doi: 10.13133/2280-6148/18135 *Journal of Mediterranean Earth Sciences 15 (2023), 81-105*

J M E S **Journal of Mediterranean Earth Sciences**

The Casal de' Pazzi mammalian fauna: biochronological and paleoecological notes, and research perspectives

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ASTRACT - This note critically reviews the biochronological range of the mammalian taxa identified thus far in the faunal assemblage found in the musealized sector of the late Middle Pleistocene fluvial deposit of Casal de' Pazzi (CdP), evaluates the similarity among the CdP fauna and that of some selected local faunal assemblages from Latium and surrounding area, and summarizes and updates our knowledge about the paleoecological hints provided by the herbivore remains. An attempt to compare CdP the ecological structure of the CdP large mammal fauna with that of the selected late Middle Pleistocene (MIS 11-MIS 7)sites, mainly from Latium, failed to provide any compelling results. This conceivably depends on the low richness of some faunal assemblages, some monotony of their taxonomical composition combined with the commonness of some taxa recorded in almost all local assemblages, and the lack of studies of the autecology of taxa recorded at each site. Accordingly, this note gives a synthesis of the principal studies that, in the future, could shed light on matters either not yet scrutinized or still unsolved. The potential results of integrated multidisciplinary research could contribute to enhancing our knowledge about the Latium mammalian fauna's evolutionary dynamics in the context of the evolution of the SW European large mammal fauna during the late Middle Pleistocene.

Keywords: Large mammals; late Middle Pleistocene; Latium; biochronology; local faunal assemblage similarity; paleoecology.

Submitted: 22 June 2023 -Accepted: 25 July 2023

1. INTRODUCTION

The site of Casal de' Pazzi (CdP hereinafter), discovered in 1982 (Anzidei, 1983, 1984; Segre, 1983a; Anzidei et al., 1984; Passarello et al., 1984; Anzidei and Ruffo, 1985), is one of the most recent among the Middle Pleistocene ones reported in the current urban area of Rome and in particular of those reported in the lower Aniene valley (e.g., Monte delle Gioie, Sedia Del Divolo, Saccopastore, Ponte Mammolo, etc.) and neighboring areas (Segre, 1983b; Anzidei et al., 2004, and references therein; Gioia and Zanzi, 2020, and references therein). Since the first decades of the last century, these sites have been a specific object of land surveys and geological research, conducted, in particular, by Barone A.C. Blanc (1906-1961). The Italian researcher conducted important geological, archeological, and paleoanthropological research on Latium Quaternary deposits and on non-marine Pleistocene sections of the Tiber and Aniene valleys (e.g., Blanc, 1955, 1957, 1958; Breuil and Blanc, 1935 a,b). These studies led to the stratigraphic asset of such deposits, which was followed by new surveys and research for more than thirty years (cf. Orombelli et al., 2023, and references therein).

Some geopaleontological investigations in the lower Aniene Valley had already been carried out in the second half of the 19th century. They led, for instance, to the discovery and systematic paleontological excavation of a fossiliferous cave at Monte delle Gioie (Indes, 1869, 1872), as well as to an accurate description of some stratigraphic sequences, such as that of Sedia del Diavolo (see, among others, Meli, 1882). In 1969, before the discovery of the CdP deposit, some mammal remains (currently stored in the collections of the Istituto Italiano di Paleontologia Umana, ISiPu) (Saracino et al., 2023) had been identified and retrieved from alluvial Pleistocene deposits exposed in the vicinity of Torre di Rebibbia (another name in the past used to indicate CdP), which at that time still was a rural area (Anzidei et al., 1984).

Although the CdP deposit was discovered more than 40 years ago, an exhaustive systematic study of all the over 2000 remains recovered in the various excavation campaigns conducted at CdP is still missing. Indeed, only some preliminary studies have been done in the past

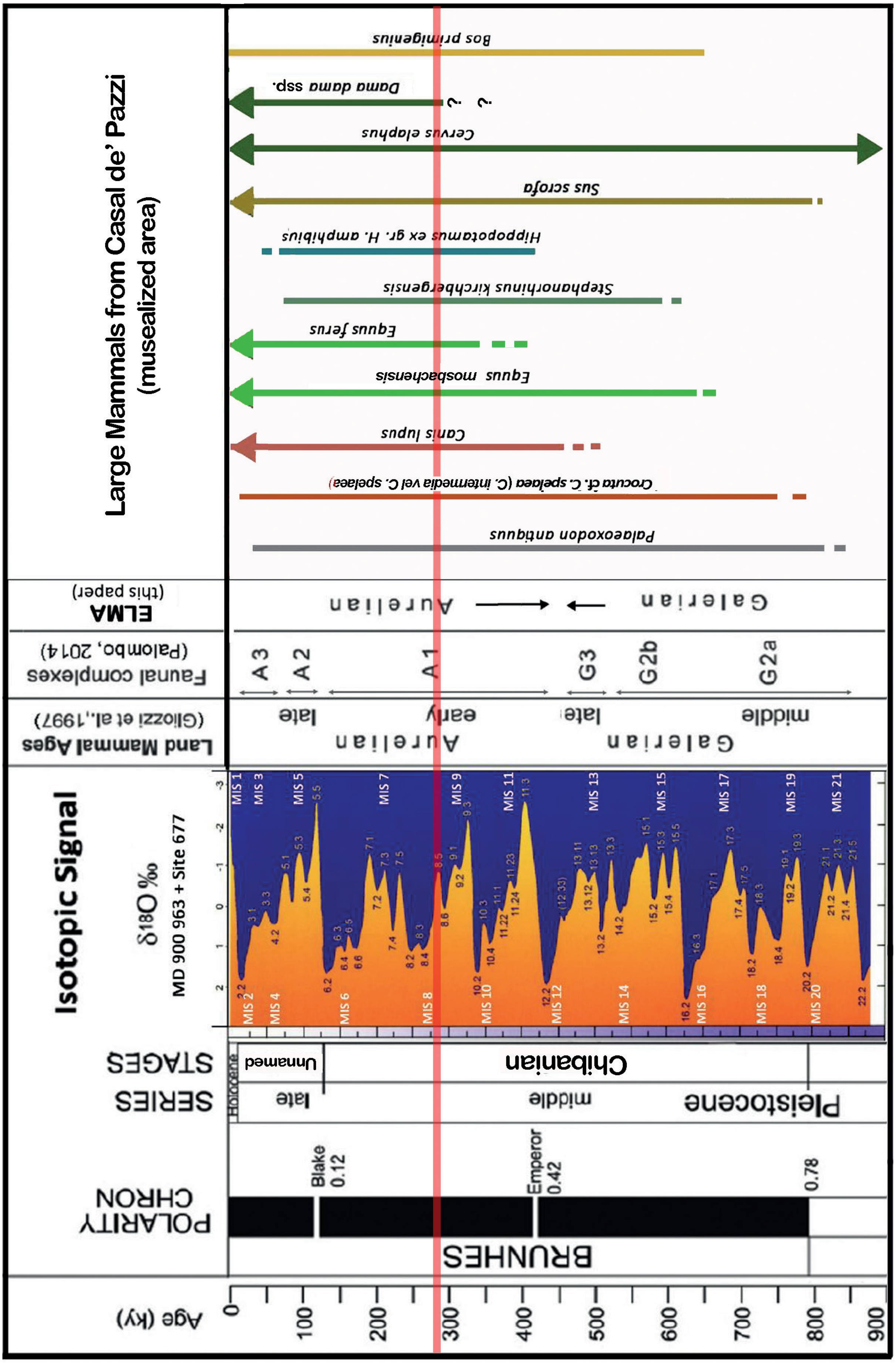

Fig. 1 - Chronological range of the large mammal species identified in the sample of bone remains found in the musealized area of the Casal de' Pazzi site (about 300 m²).

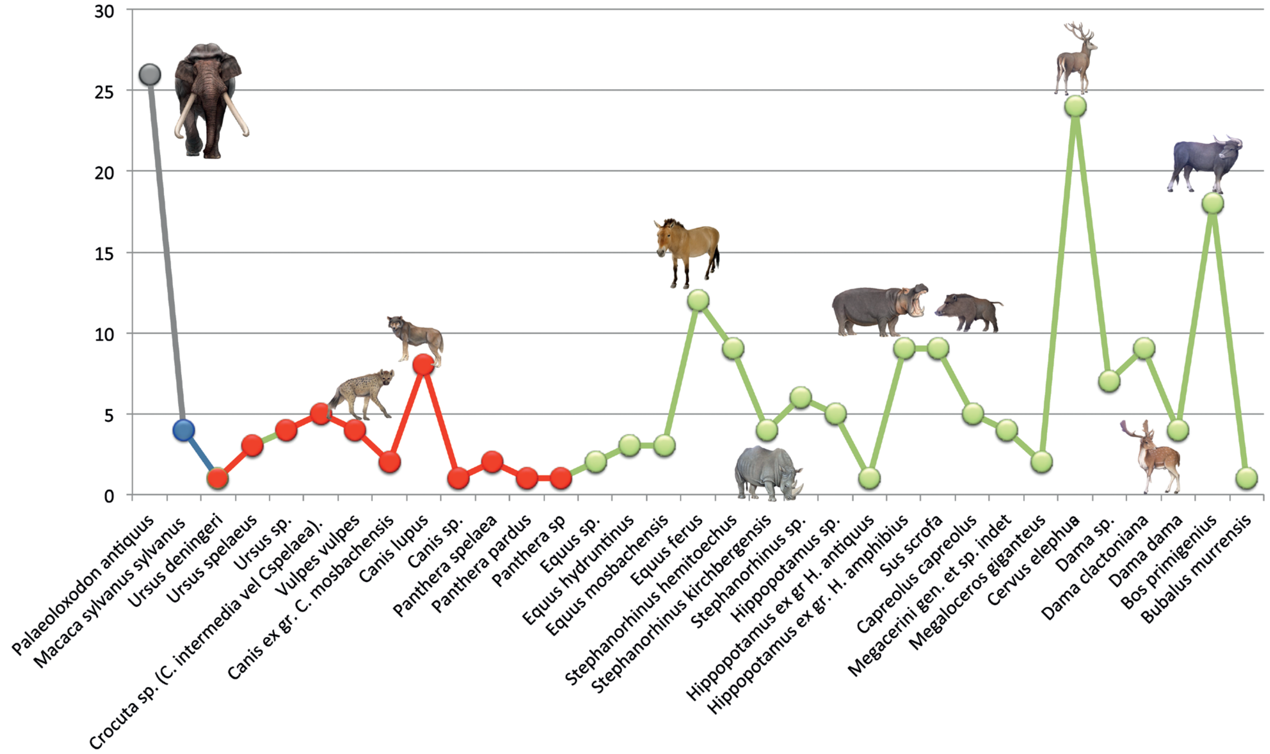

Fig. 2 - Commonness of the large mammal species recorded in the local faunal assemblages selected for this study (see Tab. 1).

(e.g., Anzidei et al., 1999, and references therein; Anzidei and Cerilli, 2001), and lists of mammalian taxa have been published in several papers dealing with the site and discussed in others dealing with the biochronology of Latium and Italian local faunal assemblages (LFAs). Recently, Pandolfi et al. (2023) examined a small sample of the remains retrieved from or still embedded in the deposit of the musealized area, which represents just a subset but is fairly representative of the whole large mammal fauna. Most of the taxa present in the previous published faunal lists (e.g., Anzidei, 1983, 1984; Anzidei and Ruffo, 1985; Anzidei et al., 1999) are present in the studied sample, with the exception of the roe deer (Pandolfi et al., 2023, and references therein).

The CdP fauna primarily consists of large mammals and also includes a few anatid birds and one reptile, the European pond turtle, *Emys orbicularis*.

