



# A Late Occurring “*Hipparion*” from the middle Villafranchian of Montopoli, Italy (early Pleistocene; MN16b; ca. 2.5 Ma)

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**KEY WORDS** - Small equid, Forsyth Major 1880 collection, early-middle Villafranchian transition, Montopoli Faunal Unit, middle Villafranchian, Italy.

**ABSTRACT** - We report here for the first time the occurrence in the Montopoli large mammal fossil assemblage of a small equid taxon identified as “*Hipparion*” sp., associated to the monodactyl large horse *Equus cf. livenzovensis*. This occurrence has been recognised on a specimen that the late De Giuli (1938-1988) identified as *Hipparion* sp. in unpublished notes available in the archives of the Vertebrate Palaeontology Laboratory of the Dipartimento di Scienze della Terra at the Università degli Studi di Firenze. Although fragmentary, the specimen documents the occurrence of “*Hipparion*” at the middle Villafranchian (early Pleistocene, ca. 2.5 Ma) site of Montopoli, one of the latest occurrences of an ipparionine horse in western Europe. The western Eurasian “*Hipparion*” evolutionary history is summarised herein.

**RIASSUNTO** - [Una forma tardiva di “*Hipparion*” nell’associazione faunistica del Villafranchiano medio di Montopoli, Italia (Pleistocene inferiore; MN16b; ca. 2.5 Ma)] - Si segnala per la prima volta la presenza nell’associazione faunistica a vertebrati di Montopoli Val d’Arno di un equide di piccolo taglio identificato come “*Hipparion*” sp., associato all’equide monodattilo di grande taglia *Equus cf. livenzovensis*. La segnalazione si basa sullo studio di un reperto che lo scomparso Claudio De Giuli (1938-1988) aveva identificato come *Hipparion* sp. in un manoscritto inedito conservato negli archivi del Laboratorio di Paleontologia dei Vertebrati del Dipartimento di Scienze della Terra dell’Università degli Studi di Firenze. Sebbene frammentario, il campione documenta chiaramente la presenza di “*Hipparion*” all’inizio del Villafranchiano medio (Pleistocene inferiore, ca. 2.5 Ma) a Montopoli, e rappresenta una delle ultime presenze di un equide ipparionino in Europa. Viene infine presentata una sintesi della storia evolutiva di “*Hipparion*” nel record fossile dell’Europa occidentale.

## INTRODUCTION

The occurrence of *Equus* from Montopoli is known from the earliest publications concerning the site. Although there has not yet been a detailed description of Montopoli *Equus* remains, reference to the occurrence of the large horse *Equus cf. livenzovensis* Bajusheva, 1978 was given in papers dealing with Villafranchian horses (Azzaroli, 1966, 1982, 1990, 2003; De Giuli, 1972; Alberdi & Palombo, 2013) and with Villafranchian biochronology and Faunal Units definition (Azzaroli, 1977; Lindsay et al., 1980; Azzaroli et al., 1988; Gliozzi et al., 1997; Rook & Martínez-Navarro, 2010).

Within a broader project on the evolution, biogeographic and palaeoclimatic context of penecontemporaneous Old World Villafranchian Plio-Pleistocene horse faunas we started a revision of the equid collections kept in the Museo di Storia Naturale at the Università degli Studi di Firenze (IGF), and the Montopoli assemblage was one of our first targeted studies. In our revision we have to acknowledge the discovery of, within the archives of the Vertebrate Palaeontology Laboratory of the Dipartimento di Scienze della Terra at the Università degli Studi di Firenze, a folder with manuscript notes by the late Prof. Claudio De Giuli (1938-1988; Rook, 2013) who drafted a brief description of the Montopoli horse remains (probably prepared in the 1970’s).

As an initial result of our revision, we report here for the first time the occurrence in the Montopoli assemblage of a small equid taxon. This occurrence has been recognised on a fragmentary specimen (IGF 15315) that De Giuli (in the above mentioned unpublished notes) already recognised as *Hipparion* sp. This identification was also confirmed (personal communication to LR) by the late Prof. Augusto Azzaroli (1921-2015; Rook, 2015).

## STRATIGRAPHIC AND GEOCHRONOLOGICAL SETTING

Montopoli Val d’Arno is a town located in Tuscany (central Italy), about 27 km east-southeast of Pisa and 40 km west-southwest of Florence (Fig. 1). Within the Neogene continental stratigraphic and vertebrate palaeontology community the name of “Montopoli” is well known as a biostratigraphic marker heralding large mammal appearances that mark the beginning of the middle Villafranchian (early Pleistocene) interval (Fig. 2). The large mammal assemblage of this interval is termed the Montopoli Faunal Unit (FU) (Rook & Martínez-Navarro, 2010).

