

Equus cf. livenzovensis from Montopoli, Italy (early Pleistocene; MN16b; ca. 2.6 Ma)

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ABSTRACT - We report here the occurrence and metric characteristics of a large species of *Equus* from Montopoli (Tuscany, Italy) correlated with the middle Villafranchian, 2.6 Ma (early Pleistocene). This species co-occurs with a rare “*Hipparion*” sp. at Montopoli. We compare the Montopoli *Equus cf. livenzovensis* with a large suite of extant *Equus* including zebras, asses and a large suite of fossil *Equus* using bivariate and log₁₀ ratio analyses of anterior and posterior 1st phalanges III. Our comparisons show that Montopoli anterior and posterior 1st phalanges III are larger than in living zebras and asses and comparable in size and proportions to the early Pleistocene large Chinese species *Equus eisenmannae* and late Pleistocene Rancho La Brea *Equus occidentale*. *Equus livenzovensis* was a larger species than *Equus stenonis* and *Equus stehlini*. *Equus cf. livenzovensis* is not represented as far as we know by skulls and dentitions in the Italian Villafranchian record.

RIASSUNTO - [*Equus cf. livenzovensis* nell’associazione faunistica di Montopoli (Pleistocene inferiore, MN16b, ca. 2,6 Ma)] - Vengono descritte le caratteristiche morfologiche dell’equide di grande taglia *Equus cf. livenzovensis* dalla località fossilifera di Montopoli, nel Valdarno inferiore, località attribuita al Villafranchiano medio, 2,6 Ma (Pleistocene inferiore). Questa specie a Montopoli è associata ad una rara forma di “*Hipparion*” sp., recentemente descritta. Il campione di *Equus cf. livenzovensis* da Montopoli viene analizzato utilizzando un ampio campione di confronto comprendente sia equidi attuali (zebre, asini e cavalli domestici), che una selezione di equidi fossili. Lo studio concentra l’analisi statistica (diagrammi bivariati e log₁₀ ratio) sulle prime e seconde falangi del terzo dito degli arti anteriori e posteriori. I risultati di queste analisi mostrano che le prime falangi III e le seconde falangi III provenienti da Montopoli sono più grandi di quelle di zebre e asini attuali e comparabili, per proporzioni, alle specie *Equus eisenmannae* (Cina, Pleistocene inferiore) ed *Equus occidentale* (Rancho la Brea, Pleistocene superiore). Sulla base delle morfologie dello scheletro postcraniale (a Montopoli non sono presenti elementi cranio-dentari), *Equus cf. livenzovensis* aveva dimensioni maggiori delle altre due specie di equidi presenti nel record fossile italiano del Pleistocene inferiore, *Equus stenonis* e *Equus stehlini*.

INTRODUCTION

The occurrence of *Equus* from the locality of Montopoli is known from the earliest publications concerning the site. Although there has not yet been a detailed description of the Montopoli *Equus* remains, reference to the occurrence of the large horse *Equus cf. livenzovensis* was given in papers reporting Villafranchian horses (Azzaroli, 1966, 1982, 1989, 2000, 2003; De Giuli, 1972; Alberdi et al., 1998; Alberdi & Palombo, 2013) and with Villafranchian biochronology and faunal units definition (Azzaroli, 1977; Lindsay et al., 1980; Azzaroli et al., 1982, 1988; Gliozzi et al., 1997; Rook & Martínez Navarro, 2010).

Within a broader project on the Evolution, Biogeographic and Palaeoclimatic Context of Old World early Pleistocene horse faunas and the origin of African zebras, we have undertaken a revision of the equid collections kept in the Museum of Natural History of the University of Florence, and the Montopoli assemblage was one of our first targeted studies. Rook et al. (2017) reported the rare occurrence of a small hipparionine horse, “*Hipparion*” sp. from Montopoli preserved in the Vertebrate Palaeontology laboratory of the Earth Sciences

Department at the University of Florence; this is the second youngest occurrence of “*Hipparion*” in Europe. The longer range goals of our Old World *Equus* project are to: 1) establish the species content of the Old World *Equus Datum* from the standpoints of the likely North American species source and oldest Old World *Equus* species in Eurasia and Africa; 2) reveal the initial evolutionary steps regionally throughout Eurasia and Africa; 3) gain a clearer understanding about the origin and evolution of extant Old World *Equus* species based on morphology and morphometrics of the skull, mandible, dentitions and postcranial elements for eventual comparison with molecular evolutionary records.

The anterior and posterior phalanges III of Montopoli *E. cf. livenzovensis* Bajgusheva, 1978 are the only complete skeletal elements of this species that we have from this locality. The significance of *E. cf. livenzovensis* lies in Montopoli’s stratigraphic position as being at the base of the Pleistocene (= base of Quaternary) as is currently realized. We will expand our studies of the Italian early Pleistocene *Equus* with study of *E. stenonis* Cocchi, 1867 and *E. stehlini* Azzaroli, 1965 abundantly represented in the Italian Villafranchian.

STRATIGRAPHIC AND GEOCHRONOLOGIC SETTING

Montopoli Valdarno 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. 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 faunas of the Triversa FU and to shallow-water marine sediments of early Pleistocene age (middle Pliocene in papers previous to the IUGS 2009 decision; cf. Benvenuti et al., 1995) (Fig. 2). 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*, and a (rare and elusive) smaller horse “*Hipparion*” sp. (Rook et al., 2017), 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); the Montopoli FU is also marked by the disappearance of some of the taxa with subtropical affinities still characterizing the previous early Villafranchian assemblages (Pradella & Rook, 2007). Montopoli, and the related faunal unit, occurs at the Gauss-Matuyama transition (Lindsay et al., 1980; Benvenuti et al., 1995) thus correlating with the recently redefined Plio/Pleistocene boundary (Gelasian Stage, GSSP at Monte san Nicola Section, Sicily; Rio et al., 1994; Gradstein et al., 2012).

HISTORICAL OVERVIEW

Vertebrate palaeontologists widely accept the Plio-Pleistocene vertebrate record from the Valdarno Basin (Tuscany, Italy) as a biochronologic and geochronologic standard (Rook & Martínez-Navarro, 2010; Rook et al., 2013). If the Upper Valdarno Basin (the Arno River trait upstream of Florence, between Rignano sull’Arno and Arezzo) is renowned for the occurrence of mammal fossil bones since Renaissance times, and fossil vertebrates from this basin have been observed, collected, discussed by early naturalists (Rook et al., 2013), the Lower Valdarno Basin (the Arno River trait downstream of Florence, from Montelupo Fiorentino to the Tuscany coast) fossil mammal record began to be mentioned in literature in the mid 1800’s.

A revision of Valdarno vertebrate faunas closely involves the ancient collections and the Museum that host the most important ones, the Florence palaeontological Museum, having its origins in the granducal collections (Cioppi & Dominici, 2011). Although “old collections” can be problematic for some degree of uncertainty, mainly concerning the exact stratigraphic provenance for some fossils, the rich Valdarno collections are presently acclaimed as an invaluable archive for the palaeobiology, palaeoecology and biochronology of the area, and even more important, they are a reference for Plio-Pleistocene western European large mammal chronology.

Throughout the 1860s and following years, the Florence palaeontological Museum vertebrate collection was about to experience an important growth with the nomination of Igino Cocchi as director of the Royal Institute of Advanced Studies. Cocchi established an Italian palaeontological collection and central library in Florence (Corsi, 2003), and set out to expand the palaeontological collections with numerous acquisitions.