Among the mammal remains identified in the Museum collection and the remains that are still embedded in the deposit (*P. antiquus, Crocuta* cf. *C. spelaea*, *Canis lupus* (small-sized), *Stephanorhinus kirchbergensis, Equus* ap., *Hippopotamus* cf. *H. amphibius, Sus scrofa, Dama dama, Cervus elaphus,* and *Bos primigenius*) (Pandolfi et al., 2023), those of elephants, mainly consisting of dental remains, predominate. *Bos primigenius* remains are rather abundant, while those of carnivores, horses, wild boar, and rhinoceros are infrequent. The identified taxa are rather common in the late Middle Pleistocene of Europe and in the large mammal assemblages of the Latium territory (Figs. 1, 2), especially in the late Middle and Late Pleistocene LFAs; hence, they fail to provide any fine chronological indication about the age of the fossiliferous layer. Marra et al. (2015) correlated it with MIS 7, but, according to Rosa's ongoing research, maybe slightly older (MIS 8.5) (Rosa, 2023).

The purpose of this note is to give some additional information about the CdP mammalian fauna retrieved from or still embedded in the deposit of the musealized area. Accordingly, the research aims to provide a synthetic overview of the taxa's chronological range and a preliminary analysis of the basic faunal structural attributes; to compare the taxonomic composition and paleoecologic structure of the CdP LFA with those of the main LFAs of the Latium and a few from surrounding territories (i.e., Guado San Nicola, Isernia, and Ciampate del Diavolo/Foresta "Devil Trails", Caserta), ranging in age from MIS 13 to MIS 7; and to discuss perspectives of research aimed at an exhaustive knowledge of the fauna and the environment surrounding the CdP watercourse at the time of the accumulation of the bones and lithic implements.

2. MATERIAL AND METHODS

This research is based on the 130 mammalian remains that Pandolfi et al. (2023) classified among those that have been retrieved from or are still embedded in the fossiliferous layer of the fluvial CdP deposits' musealized sector.

I have compared the record of the CdP-identified taxa

Tab. 1 - Chronological ordering of large mammal faunal assemblages from late Middle Pleistocene (MIS 13-MIS 7) deposits of the lower Aniene Valley, the Roman and Anagni basins, and surrounding area [i.e., Guado San Nicola, and Ciampate del Diavolo/Foresta "Devil's Trails", Caserta] selected because they are considered particularly appropriate for the purpose of this note due to their historical interest, or because they have been studied or revised recently, or they have compelling chronostratigraphic constraints, or they include species with chronological or taxonomical relevance. Symbols and abbreviations: ■= confident presence; ○= cf. (confer: presence attested by remains with some but insufficient diagnostic characters); ✪ = *Crocuta* cf. *C. spelaea*, presumable identification that has to be confirmed; **?** = doubtful presence. Green and red colors indicate the Latium sites and the Casal de' Pazzi site and its mammalian fauna, respectively.

Marine Isotopic Stage	MIS 13				MIS 11							? MIS 11 (?younger)		MIS 11- MIS 10		
Locality	Casal Selce A	Collina Barbattini and Via Aurelia km 18.9	via Aurelia km 19.3	Cava Rinaldi (upper level)	Fontana Ranuccio	Casal Selce B	Casal Lumbroso - Massimina	Castel di Guido	Malagrotta	Riano Flaminio	Via Ostiense Km 2	Cava Panzini-Pontecorvo	Pignataro Interamna	Lademagne (level1-level 2)	Guado San Nicola	Isoletta (ESR1-GA6Z -ESR4)
Chronology	MIS 13 (Milli et al 2005)	MIS 13 (Marra et al., 2018)	MIS 13 (Marra et al., 2018)	516 +/- 1 ka (Marra et al., 2014)	408 +/-10 ka (Pereira et al., 2015)	406.5 ± 2.4 ka (Iurino et al., 2022)	MIS 11 c. 400 ka (Alhaique et al., 2022)	c. 400 ka (Villa et al., 2021)	c. 380 ka, MIS 11 (Marra et al., 2022)	406±5 ka(Marra et al., 2018)	MIS 11 (Mecozzi et al., 2021)	? MIS 11 - MIS 9	? (various age have been hypotesised, from MIS 11 to MIS 5)	415- 381 ka, MIS 11 (Pereira et al., 2018)	409-371 ka- MIS 11 (Peretto et al., 2014; Pereira et al., 2016)	411- 346 ka, MIS 11-MIS 10 (Pereira et al., 2018)
Selected Large Mammal Taxa																
AFROTHERIA																
Proboscidata																
Palaeoloxodon antiquus	■	■	■	■	■		■	■	■	■		■	■	■	■	■
EUARCHONTOGLIRES																
Primates																
Macaca sylvanus sylvanus					■											
LAURASIATHERIA																
Ferae																
Carnivora-Caniformia																
Ursidae																
Ursus deningeri					■											
Ursus spelaeus				■												
Ursus sp.															■	
Hyaenidae																
Crocuta sp. *(C. intermedia vel Cspelaea)*					■											■
Canidae																
Vulpes vulpes					○											
Canis ex gr. *C.mosbachensis*					■						■					
Canis lupus						■		○								■
Canis sp.									■							
Carnivora - Feliformia																
Felidae																
Panthera spelaea								■								
Panthera pardus																
Panthera sp.					■											
Ungulata																
Perissodactyla																
Equidae																
Equus sp.																
Equus hydruntinus																
Equus mosbachensis					■							○			○	
Equus ferus		■						■	■					■		○
Rhinocerotidae																
Stephanorhinus hemitoechus			■					■	○							○
Stephanorhinus kirchbergensis		○								■					■	
Stephanorhinus sp.					■		?						■			
Cetartiodactyla (Artiodactyla)																
Hippopotamidae																
Hippopotamus sp.	■	■	■		■				■							
Hippopotamus ex gr. *H. antiquus*								○								
Hippopotamus ex gr. *H. amphibius*													■	■		
Suidae																
Sus scrofa					■			?	■			■		■		
Cervidae																
Capreolus capreolus							✪		■			✪				
Megacerini gen. et sp. indet					■							■			■	
Megaloceros giganteus																■
Cervus elephua		■	■	■	■		✪	■	■	■		■	■	■	■	■
Dama sp.		■	■				■							■	■	■
Dama clactoniana	○	■			■		○		○	■						
Dama dama ssp.																
Bovidae																
Bos primigenius		■	■	■	■		■	■	■				■		■	■
Bubalus murrensis																

Tab. 1 ...Continued

Marine Isotopic Stage	MIS 10				MIS 9		MIS 8.5			MIS ?8.5	MIS 7	
Locality	Cava Pompi	Colle Avarone	Ceprano CG9-CG10	Ciampate del Diavolo	Torre in Pietra 1	La Polledrara di Cecanibbio	Sedia del Diavolo	Prati Fiscali	Monte Sacro	Casal de' Pazzi	Campo del Conte 2	Torre in Pietra 2
Chronology	<397 +/- 10 ka (Pereira et al.,2018)	? MIS 10 (close in age to CG9-CG10, Biddittu, 2004)	>/= 353 ± 8 ka (Nomade et al., 2011; Pereira et al., 2018)	349–350 ± 3 ka (Panarello et al., 2017), MIS 10	MIS 9 (Conato et al., 1980; Caloi et al., 1998; Villa et al., 2016)	c. 330, MIS 9 (Anzidei et al., 2012; Pereira et al., 2017)	MIS 9 (Palombo et al., 2004); MIS 8.5 (upper level) (Marra et al., 2018)	MIS 8.5 (marra et al., 2018)	MIS 8.5 (marra et al., 2018)	MIS 7 (Marra et al., 2017) - attualmente in revisione	MIS 7 (?) (Palombo et al., 2003)	MIS 7 (Conato et al., 1980; Caloi et al., 1998; Villa et al., 2016)
Selected Large Mammal Taxa												
AFROTHERIA												
Proboscidata												
Palaeoloxodon antiquus	■	■	■	■	■	■	■	■	■	■	■	■
EUARCHONTOGLIRES												
Primates												
Macaca sylvanus sylvanus	■					■						■
LAURASIATHERIA												
Ferae												
Carnivora-Caniformia												
Ursidae												
Ursus deningeri												
Ursus spelaeus					○							■
Ursus sp.				■					■		■	
Hyaenidae												
Crocuta sp. *(C. intermedia vel Cspelaea)*									■	⊙		■
Canidae												
Vulpes vulpes					■	■						■
Canis ex gr. *C. mosbachensis*												
Canis lupus					■	■	○			■		■
Canis sp.												
Carnivora - Feliformia												
Felidae												
Panthera spelaea					■							
Panthera pardus								■				
Panthera sp.												
Ungulata												
Perissodactyla												
Equidae												
Equus sp.			■	■								
Equus hydruntinus							■	■	■	■		
Equus mosbachensis												
Equus ferus					■	■		○	○		■	■
Rhinocerotidae												
Stephanorhinus hemitoechus					■	○	○	■				■
Stephanorhinus kirchbergensis										■		
Stephanorhinus sp.	■		■					■	■			
Cetartiodactyla (Artiodactyla)												
Hippopotamidae												
Hippopotamus sp.												
Hippopotamus ex gr. *H. antiquus*												
Hippopotamus ex gr. *H. amphibius*			○				■	■	■	■	■	■
Suidae												
Sus scrofa					■	■	■		■	■		■
Cervidae												
Capreolus capreolus				✪						?		■
Megacerini gen. et sp. indet	■											
Megaloceros giganteus					■							
Cervus elephua	■	■	■		■	■	■	■	■	■	■	■
Dama sp.			■									
Dama clactoniana	○				○		○					
Dama dama ssp.							■	■		■		■
Bovidae												
Bos primigenius			■		■	■	■		■	■	■	■
Bubalus murrensis						■						

with those of 27 LFAs mainly from the lower Aniene Valley, the Roman and Anagni basins, and a few from the surrounding areas (e.g., Guado San Nicola, Isernia, Sala et al., 2014; Ciampate del Diavolo/Foresta "Devil's Trails", Caserta, Mietto et al., 2022). I have selected the LFAs deemed to be particularly appropriate for the purpose of this note due to their historical interest, because they have been studied or revised recently, because they have compelling chronostratigraphic constraints, or because they include single species with chronological or taxonomical relevance. The selected LFAs range in age from MIS 13 to MIS 7 (Tab. 1).

In the attempt to analyze the similarity among the selected LFAs, I have performed the classic cluster analysis using the unweighted pair group method with arithmetic mean (UPGMA) algorithm (Hair et al., 1998), the Q-Mode method, and the metric and symmetrical Jaccard index of similarity. UPGMA and the Jaccard index are particularly appropriate for paleontological analyses, basically because in UPGMA, the level at which a member (a case, i.e., a faunal list) joins an existing cluster is based on the average similarity of all the existing members, calculated from the original matrix of coefficients, and the Jaccard index is barely influenced by the sample size of the clustering procedure, which was repeated about 10,000 times (bootstrap = 9,999).

Statistical analyses were conducted with the PAST (PAleontological STatistics) 4 software (Hammer et al., 2001).

Moreover, I have carried out a very preliminary analysis of the LFAs' ecological structure, but only considering the main ecological groups (species' preferred habitat, feeding habit, and body mass) due to the low number of taxa recorded at most sites and the lack of analyses of the ecomorphological traits of the taxa recorded in the other LFAs. I have considered the following ecological categories: i) three major ecological habitat groups: forest taxa (F) [species living in forests and closed woodland (W), bush land and open woodland (Wc), and miscellaneous woodland (W-Wc)]; open landscape dwellers (O) [species inhabiting prairies (treeless grasslands), savanna (treed grasslands), steppe, or rocky landscapes], and euryoecious/"ubiquitous" taxa (U) [ecologically more flexible taxa, which can live in shrub land or woodland, as well as in an open landscape, or at the edge of both]; ii) three main trophic categories of consumers, Herbivores, Carnivores, and Omnivores (also including Carnivora that eat less than 10% of flesh); iii) and five body mass ecological groups (BM I from 5 to 15 kg; BM II from 16 to 60 kg; BM III from 61 to 250 kg; BM IV from 251 to 1000 kg; BM V>1000 kg), which subdivision was mainly based on the prey-predator relationship, considering the hunting behavior of the Middle Pleistocene predators and the size of the ordinary prey. Moreover, herbivores were classified as grazers (Gr, including species feeding on grasses and sedges, in which grass represents about 75% of diet), browsers (Br, species feeding on leaves, seeds, shoots, etc., with a reduced amount of grass), and mixed feeders (MF, species taking between about 25% and 75% of grass, which feed on grass or leaves, bark, seeds, etc. and can change preferred food seasonally, regionally, or occasionally). Carnivora were not assigned to a specific trophic group (such as species eating flesh, species that are efficient bone-crackers but a less efficient meat slicer, species grinding and committing bones but quite efficient in eating flesh meat, and flesh-eaters mainly on small mammals, sometimes feeding on invertebrates, and occasionally on fruit) because only a total of five taxa have been identified, which were documented in a few among the analyzed LFAs [i.e., *Crocuta* sp. (*C. intermedia vel C. spelaea*), *Vulpes* sp., *Canis mosbachensis*, *Canis lupus*, and *Canis* sp. (*C. mosbachensis* vel *C. lupus)* since the canid remains are recorded in a period during which both species were present and the features of remains are not taxonomically distinctive)].

