Europe include the Red Crag (Suffolk, England; ca. 3 Ma), Hungary ('*Hipparion*' *moritorium*, early Villafranchian, ca. 2.6 Ma), Sésklo (*Plesiohipparion* cf. *shanxiense*, early Villafranchian, MNQ16b; Athanassiou, 2018) and Villaroya, Spain ('*Hipparion*' *rocinantis*, 2.1 Ma). The Villaroya 'Hipparion' has been dated magnetostratigraphically at 2.1 Ma by Pueyo et al. (2016) and is the youngest European 'Hipparion', referred to *Plesiohipparion* (Bernor and Sun,

2015; Bernor et al., 2015). Recently, Cirilli et al., (in press) have recognized the occurrence of multiple Hipparionine lineages in the Plio-Pleistocene of Europe, with the species *Proboscideipparion crasum* from Perpignan (France), Suffolk, Red Crag (England) and possibly Dorkovo (Bulgaria), and *Plesiohipparion rocinantis* from Kvabebi (Georgia), Roca-Neyra (France) and Villarroya (Spain). As previously discussed above, the Montooli's fragmentary tooth remains quite enigmatic, albeit a possible genus level referral could be ?*Cremohipparion*. Indeed, Cirilli et al., (in press) have discussed the possible occurrence of the genus *Cremohipparion* in the Pliocene of Layna, due the morphology shown by the species "*Hipparion*" *fissurae*. Therefore, it can not be excluded that the genus *Cremohipparion* survived in the late Pliocene and Early Pleistocene of Europe represented by the Spanish and Italian samples.

Equus cf. *livenzovensis* at Montopoli occurs at the beginning of the Pleistocene; the faunal turnover recorded at Montopoli is marked with the disappearance of warm forest species such as *Tapirus arvernensis*, *Mammuth borsoni*, *Sus arvernensis* and *Ursus minimus*, and the first occurrence in the Villafranchian record of *Mammuthus gromovi*, *Stephanorhinus etruscus*, *Eucladoceros falconeri*, *Gazella borbonica*, and *Equus* cf. *livenzovensis*. In Europe, *E. livenzovensis* is recorded from the Spanish localities of El Rincón-1 and Huelago (Alberdi et al., 1997; Palombo and Alberdi, 2017), the France locality of Roca-Neyra (Cirilli et al., in press) and Liventsovka (Azzaroli, 2000). The Spanish locality El Rincón-1 shares a number of taxa found at Montopoli (2.58 Ma): *Nyctereutes megamastoides*, *Stephanorhinus etruscus*, and *Gazella borbonica*. These Italian and Spanish Early Pleistocene localities record the westernmost extension of *E. livenzovensis* in Europe.

Equus senezensis, preliminary identified in the Italian fossil record as *Equus senezensis* aff. *Equus senezensis stehlini* (Palombo et al., 2017), has been reported for the first time in Italy from Coste San Giacomo (CSG), dated at ca. 2.1 Ma (Bellucci et al., 2012, 2014). This datum represents the first occurrence of this species (*E. senezensis*) apart from the locality of Senèze which could suggest an early biogeographic dispersion of these Villafranchian medium-small-sized horses. Indeed, this identification seems to be well supported also from other evidence; the locality of CSG shares some taxa with the assemblage from Senèze such as *Anancus arvernensis*, and pollen data reveal a similar environmental setting for both localities (Palombo et al., 2017). The discovery of another medium-sized horse at the locality of Montecarlo, Upper Valdarno Basin (2.4–2.2 Ma; Chinassi et al., 2005), preliminarily reported by Bernor et al. (2019), re-opened the debate on the first appearance and evolutionary relationships of the small Villafranchian horses in Europe. Furthermore, the presence of *Anancus arvernensis* and *Miomys polonicus* in Montecarlo testifies to faunal similarities with CSG. These recent discoveries might be indicative of the presence of small Villafranchian horses earlier than in the Tasso FU (MNQ18, 1.8–1.6 Ma), as described in Palombo et al. (2017). The new geochronological age of the localities of Senèze reported in Nomade et al. (2014) upholds the hypothesis that the French and Italian Villafranchian localities could share a similar fossil record on the dispersion of the medium-sized horses, and their origin and evolution could be congruent with the MNQ17b–MNQ18 boundary.

Equus stenonis is one of the most common horses in middle Villafranchian European localities. The new calibration at 2.5 Ma of the French locality of Saint-Vallier (Nomade et al., 2014) includes the occurrence of *Equus stenonis vireti* Prat, 1964, and as such, it is probably the oldest evidence of this species in Europe. Eisenmann (2004) has argued that its morphology is intermediate between *E. livenzovensis* and *E. stenonis stenonis* from the Upper

Valdarno Basin. The European middle to late Villafranchian horses referred to *E. stenonis* differ in size and body proportions, while exhibiting a similar bauplan. For this reason, several subspecies have been proposed for *E. stenonis* (*Equus* s. *livenzovensis*, *E. s. stenonis*, *E. s. olivolanus*, *E. s. vireti*, *E. s. pueblensis*, *E. s. guthi*, *E. s. senezensis*, and *E. s. mygdoniensis*). Even if the validity of these subspecies is still a matter of debate (Bernor et al., 2019) they show close morphological features and their range of morphometric variability largely overlaps. Recently, Cherin et al., (2020) have reported the new occurrence of *E. stenonis* from the Italian Early Pleistocene locality of Pantalla (Central Italy).

Equus stehlini occurs at the locality of Casa Frata, Upper Valdarno Basin (De Giuli and Masini, 1986). This locality yielded a relevant number of Villafranchian taxa, many of these already reported in the Olivola FU, but the occurrences of some new species as *Praeovibos* sp., *Leptobos vallisarni*, *Pseudodama eurygonos-farnetensis*, *Lycaon falconeri*, in addition to *E. stehlini*, define the Tasso FU (Rook and Martínez-Navarro, 2010). The co-occurrences of *E. stehlini* and *E. stenonis* has been discussed by Azzaroli (1982). He hypothesized that *E. stenonis* and *E. stehlini* could share the same habitat but did not live in the same association, in contrast with the Middle and Late Pleistocene fossil record, where large- and medium-size species (e.g., *E. suessenbornensis*/*E. altidens*–*E. ferus*/*E. hydruntinus*) have been found in the same assemblages. This latter ecological perspective is also typical of the extant wild zebras *E. grevyi* and *E. quagga*, which sometimes overlap their geographic ranges. This review of the Villafranchian horses housed in IGF has revealed that some specimens identified as *E. stehlini* and *E. stenonis* come from the same Upper Valdarno localities (e.g., Terranuova and Le Ville; Table S1, Appendix A). This could be due to an ecological sympatry similar to that of Middle and Late Pleistocene horses.

The fossil record of *Equus suessenbornensis* in Italy has been improved with the identification of some specimens from the locality of Selvella-Gioiella (Val di Chiana, Tuscany; Farneta FU) and from Pirro Nord (Apulia; Alberdi and Palombo, 2013a). The probable occurrence of *E. suessenbornensis* in the Pleistocene deposits from Val di Chiana was preliminarily discussed by De Giuli (1986), even if the author identified the corresponding sample as belonging to *E. cf. stenonis*. Alberdi and Palombo (2013b) have considered the Selvella-Gioiella horse fauna equivalent with the large horse from Süssenborn (Germany) in morphology and size, and confirmed its occurrence in the Farneta FU. Moreover, the occurrence of *E. suessenbornensis* is also reported from Pirro Nord (Alberdi and Palombo, 2013a). The *E. suessenbornensis* occurrence in the Farneta and Pirro Nord represents the oldest stratigraphical datum of this species in Western Europe.

Equus altidens first occurs alongside *E. suessenbornensis* in the Farneta and Pirro Nord FU; it likewise correlates with the early late Villafranchian composite fauna. As reported in Rook and Martínez-Navarro (2010), the Pirro Nord FU marks the arrival of new taxa in addition to *E. altidens*, as *Praemegaceros verticornis*, *Lycaon lycaonides* and *Theropithecus* sp. The FAD of *E. altidens* during the Villafranchian of Italy is reported from the localities of Selvella-Gioiella and Pirro Nord, both with *E. suessenbornensis*. However, if the presence of the large *E. suessenbornensis* is still somewhat controversial and debated by different authors, the occurrence of the slender horse *E. altidens* in the Farneta and Pirro Nord was preliminarily hypothesized by De Giuli (1986) and De Giuli et al. (1986), and later confirmed by Alberdi and Palombo (2013a).

The new biochronological occurrences of 'Hipparion' and *Equus* in the Italian Villafranchian fossil record are summarized in Fig. 8, with the new updates from Alberdi and Palombo (2013a, b), Palombo et al. (2017), Rook et al. (2017), and Bernor et al. (2018).

5. Morphometry and evolutionary trends

5.1. Tapiridae

Tapirus arvernensis has been subdivided into two subspecies by some authors (Michaux et al., 1976; Guérin and Eisenmann, 1994; Guérin and Tsoukala, 2013): *T. arvernensis minor* (early Ruscinian, MN14) and *T. a. arvernensis* (late Ruscinian and early Villafranchian, MN15–MN16b). The first subspecies is smaller and slenderer than the nominal one (Michaux et al., 1976; Guérin and Eisenmann, 1994; Guérin and Tsoukala, 2013). According to Sala et al. (1990), *T. arvernensis* is likely characterized by a size increase during the Pliocene, thus providing a biochronological tool for correlating Pliocene localities. Nevertheless, Rustioni (1992) argued that available data were not enough to establish evolutionary trends, but the occurrence of tapirs are useful for climatic and environmental reconstructions. We agree with the last opinion suggesting that further discoveries are needed to undertake useful statistical analyses in order to evaluate the presence of morphometric trends within this species.

According to Rustioni (1992) the morphology and proportion of the limb bones suggest that *T. arvernensis* was one of the most cursorial species of the genus. Compared with those of the extant tapirs (*T. indicus*, *T. terrestris* and *T. bairdii*), the limb bones of *T. arvernensis* are slenderer; the ratios between the lengths of the posterior limb bones (femur, tibia and metatarsals) are usually higher than in some extant species (Rustioni 1992: p. 291). However, this comparison was based only on a very small sample of *T. arvernensis* and further investigations are needed. The body mass of *T. arvernensis* recently estimated by MacLaren et al. (2018) corresponds to 215 kg, i.e., matching the average values reported for *T. terrestris* (216.6 kg), smaller than *T. indicus* (326.4 kg) and *T. bairdii* (228.7 kg), but a little bit larger than the average estimated body weight of the mountain tapir *T. pinchaque* (202.4 kg). Anyway, the body mass of *T. arvernensis* was estimated only on one specimen and the average values of some living species (*T. pinchaque* and *T. terrestris*) were estimated on 4 or 5 specimens. The body mass of adult *T. terrestris* spans from 150 to 250 kg according to Padilla and Dowler (1994), and that of *T. pinchaque* spans from 125 to 259.8 kg according to Schauenberg (1969) and Padilla et al. (2010); different ranges were reported by de Thoisy et al. (2014), with *T. pinchaque* spanning from 136 to 250 kg and *T. terrestris* spanning from 160 to 295 kg. The body mass of *T. arvernensis*, estimated using linear regressions on humeral and femoral lengths (measurements $N = 3$, from Rustioni, 1992) described in Scott (1983), Scott (1990), suggests a weight between 253.77 and 273.22 kg, which falls into the weight range of *T. terrestris*. As recently demonstrated by MacLaren et al. (2018), *Tapirus* limb bones display significant variations not related to size but to ecological gradients, in particular in the lateral autopodium, that need to be further investigated in fossil European species. The latter species remain poorly documented and lack associated paleoenvironmental data (such as stable carbon isotope analyses on bones).

