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Late Pliocene terrestrial mammals from La Serra, a new Early Villafranchian fauna with well-documented stratigraphy near Montopoli (Tuscany, central Italy)

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KEY WORDS - Anancus arvernensis, Sus arvernensis, Procapreolus, "Pseudodama", *Triversa Faunal Unit, Piacenzian.*

ABSTRACT - The present paper focuses on the recently discovered Pliocene vertebrate site of La Serra (Valdelsa Basin, Tuscany), near the historical locality of Montopoli (Pisa Province). At La Serra, marine and terrestrial fossils co-occur within a siliciclastic succession of coastal and marginal-marine deposits. The terrestrial mammal fauna includes proboscideans and artiodactyls (suids and cervids). Specifically, the gomphothere Anancus arvernensis *is documented by bunolophodont molar fragments and postcranial bones (ribs, vertebrae and a humerus). Fragmentary maxillae and an isolated upper canine are attributed to the small-sized suid* Sus arvernensis. *Cervids are represented by an antler fragment assigned to* Procapreolus *cf.* cusanus *as well as by teeth and postcranial remains of a medium-sized Cervinae somewhat reminiscent of "*Pseudodama*". Two mammal-derived coprolites, likely produced by some herbivores, were also recovered. All identified taxa are regarded as forest-dwelling, thereby implying a wooded landscape. The taxonomic composition of the assemblage supports its attribution to the Early Villafranchian Triversa Faunal Unit, which is broadly consistent with the Piacenzian age inferred for the entombing deposits on stratigraphic grounds.*

INTRODUCTION

Little is known about the terrestrial mammal faunas that inhabited the Italian peninsula in Zanclean and Piacenzian times. Some important finds of Pliocene terrestrial mammals were gathered in the 19th century from fluvial and lacustrine sediments in the surroundings of Villafranca d'Asti, Piedmont, northern Italy (Amoretti, 1808; Pareto, 1865; Carraro, 1996). That assemblage was subsequently elected to establish the Triversa Faunal Unit (hereinafter, FU), which nowadays is included in the Early Villafranchian (= zone MNQ16a according to the biochronological scheme of Rook & Martínez-Navarro, 2010), around 3.2 Ma (Lindsay et al., 1980). Roughly coeval mammal faunas were also discovered in Tuscany, central Italy, first and foremost in the Lower Valdarno (e.g., at Ponte a Elsa: Azzaroli, 1992a; Benvenuti et al., 1995; at Case Nuove: Dominici et al., 1995a; Rustioni & Mazza 2001) and Upper Valdarno (e.g., at Santa Barbara: Albianelli et al., 1997) areas. In addition, the Lower Valdarno has historically yielded a conspicuous terrestrial fauna, dating back to around the Pliocene-Pleistocene transition, from the surroundings of Montopoli (Pisa) (Forsyth Major, 1877; Bartolini-Lucenti et al., 2022). That local fauna was elected to establish the Montopoli FU, corresponding to the beginning of the Middle Villafranchian (MNQ16b; e.g., Azzaroli, 1977; Zanchetta et al., 1995; Bartolini-Lucenti et al., 2022), whose taxonomic novelties relative to the previous Triversa FU demonstrate the climatic cooling and increasing aridity that took place around 2.6 Ma (McClymont et al., 2023, and references therein). Also worth noting is the Val di Pugna locality, in the Sienese, which has historically been home to remarkable finds of both terrestrial and marine mammals (Bianucci et al., 2001). That assemblage is referred to the beginning of the Ruscinian (MN14; Mein,

1975a, b), which in turn is broadly correlative with the Zanclean, ca. 5.3-3.6 Ma (Gliozzi et al., 1997; Azanza et al., 2004; Palombo, 2004; Rook & Martínez-Navarro, 2010). However, most of these finds are associated with weak geographic and stratigraphic information, although this is beginning to change as new terrestrial mammal sites are discovered (e.g., Arcille, near Grosseto: Pandolfi et al., 2025). Palaeontological studies of terrestrial mammal fossils from newly recognised localities are therefore greatly needed, both to expand the hitherto limited Italian Pliocene record and to unlock the full scientific potential of historical collections.

Here, we describe a new terrestrial mammal assemblage from coastal and marginal-marine deposits exposed at a quarry near La Serra (Pisa Province), a recently discovered vertebrate site near Montopoli (Merella et al., 2023; Mulè et al., in press). A comparative taxonomic analysis was undertaken to identify the specimens to the lowest possible taxonomic rank. The assemblage was then evaluated within the broader framework of the Pliocene terrestrial fossil record of the Italian Peninsula, thus enabling precise biochronological and palaeoenvironmental interpretations, and providing new insights into its palaeobiological significance.

GEOLOGICAL AND PALAEONTOLOGICAL FRAMEWORK

The La Serra quarry (San Miniato, Pisa Province; GPS geographic coordinates: 43°39′28″ N; 10°48′57″ E) is located in the northwestern sector of the Valdelsa Basin of Tuscany, central Italy (Fig. 1a). This hinterland basin of the Northern Apennines extends for about 60 × 25 km along a SE-NW trending direction. Its sedimentary fill consists of siliciclastic deposits reaching thicknesses of up to 2000 m and ranging chronostratigraphically between the Upper Miocene and the Lower Pleistocene (Benvenuti et al., 2014). The Pliocene portion of this fill comprises fine-grained marine deposits overlain by coarser sediments of both terrestrial and marine origin (Bossio et al., 1993; Dominici et al., 1994, 1995b, 2018; Benvenuti et al., 1995; Sarti et al., 2008).

Garassino et al. (2012) categorised the ca. 25 m-thick succession outcropping at La Serra into four informal stratigraphic units, numbered 1 to 4 in ascending stratigraphic order. Pending a much-needed, comprehensive reassessment of the geology of the quarry site, the fourfold partition of Garassino et al. (2012) is provisionally adopted herein. At the base of the section, mixed sands and silts overlain by cross-stratified sands and massive clays (= the 8 m-thick Unit 1) indicate an estuarine or deltaic depositional setting punctuated by marshes and ponds. The overlying stratal package (Unit 2) is comprised of a 6 m-thick sandy lithosome with high-angle cross-stratification, testifying to a barrier island with submarine longshore dunes and subaerial aeolian dunes. Unit 3, some 5.5 m thick, consists of structureless silts and silty sands that pass laterally to massive clays, hinting at a sheltered, lagoonal environment. Highly fossiliferous clayey sands are found further up section (Unit 4), reflecting a low-energy, lower shoreface to offshore transition depositional setting.

The La Serra quarry is home to a rich and diverse invertebrate record (Garassino et al., 2012; Di Cencio et al., 2021; Coletti et al., 2023) as well as by a significant assemblage of terrestrial, freshwater and marine vertebrates (Merella et al., 2023) (Fig. 1b). Specifically, fossils of the small terrapin *Mauremys* sp. were collected from Unit 1, some of which display telltale trace fossil evidence of parasitism (Collareta et al., 2020a; Mulè et al., 2025a). Remains of the tortoise *Testudo* (*Chersine*) sp. from the same unit represent the first unambiguous record of this genus in the Italian Pliocene (Mulè et al., 2025b). Teeth and postcranial bones of cervids, a suid canine and a coprolite come from the same deposits. A partial proboscidean skeleton, cervid teeth and long bones, fragmentary suid jaws, turtle shell bones and a coprolite originate from Unit 2. A deer antler was found within Unit 3, which had previously been described as barren of vertebrate remains (Garassino et al., 2012). Marine vertebrate remains are known from Unit 4 (e.g., Mulè et al., 2026), including the longest stingray stinger ever described from both the fossil and the recent records (Collareta et al., 2020b).

Garassino et al. (2012) referred the La Serra succession to the uppermost Messinian and Zanclean. However, this interpretation clashes with previous studies that had assigned the same deposits to the Piacenzian (e.g., Benvenuti et al., 1995; Dominici et al., 1995b; Abbazzi et al., 2008). More recently, the La Serra deposits were included by Dominici et al. (2018) into their S6 Synthem, which ranges across the upper Piacenzian and lower Gelasian. In particular, Dominici et al. (2018) regarded the marine strata exposed at La Serra (= Garassino et al.'s [2012] Unit 4) as latest Piacenzian in age, which in turn would imply that the entire succession belongs in a chronostratigraphically restricted interval of the Upper Pliocene. This interpretation is broadly consistent with the recognition of the CNPL zones 3 (pro parte), 4 and 5 (pro parte) in the marine deposits of Unit 4 (Di Cencio et al., 2021) as well as with the biochronological interpretation of the local faunas near Montopoli (also included in S6 deposits according to Dominici et al., 2018) as approaching the Piacenzian-Gelasian transition (De Giuli & Heintz, 1974a, b; Lindsay et al., 1980; Benvenuti et al., 1995; Bartolini-Lucenti et al., 2022).

MATERIALS AND METHODS

Institutional abbreviations

Cetona: Museo Civico per la Preistoria del Monte Cetona, Cetona, Siena Province, Italy; DST-UNIPI: Dipartimento di Scienze della Terra, Università di Pisa, Pisa, Italy; GAMPS: Gruppo AVIS Mineralogia e Paleontologia Scandicci, Scandicci, Florence Province, Italy; IFC-CNR: Istituto di Fisiologia Clinica, CNR, Area della Ricerca di Pisa, Pisa, Italy; ISEM: Institut des Sciences de l'Évolution de Montpellier, Montpellier, France; MCMV: Museo Civico "Palazzo Guicciardini", Montopoli, Pisa Province, Italy; MGGC: Collezione di Geologia "Museo Giovanni Capellini", Alma Mater Studiorum Università di Bologna, Bologna, Italy; MPM: Museo dell'Accademia Valdarnese del Poggio, Montevarchi, Arezzo Province, Italy; MRSN: Museo

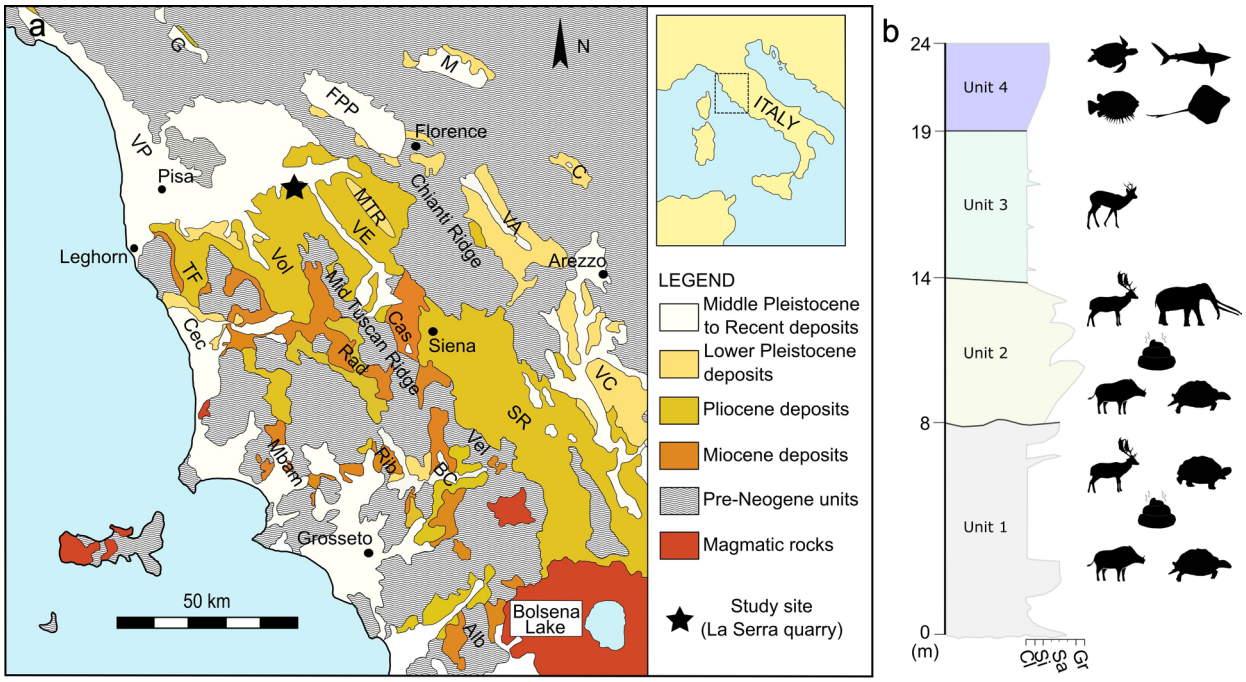


Fig. 1 - (color online) Geographic and stratigraphic setting. a) Simplified geological map of Tuscany (central Italy), redrawn and modified after Benvenuti et al. (2014: fig. 1a). The star indicates the geographic position of the study area. b) Schematic stratigraphic log of the Pliocene succession exposed at the study site, redrawn and modified after Garassino et al. (2012). The four numbers indicate the four informal units recognised by Garassino et al. (2012). The animal silhouettes schematically illustrate the nature of the vertebrate fossils retrieved from each stratigraphic unit: Unit 1 is home to remains of suids, medium-sized cervids, freshwater turtles and tortoises, and coprolites; Unit 2 is home to remains of suids, medium-sized cervids, freshwater turtles and proboscideans, and coprolites; Unit 3 is home to remains of small-sized cervids; and Unit 4 is home to remains of bony fishes, marine turtles, sharks and rays. Abbreviations: Alb, Albegna Basin; BC, Baccinello-Cinigiano Basin; C, Casentino Basin; Cec, Cecina Basin; Cl, clay; FPP, Firenze-Prato-Pistoia Basin; G, Garfagnana Basin; Gr, gravel; M, Mugello Basin; Mbam, Montebamboli Basin; MTR, Montespertoli-Tavernelle Ridge; Rad, Radicondoli Basin; Rib, Ribolla Basin; Sa, sand; Si, Silt; SR, Siena-Radicofani Basin; TF, Tora-Fine Basin; VA, Upper Valdarno Basin; VC, Valdichiana Basin; VE, Valdelsa Basin; Vel, Velona Basin; Vol, Volterra Basin ; VP, Versilia Plain.

Regionale di Scienze Naturali, Turin, Italy; MSNUP: Museo di Storia Naturale dell'Università di Pisa, Calci, Pisa Province, Italy; MUSNAF: Accademia dei Fisiocritici, Siena, Italy; NMB: Naturhistorisches Museum Basel, Basel, Switzerland; Spezia: Museo Archeologico "Ubaldo Formentini", La Spezia, Italy.

Material and repository

The fossil material dealt with herein consists of tooth fragments and postcranial bones from a single proboscidean skeleton; fragmentary maxillae and one canine of Suidae; one antler, teeth and postcranial bones of Cervidae; and two coprolites. The proboscidean remains and an associated cervid tibia are housed in the MSNUP. Each of the fifteen skeletal elements that comprise the proboscidean specimen is identified by a sequential number appended to the shared catalogue number. All other specimens are kept in the permanent exhibition of the GAMPS.

Terminology and measurement methods

Bone determinations and osteological nomenclature are based mainly on Hillson (1992, 2005) and Barone (1995). Dental nomenclature and terminology follow Biondaro et al. (1979) and Tassy (1996, 2014) for proboscideans, and van der Made (1996), Fujita et al. (2000) and Nishioka & Tomida (2022) for artiodactyls. Determination of the wear stage and sequence of tooth eruption and replacement are based on Simpson & Paula-Couto (1957) and Green (2006) for proboscideans; on Zeder & Lemoine (2020) and Wilson et al. (1982) for suids; and on Marín et al. (2024) for cervids. The cervid antler was described based on Vislobokova (2012) and Azanza et al. (2013), while the characterisation of the cervid postcrania follows the nomenclature proposed by Schmid & Garraux (1972) and Brown & Gustafson (1979). Coprolite terminology derives primarily from Jouy-Avantin et al. (2003) and Hunt & Lucas (2021). Measurements of the long bones and teeth follow the protocol introduced by von den Driesch (1976) and subsequently amended by van der Made (1996). Measurements of the proboscidean molars follow Mothé et al. (2010). All measurements were taken with a manual caliper to the nearest 0.1 mm and are reported in Tab. 1. Morphometric comparisons and taxonomic determinations refer mostly to De Guidi (1939), Tassy (1986) and Shoshani & Tassy (2005) for proboscideans; Gallai (2006), Pickford & Obada (2016), Iannucci et al. (2022) and Iannucci (2024) for suids; Stefaniak & Nauk (2015), Cherin et al. (2019) and Pandolfi et al. (2021) for cervids; Chame (2003), Hunt & Lucas (2012) and Yang et al. (2022) for coprolites. Fossil and modern materials stored in several collections were accessed for comparison (see Supplementary Online Materials [SOM] 1). Graphs were elaborated using RStudio.

Non-destructive analyses

In order to obtain histological information, we turned to Computed Tomography (hereinafter, CT). Micro-CT acquisitions were carried out at the IFC-CNR on the GAMPS-2031 coprolite using a Xalt micro-CT scanner (Panetta et al., 2012). Segmentation was performed in 3D Slicer 5.6.2. To determine its major-element composition, the GAMPS-905 coprolite was analysed by means of hand-held energy-dispersive X-ray fluorescence (HHXRF) at the DST-UNIPI, using a NITON XL3t GOLDD+ hand-held spectrometer. Instrumental performance and analytical accuracy are reported in Gemelli et al. (2017).

Photography and 3D imaging

Photographs of all specimens were taken using a Nikon D850 camera equipped with a Nikon Micro Nikkor AF-S 60 mm f/2.8 G ED macro lens. Photomicrographs of the coprolite GAMPS-905 were obtained with a Zeiss Axio Zoom.V16 macroscope equipped with a Zeiss Axiocam 305 colour camera at the DST-UNIPI.

Textured 3D models of several fossils were produced using photogrammetric and structured-light scanning techniques. As for the former method, photographic images were elaborated using Agisoft Metashape Standard (64 bit) and subsequently scaled to their natural size with Blender 3.6.1. The resulting three-dimensional models were uploaded onto the online open-access repository Figshare. A virtual cross-section of the upper canine GAMPS-580 was also made with Blender 3.6.1.

Additional abbreviations

Proboscidean teeth - ccpop = posterior posttrite central conule; ccprp = posterior pretrite central conule; Hpo = maximum height of posttrite; I = morphometric wear index (Hpo/Wpo); m = lower molar; meso = mesoconelet; po = main posttrite cusp (lingual in lower molars); pr = main pretrite cusp (labial in lower molars); Wpo = greater width of posttrite depression (dentine); WS = wear stage.

Proboscidean postcrania - H = maximum distance between ventral surface of vertebral body and apex of neural spine; L = maximum length of rib; Lvb-tc = maximum width across transverse processes; T = maximum thickness of rib at mid-point; Tmed = thickness of medial condyle of distal humeral end; Tmid = thickness of distal humeral end between condyles; Tvb = maximum thickness of vertebral body along dorsal margin; W = maximum width of rib at mid-point; Wvb1 = transverse length of vertebral body (in caudal view); Wvb2 = longitudinal length of vertebral body (in caudal view).

Artiodactyl jaws and teeth - C = upper canine; DAG = dental age group; DAPc = mesiodistal diameter at cervix (not affected by WS), measured lingually; DAPo = mesiodistal diameter in occlusal view (affected by WS); Dmd = transverse (mesiodistal) diameter of C at mid-point; DP = deciduous upper tooth (premolar); dp = deciduous lower tooth (premolar); DTa = linguolabial diameter of first pillar pair; DTp = linguolabial diameter of second pillar pair; Dvd = dorsoventral diameter of C at mid-point; Ha = height of the paraconid on labial side; Hh = height of mandible from mid-point of m1 cervix, measured lingually; Hp = height of metaconid on labial side; Ht = mandible thickness at mid-point of m1 cervix; Ld = length of canine profile along dorsal margin; Lv = length of canine profile along ventral margin; M = upper molar; m = lower molar; p = lower premolar; WG = wear group; WS = wear stage.

Cervid antler - DAD = distal anteroposterior diameter; DTW = distal transverse diameter; H = distance between base of burr and first bifurcation; PAD = proximal anteroposterior diameter; PTW = proximal transverse width.

Cervid postcranial bone - DAP = maximal anteroposterior diameter; DT = maximum transverse diameter; Lmax = maximum length.

Coprolites - L = maximum length; T = maximum thickness; W = maximum width.

SYSTEMATIC PALAEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Proboscidea Illiger, 1811
Family Gomphotheriidae Hay, 1922
Subfamily Anancinae Hay, 1922

Genus *Anancus* Aymard *in* Dorlhac, 1855

Anancus arvernensis (Croizet & Jobert, 1828)
(Figs 2, 3; Tab. 1)

Referred material - MSNUP I-16959, an incomplete skeleton including an incomplete lower third molar (MSNUP I-16959/1), a molar fragment (MSNUP I-16959/2), a cervical vertebra (MSNUP I-16959/3), a thoracic vertebra (MSNUP I-16959/4), three vertebral fragments (MSNUP I-16959/5, MSNUP I-16959/6, MSNUP I-16959/7), two fairly complete ribs (MSNUP I-16959/8, MSNUP I-16959/9), five rib fragments (MSNUP I-16959/10 to MSNUP I-16959/14) and a partial humerus (MSNUP I-16959/15). All these bones were found a few tens of centimetres apart from one another and within the same stratigraphic horizon. They are anatomically consistent with one another and suggestive of a similar ontogenetic stage (see below).

