SENCKENBERG

ORIGINAL PAPER

Late Early to late Middle Pleistocene medium-sized deer from the Italian Peninsula: implications for taxonomy and biochronology

Beniamino Mecozzi[1] · Raffaele Sardella[1] · Marzia Breda[2]

Abstract

The taxonomy of Quaternary medium-sized deer from Europe rests mainly on antler morphology, while adequate dental and postcranial diagnostic features are lacking. When complete antlers are not available, the taxonomic identifications are often attempted on chronological ground. A considerable number of mostly unpublished craniodental and postcranial remains of fallow deer from selected Italian sites from the late Early Pleistocene to the late Middle Pleistocene is here presented and discussed. The aim of this work is to test the validity of the diagnostic characters proposed in literature and to explore the variability of the fallow deer taxa. In addition, the analysis of the two reference samples from Riano and Ponte Molle allows to refine the features of *Dama clactoniana*. Finally, biometric comparison has been performed in order to investigate possible oscillations across time and/or differences among taxa.

Keywords Early-Middle Pleistocene Transition · Mediterranean area · Morphology · Cervids

Introduction

The small- and medium-sized deer are a common element of Quaternary palaeocommunities, with different forms whose taxonomic framework is still debated. Many fallow-like species have been described from the Late Pliocene to the Early Pleistocene of Europe but, despite the extensive literature dealing with them, their differences and relationships are obscure. Azzaroli (1992) united them in a single genus, *Pseudodama*, characterised by unpalmated three- to four-points antlers. Other authors, however, proposed different taxonomic opinions (e.g. de Vos et al. 1995; Pfeiffer 1999; van der Made et al. 2003; van der Made 2013), some even rearranging the described species in an array of different genera (*Rusa, Axis, Euraxis, Dama, Cervus,*

Metacervoceros, Praeelaphus, Di Stefano and Petronio 1998, 2002; Croitor 2006, 2014; Croitor et al. 2019). Disregarding the different taxonomical opinions on the *Dama*-like deer, there is however a general consensus that the position and orientation of the basal tine changes through time, being inserted quite distant from the burr and at a rather closed angle to the beam in primitive forms, to move closer and closer to the burr and at a more and more open angle to the beam in more advanced forms. The taxonomy of the fallow-like deer from the Late Pliocene to Early Pleistocene is well beyond the scope of the present work and so we will follow Azzaroli's (1992) view, not only because it finds the largest consensus (e.g. Moullé et al. 2006; Lister et al. 2010; Mazza and Ventra 2011; Bona and Sala 2016), but also because, by grouping all the species in a single genus, we avoid taking a position on the interrelationships within the group. However, if modern *Dama* derives from '*Pseudodama*', the latter is a paraphyletic stem-group thus, following Lister et al. (2010), it will be here quoted within inverted commas. In addition, we choose not to take a position on the relationship or possible synonymy between '*P.' farnetensis* and '*P.' vallonnetensis*, the two described species with advanced antler morphology from the late Early Pleistocene (roughly

✉ Beniamino Mecozzi
 beniamino.mecozzi@uniroma1.it

1 Department of Earth Sciences (PaleoFactory Lab), Sapienza University of Rome, p.le Aldo Moro 5, 00185 Rome, Italy

2 Museum of Nature and Humankind, University Museum Centre, University of Padova, Via Giotto, 1, 35121 Padova, Italy

1,6-0,9 Ma) but, pending a proper taxonomical review, we call them just "advanced '*Pseudodama*'".

The earliest species belonging to the genus *Dama* is the early Middle Pleistocene *Dama roberti* Breda and Lister, 2013, which sports an incipient palmation of the antler (a narrow but clear palmation ending in a single terminal point) and a single basal (first) tine. This species was present in western Europe during the early Middle Pleistocene (Pakefield, West Runton, Soleilhac and Mosbach - Breda and Lister 2013), and was also recorded in Italian localities, among them Valdemino cave (Breda 2015), Isernia La Pineta (Breda et al. 2015) and Contrada Monticelli (Stefanelli et al. 2021).

In the late Middle Pleistocene, a fallow deer with truly palmated antlers appears, *Dama clactoniana* (Falconer, 1868). Its European diffusion seems to be a synchronous event, since Clacton fallow deer remains have been found in Italian, French, Spanish and British localities chronologically referred to the Marine Isotope Stage (MIS) 11. This taxon differs from the extant European fallow deer (*D. dama dama*) in the distribution and size of the palmation tines (large and mainly on the upper edge rather than small and on the caudal edge as in *D. dama dama*) and in the presence (at least in British specimens from Swanscombe, close to the type locality of Clacton) of a sometimes bifurcated second tine and of an additional (third) tine departing from the anterior edge of the palmation.