5.2. Rhinocerotidae

Stephanorhinus etruscus and *Stephanorhinus jeanvireti* are easily distinguishable by the morphometric dimensions of their bones (Fig. 9). According to Guérin (1980), it is not possible to distinguish evolutionary stages of *Stephanorhinus jeanvireti* due to the short temporal distribution of this species. Nevertheless, he detected some differences between specimens collected from older localities (such as Viallette) and from younger localities (such as Montopoli and Les Etouaires): the femur is shorter with a wider diaphysis; radius and tibia are longer with narrower epiphyses;

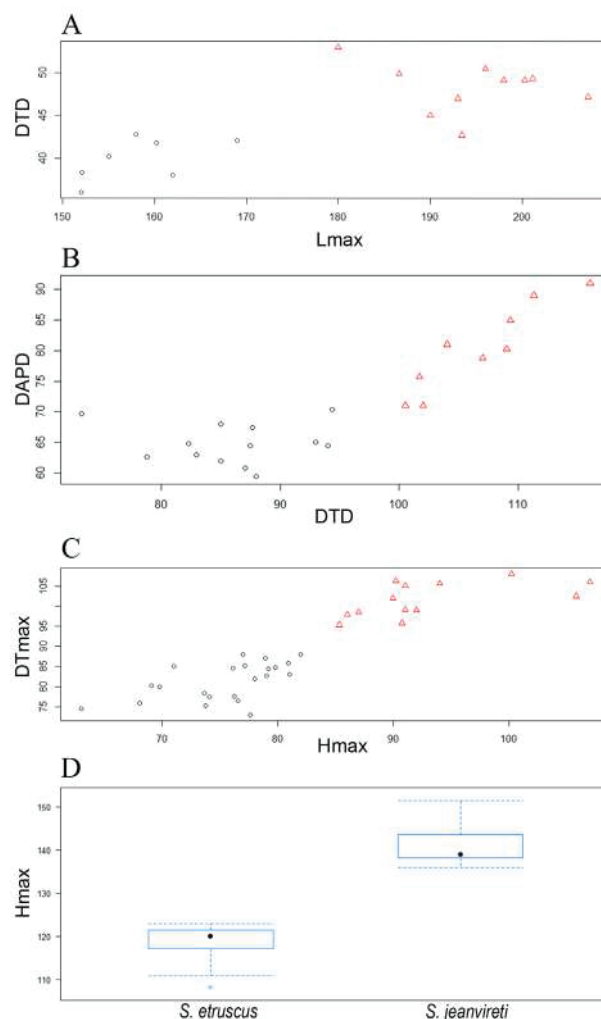


Fig. 9. Comparative dimensions of Villafranchian *Stephanorhinus etruscus* and *S. jeanvireti*. **A.** Plot of the maximal length (Lmax) and distal transverse diameter (DTD) of MCIV of *S. etruscus* (circle) and *S. jeanvireti* (triangle). **B.** Plot of the maximal distal transverse diameter (DTD) and distal antero-posterior diameter (DAPD) of tibia of *S. etruscus* (circle) and *S. jeanvireti* (triangle). **C.** Plot of the maximal height (Hmax) and maximal transverse diameter (DTmax) of astragalus of *S. etruscus* (circle) and *S. jeanvireti* (triangle). **D.** Boxplot of the calcaneus maximal height of *S. etruscus* (left) and *S. jeanvireti* (right). See Table S2 (Appendix A) for data used in these graphs.

the scaphoid is longer and slenderer; astragalus and calcaneus are narrower; MCIV and MTIV are longer with a narrower diaphysis. The available data on *S. jeanvireti* are too scarce for statistical analyses and the trends described by Guérin (1980) are not tested here; the plots suggest that there are no significant differences in dimensions among specimens of different ages.

Some differences in the postcranial elements of *Stephanorhinus etruscus* have been detected by Guérin (1980), in particular in the radius, carpals, metacarpals, some tarsals (astragalus, cuboid, navicular), and MT4 collected from Saint-Vallier and Senèze. Nevertheless, the sample size is too unbalanced and the presence of morphometric trends within the species should be studied using different statistical tools, testing the variation of multiple skeletal elements (Bernor et al., 1997; Sansalone et al., 2015; Pandolfi et al., 2015c). In addition, several localities have been redated and their ages changed during the past few years (e.g., Senèze is older than Olivola; Nomade et al., 2014). The differences reported more than thirty years ago are not useful for current biochronological correlations.

5.3. Equidae

In Equidae, morphometric analyses are provided using Log₁₀-ratio diagrams and boxplots. Eisenmann (1995), Bernor et al. (2003), and Bernor and Harris (2003) used Log₁₀-ratio diagrams to establish evolutionary relationships in different lineages of Old World Hipparionine horses. Recently, Bernor et al. (2018), Bernor et al. (2019) applied this method in their study of *Equus* in order to evaluate affinities in the evolutionary radiation of Old World *Equus*. Here, Log₁₀-ratio diagrams are undertaken on MCIII, MTIII and A1PHIII for a series of middle and late Villafranchian localities: Montopoli, Coste San Giacomo, Matassino, Casa Frata, Selvella-Gioiella, and Pirro Nord, compared to the North American *Equus simplicidens*, *Equus livezovensis* from El Rincón-1 (Spain), *Equus stenonis vireti* from Saint-Vallier (France), *Equus stenonis pueblensis* from La Puebla de Valverde (Spain), *Equus senzeensis* from Senèze (France), *Equus stenonis mygdoniensis* from Mygdonia Basin (Greece), *Equus suessenbornensis* from Süssenborn (Germany), and the extant *Equus grevyi*. Log₁₀-ratio diagrams have also been calculated on MTIII, even if the Italian fossil record does not include third metatarsals for *E. livezovensis* and *E. senzeensis* aff. *E. senzeensis stehlini* from the localities of Montopoli and Coste San Giacomo, respectively.

Boxplots are undertaken on M1 and M3 for MCIII and MTIII for the same species considered in Log₁₀-ratio diagrams, in addition with *Equus sivalensis* from Siwaliks (India), *Equus eisenmannae* from Longdan (China), *Equus stenonis guthi* from Chilhac (France), and *Equus major* from Senèze (France). These anatomical elements have been chosen because they represent the best preserved record of complete postcranial bones of Italian Villafranchian *Equus* species.

Fig. 10 shows Log₁₀-ratio diagrams for MCIII. Even if the specimens are incomplete, *E. cf. livezovensis* from Montopoli exhibits the largest dimensions of the Italian Villafranchian record. The incomplete specimen, preserved in its distal epiphysis characterized by measurements M10–M14, represents the oldest record of the genus *Equus* in Italy. This morphology is replaced by *E. stenonis* from Matassino, smaller in dimension compared to *E. livezovensis* but with similar morphological features. This sample is characterized by a large proximal articular breadth (M5) and depth (M6), a broad distal supra-articular tubercle (M10), and consequently a wide distal articulation (M11–M14). This typical stenonine log₁₀-trajectory is shown also in the sample referred to *E. altidens* from Selvella-Gioiella (Alberdi and Palombo, 2013). The variation of the dimensions is slightly lower than in *E. stenonis* from Matassino but the morphological pattern is close to the latter, except for a narrow midshaft width (M3) and a smaller proximal depth (M6), which indicate a slenderer morphology. The sample from Coste San Giacomo, referred to *E. senzeensis* aff. *E. senzeensis stehlini* (Palombo et al., 2017), exhibits a smaller and different pattern when compared to *E. stenonis*. It is less elongated (M1), with a smaller distal epiphysis (M10–M14), and a large proximal articular breadth (M5). This pattern seems to follow in *E. stehlini* from Casa Frata: the proximal articular breadth (M5) and the depth of the keel (M12) are smaller than *E. senzeensis* aff. *E. senzeensis stehlini*, but this pattern shows similarities to the sample from CSG. Nevertheless, *E. altidens* and *E. suessenbornensis* from Pirro Nord seem to be the most problematical (data from Alberdi and Palombo, 2013a, 2013b). The *Equus altidens* sample shows a great range of variability when compared to all other localities; its maximum falls within *E. stenonis* from Matassino and the minimum is the smallest of the Villafranchian fossil *Equus* record. The Pirro Nord *E. suessenbornensis* range of variability is equivalent to the *E. suessenbornensis* sample from Selvella-Gioiella.

Fig. 10(B) compares the mean values of the Italian Villafranchian horses with other Old World Fossil *Equus* and *E. grevyi*. *E. livezovensis* from El Rincón-1 has dimensions and a log₁₀-

trajectory similar to *E. cf. livezovensis* from Montopoli, larger than *E. stenonis vireti* from Saint-Vallier and *E. stenonis* from Matassino. *E. stenonis vireti* from Saint-Vallier and *E. stenonis pueblensis* from La Puebla de Valverde share a close pattern with *E. stenonis* from Matassino in their size and morphology.

Equus senzeensis from Senèze shows affinities with *E. senzeensis* aff. *E. senzeensis stehlini* from CSG in the proximal articular breadth (M5) and the depth of the keel (M12), even if its trend is somewhat larger. This latter evidence was previously mentioned by Palombo et al. (2017), even if the taxonomic attribution of the CSG sample had to be considered as provisional. This result, obtained with a different analysis (Log₁₀-ratio instead of bivariate and multivariate analysis), supports Palombo et al.'s (2017) interpretation.

The *Equus suessenbornensis* sample from Pirro Nord and Selvella-Gioiella is narrower in dimensions when compared to the *E. suessenbornensis* sample from Süssenborn (data available in Musil, 1969 and Eisenmann website [<https://vera-eisenmann.com>]). Furthermore, *E. suessenbornensis* from the type locality (0.7 Ma) is the largest European species considered in this analysis, even larger than *E. livezovensis*. Considering the evidence provided by our MCIII, MTIII and A1PHIII analyses, the specimens identified as *E. suessenbornensis* from Pirro Nord and Selvella-Gioiella appear to be smaller than the typical species from Süssenborn. More data, statistical and morphological analyses are needed to better resolve this issue.