Three-dimensional models - MSNUP I-16959/1, https://doi.org/10.6084/m9.figshare.31971249; MSNUP I-16959/2, https://doi.org/10.6084/m9.figshare.31971300; MSNUP I-16959/3, https://doi.org/10.6084/m9.figshare.31971312; MSNUP I-16959/4, https://doi.org/10.6084/m9.figshare.31971336; MSNUP I-16959/9, https://doi.org/10.6084/m9.figshare.31901203; MSNUP I-16959/15, https://doi.org/10.6084/m9.figshare.31971345.

Stratigraphic provenience - Upper Pliocene deposits exposed at La Serra; Unit 2 of Garassino et al. (2012).

Descriptive remarks - MSNUP I-16959/1 is a fairly well preserved, incomplete bunolophodont tooth fragment featuring two incomplete lophids and the fragmentary root (Fig. 2a1-a2; Tab. 1). Based on comparisons with other Pliocene and lowermost Pleistocene proboscidean teeth from museum collections (e.g., MSNUP I-12608, figured in De Guidi, 1939: pl. V; see also "Comparative materials"

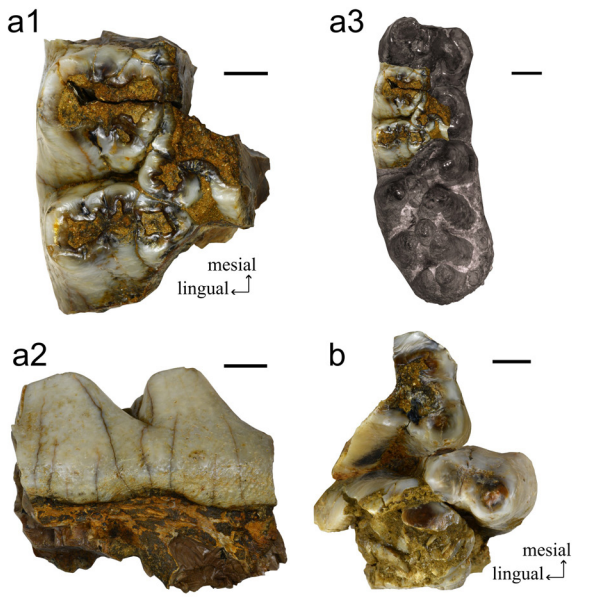


Fig. 2 - (color online) *Anancus arvernensis*, dental remains from La Serra (Tuscany). a) MSNUP I-16959/1, lower third molar fragment (m3) in occlusal (a1) and lingual (a2) views; a3) the same as (a1), superimposed on a complete m3 of *A. arvernensis* exhibiting a similar degree of occlusal wear (MRSN PU 14864 from Pralormo, Piedmont). b) MSNUP I-16959/2, fragmentary molar (m3?) in occlusal view. Scale bars = 10 mm (a1-a3); 20 mm (b).

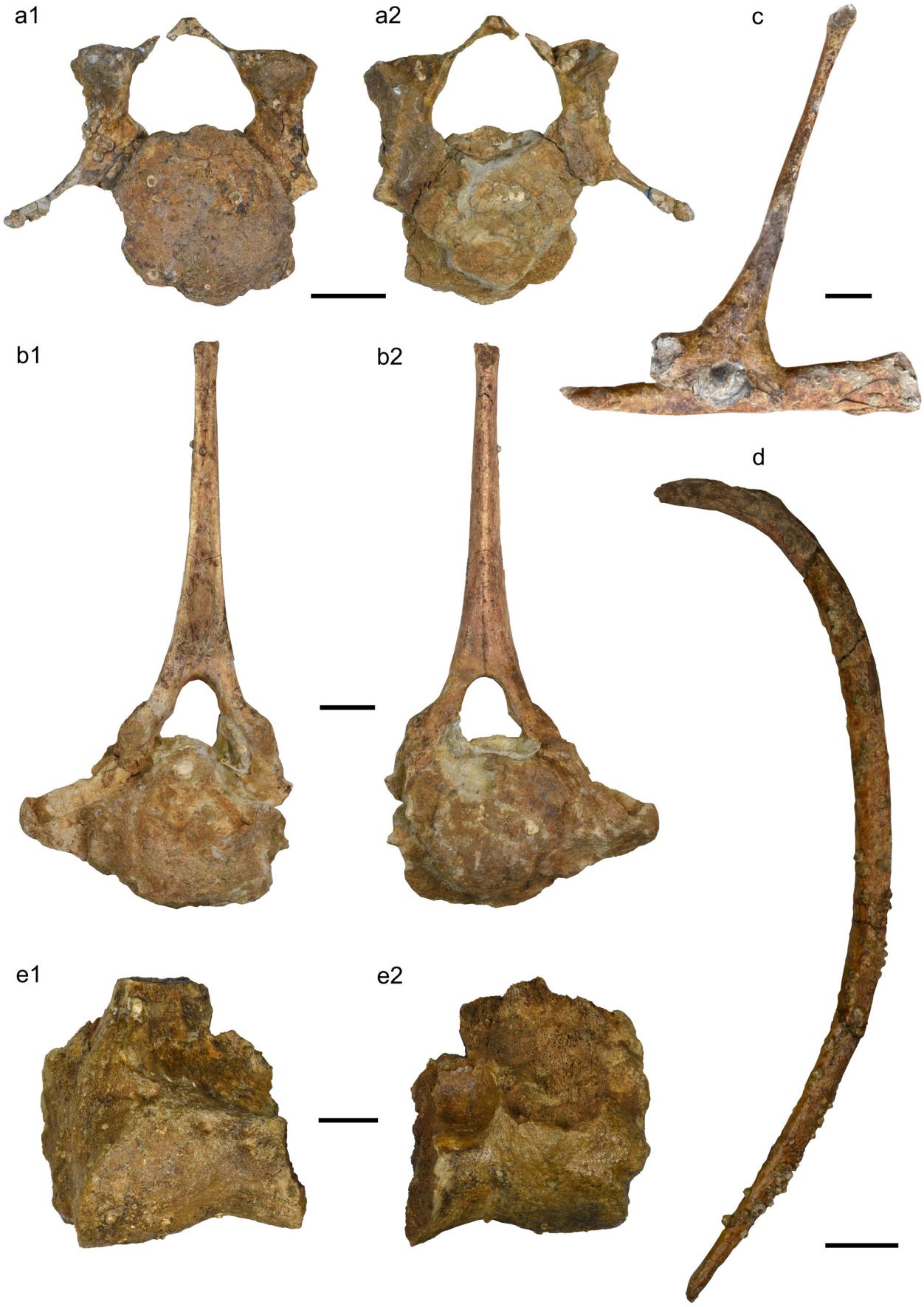
in SOM 1) and previously published illustrations (e.g., Hautier et al., 2009: fig. 4b), it is identified herein as a right m3 (Fig. 2a3). The cervix is sinuous and the crown is very high, contrasting with the generally straight cervix and shorter crown that are typical of upper molars. The cross-sections of the cuspids are circular (as characteristic of mesial cuspids) rather than triangular (as typical of distal cuspids). In occlusal view, the tooth enamel of all cusps is moderately wrinkled. The second lingual half-lophid lacks the mesial margin and exhibits a subcircular profile in occlusal view. It preserves the main cusp, the po2 and, labially, the meso2. A small ccpop2 is observed along the labiodistal margin of the fragment. A very small fragment of the second labial half-lophid is also preserved adjacent to the labiomesial margin of the second lingual lophid. The second labial half-lophid is characterised by a partially complete pr2 and a complete ccprp2. The third lingual half-lophid is separated from the second by a transversely oriented V-shaped valley. In occlusal view, the third half-lophid displays an elliptical profile, and, in lingual view, it is more mesially inclined than the second lophid. The main cusp, the po3, bears a constriction and, in the labialmost lobe, the meso3. The lingual and labial half-lophids are separated from each other by a median sulcus. MSNUP I-16959/2 is a more fragmentary bunolophodont tooth (Fig. 2b) that may be identified as a left m3 (cf. MRSN PU 14872; Loss, 1946), preserving pr3, pr4 and po4. As for the postcranial bones, MSNUP I-16959/3 is probably a third cervical vertebra. It exhibits a very short spinous process and transverse processes pierced by transverse foramina (cf. Bezuidenhout & Seegers, 1996: figs 7-10; Zehtabvar et al., 2022: figs 2, 5; Belyaev et al., 2025: fig. 2a). Its spongy bone is extensively exposed due to widespread abrasion (Fig. 3a1-a2; Tab. 1), as also observed on the thoracic vertebra MSNUP I-16959/4 (see Mulè et al., in press: fig. 3b). The latter specimen bears a long, straight spinous process and short, stocky, horizontally projecting transverse processes (Fig. 3b1-b2; Tab. 1). The shape of the vertebral foramen is sub-triangular, with a dorsally rounded profile. Based on these characters, MSNUP I-16959/4 may represent the second thoracic vertebra (cf. Bezuidenhout & Seegers, 1996: figs 11-12; Belyaev et al., 2025: fig. 2b). MSNUP I-16959/5 is an incomplete, poorly informative thoracic vertebra. MSNUP I-16959/6 and MSNUP I-16959/7 are isolated spinous processes. The latter was found contacting MSNUP I-16959/8 (Fig. 3c), which seemingly corresponds to the first right rib (cf. Sismonda, 1851: pl. IV, fig. 1; Bezuidenhout & Seegers, 1996: figs 31-32). MSNUP I-16959/9 is a long, slender left rib that lacks both the distal and proximal extremities (cf. Sismonda, 1851: pl. IV, figs 6-8; Bezuidenhout & Seegers, 1996: figs 33-34) (Fig. 3d; Tab. 1). Other collected bones include five rib fragments (MSNUP I-16959/10-14) (Tab. 1). The left humerus, MSNUP I-16959/15, only preserves the distal epiphysis (Fig. 3e1-e2; Tab. 1). The medial epicondyle is complete, while the lateral epicondyle is damaged. The humeral trochlea and radial fossa are visible.

Wear stage and age estimation - Considering the horizontal tooth displacement characteristic of proboscideans (Sanders, 2017; Schiffmann et al., 2019), MSNUP I-16959/1, recognised as an incomplete m3 fragment, likely belongs to an adult individual, because in extant elephants m3 erupts at approximately 28 years of age and is retained until death (Moss, 1996). MSNUP I-16959/1 was probably housed in a mandible where a more heavily worn m2 was still present (cf. MSNUP I-12608, figured in De Guidi, 1939: pl. V; Boeuf, 1992). It falls within tooth WS 3 as per the scheme proposed by Simpson & Paula-Couto (1957: tab. 1, p. 137) and later modified by Green (2006: tab. 1, p. 32) and Bravo-Cuevas et al. (2015). Such a wear stage is typically found in mature/senile adult individuals (Haynes, 1991), which in turn suggests an age at death of about 50 years based on American mastodons (Mothé et al., 2010: fig. 5).

The other tooth fragment, MSNUP I-16959/2, probably represents the posterior end of the left m3. That its cusplets are less worn than those of MSNUP I-16959/1, yet still consistent with an adult age at death, may be due to the fact that the anterior portions of molars begin to experience wear earlier than the posterior portions thereof (Boeuf, 1992). That said, it is also worth noting that different degrees of wear may be observed on contralateral teeth of the same proboscidean individual owing to strongly asymmetrical occlusion (Schiffmann et al., 2019). A striking example of this is provided by NMB V.J.301, an adult *A. arvernensis* mandible from the Pliocene of Asti (Piedmont, northern Italy), where the left and right m3s exhibit markedly different wear stages.

As for the postcranial bones, they display adult morphological features, such as fused epiphyses in the ribs and humerus (Roth, 1984; Lister, 1999).

Taxonomic determination and comparisons - Both MSNUP I-16959/1 and MSNUP I-16959/2 are mesodont molars with a complex bunolophodont structure, a


a1
a2
c
b1
b2
d
e1
e2

diagnostic feature of gomphothere proboscideans (Osborn, 1942; Shoshani & Tassy, 2005). The sole widely accepted gomphothere species bearing this type of molars in Western Europe is *Anancus arvernensis*, which persisted in Italy throughout the Pliocene and into the Early Pleistocene (Garrido & Arribas, 2014; Konidaris & Roussiakis, 2018). Traditionally assigned to the family Gomphotheriidae, subfamily Anancinae (Garrido & Arribas, 2014; Ros-Montoya et al., 2017; Konidaris & Roussiakis, 2018), this taxon has recently been placed within the newly erected family Tetralophodontidae by Larramendi & Ferretti (2026).

Anancus arvernensis is characterised by tetralophodont intermediate molars and upper third molars with five or six lophs. Anancoidy, defined as the alternating arrangement of labial and lingual half-loph(id)s (Maglio, 1972; Tassy, 1986; Hautier et al., 2009), is variable in the species, as are also the development of accessory cusps and the complexity of enamel folding. Four subspecies are often recognised within *A. arvernensis* based mostly on characters found on the molars (Konidaris & Roussiakis, 2018): *A. arvernensis arvernensis* (Croizet & Jobert, 1828), a strictly Pliocene (MN14-MNQ16) subspecies from eastern and southern Europe; *A. arvernensis falconeri* Osborn, 1926, from England (MNQ16-17a; Guérin, 2004); *A. arvernensis mencalensis* Garrido & Arribas, 2014, from Spain (MNQ17a); and *A. arvernensis chilhiacensis* (Boeuf, 1992), from France (MNQ17b). Several morphometric changes, including a reduction in size of M3 and a decrease in the degree of anancoidy, may be tracked along the *A. arvernensis arvernensis-A. arvernensis mencalensis-A. arvernensis chilhiacensis* lineage (Garrido & Arribas, 2014). Such changes have been proposed to represent an adaptive response to aridification at and around the beginning of the Pleistocene (Szabó et al., 2022). Nevertheless, further studies are required to better evaluate these evolutionary trends as illustrations remain scarce in the literature. The sole subspecies known to occur in Italy during the Pliocene, *A. arvernensis arvernensis*, exhibits a pronounced degree of anancoidy, five or six lophs in M3, and moderately developed to coarse enamel folds (Garrido & Arribas, 2014). In the specimens examined here, anancoidy appears to be well developed, while enamel folding is moderate, possibly supporting an attribution to *A. arvernensis arvernensis*. Furthermore, the La Serra teeth are strongly reminiscent of MRSN PU 14864, a hexalophodont m3 from Pralormo, Piedmont (Triversa FU), as well as of MSNUP I-12608, another m3 from the Tuscan site of Marti, near Montopoli (Montopoli FU) (De Guidi, 1939: pl. I). These specimens exhibit a wear stage and degree of anancoidy comparable to those observed in the La Serra material. The pattern of crown ornamentation observed in MSNUP I-16959/1 and MSNUP I-16959/2 is particularly similar to the Piedmontese molar, which displays a more obviously wrinkled enamel than the Tuscan specimen MSNUP I-12608.

As regards the ribs and vertebrae, descriptions and illustrations of proboscidean postcrania are not widespread in the literature, and where available, they often refer to taxa younger than *Anancus* (Sismonda, 1851; Zanchetta & Mazza, 1996; Göhlich, 2010; Belyaev et al., 2025; Stefanelli et al., 2026). That said, the cervical vertebra MSNUP I-16959/3 exhibits a typical proboscidean design (Bezuidenhout & Seegers, 1996) in that it is strongly compressed anteroposteriorly and disk-shaped overall (Olsen, 1979). Moreover, the shape of the vertebral foramen is dorsally rounded as observed in mastodons, rather than triangular as typical of mammoths (Olsen, 1979; Baigusheva & Titov, 2021: fig. 3). Further reminiscent of mastodons (Olsen, 1979), the thoracic vertebra MSNUP I-16959/4 features a sharp spine on the anterior face of the spinous process as well as a shallow, poorly defined concavity on the posterior face thereof. In addition, the arch is higher and thinner, and the centrum is slenderer than typically observed in mammoths. Based on direct observations of comparative material (listed in full in the SOM), the studied vertebrae and ribs are found to be morphologically consistent with those of *Anancus arvernensis*, including materials described by Boscato et al. (2008) from the Lower Pliocene of Cetona, Tuscany, as well as the Piedmontese specimens MGGC 8443 (from the surroundings of Asti) and MRSN PU 14831 (from San Paolo Solbrito).

While the proboscidean skeleton from La Serra can be confidently assigned to *Anancus arvernensis*, a more precise attribution to *A. arvernensis arvernensis* is not embraced herein. This caution is due to the limited representativeness and fragmentary nature of the molars from La Serra, as well as to the paucity of detailed studies regarding the taxonomic value of dental characters and dental evolutionary trends within *A. arvernensis*.

Order Artiodactyla Owen, 1848
Family Suidae Gray, 1821
Subfamily Suinae Gray, 1821

Genus *Sus* Linnaeus, 1758

Sus arvernensis (Croizet & Jobert, 1828)
(Figs 4-6; Tab. 1; SOM 2)

Referred material - GAMPS-580, upper canine; GAMPS-1999, fragmentary maxilla with deciduous teeth; GAMPS-2000, fragmentary maxilla with deciduous teeth and first molar.

Three-dimensional models - GAMPS-580, https://doi.org/10.6084/m9.figshare.31889695; GAMPS-1999, https://doi.org/10.6084/m9.figshare.31889713; GAMPS-2000, https://doi.org/10.6084/m9.figshare.31889725.

Fig. 3 - (color online) *Anancus arvernensis*, postcranial remains from La Serra (Tuscany). a) MSNUP I-16959/3, cervical vertebra. b) MSNUP I-16959/4, thoracic vertebra. c) MSNUP I-16959/7, fragmentary vertebra, and MSNUP I-16959/8, fragmentary rib. d) MSNUP I-16959/9, fairly complete rib. e) MSNUP I-16959/15, fragmentary humerus. Specimens are shown in cranial (a2, b2, c [for the vertebra], e1), caudal (a1, b1, d, e2) and medial (c [for the rib]) views. Scale bars = 50 mm.

Stratigraphic provenience - Upper Pliocene deposits exposed at La Serra; GAMPS-580 from Unit 1 of Garassino et al. (2012); GAMPS-1999 and GAMPS-2000 from Unit 2.

Descriptive remarks - GAMPS-580 is a large, open-rooted, dorsally bent tooth, best interpreted as a left C (Fig. 4a1-a4; Tab. 1). A longitudinal groove runs along the concave dorsal tooth surface from the base of the root to close to the tip of the crown. A leaf-shaped wear facet extends along the mesiolingual surface, from the crown apex to the central area thereof. Parallel, longitudinal enamel striae ornament the convex ventral tooth surface.

GAMPS-1999 is a fragmentary left maxilla featuring three fully erupted bunodont teeth (Fig. 4b1-b3; Tab. 1). These are interpreted as deciduous teeth. DP2 has an elliptical occlusal profile, while its outline is triangular in labial and lingual views. The main cusps are the paraconid and metacone. A prestile occupies the mesial area of the crown, being more developed on the labial side and featuring accessory cuspids. A rounded protocone is observed on the linguodistal margin of the crown, bearing smaller cusplets. DP3 exhibits a triangular profile in occlusal view. Mesially, a prestile develops on the labial side, bearing accessory cusplets. The paracone is the main cusp on the mesial side, while the metacone (labial) and the protocone (lingual) are observed more distally, beyond a transverse valley. The distal margin of DP3 is adjacent to the mesial margin of DP4 and characterised by a weakly developed cingulum. DP4 is molariform, bilobate, provided with four main tubercles, and rectangular in profile when observed in occlusal view. The main cusps are separated from each other by the transverse and longitudinal valleys, which cross each other in the central area of the crown, at the level of the tetrapreconule. The mesial and distal cingula are well developed, with accessory cusplets. The labial cusps are located more mesially than the lingual cusps. The highest and widest cusp is the paracone, which exhibits a small cusplet along the lingual margin. The enamel is characterised by additional accessory cusplets and crests that provide the crown with a somewhat folded pattern. The M1 is still unerupted, being largely embedded within the maxilla.

GAMPS-2000 is a fragmentary left maxilla preserving a fragment of the adjoining palatine (Fig. 4c1-c3; Tab. 1). Three bunodont teeth are completely erupted, conforming to tooth positions DP3, DP4 and M1. DP3 and DP4 are very similar to the corresponding teeth of GAMPS-1999, yet they display a greater degree of wear. M1 is broadly similar to DP4, yet larger and taller overall. Cingula are especially well developed along the mesial and distal margins of M1, and bear smaller cusplets, including the protopreconule and the pentapreconule. The crown is highly complicated throughout its enamelled surface. P3 is still unerupted, being largely embedded within the maxilla underneath DP3.