Two other taxa have been described from the end of the Middle Pleistocene (MIS 7), *D. dama tiberina* Di Stefano and Petronio, 1997 and *D. dama geiselana* Pfeiffer, 1998:

- *D. dama tiberina* was described on fossils from Ponte Molle (Rome) by Di Stefano and Petronio (1997), as having: a posterior direction of the palmation tines, a basal tine close to the burr; basal tine and second anterior tine less developed; flatter palm and terminal tines; smaller body-size than *D. clactoniana* and small lower third molars.
- *D. dama geiselana* was described by Pfeiffer (1998) on a rich and well preserved sample from Neumark Nord (Germany), and later upgraded by the same author (Pfeiffer-Deml 2018) to the specific rank as *D. geiselana*. It has a long and strong basal tine branching off directly above the burr and forming an obtuse angle with the beam (up to 135°); a quite robust beam; second anterior tine sometimes double or bifurcated; posterior palmation tines generally absent; a palmation bending strongly upward/forward and additional folds on the lingual wall of upper premolars.

True *D. dama* first occurs in the early Late Pleistocene (MIS 5e).

However, *D. dama tiberina* was based on the fossils from Ponte Molle (holotype MPUR 605, a partial cranium with nearly complete antlers) recently revised by Mecozzi et al. (2021a). The authors highlighted the strong morphological affinity between the antler from Ponte Molle and those of *D. clactoniana* from Fontana Ranuccio, Riano and Swanscombe, suggesting that MPUR 605 can be attributed to the same species. We agree here that the differences proposed by Di Stefano and Petronio (1997) are not enough to separate *D. dama tiberina* from *D. clactoniana* but rather fall in the intraspecific morphological variability of the latter.

The number of different evolutionary models proposed in literature for Late Pliocene and Early Pleistocene *Dama*-like deer, indicate as this theme needs to be further investigated in the future, as for instance, the relationship or possible synonymy between the advanced forms, '*P.*' *farnetensis* and '*P.*' *vallonnetensis*. An element that has contributed to the emergence of different opinions on the *Dama*-like deer lineage is the lack of adequate dental and postcranial diagnostic features. Although several attempts have been made to describe cranial and postcranial morphologies in the *Dama*-like deer group (e.g. Pfeiffer 1999; Croitor 2006; Breda and Lister 2013; Breda et al. 2020), none of them is conclusive. Thus, the taxonomy of fossil medium-sized deer of Europe still rests mainly on antler morphology, and, in the absence of complete antlers, the taxonomic identifications are often attempted on chronological ground.

Here, we present and discuss a review of the fallow deer remains from selected Italian sites from the late Early Pleistocene to the late Middle Pleistocene (Fig. 1; Table 1), including several unpublished remains. Considering the overall scarcity of complete antlers, this work attempts an identification on dental and postcranial morphology.

From a metrical point of view, statistical analysis of the fossil fallow deer material from late Early to late Middle Pleistocene sites of the Italian Peninsula has been attempted, in order to suggest possible oscillations across time and/or difference among taxa.

Materials and Methods

The fallow deer sample here analysed is housed mostly at the University Museum of Earth Sciences of Sapienza University of Rome: Batteria Nomentana, Cava Alibrandi, Malagrotta, Ponte Molle, Porta Salaria, Prati Fiscali, Riano, Sedia del Diavolo, Tor di Quinto, Torre del Pagliaccetto and Vigna San Carlo. Other fossils are housed at the PaleoFactory laboratory, Department of Earth Science of Sapienza University of Rome: Cava di Breccia - Casal Selce, Cretone,

