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LARGE MAMMAL REMAINS FROM THE EARLY PLEISTOCENE SITE OF PODERE SAN LORENZO (PERUGIA, CENTRAL ITALY)

MARCO CHERIN[1*], BEATRICE AZZARÀ[1], MARZIA BREDA[2], ALBA BROBIA ANSOLEAGA[1,3], COSTANTINO BUZI[4], LUCA PANDOLFI[5] & FAUSTO PAZZAGLIA[6]

[1*]Corresponding author. Dipartimento di Fisica e Geologia, Università degli Studi di Perugia, Via A. Pascoli, 06123 Perugia, Italy. E-mail: marco.cherin@unipg.it, beatrice.azzara@gmail.com, alba.brobiaansoleaga@unipg.it
[2]Dipartimento di Studi Umanistici, Università degli Studi di Ferrara, Via Paradiso 12, 44121 Ferrara, Italy. E-mail: marzia.breda@unife.it
[3]Department of Geography, Universitat Autònoma de Barcelona, Carrer de la Fortuna s/n, 08193 Bellaterra, Barcelona, Spain.
[4]Dipartimento di Biologia Ambientale, Sapienza Università di Roma, P.le A. Moro 5, 00185 Roma, Italy. E-mail: costantino.buzi@uniroma1.it
[5]Dipartimento di Scienze della Terra, Università degli Studi di Firenze, Via G. La Pira 4, 50121 Firenze, Italy. E-mail: luca.pandolfi@unifi.it
[6]Int. Geo. Mod. srl, Via Fratelli Cairoli 24, 06125 Perugia, Italy. E-mail: fausto.pazzaglia@gmail.com

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Keywords: Early Pleistocene; Fossil mammals; Late Villafranchian; Tiber basin, Umbria.

*Abstract***.** Most of the research on fossil mammals from Umbria (central Italy) has been carried out in the southwestern branch of the Tiber basin, due to its paleontological richness. This portion of the basin extends from Perugia to Terni and corresponds to a well-defined half-graben filled with fluvial-lacustrine deposits.

The paleontological sample presented here was discovered in a sand and gravel quarry at Podere San Lorenzo, East of the town of Deruta. The stratigraphic succession exposed in the quarry is no longer visible, but we describe here a new outcrop (Palazzone), which is not far from Podere San Lorenzo and shows comparable facies associations. The two successions were deposited in a fluvial environment characterized by an average reduction of the hydrodynamic energy from the bottom upwards. They are referred to the Early Pleistocene Santa Maria di Ciciliano Subsyntheme (Madonna dei Bagni Lithofacies).

Large mammal remains are attributed to *Mammuthus* cf. *meridionalis* (Nesti, 1825), *Stephanorhinus etruscus* (Falconer, 1859), *Equus stenonis* Cocchi, 1867, *Leptobos* cf. *etruscus* (Falconer, 1868), *'Pseudodama' nestii* (Azzaroli, 1947), and *Sus strozzii* Forsyth Major, 1881. Some hyena coprolites are also reported. The assemblage is typical of the early Late Villafranchian Land Mammal Age and can be referred to the Olivola/Tasso Faunal Units (about 2.0–1.8 Ma). This is in agreement with the alleged age of some other assemblages found in the southwestern branch of the Tiber basin (e.g., Torre Picchio, Villa San Faustino, Colle Sant'Andrea, Pantalla).

INTRODUCTION

During the Pliocene and Pleistocene, the paleogeography of central Italy was characterized by a set of NW-SE trending *én echelon* grabens whose genesis is due to the eastward migration of the extensional deformation related to the opening of the Tyrrenian Sea. This caused the opening of basins in the western part of the Peninsula, where marine sedimentation occurred during the Pliocene and the beginning of the Pleistocene; at the same time, continental deposits started to fill the extensional basins located in the eastern part, close to the recently-formed Apennine Chain (Pascucci et al. 1999; Collettini et al. 2006). Consequently, Plio-Pleistocene marine sediments today crop out in the western part of Umbria, while continental deposits are mostly found in the central and eastern portions of the Region (Ambrosetti et al. 1987).

The Tiber basin (Fig. 1) is the largest intermontane continental basin along the Apennines. It is approximately 1800 km^2 wide and extends from North to South describing an "upside-down Y" shape, splitting in a southeastern and a southwest-

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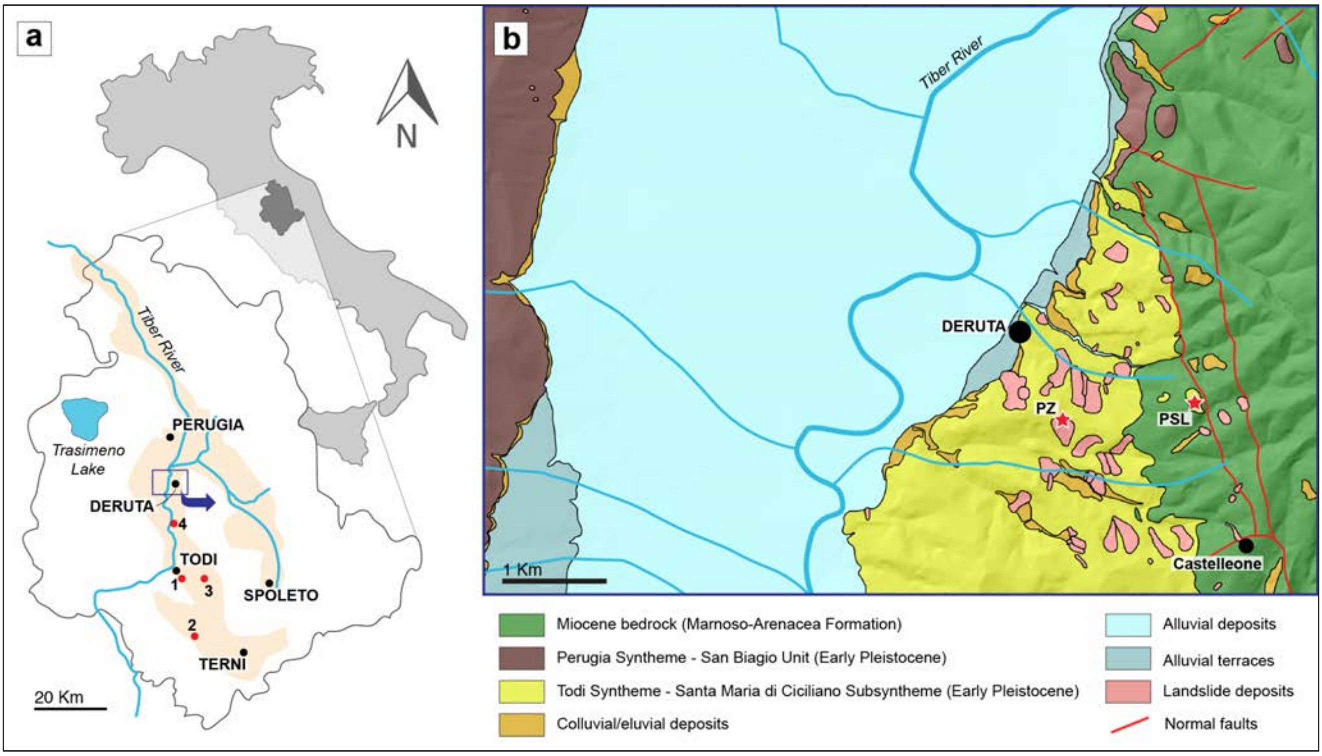


Fig. 1 - a) Geographic location of the study area. The Tiber Basin is highlighted in light orange along the middle part of Umbria. Red points refer to the paleontological sites in Tab. 1: 1, Cava Toppetti; 2, Torre Picchio; 3, Villa San Faustino and Colle Sant'Andrea; 4, Pantalla. b) Geological map superimposed on a digital elevation model of the study area. PSL, Podere San Lorenzo; PZ, Palazzone.

ern branch south of Perugia (Basilici 1997). The first geological observations on the basin date back to the beginning of the 20th century, but for a long time it has been believed that the basin was represented by a single huge lake, called the "Tiberino Lake" (Lotti 1917). Conversely, research conducted in the last 40 decades (Conti & Girotti 1977; Ambrosetti et al. 1987; Basilici 1997; Pucci et al. 2014) as well as several geological mapping projects of the Umbria Region, demonstrate that the Tiber basin was a complex depositional system deriving from the coalescence of smaller lacustrine, palustrine, and fluvial environments alternating in space and time.

Most of the fossils of Plio-Pleistocene mammals in Umbria have been recovered since the 19th century from continental deposits (gravel, sand, clay, lignite, calcareous tufa) that can be related to the Tiber basin (Cherin 2013). Even the famous French biologist Georges Cuvier, the putative "father" of vertebrate paleontology and comparative anatomy, cites some fossil proboscidean and rhinoceros remains from the Tiber basin in his book *Recherches sur les ossemens fossiles de quadrupèdes* (Paris, 4th edition, 1834).

The majority of recent scientific papers on Umbrian fossil mammals concerns the southwestern branch of the Tiber basin, thanks to the outstanding richness of paleontological sites scattered in this area (Fig. 1, Tab. 1). This portion of the basin extends from the SE of Perugia to Terni and is delimited by Mount Peglia and the Narni-Amelia Ridge to the West and by the Martani Mountains to the East. It corresponds to a well-defined half-graben filled with alluvial-lacustrine deposits referred by Basilici (1997) to four lithostratigraphic units: (1) the Fosso Bianco Unit, mainly characterized by silty, clayey deposits, ascribable to a large deep lake system, chronologically referred to the Gauss-Matuyama (i.e., Pliocene-Pleistocene) boundary (Abbazzi et al. 1997); (2) the Ponte Naja Unit, cropping out in the surroundings of the town of Todi and composed principally of gravel and sandy gravel bodies and clayey sandy silts formed on the distal part of an alluvial fan located along a lake margin around 2.15–2.10 Ma (Napoleone et al. 2003); (3) the Santa Maria di Ciciliano Unit (Early Pleistocene), unconformably overlying the Fosso Bianco Unit and composed of silty clays and clayey silts deposited in alluvial plain environments, alternating with sand lithosomes referred to meandering fluvial channels; (4) the Acquasparta

Tab. 1 - Selected Early Pleistocene localities with fossil mammal remains in the southwestern branch of the Tiber basin (Umbria, central Italy). FU, Faunal Unit; LMA, Land Mammal Age. The approximate ages of the FUs are from Rook & Martínez-Navarro (2010) and Nomade et al. (2014).

Cava Toppetti	
Mammal assemblage	*Stephanorhinus* cf. *etruscus, 'Pseudodama'* cf. *rhenana, Procapreolus* sp., *Leptobos* sp., *Apodemus dominans*
Stratigraphy	Tiberino Supersyntheme → Todi Syntheme → Fosso Bianco Subsyntheme
Biochronology	Middle Villafranchian LMA → Coste San Giacomo FU (~2.1 Ma)
References	Abbazzi et al. (1997)
Torre Picchio	
Mammal assemblage	*Canis* sp., *?Baranogale* sp., *Homotherium* sp., *?Mammuthus meridionalis*, *Equus* cf. *stenonis*, *Stephanorhinus* cf. *etruscus*, *Sus strozzii*, *Eucladoceros dicranios* vel *ctenoides*, '*Pseudodama' nestii*, Cervidae indet., *Leptobos* cf. *etruscus*, Bovidae indet., *Castor* sp., *Mimomys medasensis*, *Prolagus* sp., *Oryctolagus* cf. *lacosti*
Stratigraphy	Tiberino Supersyntheme → Todi Syntheme → Santa Maria di Ciciliano Subsyntheme
Biochronology	Late Villafranchian LMA → ?Olivola FU (~1.9 Ma)
References	Girotti et al. (2003)
Villa San Faustino	
Mammal assemblage	*Megantereon cultridens*, *Leptobos* sp., *Mammuthus meridionalis*, *Equus stenonis*, *Pseudodama* sp., '*Pseudodama' nestii*, *Eucladoceros* sp., *Stephanorhinus etruscus*, *Sus strozzii*, Cervidae indet.
Stratigraphy	Tiberino Supersyntheme → Todi Syntheme → Santa Maria di Ciciliano Subsyntheme
Biochronology	Late Villafranchian LMA → Tasso FU (~1.8 Ma)
References	Sardella et al. (1995)
Colle Sant'Andrea	
Mammal assemblage	*Pachycrocuta* cf. *brevirostris*, Cervidae indet., '*Pseudodama'* sp., *Leptobos* cf. *vallisarni*, *Castor* sp.
Stratigraphy	Tiberino Supersyntheme → Todi Syntheme → Santa Maria di Ciciliano Subsyntheme
Biochronology	Late Villafranchian LMA → Tasso FU (~1.8 Ma)
References	Sardella et al. (1995)
Pantalla	
Mammal assemblage	*Apodemus* cf. *dominans*, *Canis etruscus*, *Vulpes* sp., *Lynx issiodorensis valdarnensis*, *Acinonyx pardinensis*, *Lutraeximia umbra*, *Sus strozzii*, '*Pseudodama' nestii*, *Leptobos merlai*, *Equus* sp., *Mammuthus* cf. *meridionalis*
Stratigraphy	Tiberino Supersyntheme → Todi Syntheme → Santa Maria di Ciciliano Subsyntheme
Biochronology	Late Villafranchian LMA → Olivola/(Tasso?) FUs (~2.0-1.8 Ma)
References	Gentili et al. (1997), Cherin et al. (2013a; 2013b; 2014a; 2014b; 2016; 2018; 2019)

Unit (Early Pleistocene), represented by continental carbonates (i.e., calcareous tufa), deposited within shallow-lake and wetland environments. The most recent Umbrian geological mapping projects at a scale of 1:10000 have adopted the lithostratigraphic units described by Basilici (1997) but have integrated them into the UBSU (Unconformity Bounded Stratigraphic Units) system, widely used in continental contexts (Salvador 1994). As a consequence, the Fosso Bianco, Santa Maria di Ciciliano, and Acquasparta Units are currently classified as subsynthemes of the Todi Syntheme, while the Ponte Naja Unit is considered as a lithofacies of the Fosso Bianco Subsyntheme (Regione Umbria 2013).