Wear stage and age estimation - Considering the shape and extent of its wear facet, the upper canine GAMPS-580 likely originates from an adult individual, probably a male (cf. Iannucci, 2024: pl. 5). In turn, considering the presence of deciduous teeth (DP3 and DP4), the stage of wear of DP2 and DP3, the unworn aspect of DP4, and the unerupted M1 (which erupts at approximately four-six months of age in the extant wild boar and domestic pig; Wilson et al., 1982), the fragmentary maxilla GAMPS-1999 seemingly testifies to an age at death of a few months. Owing to the presence of deciduous teeth, the very low WS of DP3, and the unworn aspect of DP4 and M1 (WG = 1, WS = 8; Zeder & Lemoine, 2020), the fragmentary maxilla GAMPS-2000 also originates from a young individual slightly older than GAMPS-1999.

Taxonomic determination and comparisons - Three suid genera are known from the Italian Neogene and Quaternary, namely, *Eumaiochoerus*, *Propotamochoerus* and *Sus*. The monotypic *Eumaiochoerus* is a Tusco-Sardinian endemic of late Tortonian to early Messinian age (early Turolian, MN12) (Mazza & Rustioni, 1996; Gallai, 2006, 2007; Abbazzi et al., 2008). The restricted palaeogeographic and chronostratigraphic distribution of this species (Rook et al., 2006) are at odds with the depositional setting and geological age envisioned for the fossiliferous strata exposed at La Serra (Benvenuti et al., 1995; Dominici et al., 2018; Di Cencio et al., 2021). *Propotamochoerus* has been recorded at several Messinian localities of Italy, including Verduno (Sorbelli et al., 2019) in Piedmont; Baccinello-V3 (Gallai, 2006, 2007; Lazaridis et al., 2022), the Casino Basin (Iannucci et al., 2021; Lazaridis et al., 2022) and the Velona Basin (Ghetti et al., 2002) in Tuscany; and Gravitelli (Gallai & Rook, 2006; Lazaridis et al., 2022) in Sicily. Whether this genus crossed the Miocene-Pliocene transition is uncertain at present (Gallai & Rook, 2011; Iannucci et al., 2021; Lazaridis et al., 2022). *Sus* made its first documented appearance in Italy with the small-sized *Sus arvernensis* (e.g., Iannucci & Sardella, 2023). This species has been reported at Villafranca d'Asti and Bra in Piedmont (Dal Piaz, 1930; Pickford & Obada, 2016; Iannucci, 2024); Pievefosciana (= *Sus minor* Depéret, 1890 in Coltorti et al., 2008) and Val di Pugna (Azzaroli, 1992b; Gallai, 2006, 2007) in Tuscany; and Collepardo (Bellucci et al., 2012; Guérin & Tsoukala, 2013; Iannucci et al., 2022) in Latium. A larger species, *Sus strozzii* Forsyth Major, 1881, seemingly replaced *S. arvernensis* during the Early Pleistocene (e.g., Cherin et al., 2018, 2020; Azzarà et al., 2022).

According to Gallai (2006), male upper canines of *Sus* have a subcircular cross-section, while those of *Propotamochoerus* are characterised by a more triangular cross-section (cf. Iannucci et al., 2021: fig. 4b1-b3). A virtual cross-section of GAMPS-580 at mid-length reveals a subcircular profile (Fig. 5a1-a2) that is strongly reminiscent of that of NMB V.J.147, a male upper canine of *Sus arvernensis* from Villafranca d' Asti (Iannucci et al., 2024: pl. 5, fig. 7) (Fig. 5b1-b2). More generally, GAMPS-580 is morphologically close to other male upper canines of *S. arvernensis* from the same Piedmontese locality (Iannucci, 2024: pl. 5, figs 5, 8). Upper canines of *S. strozzii* (e.g., Cherin et al., 2020: fig. 3A-C) are typically larger than both GAMPS-580 and the *S. arvernensis* specimens from Villafranca d'Asti.

As for the postcanine teeth, unlike *Propotamochoerus*, which typically exhibits thicker and less complex enamel (Gallai & Rook, 2006, 2011; Pickford, 2013; Iannucci et al., 2021), GAMPS-1999 and GAMPS-2000 share the thinner and more complex enamel characteristic of *Sus*

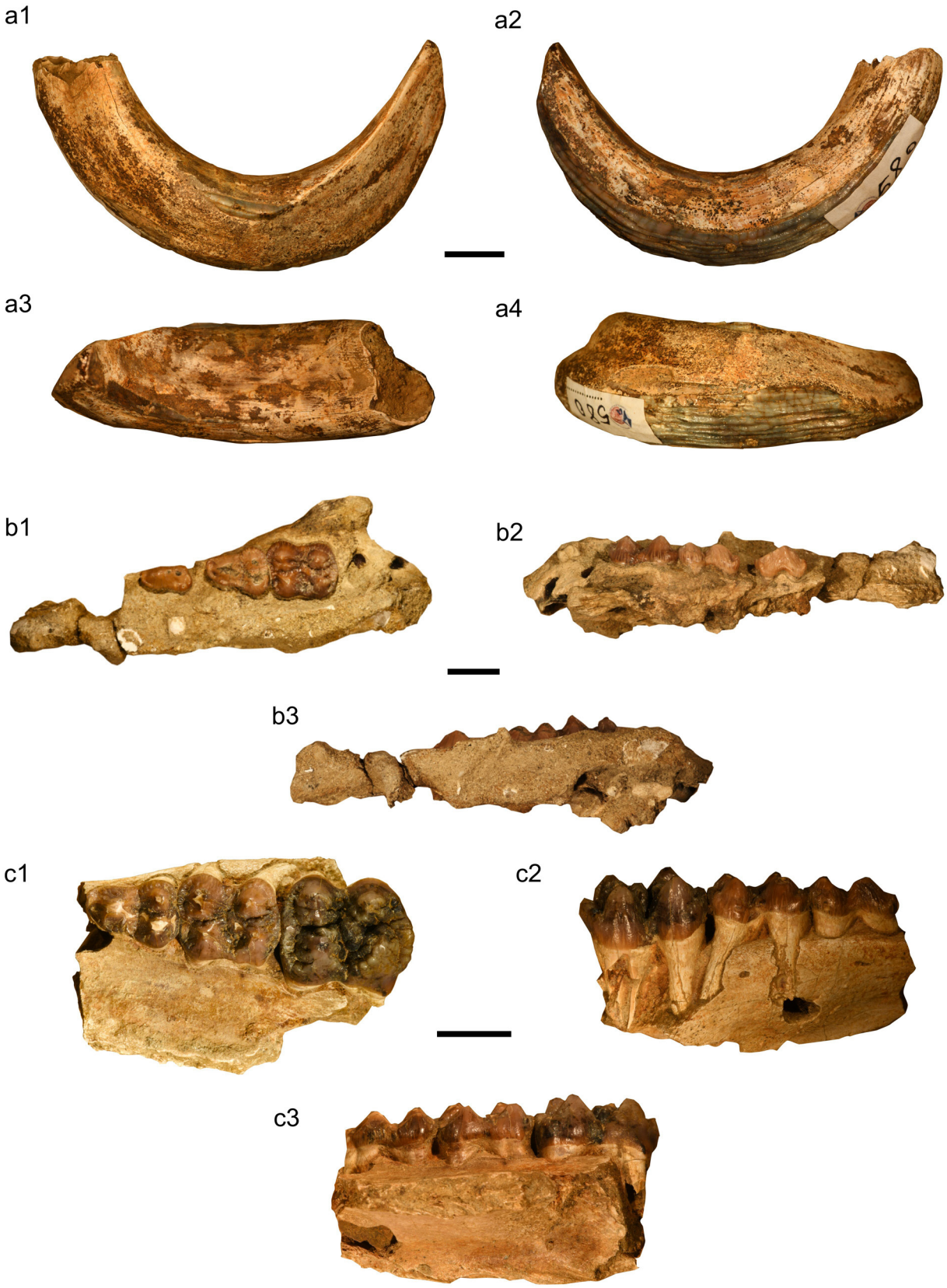


Fig. 4 - (color online) *Sus arvernensis*, dental and cranial remains from La Serra (Tuscany). a) GAMPS-580, upper canine in mesial (a1), distal (a2), dorsal (a3) and ventral (a4) views. b) GAMPS-1999, maxilla with deciduous teeth in occlusal (b1), labial (b2) and lingual (b3) views. c) GAMPS-2000, maxilla with deciduous teeth and first molar in occlusal (c1), labial (c2) and lingual (c3) views. Scale bars = 10 mm.

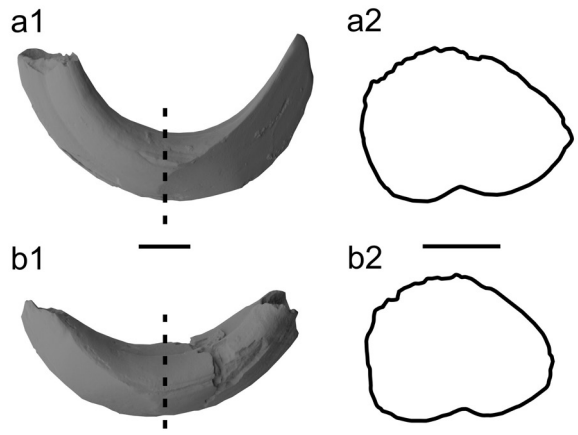


Fig. 5 - Comparisons of upper canines of *Sus arvernensis* from the Italian Pliocene. a) GAMPS-580, left upper canine from La Serra (Tuscany); medial (a1) view and digital cross-section (a2) at mid-point. b) NMB V.J.147, right upper canine from Villafranca d'Asti (Piedmont); medial (b1) view and digital cross-section (b2) at mid-point. Scale bars = 10 mm.

(Cherin et al., 2018; Iannucci, 2023, 2024). Moreover, the main morphological characters listed by Iannucci (2024) for the first upper molars of *S. arvernensis* from Villafranca d'Asti can be recognised in the suid material from La Serra. Specifically, the folded enamel pattern of GAMPS-1999 and GAMPS-2000 appears to be most consistent with that of *S. arvernensis* (cf. Montoya et al., 2006: fig. 4; Guérin & Tsoukala, 2013: fig. 16A-C; Pickford & Obada, 2016: fig. 2; Iannucci et al., 2024: pls 1-4, 6-8). Further supporting an attribution to *S. arvernensis*, the cheek teeth of *S. strozzii* typically display a higher number of accessory cuspids relative to the specimens from La Serra (cf. Cherin et al., 2020: fig. 3; Iannucci, 2023: fig. 2).

Measurements of cheek teeth, particularly deciduous premolars, are rarely reported in literature, and when they are, the measurement criteria are only sporadically specified. Dimensions of the deciduous premolars and first molars of GAMPS-1999 and GAMPS-2000, as well as of *Eumaiochoerus etruscus* (Michelotti, 1861), *Propotamochoerus* spp., *Sus arvernensis* and *Sus strozzii* from different localities, are reported in SOM 2. Most importantly, considering DAPc and DTp, M1 from La Serra (GAMPS-1999) overlaps dimensionally with *E. etruscus* and *S. arvernensis* (Fig. 6), while the corresponding dental positions are larger in *Propotamochoerus* spp. and *S. strozzii* (cf. van der Made & Moya-Solà, 1989: fig. 4; Guérin et al., 1998: fig. 2, tab.1; Montoya et al., 2006: figs 5-6; Guérin & Tsoukala, 2013: tab. 13; Pickford, 2013: fig. 16; Cherin et al., 2018: fig. 5; Cherin et al., 2020: fig. 5; Iannucci et al., 2021: fig. 5; Iannucci, 2023: fig. 4). In conclusion, the suid specimens from La Serra are confidently referred to *Sus arvernensis*.

Family Cervidae Goldfuss, 1820
Subfamily Capreolinae Brookes, 1828

Genus *Procapreolus* Schlosser, 1924

Procapreolus cf. *cusanus* (Croizet & Jobert, 1828)
(Fig. 7; Tab. 1; SOM 2)

Referred material - GAMPS-2001, incomplete antler.

Three-dimensional models - GAMPS-2001, https://doi.org/10.6084/m9.figshare.31889497.

Stratigraphic provenience - Upper Pliocene deposits exposed at La Serra; GAMPS-2001 from Unit 3 of Garassino et al. (2012).

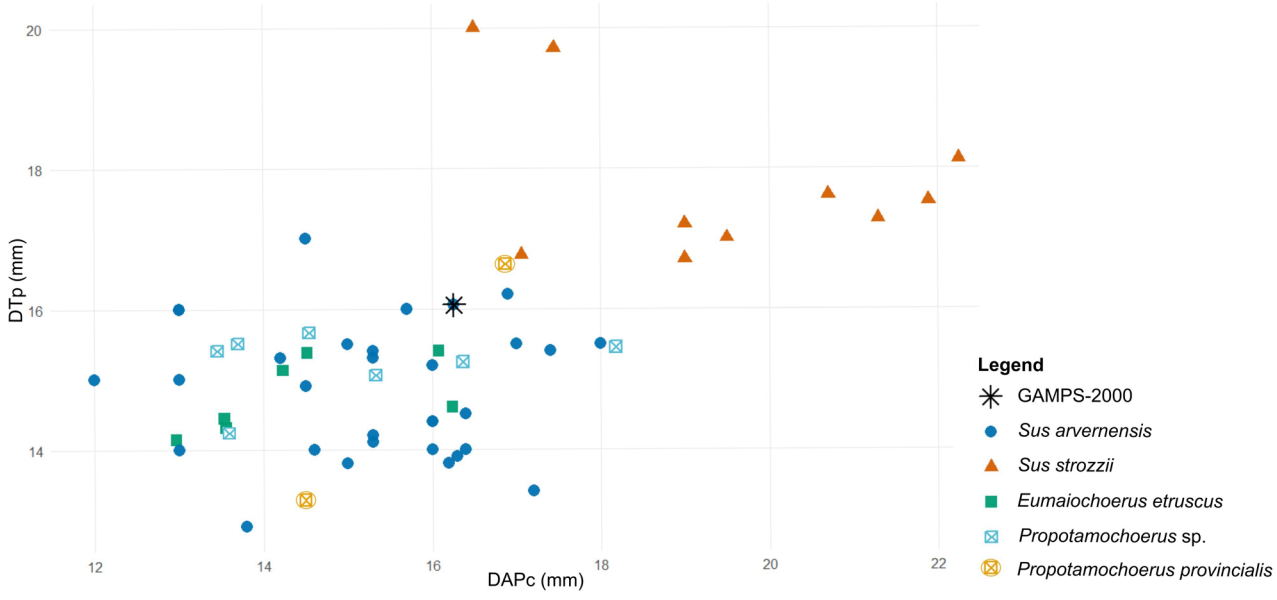


Fig. 6 - (color online) Measurements (DAPc vs DTp) of suid upper first molars (M1) from the Italian Neogene and Quaternary. See SOM 2 for data sources.

Descriptive remarks - GAMPS-2001 is an incomplete left antler, including the pedicle, burr and shaft, up to the first bifurcation (Fig. 7a1-a5; Tab. 1). The pedicle lacks most of its base. It displays a roughly cylindrical structure and a subcircular transverse section. The burr exhibits distinct pearling and a greater girth than the pedicle. Dorsal to the burr, the antler sensu stricto is only partially preserved. The beam is mediolaterally flattened and distinctly slanted backwards. The first bifurcation, located at a moderate distance from the burr, leads to a narrow, cylindrical dagger tine as well as to a wider, flatter caudal tine. The former is more laterally inclined than the latter and gives rise to the main beam. The beam exterior is characterised by well-developed ridges and furrows with V-shaped floors.

Age estimation - GAMPS-2001 displays all characters typical of antlers from mature individuals, including a well-developed burr and a fully formed beam (Cassinello et al., 2026). An antler fragment with comparable shape and measurements was illustrated by Heintz (1970: fig. 76) from the French Pliocene locality of Les Étouaires and interpreted as belonging to an adult individual with incomplete annual antler growth. The presence of the pedicle suggests that the antler was not naturally shed, but rather lost post-mortem due to breakage (Heintz, 1970; Kierdorf & Kierdorf, 2011).

Taxonomic determination and comparisons - The systematics of extinct cervids is complex and widely debated (Azzaroli, 1947; Croitor, 2014, 2018). Based on its morphology and dimensions (measurements reported in SOM 2), GAMPS-2001 differs from *Cervavitus* (Petronio et al., 2007), *Eostyloceros* (Abbazzi & Croitor, 2003; Croitor & Stefaniak, 2009), *Euprox* (Heckeberg, 2017), *Lucentia* (Azanza & Montoya, 1995), *Paracervulus* (Dong, 1996; Abbazzi, 2001), *Pliocervus* (Colombero et al., 2017), *Croizetoceros* (Heintz, 1970; Crégut-Bonnoure & Tsoukala, 2017) and "*Pseudodama*" (Abbazzi et al., 1995) in displaying a marked flattening of the beam, a moderate distance (around 7 cm) from the burr to the first bifurcation, two branches of different size, and a twisted, inclined beam.

GAMPS-2001 is particularly reminiscent of the three-pointed antlers of *Procapreolus*, which display a marked flattening of the beam as well as a short first ramification (Heintz, 1970; Abbazzi et al., 1995; Zapfe, 1997; Abbazzi, 2001). In particular, GAMPS-2001 shares the following morphological features with *Procapreolus*: 1) a relatively short, cylindrical pedicle; 2) a robust, slightly anteriorly sloping burr with distinct pearling; 3) a distance between the burr and the first bifurcation only slightly greater than the length of the pedicle; 4) a somewhat lyre-shaped beam that progressively flattens distally; 5) a laterally concave, medially flat outer beam surface; 6) a first bifurcation leading to a small, cylindrical anterior branch and to an expanded, elliptical posterior branch from which the main beam develops; 7) a shaft ornamented with longitudinal ridges and furrows; and 8) an anti-clockwise twist of the beam.

The studied specimen is very similar to an antler fragment of *Procapreolus* cf. *loczyi* Pohlig, 1911 from the uppermost Miocene of the Monticino quarry (Emilia-Romagna, Italy; Pandolfi et al., 2021: fig. 4a1-a3). However, GAMPS-2001 differs from the Monticino specimen in its greater beam inclination, more pronounced anticlockwise twist relative to the burr and stronger compression of the shaft close to the first bifurcation. GAMPS-2001 further resembles *Procapreolus* cf. *loczyi* from Baccinello-V3 (Abbazzi, 2001) by exhibiting a robust burr, a mediolaterally compressed beam that is twisted relative to the burr, and grooves and ridges ornamenting the beam's outer surface. GAMPS-2001 shares with *P. loczyi* from Mönchhof (Austria; Zapfe, 1997) a similar cross-section of the burr, but the shaft is more cylindrical in the Austrian specimen. That said, a high degree of morphological variability has been recognised in *P. loczyi* antlers by Croitor (2018) and, much earlier, by Pohlig (1911). From a morphometric perspective, GAMPS-2001 is also consistent with *Procapreolus vesti* Korotkevich, 1970, while it appears to differ from *Procapreolus cusanus* and *Procapreolus moldavicus* (Janovskaya, 1954) based on the less cylindrical cross-section of the beam and shorter distance between the base of the burr and first

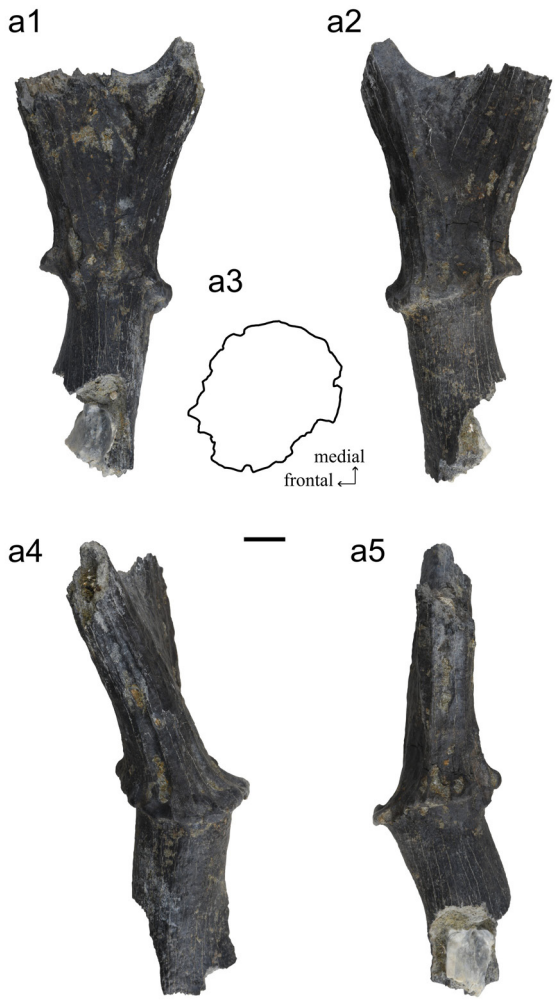


Fig. 7 - (color online) *Procapreolus* cf. *cusanus*, antler from La Serra (Tuscany). GAMPS-2001, in medial (a1), lateral (a2), frontal (a4) and caudal (a5) views. A digital cross-section of the burr is shown in (a3). Scale bar = 10 mm.

