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Vigna Nuova (Perugia): the first Middle Villafranchian mammal assemblage from the Valdichiana Basin

Abbreviated title: Mammals from Vigna Nuova

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KEY WORDS – Canis, Croizetoceros ramosus*, Early Pleistocene,* Equus senezensis*, Fossil mammals, Umbria.*

ABSTRACT - Umbria (central Italy) represents one of the most interesting areas for the study of Mediterranean Plio-Pleistocene mammal faunas thanks to the abundance of paleontological deposits distributed throughout the territory. Most of the fossils have been discovered in the Tiberino Basin, which extends over ca. 1800 km^2 along the middle part of the regional territory, and in the small Tavernelle-Pietrafitta Basin, south of Trasimeno Lake. Instead, in this paper we report on the assemblage from Vigna Nuova (Piegaro, Perugia) in the Valdichiana Basin, whose continental deposits crop out in few areas of western Umbria. Taphonomic and geological evidence, coupled *with the few available excavation notes, allow to divide the sample into two assemblages. The younger comes from the conglomerates (here called “upper layer”) still visible on the outcrop and is composed only of remains of cf.* Leptobos. *The data obtained from this fragmentary sample and some sedimentological-stratigraphic considerations suggest that it can be correlated with other well-known Valdichiana assemblages (e.g., Selvella, Farneta), dated at ca. 1.5 Ma. The older sub-sample comes from a putative paleosol (here called “lower layer”) no longer visible in the field. It includes cf.* Megantereon*,* Canis *sp., Mustelidae indet., Proboscidea indet.,* Equus *cf.* senezensis*, cf.* Leptobos*,* Croizetoceros ramosus*,* ‘Pseudodama’ *sp., Cervidae indet. (large size), and* Sus *cf.* strozzii. *This assemblage can be referred to the Coste San Giacomo Faunal Unit (late Middle Villafranchian; ca. 2.2–2.1 Ma). It represents the first well-preserved sample of this age in Umbria and one of the few in Italy, opening new interesting research perspectives on the distribution of mammals in the Peninsula and also on the stratigraphy and evolution of the Valdichiana Basin.*

> *Aggiungeva che per scavare le poche ossa che mi avrebbe subito inviate aveva dovuto faticare enormemente e lottare per due giorni contro ogni sorta di difficoltà. Ricevuto il graditissimo invio mi affrettai a consolidare e restaurare con ogni cura quelle primizie ed oggi sono lieto di poter annunziare, in così solenne adunanza, la interessante scoperta…*

> He added that in order to excavate the few bones that he would immediately send me he had had to work enormously and fight for two days against all sorts of difficulties. Having received the very welcome shipment, I hastened to consolidate and restore those fruits of the soil with every care and today I am pleased to be able to announce, in such a solemn meeting, the interesting discovery…

Giovanni Capellini (1890: 275)

INTRODUCTION

In spite of its small geographical extension (ca. 8500 km^2), Umbria represents a treasure trove of very interesting discoveries for Plio-Pleistocene vertebrate paleontology. Mentioned since the first half of the 19th century (Cuvier, 1821), in the following decades these discoveries began to draw the attention of the Italian scientific community (e.g., Verri, 1879; Pantanelli, 1886; Tuccimei, 1891, 1895; Clerici, 1894, 1895; Meli, 1895), including eminent scholars such as Giovanni Capellini, who published at least three contributions on Umbrian mammals (Capellini, 1888, 1889, 1890).

From the paleogeographic point of view, during the Plio-Pleistocene, central Italy was intersected by a set of NW-SE trending grabens related to the eastward migration of the Apennine extensional deformation (Martini & Sagri, 1993; Pascucci et al., 1999; Collettini et al., 2006). These depressions were filled by marine sediments on the west and by continental sediments on the east, with the transition between the two realms (i.e., the Tyrrenian paleocoast) crossing western Umbria from Città della Pieve south-east to Orvieto (Ambrosetti et al., 1987; Bizzarri & Baldanza, 2020). The main intermontane basin in the central-eastern part of the region is the Tiberino Basin (Fig. 1a), which extends for ca. 1800 km^2 from Sansepolcro to Terni (southwest) and Spoleto (southeast) (Basilici, 1997). This extensional basin, historically erroneously interpreted as a single huge lake ("Tiberino Lake"; Lotti, 1917), has actually been occupied at least over the last 3 Ma by a complex and dynamic system of lake, marsh, and river environments interconnected each other (Basilici, 1997). Among the smaller basins, it is worth noting the Tavernelle-Pietrafitta Basin (Fig. 1a), located south of Trasimeno Lake, characterized alternatively by lacustrine/palustrine and alluvial plain conditions during the Plio-Pleistocene. This basin hosts the most important Umbrian fossiliferous site, and one of the most important in Europe, that is, Pietrafitta (Martinetto et al., 2014; Sorbelli et al., 2021, and references therein). The Tavernelle-Pietrafitta Basin is interposed between the Tiberino

Basin to the east and the Valdichiana Basin to the west (Fig. 1a). The latter develops from north-west to south-east along the Tuscany-Umbria-Latium boundary and has been filled by shallow marine and continental sediments since the early Pliocene (Bizzarri & Baldanza, 2020).

Reports on fossil continental mammals are abundant in the literature for the Tiberino Basin (e.g., localities of Pantalla, Torre Picchio, Podere San Lorenzo, Villa San Faustino, among others) and for the Tavernelle-Pietrafitta Basin (see the aforementioned site of Pietrafitta) and, following the steps traced by the famous 19th century researchers, they have been the subject of many modern studies and revisions (e.g., Sardella et al., 1995, 2018; Girotti et al., 2003; Cherin et al., 2016, 2019a). On the contrary, in the western part of Umbria (i.e., in the Valdichiana Basin), the occurrence of marine vertebrates is known above all (fossil cetaceans from the Allerona area; Baldanza et al., 2018).

This knowledge gap is filled by the Vigna Nuova local faunal assemblage (LFA), which represents the only record of continental mammals from this portion of the regional territory. The collection was briefly mentioned by Gentili (1993). A faunal list was published by Petronio et al. (2002) and copied-and-pasted by Argenti (2004), who also stated that the Vigna Nuova LFA should be referred to the Tasso faunal unit (FU) “for its stratigraphic position with respect to Pietrafitta and its paleontological assemblage (mainly for the presence of *Megantereon cultridens*)” (Argenti, 2004: 70).

Here we provide the first systematic study of the Vigna Nuova LFA, ascertaining that, in fact, it is made up of two distinct assemblages, one of which offers some surprising biochronological information.

GEOLOGICAL SETTING AND TAPHONOMY

The Vigna Nuova LFA was unearthed in 1989 during excavation works on the front of a hill (named “Greppo Lidolfo”) for the planting of a vineyard (hence the name, which means “new vineyard”). The site is located near Piegaro (Perugia; 42°58'04.2"N, 12°04'04.7"E) at the easternmost border of the Valdichiana Basin (Fig. 1a).

Some inconsistencies exist as regards the stratigraphy of the deposits cropping out in the area. In the description of the Geological Map of Italy in 1:50,000 scale (Foglio 310, Passignano sul Trasimeno), Barchi & Marroni (2010) mention the Vigna Nuova assemblage as recovered from the Fosso Cigne Unit (Tiberino Basin, Nestore Synthem). Following Argenti (2004), the assemblage, hence the unit, is referred to the Tasso FU (ca. 1.8 Ma). Conversely, the most recent Umbrian geological mapping projects (Regione Umbria, 2013) include the Vigna Nuova locality in the Meletto Unit (Valdichiana Basin, Sanfatucchio Synthem), also referred to the Tasso FU. The Meletto Unit is very similar to and probably partially heteropic with the nearby Gioiella Unit, which yielded important samples of terrestrial mammals in the surroundings of the homonymous town, in particular at the locality of Selvella (De Giuli, 1987), which is located only 16 km north-west of Vigna Nuova (Fig. 1a). The Selvella LFA, originally dated at ca. 1 Ma (De Giuli, 1987), is today referred to the Farneta FU (ca. 1.5 Ma; Alberdi & Palombo, 2013; Cirilli et al., 2020). In fact, the lithological and sedimentological features of the Fosso Cigne and Meletto Units are quite similar. Both are mainly composed by conglomerates with a reddish medium-coarse sand matrix. Clasts are poorly sorted and predominantly made of sandstone in the first unit and carbonate in the second. The main difference is that the Fosso Cigne conglomerates have channeled geometry, while those of Meletto show no clear structures. Unfortunately, the Vigna Nuova outcrop (about 6 m in height) today is almost completely covered by vegetation, so it is not possible to describe the local stratigraphic succession. The few exposed portions (Fig. 1b) are made of conglomerates with rounded, polygenic clasts, sometimes with imbricate bedding, alternating with thin layers of medium-coarse sand. The current evidence therefore does not allow to resolve the doubts about the stratigraphic attribution of the outcrop, for which further geological studies will be necessary.