Apart from the Cava Toppetti assemblage (Tab. 1), virtually all the mammal remains found to date in the southwestern branch of the Tiber basin come from fluvial deposits of the Santa Maria di Ciciliano Subsyntheme. This work offers a further contribution to the knowledge of the paleontological, biochronological, and paleoenvironmental features of this area of the basin thanks to the description of a new mammal assemblage from the locality of Podere San Lorenzo (PSL) as well as of a new stratigraphic section (Palazzone; PZ) of the Santa Maria di Ciciliano Subsyntheme outcropping nearby (Fig. 1).

The Palazzone outcrop and notes on taphonomy.

In the area between Perugia and Todi (Fig. 1), the Tiber River course is currently set along the

Tiber basin. Between Deruta and Todi, Cencetti (1990) recognizes evidence of Quaternary tectonic activity involving both the pre-Pleistocene bedrock and Pleistocene deposits. Tectonics mainly occurs through the action of normal faults with *én echelon* arrangement, which systematically drop the western part of the whole structure and confer a terraced morphology to the eastern side of the Tiber River Valley. There are also normal NE-dipping antithetic faults, which locally determine a horst and graben structure, typical of the deformations in an extensional tectonic regime (Cencetti 1990).

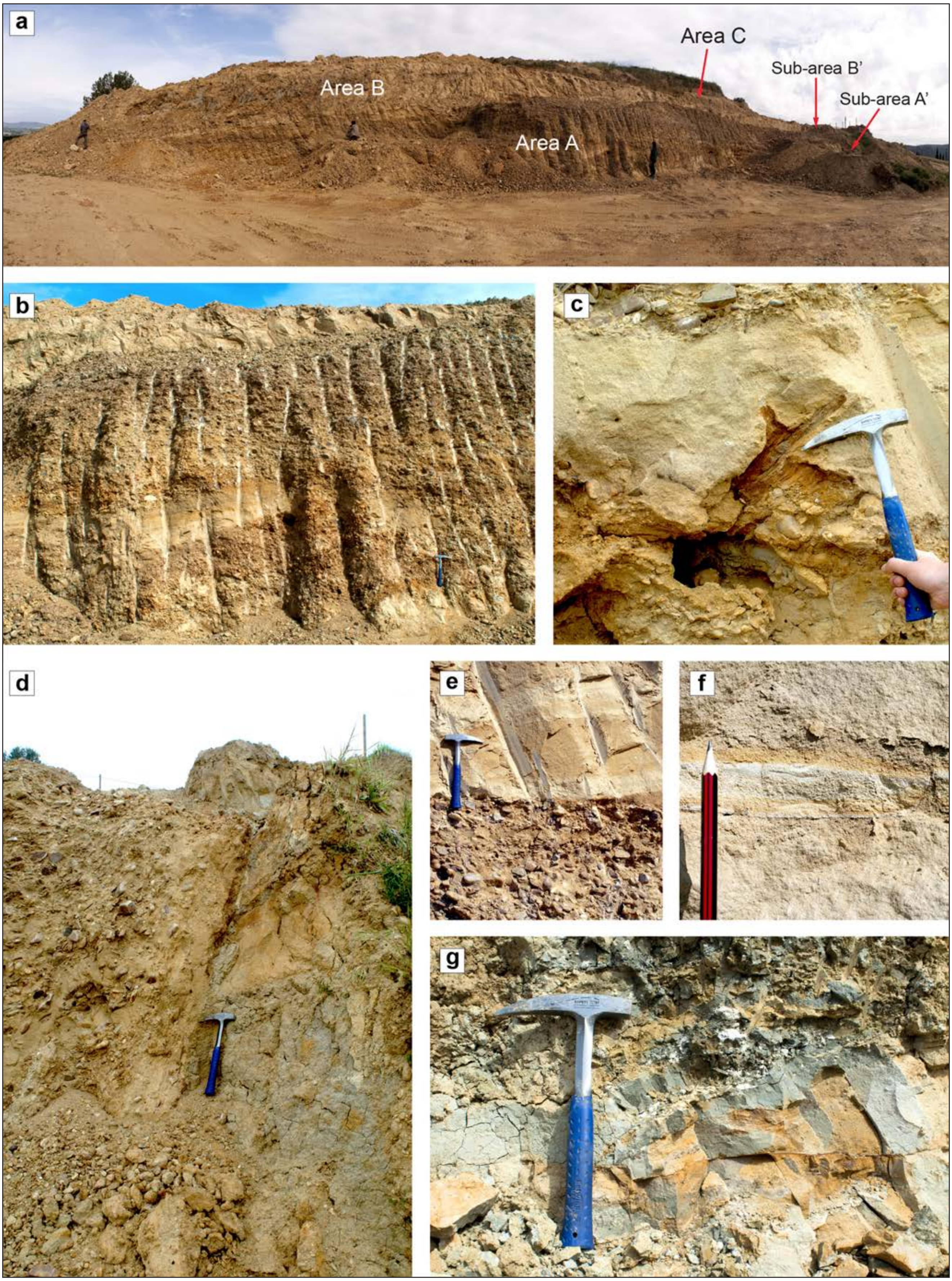
Much of the Deruta area (Fig. 1) is occupied by Pleistocene-Holocene alluvial deposits. These sediments crop out mainly in the northwestern part of the territory and form the present alluvial plain of the Tiber River. Conversely, on the hills SE of Deruta, Pleistocene deposits referred to the Santa Maria di Ciciliano Subsyntheme are mostly found (Fig. 1).

The paleontological collection here described was discovered in the 1990s in a sand and gravel quarry at PSL, East of Deruta (42°58'32.92" N - 12°26'20.87" E). Unfortunately, the quarry is currently abandoned and completely covered by vegetation, so it is not possible to describe the local stratigraphic succession, but only to make qualitative considerations based on excavation notes and photographs taken during previous surveys. However, a new section (PZ) has been identified not far from PSL (Fig. 1). The two sites show facies associations that are almost completely comparable, as confirmed by Cencetti's (1990) descriptions.

The PZ outcrop is divided into three areas, A-B-C (in ascending order), corresponding to some artificial walls excavated during slope consolidation operations (Fig. 2a). Area A develops in the West-East direction for about 30 m and for a height of about 3 m. The predominant lithology is represented by unsorted and clast-supported conglomerates organized in tabular bodies (Fig. 2b), with poor sandy matrix. The pebbles are all rounded and heterometric (centimeter to decimeter size), with a slight imbrication indicating a prevalent NE-SW paleocurrent in a high-energy hydrodynamic regime. The clasts are predominantly arenaceous, although carbonate and chert pebbles are also observed. These latter have a characteristic blackish color, an advanced state of alteration, and often a thin external oxidation reddish patina. These black pebbles are mentioned by Cencetti (1990) as peculiar to the conglomerates found in this area. Conglomerate bodies host sand lenses of various sizes (Fig. 2b), often showing cross lamination. Fossil plant remains are found in both lithologies, in the form of small branches and roots in the sands and larger fragments of branches in the conglomerates. In the eastern part of Area A, we discovered a fossil branch disposed obliquely (205/15 direction relative to the wall), with the lower part lying in conglomerates and the upper part in sands (Fig. 2c). Probably the branch, carried by the water, was embedded obliquely into the gravel bottom of the river and was then covered by a subsequent sandy deposit. This demonstrates the high dynamism of the river environment, which, in a relatively short time (i.e., less than the time required for decomposition, fragmentation or removal of the branch by the current), has decreased hydrodynamic energy, as evidenced by the conglomerate-sand transition. The fossil branch also confirms the prevalent NE-SW direction of the paleocurrent, as it is possible to observe that on its left (NE) side, the sand granulometry is finer and more homogeneous than that on the right (SW) side, where larger clasts were "trapped" by the same branch. East of Area A, in Sub-area A' (length 8 m, height 3 m), we detect a normal fault (dip notation 228/63) that puts in lateral contact the conglomerates of Area A with a massive fine-grained sand (Fig. 2d). A fault with similar characteristics is reported and mapped by Cencetti (1990) very close to PZ.

The contact between Area A and Area B (length 50 m, height 1.8 m) is marked by an erosional surface that separates the conglomerates from the overlying deposits (Fig. 2e). The latter consist mainly of a tabular fine-grained sandy body, without channel geometry, rare cross laminations, and

Fig. 2 - Palazzone outcrop at Deruta (Perugia, Italy). a) Overall view of the outcrop, detailing the areas described in the text. b) Detail of Area A: conglomerate with sandstone lens in the middle. c) Remains of a fossil branch embedded obliquely between a conglomerate (below) and a sand lens (above). d) Normal fault in Sub-area A' separating a conglomerate (left) and a fine sandstone (right). e) Stratigraphical contact between conglomerates (Area A, below) and sandstone (Area B, above). f) Thin layer of whitish claystone with bottom and top reddish portions, within the massive sandstone of Area B. g) Altered fine sandstone and claystone in Area C.


a
Area C
Sub-area B'
Sub-area A'
Area B
Area A
b
c
d
e
f
g

less abundant fossil plant remains. The sedimentological homogeneity of this body is interrupted at different heights by three 4-5 cm thick layers of grey-whitish laminated clay, delimited at the bottom and the top by reddish horizons. The three layers are related to short periods of stasis in river flow and/or periods of emersion, as suggested by the oxidation evidence in the reddish portions. The Sub-area B', to the East of the main wall and perpendicular to it, is crossed by the same normal fault identified in Sub-area A'. A thin cataclasite level consisting of red-blackish coated gravels, is visible along the fault plane.

Area C is about 50 m in length and 2.5 m in height. The outcrop is mainly composed of fine sands and silts with high clay content and poor presence of pebbles and it is crossed by numerous vertical fractures which are sub-parallel to the main fault seen in Sub-areas A'-B'. Bedding attitudes of these fractures are progressively changing from SW-NE to W-E, with a dip in direction from 180 to 230 degrees towards the fault.

The general sedimentological characteristics of the PZ and by extension, PSL sites can be referred to a fluvial depositional environment characterized by an average reduction of the hydrodynamic energy from the bottom upwards, as evidenced by the decreasing granulometry trend from Area A to C. Sand lenses within the conglomerate bodies can be related to periodic events of energy reduction and/or river bar formation. The stratigraphic discontinuity between Area A (predominantly conglomerate) and B (predominantly sands) suggests a more or less prolonged interruption of the clastic input and a subsequent recovery of solid transport, although with lower hydrodynamic energy. The transition between Areas B and C is more gradual and it records a progressive reduction in granulometry, reaching fine sand and silt size at the top. Clear evidence of pedogenesis (root traces, CaCO3 nodules, reddish portions due to oxidation processes) characterize the upper part of the sequence, testifying to more prolonged events of subaerial exposure. This may correspond to a transition towards an alluvial plain environment.

Although we did not participate in the collection of the mammal fossils from PSL, we can reasonably state that they have been recovered from the lower part of the succession. Most likely, not all fossils come from the same level, as suggested by their different color patterns and preservation. Some of the specimens, characterized by dark color with reddish and rusty coating and/or mottles, probably come from conglomerates. This is also supported by the advanced fragmentation and surface abrasion of the remains, related to transport in a high-energy regime. Other fossils, on the contrary, show brownish-yellowish color, smaller average dimensions and good state of preservation, suggesting that they have been preserved within finer grained deposits formed in lower energy context. In particular, they probably come from sand lenses within the conglomerate bodies. In fact (1) some finds still retain traces of sedimentary matrix, whose grain size and color are really similar to those of the sands observed in Area A at PZ; (2) these sands are probably deposited in fluvial bars (ideal contexts for the rapid burial and conservation of the remains; see plant macro-fossils described for Area A); (3) the tabular sandy complex observed in the higher part of the PZ section presents finer granulometry than that of the sediment associated with the fossil bones.

MATERIALS AND METHODS

Fossil preparation. Prior to the analytic study, fossils described herein were prepared using the following products and procedures:

For gluing and consolidation, we used solutions of Paraloid^{TM} B-72 mixed with acetone following Davidson & Brown (2012). In particular, we used Paraloid as "stock adhesive" (concentration 50%) to glue small to medium-sized fossil fragments (see below for large-sized specimens), as "dilute consolidant" (concentration ~5%) for the first consolidation sessions, and as "stock consolidant" (concentration ~17%) for the final consolidation session.