Anancus arvernensis							
		Hpo2	**Wpo2**	**I2**	**Hpo3**	**Wpo3**	**I3**
Lower third molar fragment (MSNUP I-16959/1)	m3	44.8	28.6	1.56	47.2	29.8	1.58
		H	**Lvb-tp**	**Tvb**	**Wvb1**	**Wvb2**	
Cervical vertebra (MSNUP I-16959/3)	vertebra	207		25	127	128	
Thoracic vertebra (MSNUP I-16959/4)	vertebra	487	292 (estimated)	52	126	118	
		L	**W**	**T**			
Fairly complete rib (MSNUP I-16959/8)	rib	382	53				
Fairly complete rib (MSNUP I-16959/9)	rib	945	38	29			
Fragmentary rib (MSNUP I-16959/10)	rib	526	43				
		Tmid	**Tmed**				
Partial humerus (MSNUP I-16959/15)	distal end	93	150				
Sus arvernensis							
		Ld	**Lv**	**Dmd**	**Dvd**		
Upper canine (GAMPS-580)	C	72.1	114.3	24.3	17.7		
		DAPo	**DAPc**	**DTa**	**DTp**	**Ha**	**Hp**
Fragmentary maxilla with deciduous teeth (GAMPS-1999)	DP2	10.81	9.67	4.54	5.5	6.55	4.57
	DP3	13.36	12.16	5.1	9.82	5.51	5.77
	DP4	14.43	14.33	11.42	11.17	5.85	5.48
Fragmentary maxilla with deciduous teeth and first molar (GAMPS-2000)	DP3	13.1	13.41	6.5	9.77	5.87	5.33
	DP4	13.55	13.28	12.17	11.79	5.86	9.15
	M1	18.09	16.26	15.21	16.05	6.13	8.9
Procapreolus* cf. *cusanus							
		L	**PAD**	**PTW**	**DAD**	**DTW**	**H**
Incomplete antler (GAMPS-2001)	pedicle	47.4	24.1	27.1	26.7	25.8	
	burr	8.2			38.1	39.5	8.2
	shaft		19.7	29.4	16.1	54.6	69.9
Cervinae gen. et. sp. indet.							
		DAPo	**DAPc**	**DTa**	**DTp**	**Hm**	
Fragmentary mandible with p4 and m1 (GAMPS-2002)	p4	13.6	13.3	7.7	8.4		
	m1	13.2	12.9	9.8	10.0		
Fragmentary mandible with m1 and m2 (GAMPS-2003)	m1	16.7	14.7	10.9	11.5		
	m2	18.8	17.4		12.9	> 21.3	
Fragmentary mandible with m2 and m3 (GAMPS-2004)	m2	14.5	13.9	12.1	11.4		
	m3			11.1			
Isolated p2 (GAMPS-2005)	p2	9.3	8.4	5.3	5.1		
Isolated m1 (GAMPS-2006)	m1	16.4	15.3	11.6	11.5		
Isolated m2 (GAMPS-2007)	m2	17.1	16.4	12.3	12.7		
Isolated molar (GAMPS-2008)	m2?	15.0	13.9	10.7	11.3		
Isolated molar (GAMPS-2009)	m2?	18.3	16.2	12.7			
Isolated molar (GAMPS-2010)	m2?			12.7			
		Lmax	**DAP**	**DT**			
Scapula (GAMPS-2013)	scapula	> 146					
	glenoid cavity		20.1	27.2			
Fragmentary distal epiphysis of humerus (GAMPS-2014)	isolated epiphysis			34.8			
Distal epiphysis of radius (GAMPS-2015)	isolated epiphysis		23.4	28.7			
Metacarpal (GAMPS-2016)	diaphysis	161.7	92 (at mid-point)	15.1 (at mid-point)			
	proximal end (without epiphysis)		18.9	25.9			
	distal end (without epiphysis)		17.9	26.3			

Tab. 1 - Measurements of selected terrestrial mammal bones from La Serra (Valdelsa Basin, Tuscany).

Cervinae gen. et. sp. indet.							
		Lmax	**DAP**	**DT**			
Fragmentary femur (GAMPS-2017)	proximal end		25.1	24.2			
Proximal epiphysis of tibia (GAMPS-2019)	isolated epiphysis		> 40	50.1			
Distal epiphysis of tibia (GAMPS-2020)	isolated epiphysis		24.3	30.4			
Calcaneus (GAMPS-2021)	proximal end		21.3	18.0			
Astragalus (GAMPS-2022)	astragalus	36.4 (medial), 38.9 (lateral)					
	proximal end		24.3	22.9			
	distal end		20.82	22.06			
Fragmentary metatarsal (GAMPS-2023)	distal end (without epiphysis)		23.1	30.0			
Phalanx I (GAMPS-2024)	phalanx	47.1					
	proximal end		15.3	17.4			
	distal end		14.3	13.2			
Phalanx I (GAMPS-2025)	phalanx	38.7					
	proximal end		16.2	16.1			
	distal end		9.3	11.1			
Phalanx III (GAMPS-2026)	phalanx	25.1					
	proximal end		11.1	17.9			
Sediment blocks with unprepared postcrania (GAMPS-2027)	isolated femur - distal epiphysis			45.2			
Sediment blocks with unprepared postcrania (GAMPS-2028)	isolated tibia - distal epiphysis			29.2			
	isolated femur - proximal epiphysis			23.1			
	isolated femur - proximal epiphysis		22.5				
Fragmentary tibia (MSNUP I-16960)	diaphysis		21.3	22.3			
	distal end		28.1	36.1			
Coprolites							
		L	**W**	**T**			
Coprolite (GAMPS-905)	whole coprolite	38	36	28.5			
Coprolite (GAMPS-2031)	whole coprolite	27.9	28.6	25.5			

Tab. 1 - Continuation.

bifurcation (Valli, 2010; Croitor, 2018: fig. 3). That said, Heintz (1970) documented several antler specimens of *P. cusanus* from Les Étouaires, which on the whole represent a broad spectrum of ontogenetic stages. In particular, GAMPS-2001 closely resembles the specimen illustrated in Heintz's (1970) figure 76, which was interpreted as belonging to an adult individual exhibiting incomplete annual antler growth. Furthermore, Croitor (2018) documented considerable variability in the position of the first tine in *P. cusanus*, which may occur 63-145 mm above the burr. This range encompasses the condition observed in GAMPS-2001, in which the distance between the burr and the first bifurcation is approximately 69 mm.

In conclusion, GAMPS-2001 can be confidently assigned to *Procapreolus*, being particular reminiscent of uppermost Miocene examples of *Procapreolus* cf. *loczyi* as well as of Pliocene examples of *P. cusanus*. Considering the morphological variability and limited diagnostic value of some antler characters, a cautious taxonomic attribution may be sensible. Accordingly, GAMPS-2001 is herein identified under open nomenclature, as belonging to *Procapreolus* cf. *cusanus*.

Subfamily Cervinae Goldfuss, 1820

Cervinae gen. et sp. indet.
(Figs 8-10; Tab. 1; SOM 2)

Referred material - GAMPS-2002, fragmentary mandible with p4 and m1; GAMPS-2003, fragmentary mandible with m1 and m2; GAMPS-2004, fragmentary mandible with m2 and m3; GAMPS-2005, isolated p2; GAMPS-2006, isolated m1; GAMPS-2007, isolated m2; GAMPS-2008, GAMPS-2009, GAMPS-2010, three isolated molars; GAMPS-2011, GAMPS-2012, two fragmentary molars; GAMPS-2013, scapula; GAMPS-2014, fragmentary distal epiphysis of humerus; GAMPS-2015, distal epiphysis of radius; GAMPS-2016, metacarpal; GAMPS-2017, fragmentary femur; GAMPS-2018, fragmentary rib; GAMPS-2019, proximal epiphysis of tibia; GAMPS-2020, distal epiphysis of tibia; GAMPS-2021, calcaneus; GAMPS-2022, astragalus; GAMPS-2023, fragmentary metatarsal; GAMPS-2024, GAMPS-2025, two phalanges I; GAMPS-2026, phalanx

III; GAMPS-2027, GAMPS-2028, two sediment blocks with unprepared postcrania; GAMPS-2029, GAMPS-2030, long bone fragments; MSNUP I-16960, fragmentary tibia.

Three-dimensional models - MSNUP I-16960, https://doi.org/10.6084/m9.figshare.32677311; GAMPS-2002, https://doi.org/10.6084/m9.figshare.31889536; GAMPS-2003, https://doi.org/10.6084/m9.figshare.31889584; GAMPS-2004, https://doi.org/10.6084/m9.figshare.31889620; GAMPS-2022, https://doi.org/10.6084/m9.figshare.31889665.

Stratigraphic provenience - Upper Pliocene deposits exposed at La Serra; Unit 1 and Unit 2 of Garassino et al. (2012).

Descriptive remarks - GAMPS-2002 is a fragmentary right mandible with fully erupted, significantly worn p4 and m1 (Fig. 8a1-a3; Tab. 1). The former tooth is high and rugose, and features a weak mesiolabial cingulum. The anterior stylid and anterior conid are separated from each other by a narrow valley. Both these elements are connected to the mesiolabial conid through an anterolabial cristid. The mesiolabial conid is not fused to the anterior stylids, revealing a lack of molarisation. A wide, transversely oriented anterior valley (trigonid basin) separates the anterior conid from the mesiolingual conid. The mesiolingual conid is laterally compressed, and bears well-developed anterolingual and mesiolingual cristids, the former being more extended than the latter. The mesiolingual conid is separated from the posterior elements by the posterior valley, which runs oblique to the longitudinal axis of the tooth. The mesiolabial conid is connected to the posterior cuspids through the posterolabial cristid. The posterior conids are separated by a back valley. The shape of m1 is trapezoidal in occlusal view and provided with a rugose crown. Featuring an anterior cingulum, this tooth exhibits labial cusps that are shorter and located more distally than the lingual cusps. The metastylid is well developed on the lingual surface of the metaconid relative to the entostylid. A lower ectostylid is present on the labial surface, between the protoconid and hypoconid; it is provided with a subcircular cross-section.

GAMPS-2003 is a fragmentary left mandibula exhibiting fully erupted m1 and m2 as well as the unerupted p4 (Fig. 8b1-b3; Tab. 1). The molars are morphologically consistent with, yet less extensively worn than, the corresponding teeth in GAMPS-2002. Their metastylids and entostilids are well developed. The m2 is larger than m1 and features a less elevated ectostylid. GAMPS-2004 is a fragmentary right mandible with heavily worn m2 and m3 (Fig. 8c1-c3; Tab. 1). The latter tooth exhibits an incomplete third lobe, only preserving the prehypoconulid cristid. As concerns the isolated teeth, GAMPS-2005 is a lower right second premolar (p2) provided with a rugose crown (Fig. 8d1-d3; Tab. 1). Its profile is elliptical in occlusal view, and triangular in lingual and labial views. The remaining teeth are isolated molars, including a right m1 (GAMPS-2006; Fig. 8e1-e3; Tab. 1) and right m2 (GAMPS-2007; Fig. 8f1-f3; Tab. 1). Both these teeth exhibit a short extostylid. The metastylid of GAMPS-2006 is well developed, as is also the slightly folded posthypocristid. GAMPS-2008, GAMPS-2009 and GAMPS-2010 are m2s that feature a well-developed metastylid and a folded posthypocristid (Fig. 8g1-i3; Tab. 1). Other small molar fragments (GAMPS-2011, GAMPS-2012) are also known from the same site. Forelimb bones include a left scapula with a complete spine and sub-circular glenoid cavity (GAMPS-2013; Fig. 9a; Tab. 1), a distal right humeral epiphysis (GAMPS-2014), a distal right radial epiphysis (GAMPS-2015) and a left metacarpal lacking the epiphyses (GAMPS-2016; Fig. 9b1-b2) (Tab. 1). As for the hindlimbs, a partly prepared, fragmentary left femur features a spherical head and a circular fovea capitis (Fig. 9c; Tab. 1). MSNUP I-16960 is a left tibia with a fused distal epiphysis that was found contacting the thoracic proboscidean vertebra MSNUP I-16959/4 (Fig. 9d1-d2; Tab. 1). GAMPS-2019 and GAMPS-2020 originate from the same anatomical district, representing isolated proximal and distal tibial epiphyses, respectively (Fig. 9e; Tab. 1). The preserved foot bones include a right calcaneus (GAMPS-2021), a right talus (GAMPS-2022; Fig. 9f1-f2; Tab. 1), a metatarsal fragment lacking the distal end (GAMPS-2023), a left first phalange (GAMPS-2024), a right first phalange (GAMPS-2025) and a right third phalanx (GAMPS-2026). Other cervid postcrania are still embedded within large sediment blocks, awaiting preparation. Among these are GAMPS-2027, which preserves the distal end of a left femur as well as two rib fragments (Fig. 9g; Tab. 1), and GAMPS-2028, which preserves a metapodial fragment, a fragmentary femural diaphysis, two proximal femur epiphyses, a distal tibial end and a sesamoid (Fig. 9h; Tab. 1). Other long bone fragments (GAMPS-2029, GAMPS-2030) were found associated with the proboscidean skeleton MSNUP I-16959, specifically with the fairly complete rib MSNUP I-16959/8.

Wear stage and age estimation - According to the age-at-death evaluation method proposed by Marín et al. (2024) for the extant red deer (*Cervus elaphus* Linnaeus, 1758), GAMPS-2002 falls within the "prime adult age group" (DAG = V; age estimation: 4.5-6.5 years) owing to the moderate wear stage of p4 and m1. GAMPS-2003 likely originates from a younger individual, because p4 is still partially unerupted, and the cuspids of m1 and m2 are only slightly worn out (DAG = IV; age estimation: 2.5-4.5 years). GAMPS-2004 is referable to the "old age group" (DAG = VII; age estimation: > 12 years) owing to its heavily worn m2 and m3. As for the isolated teeth, GAMPS-2005 (a p4) also falls within the "prime adult age group". The remaining molars may originate from adult specimens (around DAG = IV), with GAMPS-2007 being probably older considering its moderate occlusal wear.

The abundant presence of isolated epiphyses (GAMPS-2014, GAMPS-2015, GAMPS-2019, GAMPS-2020, GAMPS-2027, GAMPS-2028 and GAMPS-2029) as well as of long bone diaphyses lacking the corresponding epiphyses (GAMPS-2016, GAMPS-2023 and GAMPS-2028) suggests a very young age at death for several individuals. According to Calderón et al. (2019: tab. 3) and Tomé & Vigne (2003: tab. 9), epiphyseal fusion occurs in long bones of red and roe deer at approximately 15 months of age. Based on these postcranial

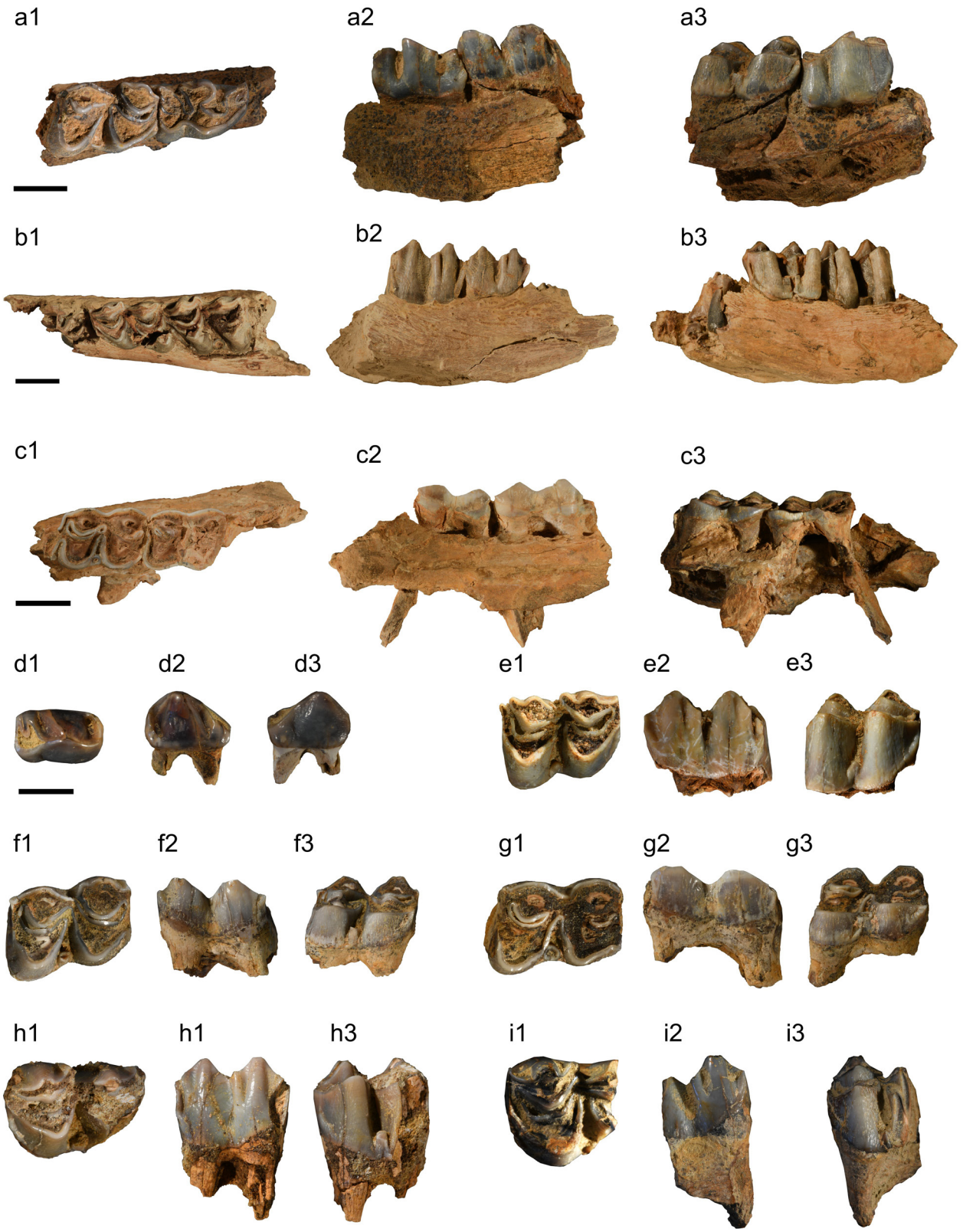


Fig. 8 - (color online) Cervinae gen. et sp. indet., dental remains from La Serra (Valdelsa Basin, Tuscany). a) GAMPS-2002, fragmentary mandible with p4 and m1. b) GAMPS-2003, fragmentary mandible with m1 and m2. c) GAMPS-2004, fragmentary mandible with m2 and m3. d) GAMPS-2005, isolated p2. e) GAMPS-2006, isolated m1. f) GAMPS-2007, isolated m2. g-i) Isolated molars (GAMPS-2008, 2009, 2010). Teeth are shown in occlusal (a1, b1, c1, d1, e1, f1, g1, h1, i1), lingual (a2, b2, c2, d2, e2, f2, g2, h2, i2) and labial (a3, b3, c3, d3, e3, f3, g3, h3, i3) views. Scale bars = 5 mm (a1-3, d1-i3); 10 mm (b1-b3, c1-3).


a
b1
b2
c
d1
d2
e
f1
f2
g
h

Fig. 9 - (color online) Cervinae gen. et sp. indet., postcranial remains from La Serra (Tuscany). a) GAMPS-2013, scapula. b) GAMPS-2016, metacarpal bone. c) GAMPS-2017, fragmentary femur. d) MSNUP I-16960, incomplete tibia. e) GAMPS-2020, distal epiphysis of tibia. f) GAMPS-2022, astragalus. g-h) GAMPS-2027 and GAMPS-2028, two sediment blocks entombing postcranial bones. Specimens are shown in cranial/anterior (a, b1, d1, f1), caudal/posterior (b2, c1, f2) and proximal (d2, e1) views. Scale bars = 10 mm (a, b1-b2, c, f1-f2); 15 mm (d1-d2, e, g, h).

specimens, a minimum of nine juvenile individuals can be confidently estimated. Other samples (MSNUP I-16960, GAMPS-2013, GAMPS-2017, GAMPS-2021, GAMPS-2022, GAMPS-2024, GAMPS-2025, GAMPS-2026, GAMPS-2029 and GAMPS-2030), accounting for a minimum of ten individuals, may instead originate from comparatively older animals.

Taxonomic determination and comparisons - As for the diagnostic characters that may be found on the cheek teeth, the p4 of GAMPS-2002 does not exhibit a molarised condition (i.e., the paraconid and metaconid are not fused), and no "*Palaeomeryx* fold" (= protoconid fold) was observed in the studied molars. The same condition occurs in most genera of Cervinae from the Upper Pliocene and Lower Pleistocene, including "*Pseudodama*", discussed below (Croitor, 2018). In contrast, both the aforementioned characters are documented in most Neogene small- or medium-sized deer, such as *Euprox* (Colombero et al., 2014, 2017; Stefaniak & Nauk, 2015), *Lucentia* (Gentry, 2005; Kostopoulos, 2006), *Pliocervus* (Colombero et al., 2014; but see Pandolfi et al., 2021 for a significant exception), *Cervavitus* (Khomenko, 1913; Dong, 2011), *Paracervulus* (Abbazzi, 2001), *Croizetoceros* (Crégut-Bonnoure & Tsoukala, 2017; Azzarà et al., 2022) and most species of *Procapreolus* (Vislobokova, 2007; Croitor & Stefaniak, 2009; Valli, 2010; Croitor, 2014), albeit Abbazzi (2001) noted that *P. cusanus* and *Procapreolus* cf. *loczyi* from Austria are exceptions to this rule. Moreover, the occurrence of a well-developed mesial cingulum and the mesial bending of the base of the entoconid allow for distinguishing the La Serra specimens from both the fallow and red deer, in which the mesial cingulum is absent, and the entoconid is straight (Breda & Lister, 2013).