Nonetheless, the taphonomic features of the Vigna Nuova mammal collection, coupled with excavation notes and labels, offer some hints on the stratigraphic context. Based on the lithology of the embedding sediment (when available), color of fossils, and their mineralization, it is possible to clearly separate the collection into two groups. The first includes fossils embedded by or maintaining traces of a whitish-yellowish sand with carbonate matrix, rich in large-sized quartz crystals and spots of black organic matter. Calcite crystals can occur as coating and infills within larger bone cavities (e.g., medullary cavity in long bones). Bones are both mineralized and impregnated (i.e., minerals and secondarily organic matter filled the smaller cavities such as trabeculae; Fig. 2), thus being very heavy. Some show root traces. Few specimens (SABAP_UMB 129847, 129849, 129852, 129853, 129869, 129881) are encrusted by a yellow-brown carbonate coating with reticular concretions. This assemblage is characterized by considerable variability in taphonomic attributes, ranging from poorly preserved isolated specimens (very abraded and broken bones) to well-preserved ones, sometimes still in anatomical connection. The weathering stages (Behrensmeyer, 1978) are heterogeneous, ranging from 0 to 4 (Fig. 2). Several taxa are recognized in this first assemblage (Supplementary Online Material), with about half of the identifiable specimens referred to Cervidae (see Systematic paleontology). On the contrary, only a bovid taxon (probably a single individual) is recognized in the second group of bones. These latter show traces of a dark-yellow to reddish sand. Mineralization is much less advanced and the inner cavities of the bones, regardless of their size, are empty. Most of the remains show evidence of abrasion and breakage typical of fluvial transport, whereas weathering is low (Fig. 2) suggesting little time spent in a sub-aerial environment prior to burial.

The observations above support the hypothesis that the two assemblages come from different stratigraphic layers. The remains of the second group certainly come from the conglomerates cropping out at Vigna Nuova. A putative fluvial depositional environment for these sediments is compatible with the taphonomic features of bovid bones. On the other side, no traces of the sediments associated to the fossils of the first group are visible today in the field. Based on original notes and labels, we know that the paleontological material was recovered near the bottom of the hill, therefore from a portion of the succession that is no longer exposed today. On the basis of the few lithological and taphonomic elements available, we can assume that this lower layer was a paleosol, but only future studies in the area could confirm this hypothesis.

The fossils of the two assemblages are treated as separate (lower layer and upper layer) hereinafter.

MATERIALS AND METHODS

The studied material is curated by SABAP_UMB and was prepared/restored and studied at the Dipartimento di Fisica e Geologia of the Università degli Studi di Perugia (Italy). For preparation details see Cherin et al. (2019a). The identification codes of the SABAP_UMB are of two types: those assigned in the past have six digits (e.g., SABAP_UMB 129842), while those recently assigned are composed of an alphanumeric code such as SABAP_UMB 22.S241-3.263 (the complete list is provided in Supplementary Online Material). In the manuscript the identifier "S241-" is omitted, thus obtaining a code like SABAP_UMB 22.3.263.

Identification of paleontological specimens is based on anatomical descriptions and morphological comparative analysis. Biometric/statistical comparisons are performed is some cases. In particular, for equids, bivariate plots and PCA were built in R Environment v. 1.4.1103 (R Core Team, 2013), using the packages *prcomp()* v. 3.6.2 (Venables & Ripley, 2008) and *ggplot2()* v. 3.3.3 (Wickham, 2016). PCA were performed on third metatarsals, using the parameter scale = T to have a unit variance before starting the analyses in R. The Log10 Ratio diagrams on third metatarsals are based on the log-transformed mean values of the Höwenegg *Hippotherium primigenium* von Meyer, 1829 (Bernor et al., 1997). The Höwenegg *H. primigenium* sample represents a well-studied, homogeneous sample of a single species of Equinae, for which the full range of descriptive statistics (mean, standard deviation, confidence limits, and minimum, maximum, and median values) are available for each bone, including the cranium, mandible, and teeth.

All measurements are taken with digital calipers and are given with a precision of 0.1 mm. Measurements are provided in Supplementary Online Material. Sources of data used for comparisons and measurement and anatomical abbreviations are indicated in the relative figure/table captions.

Anatomical and/or measurement nomenclature follows Eisenmann et al. (1988) and Bernor et al. (1997) for equids; Sala (1986), Masini (1989), and Duvernois (1990) for bovids; Heintz (1970) for cervids; Fujita et al. (2010) and Cherin et al. (2018) for suids.

Institutional abbreviations – AUT, Aristotle University of Thessaloniki, Greece; IGF, Museo di Storia Naturale, Sezione di Geologia e Paleontologia, Università di Firenze, Italy; IPS, Institut Català de Paleontologia Miquel Crusafont, Spain; LAMC, Natural History Museums of Los Angeles County, USA; MCL, Musée des Confluences de Lyon, France; NHMB, Natural History Museum Basel, Switzerland; SABAP_UMB, Soprintendenza Archeologia Belle Arti e Paesaggio dell'Umbria, Italy.

SYSTEMATIC PALEONTOLOGY (LOWER LAYER)

Class MAMMALIA Linnaeus, 1758
Order CARNIVORA Bowdich, 1821
Family FELIDAE Fischer von Waldheim, 1817
Genus *Megantereon* Croizet & Jobert, 1828
cf. *Megantereon*
(Fig. 3)

Referred material – Fragmented right upper canine (SABAP_UMB 129842).

Description – SABAP_UMB 129842 (Fig. 3a) preserves the root and a small part of the crown without appreciable crenulations on the edges. The root is moderately curved in mesiodistal direction. In mesial view, the tooth appears overall stouter and only slightly compressed labiolingually.

Comparisons and discussion – Sabertoothed felids (subfamily Machairodontinae) are a widespread group of top predators in the Plio-Pleistocene carnivoran guilds of Europe and several other parts of the world (Antón, 2013).

The fragmentary nature of the specimen from Vigna Nuova does not permit detailed comparisons. The absence/presence of crenulations along the mesial and distal edges of the crown is the more reliable criteria to differentiate Smilodontini and Homotherini, with the latter normally showing clear crenulations. However, the absence of crenulations in the small preserved portion of the crown of SABAP_UMB 129842 could be due to preservation issues. The morphology of the crown is another diagnostic character, being normally stouter and less compressed in *Homotherium* and slenderer and more labiolingually compressed in *Megantereon*. Unfortunately, this character cannot be assessed too. The curvature of the root in SABAP_UMB 129842 is intermediate between that of *Megantereon cultridens* Cuvier, 1824 from Villarroya and that of *Homotherium crenatidens* Fabrini, 1890 from the Incarcal complex as can be seen in Fig. 4a. The morphology of the tip of the root is not rounded as in Smilodontini, but more pointed as in *Homotherium* (Fig. 4a). However, the taxonomic value of this character is not discussed in the literature and we do not know its variability other than in the samples we have selected for comparison.

To solve these issues, we built a violin plot of the ratio between labiolingual with and mesiodistal length of the upper canine of Old World *Homotherium* and *Megantereon* (Fig. 4b). Our results show that the studied specimen fully falls into the range if *Megantereon* species, although it is also close to the earliest representatives of the *Homotherium* lineage (i.e., early Pliocene of Odessa Catacombs), for which however, biometric variation is virtually unknown due to poor record.

Accordingly, we confidently refer the studied specimen to cf. *Megantereon*.

Family CANIDAE Fischer von Waldheim, 1817

Genus *Canis* Linnaeus, 1758

Canis sp.

(Fig. 3)

Referred material – Articulated cervical vertebrae 3-7 (SABAP_UMB 129850); rib (SABAP_UMB 129875); thoracic vertebra 1 and rib fragments (SABAP_UMB 129877); articulated thoracic vertebrae 2-3 (SABAP_UMB 129879).

Description – The canid material from Vigna Nuova is represented only by elements of the axial skeleton, all belonging to a single individual. The articulated cervical vertebrae 3-7 (C3-7; SABAP_UMB 129850) have retained their original shape, even if they miss some portions (Fig. 3b). The spinous process is still present only in C3, while the right transverse process is preserved only in C4-6. The vertebrae have a long and stout body, which gradually became shorter and narrower towards C7 (see measurements in Supplementary Online Material). The first thoracic vertebra (T1; SABAP_UMB 129877 *partim*) preserves only the body and few fragments of the neural arch. T2 and T3 are still articulated (SABAP_UMB 129879) and in the former, a slender, long, and posteriorly directed spinous process is still visible, but half broken (Fig. 3d). The two most complete ribs (SABAP_UMB 129875 and SABAP_UMB 129877 *partim*; Fig. 3c) probably correspond to the first pair, as they perfectly articulate into the articular facets on T1-T2.

Comparisons and discussion – The first occurrence of *Canis* in Europe has long been regarded as one of the main biochronological markers of the onset of the Late Villafranchian, i.e., the so-called "wolf event" (Azzaroli, 1983; Azzaroli et al., 1988; Torre et al., 1992, 2001). Nevertheless, further discoveries such as those of *Canis* sp. in the Early Villafranchian of Vialette (France; Lacombat et al., 2008) and in the Middle Villafranchian of Coste San Giacomo (Italy; Bellucci et al., 2012, 2014), point to an earlier arrival of *Canis* in Western Europe and support a model of diachronous dispersal across the continent (Sotnikova & Rook, 2010). Aside from the aforementioned records of *Canis* *sensu stricto* in the Early-Middle Villafranchian, several species are recognized in later times, including *Canis etruscus* Forsyth Major, 1877, *Canis arnensis* Del Campana, 1913, and *Canis mosbachensis* Soergel, 1928, among others (Cherin et al., 2014; Bartolini-Lucenti & Rook, 2016; Bartolini-Lucenti et al., 2017, 2020 and references therein).

The C3 and C4 from Vigna Nuova show striking morphological resemblance with the same vertebrae of *C. etruscus* from Olivola (Italy; IGF 4523) figured by Torre (1967: plate VIII, fig. 8). In turn, the same author stated that the postcranial morphology of *C. etruscus* does not differ significantly from that of the extant wolf *Canis lupus* Linnaeus, 1758, except in relatively smaller dimensions (Torre 1967: 131). The vertebrae from Vigna Nuova are extremely similar to those of Olivola especially in the relative development of the pre- and postzygapophyses with respect to the neural arch and body, in the inclination (ca. 45° anterodorsally to posteroventrally) of the anterior and posterior articular facets in lateral view, and in the ventral projection of the posterior portion of the body relative to the anterior (i.e., the ventral edge of the body is inclined posteroventrally in lateral view) (Fig. 3e-f). In addition to the morphological similarities, the vertebrae are also very similar in size (e.g., the length of the body is 35.6 versus 34.7 mm in C3 and 31.4 versus 32.1 mm in C4 in SABAP_UMB 129850 and IGF 4523, respectively). However, despite these similarities with *C. etruscus*, the sample from Vigna Nuova does not offer sufficient diagnostic characters for identification at the species rank and is therefore referred to *Canis* sp.