For gluing large bone fragments (e.g., proboscidean long bones), we used UHU® extra All-Purpose Adhesive (mixture of methyl acetate and ethanol).

We chose to fill damaged areas with fine-grained plaster only when we found that these fractures jeopardized the stability of the specimens.

Paleontology. Identification of paleontological specimens is based on anatomical feature descriptions and morphological and morphometric comparative analysis. All measurements are taken with digital calipers and are given with a precision of 0.1 mm. Morphological and morphometric data used for comparison are from the cited literature.

The biochronological framework is based on correlations of the Villafranchian Land Mammal Age (LMA) in its most recent definition (Rook & Martínez-Navarro 2010; Martínez-Navarro et al. 2015) and the late Cenozoic and Quaternary time scale (Cohen & Gibbard 2016).

All specimens analyzed in this work are curated in the SBAU.

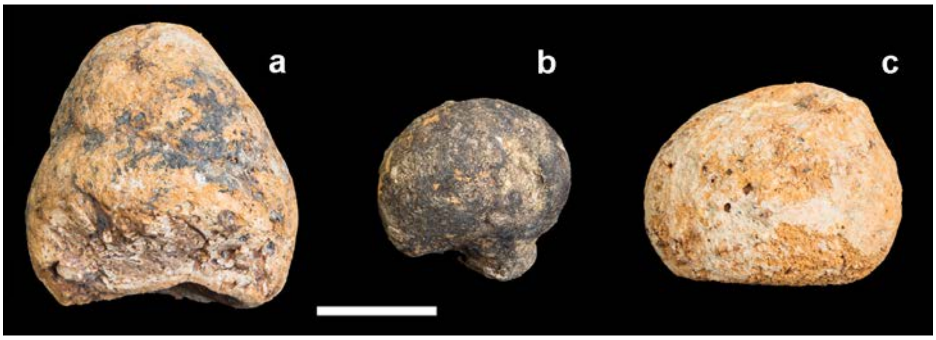


Fig. 3 - Hyaenid coprolites from Podere San Lorenzo (Italy). a) SBAU 153505; b) SBAU 153506; c) SBAU 153529. Scale bar: 3 cm.

Institutional abbreviations. IGF, Museo di Storia Naturale, Sezione di Geologia e Paleontologia, Università di Firenze; NHMB, Natural History Museum, Basel; SBAU, former Soprintendenza per i Beni Archeologici dell'Umbria (now Soprintendenza Archeologia, Belle Arti e Paesaggio dell'Umbria), Perugia.

SYSTEMATIC PALEONTOLOGY

Class **MAMMALIA** Linnaeus, 1958
Order **Carnivora** Bowdich, 1821
Family Hyaenidae Gray, 1821
Genus and species indet.

Fig. 3

Referred material: Three coprolites (SBAU 153505, SBAU 153506, SBAU 153529).

Description. The PSL collection includes three coprolites, which show a rounded/ovoid shape and a relatively flat or slightly concave side, corresponding to the contact area with the adjacent fecal pellet. Bone splinters and cavities left by the decomposition of organic material are well visible in SBAU 153505 and SBAU 153529 (Fig. 3).

The maximum length (measured by placing the caliper between the flat/concave surface and the opposite vertex) and width (measured perpendicular to the max length) of the three specimens are as follows: SBAU 153505 - 30.0 x 37.0 mm; SBAU 153506 - 50.8 x 52.2 mm; SBAU 153529 - 37.9 x 47.3 mm.

Discussion. The overall morphology of the PSL coprolites resembles that of droppings of the recent African *Crocuta crocuta* (Brain 1981). Two bone-cracking hyaenids are reported in the European Early Pleistocene: *Pliocrocuta perrieri* (late Pliocene–Early Pleistocene; about 4.2–2.0 Ma) (Turner et al. 2008; Vinuesa et al. 2014) and *Pachycrocuta brevirostris* (Early–Middle Pleistocene; about 2.0–0.8 Ma) (Turner et al. 2008; Madurell-Malapeira et al. 2010). Unfortunately, it is not possible to assign the PSL coprolites to one or the other species on the basis of morphology alone. However, the dimensions of the analyzed specimens fit those of *Pa. brevirostris* droppings from different European sites (Ceyssaguet, France; Trlica, Serbia; Untermassfeld, Germany) (Argant & Bonifay 2011).

Order **Proboscidea** Illiger, 1811
Family Elephantidae Gray, 1821
Genus *Mammuthus* Brookes, 1828

Mammuthus* cf. *meridionalis (Nesti, 1825)

Figs 4-5

Referred material: Molar fragments (SBAU 153509, SBAU 153521, SBAU 153540, SBAU 153549, SBAU 153549bis), tusk fragment (SBAU 153543), distal condyle of femur (SBAU 153541), fragments of femur diaphysis (SBAU 153542, SBAU 153553, probably belonging to the same bone), left trapezoid (SBAU 153546), fragmented proximal epiphysis of left tibia (SBAU 153547), fragmented proximal diaphysis of right femur (SBAU 153550), fragmented proximal diaphysis of right humerus (SBAU 153548), undetermined fragments of limb bone diaphyses (SBAU 153551, SBAU 153552, SBAU 153554, SBAU 153554bis).

Description. The available proboscidean material is severely damaged and incomplete, making any taxonomic attribution extremely difficult. The preserved fragments of limb bones and the left trapezoid SBAU 153546 are large and massive (Fig. 4). Specimen SBAU 153543 is a small and damaged tusk fragment (Fig. 5). Schreger lines are clearly visible thanks to the natural break of the fragment along the transverse plane; the width of Schreger angles is around 85 degrees. The most complete molar fragment is SBAU 153549bis, which preserves four almost complete lamellae. We measured the enamel thickness in various positions along

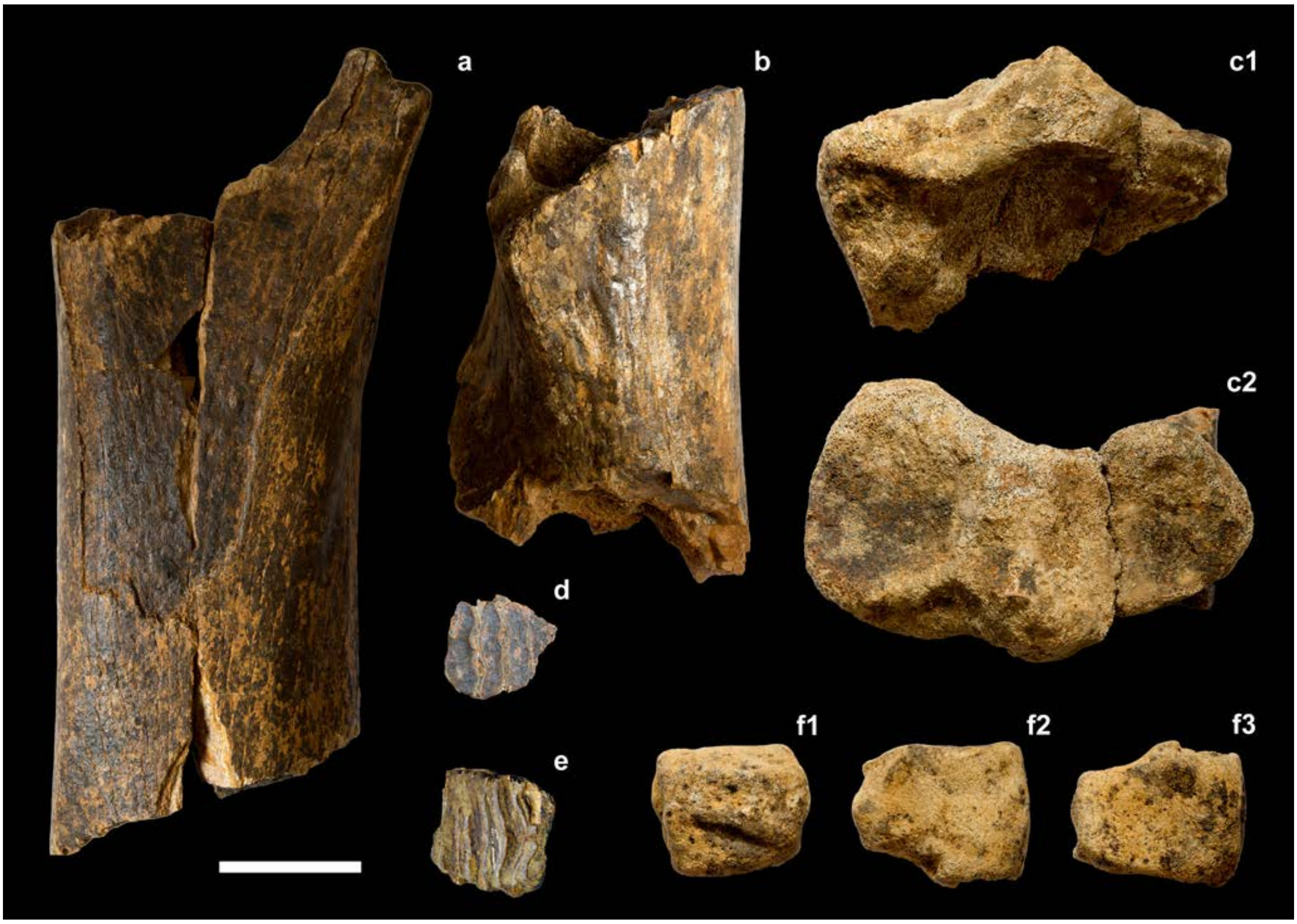


Fig. 4 - *Mammuthus* cf. *meridionalis* from Podere San Lorenzo (Italy). a) Proximal diaphysis of right femur (SBAU 153550) in anterior view. b) Proximal diaphysis of right humerus (SBAU 153548) in anterior view. c) Proximal epiphysis of left tibia (SBAU 153547) in anterior (c1) and dorsal (c2) views. d) Molar fragment (SBAU 153549) in occlusal view. e) Molar fragment (SBAU 153549bis) in occlusal view. f) Left trapezoid (SBAU 153546) in anterior (f1), dorsal (f2), and ventral (f3) views. Scale bar: 10 cm.

the occlusal lamellar surface following Palombo & Ferretti (2005) and we obtained an average value of 3.8 mm. A similar average thickness (3.7 mm) was obtained for the small tooth fragment SBAU 153521.

Discussion. Three proboscideans occur in Europe in the Early Pleistocene: *Anancus arvernensis*, *Mammuthus meridionalis*, and *Palaeoloxodon antiquus*. The gomphothere *A. arvernensis* is a common element of Pliocene mammal assemblages and became extinct in the Early Pleistocene at the beginning of the Late Villafranchian (Palombo & Ferretti 2005). However, the cheek tooth morphology of this species, characterized by lophs formed by pairs of thick conical cusps, does not fit that observed in the PSL specimens, which clearly show the typical lamellar morphology of the Elephantidae. *Mammuthus meridionalis* occurs in Europe during the entire Early Pleistocene, whereas *P. antiquus* appears in the latest Early Pleistocene (Galerian LMA) and survives until the Late Pleistocene (about 40 ka) (Palombo & Ferretti 2005; Stuart 2005). The two species are relatively similar in body size (Larramendi 2016). Although fragmented, we could take some measurements on two postcranial elements from PSL, the left trapezoid SBAU 153546 (width: 89 mm, depth: +112.5 mm, height: 77 mm) and the femur fragment SBAU 153550 (mid-shaft width: 182 mm, mid-shaft depth: 117 mm). The dimensions of both bones fall into the range of *M. meridionalis* (trapezoid - width: 72–99 mm, depth: 100–150 mm, height: 61–83 mm; femur - mid-shaft width: 120–192 mm, mid-shaft depth: 90–133 mm) and *P. antiquus* (trapezoid - width: 71–100 mm, depth: 140–144 mm, height: 70–86 mm; femur - mid-shaft width: 116–242 mm,

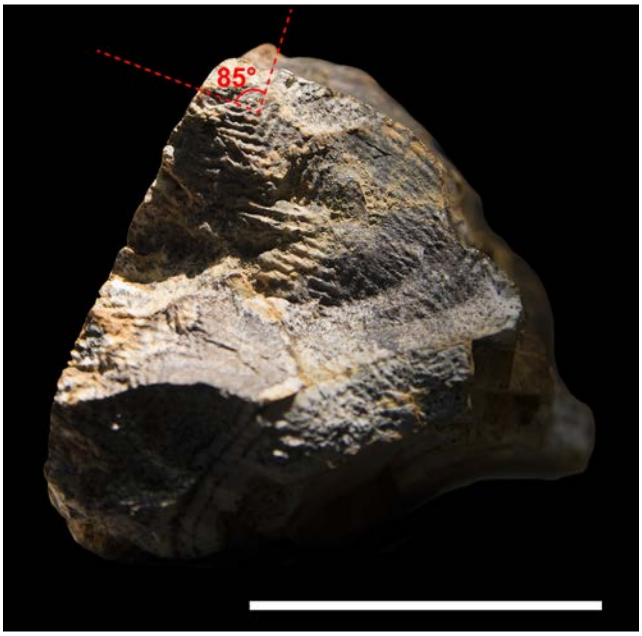


Fig. 5 - *Mammuthus* cf. *meridionalis* from Podere San Lorenzo (Italy). Tusk fragment (SBAU 153543) photographed with side lighting to highlight the Schreger lines. Values of about 85 degrees can be measured for the outer Schreger angles. Scale bar: 3 cm.

mid-shaft depth: 86–147 mm) (comparative data from Ferretti 1998 and Larramendi et al. 2017). However, Schreger angles measured on the tusk fragment SBAU 153543 are characteristic of the genus *Mammuthus* (Palombo & Villa 2001). Similarly, the average enamel thickness of the PSL molar fragments agrees with the highest values recorded for *M. meridionalis* and is significantly higher than those of *P. antiquus* (Palombo & Ferretti 2005). For these reasons, considering the fragmentary nature of the available sample, it is here referred to *Mammuthus* cf. *meridionalis*.