Tooth measurements of selected cervid taxa from the Neogene and Lower Pleistocene are reported in SOM 2. Premolar measurements are rarely published, and the corresponding specimens are typically poorly illustrated, thus making detailed comparisons unfeasible. Dimensions of m1, particularly DAPc and DTp, are more commonly available, and have been plotted into Figure 10. The lower values of DTp recorded for GAMPS-2002 relative to GAMPS 2003 and GAMPS 2006 are likely related to different wear stages. Indeed, GAMPS-2002 is far more severely worn, potentially resulting in an apparent reduction of its dimensions. GAMPS-2002 plots close to several small-sized taxa, while GAMPS 2003 and GAMPS 2006 fall within the range of variation of fallow deer-sized species (Fig. 10).

Most Villafranchian *Dama*-like deer, historically referred to as *Cervus* (Forsyth Major, 1879; Heintz, 1970), were accommodated by Azzaroli (1992a) into the then-new genus "*Psudodama*", and this is especially true of the finds from Villafranca d'Asti. That said, the validity and species content of "*Psudodama*" continue to be widely discussed, as are also its relationships with the extant deer genera (Di Stefano & Petronio, 2002; Croitor, 2018; Heckeberg, 2020; Cherin et al., 2022). Given the persistent debate regarding the taxonomic status of "*Psudodama*", we follow the approach of Cherin et al. (2019, 2022) and employ the genus name with inverted commas, thereby signalling its questioned nature (Croitor, 2018).

The taxonomic determination of the postcranial remains is even more challenging. The tibial specimens exhibit larger distal ends than other small-sized deer such as *Euprox*, *Croizetoceros* (Stefaniak & Nauk, 2015: tabs 7, 40) and some *Procapreolus* species, including *P. cusanus* (Sarti et al., 1998; Croitor & Stefaniak, 2009: tab. 2; Stefaniak & Nauk, 2015: tab. 173; Pandolfi et al., 2021). Their

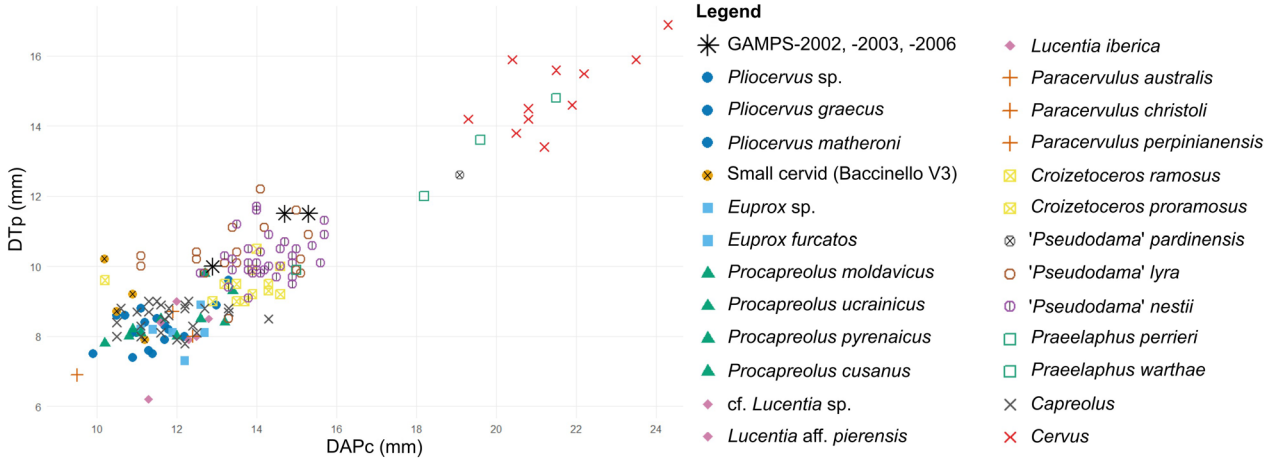


Fig. 10 - (color online) Measurements (DAPc vs DTp) of cervid lower first molars (m1) from the Italian Neogene and Quaternary. See SOM 2 for data sources.

dimensions are consistent with those of some unpublished finds from Early Villafranchian sites of Piedmont, including NMB V.J.74 (two tibiae: DAP = 26, DT = 32; DAP = 27; DT = 34) and NMB V.J.282 (DAP =33, DT = 35). The La Serra specimens and NMB V.J.74 further share with the larger forms *Praeelaphus perrieri* (Croizet & Jobert, 1828) and *Eucladoceros* sp. the occurrence of a bulge along the lateral edge of the cochlea tibiae (Pfeiffer-Deml, 2016: figs 5-6; Pfeiffer-Deml, 2020: figs 10, 12). Size-wise, the studied material is also smaller than *Praeelaphus warthae* (Czyżewska, 1968) and *Arvernoceros ardei* (Croizet & Jobert, 1828) (see measurements in Stefaniak & Nauk, 2015: tabs 81, 93, 102).

The astragalus GAMPS-2022 exhibits a strong medial lip in the proximal trochlea, which projects plantarly (Abbazzi, 2001). It is larger than the astragali of *Euprox* (Stefaniak & Nauk, 2015), *Croizetoceros* (Stefaniak & Nauk, 2015), *Lucentia* (Sen et al., 2015), *Pliocervus* (Colombero et al., 2017), *Paracervus* (Abbazzi, 2001) and *Procapreolus/Capreolus* (Croitor & Stefaniak, 2009; Stefaniak & Nauk, 2015; Pandolfi et al., 2021), including *P. cusanus* (Heintz, 1970: tab. 30), but smaller than *Praeelaphus warthae*, *Praeelaphus perrieri*, *Arvernoceros ardei* and the extant *Cervus* spp. (see measurements in Stefaniak & Nauk, 2015). In turn, measurements of GAMPS-2022 are close to those of several astragali from Villafranca d'Asti (e.g., NMB V.J.74: Lmax = [medial] 36.5, [lateral] 39, DAP [proximal end] = 22, DT [proximal end] = 21, DAP [distal end] = 24, DT [distal end] = 22; NMB V.J.282: Lmax = [medial] 39, [lateral] 42, DAP [proximal end] = 23, DAP [distal end] = 22, DT [proximal end] = 20, DT [distal end] = 27).

Considering their morphology and dimensions, the cervid teeth and postcrania from La Serra appear to be consistent with a *Dama*-like taxon in the subfamily Cervinae. That said, a genus-level assignment is problematic because of the limited diagnostic value of the studied material as well as of the many open questions that complicate the taxonomy of Pliocene deer (Croitor, 2018; Heckeberg, 2020). The studied specimens show strong similarities to the cervine remains from Villafranca d'Asti (Triversa FU), referred to "*Pseudodama*" *lyra* Azzaroli (1992a) (see also the biochronological schemes by Gliozzi et al., 1997 and Rook & Martínez-Navarro, 2010). However, given the ongoing debate surrounding the taxonomic status of "*Psudodama*", here we cautiously refer the La Serra specimens to Cervinae gen. et sp. indet.

ASSOCIATED COPROLITES

The lower portion of the Pliocene succession exposed at the La Serra quarry has also yielded two vertebrate coprolites, GAMPS-905 and GAMPS-2031.

GAMPS-905 is an essentially complete, stockily subcylindrical coprolite provided with a gently concave basal surface (Fig. 11a1; Tab. 1). A digital three-dimensional model of this coprolite is freely available at the following internet address: https://doi.org/10.6084/m9.figshare.31889329. Its outer surface is somewhat heterogeneous, with a thick outer layer (cortex) that features common tiny vesicles and rarer blackish elongated inclusions (Fig. 11a2-a3). The tiny holes that characterise the external surface of the coprolite are probably related to degassing (Farjand et al., 2024), while the elongated inclusions may represent organic matter, such as plant remains. The XRF spectrum (wt%) of the coprolite reveals high concentrations of calcium (Ca = 29.64%), and smaller but detectable abundances of iron (Fe = 2.43%) and manganese (Mn = 1.30%) (SOM 3). The high Balance (Bal) value (up to 65.32%), which accounts for elements lighter than magnesium that are not detectable by the analytical method (Gemelli et al., 2017), may indicate that light elements such as carbon contribute substantially to the total mass of the coprolite. Overall, these chemical data suggest that the tracemaker may have been an herbivore, as coprolites produced by carnivores are typically dominated by calcium phosphate, thereby exhibiting high phosphorus concentrations in their XRF spectra (Larkin et al., 2000; Sanz et al., 2016; Pineda et al., 2017; Farjand et al., 2024; Dauphin & Brugal, 2025).

GAMPS-2031 is a smaller coprolite (Fig. 11b1, Tab. 1). Its shape is best described as subspherical, with a flat base and a pointedly tapered opposite termination. The delicate cortex is darker-coloured and more homogeneous

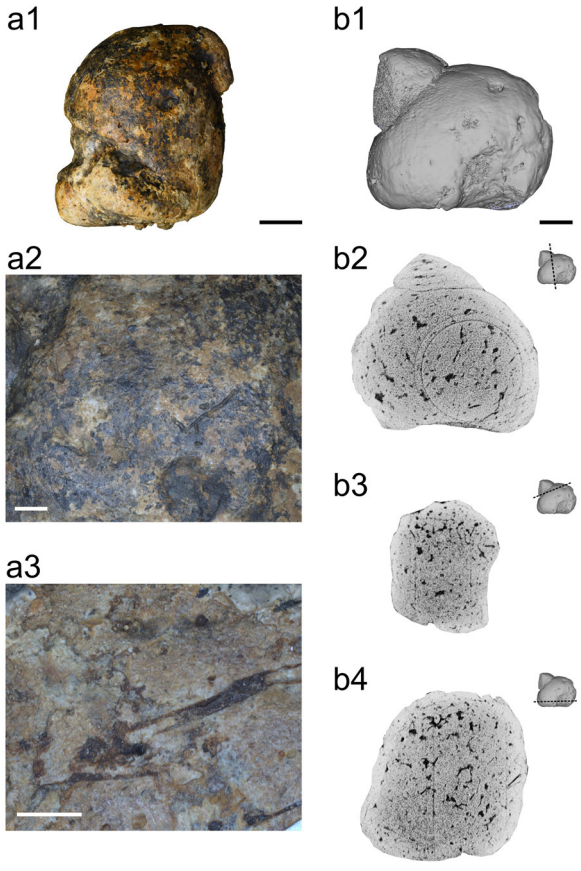


Fig. 11 - (color online) Vertebrate coprolites from La Serra (Tuscany). a) GAMPS-905, "C3"-type coprolite (sensu Hunt & Lucas, 2012); a1) overview of the coprolite; a2-a3) close-ups of the cortex, showing common tiny vesicles and rarer blackish elongated inclusions. b) Micro-CT images of the "C3"-type coprolite GAMPS-2031; b1) overview of the coprolite (solid model); b2-b4) three slices through the fossilised faecal mass. Scale bars = 10 mm (a1); 2 mm (a2-a3); 5 mm (b1).

than that of GAMPS-905. Micro-CT imaging reveals an essentially amorphous texture with widespread microvoids (Fig. 11b2-b4). The porous internal structure is suggestive of early desiccation (Farjand et al., 2024).

The morphology of the studied coprolites (GAMPS-905 and GAMPS-2031) conforms to that typical of "group V" as defined by Chame (2003), which equals Hunt & Lucas' (2012) "group C3". According to these authors, the likely producers of such coprolites are artiodactyls, excluding bovids (cf. Beltrame et al., 2022: fig. 1). Based on the size ranges reported by Chame (2003) for artiodactyl coprolites, GAMPS-2031 may have been produced by a cervid, while GAMPS-905 may have been produced by a suid. However, these assignments remain largely speculative.

DISCUSSION

For the purposes of the present Discussion, all terrestrial mammal remains recovered from La Serra are regarded as representative of a single biocoenosis. This interpretation is supported by several lines of evidence: the fossils derive from a relatively restricted stratigraphic interval (the lowermost 20 m of the succession, corresponding to Units 1-3 of Garassino et al., 2012); the succession as a whole is regarded as encompassing only a limited portion of Dominici et al.'s (2018) Synthem S6; some taxa, namely *Sus arvernensis* and medium-sized Cervinae comparable to "*Pseudodama*", occur in more than one unit; and no taphonomic evidence suggests significant reworking.

Biochronological interpretation

As already mentioned, terrestrial mammals are scarcely represented in the Italian Pliocene, and contrasting opinions are widespread concerning their biochronological interpretation (Kotsakis, 1986; Gliozzi et al., 1997; Palombo, 2004; Petronio et al., 2011; Bartolini-Lucenti et al., 2022). This situation stems primarily from a lack of accompanying stratigraphic data (Benvenuti et al., 1995; Carraro, 1996), which is often the case for historical finds such as those from most historical sites of Tuscany and Piedmont.

Accordingly, each new local fauna from temporally constrained settings represents a valuable addition to our understanding of the Italian Pliocene, including its climate and environmental diversity. In this respect, the newly discovered assemblage dealt with herein is particularly promising. Nonetheless, a reliable age interpretation of this fossil fauna is impossible without a careful reassessment of the biochronological data available for each identified taxon.

Italian biochronology of *Anancus arvernensis* - The earliest indication of the potential occurrence of the genus *Anancus* in Italy consists of small tusk and molar fragments from the Upper Miocene (MN13) of the Monticino quarry (Ferretti, 2021). Following a rather conspicuous temporal gap, the Early Villafranchian (mid-Piacenzian) Triversa FU has yielded abundant remains of *A. arvernensis* at Villafranca d'Asti and other Piedmontese localities, where this gomphotheriid species occurs alongside the mammutid "*Mammut*" *borsoni* (Hays, 1834) (Sismonda, 1851; Gastaldi, 1860; Cantamessa, 1891; Loss, 1946). *Anancus arvernensis* is also known from several localities of central Italy that broadly correlate with Triversa, including Fornaci di Barga (Tuscany; Perilli et al., 2004; Coltorti et al., 2008), Cetona (Tuscany; Boscato et al., 2008), the Upper Valdarno area (at Santa Barbara, Tuscany; Nesti, 1825; Weithofer, 1890; Rook et al., 2013) and the Spoleto Basin (Umbria; here, *A. arvernensis* co-occurs with "*M.*" *borsoni*; Pantanelli, 1886; Capellini, 1888; Mattei et al., 2023). In the Lower Valdarno, remains of *A. arvernensis*is are known from several local faunas, including some that are regarded as belonging in the Triversa FU (Ponte a Elsa; Bianucci & Landini, 2005) and others referred the subsequent Montopoli FU, where the species occurs alongside the early mammoth *Mammuthus rumanus* (Ştefănescu, 1924) (Caterini, 1924; De Guidi, 1939; Benvenuti et al., 1995; Palombo & Ferretti, 2005; Bartolini-Lucenti et al., 2022).

The timing of the disappearance of *A. arvernensis* remains controversial, with some authors placing its final occurrence in the Coste San Giacomo FU, approximately 2.2-2.1 Ma (Florindo et al., 2021; Bellucci et al., 2024), and others suggesting its persistence until the Olivola FU, around 2.0-1.8 Ma (Strani et al., 2018). As a matter of fact, a geologically young record of *Anancus* originates from Nera Montoro (Umbria), which is widely regarded as chronostratigraphically intermediate between the Coste San Giacomo and Olivola FUs (Tuccimei, 1891; Marra et al., 2018). Furthermore, while most finds of *A. arvernensis* from the Upper Valdarno are believed to originate from the Upper Pliocene Castelnuovo dei Sabbioni Synthem (Ghinassi et al., 2025), some may come from the overlying Montevarchi Synthem, which in turn correlates with the Olivola FU (Rook et al., 2013). Among these are specimens stored in the MPM that arguably originate from Terranuova Bracciolini, where the Montevarchi Synthem is extensively exposed (Ghinassi et al., 2025). As for the Aulla-Olivola Basin, Crégut-Bonnoure et al. (2025) did not report *A. arvernensis* at the Olivola locality (where a proboscidean is represented by abundant postcranial remains; see Palombo & Ferretti, 2005), yet this species occurs at La Quercia along with "*Pseudodama*" *nestii* (Azzaroli, 1947) and *Leptobos etruscus* (Falconer, 1868) (Bellucci et al., 2012; Masini et al., 2013; Iannucci, 2024). Bellucci et al. (2012) and Masini et al. (2013) regarded *L. etruscus* as characteristic of both the Olivola FU and the slightly younger Tasso FU, raising questions about the precise biochronological attribution of the assemblage. Further supporting a latest Gelasian age for the latest Italian anancines, Zanchetta & Mazza (1996) described a fragmentary skeleton of *A. arvernensis* from marginal-marine deposits approaching the Gelasian-Calabrian transition at Torrente Lama, in the Lower Valdarno. All things considered, the chronostratigraphic distribution of *A. arvernensis* spans between the mid-Piacenzian and the uppermost Gelasian.

Italian biochronology of *Sus arvernensis* - In the Italian peninsula, the small-sized suid *S. arvernensis* first appears in the Val di Pugna local fauna (Siena, Tuscany), within a mixed assemblage of marine and terrestrial mammals (Bianucci et al., 2001) of Ruscinian age (MN14; Gallai, 2006, 2007). The species is known from several Early Villafranchian localities, including Villafranca

d'Asti (Pickford & Obada, 2016; Iannucci, 2024) and Bra (Dal Piaz, 1930) in Piedmont; Pievefosciana (Coltorti et al., 2008) in Tuscany; and Collepardo (Iannucci et al., 2022; Mattei et al., 2023) in Latium. No remains of *S. arvernensis* have been documented so far from Montopoli or other time-equivalent localities (Gallai, 2006; Bartolini-Lucenti et al., 2022), while the Italian fossil record of the larger-bodied species *Sus strozzii* dates back to the geologically younger Coste San Giacomo FU (Iannucci, 2023; Bellucci et al., 2024).

Italian biochronology of Pliocene cervids - The taxonomy, systematics, and biochronology of the European Pliocene cervids are particularly intricate (Heckeberg, 2017; Croitor, 2018, 2022; Samejima & Matsuoka, 2020). The roe deer-like genus *Procapreolus* is documented in Italy from a broad chronostratigraphic interval ranging between the Upper Miocene (Sarti et al., 1998; Abbazzi, 2001; Pandolfi et al., 2021) and the Lower Pleistocene (Valli, 2010; Croitor, 2022). In particular, *Procapreolus loczyi* is known from the uppermost Miocene (Abbazzi, 2001; Pandolfi et al., 2021), while the record of *Procapreolus cusanus* embraces the Early and early Middle Villafranchian, roughly corresponding to the mid-Piacenzian to earliest Gelasian time span (Abbazzi et al., 1995; Bartolini-Lucenti et al., 2022). In the Early Villafranchian localities of Villafranca d'Asti and Aulla (Azzaroli, 1992a; Abbazzi et al., 1995), *P. cusanus* typically occurs alongside larger forms of fallow deer-like cervids that were allocated by Azzaroli (1992a) to the then-new genus "*Pseudodama*". In the Lower Valdarno, cervine remains of Early Villafranchian age are only known from a few localities assigned to the Triversa FU, such as Ponte a Elsa (the type locality of "*Pseudodama*" *lyra*) and Spicchio (Azzaroli, 1992a). By contrast, the Middle Villafranchian assemblages typically feature the occurrence of additional cervid taxa, such as *Croizetoceros ramosus* (Croizet & Jobert, 1828) and *Eucladoceros ctenoides* (Nesti, 1841) at Montopoli (Azzaroli, 1977, 1992a; Benvenuti et al., 1995; Bartolini-Lucenti et al., 2022).

Summary and implications - Overall, the terrestrial mammal assemblage from La Serra provides significant biochronological constraints. Crucially, the presence of *Sus arvernensis*, which is typically absent from the Italian Middle Villafranchian record, along with the co-occurrences of two forms of Cervidae (*Procapreolus* cf. *cusanus* and an indeterminate member of Cervinae), aligns the assemblage with the Early Villafranchian, specifically with the Triversa FU. As a matter of fact, the study site is located in the Lower Valdarno area, which is renowned for its conspicuous terrestrial mammal record of Early and Middle Villafranchian age (Benvenuti et al., 1995; Bianucci & Landini, 2005). Indeed, La Serra lies only a few kilometres away from Montopoli, which was selected by Azzaroli (1977) as the reference site for the homonymous faunal unit, marking the beginning of the Middle Villafranchian (De Giuli & Heintz, 1974a, b; Bartolini-Lucenti et al., 2022). Based on magnetostratigraphic analyses, Lindsay et al. (1980) estimated an age of approximately 2.5 Ma for the Montopoli FU, roughly corresponding to the onset of the Gelasian. However, the authors repeatedly emphasised the low magnetic intensity of the sampled sediments from Montopoli, which introduces a degree of uncertainty into the chronological interpretation. Furthermore, the precise location of some fossil-bearing deposits excavated in the late 19th century remains problematic, requiring post-hoc reconstruction (Lindsay et al., 1980; Azzaroli, 1992a).