The *Equus altidens* samples from Selvella-Gioiella and Pirro Nord compare with the pattern of *E. stenonis mygdoniensis* from the Greek locality of Gerakarou-1. Even if the Selvella-Gioiella sample shows slightly larger dimensions than the Pirro Nord and Gerakarou samples, their trends are similar in M1 and M3 dimensions. As already suggested by Gkeme et al. (2017), *E. stenonis mygdoniensis* from the Greek localities of Libakos and Polyakkos may be referred to *E. altidens*; this attribution is in accordance with the Italian data from Selvella-Gioiella and Pirro Nord. *Equus stehlini* represents the smallest Plesitocene horse in Italy, with no other reference from these European fossil localities.

Figs. 11 and 12 show Log₁₀-ratio diagrams calculated for MTIII and A1PHIII, respectively. The results concur with those of MCIII ratio diagrams. *Equus altidens* from Pirro Nord overlaps in size with *E. altidens* from Selvella-Gioiella. *Equus suessenbornensis* from Selvella-Gioiella has narrower dimensions than *E. suessenbornensis* from the type locality of Süssenborn. Moreover, the relationship between *E. senzeensis* aff. *E. senzeensis stehlini* and *E. stehlini* is noticeable, due to their metric values and morphological features. These results explain what has been discussed in the MCIII's Log₁₀-ratio analysis.

Fig. 13 gives boxplots for M1 and M3 in MCIII. All *E. stenonis* subspecies have been considered as separate populations in order to better understand their diversification. There is a significant distinction between the *E. eisenmannae*–*E. livezovensis* group and *E. stenonis vireti* (Fig. 13(A)), whereas a slight clustering can be observed between the European *E. stenonis* subspecies (*E. s. vireti*, *E. s. guthi*, and *E. s. pueblensis*) and the Italian ones (*E. s. olivolanus* and *E. s. stenonis*) in M1. The same pattern is also shown in MTIII's (Fig. 14(A)).

This evidence is partially supported by the permutational ANOVA developed on the total length (M1), both on MCIII and MTIII, for the *E. stenonis* subspecies (Table S4, Appendix A). Whereas there is no statistical difference between the European *E. stenonis* subspecies, two interesting evidences are provided by the *E. stenonis vireti*–*E. stenonis olivolanus* comparison (p-value = 9×10^{-5} on MCIII and 2×10^{-5} on MTIII) and the *E. stenonis guthi*–*E. stenonis olivolanus* comparison (p-value = 0.036 on MCIII and 0.017 on MTIII). These statistical results confirm the morphometric evidence reported in the boxplots (Fig. 13(A), 14(A)), where *E. stenonis olivolanus* has the most elongated metapodials among





Fig. 11. Log₁₀-ratio diagrams on the third metatarsal of the North American and Eurasian Plio-Pleistocene *Equus* with *E. grevyi*; the specimens are standardized on the Hoewenegg *Hippotherium primigenium* sample. Thick lines represent the log₁₀-mean of all the values analyzed from each sample, dashed lines the log₁₀-maximum, and dotted lines the log₁₀-minimum. **A.** Variability of the Italian Early Pleistocene *Equus* species in most important localities. **B.** *Equus* Italian fossil record compared with a suite of fossil *Equus* of North American and Eurasian species including *E. grevyi*. Selvella – Gioiella data from Alberdi and Palombo (2013b); Pirro Nord data from Alberdi and Palombo (2013a); data for fossil and extant *Equus* Log₁₀-ratio diagrams from Eisenmann (2004) and Bernor et al. (2019). See Table S3 (Appendix A) for data used in these graphs.

Fig. 10. Log₁₀-ratio diagrams on the third metacarpal of the North American and Eurasian Plio-Pleistocene *Equus* with *E. grevyi*; the specimens are standardized on the Hoewenegg *Hippotherium primigenium* sample. Thick lines represent the log₁₀-mean of all the values analyzed from each sample, dashed lines the log₁₀-maximum, and dotted lines the log₁₀-minimum. **A.** Variability of the Italian Early Pleistocene *Equus* species in most important localities. **B.** *Equus* Italian fossil record compared with a suite of fossil *Equus* of North American and Eurasian species including *E. grevyi*. Coste San Giacomo data from Palombo et al. (2017); Pirro Nord data from Alberdi and Palombo (2013a); Selvella – Gioiella data from Alberdi and Palombo (2013b); data for fossil and extant *Equus* Log₁₀-ratio diagrams from Eisenmann (2004) and Bernor et al. (2019). See Table S3 (Appendix A) for data used in these graphs.

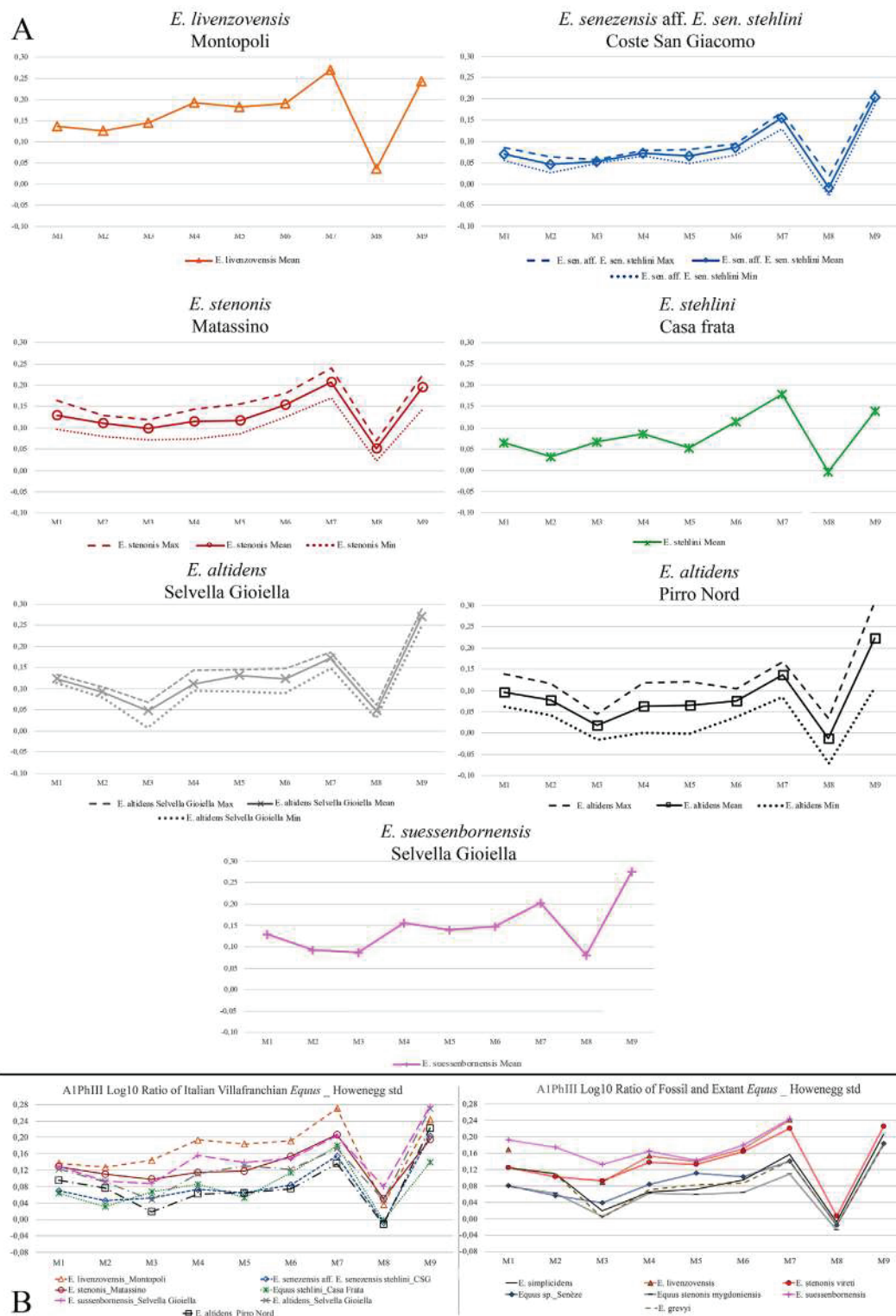


Fig. 12. Log₁₀-ratio diagrams on A1PHIII; the specimens are standardized on the Hoewenegg *Hippotherium primigenium* sample. Thick lines represent the log₁₀-mean of all the values analyzed from each sample, dashed lines the log₁₀-maximum, and dotted lines the log₁₀-minimum. **A.** Variability of the Italian Early Pleistocene *Equus* species in most important localities. **B.** *Equus* Italian fossil record compared with a suite of fossil *Equus* of North American and Eurasian species including *E. grevyi*. Coste San Giacomo data from Palombo et al. (2017); Pirro Nord data from Alberdi and Palombo (2013a); Selvella – Gioiella data from Alberdi and Palombo (2013b); data for fossil and extant *Equus* Log₁₀-ratio diagrams from Eisenmann (2004) and Bernor et al. (2019).

the *E. stenonis* subspecies. Further statistical analyses are beyond the scope of the present review. Nevertheless, we note that this indication is not reported in M3, where a trend of progressive reduction in diaphysis midshaft width can be observed from *E.*

eisenmannae–*E. livezovens* up to *E. senezensis* both in MCIII and MTIII (Fig. 13(B), 14(B)). Here, the variability of the *E. stenonis* subspecies is lower than in M1. Moreover, *E. stehlini* shows the narrowest dimensions, which in part overlap *E. senezensis*. *E. stenonis*