Order **Perissodactyla** Owen, 1848
Family Rhinocerotidae Gray, 1821
Genus *Stephanorhinus* Kretzoi, 1942

Stephanorhinus **sp.**

Fig. 6a-c

Referred material: Fragment of upper tooth and fragment of lower tooth (SBAU 153507), fragment of lower tooth (SBAU 153513), left m1 (SBAU 153514), left m2 (SBAU 153515).

Description. A few isolated and worn down teeth are included in the studied material. Length of the lower molars SBAU 153514 and 153515 is reported in Tab. 2. The preservation of the specimens and the absence of diagnostic morphological characters do not allow a specific taxonomic attribution.

Stephanorhinus etruscus (Falconer, 1868)

Fig. 6d-g

Referred material: Right M3 (SBAU 153510), left mandibular ramus with m1-m3 (SBAU 153511), left fragmentary maxilla with M2-M3 and right fragmentary maxilla with M1-M3 (SBAU 153516), left mandibular ramus with p4-m3 (SBAU 153517).

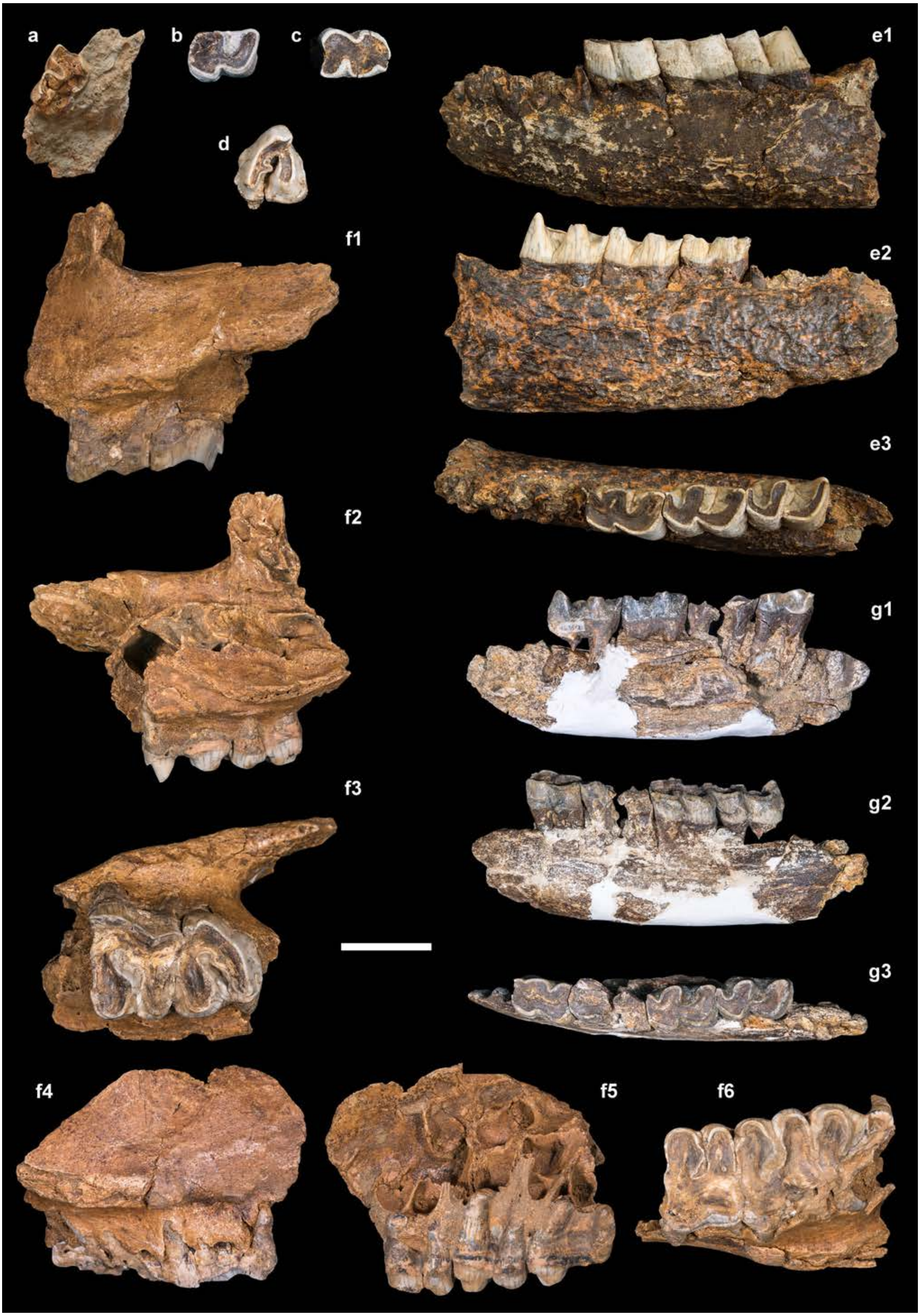
Description. The measurements are summarized in Tabs 2 and 3.

The isolated M3 SBAU 153510 (Fig. 6d) is relatively small (Tab. 3) and well preserved. It displays a mesial and a distal cingulum, a crochet, and weak accessory folds. The protocone is not constricted, the paracone fold is weak, and the parastyle is prominent.

The mandibular ramus SBAU 153511 (Fig. 6e) preserves the molars and the roots of the premolars. The surface of the bone is eroded and the ventral border of the ramus is gently convex. A mesial cingulum is present on the molars, a vestibular cingulum is present on the anterior loph of m2 and m3, and a weak lingual cingulum is present below the base of the posterior lingual valley on m2. The posterior lingual valley on m2 and m3 is V-shaped, the anterior lingual valley on m3 is broad V-shaped. The vestibular groove on the molars stretched the neck and is shallow on m2 and m3.

The left and right maxillae SBAU 153516 (Fig. 6f) belong to the same old individual. The M1s and M2s are heavily worn, the internal folds and

Fig. 6 - (pag. 498) Rhinoceros remains from Podere San Lorenzo (Italy). a-c) *Stephanorhinus* sp.: (a) fragment of lower tooth embedded in sediment (SBAU 153513); (b) Left m1 (SBAU 153514) in occlusal view; (c) Left m2 (SBAU 153515) in occlusal view. d-g) *Stephanorhinus etruscus*: (d) Right M3 (SBAU 153510) in occlusal view; (e) Left mandibular ramus with m1-m3 (SBAU 153511) in labial (e1), lingual (e2), and occlusal (e3) views; f) Left fragmentary maxilla with M2-M3 in labial (f1), lingual (f2), and occlusal (f3) views and right fragmentary maxilla with M1-M3 in labial (f4), lingual (f5), and occlusal (f6) views (SBAU 153516); g) Left mandibular ramus with p4-m3 (SBAU 153517) in labial (g1), lingual (g2), and occlusal (g3) views. Scale bar: 5 cm.


a
b
c
d
e1
e2
e3
f1
f2
f3
g1
g2
g3
f4
f5
f6

Specimen/Locality	Ltot	Lm	Lp	p2	p3	p4	m1	m2	m3
SBAU 153511	*220*	127.5	*95*	-	-		39.7	42.2	44.0
SBAU 153514	-	-	-	-	-	-		43.4	-
SBAU 153515	-	-	-	-	-	-	38.1	-	-
SBAU 153517	-	123.7	-	-	-	34.6	39.7	38.8	40.9
Stephanorhinus etruscus									
Senèze	218.0–222.0	122.1–122.7	96.0–96.4	25.7–23.3	31.3–38.65	35.1–34.4	40.8–45.3	41.6–43.2	42.6–43.2
Valdarno	-	-	-	27.2–30.4	32.3–39.6	34.7–39.6	35.2–43.7	40.3–46.0	41.1–48.4
Monte delle Piche	*240*	*135*	*105*	36.4	31.8	36.0	43.6	46.3	45.6
Valdarno	211–225	118–139	92–104	-	-	-	-	-	-
Pietrafitta	223.3	127.1	98.3	28.7	34.2–35.0	37.2–39.3	39.4–41.9	43.9–46.1	44.2–47.3
Pietrafitta	225.2	126.0	103.2	-	-	-	-	-	-
Pietrafitta	237.45	132.0	104.3	30.2	37.1	38.2	43.3	44.6	41.8
Pietrafitta	225.8	127.6	99.8	27.8	33.1–36.4	38.2–38.6	41.0–41.5	43.3–43.4	44.0–46.4
Capitone	*226*	*230*	*93*	-	-	-	-	-	-
Various localities	210.0–251.5	121.0–143.0	87.0–108.0	25.0–33.0	31.5–37.0	35.0–39.5	37.0–43.0	40.5–47.5	41.0–50.0
Stephanorhinus hundsheimensis									
Ceyssaguet	231.7	129.5	103.3	29.6	34.5	34.9	40.9	-	-
Vallonnet	-	-	-	27.4–32.3	31.2–35.6	34.0–37.0	38.3–47.35	40.2–47.2	45.1–45.7
Tour de Grimaldi	-	-	-	28.6	-	37.4	-	-	43.7
Soleilhac	-	-	107.2	29.9	35.8–36.9	38.4	42.3	46.4	46.3
Isernia	-	132.4–143	-	25.2–30.4	32.7–37.5	36.7–40.2	40.1–48.0	41.3–50.1	40.8–51.6
Durfort	-	-	-	-	-	-	-	44.2	49.0
Castellana	*238.7*	*141.2*	*98*	-	-	-	-	-	-
Castellana	-	*147*	-	-	-	-	-	-	-
Castellana	-	-	-	-	-	-	-	49.1	51.9
Süssenborn	234.5–252.9	130.0–154.6	96.5–120.1	26.5–34.6	30.0–39.8	35.3–44.2	39.0–45.0	39.8–48.8	41.7–48.2
Voigstedt	248.9	137.3	109.2	27.2	34.8	38.3	40.5	45.8	45.3
Mosbach	213.7	124.8	102.8	-	-	-	-	-	-
Mosbach	242.0	135.8	89.2	-	-	-	-	-	-
Mosbach	-	-	112.7	30.3–30.4	31.4–34.6	38.5	40.6–41.2	43.1–43.5	-
Denizli	252.0	147.0	104.0	30.0	35.0	40.0	43.0	52.0	53.0
Various localities	228.0–263.5	119.0–163.5	99.0–116.0	27.0–39.0	33.0–42.5	33.0–45.0	37.0–57.0	42.0–57.5	44.0–59.0

Tab. 2 - Measurements (length in mm) of the rhinoceros lower teeth from Podere San Lorenzo (Italy), compared with the minimum, maximum, and mean values of *Stephanorhinus etruscus* and *S. hundsheimensis* from different European sites. Ltot, length of the cheek tooth row; Lm, length of the molar row; Lp, length of the premolar row. Comparative data are from Pandolfi & Erten (2017). Estimated measurements are in italics.

Taxon/Specimen	*S. etruscus*			*S. hundsheimensis*			**SBAU 153510**	**SBAU 153516**	
Measurement	min	max	mean	min	max	mean	right	right	left
Length of cheek tooth row	220	245	-	226	263.5	-	-	-	-
Length of premolar row	100	135	-	96	119.5	-	-	-	-
Length of molar row	126	145	-	128	159.5	-	-	*126*	-
P2 length	29.0	35.0	32.0	28.5	37.5	34.5	-	-	-
P2 width	32.0	42.5	38.1	33.0	44.0	38.6	-	-	-
P3 length	35.0	41.0	38.3	35.0	46.0	40.9	-	-	-
P3 width	42.0	54.0	48.7	45.0	57.5	50.0	-	-	-
P4 length	37.0	42.5	39.9	39.0	48.5	43.1	-	-	-
P4 width	45.0	63.0	54.7	50.0	59.0	54.7	-	-	-
M1 length	41.0	50.5	48.0	44.0	57.5	49.9	-	43.9	-
M1 width	48.0	60.5	55.6	51.0	63.0	57.4	-	59.1	-
M2 length	45.5	57.0	49.9	47.0	63.0	53.9	-	*49.2*	45.4
M2 width	48.0	65.5	57.2	52.0	67.0	59.4	-	63.7	63.8
M3 length	47.0	59.0	53.3	50.5	66.0	55.7	46.7	-	54.7
M3 width	46.0	56.5	51.9	46.0	60.0	53.1	46.0	-	56.4

Tab. 3 - Measurements (mm) of the rhinoceros upper teeth from Podere San Lorenzo (Italy), compared with the minimum, maximum, and mean values of *Stephanorhinus etruscus* and *S. hundsheimensis* from different European sites. Comparative data are from Handa & Pandolfi (2016). Estimated measurements are in italics.

the postfossette cannot be distinctly observed at this stage of wear and the ectoloph profile is not indicative of a specific taxonomic attribution. The left M1 has a rectangular shape, and cingula are not observable. The left M2 displays a weak internal fold, probably a crista, a constricted protocone, and a mesial cingulum. The left M3 is damaged on its distal side and the preserved protoloph has a weak mesial cingulum. The left M2 has a weak lingual cingulum at the base of the protocone and a weakly constricted protocone. The posterior side of the ectoloph is concave. The left M3 is relatively well preserved and less worn that the other molars. The tooth has mesial and distal cingula, a few pillars inside the median valley, and a small crochet. The protocone is slightly constricted and the paracone fold is weak.