It is worth noting that the Pliocene localities in the vicinity of Montopoli have yielded finds of terrestrial mammals with varying biochronological assignments: while some are referred to the Montopoli FU, others are instead attributed to the older Triversa FU (Benvenuti et al., 1995). According to the sequence stratigraphic reconstruction by Benvenuti et al. (2014), the Montopoli local fauna and other Montopoli-correlative faunas from the Valdelsa Basin should originate from the S6 Synthem, whereas the nearby Triversa-correlative faunas should come from the underlying S5. As for the La Serra succession, Benvenuti et al. (1995) regarded it as broadly coeval with, though slightly older than, the historical Montopoli site, while Dominici et al. (2018) placed both sections within the same S6 synthem. As a matter of fact, the taxonomic composition of the La Serra assemblage is clearly more consistent with the Triversa FU than with the Montopoli FU, mainly because *Sus arvernensis* is characteristic of pre-Middle Villafranchian faunas, and the cervid assemblage consists of two taxa typical of the Early Villafranchian faunas (namely, *Procapreolus* and a medium-sized Cervinae similar to "*Pseudodama*"), while a more taxonomically diverse assemblage is often reported from Middle Villafranchian localities. At the same time, an age younger than ca. 3 Ma is further suggested by the recognition of the mid-Piacenzian Warm Period (ending about 3.025 Ma; Haywood et al., 2016) in the underlying S4 Synthem (Dominici et al., 2018). Overall, the biochronological evidence is consistent with the La Serra assemblage belonging in the Triversa FU (commonly dated to ca. 3.2 Ma), yet the stratigraphic position of the entombing sediments suggests an age reasonably close to the inception of the subsequent Montopoli FU (ca. 2.6 Ma) (Fig. 12).

Palaeoecological and palaeoenvironmental inferences

Albeit scanty, the terrestrial mammal assemblage from La Serra enables a distinctive palaeoenvironmental reconstruction. Generally speaking, all mammal taxa from La Serra are regarded as warm-loving species associated with forested environments (Caloi & Palombo, 1997). In particular, *Anancus arvernensis* is widely regarded as a woodland-dwelling species inhabiting areas close to water bodies and relying on a browse-dominated, mixed-feeding strategy. This interpretation is supported by multiple lines of evidence, including dental morphology (Saarinen & Lister, 2023), dental mesowear (Saarinen & Lister, 2023), dental microwear (Rivals et al., 2019), postcranial morphology (Ferretti & Croitor, 2001) and stable isotope analysis (Szabó et al., 2022). Likewise, *Sus arvernensis* is regarded as a forest-associated taxon (Pickford & Obada, 2016). When read against the ecological preferences of their extant counterparts, the co-occurrence of roe and fallow deer-like cervids further supports the presence of a predominantly wooded landscape (Croitor, 2018; Szabó et al., 2020).

Additional palaeoenvironmental evidence comes from the associated fauna. Specifically, the many shell

remains of the pond turtle genus *Mauremys* originating from Unit 1 suggest the presence of flooded habitats within the Pliocene landscape of La Serra (Collareta et al., 2020a; Mulè et al., 2025a). That the climate was humid is supported by the widespread occurrence of bone modifications attributable to parasites and infections on the terrapin remains, while the presence of (sub)tropical marine life forms such the extant tiger shark, *Galeocerdo cuvier* (Lesueur, 1822), the chitinophosphatic brachiopod *Lingula*? (Di Cencio et al., 2021) and pufferfishes (Mulè et al., 2026) within the fully marine Unit 4 further suggest a warm thermal regime (Merella et al., 2023).

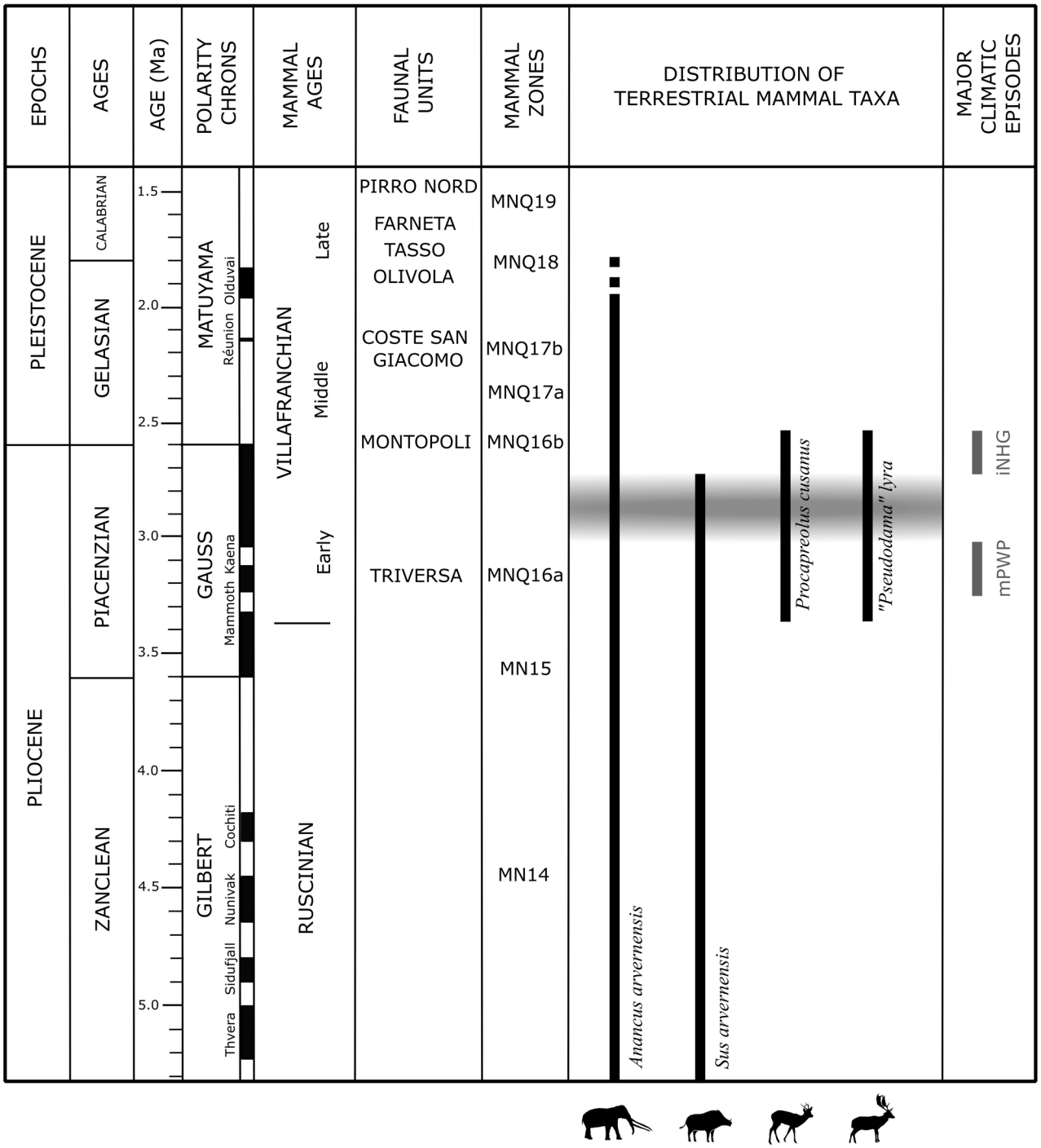


Fig. 12 - Chronological interpretation of the terrestrial mammal assemblage from La Serra (Tuscany). The biochronological framework is redrawn and modified after Rook & Martínez-Navarro (2010) and Konidaris & Roussiakis (2018). See the main text for data sources regarding each taxon. Note that the distribution of *Procapreolus cusanus* is shown to account for the range of *Procapreolus* cf. *cusanus*, while "*Pseudodama*" *lyra* (sensu Azzaroli, 1992a) is shown to account for the range of Cervinae gen. et sp. indet. The major climatic episodes are after McClymont et al. (2023). The horizontal grey band indicates the age inferred for the La Serra terrestrial mammal assemblage, which integrates biochronological evidence and stratigraphic considerations. Abbreviations: iNHG, intensification of Northern Hemisphere Glaciation; mPWM, mid-Piacenzian Warm Period.

Taken together, the autoecological traits of the terrestrial mammals from La Serra are broadly consistent with previous palaeoenvironmental and palaeoclimatic interpretations of a number of sites in the Lower Valdarno area (e.g., Ponte a Elsa; Valleri et al., 1990; Benvenuti et al., 2007) and other roughly coeval localities assigned to the Triversa FU, including Santa Barbara in the Upper Valdarno (Albianelli et al., 1997) and Villafranca d'Asti in Piedmont (Carraro et al., 1996). During most of the Piacenzian, swamp-forest ecosystems, most notably taxodiacean-dominated forests (including Taxodioideae and Sequoioideae), were widespread throughout the Italian peninsula as well as across much of the Mediterranean region (Fauquette & Bertini, 2003; Bertini, 2010; Combourieu-Nebout et al., 2015; Szabó et al., 2022; Bertini et al., 2025; Suc et al., 2026). From approximately 3 Ma onwards, progressive cooling and increasing aridification led to the gradual decline of tropical and subtropical plant taxa (Combourieu-Nebout et al., 2015; Szabó et al., 2022; Bertini & Combourieu-Nebout, 2023; McClymont et al., 2023; Bertini et al., 2025). Given the age inferred above, the La Serra assemblage predates the intensification of the Northern Hemisphere glaciation at 2.6 Ma but likely postdates the mid-Piacenzian Warm Period (Fig. 12), such that the faunal evidence for a warm, humid, predominantly wooded landscape would be consistent with the persistence of abundant forest cover during the early stages of the Plio-Pleistocene cooling trend.

CONCLUSIONS

We reported on a newly discovered terrestrial mammal fauna from Upper Pliocene deposits exposed at an active quarry site at La Serra, Pisa Province, in the Lower Valdarno area (Tuscany, central Italy). Found in association with tortoise and terrapin shell remains, the assemblage from La Serra quarry includes the gomphothere *Anancus arvernensis*, the small-sized suid *Sus arvernensis*, and two cervid taxa (*Procapreolus* cf. *cusanus* and a fallow deer-like form of Cervinae), plus two coprolites that were likely produced by some kind of herbivorous mammals. This taxonomic composition is strongly reminiscent of the Triversa Faunal Unit (MNQ16a, Early Villafranchian), yet the stratigraphic position of the entombing deposits suggests an age reasonably close to the beginning of the Middle Villafranchian. overall, the vertebrate assemblage from La Serra suggests a warm, humid climate as well as a densely forested biotope.

SUPPLEMENTARY ONLINE MATERIAL

Supplementary data are available on the BSPI website at: https://www.paleoitalia.it/bollettino-spi/bspi-vol-653/

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REFERENCES

Abbazzi L. (2001). Cervidae and Moschidae (Mammalia, Artiodactyla) from the Baccinello V-3 assemblage (Late Miocene, Late Turolian, Grosseto, Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 107: 107-123.

Abbazzi L. & Croitor R. (2003). *Eostyloceros* cf. *pidoplitschkoi* Korotkevitsch 1964 (Cervidae, Muntiacinae): new element in the Neogene mammal assemblage of lower Valdarno (Tuscany, Central Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 109: 575-580.

Abbazzi L., Ficcarelli G. & Torre D. (1995). Deer fauna from the Aulla quarry (Val di Magra, northern Apennines). Biochronological remarks. *Rivista Italiana di Paleontologia e Stratigrafia*, 101: 341-347.

Abbazzi L., Benvenuti M., Ceci M.E., Esu D., Faranda C., Rook L. & Tangocci F. (2008). The end of the Lago-Mare time in the SE Valdelsa Basin (Central Italy): interference between local tectonism and regional sea-level rise. *Geodiversitas*, 30: 611-639.

Albianelli A., Azzaroli A., Bertini A., Ficcarelli G., Napoleone G. & Torre D. (1997). Paleomagnetic and palynologic investigations in the upper Valdarno basin (central Italy): calibration of an early Villafranchian fauna. *Rivista Italiana di Paleontologia e Stratigrafia*, 103: 111-118.

Amoretti C. (1808). Su un dente e parte di mandibola d'un mastodonte trovati presso la Rocchetta nel Dipartimento del Tanaro. *Memorie dell'Istituto Nazionale Italiano*, 1: 421-430.

Azanza B. & Montoya P. (1995). A new deer from the lower Turolian of Spain. *Journal of Paleontology*, 69: 1163-1175.

Azanza B., Palombo M.R. & Alberdi M.T. (2004). Large mammal turnover and diversity from the Pliocene to the Pleistocene in Italian peninsula. *Rivista Italiana di Paleontologia e Stratigrafia*, 110: 531-546.

Azanza B., Rössner G.E. & Ortiz-Jaureguizar E. (2013). The early Turolian (Late Miocene) Cervidae (Artiodactyla, Mammalia) from the fossil site of Dorn-Dürkheim 1 (Germany) and implications on the origin of crown cervids. *Palaeobiodiversity and Palaeoenvironments*, 93: 217-258.

Azzarà B., Breda M., Cirilli O., Madurell-Malapeira J., Ruzza F., Sorbelli L., Tancredi D. & Cherin M. (2022). Vigna Nuova: the first Middle Villafranchian mammal assemblage from the Valdichiana Basin, Perugia (Italy). *Bollettino della Società Paleontologica Italiana*, 61: 223-247.

Azzaroli A. (1947). I cervi fossili della Toscana, con particolare riguardo alle specie villafranchiane. *Palaeontographia Italica*, 43: 45-82.

Azzaroli A. (1977). The Villafranchian stage in Italy and the Plio–Pleistocene boundary. *Giornale di Geologia*, 41: 61-79.

Azzaroli A. (1992a). The cervid genus *Pseudodama* n.g. in the Villafranchian of Tuscany. *Palaeontographia Italica*, 79: 1-41.

Azzaroli A. (1992b). Suids of the early Villafranchian of Villafranca d'Asti and China. *Rendiconti Lincei, Scienze Fisiche e Naturali*, 3: 109-124.

Baigusheva V.S. & Titov V.V. (2021). Late Middle–Early Late Pleistocene mammoths from the Lower Don River Region (Russia). *Quaternary*, 4: 5.

Barone R. (1995). Anatomia comparata dei mammiferi domestici. Vol. 1: Osteologia. 704 pp. Edagricole Calderini, Bologna.

Bartolini-Lucenti S., Cirilli O., Pandolfi L. & Rook L. (2022). The Montopoli site, a reference local fauna in the Pliocene and Pleistocene European large mammals biochronology, first discovered by Giovanni Capellini (1833-1922). *Bollettino della Società Paleontologica Italiana*, 61: 207-222.

Bellucci L., Mazzini I., Scardia G., Bruni L., Parenti F., Segre A.G., Naldini E.S. & Sardella R. (2012). The site of Coste San Giacomo (Early Pleistocene, central Italy): palaeoenvironmental analysis and biochronological overview. *Quaternary International*, 267: 30-39.

Bellucci L., Bona F., Conti J., Mecozzi B., Strani F. & Sardella R. (2024). The Early Pleistocene carnivoran of Coste San Giacomo (Anagni, central Italy): Biochronological implications. *Quaternary*, 7: 57.

Beltrame M.O., Tietze E., Cañal V., Barberena R. & Quintana S. (2022). Paleogenetic and microscopic studies of *Eimeria* spp. (Apicomplexa: Eimeriidae) as a tool to reveal the zoological origin of coprolites: the case study of artiodactyl coprolites from an archaeological site from Patagonia, Argentina. *The Holocene*, 32: 1144-1150.

Belyaev R.I., Boeskorov G.G., Kuznetsov A.N., Rotonda M. & Prilepskaya N.E. (2025). Comparative study of body proportions in Elephantidae and other large herbivorous mammals. *Journal of Anatomy*, 246: 63-85.

Benvenuti M., Dominici S. & Rook L. (1995). Inquadramento stratigrafico-deposizionale delle faune a mammiferi villafranchiane (Unità Faunistiche Triversa e Montopoli) del Valdarno inferiore nella zona a sud dell'Arno (Toscana). *Alpine and Mediterranean Quaternary*, 8: 457-464.

Benvenuti M., Bertini A., Conti C. & Dominici S. (2007). Integrated analyses of litho- and biofacies in a Pliocene cyclothemic, alluvial to shallow marine succession (Tuscany, Italy). *Geobios*, 40: 143-158.

Benvenuti M., Del Conte S., Scarselli N. & Dominici S. (2014). Hinterland basin development and infilling through tectonic and eustatic processes: Latest Messinian–Gelasian Valdelsa Basin, Northern Apennines, Italy. *Basin Research*, 26: 387-402.

Bertini A. (2010). Pliocene to Pleistocene palynoflora and vegetation in Italy: state of the art. *Quaternary International*, 225: 5-24.

Bertini A. & Combourieu-Nebout N. (2023). Piacenzian to late Pleistocene flora and vegetation in Italy: a moving sketch. *Alpine and Mediterranean Quaternary*, 36: 91-119.

Bertini A., Marino M., Combourieu-Nebout N., Girone A., Maiorano P., Niccolini G. & Suc J.P. (2025). Unravelling land-sea correlations during the Pliocene-Pleistocene in the Mediterranean area. *Bollettino della Società Paleontologica Italiana*, 64: 289-312.

Bezuidenhout A.J. & Seegers C.D. (1996). The osteology of the African elephant (*Loxodonta africana*): vertebral column, ribs and sternum. *Onderstepoort Journal of Veterinary research*, 63: 131-147.

Bianucci G. & Landini W. (2005). I paleositi a vertebrati fossili della Provincia di Pisa. *Atti della Società Toscana di Scienze Naturali, Memorie A*, 110: 1-21.

Bianucci G., Mazza P., Merola D., Sarti G. & Cascella A. (2001). The Early Pliocene mammal assemblage of Val di Pugna (Tuscany, Italy) in the light of calcareous plankton biostratigraphical data and paleoecological observations. *Rivista Italiana di Paleontologia e Stratigrafia*, 107: 425-438.

Biondaro M.C., Franco F. & Piccoli G. (1979). Avanzi di mastodonti nel Museo di Paleontologia dell'Università di Padova. *Memorie dell'Istituto di Geologia e Mineralogia dell'Università di Padova*, 32: 4-9.

Boeuf O. (1992). *Anancus arvernensis chilhiacensis* nov. subsp. (Proboscidea, Mammalia), un mastodonte du Plio-Pléistocène de Haute-Loire, France. *Geobios*, 25: 179-188.

Boscato P., Coltorti M. & Reggiani P. (2008). Pliocene *Anancus arvernensis* (Croizet & Jobert, 1828) remains from Cetona (Siena): stratigraphy, chronology and paleoenvironment. *Bollettino della Società Geologica Italiana (Italian Journal of Geosciences)*, 127: 151-162.

Bossio A., Costantini A., Lazzarotto A., Liotta D., Mazzanti R., Mazzei R., Salvatorini G. & Sandrelli F. (1993). Rassegna delle conoscenze sul neoautoctono toscano. *Memorie della Società Geologica Italiana*, 49: 17-98.

Bravo-Cuevas V.M., Morales-García N.M. & Cabral-Perdomo M.A. (2015). Description of *Mammut americanum* from the late Pleistocene of Hidalgo (Mexico). *Boletín de la Sociedad Geológica Mexicana*, 67: 337-347.

Breda M. & Lister A.M. (2013). *Dama roberti*, a new species of deer from the early Middle Pleistocene of Europe, and the origins of modern fallow deer. *Quaternary Science Reviews*, 69: 155-167.

Brookes J. (1828). A catalogue of the anatomical and zoological museum of Joshua Brookes. 128 pp. Richard Taylor, London.

Brown C.L. & Gustafson C.E. (1979). A Key to the Postcranial Skeletal Remains of Cattle/Bison, Elk, and Horse. 213 pp. Washington State University, Laboratory of Anthropology, Pullman, Washington.

Calderón T., DeMiguel D., Arnold W., Stalder G. & Köhler M. (2019). Calibration of life history traits with epiphyseal closure, dental eruption and bone histology in red deer. *Journal of Anatomy*, 235: 205-216.

Caloi L. & Palombo M.R. (1997). Biochronology of large mammals in the Early and Middle Pleistocene of the Italian Peninsula. *Hystrix*, n.s., 9: 3-12.

Cantamessa F. (1891). Il Mastodonte di Cinaglio d'Asti ed il *Mastodon arvernensis*: osteografia ed osservazioni. *Memorie della Reale Accademia delle Scienze di Torino*, serie 2, 41: 339-379.