In early years a very important event for the development of vertebrate palaeontology in Tuscany was the arrival in Florence of the eminent Scottish

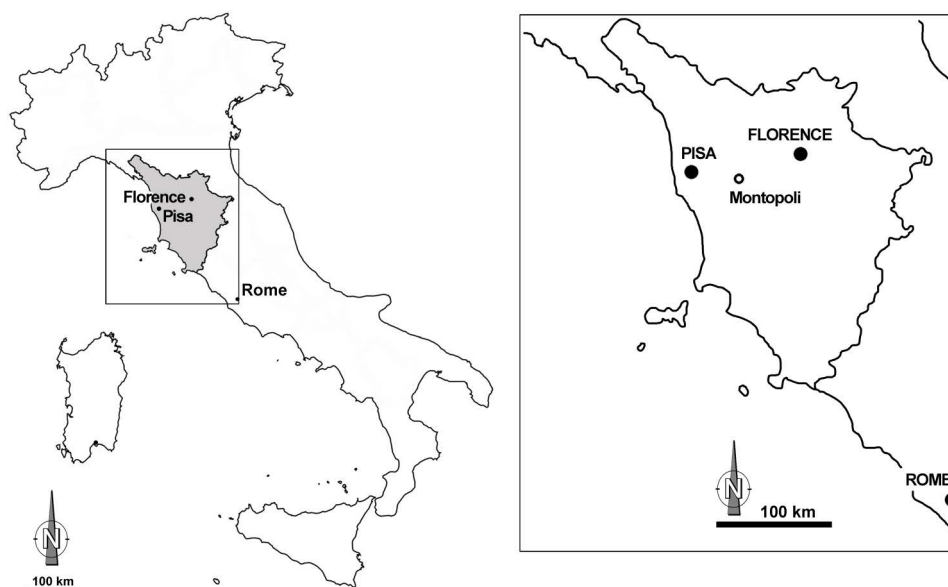


Fig. 1 - Geographical Locator Map of Montopoli.

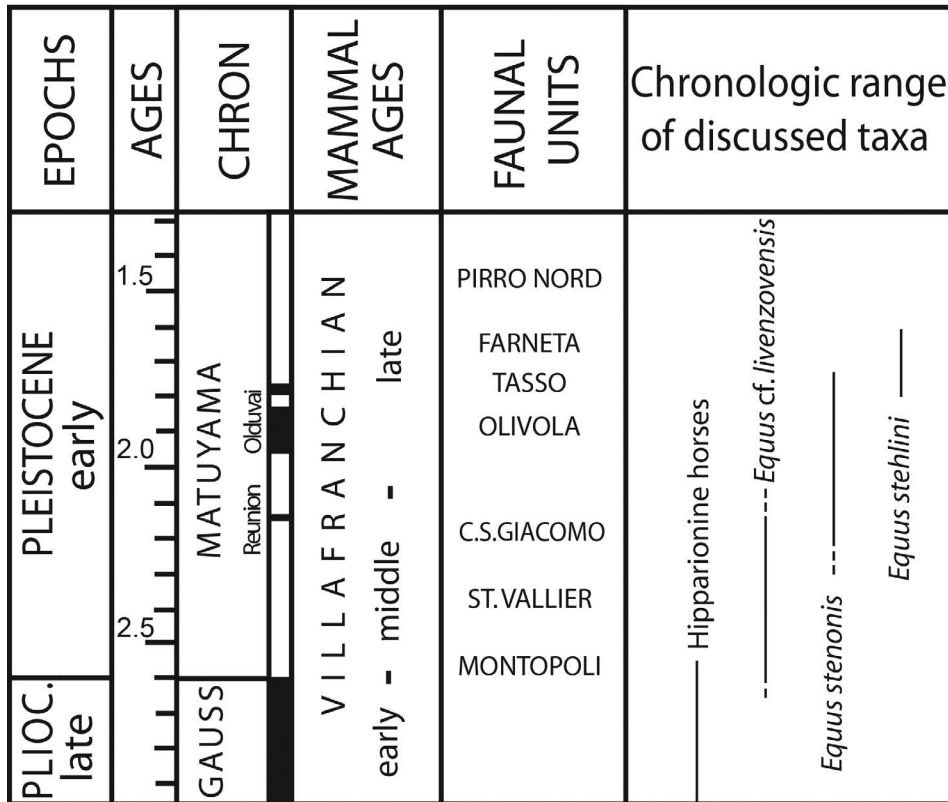


Fig. 2 - The middle Villafranchian chronology with range chart of Italian fossil equid taxa mentioned in the text.

palaeontologist Charles I. Forsyth Major, a pioneer in continental mammal stratigraphy, thanks to his interest excavation work as a necessary starting point for an exact stratigraphic placement of the mammals from Valdarno (Forsyth Major, 1877). Whilst in Florence, Forsyth Major continuously and systematically searched for new material from the main Tuscan sites, bringing to the museum hundreds of specimens (Rook, 2012), among which was the Montopoli fauna (Forsyth Major, 1885). A crucial contribution to the re-evaluation of the fossil mammals from Montopoli is dated in the years 1970s, when Augusto Azzaroli began to develop palaeontological studies on Plio-Pleistocene vertebrate faunas of Italy with a particular interest in the study of Valdarno Plio-Pleistocene fossil mammals as the basis for the biochronological subdivision of the Villafranchian, with the definition of Montopoli as a Faunal Unit, at the base of middle Villafranchian (Azzaroli, 1962, 1970, 1977; Azzaroli et al., 1982, 1988).

To order fossils in geological time, vertebrate palaeontologists usually adopt biochronological time scales based on the evolutionary stages of the faunal assemblages and on the dispersal events that characterize and define the faunal sequences. The Neogene and Quaternary continental biochronological scale of European Neogene and Quaternary has been developed since the 1960s and 1970s thanks to the pioneering works of eminent palaeontologists such as Louis Thaler, Emile Heintz and Pierre Mein in France (Agustí & Rook, 2011) and Augusto Azzaroli in Italy (Rook & Martínez-Navarro, 2010). Although its definition dates to the early 1900s (Williams, 1901), the term biochronology was rarely

used before the 1970s, when the use of radiometric dating techniques became widespread and there was the need to distinguish “radiochronology” and “biochronology” as different aspects of “geochronology”. Berggren & Van Couvering (1974) were the first to suggest an application of the term “biochron” for units of geological time based exclusively on palaeontological data, without reference to the lithostratigraphy or rock units that contain the fossils. All the chronological units developed and applied by vertebrate palaeontologists in continental sedimentation contexts are biochronological units, the so-called “Mammal Ages”. The Villafranchian “Mammal Age” is a biochronological unit based on the European large mammal fauna and spans an interval including the late Pliocene and early Pleistocene (a period of ca. 2.6 million years, roughly between 3.5 and 1 Ma).

The term Villafranchian was coined by Pareto (1865) as a continental stage referring to fluvial and lacustrine sediments with abundant mammalian fossils cropping out in the area of Villafranca d’Asti (Piedmont), although the fossil mammalian fauna of the upper and lower Valdarno in Tuscany was also included in the original description. For years, the term was considered to refer to the most recent part of the continental Pliocene, and Gignoux (1916) proposed to correlate it with the Calabrian stage (defined on the basis of marine sediments), considering the latter to represent the terminal part of the Pliocene. During the 18th International Geological Congress in London in 1948, it was decided that the base of the Calabrian should be correlative with the base of the Pleistocene, and therefore the Villafranchian was also believed to represent the continental early Pleistocene.

Since the 1960s, the work of Augusto Azzaroli (Rook, 2015) and other famous European palaeontologists (Rook & Martínez-Navarro, 2010) have demonstrated that the so-called “Villafranchian faunas” were not homogeneous and not even contemporaneous but represented a relatively long temporal interval (Azzaroli, 1970, 1977). The chronological subdivision of the Villafranchian was defined finally in the 1970s-1980s with the subdivision of the Villafranchian into successive “Faunal Units” (Azzaroli, 1977, 1983; Gliozzi et al., 1997; Torre et al., 2001) grouped respectively into early, middle and late Villafranchian. In the standard Stratigraphic Scale of geological times, the early Villafranchian now correlates with the late Pliocene (Piacenzian; from ~3.5 to ~2.6 Ma), the middle Villafranchian to the first part of the early Pleistocene (Gelasian; from ~2.6 to ~2.0 Ma) and the late Villafranchian to almost all the rest of the early Pleistocene (uppermost part of the Gelasian and almost the whole Calabrian; from ~2.0 to ~1.0 Ma). During this long interval, the composition of the mammal assemblages in Europe underwent profound changes. Even though the term “Villafranchian” has lost much of its original meaning (Azzaroli, 1977, 1992), it continues to be used for historical reasons and for nomenclatural stability; nevertheless, because the term has a stratigraphic meaning, it must always be specified to which part of it is being referred (early, middle or late Villafranchian), or better to which of the Faunal Units is being referred (Azzaroli, 1992; Rook & Martínez-Navarro, 2010). The Montopoli Faunal Unit, correlative with 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 Triversa FU to the Montopoli FU (Gliozzi et al., 1997; Rook & Martínez-Navarro, 2010) led to Montopoli being nominated as the basal unit of the middle Villafranchian (Fig. 2).