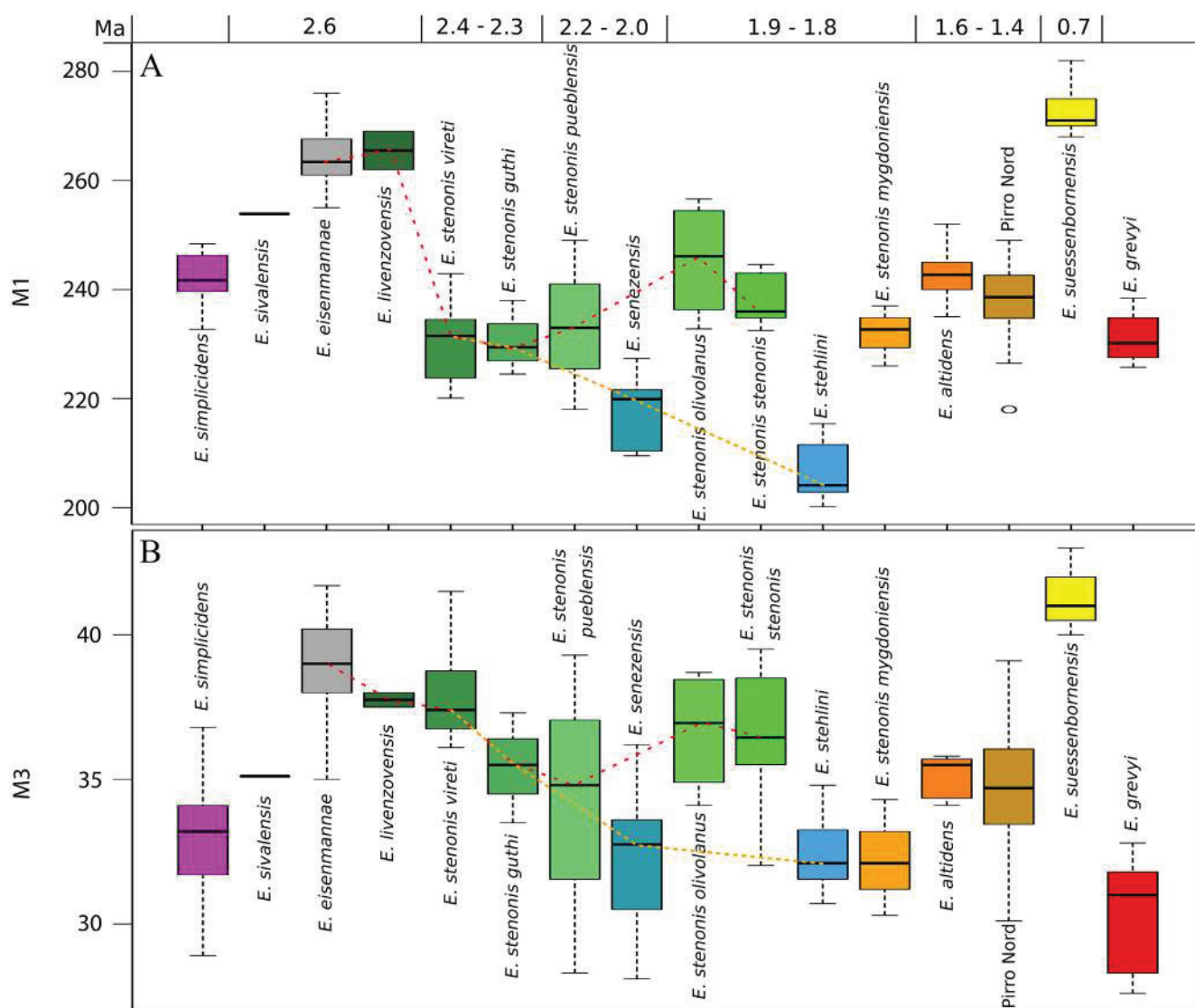


Fig. 13. M1 and M3 Boxplot diagrams on the third metacarpal of the North American and Eurasian Plio-Pleistocene *Equus* with *E. grevyi*. *E. stenonis guthi* data from Boeuf (1986); *E. stenonis pueblensis* and *E. suessenbornensis* data from Vera Eisenmann's website (Eisenmann, 2019; <https://vera-eisenmann.com>); *E. stenonis mygdoniensis* data from Koufos (1992); Pirro Nord data from Alberdi and Palombo (2013a); Selvella – Gioiella *E. altidens* data from Alberdi and Palombo (2013b). Sample sizes: *E. simplicidens*, n = 10; *E. sivalensis*, n = 1; *E. eisenmannae*, n = 12; *E. livenzovensis*, n = 2; *E. stenonis vireti*, n = 24; *E. stenonis guthi*, n = 3; *E. stenonis pueblensis*, n = 3; *E. senezensis*, n = 7; *E. stenonis olivolanus*, n = 7; *E. stenonis stenonis*, n = 9; *E. stehlini*, n = 7; *E. stenonis mygdoniensis*, n = 3; *E. altidens*, n = 19; Pirro Nord, n = 12; *E. suessenbornensis*, n = 20; *E. grevyi*, n = 10.

mygdoniensis is comparable with the Italian record of *E. altidens* from Selvella–Gioiella and Pirro Nord.

All of these relationships are supported in Fig. 13; also, *E. major* from Senèze exhibits the largest dimensions of the entire Pliocene-Pleistocene species, which are comparable to *E. suessenbornensis* (Fig. 13(A)). Regarding the *E. stenonis* group, a remarkable divergence can be observed in the *Equus* sample from Senèze (*E. senezensis*, following Alberdi et al., 1998) and *E. stehlini*, which are significantly separated from *E. stenonis vireti*, *E. stenonis guthi*, *E. stenonis pueblensis*, *E. stenonis olivolanus*, and *E. stenonis stenonis*. As pointed out in these analyses (Log₁₀-ratios, boxplots and ANOVA), the *E. stenonis* subspecies do not show significant differences in their morphometric dimensions, except for *E. stenonis olivolanus* which remains the slenderest population of the entire *E. stenonis* subspecies-complex. These preliminary morphological and statistical analyses suggest that the subspecies of *Equus stenonis* may actually represent a single polytypic species. They could prove to be different eco-morphotypes of the same species.

Finally, *Equus grevyi*'s relationship with *E. simplicidens* and *E. stenonis* sensu lato has already been suggested by Bernor et al. (2019). This hypothesis is further supported here by the Log₁₀-ratio diagrams and boxplots (Fig. 10(B), 11(B), 12(B), 13, 14). The boxplots further show that *E. grevyi*'s metapodial intraspecific variability is comparable to *E. simplicidens*, *E. stenonis* subspecies (*E. s. vireti*, *E. s. guthi*, *E. s. pueblensis*, *E. s. olivolanus* and *E. s. stenonis*), including *E. s. mygdoniensis* and *E. altidens*. These results are consistent with Bernor et al.'s (2019) conclusions in supporting the hypothesis that the North American and European *Equus stenonine* species are likely evolutionary precursors of *Equus grevyi*.

6. Concluding remarks and perspectives

Perissodactyls represent an important element of Villafranchian faunas in Eurasia. The group has been already treated in several publications (Alberdi and Palombo, 2013a, 2013b; Pandolfi and Petronio, 2011; Pandolfi and Marra, 2015; Pandolfi et al., 2015;

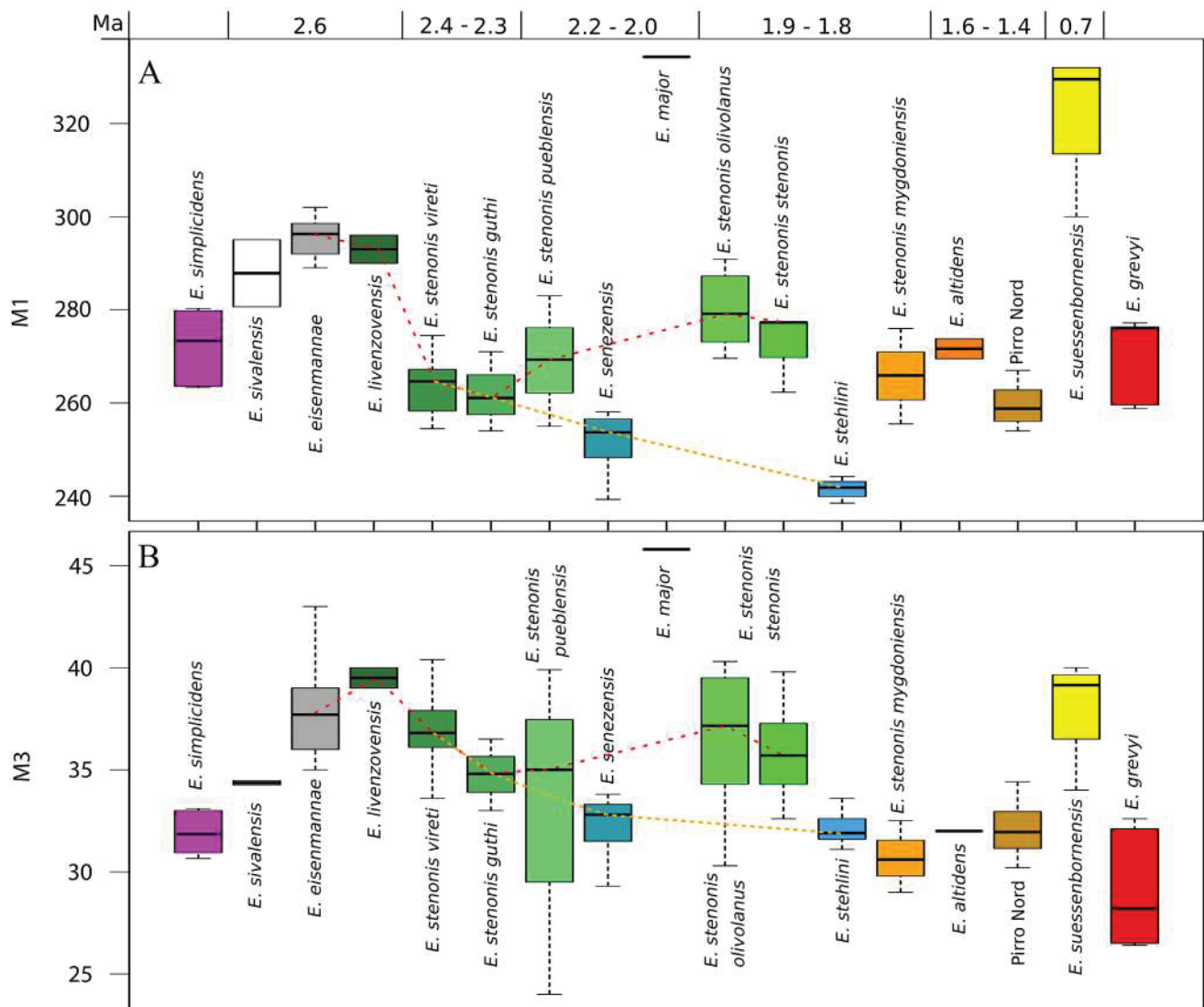


Fig. 14. M1 and M3 Boxplot diagram on the third metatarsal of the North American and Eurasian Plio-Pleistocene *Equus* with *E. grevyi*. See Fig. 13 for data sources. Sample sizes: *E. simplicidens*, n = 6; *E. sivalensis*, n = 2; *E. eisenmannae*, n = 22; *E. livezovens*, n = 2; *E. stenonis vireti*, n = 30; *E. stenonis guthi*, n = 3; *E. stenonis pueblensis*, n = 3; *E. senezensis*, n = 6; *E. stenonis olivolanus*, n = 11; *E. stenonis stenonis*, n = 6; *E. stehlini*, n = 6; *E. stenonis mygdoniensis*, n = 3; *E. altidens*, n = 2; Pirro Nord, n = 5; *E. suessenbornensis*, n = 15; *E. grevyi*, n = 6.