Capellini G. (1888). Sui resti di *Mastodon arvernensis* scoperti a Spoleto, Pontremoli e Castrocaro. *Memorie della Regia Accedemia delle Scienze di Bologna*, 4, 9: 251-258.

Carraro F. (1996). Revisione del Villafranchiano nell'area-tipo di Villafranca d'Asti. *Il Quaternario*, 9: 5-119.

Cassinello J., Caro J. & Delibes-Mateos M. (2026). Distinctive antler morphology in European roe deer: implications for evolution, conservation and game management. *European Journal of Wildlife Research*, 72: 41.

Caterini D.F. (1924). Catalogo dei proboscidiani pliocenici e quaternari conservati nel Museo di Geologia della R. Università di Pisa. *Atti della Società Toscana di Scienze Naturali, Memorie*, 35: 195-210.

Chame M. (2003). Terrestrial mammal feces: a morphometric summary and description. *Memórias do Instituto Oswaldo Cruz*, 98: 71-94.

Cherin M., Sorbelli L., Crotti M., Iurino D.A., Sardella R. & Souron A. (2018). New material of *Sus strozzii* (Suidae, Mammalia) from the Early Pleistocene of Italy and a phylogenetic analysis of suines. *Quaternary Science Reviews*, 194: 94-115.

Cherin M., Azzarà B., Breda M., Buzi C., Pandolfi L. & Pazzaglia F. (2019). Large mammal remains from the early Pleistocene site of Podere San Lorenzo (Perugia, central Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 125: 489-515.

Cherin M., Alba D.M., Crotti M., Menconero S., Moullé P.É., Sorbelli L. & Madurell-Malapeira J. (2020). The post-Jaramillo persistence of *Sus strozzii* (Suidae, Mammalia) in Europe: New

evidence from the Vallparadís Section (NE Iberian Peninsula) and other coeval sites. *Quaternary Science Reviews*, 233: 106234.

Cherin M., Breda M., Esattore B., Hart V., Turek J., Porciello F., Angeli G., Holpin S. & Iurino D.A. (2022). A Pleistocene Fight Club revealed by the palaeobiological study of the *Dama*-like deer record from Pantalla (Italy). *Scientific Reports*, 12: 13898.

Coletti G., Collareta A., Di Cencio A., Bosio G. & Casati S. (2023). Symbiont-bearing colonial corals and gastropods: an odd couple of the shallow seas. *Journal of Marine Science and Engineering*, 11: 260.

Collareta A., Casati S., Zuffi M.A.L. & Di Cencio A. (2020a). First authentic record of the freshwater turtle *Mauremys* from the Upper Pliocene of Italy, with a new occurrence of the rarely reported ichnotaxon *Thatchtelithichnus holmani*. *Carnets de Géologie*, 20: 301-313.

Collareta A., Merella M., Casati S. & Di Cencio A. (2020b). Did titanic stingrays wander the Pliocene Mediterranean Sea? Some notes on a giant-sized myliobatoid stinger from the Piacenzian of Italy. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 298: 155-164.

Colombero S., Angelone C., Bonelli E., Carnevale G., Cavallo O., Delfino M., Giuntelli P., Mazza P., Pavia G., Pavia M. & Repetto G. (2014). The upper Messinian assemblages of fossil vertebrate remains of Verduno (NW Italy): Another brick for a latest Miocene bridge across the Mediterranean. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 272: 287-324.

Colombero S., Alba D.M., D'Amico C., Delfino M., Esu D., Giuntelli P., Harzhauser M., Mazza P.A., Mosca M., Neubauer T. A., Pavia G., Pavia M., Villa A. & Carnevale G. (2017). Late Messinian mollusks and vertebrates from Moncucco Torinese, north-western Italy. Paleoecological and paleoclimatological implications. *Palaeontologia Electronica*, 20: 1-66.

Coltorti M., Pieruccini P. & Rustioni M. (2008). The Barga basin (Tuscany): A record of Plio-Pleistocene mountain building of the northern Apennines, Italy. *Quaternary International*, 189: 56-70.

Combourieu-Nebout N., Bertini A., Russo-Ermolli E., Peyron O., Klotz S., Montade V. & Sadori L. (2015). Climate changes in the central Mediterranean and Italian vegetation dynamics since the Pliocene. *Review of Palaeobotany and Palynology*, 218: 127-147.

Crégut-Bonnoure E. & Tsoukala E. (2017). The Late Pliocene Bovidae and Cervidae (Mammalia) of Milia (Grevena, Macedonia, Greece). *Quaternary International*, 445: 215-249.

Crégut-Bonnoure E., Guérin C., Argant A., Argant J., Debard E., Delson E., Eisenmann V., Faure M., Ménouret B., Mourer-Chauviré C. & Valli A. M. (2025). Biochronology of the Senèze faunal assemblage. *In* Delson E., Faure M. & Guérin C. (eds), Senèze: Life in Central France Around Two Million Years Ago, Vertebrate Paleobiology and Paleoanthropology, Springer, Cham: 633-652.

Croitor R. (2014). Deer from Late Miocene to Pleistocene of Western Palearctic: matching fossil record and molecular phylogeny data. *Zitteliana Reihe B: Abhandlungen der Bayerischen Staatssammlung fur Palaontologie und Geologie*, 32: 115-153.

Croitor R. (2018). Plio-Pleistocene Deer of Western Palearctic: Taxonomy, Systematics, Phylogeny. 140 pp. Ion Toderaș, Institute of Zoology of the Academy of Sciences of Moldova.

Croitor R. (2022). Paleobiogeography of Crown Deer. *Earth*, 3: 1138-1160.

Croitor R. & Stefaniak K. (2009). Early Pliocene deer of Central and Eastern European regions and inferred phylogenetic relationships. *Palaeontographica*, 287: 1-39.

Croizet J.B. & Jobert A.C.G. (1828). Recherches sur les ossements fossiles du département du Puy-de-Dôme. 224 pp. Thibaud Landriot, Clermont-Ferrand & Paris.

Czyżewska T. (1968). Deer from Węże and their relationship with the Pliocene and Recent Eurasiatic Cervidae. *Acta Palaeontologica Polonica*, 8: 537-593.

Dal Piaz G.B. (1930). Sopra gli avanzi di un suide scoperti nel Pliocene superiore di Bra in Piemonte. *Atti Reale Accademia delle Scienze di Torino*, 65: 299-303.

Dauphin Y. & Brugal J.P. (2025). Coprolite multimodal analysis: a tool for hyaenid predator identification. *Animals*, 15: 1145.

De Giuli C. & Heintz E. (1974a). *Croizetoceros ramosus* (Cervidae, Artiodactyla, Mammalia) de Montopoli, nouvel élément de la faune villafranchienne d'Italie. *Atti della Società Toscana di Scienze Naturali*, *Memorie A*, 81: 241-252.

De Giuli C. & Heintz E. (1974b). *Gazella borbonica* (Bovidae, Artiodactyla, Mammalia) novel element de la faune Villafranchienne de Montopoli, Valdarno inferieur, Pisa, Italia. *Atti della Società Toscana di Scienze Naturali, Memorie A*, 81: 227-237.

De Guidi G. (1939). Nuovi resti di *Mastodon arvernensis* del Valdarno. *Atti della Società Toscana di Scienze Naturali, Memorie*, 48: 1-40.

Depéret C. (1890). Les animaux pliocènes du Roussillon. *Mémoires de la Société Géologique de France*, 3: 1-164.

Di Cencio A., Dulai A., Catanzariti R., Casati S. & Collareta A. (2021). First record of the brachiopod *Lingula*? from the Pliocene of Tuscany (Italy): The youngest occurrence of lingulides in the Mediterranean Basin. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 299: 237-249.

Di Stefano G. & Petronio C. (2002). Systematics and evolution of the Eurasian Plio-Pleistocene tribe Cervini (Artiodactyla, Mammalia). *Geologica Romana*, 36: 311-334

Dominici S., Mazzanti R. & Nencini C. (1994). Carta degli elementi geologico-morfologici e storici dei dintorni di San Miniato (Pisa). Scala 1:25.000. Consiglio Nazionale delle Ricerche (CNR), Pisa.

Dominici S., Rook L., Benvenuti M. & Abbazzi L. (1995a). Tapir remains in paralic deposits (Pliocene Tuscany): Facies analysis and taphonomy. *Geobios*, Supplement 1, 28: 131-135.

Dominici S., Mazzanti R. & Nencini C. (1995b). Geologia dei dintorni di San Miniato tra l'Arno, l'Elsa e l'Era. *Quaderni del Museo di Storia Naturale di Livorno*, 14: 1-35.

Dominici S., Danise S. & Benvenuti M. (2018). Pliocene stratigraphic paleobiology in Tuscany and the fossil record of marine megafauna. *Earth-Science Reviews,* 176: 277-310.

Dong W. (1996). Les Cervides (Artiodactyla) rusciniens (Pliocène) du Languedoc et du Roussillon (France). *Bulletin du Muséum National d'Histoire Naturelle*, 18: 133-163.

Dong W. (2011). Reconsideration of the systematics of the early Pleistocene *Cervavitus*. *Estudios Geológicos*, 67: 603-611.

Dorlhac M.J. (1855). Notice géologique sur le cratère de Coupet et sur son gisement de gemmes et d'ossements fossiles. *Annales de la Société d'Agriculture, Sciences, Arts et Commerce du Puy*, 19: 497-517

Falconer H. (1868). Paleontological memoirs and notes of H. Falconer, with a biographical sketch of the author. 675 pp. Murchison, London.

Farjand A., Fu L., Rummy P., Halaçlar K., Wang J., You Q. & Bi S. (2024). First record of well-preserved canid coprolites from Eurasia: new insights into the unique ecological niche of Yuanmou Basin. *Heliyon*, 10: e30072.

Fauquette S. & Bertini A. (2003). Quantification of the northern Italy Pliocene climate from pollen data: evidence for a very peculiar climate pattern. *Boreas*, 32: 361-369.

Ferretti M.P. (2021). Il "mastodonte" di Cava Monticino (Brisighella, Ra). *In* Rook L. (ed.), La Fauna Messiniana di Cava Monticino. *Memorie dell'Istituto Italiano di Speleologia*, serie II, 37: 129-132.

Ferretti M.P. & Croitor R.V. (2001). Functional morphology and ecology of Villafranchian proboscideans from central Italy. *In* Cavarretta G., Gioia P., Mussi M. & Palombo M.R. (eds), The World of Elephants. Proceedings of the First International Congress, Rome: 103-108.

Florindo F., Marra F., Angelucci D.E., Biddittu I., Bruni L., Florindo F., Gaeta M., Guillou H., Jicha, B., Macrì P., Morigi C., Nomade S., Parenti F., Pereira A. & Grimaldi S. (2021). Environmental evolution, faunal and human occupation since 2 Ma in the Anagni basin, central Italy. *Scientific Reports*, 11: 7056.

Forsyth Major C.I. (1877). Considerazioni sulla fauna dei Mammiferi pliocenici e postpliocenici della Toscana. *Memorie della Società Toscana di Scienze Naturali*, 3: 202-227.

Forsyth Major C.I. (1879). Cervi pliocenici del Val d'Arno superiore. *Atti della Società Toscana di Scienze Naturali*, 1: 100-101.

Forsyth Major C.I. (1881). Studi sugli avanzi pliocenici del genere Sus. *Atti della Società Toscana di Scienze Naturali*, 2: 227.

Fujita M., Kawamura Y. & Murase N. (2000). Middle Pleistocene wild boar remains from NT Cave (Japan). *Journal of Geosciences, Osaka City University*, 43: 57-95.

Gallai G. (2006). Sistematica, paleoecologia, paleogeografia dei Suidae fossili italiani. 201 pp. Unpublished PhD thesis, Università di Firenze.

Gallai G. (2007). Sistematica, paleoecologia e paleogeografia dei Suidae fossili italiani. *PaleoItalia*, 17: 17-22.

Gallai G. & Rook L. (2006). *Propotamochoerus* sp. from Gravitelli (Sicily). *Rivista Italiana di Paleontologia e Stratigrafia*, 112: 317-324.

Gallai G. & Rook L. (2011). *Propotamochoerus provincialis* from Monticino Quarry. *Bollettino della Società Paleontologica Italiana*, 50: 29-34.

Garassino A., Pasini G., De Angeli A., Charbonnier S., Famiani F., Baldanza A. & Bizzarri R. (2012). The decapod community from the Early Pliocene (Zanclean) of La Serra quarry (San Miniato, Pisa, Toscana, central Italy): sedimentology, systematics, and palaeoenvironmental implications. *Annales de Paléontologie*, 98: 1-61.

Garrido G. & Arribas A. (2014). The last iberian gomphothere (mammalia, proboscidea): *Anancus arvernensis mencalensis* nov. ssp. from the earliest Pleistocene of the Guadix Basin (Granada, Spain). *Palaeontologia Electronica*, 17: 1-16.

Gastaldi B. (1860). Su alcune ossa di mammiferi fossili del Piemonte. *Atti della Società Italiana di Scienze Naturali*, 2: 213-216.

Gemelli M., Di Rocco T., Folco L. & D'orazio M. (2017). Parentage identification of differentiated achondritic meteorites by Hand-held Energy Dispersive X-Ray Fluorescence Spectrometry. *Geostandards and Geoanalytical Research*, 41: 613-632.

Gentry A.W. (2005). Ruminants of Ruabánya. *Palaeontographia Italica*, 90: 283-303.

Ghetti P., Anadón P., Bertini A., Esu D., Gliozzi E., Rook L. & Soulié-Märsche I. (2002). The Early Messinian Velona Basin (Siena, Central Italy): paleoenvironmental and paleobiogeographical reconstructions. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 187: 1-33.

Ghinassi M., Fidolini F., Papini M., Rook L. & Sagri M. (2025). The Upper Valdarno Basin: from "Azzaroli & Lazzeri (1977)" to the present understanding of a pivotal continental succession in the Pliocene-Pleistocene of Europe. *Bollettino della Società Paleontologica Italiana*, 64: 261-287.

Gliozzi E., Abbazzi L., Argenti P., Azzaroli A., Caloi L., Capasso Barbato L.C., Di Stefano G., Esu D., Ficcarelli G., Girotti O., Kotsakis T., Masini F., Mazza P., Mezzabotta C., Palombo M.R., Petronio C., Rook L., Sala B., Sardella R., Zanalda E. & Torre D. (1997). Biochronology of selected mammals, molluscs and ostracods. *Rivista Italiana di Paleontologia e Stratigrafia*, 103: 369-388.

Göhlich U.B. (2010). The Proboscidea from the Miocene of Sandelzhausen. *Paläontologische Zeitschrift*, 84: 163-204.

Goldfuss G.A. (1820). Handbuch der Zoologie. 510 pp. Schrag J.L., Nürnberg.

Gray J.E. (1821). On the natural arrangement of vertebrose animals. *The London Medical Repository*, 15: 297-310.

Green J.L. (2006). Chronoclinal variation and sexual dimorphism in *Mammut americanum*. *Bulletin of the Florida Museum of Natural History*, 46: 29-59.

Guérin C. 2004. Les Proboscidiens (Mammalia) du gisement villafranchien moyen de Saint Vallier (Drôme, France). *Geobios*, Supplement 1, 37: 306-317.

Guérin C. & Tsoukala E. (2013). Tapiridae, Rhinocerotidae and Suidae from Milia (Greece). *Geodiversitas*, 35: 447-489.

Guérin C., Faure M. & Sen S. (1998). Le gisement pliocène de Çalta (Ankara, Turquie), 8. Suidae. *Geodiversitas*, 20: 441-453.

Hautier L., Mackaye H.T., Lihoreau F., Tassy P., Vignaud P. & Brunet M. (2009). New material of *Anancus kenyensis* from Toros-Menalla (Chad). *Journal of African Earth Sciences*, 53: 171-176.

Hay O.P. (1922). Further observations on some extinct elephants. *Proceedings of the Biological Society of Washington*, 35: 97-101.

Haynes G. (1991). Mammoths, Mastodonts and Elephants. 424 pp. Cambridge University Press, Cambridge.

Hays I. (1834). Descriptions of the specimens of inferior maxillary bones of mastodons in the cabinet of the American Philosophical Society, with remarks on the genus *Tetracaulodon* (Godman). *Transactions of the American Philosophical Society*, 4: 317-339.

Haywood A.M., Dowsett H.J. & Dolan A.M. (2016). Integrating geological archives and climate models for the mid-Pliocene warm period. *Nature Communications*, 7: 10646.

Heckeberg N.S. (2017). Origination of antlerogenesis. *Journal of Morphology*, 278: 182-202.

Heckeberg N.S. (2020). The systematics of the Cervidae: a total evidence approach. *PeerJ*, 8: e8114.

Heintz E. (1970). Les Cervidés villafranchiens de France et d'Espagne. *Mémoires du Muséum National d'Histoire Naturelle*, 22: 1-303.

Hillson S. (1992). Mammal Bones and Teeth: An Introductory Guide. 132 pp. University College, London.

Hillson S. (2005). Teeth. 373 pp. Cambridge University Press, Cambridge.

Hunt A.P. & Lucas S.G. (2012). Classification of vertebrate coprolites and related trace fossils. *New Mexico Museum of Natural History and Science Bulletin*, 57: 137-146.

Hunt A.P. & Lucas S.G. (2021). The ichnology of vertebrate consumption: dentalites, gastroliths and bromalites. *Bulletin of the New Mexico Museum of Natural History and Science*, 87: 1-216.

Iannucci A. (2023). *Sus strozzii* (Suidae, Mammalia) from the historical locality of Quercia (Early Pleistocene, Italy). *Geobios*, 77: 27-36.

Iannucci A. (2024). *Sus arvernensis* from Villafranca d'Asti. *Bollettino della Società Paleontologica Italiana*, 63: 45-81.

Iannucci A. & Sardella R. (2023). What does the "Elephant-*Equus*" event mean today? Reflections on mammal dispersal events around the Pliocene-Pleistocene boundary and the flexible ambiguity of biochronology. *Quaternary*, 6: 16.

Iannucci A., Cherin M., Sorbelli L. & Sardella R. (2021). Suidae transition at the Miocene-Pliocene boundary: a reassessment of the taxonomy and chronology of *Propotamochoerus provincialis*. *Journal of Mammalian Evolution*, 28: 323-335.

Iannucci A., Bellucci L., Conti J., Mazzini I., Mecozzi B., Sardella R., & Iurino D.A. (2022). Neurocranial anatomy of *Sus arvernensis* (Suidae, Mammalia) from Collepardo (Early Villafranchian; central Italy): taxonomic and biochronological implications. *Historical Biology*, 34: 108-120.

Iannucci A., Pazonyi P. & Sebe K. (2024). The Hungarian fossil record of the Pliocene pig *Sus arvernensis* (Suidae, Mammalia). *Swiss Journal of Palaeontology*, 143: 39.

Illiger C.D. (1811). Prodromus Systematis Mammalium et Avium. 301 pp. Berolini, Berlin.

Jouy-Avantin F., Debenath A., Moigne A.M. & Moné H. (2003). A standardized method for the description and the study of coprolites. *Journal of Archaeological Science*, 30: 367-372.

Janovskaya N.M. (1954). New deer from middle Pliocene of Moldavia. *Transactions of the Palaeontological Institute*, 47: 163-171.

Khomenko J. (1913). La faune méotique du village Taraklia. *Annuaire Géologique et Minéralogique de la Russie*, 15: 107-143.

Kierdorf U. & Kierdorf H. (2011). Deer antlers–a model of mammalian appendage regeneration: an extensive review. *Gerontology*, 57: 53-65.

Konidaris G.E. & Roussiakis S.J. (2018). The first record of *Anancus* (Mammalia, Proboscidea) in the late Miocene of Greece and reappraisal of the primitive anancines from Europe. *Journal of Vertebrate Paleontology*, 38: e1534118.

Korotkevich E.L. (1970). Late Neogene deer of the North Black Sea Area. 75 pp. Naukova Dumka, Kiev.

Kostopoulos D.S. (2006). The late Miocene vertebrate locality of Perivolaki (Greece). *Palaeontographica*, 276: 151-183.

Kotsakis T. (1986). On Paleobiogeography of Italian Tertiary Mammals/Elementi di Paleobiogeografia dei mammiferi terziari dell'Italia. *Hystrix the Italian Journal of Mammalogy*, 1: 25-68.

Larkin N.R., Alexander J. & Lewis M.D. (2000). Using experimental studies of recent faecal material to examine hyaena coprolites from the West Runton Freshwater Bed, Norfolk, UK. *Journal of Archaeological Science*, 27: 19-31.

Larramendi A. & Ferretti M.P. (2026). Elephants and Their Fossil Relatives: A 60 Million Year Journey. 368 pp. Princeton University Press, Princeton.

Lazaridis G., Tsoukala E. & Kostopoulos D.S. (2022). Validation of a *Propotamochoerus* species from SE Mediterranean. *Comptes Rendus Palevol*, 21: 531-549.

Lesueur C.A. (1822). Description of a *Squalus*, of a very large size, which was taken on the coast of New Jersey. *Journal of the Academy of Natural Sciences of Philadelphia*, 2: 343-352.