The left mandibular ramus SBAU 153517 (Fig. 6g) is poorly preserved and lacks the first two premolars, while the m1 is damaged. The vestibular groove on the teeth is stretched to the neck and shallow. The p4 displays a well-developed vestibular cingulum. The m2 and m3 show a vestibular cingulum on the anterior loph and a distal cingulum. The m2 has a lingual cingulum below the base of the anterior lingual valley, whereas the m3 displays a weak mesial cingulum and a few pillars below the base of the lingual valleys. The posterior lingual valleys on m2 and m3 have a V-shaped morphology, as well as the anterior lingual valley on m2.

Discussion. Two species are commonly reported in Europe during the Early Pleistocene: *Stephanorhinus etruscus* and *S. hundsheimensis*. *Stephanorhinus etruscus* is one of the most recorded and widespread extinct European rhinoceros species and is documented since the latest Pliocene in Spain, Italy, France, and Romania (Pandolfi et al. 2017). The last appearance of *S. etruscus* is diachronic in the different Eurasian areas. Etruscan rhino populations survived until the Jaramillo subchrone (around 1.1 Ma) in France, Romania, and Hungary, and close to the Early-Middle Pleistocene transition in Spain and Italy (Pandolfi et al. 2017 and references therein). Two size-morphs (a smaller late Early Pleistocene and a larger Middle Pleistocene) of *S. hundsheimensis* have been recognized by some authors (Fortelius et al. 1993; Lacombat 2006). Nevertheless, large-sized specimens of *S. hundsheimensis* have been also collected from late Early Pleistocene deposits of Central Europe suggesting a geographic pattern of distribution of the two sizes during the late Early Pleistocene as argued by Guérin (1980) for *"Dicerorhinus etruscus brachycephalus"*. The presence of two evolutionary morphs of *S. hundsheimensis* is not confirmed by Pandolfi & Erten (2017) due to the presence of large-sized specimens (comparable to the early Middle Pleistocene ones) during the late Early Pleistocene and the re-attribution of several late Early Pleistocene findings to *S. etruscus* (Pandolfi et al. 2017). The first appearance of *S. hundshei-*

mensis in Europe is chronologically placed between 1.3 and 1.1 Ma; during that time span, the species is documented in Anatolia, Romania, Germany, France, northern Italy, and northeastern Spain (Pandolfi & Erten 2017 and references therein).

The size of the rhinoceros specimens included in this study falls within the dimensional range of *S. etruscus* and is generally smaller than *S. hundsheimensis* or close to its minimal values (Tabs 2 and 3). Diagnostic morphological characters cannot be observed on heavily worn rhinoceros teeth; among the studied material, only the M3s display a few characters (e.g., weak paracone fold; not constricted protocone; absence of crista) that confidently can be associated to *S. etruscus*. The length of the molar series falls within the dimensional range of *S. etruscus*.

Concerning the lower teeth, deep and sharp vestibular grooves are commonly recorded in *S. hundsheimensis* (Lacombat 2006), whereas in *S. etruscus* the vestibular grooves are normally open and shallow. The presence of vestibular cingula is a variable character in *S. etruscus* (Guérin 1980); nevertheless, in this species the cingula are generally absent or poorly developed. Vestibular and mesial cingula are usually present on m1s of *S. hundsheimensis* and are more frequently absent in *S. etruscus* (Lacombat 2006). V-shaped lingual valleys are a common character observable in the lower teeth of *S. etruscus*. The dimensions of the lower teeth from PSL fit well with those of *S. etruscus* rather than with those of *S. hundsheimensis*.

Family Equidae Gray, 1821
Genus *Equus* Linnaeus, 1758

Equus stenonis Cocchi, 1867

Fig. 7

Referred material: Right P2 and fragmented left M3 (SBAU 153518), distal tibia (SBAU 153535).

Description. The measurements are summarized in Tabs 4 and 5.

The right P2 (Fig. 7a) is moderately worn and has a sub-triangular occlusal outline. The root is broken. In occlusal view, the anterostyle is pronounced and rounded; the parastyle is less pronounced, pointed and directed slightly distally; conversely, the mesostyle is strong and squared, with a mesiodistal constriction in the middle; no clear metastyle is visible. The prefossette is larger than the postfossette. The distolabial corner of the former is very close to the mesiolabial corner of the latter, but they are not in touch. The fossettes bear a total of six enamel plications (two plis protoloph, one pli protoconule, two plis prefossette, one pli postfossette). Both the protoloph and metaloph are crossed by a longitudinal groove. Mesially, the hypoconal groove is well developed and deep. The protocone is relatively small and sub-rounded in occlusal shape. A very small pli caballin is visible labially to the protocone.

The left M3 (Fig. 7b) lacks the lingual half of the crown and the entire root. The stage of wear is advanced. The occlusal surface slopes distally. The parastyle, mesostyle, and metastyle are well developed and equal in size. The prefossette is slightly larger than the postfossette. There are six enamel plications (one pli protoconule, two plis prefossette, two plis postfossette, one pli hypostyle). The distolingual corner of the postfossette is elongated distally, probably due to the fusion between the fossette and a hypoconal islet. The distal wall of the tooth shows a deep vertical groove. The molar length is 28.3 mm at the crown base.

The distal fragment of left tibia SBAU 153535 (Fig. 7c) is stout and massive. The bone surface is slightly abraded. Some marks, including two subrounded holes, are visible on the anterior surface of the diaphysis (Fig. 7c) and can be interpreted as carnivore (hyena?) bite marks. In ventral view, the articular grooves are set at a marked angle to the sagittal plane of the shaft and the medial is deeper than the lateral. The synovial fossa is confined to the intermediate ridge. The medial malleolus is thick, short, and shaped as a rounded knob. It is more developed than the lateral malleolus.

Discussion. The genus *Equus* is recorded in several Early Pleistocene European faunal assemblages with various species and subspecies, whose taxonomic and phylogenetic status and chronological distribution are still debated (Palombo et al. 2017 and references therein). The most common horses occurring in Europe during the Middle-Late Villafranchian LMA (Gelasian-earliest Calabrian stages of the Early Pleistocene), belong to the "*Equus stenonis* group". According to the comprehensive taxonomic review by Alberdi et al. (1998), stenonoid

Fig. 7 - *Equus stenonis* from Podere San Lorenzo (Italy). a) Right P2 and b) fragmented left M3 (SBAU 153518). c) Distal tibia (SBAU 153535) in ventral (c1), anterior (c2), and posterior (c3) views. Carnivore (hyena?) bite marks are well visible on the anterior surface of the tibia. Scale bar: 3 cm.

horses possibly originated from the Early-Middle Villafranchian large-sized *E. livenzovensis* and then diverged into two groups, the first including relatively smaller forms (*E. stenonis*, *E. senezensis*, and *E. altidens*, in stratigraphical order), the second including larger forms (*E. major* and *E. suessenbornensis*). Members of the first group are sometimes referred to a distinct genus or subgenus, namely *Allohippus* (e.g., Eisenmann 2004 and Amirkhanov et al. 2016, respectively).

The overall morphology of the equid teeth found at PSL is consistent with that reported for *E. stenonis* from various European sites. In particular, the short protocone and the relatively low number of enamel plications are considered typical of *E. stenonis* (Azzaroli 1996). The number of plications counted in the PSL sample (6 in the P2 SBAU 153518 and 6 in the M3 SBAU 153518) is comparable to those for *E. stenonis* from other localities, such as Saint-Vallier (8 and 6, respectively; Eisenmann 1980), La Puebla de Valverde (8/9 and 6/7; Eisenmann 1980), Líbakos (5 and 5; Steensma 1988), Dafneró (6 and 6; Koufos & Kostopoulos 1993), Gerakaroú (6 and 3; Koufos 1992), Vólax (5 and 6; Koufos & Vlachou 1997). Conversely, *E. major* and *E. suessenbornensis* are characterized by a

Tab. 4 - Measurements (mm) of the equid P2 SBAU 153518 from Podere San Lorenzo (Italy) and of the comparative material used in this study. References for morphometric data: a) this work; b) Athanassiou (2001); c) Kostopoulos & Sen (1999); d) Boeuf (1986); e) Vera Eisenmann on-line database (http://vera-eisenmann.com); f) Palombo et al. (2017); g) Koufos (1992); h) Alberdi & Piñero (2012). *Equus stenonis mygdoniensis* probably belongs to the group of small-sized stenonoid horses like *E. senezensis* and *E. altidens* (Forsten 1999; Palombo et al. 2017).

Specimen/ Taxon	**Locality (Reference)**	Tooth length			Protocone length			Tooth width		
		n	min–max	mean	n	min–max	mean	n	min–max	mean
SBAU 153518	Podere San Lorenzo (Italy) (a)	1	-	42.5	1	-	7.6	1	-	27.0
Equus stenonis stenonis	Upper Valdarno (Italy) (a)	5	35.7–44.4	40.4	5	6.8–8.5	7.6	5	24.5–29.0	27.0
Equus stenonis stenonis	Olivola (Italy) (a)	3	42.5–46.0	44.3	4	6.9–9.0	7.5	4	26.6–28.5	27.2
Equus stenonis	Sésklo (Greece) (b)	4	42.0–47.0	43.9	2	7.6–7.7	7.7	4	25.5–29.0	27.5
Equus stenonis	Sarikol Tepe (Turkey) (c)	2	43.5–43.8	43.7	2	7.3–8.1	7.7	2	28.5–28.8	28.7
Equus stenonis guthi	Chilhac (France) (d)	25	37.7–46.3	40.4	25	6.0–8.2	7.3	25	24.0–30.0	26.3
Equus senezensis stehlini	Upper Valdarno (Italy) (a)	5	34.1–40.5	36.8	6	6.9–8.6	7.4	6	23.2–24.9	23.8
Equus senezensis senezensis	Senéze (France) (e)	11	35.2–43.0	38.8	9	6.5–8.0	7.1	11	23.5–28.0	26.3
Equus senezensis cf. *stehlini*	Coste San Giacomo (Italy) (f)	1	-	32.0	1	-	8.8	1	-	23.6
"Equus stenonis mygdoniensis"	Mygdonia Basin (Greece) (g)	11	36.3–40.5	37.9	11	6.0–7.1	6.6	11	22.0–27.5	25.3
Equus altidens altidens	Cueva Victoria (Spain) (h)	5	34.8–43.6	40.1	5	6.4–7.0	6.6	5	24.4–28.0	26.3
Equus altidens granatensis	Venta Micena (Spain) (e)	20	35.0–45.0	39.1	20	5.5–8.0	7.0	20	23.8–28.0	25.8

much more complicated enamel pattern on the upper cheek teeth (Azzaroli 1990; Alberdi et al. 1998). Morphometrically, the P2 from PSL is similar in size to that of *E. stenonis* from different sites (especially the early Late Villafranchian Italian localities of Upper Valdarno and Olivola) and is larger than that of *E. senezensis* and *E. altidens* (Tab. 4). The same goes for the distal tibia SBAU 153535, which falls in the upper range of variation of *E. stenonis* and is significantly larger than that of small-sized stenonoid horses like *E. senezensis*, *E. altidens*, and *E. wuesti* (Tab. 5).

In the light of morphological and morphometric data, the PSL equid sample is referred to *E. stenonis*.

Order **Cetartiodactyla** Montgelard, Catzeflis & Douzery, 1997
Family Bovidae Gray, 1821
Genus *Leptobos* Rütimeyer, 1877–1878

Leptobos cf. ***etruscus*** (Falconer, 1868)

Fig. 8a-e

Referred material: Left p3 and m3 (SBAU 153519), left M3 (SBAU 153520), right astragalus (SBAU 153526), right proximal metacarpal (SBAU 153545).

Description. The measurements are summarized in Tabs 6 and 7.