Fossil mammals from Montopoli have been analyzed by several authors since their discovery (Forsyth Major, 1885; Merla, 1949; Azzaroli, 1962; De Giuli & Heintz, 1974a, b; Ficarelli, 1984; Cherin et al., 2013; Bartolini Lucenti, 2017). According to published data the fauna is composed of the following taxa: *Acinonyx pardinensis* (Croizet & Jobert, 1828), *Puma pardoides** (Owen, 1846), *Pliocrocota perrieri* (Croizet & Jobert, 1828), *Nyctereutes megamastoides* (Pomel, 1842), *Mammuthus gromovi** (Alexeeva & Garutt, 1965), *Stephanorhinus jeanvireti* (Guérin, 1972), *S. etruscus** (Falconer, 1868), “*Hipparion*” sp., *Equus cf. livenzovensis**, *Pseudodama lyra* Azzaroli, 1992, *Croizetoceros ramosus* (Croizet & Jobert, 1828), *Eucladoceros falconeri**, *Procacpreolus cusanus* (Croizet & Jobert, 1828), *Gazella borbonica**, *Leptobos stenometopon* (Rütimeyer, 1865). Taxa marked by an * are first occurring species in the Italian Villafranchian record.

MATERIALS AND METHODS

The Montopoli sample of *Equus cf. livenzovensis* includes a large anterior 1st phalanx III (IGF11224) associated with an anterior 2nd phalanx III (IGF11225), and a large posterior 1st phalanx II (IGF11074) associated with

a posterior 2nd phalanx III (also IGF11074). We compare the Montopoli specimens of *Equus cf. livenzovensis* to our sample of extant *Equus* including extant zebras and asses and fossil *Equus* from Eurasia and Africa. Measurements of this sample are included in Table 1 of the Supplementary Online Material.

Anatomical nomenclature, osteological landmarks and ligament attachment interpretations are according Bernor et al. (1997). Measurements are all given in millimeters and rounded to 0.1 mm. Measurement numbers (M1, M2, M3, etc.) refer to those published by Eisenmann et al. (1988) and Bernor et al. (1997) for the skulls and postcrania. In various studies, Eisenmann (see Eisenmann, 1995 for a comprehensive summary) has used log10 ratio diagrams to evaluate differences in equid long bone proportions as a basis for recognizing taxa and their evolutionary relationships. Bernor et al. (2003, 2018), Bernor & Harris (2003), Bernor & Sen (2017) and Sun et al. (2018) have used multiple statistical tests, including univariate, bivariate and multivariate statistics as well as log10 ratio diagrams to evaluate and resolve the alpha systematics of equid species.

Bivariate plots include measurements (M): M1 = maximum length; M4 = proximal width. Log10 ratio diagrams include these two measurements and: M2 = anterior length, M3 = minimum breadth; M5 = proximal articular depth; M6 = distal breadth at the tuberosities; M7 = distal articular breadth; M8 = distal articular depth; M9 = minimum length of trigonum phalanges. We calculate a 95% confidence ellipse for the *Hippotherium primigenium* (Von Mayer, 1829) sample from Hoewenegg (Hegau, Germany; 10.3 Ma) for all bivariate plots and use the mean log10 values of the Hoewenegg sample for the log10 plots. The Hoewenegg sample of *Hippotherium primigenium* is statistically robust and has been applied to multiple equid analyses (Bernor et al., 1997).

Table 1 provides a listing of the extant and fossil species of *Equus* which we analyze herein.

Table 2 includes measurements on our sample of *Equus cf. livenzovensis* anterior and posterior 1st and 2nd phalanges of digit III (central digit). Table 1 of the Supplementary Online Material provides measurements of anterior and posterior 1st phalanges III of extant *Equus* including living zebras and asses, used in our statistical analyses.

Abbreviations

A1PHIII: anterior 1st phalanx of digit III; A2PHIII: anterior 2nd phalanx of digit III; P1PHIII: posterior 1st phalanx of digit III; P2PHIII: posterior 2nd phalanx of digit III; MCIII: metacarpal III; MTIII: metatarsal III; Ma: mega-annum in the geochronologic time scale (ages in m.y. usually based on radioisotopic analyses, magnetostratigraphic analyses or biochronologic units correlative to those analytical standards). AMNH: American Museum of Natural History, New York; BMNH: Natural History Museum, London; HLMD: Natural History Museum, Darmstadt, Germany; IGF: Museo di Geologia e Paleontologia dell’Università di Firenze, Sezione Geologia e Paleontologia, Florence, Italy; IVPP: Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; KNHM: Natural History Museum, Karlsruhe, Germany; RHMN: Natural

Equus Species	Abbreviation	Symbol	Country	Institutions
<i>E. burchelli</i>	Ebur	b	Africa	USNM, SMNS
<i>E. burchelli boehemi</i>	Eburboe	b	Africa	USNM
<i>E. eisenmannae</i>	Eeisen	e	China	IVPP
<i>E. grevyi</i>	Egrev	g	Africa	USNM, AMNH
<i>E. hemionus</i>	Ehem	h	Asia	USNM
<i>E. kiang</i>	Ekia	k	India	USNM
<i>E. cf. livezovenssis</i>	Eliven	l	Italy	IGF
<i>E. occidentale</i>	Eocc	o	USA	LACM
<i>E. simplicidens</i>	Esimp	p	USA	USNM
<i>E. stehlini</i>	Esteh	t	Italy	IGF
<i>E. asinus</i>	Easin	u	USA	USNM, AMNH
<i>E. sp.</i>	Esp	x	Africa	BMNH, RMNH, IGF
<i>E. zebra</i>	Ezeb	z	Africa	USNM, AMNH
<i>Hipparion</i> Standard				
<i>H. primigenium</i>		w	Hoewenegg (D)	KNHM, HLMD

Tab. 1 - Species and their abbreviations for bivariate plots.

History Museum, Leiden, the Netherlands; SMNS: Natural History Museum, Stuttgart, Germany; USNM: United States National Museum (Natural History), Washington D.C., USA.

STATISTICAL ANALYSIS

Figure 3a-b provides images of IGF11224 A1PHIII (Fig. 3a1-2) and IGF11225 A2PHIII (Fig. 3b1-2) of Montopoli *Equus cf. livezovenssis* cranial and caudal views. Figure 4a-b are bivariate plots of A1PHIII maximum length (M1) versus proximal width (M4) in relationship to the Hoewenegg *Hippotherium primigenium* 95% confidence ellipse. Figure 4a plots our complete sample of A1PHIII. The widest dimension (M4) of our entire sample is *E. cf. livezovenssis* (l) from Montopoli. Slightly longer and narrower is our sample of *E. occidentale* Leidy, 1865 (o) and a single individual of *E. eisenmannae* Qiu et al., 2004 (e). Slightly shorter but well above the Hoewenegg ellipse is our sample of *E. simplicidens* Cope, 1892 (p) and Grevy's zebra (g). There are two smaller representatives of *E. simplicidens* below this cluster with *Equus burchelli* Gray, 1824 (b), *E. kiang* Moorcroft (in Moorcroft & Trebeck, 1841) (k), *E. hemionus* Pallas, 1775 (h), *E. zebra* Linnaeus, 1758 (z) and *E. sp.* (x). The smallest individuals in our *Equus* sample are *E. asinus*

Linnaeus, 1758 (u) and *E. hemionus* (h) to the upper left, *E. stehlini* (t) to the upper right and *E. burchelli* within the upper portion of the Hoewenegg ellipse. For the most part, all species of *Equus* are larger than the Hoewenegg sample of *Hippotherium primigenium*. The Hoewenegg skeleton of *H. primigenium* has been estimated as having a standing height of between 1.30 and 1.35 meters at the whither (Bernor et al., 1997: fig. 5-3), within the range of *Equus burchelli* (1.10-1.45 meters; Nowak, 1999). While larger than many species of Old World "Hipparion", Hoewenegg *Hippotherium primigenium* had slender limbs, narrow thorax and a flexible spine that permitted rotation around its central axis. While cursorial, *Hippotherium primigenium* was well adapted to springing and leaping. Figure 4b is a bivariate plot of Italian *Equus* (l and t) and North American *E. simplicidens* (p) with the Hoewenegg population 95% ellipse. Herein we see *E. cf. livezovenssis* (l) separated from the rest of the sample by its much greater width. *Equus stehlini* (t) is placed to the right upper portion of the Hoewenegg ellipse and is much smaller than *E. simplicidens* and *E. cf. livezovenssis*.