Fig. 1 Geographic position of the main late Early to late Middle Pleistocene sites of the Italian Peninsula yielding medium-sized deer. *Pink: 'Pseudodama'; Green: Dama roberti; Blue: Dama-like deer; Orange: Dama clactoniana* (map from https://earth.google.com/web/ - acquisition date - October 2022)
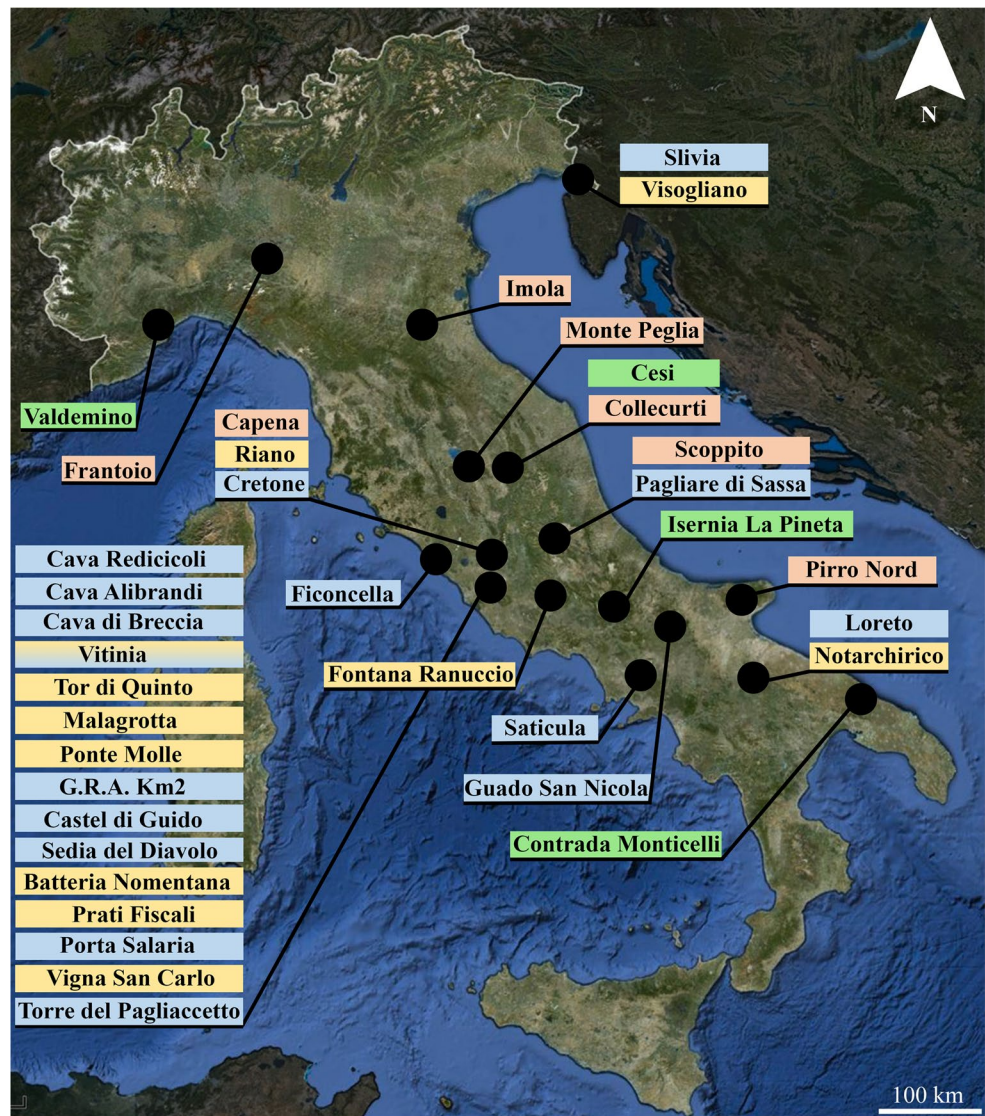
G.R.A. Km2, Saticula and Pirro Nord. Few specimens from Torre del Pagliaccetto are housed in Museum of Civilizations (former National Ethnographic Museum Luigi Pigorini).

Diagnostic characters used in this work were taken from Di Stefano (1996) and Lister (1996). We built our comparative dataset in Table 1, considering all the available literature on specimens from the late Early to late Middle Pleistocene from the Italian Peninsula.

For the metric comparison, we measured specimens of *D. dama dama* housed in the PaleoFactory laboratory, Department of Earth Sciences, Sapienza University of Rome, and used additional data taken from Di Stefano (1994). Craniodental and postcranial measurements were taken to the nearest 0.1 mm with a digital calliper, following the method proposed by von den Driesch (1976) (Table SD1).

We assessed the degree of intergroup affinity of the Italian fallow deer sample through statistical analysis on the length of the third lower molar (M_3L), which is the best identifiable tooth in deer. At first, we performed a Shapiro-Wilk test to check if the data were normally distributed. Considering the negative results (M_3L, p-value < 0.05), we used a nonparametric test (Kruskall Wallis test) to evaluate differences in size among late Early to Middle Pleistocene samples and extant *D. dama dama*. We tested the null hypothesis that the samples originate from the same distribution. The extant specimens of *D. dama dama* were chosen as corner point, and therefore compared with other fossil samples. The alternative hypothesis is that they differ in at least one distribution (p-value < 0.05). All statistical analyses were performed using the software R (R core Team 2019).