Family MUSTELIDAE Fischer von Waldheim, 1817

Mustelidae indet.

(Fig. 3)

Referred material – Crown of left upper canine (SABAP_UMB 22.3.263).

Description – An almost complete canine crown from the Vigna Nuova collection can be attributed to a small-sized carnivoran (Fig. 3g). The crown is straight and has a roughly circular section along all its height. The lingual wall is smooth, whereas the labial one shows a shallow vertical furrow in distolabial position and another groove, markedly deeper, in mesiolabial position. Neither of them reaches the apex of the crown. The latter is relatively rounded. A well-developed keel is present along the mesial margin of the tooth and a weaker one along the distal one.

Comparisons and discussion – The incompleteness of the specimen hinders any attempt at taxonomic attribution. Assuming that it is an upper canine (due to the virtually absent curvature of the crown) of the left side (due to the position of furrows and keels), the field can be restricted to small-sized carnivorans (the preserved portion of the crown is about 1 cm in height). We can exclude felids and canids, characterized by upper canines with more marked curvature, very pointed apexes, and labiolingual flattening (i.e., elliptical section). The greatest similarities are found with the mustelids, which instead have straight upper canines, with an approximately circular section and a complex of furrows corresponding, in relative position and development, to that of SABAP_UMB 22.3.263. The overall size of the latter is approximately between that of a marten and that of a badger, i.e., it approaches that of extinct forms such as *Pannonictis* (see Colombero et al., 2012).

Order PROBOSCIDEA (Illiger, 1811)

Proboscidea indet.

Referred material – Rib fragment (SABAP_UMB 22.3.264).

Description – The only available proboscidean material is a small fragment of a rib.

Comparisons and discussion – At least four proboscideans occur in the European Villafranchian mammal assemblages: *Mammut borsoni* (Hays, 1834), *Anancus arvernensis* (Croizet & Jobert, 1828), *Mammuthus rumanus* (Stefanescu, 1924), and *Mammuthus meridionalis* (Nesti, 1825) (approximately in stratigraphic order, from older to younger). Due to the fragmentation of the available specimen, it is not possible to refer it to a specific taxon.

Order PERISSODACTYLA Owen, 1848

Family EQUIDAE Gray, 1821

Genus *Equus* Linnaeus, 1758

Equus cf. *senezensis* Prat, 1964

(Fig. 5)

Referred material – Articulated left metacarpals II-III-IV, proximal part (SABAP_UMB 129840); left metacarpal III, proximal epiphysis (SABAP_UMB 129857); cervical vertebrae (SABAP_UMB 129867, SABAP_UMB 129874); left astragalus (SABAP_UMB 129869); mandible with left and right c1-i3 and left p2, divided into two pieces (SABAP_UMB 129835+129837); partial left hindlimb in anatomical connection with distal tibia, tarsus, metatarsals II-III-IV (SABAP_UMB 129856+129861+129862+129868).

Description – The mandible SABAP_UMB 129835+129837 includes a well-preserved left p2 with medium-high stage of wear. It shows a short and blunt anterostylid, the metaconid is small and rounded, and the metastylid is pointed distally. The linguaflexid is V-shaped, a feature diagnostic of stenonian horses. The ectoflexid is very shallow. The preflexid is short whereas the postflexid is longer with simple ornamented morphology. This last feature indicates an advanced wearing stage. A small *pli caballinid* is present on the mesial border of the hypoconid. The anterior portion of the mandible exhibits a slender symphysis with the left mandibular body partially preserved. The lower incisors show a high degree of wear, with the infundibulum not always present (e.g., left i1). The lower canines are visible as small blunt enamel knobs that emerge from the mandible about 1 cm behind the i3s.

SABAP_UMB 129840 includes a left third metacarpal (MC3) preserving about half diaphysis and the proximal epiphysis. It has a narrow appearance in anterior view, although not slender. The proximal epiphysis has a flat articular surface for the magnum and large articular facets for the second and fourth metacarpals (MC2, MC4). The latter are almost complete and preserved in anatomical connection.

The most complete specimen is the articulated left hindlimb SABAP_UMB 129856+129861+129862+129868. The tibia preserves the diaphysis and the distal epiphysis, lacking the proximal one. Its general appearance is rather bulky. Much information about the morphology of the distal epiphysis cannot be not observed due the presence of the astragalus and calcaneum in anatomical connection, with some sediment in between. The latter bones are complete. The calcaneum has a short and robust corpus, with a well-preserved massive *tuber calcanei*. The morphology of the other ankle elements (central, first+second, third, and fourth tarsal bones) cannot be described due to anatomical connection. The second, third, and fourth metatarsals (MT2-4) are articulated and complete. The MT3 appears robust, due the reduced maximal length, the relatively large proximal and distal epiphyses, and the wide circular diaphysis. The distal epiphysis has small medial and lateral protuberances, which are not larger than the medial and lateral trochleae. The latter are round, with a well-developed *crista sagittalis* in between. In posterior view, the long lines for the attachment of the interosseus ligaments connecting the MT2 and MT4 are partially preserved.

SABAP_UMB 129869 is a left astragalus, with incomplete and weathered articular surface for the calcaneum. The astragalus has a short and massive aspect, with small medial and lateral trochleae and a large medial *tuberculum tali* for the attachment of the *ligamentum collaterale*. The trochlear groove is large.

Comparisons and discussion – In Europe, the *Equus* Datum is marked by the appearance of the large-sized *Equus livenzovensis* Bajgusheva, 1978, occurring at the beginning of the Pleistocene (ca. 2.6 Ma) in the localities of Liventsovka (Russia), Montopoli (Italy), Roca-Neyra (France), and El-Rincón 1 (Spain) (Alberdi et al., 1997, 1998; Azzaroli, 2000; Bernor et al., 2018, 2019; Rook et al., 2019; Cirilli et al., 2021a, 2021b, 2021c). This biochronological event represents the dispersal of the monodactyl horses form North America into the Old World, with the species *Equus simplicidens* Cope, 1892 as the most likely original pool for the Eurasian species. During the Gelasian, monodactyl equids diversified in different species such as *Equus stenonis* Cocchi, 1867, *Equus major* Depéret in Delafond & Depéret, 1893 ex Boule, *Equus senezensis*, and *Equus stehlini* Azzaroli, 1964. *Equus stenonis* represents the most widespread species during this time frame, with its first occurrence in the Early Pleistocene site of Saint Vallier (France; 2.45 Ma; dating in Nomade et al., 2014). This species dispersed in western Eurasia, from Caucasus to the Iberian Peninsula, and diversified into different populations/ecomorphotypes (Palombo & Alberdi, 2017; Cherin et al., 2021; Cirilli et al., 2021a). The distribution of *E. major* is still not well defined, but at the present time it seems mostly present in Central, North, and Eastern Europe (Palombo & Alberdi, 2017). Cirilli (2022) reported some new insights on the evolution and dispersals of the Gelasian medium-small sized horses. Recent research on the Middle Villafranchian localities of Senèze (France) and Coste San Giacomo (Italy) have confirmed the presence of a medium-sized horse, intermediate between *E. stenonis* and *E. stehlini* (Palombo et al., 2017; Cirilli et al., 2021a; Cirilli, 2022), identified as *E. senezensis*. The species was originally described as a subspecies of *E. stenonis*, namely *E. stenonis senezensis*, by Prat (1964, 1980) from the locality of Senèze (France; 2.2–2.0 Ma; dating in Nomade et al., 2014). Subsequently, Alberdi et al. (1998) questioned its subspecific rank, suggesting a better attribution to the species level. This interpretation was supported by the revision of the European *E. stenonis* and *E. stehlini* samples undertaken by Cirilli et al. (2021a) and Cirilli (2022), suggesting that the medium-sized horse from Senèze truly represents a different species during the Early Pleistocene. Beside Senèze, *E. senezensis* has been reported also in Italy, from the Early Pleistocene localities of Coste San Giacomo and Montecarlo (Upper Valdarno Basin). These sites have been dated at ca. 2.2–2.1 Ma (Ghinassi et al., 2005; Bellucci et al., 2012, 2014; Fidolini et al., 2013; Florindo et al., 2021), hence similar in age with Senèze. The European medium-sized horses of the late Early Pleistocene underwent a turnover at the Gelasian-Calabrian boundary. Indeed, the first occurrence of *Equus altidens* von Reichenau, 1915 has been recognized in the paleoanthropological site of Dmanisi (Georgia; 1.85–1.76 Ma), predating the first Italian occurrences of Farneta and Pirro Nord (Bernor et al., 2021). *Equus altidens* would appear to be the most geographically widespread species in the late

Early Pleistocene, sharing its range with the last representatives of *E. stenonis* and the earliest representatives of *Equus suessenbornensis* Wüst, 1900, and being part of an extensive faunal turnover occurring at ca. 1.8 Ma in Eastern Europe and slightly later in Central and Western Europe (Alberdi & Palombo, 2013; Palombo & Alberdi, 2017; Cirilli et al., 2020; 2021a; Bernor et al., 2021; Bartolini-Lucenti et al., 2022).