Figure 5 is a log10 ratio plot of A1PHIII with the standard Hoewenegg log10 mean calculated for each variable, M1-M9. Figure 5a plots our sample of extant *Equus* A1PHIII maximum length (M1) versus proximal articular width (M4). Extant zebras are plotted with dotted lines, the longest being *E. grevyi* Oustalet, 1882, the other

Specimen Number	Bone	M1	M2	M3	M4	M5	M6	M7	M8	M9
IGF11224	A1PHIII	87.2	80.5	40.7	64.3	44.3	52.7	52.2	25.6	47.7
IGF11225	A2PHIII	54.6	41.8	48.2	58.0	37.3	45.4			
IGF11074	P1PHIII	90.8	81.9	39.8	62.9	62.0	55.1	53.4	29.0	49.7
IGF11074	P2PHIII	56.9	43.6	48.8	58.4	40.4	51.3			

Tab. 2 - *Equus cf. livezovenssis* anterior and posterior 1st and 2nd phalanges.

three being very similar in their size and proportions: *E. quagga* Boddaert, 1784, *E. zebra* and *E. burchelli*. Besides being longer than the other zebras, *E. grevyi* also has relatively elevated proximal cranio-caudal depth (M5) and distal supra-articular width (M6). *Equus kiang* plots longer than other zebras but has a narrower midshaft width, proximal articular width (M4) and depth (M5) than zebras. *Equus hemionus* has the shortest A1PHIII. Figure 5b plots our sample of fossil *Equus*. *Equus* cf. *livenzovensis* has the largest dimensions of midshaft width (M3), proximal articular width (M4) and depth (M5), distal supra-articular width (M6) and articular width (M7) of our sample. *Equus occidentale* and *E. eisenmannae* are somewhat longer but with lesser dimensions of M3-M7 and have virtually identical plot trajectories. *Equus oldowayensis* Hopwood, 1937 is shorter, but has a similar plot trajectory to *E. occidentale* and *E. eisenmannae*. North American *Equus simplicidens* is similar in length (M1 and M2) to *E. occidentale* and *E. eisenmannae* but has a lesser proximal articular width (M4) dimension. *Equus stehlini* has a plot trajectory similar to *E. occidentale*, *E. eisenmannae* and *E. oldowayensis* but is remarkably shorter.

Figure 6a-b provides images of P1PHIII (6a1-2) and P2PHIII (6b1-2) of Montopoli *Equus* cf. *livenzovensis* cranial and caudal views. Figure 7a-b shows bivariate plots of P1PHIII maximum length (M1) versus proximal articular width (M4). Figure 7b plots our sample of extant *Equus* together with *E. occidentale*, *E. cf. livenzovensis* is the longest (M1) and widest (M4) dimensions of our total sample. There is a single individual of *Equus eisenmannae* that plots immediately below the *E. occidentale*-*E. cf. livenzovensis* samples. There is a cluster plotting below these of *E. grevyi*, *E. simplicidens* and *E. zebra*; *E. grevyi* has two individuals that plot longer than this cluster. Below this cluster are *E. asinus* to the left (relatively narrow

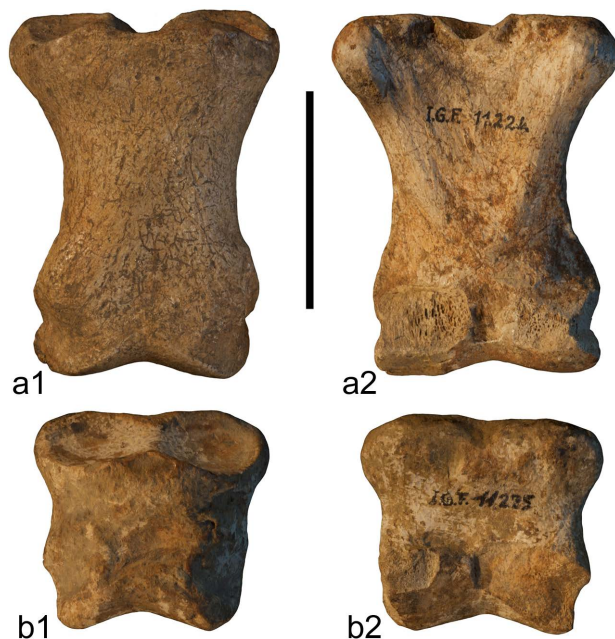


Fig. 3 (color online) - *Equus* cf. *livenzovensis* from Montopoli. a) IGF11224 A1PHIII in dorsal (a1) and palmar (a2) views. b) IGF11225 A2PHIII in dorsal (b1) and palmar (b2) views. Scale bar: 5 centimeters.

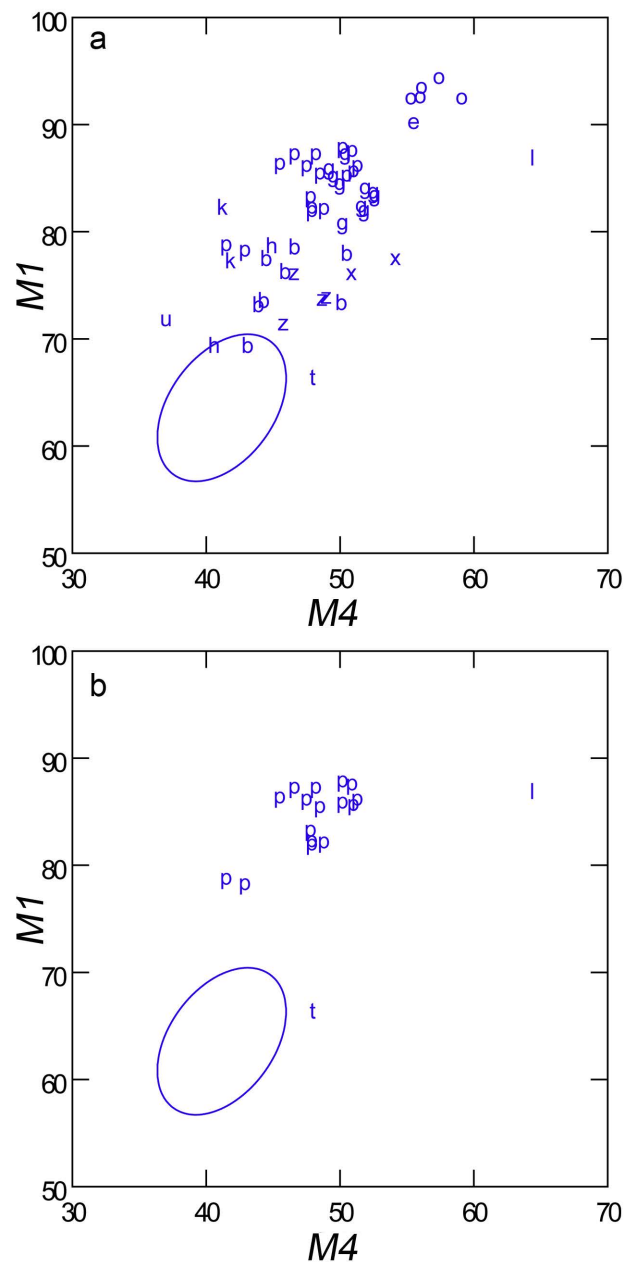


Fig. 4 (color online) - a) Bivariate plot of A1PHIII, fossil and extant *Equus* species, Hoewenegg 95% confidence ellipse; b) bivariate plot of A1PHIII, *Equus simplicidens* from Hagerman Horse Quarry and Italian *Equus* cf. *livenzovensis* and *E. stehlini*, Hoewenegg 95% confidence ellipse.