Lindsay E.H., Opdyke N.D. & Johnson N.M. (1980). Pliocene dispersal of the horse *Equus* and late Cenozoic mammalian dispersal events. *Nature*, 287: 135-138.

Linnaeus C. (1758). Systema Naturae per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. 10th edition. 338 pp. Laurentii Salvii, Stockholm.

Lister A.M. (1999). Epiphyseal fusion in *Mammuthus primigenius*. *Deinsea*, 6: 79-88.

Loss R. (1946). Resti dei Mastodonti piemontesi conservati nell'Istituto Geologico di Torino (Note preliminare). *Atti della Società Italiana di Scienze Naturali*, 85: 97-111.

Maglio V.J. (1972). Evolution of mastication in the Elephantida. *Evolution*, 26: 638-658.

Marín J., Saladié P., Azorit C. & Rodríguez-Hidalgo A. (2024). Identification of age at death in *Cervus elaphus*. *Journal of Archaeological Science*, 163: 105934.

Marra F., Petronio C., Salari L., Florindo F., Giaccio B. & Sottili G. (2018). A review of the Villafranchian fossiliferous sites of Latium in the framework of the geodynamic setting and paleogeographic evolution of the Tyrrhenian Sea margin of central Italy. *Quaternary Science Reviews*, 191: 299-317.

Masini F., Palombo M.R. & Rozzi R. (2013). A reappraisal of the early to middle Pleistocene Italian Bovidae. *Quaternary International*, 288: 45-62.

Mattei M., Fioramonti V., Cavinato G.P., Cifelli F., Mazzini I., Parotto M., Sardella R. & Sirna M. (2023). Magnetostratigraphy of the Collepardo Late Pliocene faunal assemblage (Early Villafranchian Triversa Faunal Unit), Ernici Mts., Central Italy. *Italian Journal of Geosciences*, 142: 398-410.

Mazza P. & Rustioni M. (1996). The Turolian fossil artiodactyls from Scontrone (Abruzzo, Central Italy) and their paleoecological and paleogeographical implications. *Bollettino della Società Geologica Italiana*, 35: 93-106.

McClymont E.L., Ho S.L., Ford H.L., Bailey I., Berke M.A., Bolton C.T., De Schepper S., Grant G.R., Groeneveld J., Inglis G.N., Karas C., Patterson M.O., Swann G.E.A., Thirumalai K., White M.S., Alonso-Garcia M., Anand P., Hoogakker B.A.A, Littler K., Petrick B.F., Risebrobakken B., Abell J.T., Crocker A.J., de Graaf F., Feakins S.J., Hargreaves J.C., Jones L.C., Markowska M., Ratnayake A.S., Stepanek C. & Tangunan D. (2023). Climate evolution through the onset and intensification of Northern Hemisphere glaciation. *Reviews of Geophysics*, 61: e2022RG000793.

Mein P. (1975a). Résultats du groupe de travail des vertébrés: biozonation du Néogène Méditerranéen à partir des mammifères. *In* Senes J. (ed.), Report on Activity of RCMNS Working, VIth Congress of the Regional Committee of Mediterranean Neogene Stratigraphy, Bratislava: 78-81.

Mein P. (1975b). Proposition de biozonation du Néogène Méditerranéen à partir des mammifères. *Trabajos sobre Neógeno/Cuaternario*, 4: 112-113.

Merella M., Collareta A., Casati S., Di Cencio A. & Bianucci G. (2023). Pliocene geotourism: Innovative projects for valorizing the paleontological heritage of three different-staged quarries of Tuscany (Central Italy). *Geoheritage*, 15: 82.

Michelotti G. (1861). Études sur le Miocène inférieur de l'Italie septentrionale. *Natuurkundige Verhandelingen van de Hollandsche Maatschappij der Wetenschappen te Haarlem*, 15: 1-184.

Montoya P., Ginsburg L., Alberdi M.T., Van der Made J., Morales J., & Soria M.D. (2006). Fossil large mammals from the early Pliocene locality of Alcoy (Spain) and their importance in biostratigraphy. *Geodiversitas*, 28: 137-173.

Moss C.J. (1996). Getting to know a population. *In* Kangwana K. (ed.), Studying Elephants, *African Wildlife Foundation Technical Handbook Series*, 7: 58-74.

Mothé D., Avilla L.S. & Winck G.R. (2010). Population structure of *Stegomastodon waringi* (Mammalia: Proboscidea: Gomphotheriidae) from the Pleistocene of Brazil. *Anais da Academia Brasileira de Ciências*, 82: 983-996.

Mulè F., Casati S., Bonfigli L., Di Cencio A. & Collareta A. (2025a). Terrapin aches and pains: parasite borings and other bone modifications in an Italian Pliocene population of *Mauremys* (Testudines, Geoemydidae). *Carnets de Géologie*, 25: 265-281.

Mulè F., Casati S., Bonfigli L., Di Cencio A. & Collareta A. (2025b). First unambiguous record of the tortoise genus *Testudo* from the Italian Pliocene. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 316: 87-101.

Mulè F., Casati S., Pieri A., Merella M., Di Cencio A., Bianucci G. & Collareta A. (2026). A sea of pufferfishes: new tetraodontid fossils from the Italian Pliocene shed light on an ongoing Mediterranean bioinvasion. *Carnets de Géologie*, 26: 353-364.

Mulè F., Godfrey S.J., Pandolfi L., Bianucci G., Bosio G., Bonfigli L., Casati S., Di Cencio A. & Collareta A. (in press). Episkeletozoan shadowing: a largely uninvestigated taphonomic effect of barnacle encrustation of vertebrate bones. *Paläontologische Zeitschrift*, https://doi.org/10.1007/s12542-026-00815-7

Nesti F. (1825). Lettere sopra alcune ossa fossili del Valdarno non par anco descritte: sulla nuova specie di elefante fossile del Valdarno all'illustratissimo sig. Dott. Prof. Ottaviano Targioni Tozzetti. *Nuovo Giornale de' Letterati*, 11: 195-216.

Nesti F. (1841). Report of the meeting of Sept. 25th, summarized by Savi, P. and Sismonda A. Sezione di Geologia, Mineralogia, e Geografia. *Atti della Terza Riunione degli Scienziati Italiani*, 9: 159.

Nishioka Y. & Tomida Y. (2022). Taxonomic revision of lower Miocene pecorans (Mammalia, Artiodactyla) from Japan, with a new fossil record of stem Cervidae. *Paleontological Research*, 27: 182-204.

Olsen S.J. (1979). Osteology for the Archaeologist. 192 pp. Peabody Museum Press, Cambridge.

Osborn H.F. (1926). Additional new genera and species of the mastodontoid Proboscidea. *American Museum of Natural History*, 238: 1-16.

Osborn H.F. (1942). Proboscidea: A Monograph on the Discovery, Evolution, Migration and Extinction of the Mastodonts and Elephants of the World, Vol. II: Stegodontoidea and Elephantoidea. 870 pp. The American Museum Press, New York.

Owen R. (1848). On the Archetype and Homologies of the Vertebrate Skeleton. 245 pp. Richard and John E. Taylor, London.

Palombo M.R. (2004). Biochronology of Plio-Pleistocene mammalian faunas on the Italian Peninsula: Knowledge, problems and perspectives. *Alpine and Mediterranean Quaternary*, 17: 565-582.

Palombo M.R. & Ferretti M.P. (2005). Elephant fossil record from Italy: knowledge, problems, and perspectives. *Quaternary International*, 126: 107-136.

Pandolfi L., Collareta A., Nowakowski D., Bianucci G. & Rook L. (2025). New early Pliocene Rhinocerotidae findings from Tuscany (Italy) and the Pliocene rhinocerotine record in Italy. *Geobios*, 88-89: 197-204.

Pandolfi L., Masini F. & Kostopoulos D.S. (2021). The latest Miocene small-sized Cervidae from Monticino Quarry (Brisighella, central Italy): paleobiogeographic and biochronological implications. *Historical Biology*, 33: 3368-3374.

Panetta D., Belcari N., Del Guerra A., Bartolomei A. & Salvadori P.A. (2012). Analysis of image sharpness reproducibility on a novel engineered micro-CT scanner with variable geometry and embedded recalibration software. *Physica Medica*, 28: 166-173.

Pantanelli D. (1886). Vertebrati fossili delle ligniti di Spoleto. *Atti della Società Toscana di Scienze Naturali, Memorie*, 7: 93-100.

Pareto L. (1865). Note sur les subdivisions que l'on pourrait établir dans les terrains tertiaires de l'Apennin septentrional. *Bulletin de la Société Géologique de France*, 22: 210-277.

Perilli N., Puccinelli A., Sarti G. & D'Amato Avanzi G.A. (2004). Villafranchian deposits of the Barga and Castelnuovo Garfagnana basins (Tuscany, Italy): Lithostratigraphy and sedimentary features. *Alpine and Mediterranean Quaternary*, 17: 313-322.

Petronio C., Di Canzio E. & Salari L. (2007). The Late Pleistocene and Holocene Mammals in Italy: new biochronological and paleoenvironmental data. *Palaeontographica*, 279: 147-157.

Petronio C., Bellucci L., Martinetto E., Pandolfi L. & Salari L. (2011). Biochronology and palaeoenvironmental changes from the Middle Pliocene to the Late Pleistocene in Central Italy. *Geodiversitas*, 33: 485-517.

Pfeiffer-Deml T. (2016). Deer from the Pliocene site of Bad Deutsch-Altenburg 26 (Lower Austria, Leithagebirge): Conclusions based on skeletal morphology. *Annalen des Naturhistorischen Museums in Wien*, 118: 133-173.

Pfeiffer-Deml T. (2020). Distinction of *Arvernoceros ardei* and *Cervus perrieri* (Cervidae, Mammalia) from the late Pliocene site of Perrier (France) based on the postcranial skeleton: taxonomic and phylogenetic conclusions. *Paläontologische Zeitschrift*, 94: 377-408.

Pickford M. (2013). Re-assessment of the suids from the Sables marins de Montpellier and selection of a lectotype for *Sus provincialis* Blainville, 1847. *Geodiversitas*, 35: 655-689.

Pickford M. & Obada T. (2016). Pliocene suids from Musaitu and Dermenji, Moldova: Implications for understanding the origin of African *Kolpochoerus* van Hoepen & van Hoepen, 1932. *Geodiversitas*, 38: 99-134.

Pineda A., Saladié P., Expósito I., Rodríguez-Hidalgo A., Cáceres I., Huguet R., Rosas A., López-Polín L., Estalrrich A., García-Tabernero A. & Vallverdú J. (2017). Characterizing hyena coprolites from two latrines of the Iberian Peninsula during the Early Pleistocene: Gran Dolina (Sierra de Atapuerca, Burgos) and La Mina (Barranc de la Boella, Tarragona). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 480: 1-17.

Pohlig H. (1911). Über *Cervus loczyi* Pohlig n. sp. *In* Kadic O. (ed.), Die fossile Säugetierfauna der Umgebung des Balatonsees. Paläontologische Abhandlungen. Resultate der wissenschaftlichen Erforschung des Balatonsees, Hölzel: 1-4.

Rivals F., Semprebon G.M. & Lister A.M. (2019). Feeding traits and dietary variation in Pleistocene proboscideans: A tooth microwear review. *Quaternary Science Reviews*, 219: 145-153.

Rook L. & Martínez-Navarro B. (2010). Villafranchian: the long story of a Plio-Pleistocene European large mammal biochronologic unit. *Quaternary International*, 219: 134-144.

Rook L., Gallai G. & Torre D. (2006). Lands and endemic mammals in the Late Miocene of Italy: constrains for paleogeographic outlines of Tyrrhenian area. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 238: 263-269.

Rook L., Croitor M., Delfino M., Ferretti M.P., Gallai G. & Pavia M. (2013). The Upper Valdarno Plio-Pleistocene vertebrate record: an historical overview, with notes on palaeobiology and stratigraphic significance of some important taxa. *Italian Journal of Geosciences*, 132: 104-125.

Ros-Montoya S., Martínez-Navarro B., Espigares M.P., Guerra-Merchán A., García-Aguilar J.M., Piñero P., Rodríguez-Rueda A., Agustí J., Oms O. & Palmqvist P. (2017). A new Ruscinian site in Europe: Baza-1 (Baza basin, Andalusia, Spain). *Comptes Rendus Palevol*, 16: 746-761.

Roth V.L. (1984). How elephants grow: heterochrony and the calibration of developmental stages in some living and fossil species. *Journal of Vertebrate Paleontology*, 4: 126-145.

Rustioni M. & Mazza P. (2001). Taphonomic analysis of *Tapirus arvernensis* remains from the lower Valdarno (Tuscany, Central Italy). *Geobios*, 34: 469-474.

Saarinen J. & Lister A.M. (2023). Fluctuating climate and dietary innovation drove ratcheted evolution of proboscidean dental traits. *Nature Ecology & Evolution*, 7: 1490-1502.

Samejima Y. & Matsuoka H. (2020). A new viewpoint on antlers reveals the evolutionary history of deer (Cervidae, Mammalia). *Scientific Reports*, 10: 8910.

Sanders W.J. (2017). Horizontal tooth displacement and premolar occurrence in elephants and other elephantiform proboscideans. *Historical Biology*, 30: 137-156.

Sanz M., Daura J., Égüez N. & Brugal J.P. (2016). Not only hyenids: a multi-scale analysis of Upper Pleistocene carnivore coprolites in Cova del Coll Verdaguer (NE Iberian Peninsula). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 443: 249-262.

Sarti G., Mazza P. & Rustioni M. (1998). A Miocene cervid from Torrente Morra sequence (Collesalvetti, Pisa, Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 104: 215-226.

Sarti G., Testa G. & Zanchetta G. (2008). A new stratigraphic insight of the Upper Pliocene-Lower Pleistocene succession of Lower Valdarno (Tuscany, Italy). *Geoacta*, 7: 27-41.

Schiffmann C., Hatt J.M., Hoby S., Codron D. & Clauss M. (2019). Elephant body mass cyclicity suggests effect of molar progression on chewing efficiency. *Mammalian Biology*, 96: 81-86.

Schlosser M. (1924). Tertiary vertebrates from Mongolia. *Palaeontologia Sinica*, ser. C, 1: 1-119.

Schmid E. & Garraux O. (1972). Atlas of animal bones: for prehistorians, archaeologists and quaternary geologists / Knochenatlas: für Prähistoriker, Archäologen und Quartärgeologen. 156 pp. Elsevier, Amsterdam.

Sen S., Fack F., Métais G. & Moissenet E. (2015). A late Miocene mammalian fauna from Olba in the Sarrión Depression, eastern Spain. *Paläontologische Zeitschrift*, 89: 545-562.

Shoshani J. & Tassy P. (2005). Advances in proboscidean taxonomy & classification, anatomy & physiology, and ecology & behavior. *Quaternary International*, 126: 5-20.

Simpson G.G. & Paula-Couto C. (1957). The mastodons of Brazil. *Bulletin of the American Museum of Natural History*, 112: 131-145.

Sismonda E. (1851). Osteografia di un mastodonte angustidente. *Memorie della Reale Accademia delle Scienze di Torino*, 12: 175-235.

Sorbelli L., Cherin M., Kostopoulos D.S., Pavia M. & Carnevale G. (2019). Partial cranium of *Propotamochoerus* (Cetartiodactyla, Suidae) from the late Miocene of Northern Italy. *In* Rook L. & Pandolfi L. (eds), Paleodays 2019, Abstract book: 42-43.

Stefanelli D., Marino M., Mecozzi B., Sardella R., Zazzera A. & Ferretti M.P. (2026). Reassessing diagnostic postcranial traits in Pleistocene elephants: evidence from *Palaeoloxodon antiquus* and *Mammuthus* in Italy. *Acta Palaeontologica Polonica*, 71: 155-171.

Stefanescu S. (1924). Sur la presence de l'*Elephas planifrons* et de trois mutations de l'*Elephas antiquus* dans les couches geologiques de Roumanie. *Comptes Rendus de l'Academie des Science*, 179: 1418-1419.

Stefaniak K. & Nauk P.A. (2015). Neogene and quaternary cervidae from Poland. 204 pp. Institute of Systematics and Evolution of Animals Polish Academy of Sciences, Kraków.

Strani F., DeMiguel D., Bellucci L. & Sardella R. (2018). Dietary response of early Pleistocene ungulate communities to the climate oscillations of the Gelasian/Calabrian transition in Central Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 499: 102-111.

Suc J.P., Fauquette S., Cheddadi R., Tan N., Ramstein G., Li L., Jiménez-Moreno G., Popescu S.-M. & Zheng Z. (2026). Pliocene contrasted climate conditions in space and over time: a unique pollen dataset from the NW Mediterranean Region for comparison with climate models. *Global and Planetary Change*, 259: 105328.

Szabó B., Pazonyi P., Tóth E., Magyari E.K., Kiss G.I., Rinyu L., Futó I. & Virág A. (2020). Pleistocene and Holocene palaeoenvironmental reconstruction of the Carpathian Basin based on multiproxy analysis of cervid teeth. *Historical Biology*, 33: 3307-3325.

Szabó P., Kovács J., Kocsis L., Vennemann T., Domingo L., Újvári G., Halmani A., Pirkhoffer E. & Codrea V. (2022). Pliocene-Early Pleistocene continental climate and vegetation in Europe based on stable isotope compositions of mammal tooth enamel. *Quaternary Science Reviews*, 288: 107572.

Tassy P. (1986). Nouveaux Elephantoidea (Mammalia) dans le Miocène du Kenya. *Cahiers de Paléontologie*, 10: 1-135.

Tassy P. (1996). Dental homologies and nomenclature in the Proboscidea. *In* Shoshani P. & Tassy P. (eds), The Proboscidea: Evolution and Palaeoecology of Elephants and Their Relatives, Oxford University Press, Oxford: 21-25.

Tassy P. (2014). L'odontologie de *Gomphotherium angustidens* (Cuvier, 1817) (Proboscidea, Mammalia): données issues du gisement d'En Péjouan (Miocène moyen du Gers, France). *Geodiversitas*, 36: 35-115.

Tomé C. & Vigne J.D. (2003). Roe deer (*Capreolus capreolus*) age at death estimates: new methods and modern reference data for tooth eruption and wear, and epiphyseal fusion. *Archaeofauna*, 12: 157-173.

Tuccimei G. (1891). Sui mammiferi fossili dell'Umbria e della Provincia di Roma. *Atti dell'Accademia Pontificia de' Nuovi Lincei*, 44: 274-275.

Valleri G., Bertoldi R. & Bertini A. (1990). Foraminifer and pollen assemblages from the Pliocene of Ponte a Elsa (Valdarno Inferiore, Tuscany). *Bollettino della Società Paleontologica Italiana*, 29: 321-333.

Valli A.M. (2010). Dispersion of the genus *Procapreolus* and the relationships between *Procapreolus cusanus* and the roe deer (*Capreolus*). *Quaternary International*, 212: 80-85.

van der Made J. (1996). Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie*, 33: 3-254.

van der Made J. & Moyà-Solà S. (1989). European Suinae (Artiodactyla) from the late Miocene onwards. *Bollettino della Società Paleontologica Italiana*, 28: 329-339.

Vislobokova I.A. (2007). New data on late Miocene mammals of Kohfidisch, Austria. *Paleontological Journal*, 41: 451-460.

Vislobokova I.A. (2012). Giant deer: origin and evolution, role in the biosphere. *Paleontological Journal*, 46: 643-775.

von den Driesch A. (1976). A guide to the measurement of animal bones from archaeological sites. *Peabody Museum Bulletin*, 1: 1-136.

Weithofer A. (1890). Die fossilien Proboscidier des Arnotales in Toskana. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients*, 8: 107-268.

Wilson R., Grigson C. & Payne S. (1982). Ageing and Sexing Animal Bones from Archaeological Sites. 274 pp. Bar British Series, Oxford.

Yang L., Zhang X., Zhao X. & Xiang H. (2022). Technological advance and application of coprolite analysis. *Frontiers in Ecology and Evolution*, 9: 797370.

Zanchetta G. & Mazza P. (1996). *Anancus arvernensis* remains from the basal portion of the *Arctica islandica*-bearing marine deposits of Lower Valdarno. *Bollettino della Società Geologica Italiana*, 115: 105-113.

Zanchetta G., Petrucci S., Mazza P. & Rustioni M. (1995). New Villafranchian finds from the lower Valdarno (Tuscany, central Italy). *Alpine and Mediterranean Quaternary*, 8: 449-456.

Zapfe H. (1997). Ein bemerkenswertes Cervidengeweih aus dem Pannon des Burgenlandes, Österreich. *Annalen des Naturhistorischen Museums in Wien, Series A*, 98A: 173-177.

Zeder M.A. & Lemoine X. (2020). Factors affecting molar size in *Sus scrofa*. *Journal of Archaeological Science*, 124: 105266.

Zehtabvar O., Vajhi A.R., Akbarein H.A., Ahmadian F.S., Khanamooeiashi M., Soflaei R. & Borgheie F. (2022). CT anatomy of cervical vertebrae of Asian elephant (*Elephas maximus*). *Veterinary Medicine and Science*, 8: 1750-1768.

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