The left p3 and m3 SBAU 153519, probably belonging to the same individual, are well preserved but both lack the roots. The p3 is elongated, labiolingually compressed, and sub-triangular in occlusal view. Mesially, the parastylid and paraconid are low and directed lingually and the groove between them is wide and shallow. The metaconid is well developed and pronounced with a distolingual direction and is crossed by a vertical groove on the lingual side. It is not possible to distinguish the entostylid and entoconid because they form a single distolingual triangular cuspid, separated from the metaconid by a very deep fold. The hypoconid is bulging labially and is preceded mesially by a weak fold. The labial wall of the tooth is smooth and convex and interrupted by a vertical distal groove mesial to the hypoconid. Conversely, the lingual wall is crossed by vertical grooves of variable depth: that separating the parastylid and paraconid and that crossing the metaconid are shallow, whereas those distal to the paraconid and metaconid are very deep. The latter grooves taper towards the root and close before reaching the collar. The distal wall of the p3 is slightly concave. The left m3 is moderately worn and the tip of the metaconid is broken. In occlusal view, the parastylid is particularly sharp and directed labially; the metastylid disappears about half centimeter above the collar, thus being not visible occlusally; the entostylid is pronounced and rounded, with a

Specimen/ Taxon	**Locality (Reference)**	Width			Depth		
		n	min–max	mean	n	min–max	mean
SBAU 153535	Podere San Lorenzo (Italy) (a)	1	-	84.0	1	-	50.0
Equus stenonis stenonis	Upper Valdarno (Italy) (a)	3	74.0–76.0	75.2	3	47.5–54.0	49.8
Equus stenonis stenonis	Olivola (Italy) (a)	4	80.0–83.5	81.4	4	51.0–54.5	52.4
Equus stenonis	Sésklo (Greece) (b)	23	73.3–86.0	79.1	27	49.0–56.9	52.3
Equus stenonis guthi	Chilhac (France) (c)	5	62.0–78.0	73.2	5	44.0–52.0	48.0
Equus stenonis viretii	St. Vallier (France) - old coll. (d)	22	75.0–85.0	80.5	24	47.0–55.0	52.0
Equus stenonis viretii	St. Vallier (France) - new coll. (d)	14	74.0–88.0	82.7	16	45.5–max	52.0
Equus senezensis stehlini	Upper Valdarno (Italy) (a)	2	65.0–72.5	68.8	2	49.0–43.0	46.0
Equus senezensis senezensis	Senéze (France) (e)	15	60.0–80.0	71.0	10	44.0–49.0	47.6
"Equus stenonis mygdoniensis"	Mygdonia Basin (Greece) (f)	18	63.0–72.0	66.1	19	42.4–46.0	44.3
Equus altidens altidens	Cueva Victoria (Spain) (g)	1	-	72.5	1	-	48.5
Equus altidens	Quibas (Spain) (g)	2	64.1–74.8	69.6	2	44.2–45.2	44.7
Equus altidens granatensis	Venta Micena (Spain) (e)	40	68.0–79.0	73.2	40	43.0–51.0	48.0
Equus wuesti	Untermassfeld (Germany) (h)	9	75.5–87.5	78.7	9	50.1–54.8	52.0

Tab. 5 - Measurements (mm) of the equid distal tibia SBAU 153535 from Podere San Lorenzo (Italy) and of the comparative material used in this study. References for morphometric data: a) this work; b) Athanassiou (2001); c) Boeuf (1986); d) Eisenmann (2004); e) Vera Eisenmann on-line database (http://vera-eisenmann.com); f) Koufos (1992); g) Alberdi & Piñero (2012); h) Musil (2001). *Equus stenonis mygdoniensis* probably belongs to the group of small-sized stenonoid horses like *E. senezensis* and *E. altidens* (Forsten 1999; Palombo et al. 2017).

distal direction. The metaconid and entoconid are mesiodistally compressed and protruding labially, as much as the parastylid and entostylid, respectively. Lingually, the protoconid and hypoconid are also strong and mesiodistally compressed. The mesial ectostylid between the protoconid and hypoconid is high, drop-shaped, and not fused with the conids themselves. On the other hand, the distal ectostylid between the hypoconid and hypoconulid, is not higher than one centimeter, relatively narrower, and sub-circular in occlusal shape. The two central cavities show a labiolingual compression in the middle. Distally, the hypoconulid is relatively straight labially and markedly convex lingually and exhibits a well-developed distal stylid directed distolabially.

The left M3 SBAU 153520 also lacks the root and is broken in the mesiolingual part. In occlusal view, the labial styles are rounded and bulging. The parastyle is perpendicular to the mesiodistal axis; the mesostyle and metastyle are almost equally protruding and oriented labiomesially and labiodistally, respectively. The metastyle is delimited distally by a marked vertical groove on the distal wall of the tooth. The paracone is smaller, mesiodistally shorter, and more pointed than the metacone. The metaconule has a triangular lingual outline, while the protocone is unfortunately damaged. Between them, a strong entostyle develops; it has a complex, clover-shaped occlusal outline. Also, the central cavities show complex outline in occlusal view. The distal one has a very deep bubaline fold in distolingual position. In labial view, the styles are strong and the ribs of the paracone and metacone become flatter and wider towards the root.

The right astragalus SBAU 153526 is broken in the distolateral part and is moderately weathered. In anterior view, the proximal trochlea is asymmetric, with the lateral trochlear ridge higher and more pointed than the medial one. The proximal trochlear ridges are parallel to the sagittal plane. The intertrochlear fossa is narrow and V-shaped. The posterior surface is almost completely occupied by the wide articular facet for the calcaneum, which is sub-quadrangular and convex. The distolateral margin of this facet is marked by a groove perpendicular to the sagittal axis, which separates the facet from the distal trochlea.

The right metacarpal SBAU 153545 is severely weathered and lacks the distal half. However, the proximal articulation can be described. In proximal view, the proximal diaphysis is D-shaped and hosts two large articular facets, which border a wide nutrient foramen located at about one third from the posterolateral corner. The medial articular facet is wider than the lateral one and its anteroposterior diameter is almost equal to the mediolateral diameter. In posterior view, there is a shallow unobstructed groove connecting the proximal nutrient foramen with another faintly visible, foramen on the posterior surface.

Discussion. The extinct bovid *Leptobos* is one of the most characteristic elements of European Villafranchian faunal assemblages. Masini (1989) and Masini et al. (2013) recognize two different groups. The first includes *L. stenometopon*, *L. merlai*, and *L. furtivus*, the second *L. etruscus* and *L. vallisarni*. However, the validity of *L. furtivus* as a good species has been questioned by Cherin et al. (2019). Two other European species, namely *L. bravardi* and *L. elatus*, are represented by very scanty remains, which are not sufficient to confidently refer them to one or the other groups (Cherin et al. 2019). The two groups of species (*L. stenometopon*-*L. merlai* and *L. etruscus*-*L. vallisarni*, respectively) can be easily distinguished on the basis of morphological characters of the cranium, teeth, and some postcranial elements (Masini 1989; Duvernois 1990; Masini et al. 2013; Cherin et al. 2019). The morphology of the bovid teeth from PSL agrees with the information reported in the above literature for *L. etruscus*, i.e., p3 with sub-triangular occlusal outline, shallow groove separating parastylid and paraconid, entostylid indistinguishable from the entoconid, protruding hypoconid preceded by a vertical groove on the labial wall, deep sub-triangular grooves on the lingual wall; m3 with pointed parastylid, very low and faint metastylid, and large entostylid, constricted lingual lobes, third lobe with straight labial margin, convex lingual margin, and marked distal stylid, presence of two ectostylids, with the distal much smaller than the medial; M3 with marked constriction of lingual lobes, frequent end deep infoldings in the central cavities, complex occlusal outline of the entostyle, strong labial styles, metastyle followed by a vertical groove on the distal wall of the tooth. Measurements of the PSL m3 SBAU 153519 and M3 SBAU 153520 also fall into the variability range of *L. etruscus* from various European sites (Tab. 6). The same goes for the astragalus SBAU 153526 (Tab. 7). Unfortunately, the proximal metacarpal SBAU 153545 is too damaged and weathered to be measured. Considering the relatively poor preservation, the PSL bovid material is here referred to *Leptobos* cf. *etruscus*.

Specimen/Taxon	Alveolar length			Alveolar max width		
	n	min–max	mean	n	min–max	mean
p3						
SBAU 153519	1	-	18.2	1	-	10.1
L. etruscus (a)	9	17.5–19.5	17.9	9	10.0–12.5	10.9
L. merlai (b)	2	15.5–17.0	16.2	2	10.5–10.5	10.5
"L. furtivus" (b)	10	13.5–17.5	15.7	10	10.0–12.0	10.8
L. elatus (b)	6	15.0–17.5	16.2	7	10.0–11.5	11.1
m3						
SBAU 153519	1	-	38.5	1	-	16.5
L. etruscus (a)	10	37.5–45.0	41.0	11	13.5–19.5	16.1
L. vallisarni (c)	2	32.7–36.2	35.1	2	15.5–15.8	15.7
L. cf. *stenometopon* (c)	2	36.0–39.0	37.2	2	17.0–18.0	17.5
L. merlai (b)	2	37.5–39.0	38.2	2	17.5–17.5	17.5
"L. furtivus" (a)	13	33.0–37.5	35.4	14	14.5–17.5	16.1
L. elatus (b)	8	35.5–39.5	37.9	7	16.5–18.5	17.5
M3						
SBAU 153520	1	-	30.4	1	-	24.7
L. etruscus (a)	10	28.0–34.0	30.0	10	18.5–27.5	22.8
L. vallisarni (c)	3	24.6–29.6	26.5	3	23.2–27.0	25.1
L. cf. *stenometopon* (c)	1	-	27.0	1	-	23.0
L. merlai (b)	4	25.5–29.0	27.0	4	24.0–26.5	24.9
"L. furtivus" (b)	7	24.0–30.0	26.7	7	19.5–25.0	22.1

Tab. 6 - Measurements (mm) of the bovid teeth from Podere San Lorenzo (Italy) and of the comparative material used in this study. References for morphometric data: a) Duvernois & Guérin (1989); b) Duvernois (1990); c) Masini (1989). The validity of the species *"Leptobos furtivus"* is debated (see Cherin et al. 2019).

Family Cervidae Goldfuss, 1820
Genus *'Pseudodama'* Azzaroli, 1992

'Pseudodama' nestii (Azzaroli, 1947)
Fig. 8f-j

Referred material: Right frontal bone with almost complete antler (SBAU 153527), basis of a left shed antler (SBAU 153528), fragment of left mandible with p4 and m1 (SBAU 153522), left m2

Specimen/Taxon	Length			Proximal width		
	n	min–max	mean	n	min–max	mean
SBAU 153526	1	-	66.5	1	-	41.2
L. etruscus (a)	31	61.7–72.0	66.5	31	39.3–48.0	43.5
L. cf. *vallisarni* (a)	3	63.6–66.6	65.6	3	42.0–45.0	43.5
L. cf. *stenometopon* (a)	10	59.2–67.7	62.7	10	37.0–44.0	41.2
L. merlai (b)	17	59.5–70.0	63.9	15	36.5–43.0	39.2
"L. furtivus" (b)	9	55.5–62.0	60.3	9	34.5–39.5	37.1
L. elatus (b)	9	60.5–67.5	63.6	9	36.5–40.0	38.9

Tab. 7 - Measurements (mm) of the bovid astragalus SBAU 153526 from Podere San Lorenzo (Italy) and of the comparative material used in this study. References for morphometric data: (a) Masini (1989); (b) Duvernois (1990). The validity of the species *"Leptobos furtivus"* is debated (see Cherin et al. 2019).

(SBAU 153523), four isolated tooth fragments (SBAU 153524), right astragalus (SBAU 153530).

Description. The measurements are summarized in Tabs 8 and 9.

The right frontal bone with antler SBAU 153527 is quite fragmentary, preserving basically only the pedicle, which ends anteriorly and medially well before, respectively, the orbital rim and the suture surface to the other frontal. A portion of the suture surface to the parietal and temporal bones is preserved. On the internal side of the bone, the endocranial cast can be seen. The burr is quite well developed but incomplete, missing the lateral portion. The antler preserves the very base of the first tine, located a few centimeters above the burr (33 mm from the burr, on the anterior side), the very base of the second tine and a stump of beam roughly 5 cm long. In lateral view, the beam is roughly straight, with its posterior (ventral) edge mildly convex between the insertion of the two tines. In rostral view, the basal portion of the beam is aligned with the pedicle up to the base of the first tine; between first and second tine the beam mildly bends laterally, then it bends back medially at the level of the insertion of the second tine. The overall rostral outline is thus somewhat sigmoid.

The left shed antler SBAU 153528 preserves the shedding surface, the rather abraded burr, most of the first tine, departing at 20 mm from the burr and at roughly 80 degree angle to the beam, and a further piece of the beam. The tine points forward and slightly laterally and is regularly bent upward.

The left mandible SBAU 153523 consists in a ca. 5 cm long portion of the ramus from half the alveolus of the missing p3 to that of the missing m2. The p4 and m1 are complete, well preserved, and at a medium wear stage. In the p4, the anterior wing of the paraconid elongates mesially creating a small enamel island with the parastylid, visible in occlusal view; the lingual wall is open (the so called "unmolarized" condition), because of the lack of fusion between paraconid and metaconid; the entoconid elongates at about 45 degrees to the axis of the tooth. The m1 has a developed mesial cingulum (with accessory tubercles), well evident in labial view, a mesial bending of the base of the entoconid, visible in lingual view, and a strong ectoconid between the mesial and distal lobes.