Pandolfi et al., 2017; Pandolfi et al., 2019; Pandolfi and Erten, 2017; Rook et al., 2017; Bernor et al., 2018, 2019; Cirilli et al., 2020), and the present article provides an overview on the current knowledge of this group in Italy to depict a comprehensive framework, highlighting the following points:

- *Tapirus arvernensis* is documented in Italy during the early Villafranchian, as reported by previous papers;
- *Stephanorhinus jeanvireti* characterizes the early and middle Villafranchian (Triversa and Montopoli FUs), despite being documented in Italy by only a few remains;
- *Stephanorhinus etruscus* appears in Italy during the early Villafranchian (despite older references suggested its first occurrence since the middle Villafranchian) and dominates throughout the middle and late Villafranchian, until the beginning of the Middle Pleistocene;
- Evolutionary trends and morphometric variations among Rhinocerotidae cannot be tested due the scarcity of fossil collections; however, the two Villafranchian species can easily be distinguished by their morphometrical characters;
- ‘*Hipparion*’ sp. recovered in Montopoli represents the last reported occurrence of this genus in Italy and perhaps one of the last in Europe, together with the Roca-Neyra *Plesiohipparion* cf. *P. rocinantis*, the *Plesiohipparion* cf. *shanxiense* from Sésiklo, and *Plesiohipparion rocinantis* from Villaroya; these are the youngest European ‘*Hipparion*’ and ultimately they may all be referred to the genus *Plesiohipparion*;
- *Equus* cf. *livezovens* from Montopoli (MNQ16b; 2.58 Ma) represents the *Equus* Datum in the Italian Villafranchian fossil record and, more broadly, in Europe. It shows the primitive bauplan for the “Old World *Equus* stenonine group” and its dimensions are comparable with *E. eisenmannae* from Longdan (China; 2.55 Ma). The morphometrical analysis show that these two species, which mark the *Equus* Datum in Europe and China, could have similar proportions. The occurrence of *E. livezovens* from Montopoli together with the French locality of Roca-Neyra and the Spanish sites of Huelago-1 and El Rincon represent the westernmost dispersion of this lineage in Europe.;
- *Equus stenonis* from Matassino and Olivola share features and morphometric characteristics with other European stenonine

horses such as *E. stenonis vireti* (Saint-Vallier), *E. stenonis guthi* (Chilhac) and *E. stenonis pueblensis* (La Puebla de Valverde). The analyses carried out herein have shown that the range of variability between these subspecies is not large, except for *E. stenonis olivolanus* which shows the most elongated metapodial among *E. stenonis* subspecies. More morphometrical and morphological analysis are needed to resolve this issue, but by the present evidence, it cannot be excluded that these subspecies can be attributable to population variability over time. A synthetic list of *E. stenonis* subspecies is given in Table S5 (Appendix A);

- *Equus senezensis* aff. *E. senezensis stehlini* from Coste San Giacomo is the first record of *E. senezensis* in Europe apart from Senèze. As previously reported in Palombo et al. (2017), the horse from CSG shares morphological features with *E. senezensis* and *E. stehlini* from Casa Frata. This evidence, which needs to be reviewed and supported by further analysis, suggest a close relationship between these two species and may provide new biogeographical and biochronological insights on the evolution of the Villafranchian small- to medium-sized horses;
- *Equus stehlini* is considered here to be a different species and not a subspecies of *E. senezensis*. It is a gracile horse in the Italian Villafranchian fossil record. At the present knowledge, its biochronological and biogeographical range seems to be limited to a few Italian localities;
- The occurrence of *Equus suessenbornensis* in the Italian Villafranchian fossil record remains uncertain because of the nature of the Süssenborn sample. More morphological, morphometrical and statistical investigations are required to resolve this issue;
- The presence of *Equus altidens* in the localities of Selvella-Gioiella and Pirro Nord is confirmed. This observation is also supported by the new identification of *E. altidens* from the Early Pleistocene of Greece (Gkeme et al., 2017).

Our current knowledge of the Italian Villafranchian perissodactyl biochronological ranges is given in Fig. 8.

CRedit authorship contribution statement

OC and LP conceived the study; LP wrote the Tapiridae and Rhinocerotidae sections; OC and RB wrote the Equidae sections; all the authors equally contributed to develop ideas, discuss the results and review the final version of 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.

Acknowledgements

We thank several institutions in Italy and Europe which have provided access to the collection (see main text and Appendix A), with regards to E. Cioppi and L. Bellucci for access to collection at the Palaeontology section of the Museo di Storia Naturale of the University of Florence. O.C. thanks D. Berthet (Musée des Confluences, Lyon) and E. Robert (Université Claude Bernard Lyon 1). L. P. thanks M. Gasparik (HNHM), E. Bodor (MFGI), O. Hampe (MfN), C. Sarti (MGGC), P. Pérez Dios (MNCN), R. Manni (MPUR), F. Farsi (MSNAF), P. Brewer (NHMUK), U. Göhlich (NHMW) and L. Costeur (NMB) for their help and assistance during his visits to the rhinoceros fossil collections. L.P. thanks the European Commission's Research Infrastructure Action, EU-SYNTHESYS projects AT-TAF-2550, DE-TAF-3049, GB-TAF-2825, HU-TAF-3593, HU-TAF-

5477, and ES-TAF-2997; part of this research received support from the SYNTHESYS Project (<http://www.synthesys.info/>) which is financed by European Community Research Infrastructure Action under the FP7 “Capacities” Program. This paper has been developed within the research project “Ecomorphology of fossil and extant Hippopotamids and Rhinocerotids” granted to L.P. by the University of Florence (“Progetto Giovani Ricercatori Protagonisti” initiative).

This manuscript results from a continuous collaboration of RLB with the Earth Sciences Department of the University of Florence. RLB's research has likewise been supported by NSF grants EAR0125009, 1113175, 1138908 and 1558586 for the study of fossil horses, and currently the FuTRES NSF sponsored database NSF DBI-ABI:1759882. Background work crucial for the results presented here has been supported by grants from the University of Pisa and the University of Florence (Fondi di Ateneo). Finally, we thank the Editor, Prof. P.-O. Antoine for considering this contribution and the two reviewers, Prof. D. Kostopoulos and Prof. M.T. Alberdi, for their useful comments and suggestions which have increased the quality of the present manuscript. This is the FuTRES publication n° 16.

Appendix A. Supplementary data

Supplementary data (including Tables S1–S5) to this article can be found online at <https://doi.org/10.1016/j.geobios.2020.09.001>.

References

- Alberdi, M.T., Caloi, L., Palombo, M.R., 1988. The Quaternary fauna of Venosa: Equidae. *Bulletin du Musée d'Anthropologie préhistorique de Monaco* 31, 5–39.
- Alberdi, M.T., Cerdeño, E., López-Martínez, Morales, J., Soria, M.D., 1997. La Fauna Villafranchiense de El Rincon-1 (Albacete, Castilla – La Mancha). *Estudios Geológicos* 53, 69–93.
- Alberdi, M.T., Ortiz-Jaureguizar, E., Prado, J.L., 1998. A quantitative review of European stenonoid horses. *Journal of Paleontology* 72, 371–387.
- Alberdi, M.T., Azanza, B., Cervantes, E., 2016. Villaroya, yacimiento clave de la Paleontología riojana. *Instituto de Estudios Riojanos Logroño*, 317 p.
- Alberdi, M.T., Palombo, M.R., 2013a. The Early Pleistocene Equidae from Pirro Nord (Apricena, Southern Italy). *Palaeontographica Abteilung* 298, 147–167.
- Alberdi, M.T., Palombo, M.R., 2013b. The late Early to early Middle Pleistocene stenonoid horses from Italy. *Quaternary International* 288, 25–44.
- Antoine, P.-O., 2002. Phylogénie et évolution des Elasmotheriina, Mammalia, Rhinocerotidae. *Mémoires du Muséum d'histoire Naturelle* 188, 1–359.
- Antoine, P.-O., Saraç, G., 2005. Rhinocerotidae (Mammalia, Perissodactyla) from the late Miocene of Akkasdagı, Turkey. *Geodiversitas* 27, 601–632.
- Azzaroli, A., 1962. Rhinoceroti pliocenici del Valdarno inferiore. *Palaeontographia Italica* 57, 11–20.
- Azzaroli, A., 1964. The two Villafranchian Horses of the Upper Valdarno. *Palaeontographia Italica* 59, 1–12.
- Azzaroli, A., 1982. On Villafranchian Palaeartic Equids and their allies. *Palaeontographia Italica* 72, 74–97.
- Azzaroli, A., 1983. Quaternary mammals and the “end-Villafranchian” dispersal event. A turning point in the history of Eurasia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 44, 117–139.
- Azzaroli, A., 1984. On some vertebrate remains of Middle Pleistocene age from the Upper Valdarno and Val di Chiana, Tuscany. *Paleontographia Italica* 73, 104–115.
- Azzaroli, A., 1989. The Genus *Equus* in Europe. In: Lindsay, E.H., Fahlbusch, V., Mein, P. (Eds.), *European Neogene Mammal Chronology*. Plenum Press, New York, pp. 339–356.
- Azzaroli, A., 2000. On *Equus livezovensis* Baigusheva 1978 and the “stenonid” lineage of Equids. *Paleontographia Italica* 87, 1–17.
- Azzaroli, A., 2003. Phylogeny of the genus *Equus* L. *Palaeontographia Italica* 84, 11–16.
- Baigusheva, V.S., 1971. Iskopaemaja Teriofauna Livezovskogo Karera (Severo-Vostochnoe Priazovije) SSSR. *Trudy Zoological Institute* 49, 5–23 (in Russian).
- Baigusheva, V.S., 1978. Krupnaja Loshad Khaprovskogo Kompleksa is alluvija SeveroVostochnoto Priazovija. *Invesija Servo-Kavkazkogo Nauchnogo Zentra Vychei Shkoly* 1, 98–92 (in Russian).
- Ballatore, M., Breda, M., 2016. *Stephanorhinus elatus* (Rhinocerotidae, Mammalia): proposal for the conservation of the earlier specific name and designation of a lectotype. *Geodiversitas* 38, 579–594.
- Bellucci, L., Mazzini, I., Scardia, G., Bruni, L., Parenti, F., Segre, A.G., Segre Naldini, E., Sardella, R., 2012. The site of Coste San Giacomo (Early Pleistocene, central Italy): palaeoenvironmental analysis and biochronological overview. *Quaternary International* 267, 30–39.