3. BIOCHRONOLOGICAL NOTES

A sum of evidence highlights the gradual, sometimes asynchronous/diachronous modification of the taxonomic and structural composition of the mammalian paleocommunities, which led to the configuration of the late Middle Pleistocene European faunal complex, since the latest Early Pleistocene and throughout the early Middle Pleistocene. This faunal complex has commonly been indicated as the Aurelian European Land Mammal Age (ELMA), especially regarding the Italian LFAs. The long-lasting, progressive phase of renewal and the objective instability of any biochronological scheme based on continental large mammal first and last appearances make it problematic to identify potential biologic chronostratigraphic markers (*sensu* Lindsay, 2003) for the transition from the Galerian to the Aurelian ELMA, which was already completed shortly before MIS 11 (Palombo, 2018). Indeed, the known stratigraphic lowest or highest occurrence of a taxon does not necessarily correspond to its actual first/last appearance in time. As a result, new discoveries, the revision of taxa, and new absolute dating of fossiliferous levels may modify the chronological extent (biochron) of a biochronological unit and, in turn, any scheme previously proposed (e.g., Palombo, 2016a, and references therein). Accordingly, the present biochronological notes are merely a synthetic report of the current status of knowledge.

3.1. CHRONOLOGICAL RANGE OF TAXA IDENTIFIED IN THE CASAL DE' PAZZI MUSEUM COLLECTION

3.1.1. *Palaeoloxodon antiquus*

The straight-tusked elephants originated from the African *Palaeoloxodon recki* lineage, whose representatives dispersed out of Africa towards Eurasia in the post-Jaramillo Early Pleistocene. A *P. recki* population was presumably present in Israel around 0.8 Ma (MIS 21), as inferred from the presence of a *Palaeoloxodon* partial skull at the well-known Gesher Benot Ya'aqov site. Although several authors considered it a primitive *P. antiquus* (e.g., Goren-Inbar et al., 1994; Saegusa and Gilbert, 2008), the proportionally narrow isthmus frontalis, which gives the skull a more vertical elongate appearance of the front compared to other continental Eurasian *Palaeoloxodon*, as well as the moderate extrusion of the parieto-occipital crest, indicate it belongs to the *P. recki* lineage (Larramendi et al., 2020). *P. recki* has been generally considered the progenitor of subsequent *Palaeoloxodon* Eurasian species (e.g., Saegusa and Gilbert, 2008; Ferretti, 2008; Lister, 2015). The hypothetical occurrence of *P. antiquus* in Turkey at about 0.9 Ma (a last molar from Dursunlu) (Albayrak and Lister, 2012), if confirmed by more compelling specimens, might complicate the out of Africa dispersal scenario of *P. recki*.

A molar discovered in the Slivia LFA (north-western Italy) provides reliable evidence of *P. antiquus* presence in Europe around 0.8 Ma (Bon et al., 1992) (pre-Bruhnes age of the site inferred according to the small mammal association). Indeed, the Spanish elephant remains from the slightly older sites of Huescar (1.0-0.9 Ma) and Vallparadis (1.1-1.0 Ma) belong to *Mammuthus meridionalis* (see Palombo, 2014; Ros Montoia et al., 2018).

P. antiquus inhabited mildly humid, warm to warm-temperate, and wooded environments, as well as moderately wooded, sometimes rather arid, grasslands. The ecological adaptive flexibility of the species accounts for the wide geographic distribution of its populations. The geographical range extended northwards as far as the 55° meridian, eastwards possibly as far as the 75° meridian, and southwards till Iran (Palombo et al., 2010, and references therein). The straight-tusked elephant remains are particularly abundant in the South European faunal assemblage, while in central and eastern Europe they are mainly recorded during interglacial phases, especially, if not exclusively, during the pronounced climatic warming of the last interglacial (MIS 5e) (e.g., Palombo et al., 2010, and references therein; Palombo 2014, and references therein).

The last glacial-marked climate change (MIS 4-MIS 2) significantly affected the straight-tusked elephant populations in Europe, their numerical consistency, distribution, and local extirpation. By the end of the late last interglacial, in response to the MIS 5a climatic cooling, most populations had gradually reduced their geographic range to core refugial areas, mainly located in southern Europe. Straight-tusked elephants were still present in the Iberian Peninsula during the late MIS 3 (e.g., an unworn upper molar plate was found in layers dated at about 33-34 ka Foz do Enxarrique, Portugal) (Brugal and Raposo, 1999). In Italy, some remains have been found in the Balzi Rossi, Grimaldi cave, in deposits ranging from MIS 5 to MIS 3 (cf. Moussous et al., 2014), while there is no compelling evidence of a straight-tusked elephant presence in the Italian peninsula later than MIS 5a to MIS 4 (Braun and Palombo, 2012, and references therein). In Greece, *P. antiquus* has not been reported during the last glacial phase (e.g., Tsoukala et al., 2011).

3.1.2. *Crocuta* cf. *C. spelaea*

Lewis and Werdelin (2022) recently examined the Eurasian *Crocuta* species in the context of the revision of the genus *Crocuta*. The analysis results allowed the authors to assert that *Crocuta crocuta* did not expand its geographical range out of Africa and that two different spotted hyaena species inhabited Europe, i.e., *Crocuta intermedia*, present during the Middle Pleistocene, and the larger *Crocuta spelaea,* recorded during both the Middle and the Late Pleistocene. The relationships between the two species are still unclear.

The oldest European spotted hyaena remains are those found in the TD4W level of Trinchera de Ferrocarril (Atapuerca, Northern Spain) (García and Arsuaga, 2001; García, 2003), dated to about 0.9 Ma (Berger et al., 2008). In Italy, some *Crocuta* remains (two incomplete hemimandibles and an ulna) are reported slightly later, just after the Matuyama-Bruhnes boundary, in the Cava di Breccia-Casal Selce deposits (Ponte Galeria, Roman Basin) (Palombo and Milli, 2011; Sardella and Petrucci, 2012). According to Lewis and Werdelin (2022), these specimens cannot be assigned to a species-level taxon at present, though the dimensions of the lower chewing teeth from Casal Selce roughly match or are slightly smaller than those of the *C. intermedia* teeth from Lunel Viel (Bonifay, 1971). The cave-spotted hyaena was present not long after in eastern North Europe (e.g., in Hungary and Germany). *C. spelaea* is recorded in several Middle Pleistocene sites, in particular from the Mosbach early Middle Pleistocene deposits (MIS 15-MIS 13), the type locality of *C. spelaea praespelaea,* a subspecific name that could be conventionally used to distinguish the Middle cave hyaena remains from the typical Late Pleistocene ones. The latter, well-known since the first illustrations of its remains by Esper (1774), was a widespread species and a common component of most Late Pleistocene European large mammal paleocommunities, especially in cave sedimentary sequences, where it was the main accumulator of bone remains in non-anthropic depositional contexts.

According to Stuart and Lister (2014), most, if not all, *Crocuta* populations disappeared in North and Central Europe around 32 ka. Later, during MIS 2, the species distribution was mainly restricted to Southern Europe, where the cave hyaena is last recorded at about 12.780 cal. ka BP in the Las Ventanas Cave mammalian fauna (Granada, Spain) (Carrión et al., 2001).

3.1.3. *Canis* cf. *C. lupus*

In the late 20th century, the first appearance of the modern wolf was considered a significant biochronological event. Indeed, Gliozzi et al. (1997) regarded it as one of the bioevents marking (together with those of *Ursus spelaeus* and *Magaloceros giganteus*) the transition from the Galerian to the "modern large mammal fauna" and the beginning of the new proposed biochronological unit

Aurelian. The authors based this hypothesis mainly on the large mammals found in Italian LFAs, roughly coincident with MIS 9. However, available evidence dates back the *C. lupus* appearance in Europe much earlier, possibly about 0.500 Ma ago. Hence, the species is reported in Spain at Galería GII (?MIS 14-MIS 13; Rodriguez et al., 2011; Álvarez-Posada et al., 2018) and Sima de los Huesos, in levels correlated with MIS 13 and dated to about 0.5 Ma (Falguères et al., 2010) or 0.430 Ma (Arnold et al., 2014). The modern wolf is also recorded during MIS 11 in some British LFAs, where *M. giganteus* is sometimes present (Stewart, 2008, and references therein), in Spain in the LFAs of Ambrona, Gran Dolina TD10-11, and Cova del Angel, in France in the upper complex of the Arago cave's sedimentary sequence, and in the LFAs of Terra Amata and Lunel Viel (Palombo, 2014, and references therein). In the latter site, Bonifay (1971) identified a small wolf, *Canis lupus lunellensis*, showing some morphological features that exclude its attribution to the small *Canis mosbachensis*. The revision of the entire Lunel Viel canid sample by Boudadi-Maligne (2010) supports Bonifay's (1971) identification. During MIS 11, *Canis lupus* was also recorded in some Latium LFAs (Tab. 1), but in various cases the remains are not sufficiently diagnostic for a confident specific attribution to *C. lupus* or *C. mosbachensis*, a species that last occurred in Italy during MIS 11 (via Ostiense, Rome) (Mecozzi et al., 2021a). The finding of a partial cranium at Casal Selce-Ponte Galeria (Rome), in a deposit dated at 406.5±2.4 ka, definitely confirms, on the one hand, the presence of modern wolf populations in Italy during MIS 11 (Iurino et al., 2022), and, on the other hand, the presumable coexistence for a while of two species, *C. lupus* and *C. mosbachensis*, of different size and possibly behavior, in the same restricted territory.

In the late Middle and Late Pleistocene, the modern wolf became one of the most common components of the European LFAs, showing, during the Late Pleistocene, a general dimensional increase. The widespread distribution of the species, as well as its presence in different ecological contexts, are likely related to its ecological flexibility, mixed-feeding dietary behavior, and well-structured social structure, which also facilitates its pack hunting abilities.

3.1.4. *Equus* sp.

The caballine horses appeared in Europe at the beginning of the Middle Pleistocene, as supposed by almost all authors and confirmed by molecular genetic data (e.g., Eisenmann, 2006). The oldest representative of the phyletic lineage is the large horse *Equus mosbachensis* that was present around 0.65 Ma (MIS 16) in Southern Italy at Notarchirico, (0.65 Ma, Pereira et al., 2015; 670-695 ka (lowest layers) Moncel et al., 2023), and in Germany at the slightly younger Süssenborn site (0.64-0.62 Ma). The species, widely recorded in LFAs dated between MIS 16 - MIS 9, is reported until MIS 6 (e.g., Guadelli, 2007) but authors disagree about the real persistence of the species after MIS 9 (Boulbes and van Asperen, 2019).

Reichenau (1915) created the taxon for the horse remains found at the German Mosbach 2 site (MIS 15-MIS 13). The German paleontologist considered it a subspecies of the modern "*Equus caballus*" (recte *Equus ferus*) since the morphology of the cranium and limb bones was somewhat similar to that of more recent caballine horses, though the chewing teeth show more primitive characters, and a few differences characterize the morphology and proportion of the skull and limb bones. The subspecific rank was rejected some years later when two *E. mosbachensis* subspecies were described in the French sites of Lunel Viel by Bonifay (1980) (*E.m. palustris*) and Caune de l'Arago by Eisemnann and colleagues (Eisenmann et al., 1985) (*E. m. tautavelensis*). However, some other researchers considered the differences shown by the Mosbach hotse not compelling enough to substantiate its specific rank (e.g., Azzaroli, 1989).