Sediments that yielded the Montopoli FU in the local stratigraphic setting (Benvenuti et al., 1995) are stratigraphically superposed on sediments yielding

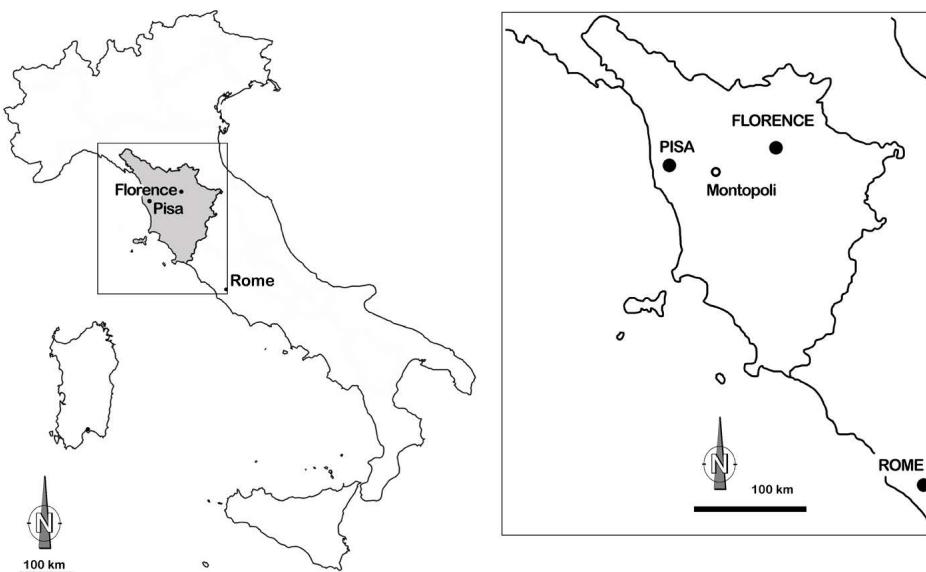


Fig. 1 - Location map of Montopoli site.

faunas of the Traversa FU and to shallow-water marine sediments of early Pleistocene age (middle Pliocene in papers previous to the IUGS 2009 decision; cfr. Benvenuti et al., 1995). This fauna is celebrated in literature for its important signal of environmental change given by marked mammalian dispersals. In addition to the monodactyl horse *Equus cf. livenzovensis*, also occurring is a primitive species of the genus *Mammuthus* (Palombo & Ferretti, 2005), the large deer *Eucladoceros falconeri* (Dawkins, 1868) (De Giuli & Heintz, 1974a), and *Gazella borbonica* Depéret, 1884 (De Giuli & Heintz, 1974b), as well as the disappearance of some of the taxa with subtropical affinities still characterizing the previous early Villafranchian assemblages (Pradella & Rook, 2007).

The Montopoli Faunal Unit, corresponding to the MN16b unit in the European MN sub-division, was originally included in the early Villafranchian (Azzaroli, 1977; Azzaroli et al., 1988), but the marked faunal turnover characterizing the transition from the early Villafranchian Traversa FU to Montopoli FU led to Montopoli being nominated as the basal unit of the middle Villafranchian (Gliozzi et al., 1997; Rook & Martínez-Navarro, 2010). Montopoli, and the related Faunal Unit, occurs at the Gauss-Matuyama transition (Lindsay et al., 1980; Benvenuti et al., 1995) thus correlating with the redefined Plio/Pleistocene boundary (Gelasian Stage, GSSP at Monte San Nicola Section, Sicily; Rio et al., 1994; Gibbard et al., 2010).

## HISTORICAL OVERVIEW

Most of the Montopoli collection comes from excavations made by Forsyth Major in the latest decades of the 19<sup>th</sup> century and was found in gravelly sands alternating with marine littoral deposits. Continental mammal-bearing sands outcropped in at least two localities: "L'Uccellatoio" Hill and "Poggio di Montevicchio", both located a few kilometres southeast of the town

of Montopoli (De Giuli & Heintz, 1974a, b). Whereas specimens of *Equus cf. livenzoensis* have been known from Montopoli (Azzaroli, 2000), the appearance of "*Hipparrison*" has thus far not been published. According to the record notes in the Florence Museum inventory, the "*Hipparrison*" specimen described in the present paper comes from the excavations carried out in 1880 by Forsyth Major at L'Uccellatoio. Fossil mammals from Montopoli have been analysed by several authors since their discovery (Forsyth Major, 1885; Merla, 1949; De Giuli & Heintz, 1974a, b; Azzaroli, 1977; Ficcarelli, 1984; Cherin et al., 2013; Bartolini Lucenti, 2017). According to published data the fauna is composed of the following taxa (first occurring taxa are marked with an asterisk): *Acinonyx pardinensis* (Croizet & Jobert, 1828), *Puma pardoides*\* (Owen, 1846), *Pliocrocuta perrieri* (Croizet & Jobert, 1828), *Nyctereutes megamastoides* (Pomel, 1842), *Mammuthus gromovi*\* (Alexeeva & Garutt, 1965), *Stephanorhinus jeanvireti* (Guérin, 1972), *S. etruscus*\* (Falconer, 1868), *Equus cf. livenzovensis*\*, *Pseudodama lyra* Azzaroli, 1992, *Crozetoceros ramosus* (Croizet & Jobert, 1828), *Eucladoceros falconeri*\*, *Procapreolus cusanus* (Croizet & Jobert, 1828), *Gazella borbonica*\*, *Leptobos stenometopon* (Rütimeyer, 1865).