- 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. *Quaternary Science Reviews* 96, 72–85.
- Berggren, W.A., Van Couvering, J.A., 1974. The late Neogene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 16, 1–215.
- Bernor, R.L., Kovar, J., Lipscomb, D., Rögl, F., Tobien, H., 1988. Systematic, stratigraphic and paleoenvironmental contexts of first appearing *Hipparion* in the Vienna Basin, Austria. *Journal of Vertebrate Paleontology* 8, 427–452.
- Bernor, R.L., Lipscomb, D., 1991. The systematic position of “*Plesiohipparion*” aff. *huangeense* (Equidae, Hipparionini) from Gülyazi, Turkey. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Histor. Geologie* 31, 107–123.
- Bernor, R.L., Fahlbusch, V., Andrews, P., De Bruijn, H., Fortelius, M., Rögl, F., Steininger, F.F., Werdelin, L., 1996. The evolution of Western Eurasian Neogene mammal faunas: a chronologic, systematic, biogeographic, and paleoenvironmental synthesis. In: Bernor, R.L., Fahlbusch, V., Mittman, H.W. (Eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York, pp. 449–469.
- 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., Harris, J.M., 2003. Systematics and evolutionary biology of the Late Miocene and Early Pliocene hipparionine horses from Lothagam, Kenya. In: Leakey, J.M., Leakey, M.G. (Eds.), *Lothagam – The Dawn of Humanity in Eastern Africa*. Columbia University Press, New York, pp. 387–438.
- Bernor, R.L., Scott, R.S., Fortelius, M., Kappelman, J., Sen, S., 2003. Systematics and evolution of the Late Miocene Hipparions from Sinap, Turkey. In: Fortelius, M., Kappelman, J., Sen, S., Bernor, R.L. (Eds.), *The Geology and Paleontology of the Miocene Sinap Formation, Turkey*. Columbia University Press, New York, pp. 220–281.
- Bernor, R.L., Armour-Chelu, M., Gilbert, H., Kaiser, T.M., Schulz, E., 2010. Equidae. In: Werdelin, L., Sanders, W.J. (Eds.), *Cenozoic Mammals of Africa*. University of California Press, Berkeley, pp. 685–721.
- Bernor, R.L., Meshida, K., Sun, B., 2015. Phylogenetic signature in the juvenile skulls and cheek teeth of Pleistocene *Proboscideipparion sinense*, China. *Rivista Italiana di Paleontologia e Stratigrafia* 121, 255–264.
- Bernor, R.L., Sun, B., 2015. Morphology through ontogeny of Chinese *Proboscideipparion* and *Plesiohipparion* and observations on their Eurasian and African relatives. *Vertebrata Palasiatica* 53, 73–92.
- Bernor, R.L., Sen, S., 2017. The early Pliocene *Plesiohipparion* and *Proboscideipparion* (Equidae, Hipparionini) from Çalta, Turkey (Ruscinian Age, c. 4.0 Ma). *Geodiversitas* 39, 285–314.
- Bernor, R.L., Göhlich, U.B., Harzahauser, M., Semprebon, G.M., 2017. The Pannonian C hipparions from the Vienna Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology* 476, 28–41.
- Bernor, R.L., Cirilli, O., Wang, S.Q., Rook, L., 2018. *Equus cf. livezovenzsis* from Montopoli, Italy (early Pleistocene; MN16b; ca. 2.6 Ma). *Bollettino della Società Paleontologica Italiana* 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. *Frontiers in Ecology and Evolution* 7, 166.
- Boeuf, O., 1986. L'Equidé du site Villafranchien de Chilhac (Haute-Loire, France). *Annales de Paléontologie* 72, 29–67.
- Campanino, F., Forno, M.G., Mottura, A., Ormezzano, D., Sala, B., 1994. *Stephanorhinus jeanvireti*, Guérin, 1972 (Rhinocerotidae, Mammalia) from Roatto near Villafranca d'asti, NW Italy – Revision of the specimen from Dusino. *Bollettino del Museo Regio di Scienze Naturali di Torino* 12, 439–499.
- Capellini, G., 1881. Resti di Tapiro nella Lignite di Sarzanello. *Memorie della Regia Accademia dei Lincei* 9, 76–80.
- Capellini, G., 1894. Rinoceronti fossili del Museo di Bologna. *Memorie della Regia Accademia delle Scienze dell'Istituto di Bologna* 5, 337–349.
- Capellini, G., 1920. Rinoceronte fossile di Monte San Pietro. *Rendiconti della 9.a Sessione della Regia Accademia delle Scienze dell'Istituto di Bologna*, pp. 79–84.
- Capellini, E., Welker, F., Pandolfi, L., Ramos-Madrugal, J., Samodova, D., Ruther, P. L., Fotakis, A. K., Lyon, D., Moreno-Mayar, J.V., Bukhsianidze, M., Jersie-Christensen, R.R., Mackie, M., Ginolhac, A., Ferring, R., Tappen, M., Palkopoulou, E., Dickinson, M.R., Stafford, T. W. jr., Chan, Y.L., Götherström, A., Nathan Senthilvel, K.S.S., Heintzman, P.D., Kapp, J. D., Kirillova, I., Moodley, Y., Agusti, J., Kahlke, R.-D., Kiladze, G., Martínez-Navarro, B., Liu, S., Velasco, M.S., Sinding, M.-H. S., Kelstrup, C.D., Allentoft, M.E., Orlando, L., Penkman, K., Shapiro, B., Rook, L., Dalén, L., Gilbert, M.T.P., Olsen, J.V., Lordkipanidze, D., Willerslev, E., 2019. Early Pleistocene enamel proteome from Dmanisi resolves *Stephanorhinus* phylogeny. *Nature* 574, 103–107.
- Cerdeño, E., 1989. Revisión de la sistemática de los rinocerontes del Neógeno de España. Tesis Doctoral, Universidad Complutense de Madrid 306/89, 429 p. (unpubl.).
- Cerdeño, E., 1992. Spanish Neogene Rhinoceroses. *Palaeontology* 35, 297–308.
- Cerdeño, E., 1993. Remarks on the Spanish Plio-Pleistocene *Stephanorhinus etruscus*, Rhinocerotidae. *Comptes Rendus de l'Académie des Sciences* 317, 1363–1367.
- Cherin, M., Cirilli, O., Azzarà, B., Bernor, R.L., 2020. *Equus stenonis* (Equidae, Mammalia) from the Early Pleistocene of Pantalla (Italy) and the dispersion of stenonis horses in Europe. *Bollettino della Società Paleontologica Italiana*. <https://doi.org/10.4435/BSPI.2020.21>.
- Cirilli, O., Bernor, R.L., Rook, L., n.d. New insights on the Early Pleistocene equids from Roca-Neyra (France, central Europe): implications for the Hipparion LAD and the Equus FAD in Europe. *Journal of Paleontology*. <https://doi.org/10.1017/jpa.2020.99>. In press.
- Cirilli, O., Melchionna, M., Serio, C., Bernor, R.L., Bukhsianidze, M., Lordkipanidze, D., Rook, L., Profico, A., Raia, P., 2020. Target deformation of the *Equus stenonis* holotype skull: A virtual reconstruction. *Frontiers in Earth Science* 8, 247.
- Cocchi, L., 1867. L'uomo fossile dell'Italia Centrale. *Memorie della Società Italiana di Scienze Naturali* 2, 1–180.
- Croizet, J.B., Jobert, A., 1828. Recherches sur les ossements fossiles du département du Puy-de-Dôme. Adolphe Delahays, Paris, p. 226.
- De Giuli, C., 1972. On the type form of *Equus stenonis* Cocchi. *Palaeontographica Italica* 48, 35–49.
- De Giuli, C., Masini, F., Torre, D., 1986. The latest Villafranchian Faunas in Italy: the Pirro Nord Fauna (Apricena, Gargano). *Palaeontographica Italica* 74, 51–62.
- De Giuli, C., 1986. Late Villafranchian faunas of Italy: the Selvella local Fauna in the southern Chiana Valley, Umbria. *Palaeontographica Italica* 74, 11–50.
- De Giuli, C., Masini, F., 1986. Late Villafranchian faunas in Italy: the Casa Frata local Fauna (Upper Valdarno, Tuscany). *Palaeontographica Italica* 74, 1–9.
- Del Campana, D., 1910. I tapiri del Terziario italiano. *Palaeontographica Italica* 16, 147–204.
- Delafond, F., Depéret, C., 1893. Les terrains tertiaires de la Bresse et leurs gîtes de lignites et de minerais de fer. *Etudes des Gîtes Minéraux de la France*. Imprimerie Nationale, Paris, 332 p.
- Delson, E., Faure, M., Guérin, C., Aprile, L., Argant, J., Blackwell, B.A.B., Debar, E., Harcourt-Smith, W., Martin-Suarez, E., Monguillon, A., Parenti, F., Pastre, J.F., Sen, S., Skinner, A.R., Swisher, C.C., Valli, A.M.F., 2006. Franco-American renewed research at the Late Villafranchian locality of Senèze (Haute-Loire, France). *Courier Forschungsinstitut Senckenberg* 256, 275–290.
- Dominici, S., Rook, L., Benvenuti, M., Abbazzi, L., 1995. Tapir remains in paralic deposits of Pliocene age in Lower Valdarno (Tuscany, Italy): Facies analysis and taphonomy. *Geobios* 18, 131–135.
- 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.
- Eisenmann, V., Guérin, C., 1992. *Tapirus priscus* Kaup from the Upper Miocene of Western Europe: palaeontology, biostratigraphy, and palaeoecology. *Paleontologia i Evolució* 24–25, 113–122.
- Eisenmann, V., 1995. What metapodial morphometry has to say about some Miocene hipparions. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), *Paleoclimate and Evolution: With Emphasis on Human Origins*. Yale University Press, New Haven, pp. 148–163.
- Eisenmann, V., 2004. Les Equidés (Mammalia, Perissodactyla) de Saint-Vallier (Drôme, France) et les Equidés Plio-Pleistocènes d'Europe. *Geobios* 37, 279–305.
- Eisenmann, V., 2019. Personal website, <https://vera-eisenmann.com>.
- Eronen, J., Evans, A.R., Fortelius, M., Jernvall, J., 2009. The impact of regional climate on the evolution of mammals: a case study using fossil horses. *Evolution* 64, 398–408.
- Falconer, H. (1868). On the European Pliocene and Post-Pliocene species of the genus *Rhinoceros*, in: C. Murchison, ed., *Palaeontological Memoirs and Notes of the late Hugh Falconer*, Vol. 2, Mastodon, Elephant, Rhinoceros, Ossiferous Caves, Primeval Man and His Contemporaries. Robert Hardwicke, London, pp. 309–403.
- Fejfar, O., 1964. Early-Villafranchian vertebrates from Hajnáčka near Filakovo in Southern Slovakia. *Rozprawy Ústředního Ústavu Geologického* 30, 1–115.
- Forsyth Major, C., 1885. On the mammalian Fauna of the Val d'Arno. *Quarterly Journal of the Geological Society of London* 41, 1–8.
- Fortelius, M., Mazza, P., Sala, B., 1993. *Stephanorhinus* (Mammalia: Rhinocerotidae) of the Western European Pleistocene, with a revision of *S. etruscus*, Falconer, 1868. *Palaeontographica Italica* 80, 63–155.
- Geraads, D., 1988. Révision des Rhinocerotidae (Mammalia) du Turolien de Pikermi : Comparaison avec les formes voisines. *Annales de Paléontologie* 74, 13–41.
- Ghinassi, M., Abbazzi, L., Esu, D., Gaudant, J., Girotti, O., 2005. Facies analysis, stratigraphy and paleontology (molluscs and vertebrates) in the upper Pliocene sandy flood-basin deposits of the Upper Valdarno basin (Northern Apennines). *Rivista Italiana di Paleontologia e Stratigrafia* 11, 463–483.
- Gibbard, P.L., Head, M.J., Walker, M.J.C., 2010. Formal ratification of the Quaternary System/Period and the Pleistocene Series/Epoch with a base at 2.58 Ma. *Journal of Quaternary Science* 25, 96–102.
- Gliozzi, E., Abbazzi, L., Argenti, P., Azzaroli, A., Caloi, L., Capasso Barbato, L., Di Stefano, G., Esu, D., Ficarelli, G., Girotti, O., Kotsakis, T., Masini, F., Mazza, P., Mezzabotta, C., Palombo, M.R., Petronio, C., Rook, L., Sala, B., Sardella, R., Zanolza, 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. *Rivista Italiana di Paleontologia e Stratigrafia* 103, 369–388.
- Gkeme, A., Koufos, G.D., Kostopoulos, D.S., 2017. The Early Pleistocene stenonoid horse from Libakos (Western Macedonia, Greece): Biochronological and palaeoecological implications and dispersal events. 15th RCMNS Congress, Athens, 2017, Abstract Book, p. 67.
- Gómez De Soler, B., Campeny, Vall-Llosera, G., Made, J. Van der., Oms, O., Agustí, J., Sala, R., Blain, H.A., Burjachs, F., Claude, S., García Catalán, S., Riba, D., Rosillo, R., 2012. A new key locality for the Pliocene vertebrate record of Europe: the Camp dels Ninots maar, NE Spain. *Geologica Acta* 10, 1–17.
- Gromova, V.I., 1949. Istorija loshadej (roda *Equus*) v Starom Svete. Chast' 1. Obzor i opisaniye form. *Trudy paleontologicheskogo Instituta* 17, 1–373 (in Russian).