M4 dimension), then to the right *E. kiang* and further to the right small representatives of *E. simplicidens* and *E. burchelli*. There are small representatives of *E. asinus* to the left and *E. burchelli* to the right of the upper portion of the Hoewenegg ellipse. Some *E. burchelli* and *E. hemionus* plot within the Hoewenegg ellipse. Figure 7b plots the relationships between the Hoewenegg 95% confidence ellipse and the distribution of *E. simplicidens*, *E. cf. livenzovensis* and *E. stehlini*. This figure emphasizes the relatively large size of *E. cf. livenzovensis* compared to the ancestral North American population and Italian *E. stehlini*.

Figure 8 is a log10 ratio plot of P1PHIII with the Hoewenegg log10 mean calculated for each variable, M1-

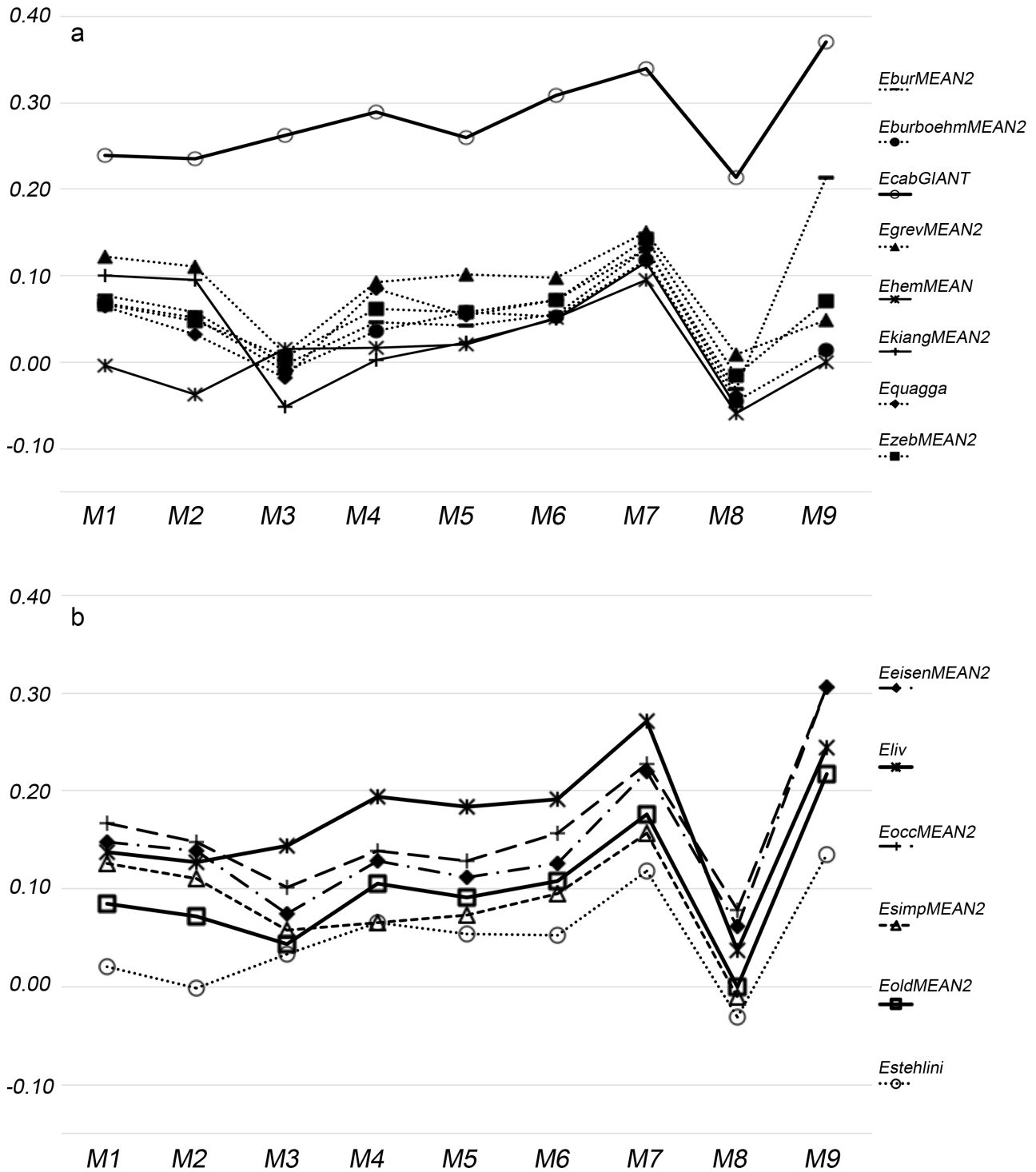


Fig. 5 - a) Extant *Equus* A1PHIII means, log10 ratios (Hoewenegg as Standard); b) fossil *Equus* A1PHIII log10 ratios (Hoewenegg as Standard).

M9. Figure 8a plots our sample of extant *Equus*. *Equus grevyi* has the longest P1PHIII (M1 and M2) and overlaps with *E. quagga* in other dimensions. *Equus burchelli* and *E. burchelli boehemi* are somewhat smaller than *E. grevyi* and *E. quagga*, plot very close to one another and show the same trajectory as *E. grevyi* and *E. quagga*. *Equus zebra* is essentially identical in its dimensions and trajectory to *E. quagga* and *E. burchelli*. *Equus kiang*, *E. hemionus* and *E. asinus* have similar plot trajectories and are remarkable for

their narrow midshaft (M3), small proximal width (M4) and depth (M5) and small supra-articular (M6) dimensions (*E. hemionus* and *E. asinus*). Figure 8b plots our sample of fossil *Equus* P1PHIII. *Equus cf. livenzovensis* and *E. occidentale* exhibit close similarities in length (M1 and M2), midshaft width (M3), proximal articular width (M4) and depth. *Equus cf. livenzovensis* has relatively greater dimensions of supra-articular width (M6) and distal articular width (M7) compared to *E. occidentale*. *Equus*



Fig. 6 (color online) - *Equus* cf. *livenzovensis* from Montopoli. a) IGF11074 P1PHIII in dorsal (a1) and palmar (a2) views; b) P2PHIII in dorsal (b1) and palmar (b2) views. Scale bar: 5 centimeters.

eisenmannae has a length (M1 and M2) nearly as great as *E. cf. livenzovensis* and *E. occidentale*, but midshaft (M3), proximal articular dimensions (M4 and M5) and distal articular dimensions (M6-8) and length of trigonum phalanges (M9) is less. *Equus simplicidens* has somewhat shorter length dimensions (M1 and M2) than these taxa but has a log10 profile closely resembling *E. eisenmannae*. *Equus stehlini* has the shortest length dimensions (M1 and M2) and has a similar profile to *E. simplicidens*.

DESCRIPTION AND COMPARISONS

The Montopoli sample of *Equus* cf. *livenzovensis* includes an A1PHIII, IGF11224 and A2PHIII, IGF11225 (Fig. 3a-b) and a P1PHIII and P2PHIII, both IGF11074 (Fig. 6a-b). These bones are similar in their preservation and articulate with one another well. They are derived potentially from the same individual. The A1PHIII is very large and robust. The dorsal surface (Fig. 3a1) presents a number of swellings. Proximally, the articular surface is expanded medially and laterally for articulation with distal MCIII. Immediately distally, the supra-articular tubercles (points for measuring M6) are greatly expanded for attachment of the ligamentum sesamoideum centrale. The distal articular tubercles are likewise expanded for attachment of the medial and lateral collateral ligaments. The supra-articular and articular dimensions are virtually the same. The palmar surface is dominated by a very long, deeply depressed “V” scar for attachment of the ligamentum sesamoideum obliquum. Superiorly, and proximally on both the medial and lateral aspect of the “V” scar are robust swellings for attachment of the ligamentum collaterale of the fetlock joint. Proximally,

the palmar groove for the crista sagittalis is a broad U-shape. The distal articular surface describes a gentle sinuous groove.