Morphometric comparisons on the Vigna Nuova equid remains are here provided based on the most relevant elements, namely the p2 and the complete MT3. Fig. 6a plots the maximum width (M6) versus maximum length (M1) for p2, comparing the Vigna Nuova specimen with the European Early Pleistocene species. SABAP_UMB 129835 is included in the range of variation of *E. senezensis* from Senèze, and plots close to the largest *E. stehlini* (Upper Valdarno Basin) and the smallest *E. altidens* (Dmanisi and Venta Micena). It is well separated from the European *E. stenonis*, thus far highlighting its attribution to a medium-small sized species. *Equus suessenbornensis* represents the largest species considered in the plot, whereas *E. stenonis mygdoniensis* from Gerakarou-1 (Mygdonia Basin, Greece) overlaps the morphometric range of variation of *E. stehlini* and *E. altidens*.

More interesting results are depicted in the multivariate analyses on the MT3s. Fig. 6b shows the results for the MT3 PCA, with PC1 and PC2 accounting for 85.4% of the total variance (PC1 = 80.4%; PC2 = 5.0%). The loading distribution is reported as an inset in Fig. 6b and in Supplementary Online Material within the variance components. PC1 separates species by maximal length from negative to positive values (less to more elongate), whereas PC2 denoted a slenderer morphology from positive to negative values. The Vigna Nuova specimen is included in the range of variation of *E. senezensis*, distinct from the *E. stehlini* sample from Upper Valdarno and close to the smallest *E. altidens* individuals from Dmanisi. *Equus senezensis* occupies an intermediate position between *E. stenonis* and *E. stehlini*, confirming the previous results obtained by Cirilli et al. (2021b) and Cirilli (2022). *Equus stehlini* is well separated from the rest of the comparative sample and shows a narrow and massive MT3 morphology, with the largest *E. stehlini* specimens overlapping the smallest *E. senezensis*. On the other hand, the medium-sized *E. altidens* shows a slenderer morphology, with a more elongated maximal length a reduced diaphysis. The Dmanisi and Pirro Nord populations overlap their range of variation, whereas the sample from Venta Micena (Spain) is somewhat larger. The Gerakarou-1 medium-sized *E. stenonis mygdoniensis* is included in the range shown by the European *E. altidens* samples. The European *E. stenonis* samples (Saint Vallier, Olivola, Matassino, and Upper Valdarno Basin) overlap in their range of variation, characterized by larger dimensions and more robust morphology than the medium-sized *E. senezensis* and *E. altidens*. *Equus eisenmannae* Qiu et al., 2004 from Longdan (China) and *E. livenzovensis* exhibit again longer MT3s when compared with *E. simplicidens* and *E. stenonis*, whereas *E. major* and *E. suessenbornensis* remain the largest equid species from the European Early Pleistocene.

These results are also confirmed in the Log10 ratio diagrams on MT3. Fig. 6c plots the mean values of the European Gelasian *Equus* species, whereas Fig. 6d shows the Calabrian ones. Both diagrams include the complete MT3 from Vigna Nuova (SABAP_UMB 129856+129861+129862+129868 *partim*). As shown in Fig. 6c, the Vigna Nuova MT3 has a pattern close to that of *E. senezensis* from Senèze, characterized by a reduced maximum length (M1) and robust diaphysis, proximal, and distal epiphyses (M3-M14). It is overall larger than that of *E. stehlini* (Upper Valdarno), whereas the incomplete MT3 from Montecarlo (Upper Valdarno Basin) plots in between. The Vigna Nuova MT3 is smaller than that of *E. stenonis*, although showing a similar pattern. Fig. 6d compares the Vigna Nuova MT3 with the *E. altidens* samples and *E. suessenbornensis*. Although SABAP_UMB 129856+129861+129862+129868 *partim* shows similar dimensions in the proximal and distal epiphyses than *E. altidens*, but its M1-M3 pattern is much different form the *E. altidens* samples, which show a slender morphology with a more elongated M1 and reduced M3. SABAP_UMB 129856+129861+129862+129868 *partim* exhibits the same M3 values of *E. altidens* from Venta Micena, the largest among the *E. altidens* samples. As reported in the PCA, *E. stenonis mygdoniensis* from Gerakarou-1 is included in the European *E. altidens* samples.

Considering this evidence, we ascribe the medium-sized equid from Vigna Nuova to *E.* cf. *senezensis*, recognizing their close similarities, especially in the postcranial elements.

Order ARTIODACTYLA Owen, 1848

Family BOVIDAE Gray, 1821

Genus *Leptobos* Rütimeyer, 1877-1878

cf. *Leptobos*

(Fig. 7)

Referred material – Horn core fragment (SABAP_UMB 129851).

Description – The only bovid fossil from the Vigna Nuova lower layer is a fragment of horn core. Unfortunately, it is so heavily weathered and abraded that the surface is no longer visible. Faint parallel furrows are visible along one of the edges. The horn core is virtually straight and does not show clear spiralization.

Comparisons and discussion – Based on the absence of curvature and spiralization, specimen SABAP_UMB 129851 is here referred to cf. *Leptobos* (see detailed discussion in the section on the bovid remains from the upper layer of Vigna Nuova).

Family CERVIDAE Goldfuss, 1820

Genus *Croizetoceros* Heintz, 1970

Croizetoceros ramosus (Croizet & Jobert, 1828)

(Fig. 7)

Referred material – Left maxilla with P2-M3 (SABAP_UMB 129863).

Description – Specimen SABAP_UMB 129863 belongs to an adult individual with teeth in moderate stage of wear. The upper premolars are relatively large and similar in size to each other. In occlusal view, the P3 and especially the P2 stand out for the pointed lingual margin. The P4 has a more squared lingual margin, with a slight hint of molarization (i.e., a faint vertical groove crosses the lingual wall of the tooth). On the labial side, the three premolars show pointed parastyle and metastyle and, between them, a strong pillar of the paracone, which is mesially shifted and points forward. The upper molars are similar to each other in overall morphology and exhibit lingual cones with trapezoidal shape. The protoconal fold (*pli protoconal*) is noticeable in the M3, present but not marked in the M2, and not visible in the M1 due to the more advanced wear. A sharp entostyle is developed in all molars, while no lingual cingula are present.

Comparisons and discussion – Croizetoceros is an extinct cervid with uncertain phylogenetic relationships and body size smaller than the *Dama*-like deer (see section on *'Pseudodama'* below). The genus is reported in Europe since the late Miocene with scanty remains (Azanza, 2000) and becomes a relatively common element of the Early-Middle Villafranchian assemblages with the species *C. ramosus*, ranging from Spain to Greece, with different samples sometimes referred to different subspecies (Valli, 2004 and references therein). *Croizetoceros* sp. is reported based on a single tooth from the Pliocene of Burdur (Turkey; Mayda et al., 2017).

The main dental features of *C. ramosus* are well described by Heintz (1970) on the basis of several samples from France and Spain, and resumed by Valli (2004) with reference to the richest European collection, namely that of Saint Vallier (France). Most of the recognized features can be found also in the Vigna Nuova specimen, including the asymmetrical development of the strong pillar of the paracone in the premolars, the presence of the protoconal fold in the molars, the relative development of the styles on the labial wall of the molars. In particular, the maxilla from Vigna Nuova shows striking morphological similarities with some known specimens of *C. ramosus* such as NHMB Prr.346 from the type locality of Les Etouaires (France), MCL QSV-766 from Saint Vallier, AUT GER-188 from Gerakarou (Greece), IPS28245/740b from La Puebla de Valverde (Spain) (see Fig. 8 for comparisons). Dimensionally, the Vigna Nuova specimen falls into the lower part of the range of *C. ramosus*, approaching in particular to the material from Gerakarou (measurements in Supplementary Online Material). However, it must be noted that the apparently larger size of the specimens from the French localities of Saint Vallier, Pardines, and Les Etouaires could be due to a slightly different measuring technique (Supplementary Online Material). The same applies to the ratio between the premolar and molar length (LP/LM), which is 0.70 in SABAP_UMB 129863 and between 0.69 and 0.79 in *C. ramosus* from several localities (Heintz, 1970; Kostopoulos, 1996; Kostopoulos & Athanassiou, 2005).

The overall size of SABAP_UMB 129863 is also similar to the average values of small-sized cervids of the roe deer lineage (i.e., *Procapreolus*, *Capreolus*). However, these latter taxa are well recognizable in the more articulated occlusal pattern of the upper teeth (e.g., numerous enamel folds that develop into the fossae), unlike the relatively simple morphology observed in SABAP_UMB 129863. Moreover, roe deer have more elongated premolar series with respect to molars. For instance, the average LP/LM is 0.92 in *Procapreolus cusanus* from Les Etouaires (Heintz, 1970), 0.89 in *Capreolus cusanoides* from Untermassfeld (Germany) and 0.84 in *Capreolus suessenbornensis* from Süssenborn (Germany) (personal data).

The above lines of evidence allow us to confidently refer the Vigna Nuova maxilla to *C. ramosus*, of which it represents one of the most complete and better-preserved specimens in Italy.

Genus *'Pseudodama'* Azzaroli, 1992

'Pseudodama' sp.

(Fig. 7)

Referred material – Left i2 (SABAP_UMB 129841); right frontal bone fragment with basal antler (SABAP_UMB 129843); left frontal bone fragment with basal antler (SABAP_UMB 129844); left frontal bone fragment with basal antler (SABAP_UMB 129845); right frontal bone fragment with basal antler (SABAP_UMB 129846); right hemimandible with p3-m3 (SABAP_UMB 129848); antler fragments (SABAP_UMB 129849, SABAP_UMB 129853, SABAP_UMB 129881); left hemimandible fragment with dp4 (broken), m1, and m2 (SABAP_UMB 129860+129865), right M1

(SABAP_UMB 129870); broken left m3 (SABAP_UMB 129871); left i3 (SABAP_UMB 129872); left i1 (SABAP_UMB 129873); right antler fragment (SABAP_UMB 129880).