Table 1 Medium-sized deer from the late Early Pleistocene to the Middle Pleistocene sites of the Italian Peninsula, with chronological attribution, previous and present taxonomical attribution, references and present location of the material. *Pink: 'Pseudodama' sp.; Green: Dama roberti; Orange: Dama clactoniana; Blue: Dama-like deer*

Previous attribution	References for previous attribution	Site	Geochronology	Age (Ma)	MIS	References for chronological assigment
Axys eurygonos	Petronio et al. (2002) [*Dama nestii eurygonos* in Petronio (1979)]	Capena	Early Pleistocene	1.3		Petronio (1979)
Axys eurygonos	Petronio et al. (2013)	Pirro Nord	Early Pleistocene	1.3		Arzarello et al. (2009)
Pesudodama ex gr. *nestii*	Mazza and Ventra (2011)	Colle Curti	Early Pleistocene	1.1		Mazza and Ventra (2011)
Axis eurygonos	Petronio et al. (2020)	Monte Peglia	Early Pleistocene	~ 1.1		Sala and Masini (2007)
Axis eurygonos	Mancini et al. (2012)	Scoppito – undefined deposit	Early Pleistocene	~ 1.1		Mancini et al. (2012)
Axis eurygonos	Russo Ermolli et al. (2010)	Saticula	Early Pleistocene			Russo Ermolli et al. (2010)
Pseudodama farmetensis	Bona and Sala (2016)	"Frantoio" locality	Early Pleistocene	0.990		Bona and Sala (2016)
Dama sp.	Ambrosetti et al. (1979); Bon et al. (1992)	Slivia	Early Pleistocene	0.900		Ambrosetti et al. (1979)
Pseudodama sp.	Palombo et al. (2002) [*Cervus* sp. in Azzaroli and Berzi (1970)]	Imola	Early Pleistocene	~ 0.850		Muttoni et al. (2011)
Dama nesti eurygonos	Caloi et al. (1979)	Cava Redicicoli	Early Pleistocene	~ 0.800	20/19	Marra et al. (2014)
Axis eurygonos	Marra et al. (2014)	Cava di Breccia – Casal Selce 1	Middle Pleistocene	~ 0.700	18.2–17.3	Marra et al. (2014)
Axis eurygonos	Marra et al. (2014) [*Dama nesti eurygonos* in Capasso Barbato and Petronio (1983)]	Cava Alibrandi	Middle Pleistocene	~ 0.700	18.2–17.3	Marra et al. (2014)
Dama sp.	Ambrosetti (1967)	Fossiliferous deposits of Ponte Galeria area	Middle Pleistocene	~ 0.700	18.2–17.3	Marra et al. (2014)
Dama sp.	Palombo et al. (2001) (taxon not reported in Palombo et al. [2010])	Pagliare di Sassa	Middle Pleistocene	~ 0.700		Palombo et al. (2001)
Dama roberti	Breda and Lister (2013) [*Dama clactoniana* in Ficcarelli et al. (1997)]	Cesi	Middle Pleistocene	~ 0.700		Ficcarelli et al. (1997)
Axys sp.	Marra et al. (2014) [*Dama* sp. in Caloi et al. (1981)]	Vitinia – lower level	Middle Pleistocene	0.650 - 0.620	16-15	Marra et al. (2014)
Dama clactoniana	Cassoli et al. (1999)	Notarchirico	Middle Pleistocene	?0.658 -0.612	16-15?	Moncel et al. (2020)
Dama cf. *roberti*	Breda et al. (2015) [*Dama clactoniana* in Abbazzi and Masini (1997)]	Isernia La Pineta	Middle Pleistocene	0.600	15	Coltorri et al. (1982, 2005)
Dama roberti	Breda (2015) [*Dama clactoniana* in Abbazzi (1995)]	Valdemino	Middle Pleistocene	~ 0.600	15	Sala and Masini (2007)
Dama cf. *roberti*	Stefanelli et al. (2021)	Contrada Monticelli	Middle Pleistocene	~ 0.600	15	Mecozzi et al. (2017)
Dama sp.	Strani et al. (2021) [*Axis eurygonos* in Marra et al. (2014)]	Cava di Breccia – Casal Selce 2	Middle Pleistocene	~ 0.600	15	Marra et al. (2014)
Dama sp.	Aureli et al. (2016)	Ficoncella	Middle Pleistocene	~ 0.441	13	Aureli et al. (2016)
Dama sp.	Caloi and Palombo (1986)	G.R.A. Km2	Middle Pleistocene	0.517 - 0.499	13	Marra et al. (2014)
Dama clactoniana	Mecozzi et al. (2021) [*Dama dama tiberina* in Di Stefano and Petronio (1997)]	Ponte Molle	Middle Pleistocene	0.540 - 0.460	13	Mecozzi et al. (2021a)
Dama dama spp.	Di Stefano et al. (1998)	Tor di Quinto	Middle Pleistocene	0.560 - 0.500	13	Pandolfi and Marra (2015)
Dama clactoniana	Di Stefano (1994)	Visogliano	Middle Pleistocene	~ 0.500 - 0.400	13-11	Falguères et al. (2008)
Dama sp.	Capasso Barbato and Petronio (1981)	Castel di Guido	Middle Pleistocene	0.451 - 0378	11	Villa et al. (2021)
Dama clactoniana	Di Stefano (1994)	Fontana Ranuccio	Middle Pleistocene	0.407	11	Di Stefano (1994)
Dama sp.	Sala et al. (2014)	Guado San Nicola	Middle Pleistocene	400 ± 9 ka – 345 ± 9 ka	11	Nomade and Pereira (2014)
Dama sp.	Palombo et al. (2002)	Loreto	Middle Pleistocene	~ 0.600	11	Palombo et al. (2002)
Dama cf. *clactoniana*	Caloi and Palombo (1980)	Malagrotta	Middle Pleistocene	0.451 - 0378	11	Villa et al. (2021)
Dama clactoniana	Leonardi and Petronio (1976)	Riano	Middle Pleistocene	~ 0.406	11	Marra et al. (2018)
Dama cf. *D. clactoniana*	Di Canzio et al. (2003)	Cretone	Middle Pleistocene	~ 0.350	9	Di Canzio et al. (2003)
		Torre del Pagliaccetto – lower level	Middle Pleistocene		9	This work
Dama dama	Caloi and Palombo (1978)	Vitinia – middle level	Middle Pleistocene		9	Caloi & Palombo (1981)
Dama dama spp.	Di Stefano et al. (1998) [*Dama dama tiberina* in Di Stefano and Petronio (1997)]	Batteria Nomentana	Middle Pleistocene	0.370 - 0.290	9-8	Pandolfi and Marra (2015)
Dama dama spp.	Di Stefano et al. (1998) [*Dama dama tiberina* in Di Stefano and Petronio (1997)]	Porta Salaria	Middle Pleistocene	0.370 - 0.290	9-8	Pandolfi and Marra (2015)
Dama dama spp.	Di Stefano et al. (1998) [*Dama dama tiberina* in Di Stefano and Petronio (1997)]	Prati Fiscali	Middle Pleistocene	0.370 - 0.290	9-8	Pandolfi and Marra (2015)
Dama dama tiberina	Di Stefano and Petronio (1997) [*Dama* sp. in Caloi et al. (1980)]	Sedia del Diavolo – upper gravels	Middle Pleistocene	0.370 - 0.290	9-8	Pandolfi and Marra (2015)
Dama dama tiberina	Di Stefano and Petronio (1997); Di Stefano et al. (1998)	Vigna San Carlo	Middle Pleistocene	0.370 - 0.290	9-8	Pandolfi and Marra (2015)
Dama dama tiberina	Di Stefano and Petronio (1997) [*Dama dama* in Caloi and Palombo (1978)]	Torre del Pagliaccetto – upper level	Middle Pleistocene	0.270 -0.240	7	Villa et al. (2016)
Dama dama tiberina	Di Stefano and Petronio (1997) [*Dama* sp. in Caloi et al. (1981)]	Vitinia – upper level	Middle Pleistocene	0.250 - 0.190	7	Pandolfi and Marra (2015)