## MATERIAL AND METHODS

The IGF original paper catalogue under the record number IGF 15315 reports the identification of "*Equus* (?) / Montopoli 1880". We compare the Montopoli specimen to our available database including a relevant group of late Miocene and Pliocene Old World hipparrisonine taxa (localities and ages discussed in several previous studies: Bernor et al., 1988, 1993, 1996, 1997, 2003a, b, 2011; tooth measurements and description follow the standard defined in Bernor et al., 1997). Since the nomen *Hipparrison* has been used in a variety of ways by different authors, it is worth mentioning here that we

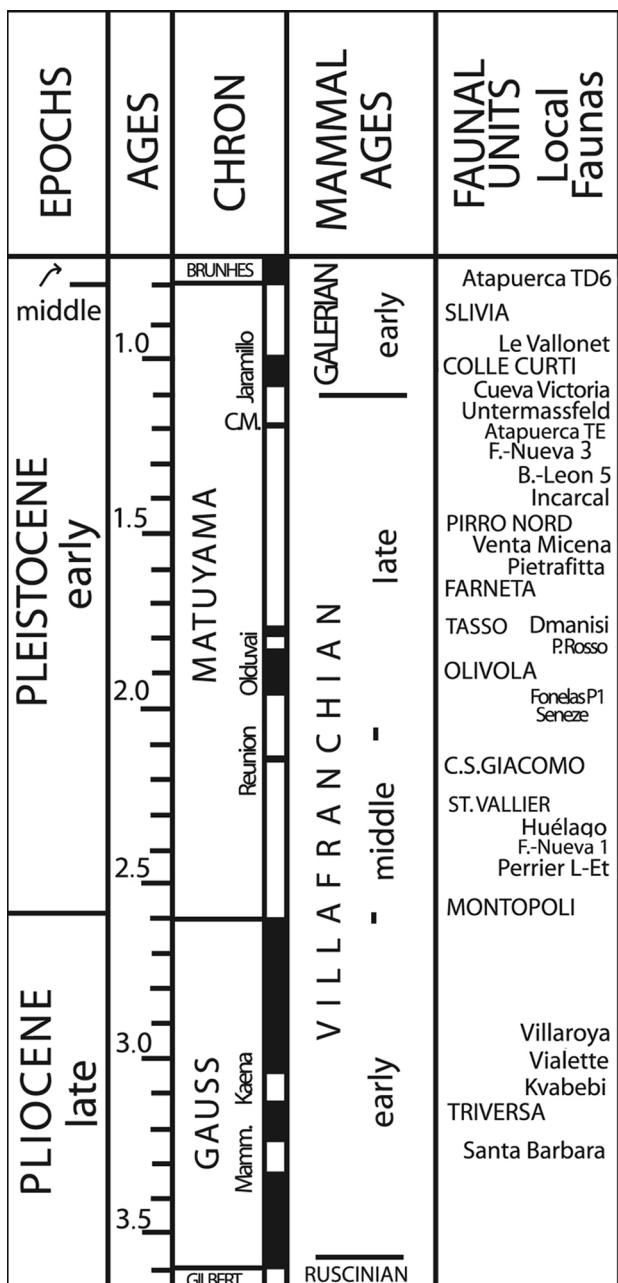


Fig. 2 - Villafranchian biochronological scheme with chronology of the Montopoli Faunal Unit (modified from Rook & Martínez-Navarro, 2010).

follow characterizations and definitions for hippariumine horses as provided in Bernor et al. (1996, 1997), and that "*Hipparium*" is a general taxonomic term not relating to the genus *Hipparium* s.s. (cfr. Bernor et al., 2011).

#### DESCRIPTION

In our revision of the equid material from Montopoli, the small equid left M1 (IGF 15315; Fig. 3) is distinct in its small size and morphology. The tooth is damaged lacking the entire lingual portion. The protocone is missing from the occlusal level to base. There is no cementum remaining on the tooth, parastyle and mesostyle are very

slender, pre- and postfossettes have very few plications due to the later stage of wear. The tooth is heavily worn but apparently the roots are not completely closed. The slight distalward angle of the mesial and distal walls of the tooth suggest it is an M1 (as originally observed by De Giuli; Figs 4-5). Measurements and features taken on the equid tooth are: occlusal length = 20.4 mm; basal length = 18.0 mm; mesostyle height = 21.3 mm; prefossette plis: 0 mesially, 2 distally; postfossette plis: 2 mesially, 1 distally.