Assuming it is true that *E. mosbachensis* could be a bona fide species, as believed by most authors, a question arises about the time of *E. ferus* first occurrence. The species was widely present during the Late Pleistocene and also during the last glacial in a wide range of environments under different climatic conditions (e.g., Boulbes and van Aspersen, 2019, and references therein). Its great ecological flexibility and morphological plasticity are documented by the wide morphological and dimensional variation range characterizing local populations that led to the creation of various Late Pleistocene subspecies, most of which might, in fact, represent different ecomorphotypes. Some variability also characterizes the late Middle Pleistocene caballine horses. Moreover, in some LFAs, few horse remains are present, often showing insufficient taxonomical features, as for instance in the majority of the MIS 11 to MIS 7 Latium sites reporting the presence of *E. ferus* (Tab. 1). A thorough analysis of the remains has only occasionally been done at a few sites with abundant horse samples (for example, the sample from the lower level of the Torre in Pietra, where an alleged subspecies, *E. ferus malatestae*, was proposed in 1997 by Caloi). At other sites, the caballine remains lack a formal description, and at still other sites, they are taxonomically insignificant. Therefore, the hypothesis that *E. mosbachensis* occurred at least in some of these localities cannot be completely rejected. The contemporary presence of populations of equids with primitive characters and a size within the variation range of *E. mosbachensis* and populations with more advanced characters may have hypothetically been possible at least during MIS 9-MIS 7, though no evidence support this purely academic supposition. The evolutionary scenario of European caballine populations during the Middle Pleistocene gets further complicated by the presence of species with characters rather more primitive than those of *E. mosbachsis*, such as *Equus steinheimensis* (MIS 11-MIS 4) and *Equus torralbae*, typified by the horse from the Torralba (Spain) eponymous site in levels correlated with MIS7 (Santonja et al., 2014). A discussion about the systematics and the evolutionary dynamics of the Middle and Late Pleistocene caballine horses is, however, beyond the purpose of this note.

3.1.5. *Stephanorhinus kirchbergensis*

The large rhinoceros *Stephanorhinus kirchbergensis* was a rare component of the Middle and Late Pleistocene west and southern European LFAs, despite its wide geographical distribution across the middle latitude Eurasian territories, from Western Europe to China, where it is mostly recorded in Russia and former Soviet Union regions (Billia, 2011; Billia and Zervanova, 2015). The species was also reported in Siberia at about 64° N (Dubrovo, 1957), and the northernmost known site is the late glacial deposits of the Chandon Valley (Artic Yakutia, Russia), just above the 70th parallel (Kirillova et al., 2017). Martínez-Navarro (2004) included the Merck's rhinoceros in the list of mammals found at the Israeli Gesher Benot Ya'aqov site (c. 0.8-0.7 Ma) (*S. merckii*, Martínez-Navarro, 2004, table 1, p. 41). If confirmed, the identification would correspond to the earliest and southernmost occurrence of the species. However, Guérin and Faure (1988) ascribed the Gesher Benot Ya'aqov rhinoceros remains to *Dicerorhinus* cf. *hemitoechus* and Rabinovich and Biton (2011) to *Stephanorhinus* sp., and Pandolfi rejects the attribution to the Merck rhinoceros (L. Pandolfi, personal communication, 2023). No other *S. kirchbergensis* specimens have been recorded in North Africa thus far.

The two mandible fragments from the early Middle Pleistocene site of Biliayivka (Ukraina) (MIS 17) (Stefaniak et al., 2023) document one of the earliest occurrences of the Merck's rhinoceros in East Europe. In West Europe, the species might have first been present in the German Mauer LFA, dated to about 0.609 Ma+/-40 ka (MIS 15) (Wagner et al., 2010). At the site, the majority of specimens belong to *Stephanorhinus hundsheimensis*, but some can be assigned to Merck's rhinoceros (Schreiber, 2005; Billia, 2011, and references therein). The skull found in the Mosbach 2 LFA confirms the occurrence of the species in Germany during MIS 13.

In Italy, *S. kirchbergensis* might have occurred earlier, around MIS 15, assuming as correct the attribution to *S.* cf. *S. kirchbergensis* of a large but incomplete metapodial from Valdemino Cave (? MIS15, Nocchi and Sala, 1997) (Sala, 1992). More compelling remains were present shortly later, ca. 0.56-0.5 Ma (MIS14-MIS13), at Tor di Quinto, in the Rome urban area (Pandolfi and Marra, 2015).

The disappearance of Merk's rhinos in Eurasia was likely diachronous, though not clearly defined. With the Last Glacial climate worsening, *S. kirchbergensis* populations disappeared from most European territories but were still present about 40 ka throughout Asia and north Siberia, while survived during MIS 2 in China (Stefaniak et al., 2023).

3.1.6. *Hippopotamus amphibious*

There is not a general consensus about the number of hippopotamus dispersals (one, two, or three) from Africa towards Eurasia, the species that moved out of Africa, and, in turn, about the phyletic relationships of the European species and the African ancestor(s) that gave rise to the European hippopotamuses. These issues and the number of species that inhabited Europe during the Pleistocene have been the subject of a long debate in the last decades (see Fidalgo et al., 2021, 2023; Martino et al., 2022, and references therein for a discussion). Nonetheless, most authors currently concur on the presence of two continental species in the European Pleistocene, *Hippopotamus antiquus* and *Hippopotamus amphibius*, which colonized at different times some Mediterranean islands, giving rise to diminutive endemic subspecies (cf. Palombo and Monculli-Solé, 2023, and references therein).

H. antiquus, which is possibly related to or evolved from the African species *Hippopotamus gorgops*, first occurred in Europe around 2.1 Ma, as documented by the remains from the Italian site of Coste San Giacomo (Anagni basin) (ca. 2.1 Ma) (Bellucci et al., 2012) and the skull from the Greek Elis site (Peloponnesus) (2.00–0.8 Ma). The species was last recorded in a few sites correlated with MIS 11 (e.g., Condeixa, Portugal, and Castel di Guido, central Italy) (Martino et al., 2022). At that time, *H. amphibius* was reported in the Italian Fontana Ranuccio site, dated to 408+/-10 ka (Pereira et al., 2015), as well as in some sites of the Roman basin, such as Malagrotta (MIS 11). However, the attribution of such remains to *H. amphibius* is doubtful because they lack firm diagnostic characters (Martino and Pandolfi, 2022). Herein, they are informally indicated as *Hippopotamus* sp. (Tab. 1). If confirmed by more compelling findings, the almost contemporaneous presence of both species in a rather restricted geographic area would give some support to a probable dispersal from Africa of *H. amphibius* during MIS 11. The species has rarely been reported during MIS 11 in some European LFAs, but the identification of the remains has sometimes been questioned. *H. amphibius* would be present in the Swanscombe LFA (Britain), though, according to Bridgland and Schreve (2001), the species would be a chronological marker of MIS 5e in the British LFAs biochronological scenario.

In the following Middle Pleistocene, *H. amphibius* was rather common during the interglacial phase in the South European LFAs (especially in Italy and Greece), and reached its maximum diffusion during MIS 5e, when the species was rather common also in Western and central Europe and the geographical range roughly extended from about 55° N to 10° E and 45° E (Pushkina, 2007). By the end of the last interglacial, the geographical range had fragmented and was reduced to temperate, not arid, areas. The species is still recorded during MIS 5a, MIS 4, and MIS 3 in some Italian LFAs, though Martino and Pandolfi (2022) believed that the remains found in levels dated between 69 ka and 40 ka at Grotta Romanelli (Apulia) may document its last occurrence. *H. amphibius* probably disappeared later in Greece, where a rich *H.*

amphibius sample radiometrically dated to 32 ka was found at Dyrós Cave (South Peloponnesus) (Athanassiou, 2022, and references therein).

3.1.7. *Sus scrofa*

The wild boar, *Sus scrofa*, originated in Southeast Asia in the Early Pleistocene and first dispersed into India, then moved westwards to the Levantine Corridor (Gesher Benot Ya'akov, Israel, Tchernov, 1992) and Europe.

The time of arrival in Europe of the Asian scrofic suids and the processes leading to their replacement of the Villafranchian European verrucosous suid, *Sus strozzii*, is somehow controversial and still a matter of debate. The uncertainties basically depend on the poor suid record in the period roughly between 1.6 Ma and 1.2 Ma, as well as on the peculiar morphological characteristics of some Jaramillo specimens, identified by authors either as scrofic or verrucosous suid. The first scrofic suid representative would be present at about 1.2 Ma in the mammalian fauna of layer TE9 of Sima del Elefante (Atapuerca, Northern Spain). Rosas et al. (2006) reported such remains as *Sus* sp., while Martinez-Navarro et al. (2015) regarded the Sima del Elefante suid as phylogenetically related to *Sus* ex gr. *S. scrofa*. Other remains with a controversial identification had been recorded at the France site of Le Vallonnet (Cobb Mountain, about 1.221-1.118 Ma or Jaramillo, about 1.070-0.990 Ma), and *Sus* sp. had been reported from the Spanish Vallparadís Estació (ca. 1.1-1.0 Ma, MIS 31). The Le Vallonnet remains were first ascribed to *S. strozzii*, but Moullè et al. (2006) considered the identification doubtful and the species undetermined (*Sus* sp.). A large and rather primitive wild board, *S. scrofa priscus*, would be present in the Untermassfel fauna (Germany) (Guerin and Faure, 1997), which several researchers considered the epitome of the Epivillafranchian ELMA (Kahlke, 2007). Accepting the occurrence of scrofic suids at those sites, the dispersal into Western Europe of scrofic suids was considered a bioevent that occurred roughly at the time of the Jaramillo paleomagnetic event, when *S. strozzii* was supposed to have already disappeared.

Later, S. *strozzii* was identified in the about 0.99 Ma old mammalian fauna from Frantoio (Adda River, Italy) (Bona and Sala, 2016; Cherin et al., 2020). Moreover, the revision of suid samples from Vallparadís Estació (Cherin et al., 2020), Untermassfield (Iannucci, 2022), and Le Vallonet (Moullé et al., in press) indicated that they belong to *S. strozzii*, even if they show some morphological differences from typical Villafranchian *S. strozzii* populations (see Iannucci, 2022 for a discussion). As a result, the dispersal of *S. scrofa* into Western Europe was likely part of the mammalian fauna renewal that marked the transition from the Early to the Middle Pleistocene. The wild boar first occurred in Europe possibly slightly earlier than 0.8 Ma [e.g., in Spain at Gran Dolina TD6B (dated about 0.85 Ma by Berger et al., 2008) and Cueva Negra (with an age between 0.99 Ma and 0.78 Ma, according to Walker et al., 2013), and in Italy at Slivia (Ambrosetti et al., 1979).

During the Middle Pleistocene and the last interglacial, the species became rapidly widespread in Europe, where it was present, especially during the interglacial phases and in closed (e.g., Macchia Mediterranean) or even open wooded environments. It was generally believed that the size and range of the European populations reduced during the last glacial, and South European territories (e.g., Spain, South France, Italy, and the Balkans) acted as "glacial refugia" for large populations during the Last Glacial Maximum and as a potential source for the massive European recolonization in the Holocene. Recent studies on the spatial genetic structure of extant populations failed to fully confirm such a hypothesis, though they suggest that two main dispersal routes, from South France and the Balkans, played an important role in the recolonization of the European regions (de Jong et al., 2023).

3.1.8. *Dama dama* ssp.