Localities yielding Fallow deer in the Italian Peninsula

Pirro Nord

Pirro Nord is located within the Apricena-Lesina-Poggio Imperiale quarrying district on the Apricena Horst, in a quarry called Dell'Erba (Foggia, Apulia). The site consists of a karstic network developed in the Mesozoic and Neogene Formation, which was filled by continental sediment (Abbazzi et al. 1996; Pavia et al. 2010). Two different karst cycles were recognised: the lower residual "Terre Rosse", where a late Miocene to Early Pliocene "*Mikrotia* fauna" was found, and the upper sandy-clayey complex, where a rich Early Pleistocene mammal faunal assemblage was recovered. More than 100 different taxa were identified, including amphibians, birds and mammals (Abbazzi et al. 1996; Arzarello et al. 2012). The faunal assemblage from Pirro Nord defines the latest Villafranchian Faunal Unit (Pirro Nord FU), which is characterised by the first occurrence of *Bison degiulii*, *Capreolus* sp., *Equus altidens* and *Meles meles*. Associated to faunal remains, also lithic artefacts were found. The Pirro Nord deposit was dated between 1.6 and 1.3 Ma by Arzarello et al. (2009), but considered slightly more recent by other authors (e.g. Masini and Sala 2007 - 1.5-1.2 Ma; Bertini et al. 2010 - 1.5-1.3 Ma). Anyway, the Pirro Nord locality currently represents one of the earliest human occupations of western Europe (Arzarello et al. 2012). The excavation activity at Pirro Nord was carried out by several Institutions and the remains are stored in different Museums: PaleoFactory laboratory, Sapienza University of Rome; Paleontology Museum, University of Turin; Department of Human Studies, University of Ferrara; Museum of Natural History (section of Geology and Paleontology), University of Florence. Petronio et al. (2013) attributed to *Axis eurygonos* (= '*P.' farnetensis*) the remains from Pirro Nord excavated in the 1970s, 1990s, and 2000s and stored in Florence and Rome. Here, we consider only the material stored in Rome collected during the 1990s and 2000s.