The small size of this sample clearly distinguishes it from the other equid remains from Montopoli. It certainly belongs to a species differing from the large monodactyl horse *Equus* cf. *livenzovensis* occurring at Montopoli (albeit the Montopoli large *Equus* teeth are heavily damaged and cannot be measured, their size is much larger than IGF 15315), but its specific determination cannot be ascertained easily. To be certain that it is actually a species of "*Hipparium*" it would be desirable to have a preserved, isolated protocone. Yet the IGF 15315's size, the occurrence of fossette plications in this late stage of wear, and the very thin parastyle and mesostyle all suggest that the attribution to "*Hipparium*" s.l. is accurate.

#### DISCUSSION

Hippariumine horses first appear in the Old World between 11.4 and 11.0 Ma as recorded in the Vienna Basin Pannonian C (Bernor et al., 1988; Woodburne, 2007, 2009; Bernor et al., 2017). Bernor et al. (2017), following Woodburne (2009), have identified North American *Cormohipparium* as the presumptive genus that founded the Old World "*Hipparium*" radiation. The *Cormohipparium* Datum - replacing the *Hipparium* Datum of Berggren & Van Couvering (1974) after Bernor et al. (2017) - extended across all of Eurasia and Africa during a short geochronologic interval of time. Bernor et al. (1989, 1996) outlined the multiple Eurasian and African lineages in geographic distance and chronologic time that evolved in the 11-1 Ma interval. "*Hipparium*" diversification reached its apogee in the late Miocene and underwent a collapse in diversity at the very end of the late Miocene (Bernor et al., 1996, 2010; Eronen et al., 2009). The Pliocene interval had far fewer lineages of Old World "*Hipparium*" and the disappearance of Western Eurasian *Hippotherium*, *Cremohipparium* and *Hipparium* s.s. was accompanied by the biogeographic



Fig. 3 - "*Hipparium*" sp.: left M1 (IGF 15315) from Montopoli in labial (left) and occlusal (right) views. Scale bar equals 2 cm.