The A2PHIII is a short bone, expanded mediolaterally proximally and distally. The proximal articular surface is inclined from the dorsal to palmar aspect. Dorsally, the distal aspect presents the medial and lateral hollowed scars for attachment of the ligamentum collaterale which binds the 2nd and 3rd phalanges III. The distal articular facet presents as a gentle sinuous curve in dorsal view. The proximal palmar aspect presents robust swellings for the medial and lateral scar for the ligamentum collaterale of digit III phalanx 1/phalanx 2 articulation.

The P1PHIII is very large and robust and, as is common in *Equus*, is distinguished from A1PHIII by having a greater length (M1 = 90.8 mm versus 87.2 mm) and more slender midshaft dimension (M3 = 39.8 versus 40.7 mm; Fig. 6a1-2). Other than these contrasts in dimensions, the anatomical features are much the same. Dorsally (Fig. 6a1), the proximal articular surface is expanded medially and laterally for articulation with distal MTIII. Distally, the supra-articular tubercles (points for measuring M6) are similarly expanded for attachment of the ligamentum sesamoideum centrale. The distal articular tubercles are likewise expanded for attachment of the medial and lateral collateral ligaments. The distal supra-articular and articular dimensions are virtually the same. The palmar surface (Fig. 6a2) “V” scar is likewise deeply excavated for attachment of the ligamentum sesamoideum obliquum. The proximal medial and lateral attachments for the ligamentum collaterale of the fetlock joint are likewise robust. The proximal palmar groove for the crista sagittalis has a shallower U-shape than in the A1PHIII. The distal articular surface again describes a gentle sinuous groove.

As in A2PHIII the P2PHIII is a short bone, expanded proximally and distally. The anatomy of P2PHIII is similar in several features: it is expanded mediolaterally proximally and distally; the proximal articular surface is inclined from the dorsal to palmar aspect; dorsally, the distal aspect presents the medial and lateral hollowed scars for attachment of the ligamentum collaterale which binds the 2nd and 3rd phalanges III; the distal articular facet presents as a gentle sinuous curve; proximal palmar aspect presents robust swellings for the medial and lateral scar for the ligamentum collaterale of phalanx 1/phalanx 2 of digit III articulation; distally the articular facet is divided into a medial and lateral aspect by a deep U-shaped, non-articular depression not clearly preserved on A2PHIII.

We have undertaken a statistical analysis of A1PHIII and P1PHIII. The A2PHIII and P2PHIII offer too little information for statistical analyses to be useful in distinguishing species. We have contrasted in both the bivariate (Figs 4a-b and 7a-b) and log10 ratio plots (Figs 5a-b and 8a-b) comparisons between extant and fossil species of *Equus*. In both bivariate and log10 plots, *Equus* cf. *livenzovensis* is one of the largest species of *Equus* that we have analyzed herein. In bivariate plots of A1PHIII (Fig. 4a-b), *E. cf. livenzovensis* has absolutely the widest proximal articular surface dimension (M4) and is only slightly shorter than *E. occidentale* and *E. eisenmannae*. *Equus* cf. *livenzovensis* is more robustly built in midshaft (M3), proximal (M4 and M5) and distal articular (M6 and

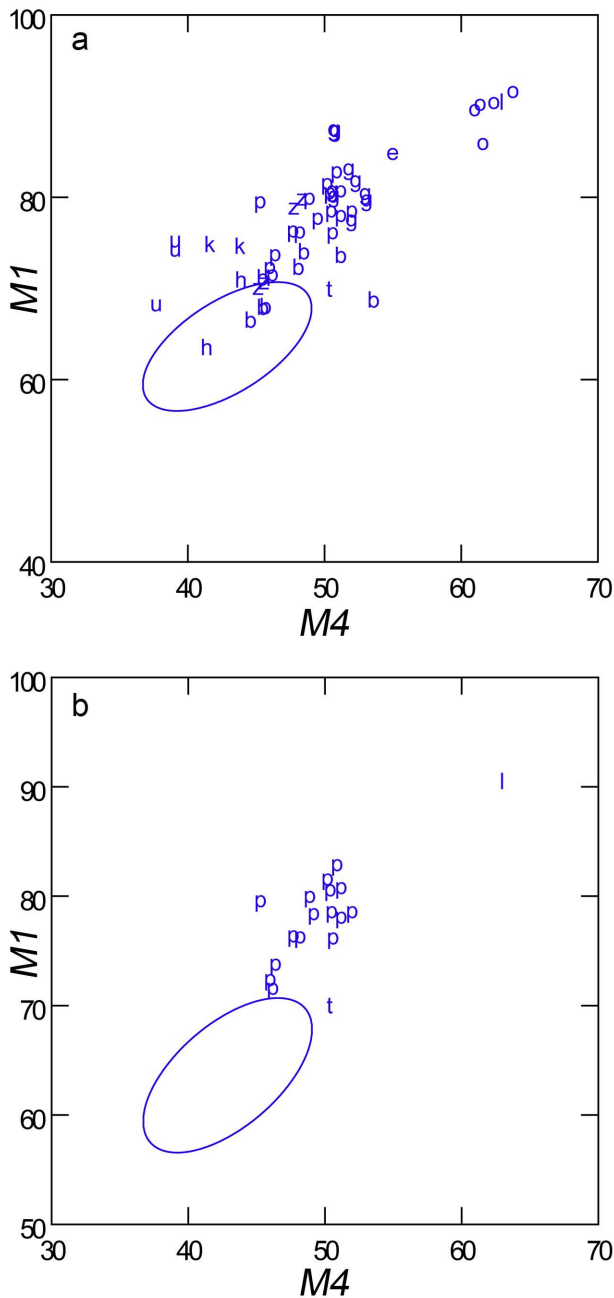


Fig. 7 (color online) - a) Bivariate plot of P1PHIII, fossil and extant *Equus* species, Hoewenegg 95% confidence ellipse; b) bivariate plot of P1PHIII, *Equus simplicidens* from Hagerman Horse Quarry and Italian *Equus cf. livenzovensis* and *E. stehlini*, Hoewenegg 95% confidence ellipse.

M7) dimensions than all of our fossil species. Together with *E. occidentale*, *E. eisenmannae* and *E. oldowayensis*, *E. cf. livenzovensis* has a longer A1PHIII than most zebras except *E. grevyi*. *Equus occidentale*, *E. eisenmannae* and *E. oldowayensis* have very similar log10 plot trajectories differing from the primitive species *E. simplicidens* only in their relatively greater proximal articular dimension (M4).

In bivariate plots of P1PHIII (Fig. 7a-b), *Equus cf. livenzovensis* plots within the *Equus occidentale* plot and well above *Equus eisenmannae*. Likewise, *E. cf. livenzovensis* plots well above our sample of *E.*

simplicidens and other extant and fossil *Equus*. Figure 7b reveals that *E. cf. livenzovensis* plots above the *E. simplicidens* sample and one specimen of *E. stehlini*. In terms of log10 ratios, *E. cf. livenzovensis* again plots most similarly with *E. occidentale*, differing only in its greater distal supra-articular (M6) and distal articular (M7) width dimensions. *Equus stehlini* plots significantly smaller than *E. cf. livenzovensis* (Fig. 8b). Of the zebras, *E. grevyi* has the longest P1PHIII with a midshaft dimension (M3) strikingly more narrow than *E. cf. livenzovensis* and *E. occidentale* but similar in its log10 trajectory to *E. eisenmannae*.