Saticula

The deposit, discovered during the construction of the Italian-Agerian gas pipeline realised by ENI society, is located at Saticula near Sant'Agata de' Goti village (Benevento, Campania). Mammal fossil remains were quite scarce, but several species were identified: Hyaenidae indet. (coprolites), Elephantidae indet., *Stephanorhinus* cf. *hundsheimensis*, *Equus sussenbornensis*, *Hippopotamus antiquus*, Megacerine indet. and *Axis eurygonos* (= '*P.' farnetensis*) (Russo Ermolli et al. 2010). The deposit was chronologically referred to the Colle Curti Faunal Unit (about 1.1 Ma – late Early Pleistocene; Russo Ermolli et al. 2010).

Cava di Breccia di Casal Selce

The 40 m thick sedimentary succession in a working quarry at Cava di Breccia (Rome, Latium) yielded fossil remains from two different levels (Milli et al. 2004; Sardella and Petrucci 2012):

– The lower level consists of pebble gravels and sands with cross laminations (level d in Milli et al. 2004). The faunal assemblage, known as Cava di Breccia – Casal Selce 1, includes *Mammuthus trogontherii, Hemibos galerianus, Praemegaceros verticornis, Megaloceros savini, Axis eurygonos* (='*P.' farnetensis*) and *Crocuta crocuta* (Petronio and Sardella 1998, 1999; Martínez-Navarro and Palombo 2004; Sardella and Petrucci 2012). The faunal assemblage from level d correlates to the Ponte Galeria Faunal Unit. The stratigraphic and palaeomagnetic data provide an age between 763 ±8 ka and c.a 700 ka (MIS 18-17).

– The upper fossiliferous level, known as Cava di Breccia – Casal Selce 2, consists of salmon sands (level f in Milli et al. 2004). Many mammal taxa have been recognised: *Macaca sylvanus, Vulpes* sp., *Canis* sp., *Lynx pardinus, Meles meles, Stephanorhinus* sp.*, Equus* cf. *altidens, Equus mosbachensis, Sus scrofa, Hippopotamus antiquus, Capreolus* sp., *Dama* sp.*, Cervus elaphus, Praemegaceros* sp. and Bovidae indet. (Strani et al. 2021). Level f is dated about 0.615–0.611 Ma (MIS 15) (Marra et al. 2014). The studied material comes from both fossiliferous levels (d and f).

Cava Alibrandi

Fossil remains from Cava Alibrandi were recovered during the 70-80s in a quarry at Kilometer 13.5 of the via Aurelia (Rome, Latium) (Capasso Barbato and Petronio 1983). The finds were collected from the gravels and sands, which were chronologically referred to 763 ± 8 ka and c.a 700 ka, based on stratigraphic and palaeomagnetic data (Marra et al. 2014). Capasso Barbato and Petronio (1983) identified the following mammal taxa: *Elephas* sp. (=*Palaeoloxodon* sp.), *Equus* (*Equus*) cf. *altidens, Hippopotamus* sp.*, Cervus* (*Dama*) *nestii eurygonos* (= '*P.' farnetensis*), *Megaceros savini* and *Bos primigenius.* The faunal list from Cava Alibrandi was partially revised by Marra et al. (2014), which referred the cervid remains to *Axis eurygonos* (= '*P.' farnetensis*) and the fossils horse to *Equus altidens*.

G.R.A. Km2

The site, located in the urban area of Rome (Latium), was discovered during building work on the Rome beltway

called "Grande Raccordo Anulare" (G.R.A.) approximately at kilometer 2 (Caloi and Palombo 1986) (Fig. 1). Fossil remains were found in a lacustrine level belonging to the Ponte Galeria Formation (Caloi and Palombo 1986). Marra et al. (2014) carried out the revision of the Ponte Galeria Formation deposits cropping out in the Campagna Romana, suggesting the faunal assemblage from G.R.A. Km2 could be referred to MIS 13 (Middle Pleistocene). Other mammals were also found at G.R.A. Km2, *Hyaena prisca*, *Meles meles* and *Bos primigenius* (Caloi and Palombo 1986; Iannucci et al. 2021; Mecozzi 2021).