Description – Fossils of a medium-sized deer are relatively common in the Vigna Nuova collection. The antler remains SABAP_UMB 129843, SABAP_UMB 129844, SABAP_UMB 129845, and SABAP_UMB 129846 are quite similar to each other both in shape and dimensions (measurements in Supplementary Online Material). All show a basal portion of the beam with an almost circular section and the insertion of the first tine (unfortunately never preserved) at a certain distance above the burr. The pedicles are also roughly circular in section (measurements in Supplementary Online Material). The most complete specimen (SABAP_UMB 129880) is a long fragment of right antler with basis of the basal tine, but missing the burr. The basal tine branches at about 3 cm from the bottom edge of the antler. Above the basal tine, the beam runs roughly vertical, with a slight lateral curvature in the first part and a medial curvature in the second.

The only upper tooth is the isolated right M1 SABAP_UMB 129870. It is virtually unworn and shows mesiodistally compressed lingual cones, between which a small entostyle develops. Mesiolingual, lingual, and distolingual cingula are present but weak. The labial styles are instead very prominent, as are the pillars of the labial cones.

The right hemimandible SABAP_UMB 129848 bears the complete cheek tooth row, but in a very advanced stage of wear (the m1 is almost completely worn out). This prevents a detailed description of the dental morphology. In occlusal view, the lingual wall of the paraconid is open, that is, the paraconid and metaconid are not fused (i.e., “unmolarized” condition). Lingual cingula and a faint ectostylid are still visible in the m2 and m3, but not in the m1 due to wear. The lower molar morphology is better recognizable in the hemimandible fragment SABAP_UMB 129865+129860, bearing a fragmented dp4 and complete m1 and m2. Both molars show a mesial cingulum and a prominent ectostylid in labial view.

The lower incisors SABAP_UMB 129841, SABAP_UMB 129872, and SABAP_UMB 129873 may belong to the same individual based on preservation, relative size, and absent wear.

Comparisons and discussion – Pliocene and Pleistocene cervids with overall morphology and size similar to the extant fallow deer are known as *Dama*-like deer. Villafranchian and Epivillafranchian forms from Europe are characterized by un-palmated antlers with three or four points. These forms have been allocated into a variety of genera (e.g., *Cervus*, *Dama*, *Axis*, *Rusa*, *Metacervocerus*, *Praeelaphus*, etc.) and species, whose relationships with each other and with present-day species are not clear (see a summary in Cherin et al., 2019a). Azzaroli (1992) proposed to refer all these species to the genus *Pseudodama*, including the "Italian" lineage - with the species *Pseudodama lyra* Azzaroli, 1992, *Pseudodama nestii* (Azzaroli, 1947), and *Pseudodama farnetensis* Azzaroli, 1992 - and the "French" lineage - with the species *Pseudodama pardinensis* (Croizet & Jobert, 1828), *Pseudodama rhenana* (Dubois, 1904), and *Pseudodama perolensis* (Bout & Azzaroli, 1952). Although we believe that some of the aforementioned species could probably be synonymized, we follow Azzaroli's concept, recognizing significant similarities between them all (Breda & Lister, 2013; Breda, 2015), but also including the Epivillafranchian *Pseudodama vallonnetensis* (de Lumley et al., 1988) (Breda et al., 2020). However, pending a comprehensive phylogenetic analysis, we prefer to indicate the genus *'Pseudodama'* with inverted commas (following Breda et al., 2015, 2020; Cherin et al., 2019a, among others).

The morphology and size of the identifiable material of middle-sized deer from Vigna Nuova are clearly akin to the genus *'Pseudodama'*. On the other hand, the available fossils do not retain characters that allow for an attribution at the species rank, for which more complete craniodental remains (especially antlers) would have been needed. The antlers from Vigna Nuova differ from those of derived species of '*Pseudodama'* such as *'P.' farnetensis* and *'P.' vallonnetensis*, in which the basal tine is normally inserted very close to or even leaning against the burr, as in the extant *Dama*. Similarly, the sub-vertical morphology of the best-preserved antler (SABAP_UMB 129880) also recalls the earlier forms of '*Pseudodama'* rather than the later ones, in which the antlers tend to diverge greatly posteriorly and laterally. However, these features must be considered with thoughtfulness because they can also be subject to ontogenetic variation.

Other primitive characters of the *Dama*-like deer from Vigna Nuova lie in the teeth and include the development of labial cones and styles and lingual cingulum in the upper molar (SABAP_UMB 129870), enlarged i1 (SABAP_UMB 129873), and un-molarized p4 (SABAP_UMB 129848) (Azzaroli, 1947, 1992; Croitor, 2006; Pfeiffer, 2016). Another primitive condition is the high ratio between the lower premolar and molar lengths measured in SABAP_UMB 129848 (Lp/Lm=0.69), which exceeds the average values available for *'P.' lyra* from Montopoli (Italy; Lp/Lm=0.64, n=2), *'P.' rhenana* from Saint Vallier (Lp/Lm=0.68, n=18) and Senèze (Lp/Lm=0.65, n=11), *'P.' nestii* from Pantalla (Italy; Lp/Lm=0.68, n=3), Olivola (Italy; Lp/Lm=0.62, n=5) and Upper Valdarno (Italy; Lp/Lm=0.63, n=16). On the contrary, later forms of *'Pseudodama'* show relatively shorter premolar rows, as can be seen in *'P.' farnetensis* from Pietrafitta (Italy; Lp/Lm=0.63; n=5) and Pirro Nord (Italy; Lp/Lm=0.58; n=2) and *'P.' vallonnetensis* from Untermassfeld (Germany; Lp/Lm=0.59; n=21) and Vallparadís Estació (Spain; Lp/Lm=0.57; n=9) (Breda, 2015; this paper).

In summary, the material of *'Pseudodama'* of Vigna Nuova is suggested to belong to a basal species of the genus (e.g., *'P.' lyra*, *'P.' rhenana*), but the incompleteness of the specimens requires a cautious attribution to *'Pseudodama'* sp.

Cervidae indet.

(Fig. 7)

Referred material – Left maxilla with dP2-M2 (SABAP_UMB 129866).

Description – Specimen SABAP_UMB 129866 is particularly interesting. It is a left maxillary fragment of a large-sized deer with deciduous premolars dP2-dP4, slightly worn M1, and freshly erupted M2. The dP2 is heavily worn and shows a distal lobe which is only slightly wider than the mesial one. Labially, the parastyle, paracone, and metastyle are pointed, while the metacone does not form a pillar on the labial wall. In the dP3, the distal lobe is significantly wider and shorter than the mesial one. On the labial wall, the pillar of the paracone and the mesostyle are particularly prominent and are oriented mesially. A similar morphology characterizes the labial wall of the dP4, in which however, the two lingual cones are almost equally developed and constricted mesiodistally. In the M1, a low and rounded entostyle develops between the protocone and hypocone. The parastyle and mesostyle are very strong and stretch in labial direction. The M2 looks like a slightly larger version of the M1, although the entostyle is replaced by a lingual cingulum. In all teeth, the enamel on the lingual walls is rough.

Comparisons and discussion – The most common large-sized deer occurring in the Villafranchian is *Eucladoceros*, characterized by spectacular comb-like antlers (Azzaroli & Mazza, 1992; Croitor, 2018). Nevertheless, other groups of cervids of comparable size can be found in the same time interval, although their record is poorer. These include the enigmatic *Arvernoceros*, whose systematic status and chronological occurrence are debated (Heintz, 1970; Petronio & Pandolfi, 2011; Croitor, 2018). The genus *Praemegaceros* seems to replace *Eucladoceros*, at least in southwestern Europe, in the late Late Villafranchian (Abbazzi, 2004). Unfortunately, the diagnostic characters of all these forms reside mainly in the antlers, of which we have no evidence in Vigna Nuova. No peculiar character can be identified in the upper deciduous or permanent dentition, neither in shape nor in size. For this reason, the large-sized deer of Vigna Nuova remains unidentifiable.

Family SUIDAE Gray, 1821

Genus *Sus* Linnaeus, 1758

Sus cf. *strozzii* Forsyth Major, 1881

(Fig. 7)

Referred material – Fragmented right maxilla with P4-M2 and broken M3 (SABAP_UMB 129847) and fragmented left maxilla with broken M3 (SABAP_UMB 129852).

Description – SABAP_UMB 129847 shows teeth with an advanced stage of wear that prevents a detailed description of the occlusal pattern. However, wear makes it possible to appreciate the considerable thickness of the enamel in all preserved teeth. The P4 has a squarish occlusal outline, but appears slightly wider than long. A mesial cingulum and a distal cingulum are visible. The mesial one has a slight constriction in the middle. A hinted protoprestyle is visible. The protofossa is narrow, long and positioned lingually in the middle-mesial part of the tooth. The M1 is very worn (wear stage: 16, wear group: 4; Zeder & Lemoine, 2020), so much that the main cusps are unrecognizable. The tooth has a figure-eight shape in occlusal view, with the mesial lobe smaller than the distal one and a labial constriction between them. The M2 is similar in shape to the M1, but larger. Also in this molar, none of the four main cusps can be described in detail due to the state of wear (wear stage: 12, wear group: 2; Zeder & Lemoine, 2020). However, the difference in width between the mesial and distal lobe is more marked than in the M1. The mesial cingulum is flat and does not seem to bear a protopreconule. The oval-shaped paracone is narrow and in contact with the lingual cingulum. The residue of the protocone is pointed, tiny and slightly visible. The labial cingulum of the mesial lobe is broken but it is possible to recognize that a hypoectoconid was present. The transverse valley between the paracone and metacone is wide lingually and ends exactly halfway through the tooth; no tetrapreconule is visible. The tetracone is central and rectangular. In all the teeth no styles are visible in lingual and labial view.