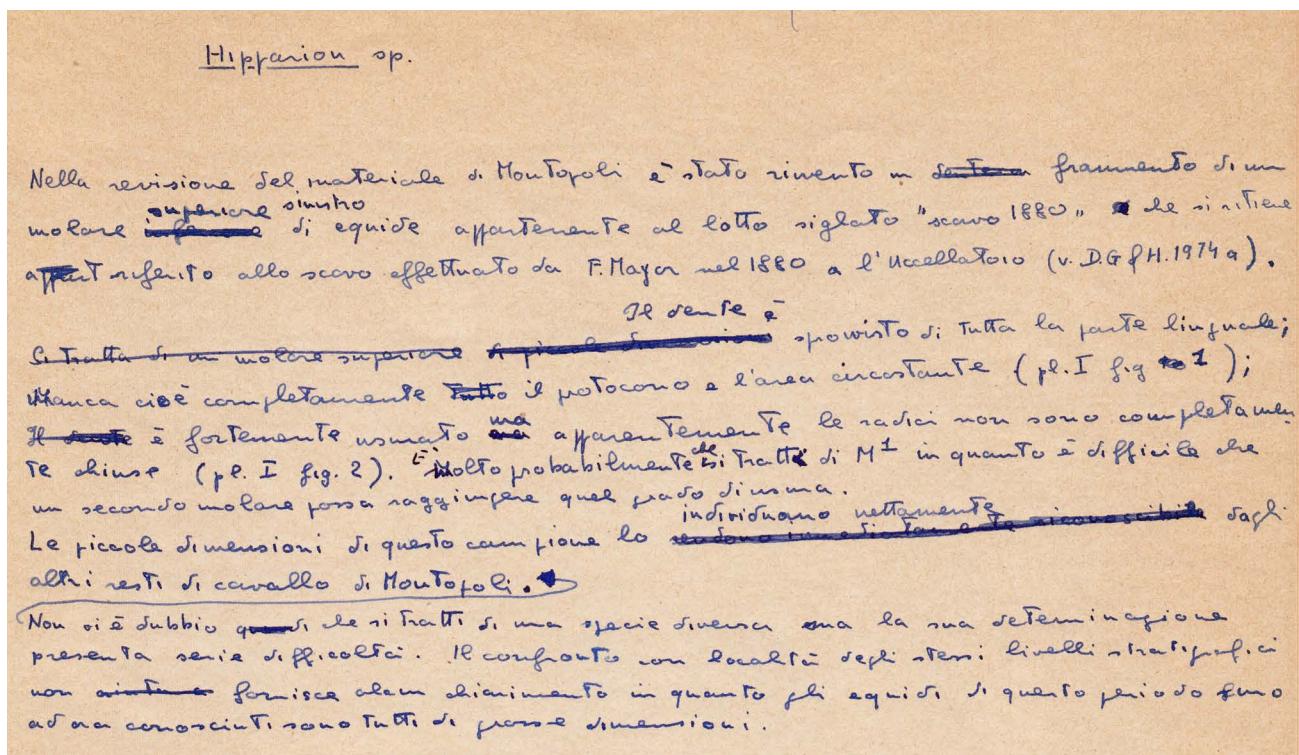


Fig. 4 - Original manuscript by late Claudio de Giuli describing IGF 15315. For the completeness of the record we report here the translation in English of the original handwritten notes:

*Hipparium* sp. - "Revising the material from Montopoli, has been identified a fragment of an upper left molar of an equine from the lot labelled "excavation 1880", which is reported as being excavated by Forsyth Major in 1880 at the site called "l'Uccellatoio".

The tooth is damaged and lacks the entire lingual part, i.e. it completely lacks the protocone and the surrounding area. It is heavily worn but apparently the roots are not completely closed. It is very likely that it is an M1 because it is difficult for a second molar to reach that degree of wear.

Because of the small size this sample is clearly distinguishable from all other remains from Montopoli. There is no doubt that it is a different species, but its determination has serious difficulties. The comparison with localities of the same stratigraphic levels does not provide any clarification given that the equids of this period so far known are all of larger size."

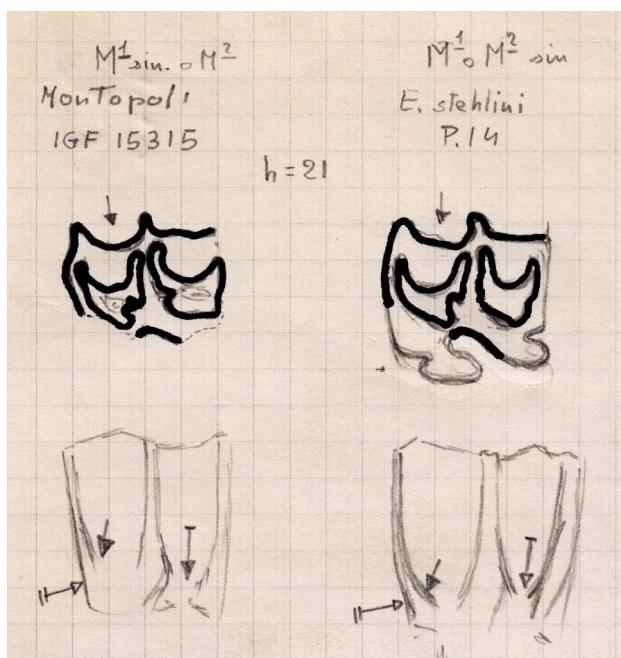


Fig. 5 - Original drawing by late Claudio de Giuli illustrating IGF 15315 morphological characteristics (in comparison with an upper molar of *Equus stehlini* Azzaroli, 1964).

extension of the Chinese lineages of *Plesiohipparion* and *Proboscidipparion* into Turkey (Bernor & Lipscomb, 1991; Bernor & Sen, 2017) and *Plesiohipparion* into Spain (Bernor & Sun, 2015; Bernor et al., 2015). Africa retained the late Miocene lineage *Eurygnathohippus* from the late Miocene until the middle Pleistocene, ca. 1 Ma (Gilbert & Bernor, 2008; Bernor et al., 2012).

Von Koenigswald (1970) has addressed the Villafranchian occurrences of "*Hipparium*" from the Red Crag (Suffolk, England; ca. 3 Ma), Hungary ("*Hipparium* moritorum Kretzoi, 1954, early Villafranchian) and Spain ("*Hipparium* rocinantis Hernández-Pacheco, 1921). Bernor & Lipscomb (1991) also identified an "*Hipparium*" from Gülyazi, Turkey as being *Plesiohipparion* aff. *huangheense* Qiu, Weilong & Zihui, 1988, known elsewhere from China (Qiu et al., 1988) from early middle Villafranchian (MN16b, ca. 2.5 Ma) horizons co-occurring with *Equus*. Bernor & Sun (2015) and Bernor et al. (2015), following Zhegallo (1978) and Qiu et al. (1988), identified Spanish Villafranchian "*Hipparium*" from Villarroya as being attributable to the genus *Plesiohipparion*. Pueyo et al. (2016) calibrated the age of the Villaroya assemblage to the Réunion chron C2r.1n, with equivalent age of 2.128-2.148 Ma. The authors' attribution of the latter as being the youngest occurring hipparium in Europe is supported by all known evidence. However, the genus

*Proboscidipparrison* persisted in China until 1 Ma (Qiu et al., 1988) and *Eurygnathohippus* occurred in Africa until at least 1 Ma (Gilbert & Bernor, 2008; Bernor et al., 2010).