The taxonomy and systematics, phylogenetic relationships, and biochronology of the Early Pleistocene *Dama*-like deer and the Middle Pleistocene fallow deer have been extensively discussed. The authors have proposed several evolutionary models, especially for the early Pleistocene species with unpalmated, four-point antlers and, to a lesser extent, for the Middle Pleistocene ones with narrow and flattened, or fully palmated antlers (e.g., Pfeifer, 1999, 2005; Di Stefano and Petronio, 2002; van der Made et al., 2014; Stefaniak et al., 2015; Croitor, 2014, 2018; Heckenberb, 2020; Van der Made et al., 2023, and references in those papers). Whatever the taxonomy and nomenclature of the Early and Middle Pleistocene fallow deer could be adopted, the available data indicate that the Middle Pleistocene fossil record includes five taxa: *Dama roberti, Dama celiae, Dama clactoniana (*by some supposed to be a subspecies*, Dama dama clactoniana*, but herein considered a species)*, Dama dama geiselana*, and *Dama dama tiberina*.

Breda and Lister (2013) proposed the new species *Dama roberti*, a fallow deer with two-point, unforked but fattened, narrow blade-like shovel antlers, on the basis of the sample from the early Middle Pleistocene site of Pakefield (Suffolk coast, United Kingdom). The species' authors deemed it derived from the Early Pleistocene *Dama*-like deer lineage and was the putative ancestor of the modern fallow deer *Dama dama*. Afterward, new evidence led to the species identification in a few other early Middle Pleistocene sites, such as the Italian sites of Valdemino (northwestern Italy) (? MIS 15) (Breda, 2015) and Isernia la Pineta (Molise) (Breda et al., 2015) (MIS 15), as well as in the Contrada Monticelli LFA (Apulia) (Mecozzi et al., 2021b).

The presence of the large-sized deer, *Dama clactoniana* at Notarchirico (Basilicata) (MIS 16) (Pereira et al., 2015 but see Moncel et al., 2023), implies the occurrence of both fallow deer species in the early Middle Pleistocene of Southern Italy. The presumable co-occurrence of two differently sized deer in the same territory gives some support to the hypothesis that *D. roberti* was a dead branch of the fallow deer-like deer of the *"Pseudodama"* group and *D. dama* perhaps stemmed from a different and older *"Pseudodama"* stock (Breda and Lister, 2013; van der Made et al., 2023). Recently, van Made et al. (2023) described the new fallow deer species, *Dama celiae*, from the MIS 9 sites of Pedro Jaro I and Orcasitas (Manzanares River, Spain). The author considered the species a *D. roberti* descendant and the end member of the long-lasting *"Pseudodama"* lineage that persisted from the early to the Middle Pleistocene, while the fallow deer with more complex and palmate antlers would have evolved from a parallel *Dama*-like lineage.

The researchers disagree about the possible ancestor of the palmate fallow deer, which has been traced back to a different genus; thus, their origin is still unclear.

A wide time gap separates the putative ancestor and the earliest occurrence of the first palmate fallow deer, the large-sized *Dama clactoniana*. The Clacton fallow deer is reported first in Italy at Notarchirico (MIS 16), rarely during MIS 14-MIS 13 (e.g., at Caune de L'Arago CMI, France, and Visogliano, and perhaps at Collina Barbattini, Italy), and especially recorded in sites correlated with MIS 11-MIS 9. It would be still present during MIS 7 (e.g., Galería GIII and TZ, Spain) (Cuenca-Bescòs and Garcìa, 2007), at the same time that its putative descendants, *D. dama tiberina*, rather smaller in size, is already recorded in Italy (Di Stefano and Petronio, 1997), and *D. dama geiselana* was present at Neumark Nord I (Germany), a site that some researchers conversely refer to MIS 5e (e.g. Gaudzinski-Windheuser et al., 2014, and references therein).

In the Roman basin, some small-size fallow deer remains have been reported since MIS 13, such as at Collina Barbattini, a site where also *D. clactoniana* has been identified (Anzidei et al., 1993). Fallow deer remains with a size slightly smaller than the average size of *D. clactoniana* are recorded in other Latium MIS 13-MIS 10 LFAs. However, complete antlers are missing, and remains generally lack compelling diagnostic characters, precluding any sound identification of these fallow deer specimens. As a result, based on the available data, a hypothetical occurrence of modern fallow deer before MIS 8.5 cannot be confirmed or excluded.

During MIS 8.5 and MIS 7, the primitive *D. dama* representative, *D. d. tiberina*, was reported mainly from Italian LFAs. Di Stefano and Petronio (1997) described the subspecies based on a partial skull with complete antlers from the Ponte Molle gravels (Rome). Portis (1920) had already named it *Cervus (Dama) quirinus,* a species to which the author, however, referred other cervid remains from the Roman Basin without a formal description. *D. d. tiberina* shows a peculiar mixture of plesiomorphic and apomorphic features somehow intermediate between those of the Clacton and the extant fallow deer. Although the subspecies probably disappeared by the end of the Middle Pleistocene, replaced by the modern *D. dama dama*, during MIS 5e, or shortly after, a peculiar fallow deer, *Dama dama* cf. *tiberina*, previously assigned to the endemic giant deer "*Megaceros calabriae*", has been reported in some Calabria LFAs (Marra, 2009).

The extant subspecies, *D. dama dama*, occurred for the first time in the early Late Pleistocene. During the MIS 5e climatic optimum, the modern fallow deer had its maximum distribution in Western Europe. Later, the fallow deer's geographical range was reduced, the populations became more and more rare, and the deer disappeared from most of Europe with the onset of the worsening climate. Few populations persisted sometimes in South Europe during the last glacial [e.g., in Italy, the species is reported during MIS 3 in the Aurignacian levels of Cala Cave, Salerno (Benini et al. 1997)] and, even during the Last Glacial Maximum, in very few southeastern Mediterranean territories (Fernández-García, 2012).

3.1.9. *Cervus elaphus*

Red deer have today, as they did at least in the Late Pleistocene, an extremely wide geographic range that extends throughout much of the northern hemisphere, from Europe through northern Africa, Asia, and North America. The red deer populations mainly inhabited open woodlands through a large range of elevations, from sea level to about 3000 m. The ecological flexibility of this mixed-feeder species was probably a key factor allowing the presence of large red deer herds across such a large territory and, in turn, the differentiation of several ecomorphotypes. *Cervus elaphus* is, indeed, a rather polymorph species that shows morphological and dimensional variation both across its wide geographic range and during its evolutionary history. As a result, various subspecies have been proposed with either geographical or chronological significance, the latter mainly based on the progressive evolution of the ramusing antlers.

After the dispersal of elaphine populations from Asia, where the species possibly originated, *C. elaphus* had a rather long evolutionary history that, in Europe, was documented during about 1 Ma. The diffusion into Europe probably took place at some point in the late Early Pleistocene, as suggested by the occurrence around 1 Ma ago of elaphine deer at Saint Prest (France) (Guerin et al., 2003) and Barranc de la Boella (Spain) (Vallverdú et al., 2014). Shortly after, around 0.9 Ma, the first chronosubspecies appeared, *Cervus elaphus acoronatus*, characterized by five points and crownless antlers with a terminal fork with only two points. At that time, the subspecies may have already reached a rather wide distribution, having been recorded from Germany (Dorn-Dürkheim, Franzen et al., 2000) to Israel (*Cervus* cf. *C. elaphus*, Gesher Benot, Ya'akov, Hooijer, 1959). In SW Europe, *C. e. acoronatus* occurred in Spain [Ponton de la Oliva (>0.9 Ma, cf. Torres et al., 1995) and Gran Dolina TD3-4 TD5-TD6 (<0.9 and >0.85 Ma, Berger et al., 2008)] and Italy (Slivia, pre-Bruhnes, age inferred according to small mammal assemblage). In France, the most complete antler found in the Arago Cave LFA ("Complex moyen" II, MIS 13, Falguères et al., 2015; Deldique et al., 2021) has two points at the top. Consequently, it may belong to this subspecies, but the presence at the apex of a fork might depend on the specimen's juvenile age, and the crown might still not have formed due to the young age of the individual (Magniez et al., 2013). *C. e. acoronatus* would still be present in the Italian Guado San Nicola LFA (MIS 11–MIS 10 transition, Pereira et al., 2016) (cf. Sala et al., 2014). However, roughly at the same time (MIS 11, Pereira et al., 2018), some deer remains found in the Italian site of Fontana Ranuccio (in particular four incomplete antlers, the most complete broken near the trez tine) have been ascribed by Di Stefano and Petronio (1993) to a more advanced subspecies, *Cervus elaphus eostephanoceros*, that the Italian paleontologists had created for the well-preserved antler from Cava Nera Molinario (Rome) (MIS 11 in Marra et al., 2018), and to which also the remains from the early Middle Pleistocene site of Notarchirico (Basilicata Italy) (MIS 16, Pereira et al., 2015 but see Moncel et al., 2023) were ascribed. The presence in Italy of an alleged primitive red deer with crowned antler, *Cervus elaphus rianensis*, a subspecies created by Leonardi and Petronio (1974) for the rich deer sample from Riano Flaminio (Rome) (MIS 11, Marra et al., 2018), further complicates understanding the actual chronological significance of the *C. e. eostephanoceros* subspecies, which some had regarded as one of the biochronologic markers of the late Galerian. This still confusing scenario suggests great caution in the taxonomic identification of fossil elaphine subspecies if based on incomplete or fragmentary antlers, also considering the great individual variability of red deer antlers. Furthermore, the not yet-defined chronological range of the alleged subspecies makes it challenging to imagine when modern red deer (i.e., *Cervus elaphus elaphus*) actually first occurred in Europe. However, it seems rather certain that modern deer populations were present during MIS 11 in Italy and in the Latium territories.

3.1.10. *Bos primigenius*

Bos primigenius is a well-known species, recorded in the Eurasian large mammal fauna from about 0.65 Ma until historic times (late 17th century), which was extremely common in LFAs, especially during the Middle and Late Pleistocene.

The species, likely phylogenetically linked to *Pelorovis olduwayensis* (Martinez-Navarro et al., 2007), originated in Africa, where its direct ancestor, *Bos buiensis*, is recorded at Buia (Eritrea, eastern Africa) about 1.0 Ma (Martinez-Navarro et al., 2010). *Bos primigenius* was first documented about 0.7 Ma by the nearly complete, large-sized skull found in the Wadi Sarrat site (Tunisia) (Martinez-Navarro et al., 2014), if not the skull fragment ASB-198-1 from Asbole (Ethiopia) (0.8-0.6 Ma) (Geraads et al., 2004). From North Africa, the species probably dispersed towards Eurasia shortly after. The oldest auroch fossil records are those from Italy, where the species is present in the Notarchirico LFA (Basilicate) (Cassoli et al., 1999), dated at about 0.65 Ma (MIS 16) (older than 0.614 +/- 0.4, Pereira et al., 2015) but were the lowermost levels have been recently dated to 670-695 ka by Moncel et al. (2023), and in the slightly younger LFA of the Valdemino Cave (? MIS15, Nocchi and Sala, 1997) (Sala, 1992).

During the Middle Pleistocene, the auroch was present in the Latium area at some sites correlated with MIS 15-MIS 13 (e.g., Ficoncella, Aureli et al., 2015), as well as in the several early Aurelian LFAs (Tab. 1). Often, its commonness equals or is slightly inferior to that of the straight-tusked elephants.

The species was widely present in Eurasia and North Africa during the Late Pleistocene, even though the density decreased in the northernmost regions during the most severe cold phase and the geographical range sometimes shifted towards the south, while it enlarged during the Early Holocene.

In the Neolithic period, with the beginning and intensification of the domestication practice, large populations were still recorded, for instance, in Germany, but the average size of aurochs decreased. The wild cattle populations were still present in historical times, although the number and size of the population progressively decreased, and the geographical range fragmented. Since the 13th century, the wild cattle's range has been limited to the forests of Poland, Lithuania, Moldova, and Eastern Prussia. Although the hunting of species was first permitted only to nobles and then forbidden, the number of individuals dramatically decreased during the 16th century. The last individual, a female, died in Poland in 1627.

3.2. SIMILARITY

I performed the cluster analysis in an attempt to scrutinize if the taxonomical composition of the Latium LFAs selected for this study might lead to their hierarchical assessment in some chronological or geographical order. In the two-step analysis, first I considered all the LFAs (28 LFAs, Tab. 1) (Sample A), including those that include just one or very few taxa, and then I limited the analysis to the LFAs counting at least six taxa (20 LFAs) (Sample B).