No descriptions can be provided for SABAP_UMB 129852 as the specimen preserves only a distal splinter of the M3, which however is dimensionally comparable to the corresponding tooth of SABAP_UMB 129847 and shows a similarly high enamel thickness. Based on preservation features, it is likely that the two specimens belonged to the same individual.

Comparisons and discussion – The genus *Sus*, of putative Asian origin, spread rapidly towards Europe since the Pliocene and became a common element in the Early Pleistocene faunal assemblages throughout the continent (Cherin et al., 2020). The earliest member of this group is *Sus arvernensis* (Croizet & Jobert, 1828), occurring in Eurasia during the Ruscinian and Early Villafranchian. At the beginning of the Early Pleistocene, this species was replaced by the larger-sized *S. strozzii*. The latter survived in Europe at least until the end of the Early Pleistocene, although its presence during the latest Villafranchian (i.e., ca. 1.7–1.3 Ma) is yet not confirmed [see the so-called "suid gap" hypothesis by Martinez-Navarro et al. (2015)] (Cherin et al., 2018, 2020). Starting from the Middle Pleistocene, the wild boar *Sus scrofa* Linnaeus, 1758 replaced *S. strozzii* rapidly expanding throughout Eurasia up to the present day (Cherin et al., 2020; Iannucci et al., 2020).

The distinction between the closely-related *S. arvernensis* and *S. strozzii* on one side and *S. scrofa* on the other, is easy when lower canines are available, even in the absence of complete skulls. This is because the first two species show a "verrucosic" morphology of lower canines, as opposed to the "scrofic" condition of *S. scrofa* (see Cherin et al., 2020). The lack of lower canines in the Vigna Nuova collection leads to rely only on biometric considerations (also because the advanced state of wear of the teeth in SABAP_UMB 129847 prevents any detailed comparisons in dental morphology). The box-plots in Fig. 9 clearly show that the Pliocene *S. arvernensis* can be distinguished from *S. strozzii* and *S. scrofa* by its smaller size (especially molar length). SABAP_UMB 129847 has relatively large-sized teeth, which fall in the ranges of these two latter species. Although in the literature there are several works in which an attempt has been made to recognize *S. strozzii* and *S. scrofa* on a dimensional basis (e.g., Ambrosetti et al., 1979; Faure & Guérin, 1983; Van der Made, 1999; Van der Made et al., 2017), Cherin et al. (2020) showed that this approach alone cannot be sufficient, especially when large samples are considered both geographically and chronologically (the wild boar shows enormous dimensional variation over time and space). As far as current knowledge is concerned, only the dimensions of the dp4 can be used for a statistically significant distinction between *S. strozzii* and *S. scrofa* (Iannucci et al., 2020). In this context, the length of the teeth of SABAP_UMB 129847 alone is not decisive for the taxonomic identification of the specimen, while considerations on their proportions can be. In particular, the P4 exhibits a relatively low length-to-width ratio (i.e., it is more rectangular in occlusal view; Fig. 9). In this, it resembles *S. strozzii* rather than *S. scrofa*, which instead has a squarer P4. This evidence – associated with the very thick enamel possessed by the cheek teeth [i.e., one of the diagnostic characters of *S. strozzii*; Cherin et al. (2018)] – allows to refer the Vigna Nuova material to *S.* cf. *strozzii*.

SYSTEMATIC PALEONTOLOGY (UPPER LAYER)

Order ARTIODACTYLA Owen, 1848

Family BOVIDAE Gray, 1821

Genus *Leptobos* Rütimeyer, 1877-1878

cf. *Leptobos*

(Fig. 10)

Referred material – Left hemimandible with p4-m3 and roots of p2-p3 (SABAP_UMB 129836); right metacarpal (SABAP_UMB 129838); atlas (SABAP_UMB 129839); intermediate phalanx (SABAP_UMB 129854); left P2 (SABAP_UMB 129855); left tibia, proximal epiphysis (SABAP_UMB 129858); left tibia diaphysis (SABAP_UMB 129876); humerus distal diaphysis (SABAP_UMB 129878); horn core fragments (SABAP_UMB 22.3.248–22.3.252, 22.3.267); distal phalanx fragments (SABAP_UMB 22.3.256, SABAP_UMB 22.3.266); cranium fragment (SABAP_UMB 22.3.265); left medial malleolus fragment (SABAP_UMB 22.3.268).

Description – An incomplete hemimandible and an isolated P2 were recovered from the Vigna Nuova upper layer. The mandible (SABAP_UMB 129836) includes the molars and the p4 with root fragments of p2-p3. The teeth are all heavily worn. In the p4, the parastylid and paraconid are separated by a shallow furrow, the protoconid is quite developed. The lingual valley between the paraconid and protoconid strongly indents mesially. The metaconid is large and has the shape of a blade, emerging lingually and strongly curving distally. The furrow separating the metaconid and entoconid is quite deep and narrow due to the distal shift of the former. The entostylid and entoconid are completely fused. The distal labial groove separating the protoconid from the hypoconid is strong. The molars are mesiodistally elongated with well-separated lobes. The parastylid is well developed and mesially projecting. The protoconid and hypoconid are morphologically similar except for a slight mesiodistal constriction of the latter. The ectostylid emerges mesially from the distal lobe and lies almost attached to the protoconid. The entostylid is smaller than the parastylid and projects lingually. The inner enamel islets are halfmoon shaped. The mesial one is characterized by a constriction in the mid part. The islet of the distal lobe in m3 is marked by a bubaline fold (*sensu* Masini, 1989) in the distal portion. The cement is present in all the teeth, on both sides. The P2 SABAP_UMB 129855 has an advanced stage of wear. The paracone and parastyle lie almost attached, separated by a shallow furrow that reaches the base of the tooth. The metacone is strongly reduced. The metastyle projects distally.

Several horn core fragments are part of the collection. Most of them present nutrient foramina and/or furrows on the outer side (e.g., SABAP_UMB 22.3.248 and SABAP_UMB 22.3.249) and clear sign of pneumatization in the inner portion (e.g., SABAP_UMB 22.3.248 and SABAP_UMB 22.3.251). Despite their scanty preservation, it is possible to state that all of the remains are characterized by a quite low degree of curvature and do not present evidences of spiralization.

The atlas SABAP_UMB 129839 preserves most of the body and the left wing. Dorsally, the atlas is characterized by two large openings, on each wing, shifted towards the anterior portion of the bone, in which two foramina are located. The left wing projects posteriorly but not far from the posterior zygapophyses. The dorsal tubercle and the dorsal portion of the neural arch are missing. The alar fossae, visible on the ventral side of the wings, are large and relatively deep depressions. The posterior tubercle is partially preserved and not well developed. The anterior articular surface is almost complete and extends on the ventral side. The area connecting the two posterior zygapophyses is broad and flat.

The only complete metacarpal (SABAP_UMB 129838) is relatively slender. It has an hourglass shape, with the two epiphyses having approximately the same width, mediolaterally wider than the diaphysis. The proximal epiphysis, seen from above, is D-shaped; the anterior margin is sub-rounded whereas the posterior one is straight. The lateral articular facet is triangular and much smaller than the medial, which is sub-quadrangular with rounded anterior margin. The two facets are separated by a small crest perpendicular to the major axis of the articulation. The crest ends posteriorly in a deep, narrow groove which hosts the proximal nutrient foramen. Another foramen is present distally to the proximal end, connected with the former through a very narrow furrow. All the anterior border of the proximal epiphysis is characterized by a wrinkled tuberosity. The diaphysis has its minimum mediolateral width slightly above the mid-point. There are two shallow grooves in the proximo-anterior portion of the diaphysis. The anterior vascular groove at the distal shaft is narrow and shallow, getting deeper and marked by sharp edges distally. The ovoidal foramen is located just above the distal end of the vascular groove, covered by sediment. The mediolateral width at the contact area between the diaphysis and the distal epiphysis is slightly smaller than that across the trochleae. The intertrochlear margins as well as the crests are subparallel. The lateral and medial trochlear pits are deep and marked by faint radial rugosities. The lateral abaxial hemicondyle is anteroposteriorly thinner than the medial one.

The tibia remains includes a fragment of the diaphysis (SABAP_UMB 129876) and a partial proximal epiphysis (SABAP_UMB 129858). The articulation surface of the latter is composed by the two large condyles. Neither of these elements are complete. The proximally projected intercondylar eminences are partially preserved. The diaphysis fragment represents the proximal half of the tibia due to the visible crest running along one side of the shaft.

The intermediate phalanx SABAP_UMB 129854 is complete and well preserved. The bone is stout, having a short and thick diaphysis. The proximal articulation is divided by the sagittal crest into two facets for the articulation with the proximal phalanx (abaxial and axial glenoid cavities). Posteriorly to the crest there is a deep U-shaped furrow. The abaxial cavity is slightly larger than the axial. The abaxial tubercle and the axial pit are visible although not well developed. The distal articular surface is subtriangular. The abaxial lobe has a pointed tip developing toward the diaphysis of the phalanx.

The other available specimens are heavily fragmented and do not allow for any detailed description.