## CONCLUSIONS

The occurrence among the Montopoli large mammal fossil assemblage of a small equid identified as "*Hipparrison*" sp. associated to the monodactyl large horse *Equus* cf. *livenzovensis*, is reported here for the first time (albeit we acknowledge its original identification by the late Prof. Claudio De Giuli as testified by an unpublished manuscript).

A single fragmentary specimen from the early excavation by Forsyth Major at Montopoli in 1880 and retained in the collections of the Palaeontology Section at the Museo di Storia Naturale of the Università degli Studi di Firenze preserves enough morphology to allow documenting one of the latest occurrences of an hipparrisonine horse in western Europe in the middle Villafranchian (early Pleistocene, ca. 2.5 Ma) of Montopoli.

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## REFERENCES

- Alberdi M. & Palombo M.R. (2013). The late Early to early Middle Pleistocene stenonoid horses from Italy. *Quaternary International*, 288: 25-44.
- Alexeeva L.I. & Garut V.E. (1965). Novye dannye ob evolucii slonov roda *Archidiskodon*. *Byulleten komissii po lzucheniiu Chetvertichnogo Perioda AN SSSR*, 30: 161-166 [in Russian].
- Azzaroli A. (1964). The two Villafranchian Horses of the Upper Valdarno. *Palaeontographia Italica*, 59: 1-12.
- Azzaroli A. (1966). Pleistocene and living horses of the world - An essay of a classification based on skull characters. *Palaeontographia Italica*, 61: 1-15.
- Azzaroli A. (1977). The Villafranchian stage in Italy and the Plio-Pleistocene boundary. *Giornale di Geologia*, 41: 61-79.
- Azzaroli A. (1982). On Villafranchian Palaearctic Equids and their allies. *Palaeontographia Italica*, 72: 74-97.
- Azzaroli A. (1990). The genus *Equus* in Europe. In Lindsay E., Fahlsch V. & Mein P. (eds), European Neogene Mammal Chronology. Plenum Press, New York: 339-356.
- Azzaroli A. (1992). The cervid genus *Pseudodama* n.g. in the Villafranchian of Tuscany. *Palaeontographia Italica*, 79: 1-41.
- Azzaroli A. (2000). On *Equus livenzovensis* Baigusheva 1978 and the "stenonid" lineage of equids. *Palaeontographia Italica*, 87: 1-17.
- Azzaroli A. (2003). Phylogeny of the genus *Equus* L. *Palaeontographia Italica*, 84: 11-16.
- Azzaroli A., De Giuli C., Ficcarelli G. & Torre D. (1988). Late Pliocene to early Mid-Pleistocene mammals in Eurasia: faunal succession and dispersal events. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 66: 77-100.
- Bajgusheva V.S. (1978). Krupnaja Loshad Khaprovskogo Kompleksa is alluvija Severo Vostochnogo Priazovija. *Izvestija Severo-Kavkazkogo Nauchnogo Zentra Vyschei Shkoly*, 1: 98-102 [in Russian].
- Bartolini Lucenti S. (2017). *Nyctereutes megamastoides* (Canidae, Mammalia) from the early and eiddle Villafranchian (late Pliocene and early Pleistocene) of the Lower Valdarno (Firenze and Pisa, Tuscany, Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 123: 211-218.
- Benvenuti M., Dominici S. & Rook L. (1995). Inquadramento stratigrafico-deposizionale delle faune a mammiferi villafranchiane (unità faunistiche Traversa e Monopoli) del Valdarno Inferiore nella zona a sud dell'Arno (Toscana). *Il Quaternario*, 8: 457-464.
- Berggren W.A. & Van Couvering J.A. (1974). The late Neogene. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 16: 1-215.
- Bernor R.L., Armour-Chelu M., Gilbert H., Kaiser T.M. & Schulz E. (2010). Equidae. In Werdelin L. & Sanders W.L. (eds), Cenozoic mammals of Africa. University of California Press, Berkeley: 685-721.
- Bernor R.L., Armour-Chelu M., Kaiser T.M. & Scott R.S. (2003a). An Evaluation of the Late MN 9 (Late Miocene, Vallesian Age), Hipparrison Assemblage from Rudabánya (Hungary): Systematic Background, Functional Anatomy and Paleoecology. *Coloquios de Paleontología*, Volumen extraordinario, 1: 35-45.
- Bernor R.L., Boaz N. & Rook L. (2012). *Eurygnathohippus feibeli* (Perissodactyla, Mammalia) from the late Miocene of Sahabi (Libya) and its evolutionary and biogeographic significance. *Bollettino della Società Paleontologica Italiana*, 51: 39-48.
- Bernor R.L., Fahlsch 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., Fahlsch V. & Mittmann H.W. (eds), The Evolution of Western Eurasian Neogene Mammal Faunas, Columbia University Press, New York: 449-469.
- Bernor R.L., Göhlich U., Harzhauser M. & Semperbon G.M. (2017). The Pannonian C hipparions from the Vienna Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 476: 28-41.
- Bernor R.L., Kaiser T., Nelson S. & Rook L. (2011). Systematics and Paleobiology of *Hippotherium malpassii* n. sp. (Equidae, Mammalia) from the latest Miocene of Baccinello V3 (Tuscany, Italy). *Bollettino della Società Paleontologica Italiana*, 50: 175-208.
- Bernor R.L., Kovar J., Lipscomb D., Rögl F. & Tobien H. (1988). Systematic, stratigraphic and paleoenvironmental contexts of first appearing *Hipparrison* in the Vienna Basin, Austria. *Journal of Vertebrate Paleontology*, 8: 427-452.
- Bernor R.L. & Lipscomb D. (1991). The systematic position of "*Plesiohipparrison*" aff. *huangeense* (Equidae, Hipparrisonini) from Gülyazi, Turkey. *Mitteilungen der Bayrischen Staatsammlung für Paläontologie und Historische Geologie*, 31: 107-123.
- Bernor R.L., Meshida K. & Sun B. (2015). Phylogenetic signature in the juvenile skulls and cheek teeth of Pleistocene *Proboscidipparrison sinense*, China. *Rivista Italiana di Paleontologia e Stratigrafia*, 121: 255-264.
- Bernor R.L., Mittmann H.-W., Kretzoi M. & Tobien H. (1993). A preliminary systematic assessment of the Rudabánya