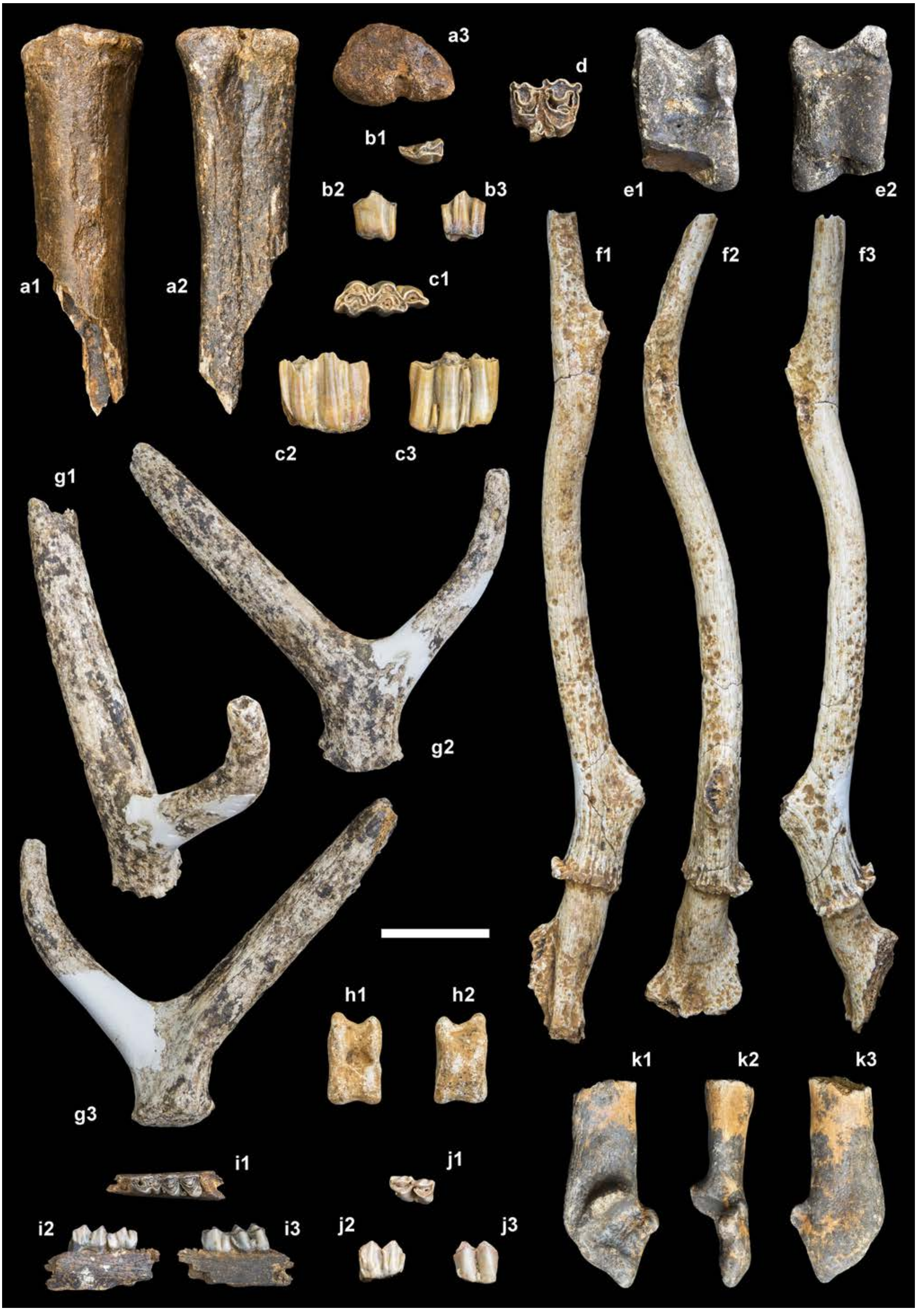
The isolated left m2 SBAU 153523 is almost unworn and the roots are missing, probably because they were not completely formed yet. Like the above described m1, this tooth has a developed mesial cingulum (with a visible accessory tubercle on it) and a mesially bent base of the entoconid, but a smaller ectoconid.

Both of the above dental specimens show a mild roughness of the labial wall. The isolated tooth fragments SBAU 153524 do not allow any measurement or morphological observation but are compatible in size with a fallow deer.

The right astragalus SBAU 153530 is complete but badly abraded, so that particular morphologies cannot be detected. Its porous appearance suggests that it belonged to a juvenile specimen.

Discussion. The so called *Dama*-like deer are an important element of the late Pliocene to Middle Pleistocene fauna of Europe, with roughly the size of modern fallow deer but three to four

Fig. 8 - Cetartiodactyla from Podere San Lorenzo (Italy). a-e) *Leptobos* cf. *etruscus*: (a) Right proximal metacarpal (SBAU 153545) in anterior (a1), posterior (a2), and dorsal (a3) views, (b) Left p3 and (c) left m3 (SBAU 153519) in occlusal (b1, c1), labial (b2, c2), and lingual (b3, c3) views; (d) Left M3 (SBAU 153520) in occlusal view; (e) Right astragalus (SBAU 153526) in anterior (e1) and posterior (e2) views. f-j) *'Pseudodama' nestii*: (f) Right frontal bone with antler (SBAU 153527) in lateral (f1), anterior (f2), and medial (f3) views; g) Left shed antler (SBAU 153528) in anterior (g1), medial (g2), and lateral (g3) views; h) Right astragalus (SBAU 153530) in anterior (h1) and posterior (h2) views; i) Left mandible with p4 and m1 (SBAU 153522) in occlusal (i1), labial (i2), and lingual (i3) views; (j) Left m2 (SBAU 153523) in occlusal (j1), labial (j2), and lingual (j3) views. k) *Sus strozzii*: Right calcaneum (SBAU 153531) in medial (k1), anterior (k2), and lateral (k3) views. Scale bar: 5 cm.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Locality	**Specimen**	**p4 length**	**p4 width**	**m1 length**	**m1 width**
Podere San Lorenzo	**SBAU 153523**	12.6	8.2	14.9	9.8
'Pseudodama' lyra					
Spicchio	IGF 1471v	12.1	8.9	13.4	11.1
Montopoli, Lower Valdarno	IGF 1406	12.5	7.8	15.1	9.8
Montopoli, Lower Valdarno	IGF 1407	12.6	8.2	12.7	9.8
Montopoli, Lower Valdarno	IGF 1409	13.3	8.9	15.3	10.9
Lower Valdarno	IGF 2805v	13.3	10.6	15.0	11.6
Lower Valdarno	IGF 2806v	12.9	8.3	15.1	10.2
Lower Valdarno	IGF 2817v	12.6	8.5	14.7	10.7
'Pseudodama' nestii					
Olivola	IGF 1385	13.4	9.3	-	-
Olivola	IGF 1388	-	-	15.7	10.9
Olivola	IGF 1394	13.4	9.2	15.0	10.5
Olivola	IGF 1395	13.0	8.2	14.6	10.5
Olivola	IGF 1396	12.9	8.6	15.0	9.9
Olivola	IGF 1397	13.4	9.6	13.4	9.9
Olivola	IGF 1476	12.5	8.5	13.5	11.2
Olivola	IGF 1477	12.0	10.0	-	-
Olivola	IGF 1479	12.0	8.2	-	-
Olivola	IGF 1523	-	-	15.0	9.9
Olivola	IGF 1527	-	-	15.6	10.1
Olivola	IGF 1526	13.9	8.5	15.7	11.3
Upper Valdarno	IGF 227	11.7	7.7	-	-
Upper Valdarno	IGF 228	-	-	14.0	9.9
Upper Valdarno	IGF 229	11.3	7.0	13.2	10.3
Il Tasso, Upper Valdarno	IGF 230	13.0	9.5	13.8	10.5
Upper Valdarno	IGF 231	13.0	8.9	14.3	10.9
Il Tasso, Upper Valdarno	IGF 233	13.0	8.8	14.9	9.5
San Giovanni, Upper Valdarno	IGF 237	11.2	7.8	12.6	9.8
San Giovanni, Upper Valdarno	IGF 238	14.0	9.8	-	-
Il Tasso, Upper Valdarno	IGF 240	14.1	10.4	14.0	11.6
Figline, Upper Valdarno	IGF 242	12.2	9.0	14.9	10.1
Figline, Upper Valdarno	IGF 243	12.6	8.1	14.5	9.7
Figline, Upper Valdarno	IGF 243	13.3	8.4	14.9	9.7
Le Ville, Upper Valdarno	IGF 251	12.1	9.4	14.3	10.0
Upper Valdarno	IGF 252	13.3	9.0	13.8	9.1
Upper Valdarno	IGF 253	-	-	14.2	9.9
Figline, Upper Valdarno	IGF 254	12.5	8.4	13.9	9.8
Upper Valdarno	IGF 1156	12.4	7.3	13.8	9.9
Upper Valdarno	IGF 1168	12.7	8.5	13.8	10.1
Upper Valdarno	IGF 1170	13.8	8.2	-	-
Upper Valdarno	IGF 1175	12.5	7.8	14.9	10.3
Upper Valdarno	IGF 1179	12.1	7.6	14.1	9.8
Upper Valdarno	IGF 1187	12.6	8.2	14.0	10.1
Upper Valdarno	IGF 1228	-	-	15.4	10.6
Upper Valdarno	IGF 5v	11.4	7.7	13.3	9.4
Upper Valdarno	IGF no num.	11.5	7.3	14.1	10.4
Upper Valdarno	IGF no num.	12.6	8.2	14.7	10.7
Upper Valdarno	IGF 8920v	12.0	8.2	-	-
Upper Valdarno	IGF 8921v	12.4	7.9	14.6	10.0
Upper Valdarno	IGF 8922v	12.6	9.2	14.0	11.7
Upper Valdarno	IGF 8924v	11.4	7.4	13.4	10.2

Tab. 8 - Measurements (mm) of the cervid p4 and m1 SBAU 153526 from Podere San Lorenzo (Italy) and of the comparative material used in this study.

pointed and un-palmated antlers. Different species replace each other chronologically, but their taxonomic allocation and interrelationships are far from being clarified. Azzaroli (1992) proposed unifying all the species into the genus *Pseudodama*, type species *P. nestii* from the Upper Valdarno. This author suggested the presence of two lineages, each with ancestor-descendant relationships: an "Italian" lineage with (in chronological order) *P. lyra*, *P. nesti*, *P. farnetensis*, and a "French" lineage with *P. pardinensis*, *P. philisi* (= *P. rhenana*), *P. perolensis*. In both the lineages, there is an evolution in the position and orientation of the basal tine that, in the earliest representatives, departs at a certain distance from the burr and makes an acute angle with the beam, to became closer to the burr and creating an open angle

Tab. 9 - Measurements (mm) of the cervid astragalus SBAU 153530 from Podere San Lorenzo (Italy) and of the comparative material used in this study.

Locality	Specimen	Distal width	Max lateral length
Podere San Lorenzo	**SBAU 153530**	23.0	39.5
'Pseudodama' lyra			
Montopoli, Lower Valdarno	IGF 2809v	27.3	46.1
Montopoli, Lower Valdarno	IGF 2810v	27.1	43.7
'Pseudodama' nestii			
Olivola	IGF 1389	27.5	43.9
Olivola	IGF 1846	25.9	43.5
Olivola	IGF 1847	25.5	41.2
Il Tasso, Upper Valdarno	IGF 393	25.1	40.3
Il Tasso, Upper Valdarno	IGF 398	24.9	40.3
Il Tasso, Upper Valdarno	IGF 399	25.5	40.7
Upper Valdarno	IGF 19v	26.1	41.7
Upper Valdarno	IGF 107v	24.7	42.4
Upper Valdarno	IGF 20v	26.9	41.6
Upper Valdarno	IGF 59v	23.9	38.9
Upper Valdarno	IGF 68v	24.0	37.7

with the beam in later representatives of the group (Azzaroli 1992; Van der Made 1999). However, Azzaroli (1992) did not explain what distinguishes the Italian and French lineages. Surprisingly, Azzaroli (1992) does not include in *Pseudodama* (nor discusses at all) the small deer from Le Vallonnet which had been recently described as '*C.*' *vallonnetensis* but already suggested to be related to the fallow deer group (De Lumley et al. 1988).