Ponte Molle

The site, located in the urban area of Rome (Latium), was described by Portis (1893), and, due to the intense urbanization process, the outcropping was destroyed during the early 1900s. The sedimentary succession testifies that the delta Palaeo-Tiber River evolution began during the early Middle Pleistocene (800 ka), mainly including sedimentation linked to sea-level rise during the Pleistocene glacial terminations (Pandolfi and Marra 2015). The lowermost level of the stratigraphic succession, called "cosidette ghiaie diluviali di Ponte Molle", consists of tufaceous gravel and sand and yielded fossil remains generically reported as Elephant, Rhinoceros, Bovidae, Hippo, Cervidae and Carnivorans by Portis (1893). New geological and stratigraphical data suggest an age between 0.540 and 0.460 Ma for the "cosidette ghiaie diluviali di Ponte Molle" level (Mecozzi et al. 2021a). A review of the fauna records *Palaeoloxodon antiquus, Hippopotamus* ex gr. *antiquus, Stephanorhinus kirchbergensis, Stephanorhinus hemitoechus, Stephanorhinus* sp.*, Bos primigenius, Sus scrofa, Cervus elaphus acoronatus, Cervus elaphus eostephanoceros, Dama clactoniana, Capreolus capreolus, Equus mosbachensis, Equus hydruntinus, Lepus* sp.*, Castor fiber, Canis* cf. *mosbachensis, Crocuta crocuta, Lynx* sp. and *Meles meles* (Mecozzi et al. 2021a). The relative abundance of species usually widespread during warm periods suggest that the mammal record from Ponte Molle was accumulated during an interglacial stage (MIS 13).

Tor di Quinto

The historical site of Tor di Quinto (=Torretta di Quinto; Rome, Latium) was firstly described by Portis (1893). Unfortunately, the deposit was destroyed by human activity during the early 1900s. Based on the age of volcanic sediments, the deposit was recently reassigned to the Valle Giulia Formation (Marra and Rosa 1995), dated at about 0.560-0.500 Ma (Pandolfi and Marra 2015). The faunal assemblage of Tor di Quinto was preliminarily listed by Di Stefano et al.

(1998): *Ursus spelaeus, Stephanorhinus* sp., *Stephanorhinus hemitoechus, Equus* sp., *Sus scrofa, Hippopotamus* sp., *Hippopotamus antiquus, Megaceroides* sp., *Dama dama* ssp., *Cervus elaphus* and *Elephas* (=*Palaeoloxodon*) sp. In the last decade, the rhinoceros specimens were assigned to *Stephanorhinus kirchbergensis* and *Stephanorhinus* sp. by Pandolfi and Marra (2015).

Malagrotta

The fossiliferous sedimentary succession, located near the Malagrotta locality (Rome, Latium), was discovered during the 1960s (Caloi and Palombo 1980). Preliminary fieldwork activities were conducted by A. Radmilli, but a systematic excavation was never performed. The fossils were collected from a gravel and sand level attributed to the Ponte Galeria Formation (Caloi and Palombo 1980). In the revision carried out by Marra et al. (2018), the deposit of Malagrotta was chronologically referred to about 0.516 Ma (MIS 13), but Villa et al. (2021) attributed the site to MIS 11 (0.451 – 0.378 Ma). Caloi and Palombo (1980) recorded the following mammal taxa: *Elephas* (=*Palaeoloxodon*) *antiquus, Equus caballus* (=*Equus ferus*)*, Dicerorhinus* (=*Stephanorhinus*) cf. *hemitoechus, Hippopotamus* sp.*, Cervus elaphus, Dama* cf. *clactoniana, Capreolus capreolus, Bos primigenius, Sus scrofa* and *Canis lupus*. In the revision carried out by Marra et al. (2018), the canid sample was referred to *Canis* sp., whereas two additional taxa were identified: *Castor* sp. and *Oryctolagus* sp.

Riano

The diatomiferous lacustrine deposits were exposed by quarry excavations near the town of Riano (Rome, Latium) during the 60s (Accordi and Maccagno 1962). Among the fossils discovered in the site, three complete skeletons of red deer and one of Clacton fallow deer were found in anatomical connection (Accordi and Maccagno 1962; Leonardi and Petronio 1971, 1976). Historically, the faunal assemblage from Riano was attributed to MIS 9 (Leonardi and Petronio 1976), but the recent revision carried out by Marra et al. (2018) suggested instead an older age (406 ± 5 ka; MIS 11).