In the dendrogram obtained by using all LFAs, it is challenging to find a chronological or geographical hierarchical order (Fig. 3). All the analyzed LFAs fall in the main group A unless the two LFAs with a single taxon from via Ostiense, which sets apart, like an "out-group", and Casal Selce B, detached from A as a separate ramus. The peculiar setting of via Ostiense LFA likely depends on the presence of a single species, *C. mosbachensis,* at the site. The species is also recorded in the Fontana Ranuccio LFA, which is, however, the richest among the analyzed LFAs and consists of almost all the taxa most common in the Latium mammalian assemblages (Figs. 2, and 3). At Casal Selce B, the single species present, *C. lupus*, justifies its position since the species is recorded in several other LFAs of the large cluster A.

The main group A includes two sister clusters, A1 and A2, as well as the Ciampate Del Diavolo LFA (four taxa) as a separate ramus. The cluster A2 gathers a few LFAs, mostly ranging in age from MIS 13 to MIS 10. Within A1, A1.2 includes only four LFAs, all from the Roman basin and correlated to MIS 13 and MIS 11. A1.1 includes

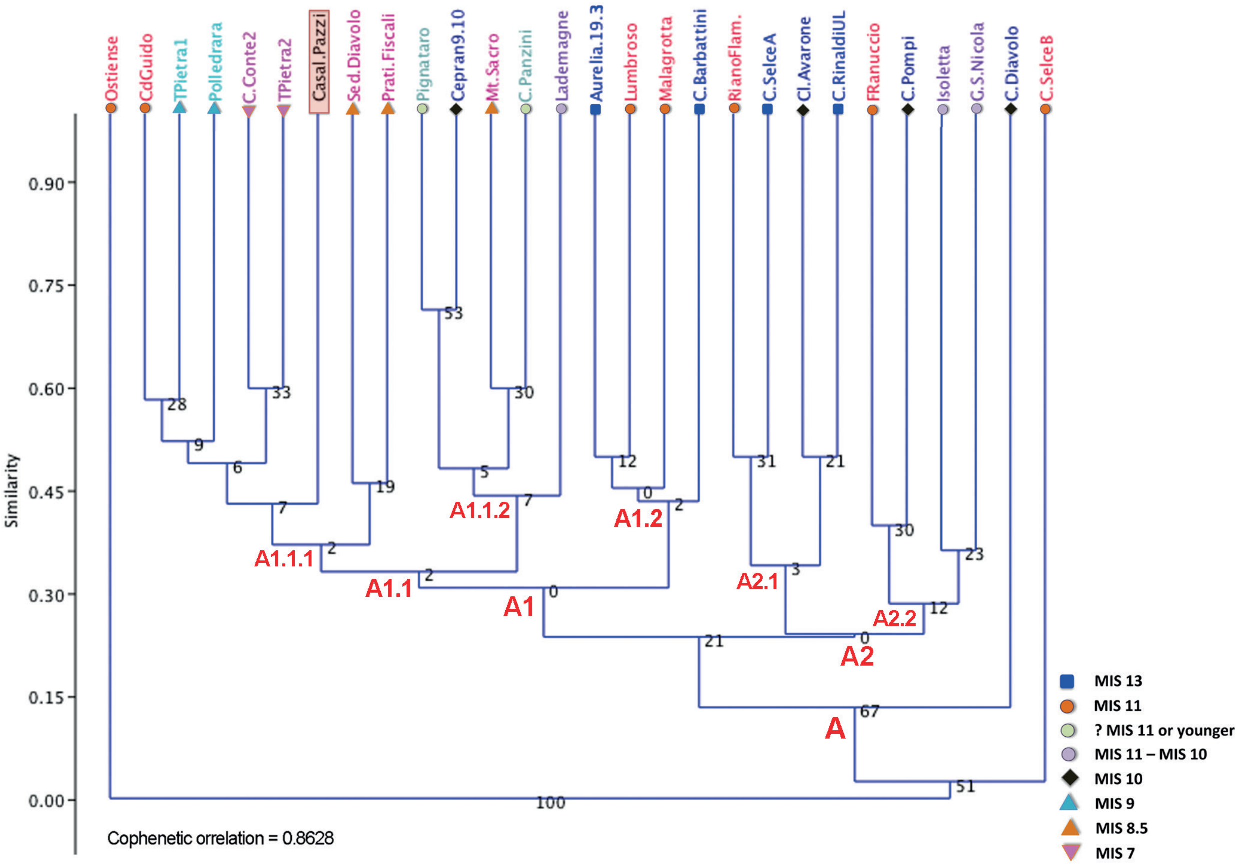

Fig. 3 - Q-mode dendrogram showing how the selected late Middle Pleistocene (MIS 13-MIS7) local faunal assemblages (Latium and surrounding area) cluster each other based on the species they include. Clusters are joined based on the average distance between all members in the groups (unweighted pair-group average, UPGMA).

two groups, A1.1.1 and A1.1.2. The first gathers LFAs ranging in age from MIS 9 to MIS 7, as well as the Castel di Guido LFA (MIS 11) as a sister LFA of La Polledrara di Cecabbio (MIS 9). Both LFAs show the highest similarity with Torre in Pietra 1 (lower levels) (MIS 9), another mammalian fauna from the same region. The three LFAs share, indeed, a somehow similar fauna's taphonomic structure and assemblage context. CdP fauna also falls into this group but as a separate ramus. The group A1.1.2 is much more heterogeneous, as the five LFAs range in age from late MIS 11 to MIS 8.5. However, it is unclear which factors allowed their gathering because they share the three most common species (*P. antiquus, C. elaphus*, and *Bos primigenius*), though LFAs differ in richness and in the presence or absence of other taxa (Tab. 1).

All things considered, the presence or absence of taxa in each LFA and the LFAs' richness and diversity, which are mainly influenced by the depositional context and biostratinomic processes, are likely the main factors that determine the LFAs clustering.

To reduce biases due to the presence of LFAs with a high number of missing taxa, I carried out the analysis, including as cases the LFAs recording at least six taxa. The results obtained provide a few chronological hints, though the cophenetic correlation coefficient is lower (CCC= 0.7858) than that resulting from the analysis of all LFAs (CCC=0.8628) (Fig. 4). In the dendrogram, two well-separated clusters are detectable, A and B, each gathering a notably different number of mammal assemblages. Cluster B comprises only three LFAs from the Anagni basin, ranging in age from MIS 11 to MIS 10. The cluster A includes the sister clusters AI, the richest, and A2. In cluster A1, the two sister subclusters A1.1, gathering the LFAs ranging in age from MIS 11 (Castel di Guido) to MIS 9, and A1.2, including the more recent LFAs, correlate with MIS 8.5 and MIS 7 that fall into two separate subgroups, i.e., A1.2.1 and A1.2.1, respectively. The CdP LFA joins as a separate ramus the small groups of Sedia del Diavolo and Monte Sacro LFAs. In A2, the five LFAs fall into two groups. The small one gathers the Malagrotta (MIS 11) and Collina Barbattini (MIS 13) LFAs from the Roman basin, and the slightly larger and heterogeneous one includes MIS 13-MIS 10 LFAs. Although the LFA clusters' arrangement does not show a full chronological order, the hierarchical assessment reveals the tendency to cluster each other of either the most recent LFAs or some fauna that include the most common taxa and have a similar taxonomical composition.

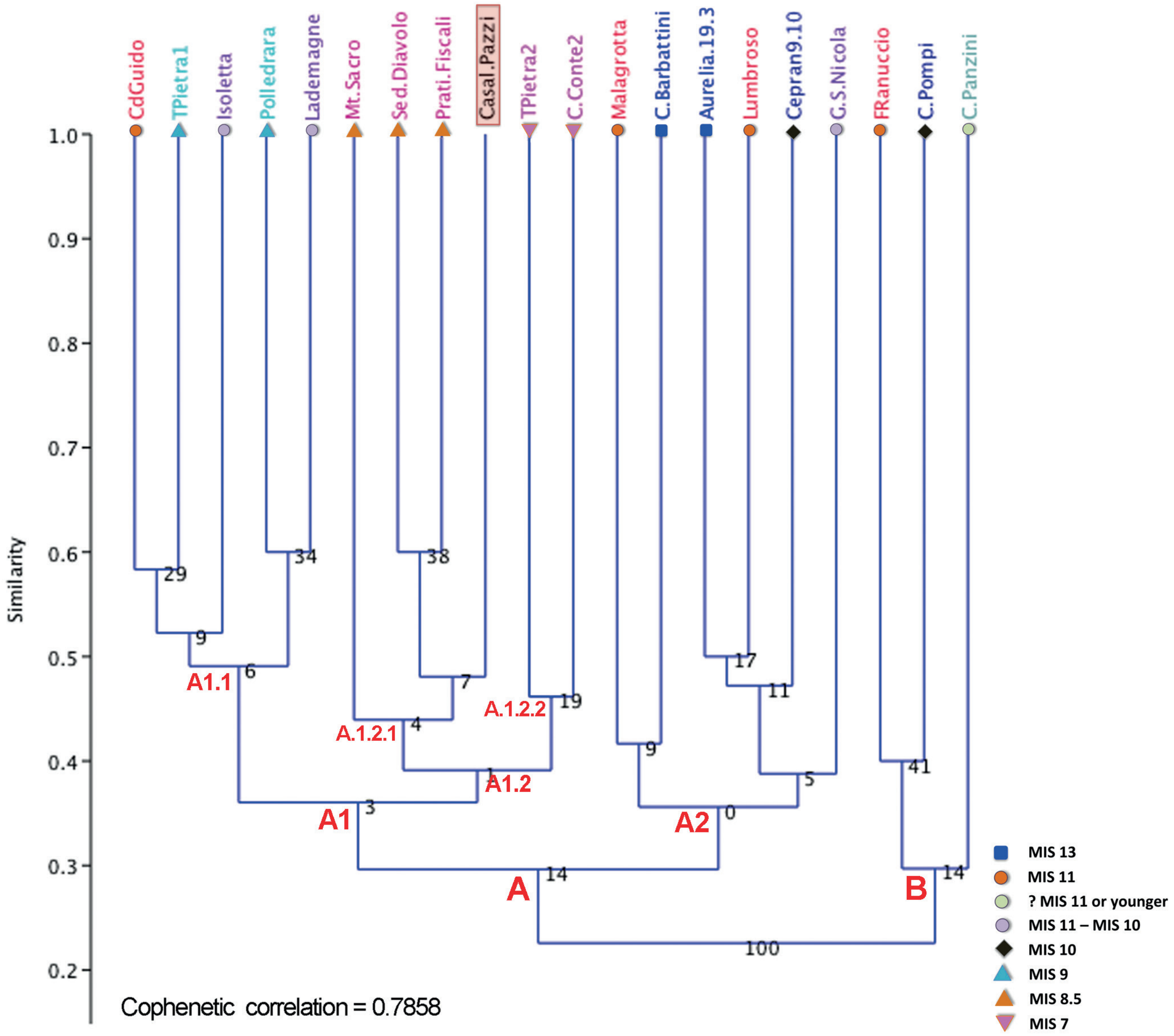

Fig. 4 - Q-mode dendrogram showing the hierarchical ordering obtained for the late Middle Pleistocene (MIS 13-MIS7) local faunal assemblages from Latium and surrounding areas, selected because they include at least six large mammal taxa. Clusters are joined based on the average distance between all members in the groups (unweighted pair-group average, UPGMA).

3.3. REMARKS

The CdP large mammal remains, as well as those of the selected LFAs, were retrieved from attritional fluvio-lacustrine deposits (including braided systems). The formation of attritional assemblages mainly depends on the nature of the depositional context and the sedimentary processes that influenced the bone accumulation, burial, and preservation processes and, in turn, greatly affected the taxonomic composition of fossil assemblages. As a result, the composition of a mammal fauna retrieved from attritional deposits may not be faithful to the original compositions of the ancient communities. This is particularly evident when the richness and diversity of the fauna are particularly low. In these cases, the fauna might mainly consist of remains particularly resistant to potentially damaging biostratinomic processes, such as teeth or long bones, as well as remains of the gregarious large mammal showing a high density on the territory surrounding the site.