Most later authors use Azzaroli's generic name *Pseudodama* (e.g., Lister et al. 2010; Kahlke et al. 2011), whereas some include all these species in *Dama*, confirming a strict relationship with modern fallow deer (e.g., Pfeiffer 1999; Van der Made 1999; Van der Made et al. 2014), or keep the genus *Pseudodama* for Azzaroli's Italian lineage and prefer the name *Metacervoceros* for the French lineage (e.g., Palombo 2014), or even reallocate the species of the two lineages into the Asiatic genera *Axis* and *Rusa* respectively (Di Stefano & Petronio 2003). Conversely, Croitor (different papers) splits variously the *Pseudodama* group into many different taxa following patterns and groupings different from paper to paper and from any other author, his last review including four apparently unrelated genera (*Dama*, *Metacervoceros*, *Praeelaphus*, *Cervus*) (Croitor 2018). We choose to use here the name '*Pseudodama*' for this morphologically conservative group of deer which, as demonstrated by Breda & Lister (2013) and Breda (2015), shares many features with the genus *Dama*, suggesting a strict relationship. Since the main morphological characters that differentiate '*Pseudodama*' from later *Dama* are primitive features, '*Pseudodama*' is probably a paraphyletic stem-group, so, in the absence of a proper phylogenetic analysis, we follow Breda & Lister (2013) and Breda et al. (2015), in using the name '*Pseudodama*' within inverted commas.

The fallow deer material from PSL is consistent in size and morphology with '*P.*' *nestii* as detailed below.

The weak pedicle and antler of SBAU 153527 suggests a juvenile age. The relatively high position of the first tine, which apparently formed an acute angle to the beam, is consistent with the earliest species of the genus '*Pseudodama*', '*P.*' *nestii* and '*P.*' *lyra*. The sigmoid outline of the antler in frontal view suggests referral to the former species, since the latter species has a lyrate rostral outline instead. Shed antler SBAU153528 probably belongs to a more mature individual, as suggested by the stronger diameter of the beam and by the relatively lower insertion of the first tine.

The p4 from PSL conforms to '*Pseudodama*' due to its obliquely oriented entoconid, the entoconid being perpendicular to the tooth row in the red deer, aligned to it in modern *Dama* (Lister 1996) and variable from oblique to aligned to the tooth row in the '*Pseudodama*' species (Breda & Lister 2013); a specific attribution on this character is not possible. The un-molarized condition of the lingual wall is usually considered to be an ancestral character as opposed to the molarized condition. However, molarization of p4 is more frequent in '*Pseudodama*' than in modern *Dama* (Breda 2015) and the p4 morphology is prone to significant intraspecific variability (e.g., Janis & Lister 1985 for *C. elaphus*; Pfeiffer 2005 for *D. dama*), so the situation of the lingual wall does not give clear clues to the antiquity (and thus specific attribution) of this specimen. The lingual bifurcation of the p4 parastylid is absent in '*P.*' *lyra* from Lower Valdarno (6 specimens) and in '*P.*' *nestii* from Olivola (6 specimens), while it is variably present in '*P.*' *nestii* (3/3 specimens from Casa Frata, 3/25 from Upper Valdarno, 1/2 from Selvella), and again absent in '*P.*' *farnetensis* (4 specimens from Pietrafitta, 2 from Pirro, 2 from Capena), '*P.*' *vallonnetensis* (15 specimens from Untermassfeld, 7 from Vallparadis), *Dama roberti* (11 specimens from different localities), and later *Dama* (Breda, personal observation). Thus, the bifurcation of the p4 parastylid shared by the PSL specimen apparently characterizes '*P.*' *nestii* from the Tasso FU.

In the lower molars, the developed mesial cingulum and the mesial bending of the base of the entoconid, distinguish the fallow deer (both *Dama* and '*Pseudodama*') from the red deer in which the mesial cingulum is weaker and the entoconid is straight (Lister 1996; Breda & Lister 2013). The ectoconid, stronger on m1 than m2, also suggests attribution to a fallow deer because in the red deer it is the opposite (Lister 1996; Breda & Lister 2013). The nearly unworn condition of m2 allows measuring the tooth height and calculating the hypsodonty index as the ratio between crown height along the lingual pillar of the metaconid and crown width, which corresponds to 1.31. This index is slightly higher than in the only two coeval m2 *Dama*-like specimens from Olivola and Upper Valdarno (1.25 in Olivola IGF 1527 and 1.21 in Upper Valdarno IGF 242).

The mild roughness of the labial wall of the teeth is often present in '*P.*' *nestii* and '*P.*' *lyra* from Upper Valdarno and Olivola, with which these teeth are consistent in size (Tab. 8).

The size of the astragalus SBAU 153530 fits in the lower end of the range of *Dama*-like deer from Upper Valdarno and Olivola (Tab. 9) confirming that it belonged to a juvenile specimen.

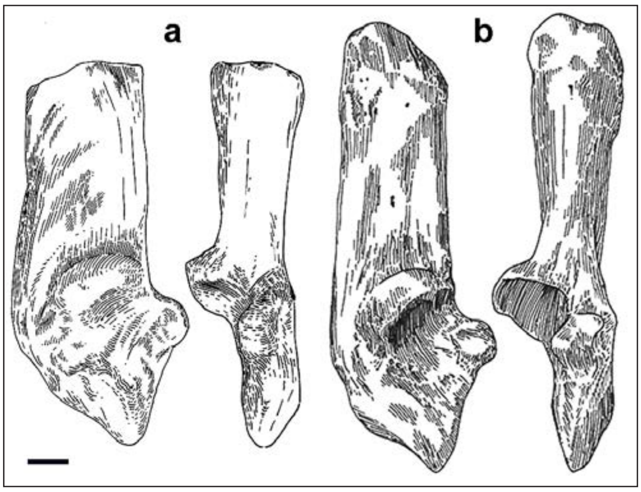

Fig. 9 - a) Suid calcaneum (SBAU 153531) from Podere San Lorenzo (Italy) compared with b) calcaneum of *Sus strozzii* (NHMB Se1775) from Senéze (France) redrawn from Azzaroli (1954). Medial view on the left, anterior view on the right. Scale bar: 1 cm.

Family Suidae Gray, 1821
Genus *Sus* Linnaeus, 1758

Sus strozzii Forsyth Major, 1881
Figs 8k-9

Referred material: Right calcaneum (SBAU 153531).

Description. The calcaneum (Fig. 8k) is severely weathered and the proximal extremity including the *tuber calcanei*, is missing. In medial view, the anterior and posterior margins of the body are subparallel, although the posterior one tends to enlarge posteriorly at the level of the *sustentaculum tali*. As in all suids (Schmid 1972), the latter is anteroposteriorly very short and does not reach the posterior margin of the calcaneum in medial view. The posteroventral margin of the bone is more inclined than the anteroventral margin with respect to the main axis of the calcaneum, giving to the ventral part an asymmetrical triangular appearance. The small anterior process has a semicircular profile in medial and lateral views. The articular facets are not well visible due to poor preservation. The facet for the astragalus is subcircular, with the anteroposterior diameter slightly longer than the mediolateral one. The trochlear facet of the anterior process has the shape of a small circular and smooth area ventral to the process itself. Posteroventrally, the articulation for the navicular is dorsoventrally elongated and leaf-shaped.

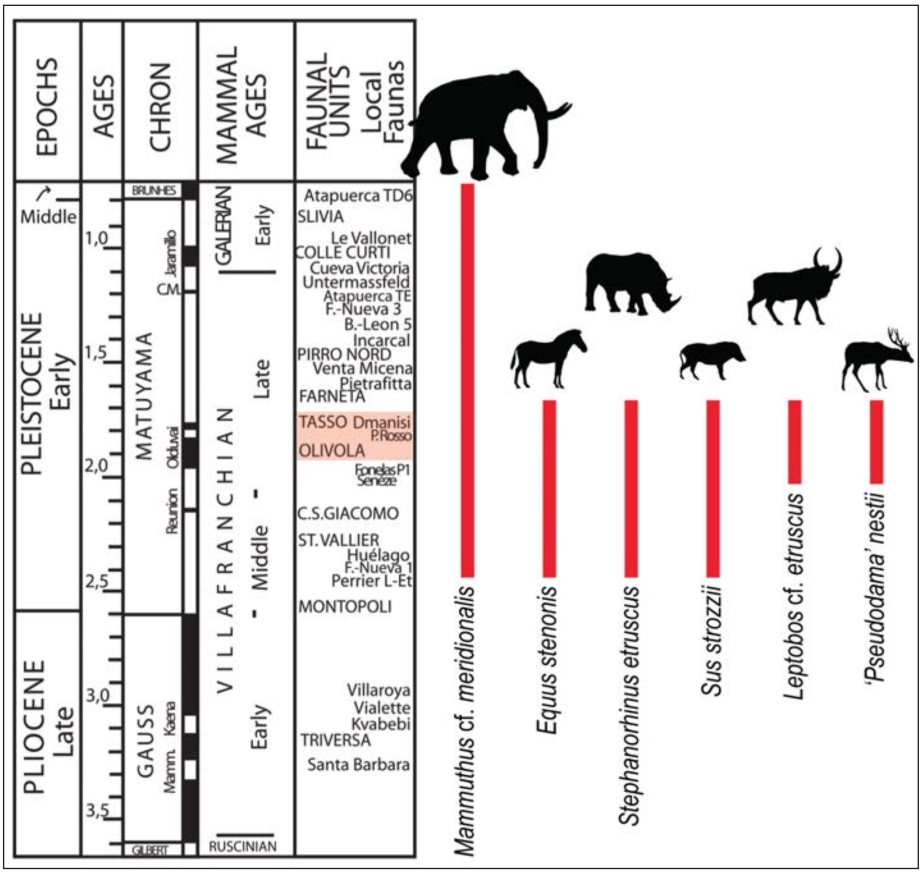

Fig. 10 - Biochronological range chart of large mammals found in Podere San Lorenzo (Italy). The chronological/biochronological scheme on the left is modified from Rook & Martínez-Navarro (2010).

Discussion. The Villafranchian LMA is distinguished by the occurrence of two suid species, apparently without stratigraphic overlap: the small-sized *Sus arvernensis* originates in the Ruscinian LMA and continued in the Early Villafranchian LMA (Pliocene); the larger and closely-related *S. strozzii* is a common element of the Middle to early Late Villafranchian LMA (Gelasian stage of the Early Pleistocene) (Cherin et al. 2018). Suid remains are virtually unknown in Europe during the last part of Villafranchian (approx. 1.8–1.2 Ma), conversely to what is observed before and after this interval when these animals are almost ubiquitous (Martínez-Navarro et al. 2015).

The suid calcaneum from PSL is morphologically very similar to that of the sub-complete skeleton of *S. strozzii* NHMB Se1775 from the French locality of Senéze (about 2.1 Ma; Nomade et al. 2014) figured by Azzaroli (1954: 67) (Fig. 9). The linear dimensions of SBAU 153531 (length: >89 mm; max width: 24.8 mm; max depth: 40.4 mm) are also very similar to NHMB Se1775 (length: 99 mm; max width: 25.5 mm; max depth: 37.5 mm), and significantly larger than those of the two calcanei of *S. arvernensis* published by Gallai (2006) (length: 71.2/71.9 mm; max width: 18.6/18.8 mm; max depth: 27.7/26.6 mm, respectively). Specimen SBAU 153531 is thus attributed to *S. strozzii*, of which it represents the first calcaneum discovered so far in Italy.

CONCLUSIONS

Umbria is a key area for the study of Plio-Pleistocene European terrestrial mammal communities. Thanks to its geographic position in the middle of the Italian Peninsula, the Region has probably acted as a crossroads for the dispersal and evolution of mammals during this time span, characterized by strong climatic and ecological changes.

Most of the importance of Umbria in disclosing information on Plio-Pleistocene mammals is due to the extensive deposits of the wide Tiber basin, from which paleontologists have recovered a great number of fossils testifying to the evolution of terrestrial ecosystems during the last 3 Ma.

The mammal assemblage from PSL described in this paper represents a valuable example of the diversity and richness of the Umbrian fossil mammal record. The remains from the site have been referred to the following taxa: *Mammuthus* cf. *meridionalis*, *Stephanorhinus etruscus*, *Equus stenonis*, *Leptobos* cf. *etruscus*, *'Pseudodama' nestii*, and *Sus strozzii*. Some hyaenid (*?Pachycrocuta brevirostris*) coprolites have been also reported. Except for the mammoth, the other species have a biochronological distribution that spans the Middle and early Late Villafranchian (Fig. 10). In particular, the occurrence of *L.* cf. *etruscus* and *P. nestii* allows referral of the PSL assemblage to the Olivola-Tasso Faunal Units (about 2.0–1.8 Ma). This result is in accordance with the age of some other assemblages found in the southwestern branch of the Tiber basin (e.g., Torre Picchio, Villa San Faustino, Colle Sant'Andrea, Pantalla) (Tab. 1).

Although the original outcrop is no longer accessible, the nearby PZ outcrop has been described herein. The overall sedimentological features of the two sites can be referred to a fluvial depositional environment characterized by a gradual passage from predominant conglomerates to fine sands and silts (i.e., average reduction of the hydrodynamic energy) from the bottom upwards. The two outcrops have been referred to the Madonna dei Bagni Lithofacies (Tiberino Supersyntheme - Todi Syntheme - Santa Maria di Ciciliano Subsyntheme; Early Pleistocene). The taphonomic features of the mammal remains suggest that they most likely come from conglomerates or sand lenses within conglomerate bodies of the lower part of the succession, deposited in a fluvial environment with relatively high energy.

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