Comparisons and discussion – The largest forms of bovids are part of the subfamily Bovinae which, during the earliest Pleistocene of Europe, was mainly represented by the genus *Leptobos*. This extinct taxon was populating most of the subtropical and temperate areas of Eurasia, spanning from the Iberian Peninsula to China, from Northern India to, possibly, British Islands (Cherin et al., 2019b). Although *Leptobos* has been matter of interest in numerous works (Merla, 1939; Pilgrim 1939; Masini, 1989; Duvernois, 1990; Cherin et al., 2019b, among others), there is still no consensus about its systematics and evolutionary history. Most of the scholars divide European *Leptobos* into two lineages/groups or subgenera (Masini, 1989; Duvernois, 1990, 1992; Masini et al., 2013; Cherin et al., 2019b; Sorbelli et al., 2021). The first includes the species *Leptobos stenometopon* (Sismonda, 1846), *Leptobos elatus* (Pomel, 1853), *Leptobos merlai* De Giuli (1987), and *Leptobos furtivus* Duvernois (1989) (called *Leptobos* ex gr. SEM hereinafter) constrained to the Early-Middle Villafranchian of Central and Western Europe; the second includes *Leptobos etruscus* (Falconer, 1868) and *Leptobos vallisarni* Merla (1949) (called *Leptobos* ex gr. EV hereinafter), limited to the Late Villafranchian of Europe and, as concerning the latter species, Asia (Masini et al., 2013; Tong et al., 2016; Sorbelli et al., 2021). Species of *Leptobos* ex gr. SEM are characterized by elongated neurocranium, “taurine” horns (i.e., laterally emerging, with strong anticlockwise spiralization), and slender limbs, whereas species of *Leptobos* ex gr. EV share shorter postcornual portion of the cranium, posterolaterally emerging horns with single curvature, and stouter limb proportions. During the last stages of the Villafranchian, a new group of large bovids reached Europe from Asia. These bovines represented the first western dispersal of *Bison* which, most probably, evolved in mainland Asia from a derivate stock of *Leptobos* at the end of the Pliocene (Sorbelli et al., 2021 and references therein). These forms of large and stout bovids, grouped in the subgenus *Bison* (*Eobison*), were well adapted to the harshened environmental condition that started to affect Europe during the Late Villafranchian and rapidly replaced *Leptobos* in all the herbivore guilds of the continent. With the faunal turnover of the Early-Middle Pleistocene Transition (i.e., during the Epivillafranchian), *Eobison*, in turn, was replaced by the “true” *Bison*, which will be the dominant large bovids in all the Holarctic realm until the Holocene (Sorbelli et al., 2021).

Due to their general morphology and size, the sample from Vigna Nuova is referable to a large bovid. As already remarked, during the Early Pleistocene, the only European representatives of this group are *Leptobos* and *Bison* (*Eobison*). The proportions of metapodials, in particular metacarpals, are a useful taxonomic tool in order to discriminate between the various species belonging to these genera (Maniakas & Kostopoulos, 2017; Sorbelli et al., 2021). However, due to the high intraspecific variation that characterizes bovids, a cautious approach is recommended when dealing with small samples, as in the Vigna Nuova case. The single metacarpal from this locality shows a relatively slender built, with a long and thin diaphysis. In order to assess the robusticity of this element, a biplot diagram comparing the total length of the metacarpal and the ratio between the transversal width and the length is provided (Fig. 11). The Vigna Nuova specimen falls within the range of the largest *Leptobos*, in the area overlapping with *Eobison* and the slenderest specimens of *Bison schoetensacki* Freudenberg, 1914. The most imponent and robust species of *Leptobos* are those belonging to the EV group. While the postcranial skeleton of *L. etruscus* is well known, that of *L. vallisarni* is still poorly represented in the fossil record. Moreover, few limb bones referred to *L. vallisarni* are quite similar to those of *L. etruscus*, thus, without complete cranial elements or a large sample of postcranial remains, it is virtually impossible to discern the two taxa.

The lower dentition of *Leptobos* and *Bison* are quite similar, except for the evident increasing of hypsodonty and larger average size in the latter. The morphology of the p4 has been used as tool in order to differentiate the two groups of *Leptobos* (Masini, 1989; Duvernois, 1990). The distally projected metaconid, the strong hypoconid, and the deep distolabial groove are characters shared between the Vigna Nuova and *Leptobos* ex gr. EV. Nonetheless, several scholars underlined the strong variability affecting the tooth morphology of large bovids, remarking how taxonomic inferences based on dentognathic remains should be taken cautiously (Skinner & Kaisen, 1945; Olsen, 1990; Sher, 1997, among others)

The horn core morphology is one of the most useful tools for taxonomic purposes. *Leptobos* ex gr. SEM features long, spiralized horns emerging posterolaterally. On the contrary, *Leptobos* ex gr. EV shows crescent moon-shaped cores with no or little torsion, emerging in a more posterior position than in the former group (i.e., smaller angle between the sagittal plane and the core's mid line) and gently curving inwards. *Eobison* is characterized by relatively small and stout horns, projecting laterally with strong upward bending and slight anticlockwise torsion. The horn core fragments from Vigna Nuova show a low degree of bending and no sign of torsions, as in *Leptobos* ex gr. EV. Other skeletal elements from Vigna Nuova do not bear/preserve diagnostic characters and are not discussed furtherly.

Despite their scantiness, the analyzed elements evidence that the bovid from the upper layer of Vigna Nuova has affinities with *Leptobos* ex gr. EV. However, due to the limited number and preservation of the fossils and the strong variation that characterizes this group of large bovids, we prefer to cautiously refer the sample to cf. *Leptobos* pending for new material from the locality.

CONCLUSIONS

The fossil mammals from Vigna Nuova, collected more than thirty years ago, have revealed new extremely intriguing data. First of all, the combination of taphonomic, historical, and, to a lesser extent, geological data made it possible to divide the sample into two different assemblages. The one coming from what we have called the "upper layer" of Vigna Nuova (i.e., the only portion still visible in the outcrop), is made up of 18 identifiable remains, plus about 25 unidentifiable ones. The identifiable material is all assigned to cf. *Leptobos* in the light of morphological affinities with this genus of Villafranchian bovines. In particular, especially as regards the dimensions of the metacarpal

(Fig. 11), the remains of Vigna Nuova upper layer are similar to those of the most derived forms of the group, namely *L. etruscus* and *L. vallisarni*. Remains of the latter species are reported from the nearby locality of Selvella (De Giuli, 1987; Masini et al., 2013) (Fig. 1), whose referral to the Farneta FU (ca. 1.5 Ma) is supported by biochronological data on fossil horse (Alberdi & Palombo, 2013; Cirilli et al., 2020).

The assemblage from the "lower layer" (unfortunately not more cropping out at Vigna Nuova) includes at least ten taxa, some of which carrying crucial biochronological information. The co-occurrence of *C. ramosus* and *E.* cf. *senezensis* allows an attribution of the fauna to the second part of the Middle Villafranchian, matching a correlation with the Coste San Giacomo FU in the Italian biochronological framework. This result contrasts with the first hypotheses on a younger age of the fauna (Tasso FU; Argenti, 2004), probably also failing to recognize the division into two assemblages.

In Italy, scanty remains of *Croizetoceros ramosus* are reported only from Montopoli (ca. 2.6. Ma; De Giuli & Heintz, 1974) and Coste San Giacomo (ca. 2.1 Ma; Bellucci et al., 2012, 2014). Therefore, the well-preserved maxilla with upper dentition (SABAP_UMB 129863) from Vigna Nuova allows to confirm the presence of this enigmatic species in the Italian Middle Villafranchian. Similarly, the horse *E. senezensis* is rare in Italy, having been reported with scanty remains only in Coste San Giacomo and Montecarlo fossil sites, in contrast to the rich French sample from Senèze (Palombo et al., 2017; Cirilli et al., 2021a; Cirilli, 2022). The occurrence of this species in Vigna Nuova provides a new support of the dispersion of this species in the Italian peninsula, which may have been the source for the origin of *E. stehlini* (Cirilli, 2022).

Some primitive characters of the sample of *'Pseudodama'* from Vigna Nuova suggest that it may be referred to a primitive species of the genus, thus supporting the attribution of the assemblage to the Middle Villafranchian. On the other hand, this hypothesis can only be confirmed by the discovery of more complete fossils.

Finally, the discovery of the remains of *Canis* sp. is noteworthy. Although these predators probably arrived in Europe already in the Early Villafranchian as evidenced by the Vialette record

(Lacombat et al., 2008; Sotnikova & Rook, 2010), there is no trace of them in Italy before the second part of the Middle Villafranchian. Indeed, the record of *Canis* sp. from Coste San Giacomo (Bellucci et al., 2021, 2014) marks the first occurrence of the genus *Canis* in Italy, which is confirmed here by the Vigna Nuova fossils.

The recognition of a Middle Villafranchian assemblage in Umbria is novel information, given that the majority of the other LFAs in the region, especially those from the Tiberino Basin, have been attributed to the Late Villafranchian (see Cherin et al., 2019a for a summary). The only exception is represented by the small assemblage from the upper layers of Cava Toppetti near Todi (Perugia), which was referred to the Coste San Giacomo FU (Abbazzi et al., 1997). However, in our opinion, the sample is too small and the fossils too fragmentary to confirm such biochronological conclusion.

Our chronological results also open up stimulating research prospects in the stratigraphic field. To date, the continental deposits of the Valdichiana Basin were generically referred to the Calabrian, especially on the basis of biochronological data on mammals (e.g., Selvella, Farneta, Cava Liberatori LFAs, all dated to ca. 1.5. Ma; Masini & Sala, 2007). On the other hand, recent studies focused on the paleoenvironmental history of the marine portion of the Basin, which underwent a complex depositional history at least throughout the Early Pleistocene (Gelasian and Calabrian; Bizzarri & Baldanza, 2020). Further research is needed to identify in the field the deposit that yielded the fossils of the "lower layer" of Vigna Nuova, here dated to the Gelasian (ca. 2.2–2.1 Ma), and to understand its stratigraphic relationships with the surrounding marine and continental units of the Valdichiana Basin.