- hipparions. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie*, 33: 1-20.
- Bernor R.L., Scott R.S., Fortelius M., Kappelman J. & Sen S. (2003b). Systematics and evolution of the Late Miocene Hipparians 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: 220-281.
- Bernor R.L. & Sen S. (2017). The Early Pliocene *Plesiohipparion* and *Proboscidippiparion* (Equidae, Hipparrisonini) from Çalta, Turkey (Ruscinian Age, c. 4.0 Ma). *Geodiversitas*, 39: 285-314.
- Bernor R.L. & Sun B. (2015). Morphology through ontogeny of Chinese *Proboscidippiparion* and *Plesiohipparion* and observations on their Eurasian and African relatives. *Vertebrata Palasatica*, 53: 73-92.
- 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., Tobien H. & Woodburne M.O. (1989). Patterns of Old World hipparrisonine evolutionary diversification. In Lindsay E., Fahlbusch V. & Mein P. (eds), *European Neogene Mammal Chronology*. Plenum Press, New York: 263-319.
- Cherin M., Iurino D.A. & Sardella R. (2013). Earliest occurrence of *Puma pardoides* (Owen, 1846) (Carnivora, Felidae) at the Plio/Pleistocene transition in western Europe: New evidence from the middle Villafranchian assemblage of Montopoli, Italy. *Comptes Rendus Palevol*, 12: 165-171.
- Croizet J.B. & Jobert A. (1828). Recherches sur les ossements fossiles du département du Puy-de-Dôme. 224 pp. Principaux Libraires, Paris.
- Dawkins W. (1868). On a new species of deer from the Norwich Crag. *Quarterly Journal of the Geological Society of London*, 24: 516-518.
- De Giuli C. (1972). On the type form of *Equus stenonis* Cocchi. *Palaeontographia Italica*, 68: 35-49.
- De Giuli C. & Heintz E. (1974a). *Crozetoceros ramosus* (Cervidae, Artiodactyla, Mammalia) de Montopoli, nouvel élément de la faune villafranchienne d'Italie. *Atti della Società Toscana di Scienze Naturali, Memorie, ser. A*, 81: 241-251.
- De Giuli C. & Heintz E. (1974b). *Gazella borbonica* (Bovidae, Artiodactyla, Mammalia) nouvel élément de la faune villafranchienne de Montopoli, Valdarno Inferieur, Pisa, Italie. *Atti della Società Toscana di Scienze Naturali, Memorie, ser. A*, 81: 227-237.
- Depéret C. (1884). Nouvelles études sur les Ruminants pliocènes et quaternaires d'Auvergne. *Bulletin de la Société Géologique de France*, 12: 247-284.
- 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). Palaeontological memoirs of the late Hugh Falconer, A.M., M.D., with a biographical sketch of the author. Vol. II, Mastodon, Elephant, Rhinoceros, Ossiferous caves, primeval man and his contemporaries. 860 pp. Robert Hardwicke, London.
- Ficcarelli G. (1984). The Villafranchian cheetahs from Tuscany and remarks on the dispersal and evolution of the genus *Acinonyx*. *Palaeontographia Italica*, 73: 94-103.
- Forsyth Major C.J. (1885). On the mammalian fauna of the Val d'Arno. *Quarterly Journal of the Geological Society of London*, 41: 1-8.
- Gibbard P.L., Head M.J., Walker M.J.C. & the Subcommission on Quaternary Stratigraphy (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.
- Gilbert H. & Bernor R.L. (2008). Equidae. In Gilbert H. & Asfaw B. (eds), *Homo erectus* - Pleistocene evidence from the Middle Awash, Ethiopia. University of California Press, Berkeley: 133-166.