- Guérin, C., Heintz, E., 1971. *Dicerorhinus etruscus* (Falconer, 1859), Rhinocerotidae, Mammalia, du Villafranchien de La Puebla de Valverde, Turuel, Espagne. Bulletin du Muséum d'Histoire naturelle série 3, n. 18. Sciences de la Terre 2, 13–22.
- Guérin, C., 1972. Une nouvelle espèce de rhinocéros, Mammalia, Perissodactyla à Viallette, Haute-Loire, France) et dans d'autres gisements du Villafranchien Inférieur européen : *Dicerorhinus jeanvireti* n. sp. Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon 49, 53–161.
- Guérin, C., 1980. Les Rhinocéros, Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale. Comparaison avec les espèces actuelles. Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon 79, 1–1185.
- Guérin, C., 1982. Première biozonation du Pléistocène Européen, principal résultat biostratigraphique de l'étude des Rhinocerotidae (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène Supérieur d'Europe occidentale. Geobios 15, 593–598.
- Guérin, C., Eisenmann, V., 1994. Les tapirs, Mammalia, Perissodactyla) du Miocène supérieur d'Europe occidentale. Geobios 27, 113–127.
- Guérin, C., 2004. Les rhinocéros (Mammalia, Perissodactyla) du gisement villafranchien moyen de Saint-Vallier, Drôme. Geobios 37, 259–278.
- Guérin, C., Tsoukala, E., 2013. The Tapiridae, Rhinocerotidae and Suidae (Mammalia) of the Early Villafranchian site of Milia, Grevena, Macedonia, Greece. Geodiversitas 35, 447–489.
- Guerrero-Alba, S., Palmqvist, P., 1997. Estudio morfológico del caballo de Venta Micena (Orce, Granada) y su comparación con los équidos modernos y del Plioceno en el viejo mundo. Paleontología y Evolución 30–31, 93–148.
- Heissig, K., 1996. The stratigraphical range of fossil rhinoceroses in the late Neogene of Europe and the Eastern Mediterranean. In: Bernor, R.L., Fahlbusch, V., Mittmann, H.-W. (Eds.), The Evolution of Western Eurasian Neogene Mammal Faunas. Columbia University Press, New York, pp. 339–347.
- Heissig, K., 1999. Family Rhinocerotidae. In: Rössner, G.E., Heissig, K. (Eds.), The Miocene Land Mammals of Europe. Pfeil, Munich, pp. 175–188.
- Heintz, E., Guérin, C., Martin, R., Prat, F., 1974. Principaux gisements villafranchiens de France : listes fauniques et biostratigraphie. Mémoires du Bureau de Recherches géologiques et minières 78, 169–182.
- Hulbert Jr., R.C., 2010. A new early Pleistocene tapir (Mammalia: Perissodactyla) from Florida, with a review of Blancan tapirs from the state. Bulletin of Florida Museum of Natural History 49, 67–126.
- Hürzeler, J., Engesser, B., 1976. Les faunes de mammifères néogènes du Bassin de Baccinello, Grosseto, Italie. Compte Rendus de l'Académie des Sciences, série D 283, 333–336.
- Jánossy, D., Krollop, E., 1981. Die pleistozänen Schnecken- und Vertebraten-Faunen von Süttö, Travertine, Deckschichten und Spalten. Fragm. Mineral. Paleontology 10, 31–58.
- Jukar, A., Sun, B., Bernor, R.L., 2018. The first occurrence of *Plesiohipparion huangheense* (Qiu, Huang and Guo, 1987) (Equidae, Hipparionini) from the late Pliocene of India. Bollettino della Società Paleontologica Italiana 57, 125–132.
- Kirillova, I.V., Chernova, O.F., van der Made, J., Kukarskih, V.V., Shapiro, B., van der Plicht, J., Shidlovskiy, F.K., Heintzman, P.D., van Kolschoten, Thijis, 2017. Discovery of the skull of *Stephanorhinus kirchbergensis* (Jäger, 1839) above the Arctic Circle. Quaternary Research 88, 537–550.
- Lacombat, F., 2005. Les Rhinocéros fossiles des sites préhistoriques de l'Europe méditerranéenne et du Massif central, paléontologie et implications biochronologiques. British Archaeological Reports 1419, 1–175.
- Lacombat, F., Mörs, T., 2008. The northernmost occurrence of the rare Late Pliocene rhinoceros *Stephanorhinus jeanvireti*, Mammalia, Perissodactyla. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 249, 157–165.
- 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.
- Made, J. Van der, Stefanovic, I., 2006. A small tapir from the Turolian of Kreka (Bosnia) and a discussion on the biogeography and stratigraphy of the Neogene tapirs. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 240, 207–240.
- Mazza, P., 1988. The Tuscan Early Pleistocene rhinoceros *Dicerorhinus etruscus*. Palaeontographia Italica 75, 1–87.
- Mazza, P., Varola, A., 1999. Revision of the Middle Pleistocene rhinoceros remains from Contrada Monticelli, Castellana, Bari, Southern Italy. Il Quaternario 12, 99–104.
- Maclaren, J.A., Hulbert, R.C., Wallace, S.C., Nauwelaerts, S., 2018. A morphometric analysis of the forelimb in the genus *Tapirus* (Perissodactyla: Tapiridae) reveals influences of habitat, phylogeny and size through time and across geographical space. Zoological Journal of the Linnean Society 184, 499–515.
- Meneghini, G., 1880. Resti di tapiro e d'istrice nella lignite di Ghivizzano. Atti della Società Toscana di Scienze Naturali 2, 23.
- Michaux, J., Sigé, B., Sudre, J., 1976. Présence de *Tapirus arvernensis* (Mammalia, Perissodactyla) dans le Pliocène supérieur de Bassan, Hérault. Comptes Rendus sommaires de la Société Géologique de France 18, 9–11.
- Musil, R., 1969. Die Equiden-Reste aus dem Pleistozän n von Süssenborn bei Weimar. Paläontologische Abhandlungen, A Paläozoologie 3, 617–666.
- Nobis, G., 1971. Vom Wildpferd zum Hauspferd. Fundamenta 6, 1–96.
- Nomade, S., Pastre, J.F., Guillou, H., Faure, M., Guérin, C., Delson, E., Debard, E., Voinchet, P., Messager, E., 2014. Ar-40/Ar-39 constraints on some French landmark Late Pleistocene to Early Pleistocene large mammalian paleofaunas: Paleoenvironmental and paleoecological implications. Quaternary Geochronology 21, 2–15.
- Padilla, M., Dowler, R.C., 1994. *Tapirus terrestris*. Mammalian Species 481, 1–8.
- Padilla, M., Dowler, R.C., Downer, C.C., 2010. *Tapirus pinchaque* (Perissodactyla: Tapiridae). Mammalian Species 42, 166–182.
- Palombo, M.R., Alberdi, M.T., Bellucci, L., Sardella, R., 2017. An intriguing middle-sized horse from Coste San Giacomo (Anagni Basin, central Italy). Quaternary Research 87, 347–362.
- Palombo, M.R., Alberdi, M.T., 2017. Light and shadows in the evolution of South European stenonoid horses. Fossil Imprint 73, 115–140.
- Pandolfi, L., Petronio, C., 2011a. *Stephanorhinus etruscus*, Falconer, 1868, from Pirro Nord, Apricena, Foggia, Southern Italy) with notes on the late Early Pleistocene rhinoceroses of Italy. Rivista Italiana di Paleontologia e Stratigrafia 117, 173–187.
- Pandolfi, L., Petronio, C., 2011b. The small-sized rhinoceroses from the Late Pleistocene of Apulia (southern Italy). Rivista Italiana di Paleontologia e Stratigrafia 117, 509–520.
- Pandolfi, L., 2013a. New and revised occurrences of *Dihoplus megarhinus* (Mammalia Rhinocerotidae) in the Pliocene of Italy. Swiss Journal of Palaeontology 132, 239–255.
- Pandolfi, L., 2013b. Rhinocerotidae (Mammalia, Perissodactyla) from the Middle Pleistocene site of Ponte Milvio, Central Italy. Bollettino della Società Paleontologica Italiana 52, 219–229.
- Pandolfi, L., Marra, F., 2015. Rhinocerotidae (Mammalia, Perissodactyla) from the chrono-stratigraphically constrained Pleistocene deposits of the urban area of Rome, Central Italy. Geobios 48, 147–167.
- Pandolfi, L., Tagliacozzo, A., 2013. Earliest occurrence of the woolly rhino (*Coelodonta antiquitatis*) in Italy (Late Pleistocene, Grotta Romanelli site). Rivista Italiana di Paleontologia e Stratigrafia 119, 125–129.
- Pandolfi, L., Tagliacozzo, A., 2015. *Stephanorhinus hemiteochus*, Mammalia, Rhinocerotidae) from the Late Pleistocene of Valle Radice, Sora, Central Italy) and re-evaluation of the morphometric variability of the species in Europe. Geobios 48, 169–191.
- 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., Gasparik, M., Piras, P., 2015a. Earliest occurrence of “*Dihoplus*” *megarhinus* (Mammalia, Rhinocerotidae) in Europe, Late Miocene, Pannonian Basin, Hungary): Palaeobiogeographical and biochronological implications. Annales de Paléontologie 101, 325–339.
- Pandolfi, L., Grossi, F., Frezza, V., 2015b. New insights into the Pleistocene deposits of Monte delle Piche, Rome, and remarks on the biochronology of continental *Hippopotamus* (Mammalia, Hippopotamidae) and *Stephanorhinus etruscus* (Mammalia, Rhinocerotidae) in Italy. Estudios Geológicos 71, e026.
- Pandolfi, L., Maiorino, L., Sansalone, G., 2015c. Did the Late Pleistocene climatic changes influence evolutionary trends in body size of the red deer? The study case of the Italian Peninsula. Palaeogeography, Palaeoclimatology, Palaeoecology 440, 110–115.
- Pandolfi, L., Kotsakis, T., 2016. A mandible of *Tapirus arvernensis* from central Italy. Italian Journal of Geosciences 136, 131–133.