Such taphonomic biases also influence the results of the clustering analysis. Using the Jaccard index, indeed, the similarity degree among cases (LFAs) and, in turn, the results obtained depend on the presence or absence of taxa at each site. Moreover, the hierarchical ordering is greatly influenced by the taxa most frequently recorded, such as *P. antiquus, Bos primigenius*, and *C. elaphus*, in the LFAs of the analyzed sample. The effect exerted by depositional context and related taphonomic biases may also give an account of some faunal monotony that could be at least partially related to the low number of rich and diversified faunal assemblages (Tab. 1).

Although the CdP mammalian fauna is bio-chronologically poorly significant, since most taxa were present in Europe at least from MIS 11 (Fig. 1), two taxa could have potential chronological relevance: *Equus ferus*, assuming that it is actually present in the CdP fauna

(Anzidei et al., 1999) and appeared around MIS 9, and *Dama dama*, which seems to not have been present in Italy before MIS 8.5. The latter species, however, would have occurred in Spain earlier, but it is reported from sites with a debated chronology, such as, for instance, Solana del Zamborino, believed to be 480-300 kyr old by Álvarez-Posada et al. (2017).

All things considered, the obtained results, though biased by the low LFA richness and the small size of the sample, on the one hand, support the suggested correlation of the CdP site with MIS 8.5 and, on the other hand, highlight some uniformity of the analyzed mammalian assemblages, especially during MIS 9, which confirms the inconsistency of any subdivision in low-rank biochronological units for a geologically short time (i.e., the second half of the Middle Pleistocene).

4. PALEOECOLOGICAL NOTES

Hitherto, the study of the ecomorphological traits of CdP species has been limited to the analysis of microwear patterns and $\delta^{13}C$ and $\delta^{18}O$ (phosphates and carbonates) stable isotopes of the tooth enamel of *P. antiquus*. The first study was done to infer their dietary behavior and the paleoenvironment they inhabited (Palombo et al., 2005). Recently, Briatico and Bocherens (2023) analyzed the stable carbon and oxygen ($\delta^{13}C$ and $\delta^{18}O$) isotopic abundances in the tooth enamel of all herbivore species recorded at CdP.

Data provided by Palombo et al. (2005) indicated that the amount of gramineae, or vegetables relatively rich in phytoliths, was important in the daily diet of the CdP elephants. Grube et al. (2010) compared the CdP and La Polledrara data with those obtained for the sample from Neumark Nord 1 (Germany) and data available for extant herbivores. In the PCA based on all microwear variables (different types of scratches, pits, and gouges), CdP specimens fall into the overlapping ecomorphospaces of occasional (meat by meat) mixed-feeders and browsers, while, considering the ratio between the average number of scratches and pits, they fall close to the ecomorphospace of meat by meat mixed-feeders. However, in the CdP sample, coarse and fine scratches and pits have a high and rather low percentage, respectively, while in the La Polledrara sample, pits occur about in the same percentage as the striations, among which coarse and crossed scratches prevail (Palombo et al., 2005). Accordingly, the microwear patterns of the two populations suggest that the CdP elephants ate more graminaee, or vegetables rich in phytoliths, than those of La Polledrara did. In extant elephants, the percentage of browse varies depending on the availability of different kinds of plants and on climatic conditions, increasing during arid periods when grasses dry out. The results of $\delta^{13}C$ and $\delta^{18}O$ (phosphates and carbonates) isotope analysis could support the hypothesis of a fairly less humid climatic condition at La Polledrara than at CdP (Palombo et al., 2005). The C3 plants generally have a high carbon isotope composition in xeric climates; thus, the $\delta^{13}C$ value obtained for the straight elephants from the two sites, lower in the CdP sample than in the La Polledrara one, indicates the prevailing of a more closed canopy forest at CdP or of a more arid climate at La Polledrara. The results of oxygen isotope analysis support the latter hypothesis, suggesting a difference in terms of temperature and/or humidity between the two sites: warmer and/or more arid conditions at La Polledrara and colder and/or wetter conditions at CdP.

The results of the $\delta^{13}C$ and $\delta^{18}O$ analyses carried out by Briatico and Bocherens (2023) suggest the presence of closed and open C3 environments at both sites. Straight-tusked elephants occasionally moved from one habitat to another according to the period's climatic conditions as well as their dietary preferences, increasing grazing and browsing during humid and dry periods, respectively.

4.1. A GLANCE TO THE FAUNA'S ECOLOGICAL STRUCTURE

The taxonomic composition of faunal assemblages in a region may differ from site to site, while the ecological structure may be the same. In such cases, the taxon-free analysis of taxon ecomorphological traits in each LFA and their consequent arrangement into functional groups may be useful for scrutinizing the amount of inter-specific variation in taxa functional traits (Functional Diversity, FD). FD could also be a useful tool for inferring the ecological structure of fossil ecological communities, as well as the factors behind changes in the ecological group's relative abundance across a region or over time (Palombo, 2016b). However, in the case of CdP and the analyzed LFAs, the low number of taxa identified in most sites and the lack of exhaustive studies of their ecomorphological traits prevent any compelling FD analysis. Consequently, I have performed a first preliminary evaluation of the CdP relative abundance of ecological groups by using as variables the average data available in the literature for the basic ecological categories (taxa's feeding habits, habitat preferences, and body mass).

The comparison among the habit, trophic, and body mass structure of the CdP LFA and those of the selected MIS 13 to MIS 7 LFAs evidences a high variability among the relative abundance of ecological groups present in each local large mammal assemblage (Figs. 5, and 6). As regards habitat preferences, ubiquitous taxa are dominant in most LFAs, with the exception of Prati Fiscali (MIS 8.5), Castel di Guido (MIS 11), and Campo del Conte 2 (MIS 7). In the Prati Fiscali and Castel di Guido LFAs, the open landscape dwellers are the dominant group, while at Campo del Conte 2, their relative percentage equals that of ubiquitous taxa. The open landscape and forest dweller ecological categories have the same relative abundance in the LFAs of Lademagne (MIS 11-MIS 10) and Ciampate del Diavolo (MIS 10). Among the main trophic categories, primary consumers are always the main represented trophic group, as expected, while the few carnivores and omnivores have a discontinuous presence, being reported from about half of the analyzed LFAs (Fig. 5). Among

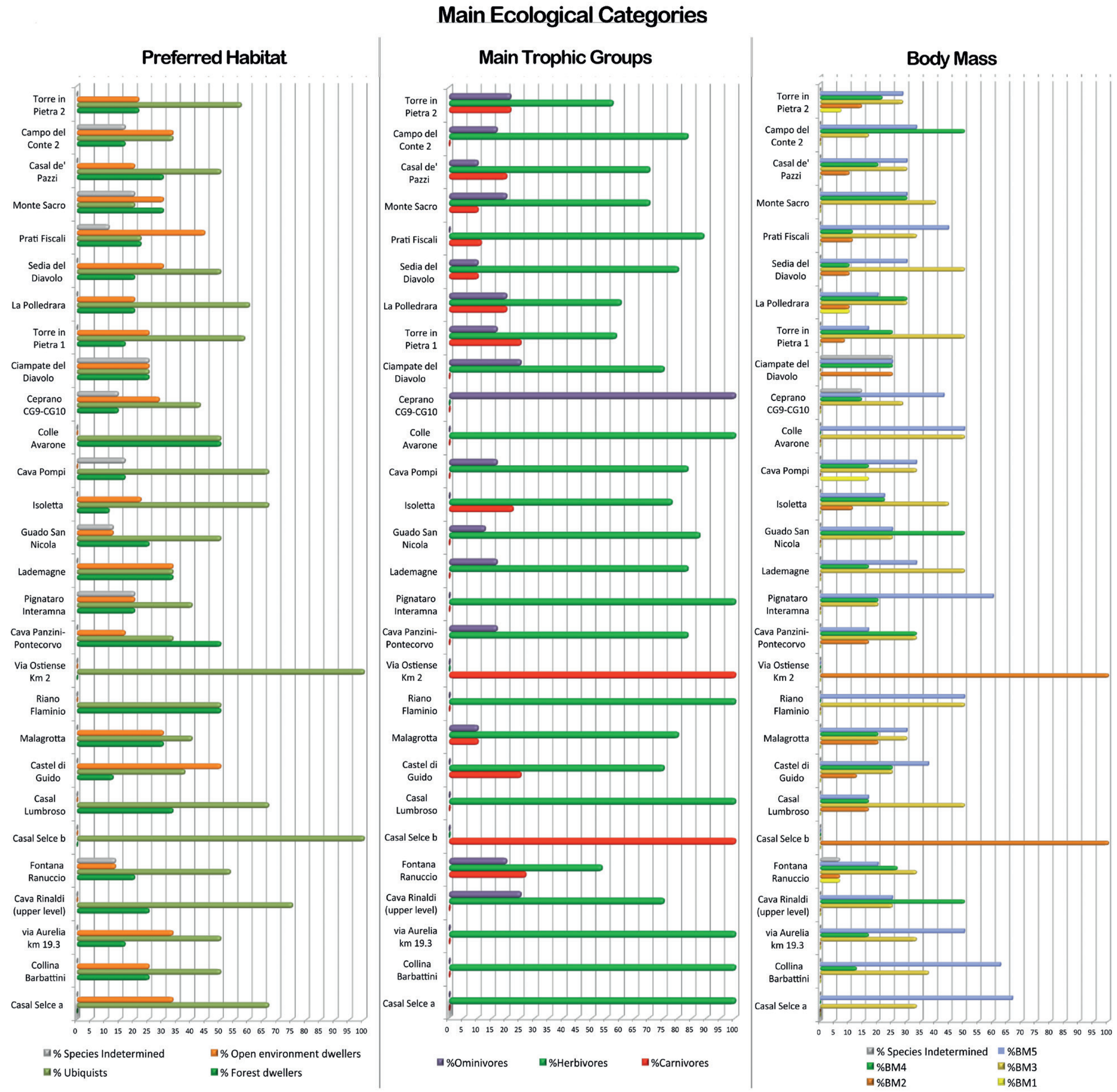

Fig. 5 - Relative percentage of the main large mammal ecological groups (i.e., species' preferred habitat, feeding habit, and body mass) present in the studied local faunal assemblages.

herbivores, taxa forming large herds, which may suggest the presence of open landscapes, prevail, as do taxa able to change their diet occasionally or seasonally (mixed-feeders). The latter ones are numerous, especially in the oldest (MIS 13-MIS 10) LFAs, except for the not-rich LFAs of Ceprano CG9-CG10 (7 taxa) and Ciampate del Diavolo (3 taxa), where the mixed feeders percentage equals that of grazers, as it occurs at La Polledrara and CdP. Grazers are the dominant group only in the Monte Sacro and Campo di Conte 2 LFAs (Fig. 6). Even the percentages relating to the BM categories, which are greatly influenced by the taxonomic composition and richness of the fauna, are scarcely informative. For instance, Torre in Pietra 2 (MIS 7) and Fontana Ranuccio (MIS 11), two of the richest LFAs, are the only ones recording a taxon weighting less than 15 kg (BM 1), but in the first, taxa weighting at least 251 kg or more (BM 4 and BM 5) prevail. In the second, taxa with a weight ranging from 251 kg to 1000 kg (BM 4) are the most represented, followed by those ranging in weight from 61kg to 250 kg (BM 3).

The obtained results are sometimes contradictory (e.g., the prevalence of ubiquitous and mixed-feeder taxa, but also that of taxa forming large herds). They fail to detect any differences between the sites based on geographical or chronological factors, giving only general indications about the presence on the territory of environments with a mixed vegetation cover (grasslands, wooded grasslands, and woodlands).