AUTHORS' CONTRIBUTIONS

M.C. and B.A. conceived the study. F.R., D.T., M.C., and B.A. prepared the fossils. B.A., M.C., and F.R. collected the data. B.A., M.C., J.M.M., L.S., and O.C. made the figures. M.C., B.A., M.B., J.M.M., L.S., and O.C. developed the methods and performed the analyses. B.A. and M.C. wrote the

final version of the manuscript with input from the other authors. All authors contributed equally to develop the ideas, discussed the results, and reviewed the final version of the manuscript.

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CAPTIONS

Fig. 1 - (color online) Location of the study area. a) The extensional basins cited in the text are highlighted. Red star: Vigna Nuova; black star: Selvella. b) Detail of the Vigna Nuova outcrop.

Fig. 2 - (color online) Taphonomy of the Vigna Nuova assemblages. a) Detail of the inner part of a proboscidean bone (SABAP_UMB 22.3.264) showing heavy mineralization and filling of trabeculae by minerals and organic matter. b) Distribution of weathering stages (following Behrensmeyer, 1978) in the fossils from the two fossiliferous layers of Vigna Nuova.

Fig 3 - (color online) Carnivorans from Vigna Nuova (Italy), lower layer. a) cf. *Megantereon*: right upper canine (SABAP_UMB 129842) in labial (a1) and distal (a2) views. b-d) *Canis* sp.: cervical vertebrae 3–7 (SABAP_UMB 129850) in dorsal view (b); left rib (SABAP_UMB 129875) in lateral view (c); thoracic vertebrae 2–3 (SABAP_UMB 129875) in lateral view (d). Scale bar: 2 cm. e-f) Comparison between the vertebrae C3-C4 from Vigna Nuova (SABAP_UMB 129850) (e) and those of *Canis etruscus* from Olivola (IGF 4523) (f) in left lateral view. Vertebrae are shown in anatomical connection, as they were discovered; the relative position of the vertebrae in the two specimens is slightly different (C4 is rotated clockwise with respect to C3 in SABAP_UMB 129850, while the two vertebrae are almost aligned in IGF 4523). Red asterisks indicate broken portions. The morphology of the posterior edge of C4 in SABAP_UMB 129850 is estimated (dotted line) because it is partially covered by C5. Scale bar: 2 cm. g) Mustelidae indet., left upper canine (SABAP_UMB 22.3.263) in mesial view. Scale bar: 1 cm.

Fig. 4 - (color online) Comparisons between Machairodontinae upper canines. a) From left to right: *Smilodon fatalis* Leidy, 1868 from La Brea Tar Pits (LAMC Hc1142); *Megantereon cultridens* from Villarroya (IPS36785); *M. cultridens* from Villarroya (IPS36784); cf. *Megantereon* from Vigna

Nuova (SABAP_UMB 129842; reversed); *Homotherium crenatidens* from Incarcal-I (IPS IN-I1542); *H. crenatidens* from Incarcal-I (IPS IN-I-421). Scale bar: 2 cm. b) Violin plot for the width/length ratio of the upper canine (measured at the cervix) in Pliocene to Middle Pleistocene *Homotherium*, *M. cultridens*, *Megantereon adroveri* Pons-Moyà, 1987, and the Vigna Nuova specimen. Legend: Epi, Epivillafranchian; EVal, Early Villafranchian; Gal, Galerian; LVal, Late Villafranchian; MVal, Middle Villafranchian. Sources of data: Ballesio (1963); de Bonis (1976); Ficcarelli (1979); Hemmer (2001); Sardella & Iurino (2012).

Fig. 5 - *Equus* cf. *senezensis* from Vigna Nuova (Italy), lower layer. a) Left hindlimb with distal tibia, tarsus, metatarsals II-III-IV (SABAP_UMB 129856+129861+129862+129868): specimen in anatomical connection, lateral view (a1); metatarsals in anterior (a2) and posterior (a2) views. b) Left astragalus (SABAP_UMB 129869) in anterior (b1) and medial (b2) views. c) Left metacarpals II-III-IV (SABAP_UMB 129840) in anterior (c1) and posterior (c2) views. d) Mandible (SABAP_UMB 129835+129837): incisor arcade in occlusal (d1) and ventral (d2) views; left corpus fragment with p2 in labial (d3) and occlusal (d4) views. Scale bar: 5 cm.

Fig. 6 - (color online) Biometric comparisons between the horse from Vigna Nuova and several *Equus* samples from the Plio-Pleistocene of Eurasia. a) Bivariate plot comparing the maximum width (M6) versus maximum length (M1) of the p2. b) PCA performed on ten measurements of the third metatarsal (M1, maximum length; M3, midshaft width; M4, depth of the diaphysis at level of M3; M5, proximal articular width; M6, proximal articular depth; M10, distal maximal maximum supra-articular width; M11, distal maximum articular width; M12, distal maximum keel depth; M13, distal maximum depth of the lateral condyle; M14, distal maximum depth of the medial condyle). c-d) Log10 ratio diagrams of third metatarsal measurements in European Gelasian (c) and Calabrian (d) equids. In addition to the measurements used in the PCA, this analysis includes M7 (maximum

diameter of the articular facet for the third tarsal) and M8 (diameter for the anterior facet for the fourth tarsal).

Fig 7 - (color online) Artiodactyls from Vigna Nuova (Italy). a) cf. *Leptobos*: horn core fragment (SABAP_UMB 129851). b) *Croizetoceros ramosus*: maxilla with P2-M3 (SABAP_UMB 129863) in occlusal (b1) and labial (b2) views. c-h) *'Pseudodama'* sp.: right hemimandible with p2-m3 (SABAP_UMB 129848) in occlusal (c1) and labial (c2) views; left hemimandible with dp4 (fragmented), m1-m2 (SABAP_UMB 129865+129860) in occlusal (d1) and labial (d2) views; left frontal fragment with antler basis (SABAP_UMB 129845) in medial (e1) and anterior (e2) views; right antler fragment (SABAP_UMB 129880) in lateral (f1) and anterior (f2) views; right M1 (SABAP_UMB 129870) in occlusal view (g). h) Cervidae indet. (large size): left maxilla with dP2-M2 (SABAP_UMB 129866) in occlusal (h1) and labial (h2) views. j) *Sus* cf. *strozzii*: maxilla with P4-M2 and M3 fragment (SABAP_UMB 129847) in occlusal view. Scale bar: 2 cm.

Fig. 8 - Comparisons between *Croizetoceros ramosus* upper tooth rows. a) SABAP_UMB 129863 from Vigna Nuova. b) NHMB Prr.346 from Les Etouaires (France; reversed). c) MCL QSV-766 from Saint Vallier (France). d) AUT GER-188 from Gerakarou (Greece). e) IPS28245/740b from La Puebla de Valverde (Spain; reversed). The fossils are drawn not to scale to highlight morphological similarities.

Fig. 9 - (color online) Boxplots of upper tooth measurements (mm) comparing the suid from Vigna Nuova with *Sus arvernensis*, *Sus strozzii*, and *Sus scrofa*. Boxplots show minimum, median, and maximum values with 25th and 75th percentile of each sample. L, length; W, width.

Fig. 10 - (color online) cf. *Leptobos* from Vigna Nuova (Italy), upper layer. a) Left hemimandible with p4-m3 (SABAP_UMB 129836) in labial (a1) and occlusal (a2) views. b) Left P2 (SABAP_UMB

129855) in occlusal view; c) Atlas (SABAP_UMB 129839) in ventral (c1) and dorsal (c2) views. d) Right metacarpal (SABAP_UMB 129838) in proximal (d1) and anterior (d2) views. e) Horn core fragment (SABAP_UMB 22.3.248). f) Horn core fragment (SABAP_UMB 22.3.249). g) Intermediate phalanx (SABAP_UMB 129854) in abaxial (g1) and axial (g2) views. Scale bar: 5 cm.

Fig. 11 - (color online) Bivariate plot comparing the maximum length (Lmax; in mm) versus the ratio between the distal end width (DEW) and maximum length of the metacarpal in several samples of Eurasian bovines. The sample of *Leptobos etruscus* includes data from Faella/Matassino and Olivola (Italy), Senèze (France), and Fonelas P-1 (Spain). The sample of *Leptobos vallisarni* includes data from Upper Valdarno and Farneta (Italy). The sample of *Leptobos* ex gr. SEM includes the following sub-samples: *Leptobos* cf. *stenometopon* from Montopoli (Italy); *Leptobos stenometopon/elatus* from Upper Valdarno (Italy; several sites); *Leptobos elatus* from Les Etouaires (France) and Villarroya (Spain); *Leptobos merlai* from Saint Vallier (France); *Leptobos* cf. *furtivus* from Senèze and Olivola; *Leptobos* aff. *furtivus* from Upper Valdarno and Carsoli (Italy). The sample of *Eobison* includes the following sub-samples: *Eobison* sp. from Venta Micena (Spain), *Eobison degiulii* from Pirro Nord (Italy); *Eobison* cf. *degiulii* from Capena (Italy) and Mygdonia Basin (Greece); *Eobison georgicus* (Burchak-Abramovich & Vekua, 1994) from Dmanisi (Georgia); *Eobison palaeosinensis* Teilhard de Chardin & Piveteau, 1930 from Nihewan Basin (China). The sample of *Bison menneri* includes data from Untermassfeld (Germany). The sample of *Bison schoetensacki* includes data from Süssenborn and Mauer (Germany), Vallparadís composite section (Spain), Le Vallonnet, Le Vassirie, and Durfort (France). Source of data: Sorbelli et al. (2021), and references therein.