- Gliozzi E., Abbazzi L., Argenti P., Azzaroli A., Caloi L., Capasso Barbato L., Di Stefano G., Esu D., Ficcarelli G., Girotti O., Kotsakis T., Masini F., Mazza P., Mezzabotta C., Palombo M.R., Petronio C., Rook L., Sala B., Sardella R., Zanalda E. & Torre D. (1997). Biochronology of selected mammals, molluscs and ostracods from the middle Pliocene to the late Pleistocene in Italy. The state of the art. *Rivista Italiana di Paleontologia e Stratigrafia*, 103: 369-388.
- 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.
- Hernández-Pacheco E. (1921). La Llanura manchega y sus mamíferos fósiles: yacimiento de La Puebla de Almoradier. *Comisión de Investigaciones Paleontológicas y Prehistóricas, Memoria* 28: 1-41.
- Kretzoi M. (1954). Bericht über die Calabrische (Villafranchische) Fauna von Kislang, Kom. Fejer. *Magyar Állami Földtani Intézet, Évi Jelenése*, 1: 213-265.
- 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.
- Merla G. (1949). I *Leptobos* Rütimeyer italiani. *Palaeontographia Italica*, 46: 41-155.
- Owen R. (1846). A History of British Fossil Mammals, and Birds. 560 pp. John Van Voorst, London.
- Palombo M.R. & Ferretti M.P. (2005). Elephant fossil record from Italy: knowledge, problems, and perspectives. *Quaternary International*, 126/128: 107-136.
- Pomel M. (1842). Nouvelle espèce de chien fossile découverte dans les alluvions volcaniques de l'Auvergne. *Bulletin de la Société Géologique de France*, 14: 38-41.
- Pradella C. & Rook L. (2007). *Mesopithecus* (Primates, Cercopithecoidea) from Villafranca d'Asti (Early Villafranchian; NW Italy) and palaeoecological context of its extinction. *Swiss Journal of Geosciences*, 100: 145-152.
- Pueyo E.L., Muñoz A., Laplana C. & Parés J.M. (2016). The Last Appearance Datum of *Hipparrison* in Western Europe: magnetostratigraphy along the Pliocene-Pleistocene boundary in the Villarroya Basin (northern Spain). *International Journal of Earth Sciences*, 105: 2203-2220.
- Qiu Z., Weilong H. & Zihui G. (1988). Chinese hipparrisonines from the Yushe Basin. *Palaeontologica Sinica, Series C*, 175: 1-250.
- Rio D., Sprovieri R. & Di Stefano E. (1994). The Gelasian stage: a proposal of a new chronostratigraphic unit of the Pliocene series. *Rivista Italiana di Paleontologia e Stratigrafia*, 100: 103-124.
- Rook L. (2013). The 1980s field researches at Pirro Nord were developed thanks to the inspired and energetic activity of Claudio De Giuli (1938-1988). *Palaeontographica Abteilung A*, 298: 1-3.
- Rook L. (2015). Dedication to Augusto Azzaroli (1921-2015). *Bollettino della Società Paleontologica Italiana*, 54: 147-159.
- Rook L. & Martínez-Navarro B. (2010). Villafranchian: The long story of a Plio-Pleistocene European large mammal biochronologic unit. *Quaternary International*, 219: 134-144.
- Rütimeyer L. (1865). Beiträge zu einer palaontologischen Geschichte der Wiederkauer zunächst an Linne's Genus *Hemibos*. *Verhandlungen der Naturforschenden Gesellschaft in Basel*, 2: 299-354.
- Von Koenigswald G.H.R. (1970). *Hipparrison* from the Pleistocene of Europe, especially from the Red Creag of East Anglia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 8: 261-264.

- Woodburne M.O. (2007). Phylogenetic 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 Valesian vertebrates of Atzelsdorf (Late Miocene, Austria), 9. *Hippotherium* (Mammalia, Equidae). *Annalen des Naturhistorischen Museums in Wien*, 111A: 585-604.
- Zhegallo V.I. (1978). Gippariony Tsentral'noj Azii. Sovmestnaya Sovetsko-Mangolskaya paleontologicheskaya Ekspeditsiya, Trudy 7: 1-152 (in Russian).

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