- Pandolfi, L., Gasparik, M., Magyar, I., 2016. Rhinocerotidae from the upper Miocene deposits of the Pannonian Basin (Hungary): implications for migration routes and biogeography. Geologica Carpathica 67, 69–82.
- Pandolfi, L., Rook, L., 2017. Rhinocerotidae (Mammalia, Perissodactyla) from the latest Turolian localities (MN 13; late Miocene) of central and northern Italy. Bollettino della Società Paleontologica Italiana 56, 45–56.
- Pandolfi, L., Cerdeño, E., Codrea, V., Kotsakis, T., 2017a. Biogeography and chronology of the Eurasian extinct rhinoceros *Stephanorhinus etruscus*, Mammalia, Rhinocerotidae. Comptes Rendus Palevol 16, 762–773.
- Pandolfi, L., Spadi, M., Martinetto, E., Kotsakis, T., Esu, D., 2017b. New data on the lower Pleistocene (Gelasian) lignite beds of Castel San Pietro, Rieti, Central Italy. Rivista Italiana di Paleontologia e Stratigrafia 123, 335–345.
- Pandolfi, L., Popescu, A., Codrea, V., 2019. *Stephanorhinus jeanvireti* (Mammalia, Rhinocerotidae) from the early Pleistocene of Colești, southwestern Romania. Comptes Rendus Palevol 18, 1041–1056.
- Pandolfi, L., Rivals, F., Rabinovich, R., 2020. A new species of rhinoceros from the site of Bethlehem: “*Dihoplus*” *bethlehemsis* sp. nov. (Mammalia, Rhinocerotidae). Quaternary International 537, 48–60.
- Pantanello, D., 1879. Sugli strati miocenici del Casino (Siena) e considerazioni sul Miocene superiore. Memorie della Regia Accademia dei Lincei serie 3, 1–21.
- Pareto, I., 1865. Note sur les subdivisions que l'on pourrait établir dans les terrains tertiaires de l'Appénin septentrional. Bulletin de la Société Géologique de France 22, 210–277.
- 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.
- Pueyo, E.L., Muñoz, A., Laplana, C., Parés, J.M., 2016. The Last Appearance Datum of *Hipparion* in Western Europe: magnetostratigraphy along the Pliocene-Pleistocene boundary in the Villarroja Basin (northern Spain). International Journal of Earth Science 105, 2203–2220.
- Qiu, Z., Weiling, H., Zhihui, G., 1988. Chinese hipparionines from the Yushe Basin. Palaeontologica Sinica, Series C 175, 1–250.
- Qiu, Z.-X., Deng, T., Wang, B.-Y., 2004. Early Pleistocene mammalian Fauna from Longdan, Dongxiang, Gansu, China. Palaeontologia Sinica, New Series C 27, 1–198.
- Radulescu, C., Samson, P.M., Petculescu, A., Stăucă, E., 2003. Pliocene large mammals of Romania. Colloquio de Paleontologia 53, 549–558.
- von Reichenau, W., 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.). Abhandlungen der Großherzoglich Hessischen Geologischen Landesanstalt zu Darmstadt 7, 1–55.
- Rook, L., Rustioni, M., 1991. *Tapirus* cf. *arvernensis* remains from the late Turolian Baccinello V3 Faunal Assemblage (Grosseto, Tuscany). Bollettino della Società Paleontologica Italiana 30, 325–327.
- Rook, L., Martínez-Navarro, B., 2010. Villafranchian: The long story of a Plio-Pleistocene European large mammal biochronologic unit. Quaternary International 219, 134–144.
- Rook, L., 2015. Dedication to Augusto Azzaroli (1921–2015). Bollettino della Società Paleontologica Italiana 54, 147–159.
- Rook, L., Cirilli, O., Bernor, R.L., 2017. A late occurring “*Hipparion*” from the middle Villafranchian of Montopoli, Italy (early Pleistocene; MN16b; ca. 2.5 Ma). Bollettino della Società Paleontologica Italiana 56, 333–339.
- 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. Frontiers in Ecology and Evolution 7, 268.
- Ros-Montoya, S., Martínez-Navarro, B., Espigares, M.-P., Guerra-Merchán, A., García-Aguilar, J.M., Piñero, P., Rodríguez-Rueda, A., Agustí, J., Oms, O., Palmqvist, P., 2017. A new Ruscinian site in Europe: Baza-1 (Baza basin, Andalusia, Spain). Comptes Rendus Palevol 16, 746–761.
- Ruiz Bustos, A., 1973. Estudio de unos restos de *Dicerorhinus etruscus* Falconer, encontrados en Granada. Cuadernos de Ciencias Biológicas 2, 2–89.
- Rustioni, M., 1992. On Pliocene tapirs from France and Italy. Bollettino della Società Paleontologica Italiana 31, 269–294.
- Rustioni, M., Mazza, P., Ciofini, R., 1996. Synopsis of the stratigraphical distribution of the Villafranchian Equids, Tapirids and Rhinocerotids of Western Europe. II Quaternario 8, 357–366.
- Rustioni, M., Mazza, P., 2001. Taphonomic analysis of *Tapirus arvernensis* remains from the Lower Valdarno, Tuscany, Central Italy. Geobios 34, 469–474.
- Sala, B., Ungaro, S., Vincenzi, L., 1990. *Tapirus arvernensis* Croizet and Jobert del Villafranchiano inferiore di Vignola, Modena. Bollettino della Società Paleontologica Italiana 29, 129–136.
- Sala, B., Fortelius, M., 1993. The rhinoceroses of Isernia La Pineta, early Middle Pleistocene, Southern Italy. Palaeontographia Italica 80, 157–174.
- Samson, P., 1975. Les Equidés fossiles de Roumanie. Geologica Romana 14, 165–352.
- Sansalone, G., Berté, D., Maiorino, L., Pandolfi, L., 2015. Evolutionary trends and stasis in carnassial teeth of European Pleistocene wolf *Canis lupus* (Mammalia, Canidae). Quaternary Science Reviews 110, 36–48.
- Santafé-Llopis, J., Casanovas-Cladellas, Vte M.L., 1987. *Dicerorhinus etruscus brachycephalus*, Mammalia, Perissodactyla) de los yacimientos pleistocénicos de la cuenca Guadix-Baza, Venta Micénay Huéscar), Granada, Espana. Paleontologia i Evolució. Mem. Esp. 1, 237–254.
- Sardella, R., Di Stefano, G., Petronio, C., 1996. The Villafranchian Mammal Faunas from the Tiber River Basin (Umbria, Central Italy). II Quaternario 8, 509–514.
- Schauenberg, P., 1969. Contribution à l'étude du tapir pinchaque, *Tapirus pinchaque* (Roulin 1829). Revue Suisse de Zoologie 76, 211–256.
- Schwarz, E., 1928. Über diluviale Pferde der Equus caballus-Gruppe. Jarburch preuss. geologische Landenstaat 48, 429–476.
- Scott, K.M., 1983. Prediction of body weight of fossil Artiodactyla. Zoological Journal of the Linnean Society 77, 199–215.
- Scott, K.M., 1990. Postcranial dimensions of ungulates as predictors of body size. In: Damuth, J., MacFadden, B.J. (Eds.), Body Size in Mammalian Paleobiology: Estimation and Biological Implications. Cambridge University Press, Cambridge, pp. 301–335.
- Stehlin, H.G., Graziosi, P., 1935. Ricerche sugli Asinidi fossili d'Europa (Studies on the fossil European asses). Memoires de la Société Paléontologique Suisse 56, 1–73.
- Šujan, M., Rybár, S., Šarinová, K., Kováč, M., Vlačiky, M., Zervanová, J., 2013. Uppermost Miocene to Quaternary accumulation history at the Danube Basin eastern flanks. In: Fodor, L., Kövér, Sz. (Eds.), 11th Meeting of the Central European Tectonic Studies Group (CETeG). Abstract book, Geological and Geophysical Institute of Hungary, Budapest, pp. 66–68.
- Szabó, P., Kocsis, L., Vennemann, T., Pandolfi, L., Martinetto, E., Újvári, G., Demény, A., 2017. Pliocene-Early Pleistocene climatic trends in Italy based on oxygen and carbon stable isotopes of rhinoceros and proboscidean teeth enamel. Quaternary Science Reviews 157, 52–65.
- de Thoisy, B., Pukazhenthi, B., Janssen, D.L., Torres, I.L., May Jr., J.A., Medici, P., Mangini, P.R., Marquez, P.A.B., Vanstreels, R.E.T., Fernandes-Santos, R.C., Hernandez-Divers, S., Quse, V., 2014. Tapir Anatomy. In: Quse, R.C., Fernandes-Santos, V. (Eds.), Tapir Veterinary Manual. second ed. IUCN/SSC Tapir Specialist Group, Campo Grande, pp. 14–149.
- Tsoukala, E., 2018. Rhinocerotidae from the Late Miocene and Late Pliocene of Macedonia, Greece. A revision of the Neogene-Quaternary Rhinocerotidae of Greece. Revue de Paléobiologie 37, 609–630.
- Vlačiky, M., Sliva, L., Tóth, Cs, Karol, M., Zervanová, J., 2008. Fauna a sedimentológia lokality Nová Vieska (vilafrank, SR) [The fauna and sedimentology of the locality Nová Vieska (Villafranchian, SR). Acta Musei Moraviae, Scientiae Geologicae 93, 229–244 (in Slovak, with English summary).
- Wang, S.-Q., Deng, T., 2011. Some evolutionary trends of *Equus eisenmannae* (Mammalia, Perissodactyla) in the stratigraphic sequence of Longdan, China, in comparison to modern *Equus*. Journal of Vertebrate Paleontology 31, 1356–1365.
- Woodburne, M.O., 2007. Phyletic diversification of the *Cormohipparion occidentale* Complex (Mammalia, Perissodactyla, Equidae), Late Miocene, North America, and the origin of the Old World *Hippotherium* Datum. Bulletin of the American Museum of Natural History 306, 1–138.
- Woodburne, M.O., 2009. The early Vallesian vertebrates of Atzelsdorf (Late Miocene, Austria), 9. *Hippotherium* (Mammalia, Equidae). Annalen des Naturhistorisches Museum in Wien 111A, 585–604.

Further reading

- Lacombat, F., Abbazzi, L., Ferretti, M.P., Martínez-Navarro, B., Mouille, P.E., Palombo, M.R., Rook, L., Turner, A., Valli, A.M.F., 2008. New data on the Early Villafranchian fauna from Viallette (Haute-Loire, France) based on the collection of the Crozatier Museum (Le Puy-en-Velay, Haute-Loire, France). Quaternary International 179, 64–71.