Of the *Equus* species that we have studied herein, the Montopoli *Equus cf. livenzovensis* has the most robustly built anterior and posterior 1st phalanges III. Remarkable is the closeness in size and proportions of the Montopoli phalanges to the latest Pleistocene North American horse (Rancho La Brea) *Equus occidentale*. Given the geographic and chronologic separation of *E. cf. livenzovensis* and *E. occidentale*, the similarity is most likely due to convergent evolution in the size of these two horses.

DISCUSSION

The lower boundary of the Quaternary (= Pleistocene of current usage) is marked by a striking climatic change that marks the disappearance of warm forest species *Mammuthus borsoni* (Hays, 1834), *Tapirus arvernensis* Croizet & Jobert, 1828, *Sus minor* Depéret, 1890 and *Ursus minimus* Devèze & Bouillet, 1827 and the migratory first occurrence of a primitive elephant (*Mammuthus gromovi*), gazelle (*Gazella borbonica*), and the monodactyl equid (*Equus cf. livenzovensis*) (Azzaroli, 1983). The first appearance of *Equus* in Eurasia had its origin from North America and was heralded as being a stratigraphic marker termed the *Equus* Datum (Berggren & Van Couvering, 1974). Lindsay et al. (1980) calibrated this event as being 2.6 Ma.

Azzaroli (1982) recognized the occurrence of a very large *Equus* in the Montopoli fauna, ca. 2.6 Ma which he referred to *Equus cf. livenzovensis*. He explained that *Equus livenzovensis* included two skulls described from the "late Pliocene" (current early Pleistocene) deposits of southern Russia (= Ukraine). One skull, from Khapry near the Azov Sea, was described as *Equus stenonis cf. major* Boule by Gromova (1949). The skull second was derived from a sand pit at Livensovka near Rostov on Don and described as *E. cf. bressanus* Viret by Bajgusheva (1971), and again as a new species *Equus livenzovensis* (Bajgusheva, 1978). There were no figures given in Bajgusheva (1971). Only Bajgusheva (1978) is valid because illustrations of the material are included therein (Azzaroli, 1982). Azzaroli (1982) noted that the skulls of *Equus livenzovensis* are somewhat larger than *E. namadicus* Azzaroli, 1982 and *E. stenonis* but otherwise similar. The Khapry skull has a well-developed preorbital fossa and a distinct median nasal groove. The dental features are similar to those of Italian *E. stenonis* and North American *E. simplicidens*. *Equus simplicidens* has been proposed as the North American source of Old World *Equus* (Azzaroli & Voorhies, 1993).

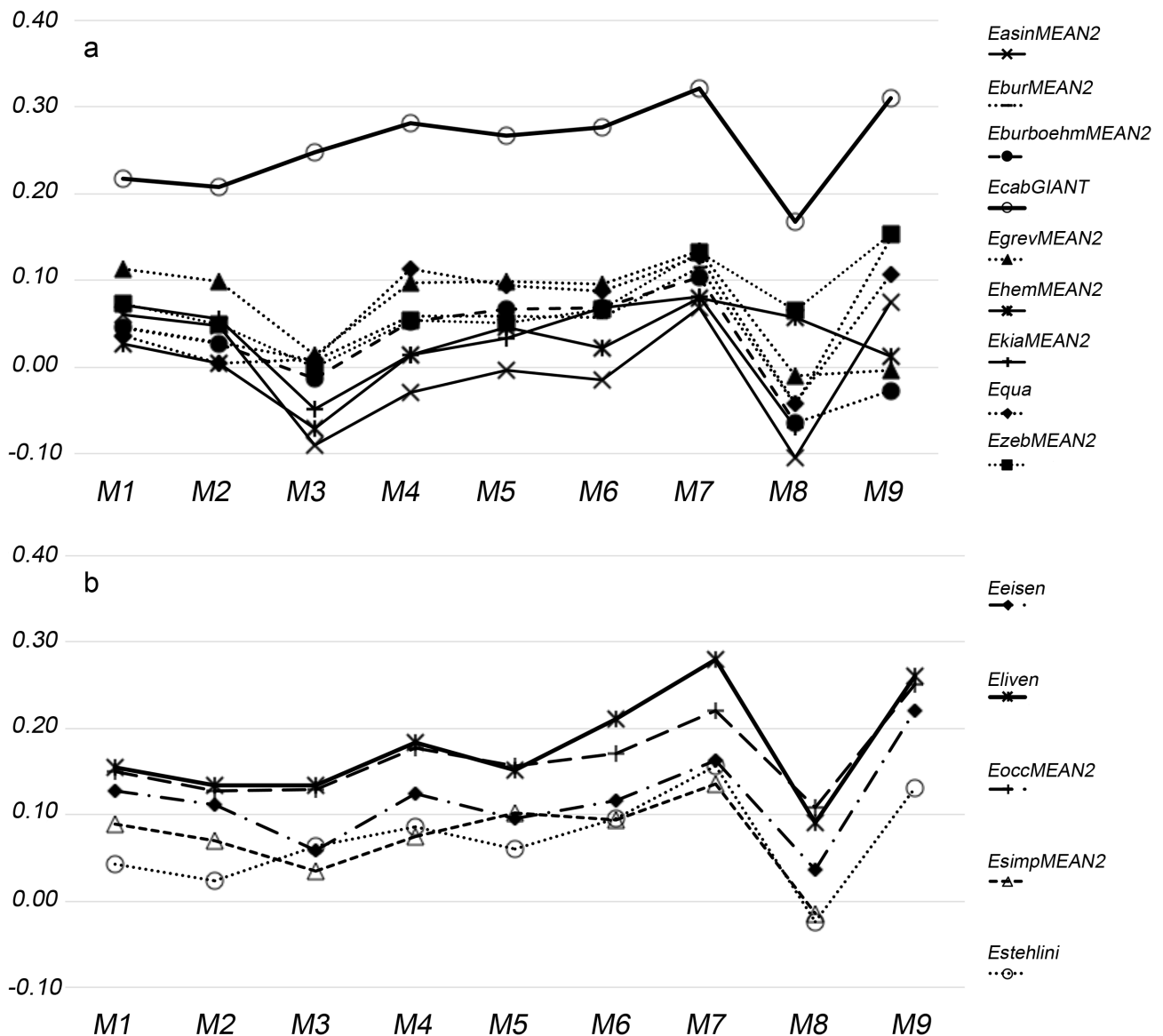


Fig. 8 - a) Extant *Equus* P1PHIII means, log10 ratios (Hoewenegg as Standard); b) fossil *Equus* P1PHIII log10 ratios (Hoewenegg as Standard).

Azzaroli (1982, 1989, 2000) provided a detailed discussion on the origin of Old World *Equus*, including interpretations that follow herein. The genus *Equus* originated in North America, and it was derived from the late Miocene genus *Dinohippus* which had already developed monodactyl limbs. The North American genus *Pliohippus* and South American genera *Onohippidium* and *Hippidion* had also evolved monodactyly. Azzaroli has through his various publications, but specifically in Azzaroli (2000) and Azzaroli & Voorhies (1993), consistently favored Pliocene *Equus* (*Dolichohippus*) *simplicidens* as the founding stock for Old World *Equus*. The Hagerman Horse Quarry from the Glens Ferry Fm., Idaho has the most abundant sample of *E. simplicidens* known and the extensive USNM sample has been used herein in our analysis of extant and fossil *Equus*. Azzaroli & Voorhies (1993) have reported that the oldest occurrence of *E. simplicidens* in the Glens Ferry Fm. is 3.7 m.y., while the age of the extensive Hagerman Horse quarry is just less than 3.4 Ma.