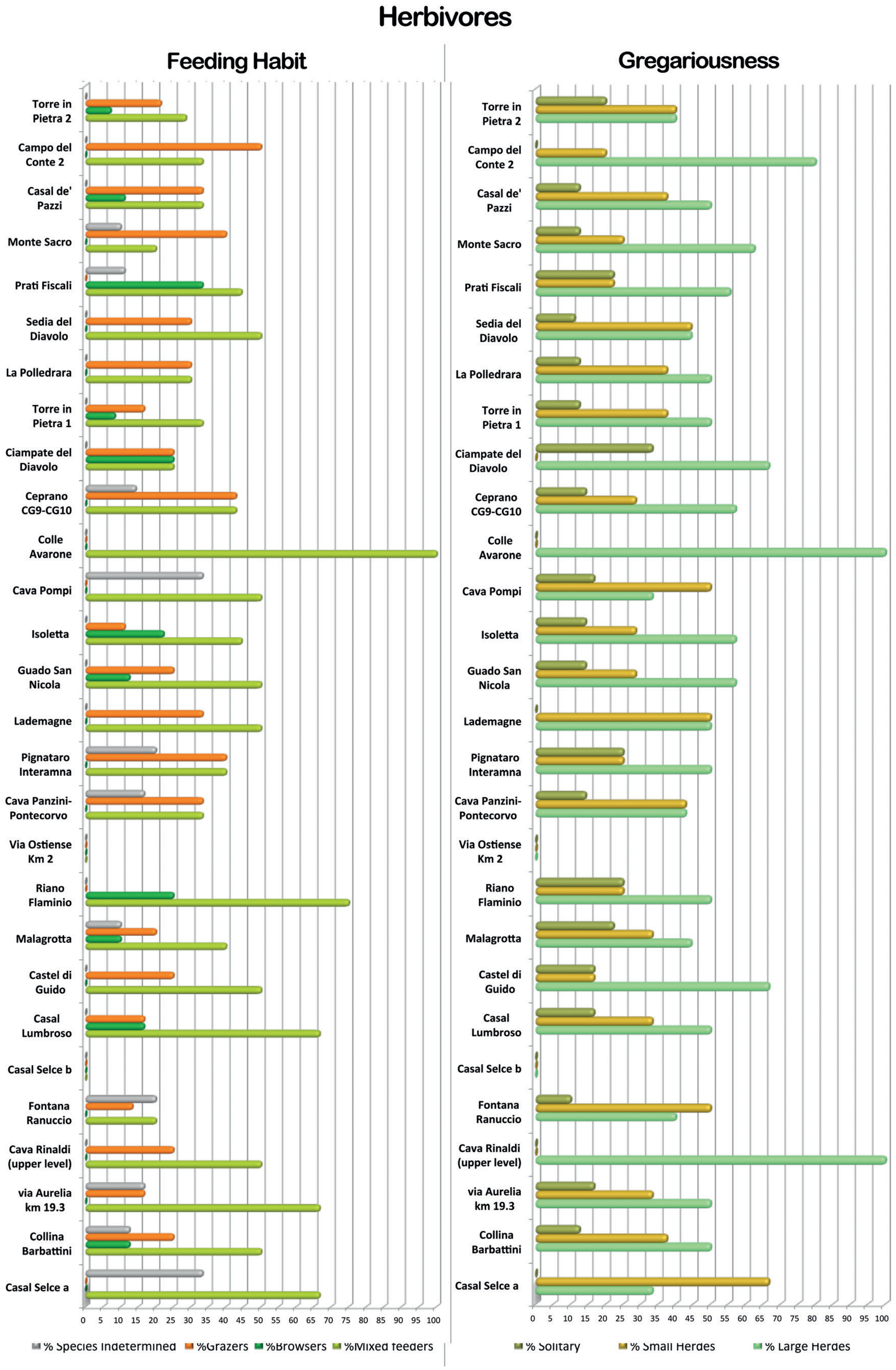

Figure 6 - Relative percentage of the ecological categories related to the trophic habit and the gregariousness of herbivore species recorded in the studied local faunal assemblages.

4.2. REMARKS

It is challenging to determine which of the many potential variables (taphonomy, chronology, regional microclimate, etc.) may have had the most impact on the relative percentage of ecological categories in each LFA. Furthermore, the lack of research on the autoecology of the taxa in each LFA hampers drawing conclusions about the actual LFAs' ecological structure. In fact, the data on species average characteristics are less useful for differentiating LFAs with closely related taxonomic compositions, and this in turn limits their potential for advancing our understanding of the paleoenvironment. Data on the macrovegetation or pollen content of fossiliferous layers are only available from a few sites, so it is hardly possible to find adequate support for the interpretation of the obtained results. The only available data concern Riano Flaminio (Follieri, 1958), Campo di Conte 2 (Palombo et al., 2000-2002), and Guado san Nicola (Orain et al., 2013). They indicate the occurrence of a Colchic forest, scattered woodlands dominated by mixed oak forest, and both wooded zones along rivers and grasslands at Riano, Campo di Conte 2, and Guado San Nicola, respectively. The data on the pollen sequences from Fontana Ranuccio (Corrado and Magri, 2011) and Ceprano (Margarari et al., 2018) refer to levels underlying the fossiliferous ones. In the lower levels of the Isoletta's stratigraphic sequence (lacustrine phase, MIS 11), the pollen record suggests a prevalent presence of conifers and deciduous wooded areas, as well as some open landscapes (Zarattini et al., 1999).

Future multidisciplinary research on the CdP fauna could provide some useful clues for better depicting the taxa's ecological traits, delineating the environmental features at the time of fossiliferous level deposition, and adding some clues to enlarge our knowledge on the paleoenvironmental evolution of the low Aniene valley in the late Middle Pleistocene (MIS 11-MIS 7).

5. PERSPECTIVES

Two matters have preeminent relevance, i.e., systematics and taphonomy, for evaluating which should be the meaning of the CdP large mammal assemblage in the context of the evolutionary dynamics of Italian and South European Middle Pleistocene fauna. Before scrutinizing any other topic (e.g., biochronology, paleoecology, et cetera), it is crucial to know the taxonomic composition of the whole fauna, understand the time and processes that lead to bone accumulation, and verify the reciprocal chronological consistency of remains and the structural conformity of CdP large mammal assemblages with the community from which they originated.

A thaphonomic study can enable us to evaluate whether the taxonomical data are suitable or not for further paleo-synecological studies and paleoenvironmental inferences. To deconstruct the biostratinomic processes leading to the attritional bone assemblage formation in the CdP fluvial deposit could clarify their geographic provenance and whether all remains are of primary deposition or some were reworked from earlier deposits. Thus far, the taphonomic signatures of the CdP mammalian remains have only been preliminary analyzed by Anzidei and Cerilli (2001), who only focused on their degree of rolling and abrasion. However, a glance at CdP remains gives an inkling of the possibility that several large mammal bones might undergo different biostratinomic and fossilization processes. The differences in taphonomic signatures affected the remains of all the species, so a thorough study is essential to confirm whether the age of the deposits could be the same age as that of all the specimens found in the mammalian assemblages. The further taphonomic analysis could depict the taphonomic history of remains and the dynamics of the biostratinomic processes leading to remains accumulation (e.g., transport signatures, spatial distribution of remains, weathering degree, trampling, burning, butchering marks, et cetera), as well as the diagenetic processes, such as the type of permineralization, to verify its basic uniformity across remains. Moreover, a stale isotope analysis (^{87}Sr/^{86}Sr) could be suitable for determining what should have been the remains' provenance.

Knowing the autoecology of each taxon and, in turn, the ecological structure of the CdP mammalian fauna could facilitate its comparison with the main late Middle Pleistocene (MIS 11-MIS 7) faunas of central Italy. Indeed, the amount of inter-specific variation in functional traits in an ecological community (FD) can provide useful information about the processes that structured past faunal complexes and promoted their dynamics by analyzing the functional diversity of mammalian paleocommunities throughout time and across geographic regions. Several methods are suitable for inferring the ecological role that a taxon has in its community from the ecomormological traits of its remains. For instance, some analyses, such as the mesowear of no-carnivore teeth, microwear, and enamel Hunter-Schreger Bands, as well as the mechanical advantage and size of the temporalis and masseter masticatory muscles and mandibular force in carnivores, and cranial and mandibular features distinctive of browsers and grazers, are useful for deducing a taxon's feeding aptitude, as are the analysis of isotopes (e.g., ^{12}C/^{13}C ratio, δ^{15}N) and Ca/Sr ratio for inferring trophic relationships among the mammals present in a community and the flow of energy through a food web. The δ^{18}O, C isotope analysis can help reconstruct past environmental and climatic conditions. Moreover, knowledge about the taxon niche could be enhanced by applying the most appropriate among the variety of methods that have been developed to use mammal postcranial elements in the functional morphology approach for paleohabitat predictions and inferences about their gait.

All things considered, the integration of the taphonomic, paleoecologic, and geochemical data could provide some useful clues for better depicting, at the very least, the evolution of the ecological structure of the mammalian paleocommunities in the Latium territory, the basic ecosystem characteristics, and maybe the suitability of the environment for Paleolithic man.

6. CONCLUSIVE REMARKS

The data analyzed in this note provide a few additional pieces of information about three focal points: the chronological range of the large mammal species identified in the sample of bone remains found in the musealized CdP deposit (about 300 m^2); the similarity degree of the CdP fauna with those of some Middle Pleistocene (MIS 13-MIS 7) LFAs mainly from Latium; and the basic paleoecological structure of the CdP mammalian fauna. Most CdP taxa were present in Europe at least since MIS 11, but two taxa could have potential chronological relevance: *Equus ferus*, accepting that it appeared around MIS 9 and was actually present in the CdP fauna (Anzidei et al., 1999), and *Dama dama* ssp., which seems to have been hardly present in Italy before MIS 8.5. The small size of the sample, the low richness of most LFAs, possibly related to the deposit context and related taphonomic biases, and, in turn, some uniformity in the taxonomical composition of the analyzed mammalian assemblages, especially those correlated with MIS 9, reduce the significance of the results of similarity analysis based on all LFAs. They, indeed, fail to provide any chronologic or geographic ordering, while they are rather more compelling when examining the richest LFAs. The above-mentioned factors, as well as the lack of data about the autoecology of the taxa recorded in each LFA and the nonspecific identification of some remains, may also account for the generic indications resulting from the attempt to infer and compare the paleoecological structure of the CdP large mammal assemblage. For instance, the information obtained from the analysis of the herbivore species is sometimes contradictory and suggests the presence of environments with a mixed vegetation cover (grasslands, wooded grasslands, and woodlands) on the territory. In brief, the available data could support a correlation of the CdP site with MIS 8.5, in spite of some taxonomic uniformity of most of the MIS 9-MIS 7 analyzed mammalian assemblages, as well as the presence in the CdP surroundings of some canopy forest, grasslands, and streams in a fairly wet and cool environment.

In the end, further studies will be essential to shed light on key issues, such as the taphonomy of the fauna, its systematic taxonomic composition, and its similarities and differences with other LFAs, enabling us to better understand the significance of the CdP fauna assemblage. Appropriate multidisciplinary studies of all the vertebrate remains found in the CdP deposit (systematics, taphonomy, paleoecology, and geochemistry) could clarify some crucial issues. For instance, the chronologic consistency and provenance of the remains, the ecological fidelity of large mammal assemblages with respect to the communities living in the CdP territory at the time of the deposit formation, as well as the palaeocommunity functional diversity, the energy flow through the food web, thus the ecosystem functioning, and the paleoenvironment evolutionary dynamic throughout time and across the analyzed territory.

ACKNOWLEDGEMENTS - I thank the two anonymous reviewers for their constructive comments to the manuscript and L. Pandolfi for critically reading the paragraph dealing with *Stephanorhinus kirchbergensis*. I am thankful to the organizers of the conference “40 Years of Casal de’ Pazzi in the framework of Pleistocene archaeo-palaeontological sites (400,000-40,000 BP)” for inviting me to participate and the journal Editor, Salvatore Milli, for accepting to publish the conference proceedings and revising and editing the manuscript. This paper is dedicated to the memory of Anna Paola Anzidei (1946- 2017).

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