The Montopoli phalanges that we have analyzed herein are clearly the largest of our analytical sample. However, it should be made clear that the 2.55-1.85 Ma sample of *Equus eisenmannae* from Longdan (Linxia Basin, China) rivals the *E. cf. livenzovensis* phalanges from Montopoli, Italy in their size: basal skull length exceeds 590 mm (Wang & Deng, 2011). Azzaroli (1982) further noted that *Equus sanmeniensis* Teilhard & Piveteau, 1930, from the Nihowan, northern China (ca. 2.0 Ma) is yet another very large early Pleistocene species of *Equus* which is likely related to *E. cf. livenzovensis* and resembles extant *Equus grevyi*. Kenyan *Equus koobiforensis* (Eisenmann, 1983) recovered from below the KBS tuff (1.87 Ma; Feibel et al., 1989) is another early derived *Equus* that Azzaroli (1982, 1989, 2000) believes is closely related to *Equus* (*Dolichohippus*) *grevyi* and China *Equus sanmeniensis*. Azzaroli (1982) found that the Koobi Fora skull resembles extant *Equus* (*Dolichohippus*) *grevyi* and moreover concludes that *E. grevyi*, *E. sanmeniensis* and

E. koobiforensis represent a remarkably homogeneous assemblage of species ultimately derived from North American *Equus simplicidens*. It should be further noted that *Equus koobiforensis* may prove to be the junior synonym of *Equus oldowayensis*.

Recently, Alberdi & Palombo (2013) reviewed European Pleistocene stenorine horses. The species that they have included in this group are *Equus livenzovensis*, *Equus stenonis*, *Equus stehlini*, *Equus altidens*, the large-sized horses generally referred to as the so-called *Equus* ex gr. *Equus major* (*Equus bressanus*) and *Equus suessenbornensis*. With regards to the biochronology of stenorine *Equus* in Italy, they report in their Figure 2 the following chronologic ranges: *E. cf. livenzovensis*: 2.6-2.4 (Montopoli); *E. stenonis* 2.4-1.7; *E. stehlini* 1.8-1.6 (last two at Olivola and Tasso), *E. altidens* and *E. suessenbornensis* 1.6-0.6. *Equus livenzovensis* appears to be at the base of the radiation of this group.

Figure 9 herein reproduces Azzaroli's (2003) last version of the phylogeny of the genus *Equus* with geographical and stratigraphical distribution (modified from Azzaroli, 1995). This phylogeny takes into consideration the major lineages of North and South America, Eurasia, India and Africa and is a suitable starting point for further research aimed at study and analysis of the morphology of early Pleistocene Old

World *Equus*, the taxonomic context of the Old World *Equus* Datum, and the origin of extant Old World *Equus* clades. We appreciate Alberdi & Palombo's (2013) recent detailed contribution on the taxonomic contents, evolution and biochronology of European stenorine horses which advances our understanding of Old World *Equus* evolution in this regard.

CONCLUSIONS

Equus cf. *livenzovensis* first occurs in Italy and Southwest Russia 2.6 Ma and constitutes the regional *Equus* Datum. *Equus eisenmannae* is another very large horse that occurs 2.55-1.85 Ma at Longdan in the Linxia Basin, China. These species of *Equus* are stenorine horses of larger size than *Equus stenonis* sensu strictu. Our statistical analyses of A1P1HIII and P1P1HIII confirm the large size of *Equus* cf. *livenzovensis* and close size comparison to *Equus eisenmannae*. Our direct comparisons to North American *Equus simplicidens* derived from the Glenns Ferry Fm. Hagerman Horse fauna (ca. < 3.4 Ma) confirms Azzaroli & Voorhies (1993) conclusion that morphologically it represents a plausible ancestral stock for the Old World *Equus* Datum. Moreover, our comparisons based on the phalanges have revealed

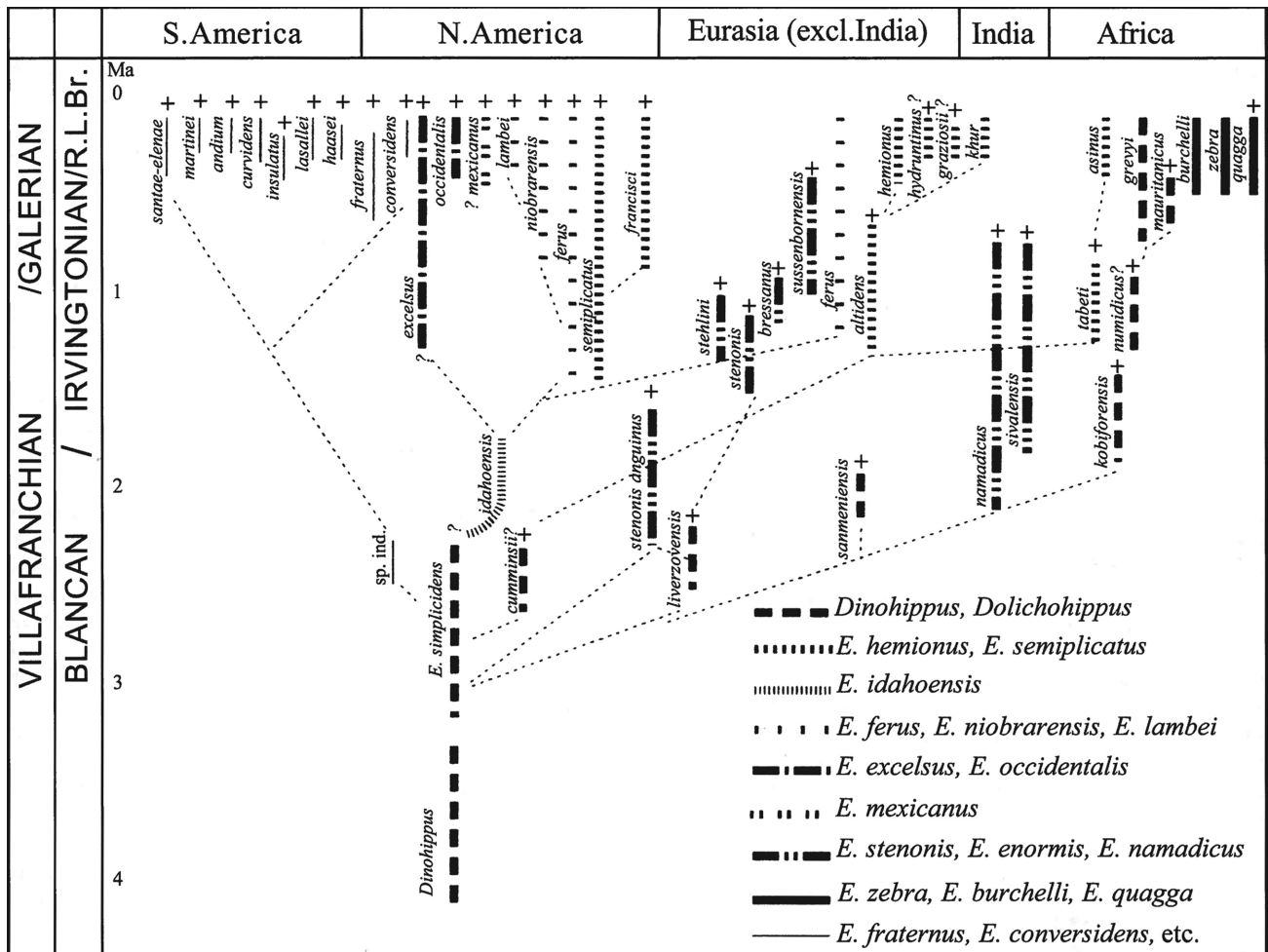


Fig. 9 - Azzaroli (2003; fig. 1: XIII) phylogeny of the genus *Equus* with geographical and stratigraphical distribution.

that *E. simplicidens* conforms in basic morphology to extant zebras, and mostly *E. grevyi*. Whereas a future analysis of skulls, dentitions and other skeletal elements is needed, we believe that African *E. oldowayensis*, *E. koobiforensis* and *E. grevyi* could well prove to be derived from stenorine horses with *E. simplicidens* representing the original North American stock. Our review of the literature together with our initial analysis herein opens questions about the efficacy of a single early Pleistocene *Equus* Datum and the monophyly of asses. Future analyses of North American Pliocene *Equus*, Eurasian stenorine horses and African fossil and extant *Equus* will be aimed at analyzing these relationships.

SUPPLEMENTARY ONLINE MATERIAL

All the Supplementary data of this work are available on the BSPI website at <http://paleoitalia.org/archives/bollettino-spi/>

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