Cretone

The fossil material was recovered from a fluvio-lacustrine deposit, located along the Tiber river near the Cretone village (Rome, Latium). The following mammal taxa were identified: *Lepus* cf. *corsicanus, Mustela putorius, Felis silvestris, Canis* sp., *Ursus* cf. *spelaeus, Elephas antiquus* (=*Palaeoloxodon antiquus*)*, Stephanorhinus hemitoechus, Dama* cf. *clactoniana, Cervus elaphus* ssp. and *Bison priscus* (Di Canzio et al. 2003). The faunal assemblage has

been biochronologically referred to the Torre in Pietra FU (MIS 9) (Di Canzio et al. 2003). Recently, other fossiliferous deposits have been described by Marra et al. (2016), who carried out new radiometric dating and recorded new fossil material. In particular, the authors recognised *Axis eurygonios (= 'P.' farnetensis)* from Osteria Moricone and *Dama* sp. from Camporioccio, Fosso Casa Cotta, Fosso delle Bufala, Osteria Moricone and Sferracavallo (Marra et al. 2016).

Torre del Pagliaccetto

Systematic excavations at Torre del Pagliaccetto (= Torre in Pietra; Rome, Latium) have been conducted during the 50-60s (Caloi and Palombo 1978). Two fossiliferous levels were identified, dated by Villa et al. (2016), who referred the lowermost part of the succession to MIS 9 (approximately 350 ka) and the upper level to MIS 7 (270-240 ka). Fossils of *Dama dama* were described from the upper levels by Caloi and Palombo (1978), whereas the presence of fallow deer in the lower level is here reported for the first time. Mammal fossils from the lower level were attributed to *Ursus* cf. *spelaeus, Canis lupus, Vulpes vulpes, Panthera leo spelaea, Lepus* cf. *capensis, Oryctolagus cuniculus, Elephas antiquus* (=*Palaeoloxodon antiquus), Equus caballus* (=*Equus ferus), Dicerorhinus hemitoechus* (=*Stephanorhinus hemitoechus), Sus scrofa, Cervus elaphus, Megaloceros* cf. *giganteus, Bos primigenius* (Caloi and Palombo 1978). Mammal faunal assemblage from the upper level included: *Erinaceus europaeus, Macaca sylvana* (=*Macaca sylvanus), Castor fiber, Martes* cf. *foina, Meles meles, Ursus* sp., *Crocuta crocuta, Canis lupus, Vulpes vulpes, Oryctolagus cuniculus, Elephas antiquus* (= *Palaeoloxodon antiquus), Equus caballus* (=*Equus ferus), Dicerorhinus hemitoechus* (=*Stephanorhinus hemitoechus), Sus scrofa, Hippopotamus amphibius, Cervus elaphus, Capreolus capreolus* and *Bos primigenius* (Caloi and Palombo 1978; Mecozzi 2021).

Batteria Nomentana

The Batteria Nomentana deposit outcropped near the crossroad between the homonymous road (Batteria Nomentana) and Nomentana road (Rome, Latium). As reported by Meli (1886), the stratigraphic succession was the same recognised at Sedia del Diavolo (above described – about 500 m from Batteria Nomentana). The deposit was destroyed or buried below anthropogenic deposits during the early decades of 1900. Mammal remains were recovered above the Tufo Lionato deposit. A preliminary mammal list was reported by Meli (1886): *Rhinoceros megarhinus* (=*Dihoplus megarhinus), Rhinoceros etruscus* (=*Stephanorhinus etruscus), Equus caballus* (=*Equus*

ferus), Hippopotamus (Tetraprotodon) *major* (=*Hippopotamus antiquus), Cervus elaphus, Bos primigenius* and *Elephas* (*Euelephas) antiquus* (=*Palaeoloxodon antiquus*). The rhino fossils were revised by Pandolfi and Marra (2015) and attributed to *Stephanorhinus* sp., whereas fallow deer remains were referred to *Dama dama tiberina* by Di Stefano and Petronio (1997). Following the geochronologic constraint provided by Pandolfi and Marra (2015), the age of Batteria Nomentana faunal assemblage spans approximately from 367 to 287 ka.

Porta Salaria

The Porta Salaria site, today destroyed or buried below anthropogenic deposits, was located nearby the homonymous gate, part of ancient Roman walls (Rome, Latium). In this area, especially along the via Salaria, many quarries were opened for the extraction of the gravel during 1894-1896, levels that were stratigraphically above the Tufo Lionato pyroclastic-flow deposit (Portis 1907). These quarries were called "Vigne Torte", as well as the levels where fossil mammals bearing (Vigne Torte tuffaceous levels) (Portis 1907). Di Stefano et al. (1998) reported the following taxa from Porta Salaria: *Equus* sp., *Cervus elaphus, Bos primigenius* and *Elephas antiquus* (=*Palaeoloxodon antiquus*). The presence of other taxa from Vigne Torte was also reported: *Felis* sp., *Stephanorhinus* sp., *Equus* sp., *Hippopotamus* sp., *Cervus elaphus, Bos primigenius* and *Elephas antiquus* (=*Palaeoloxodon antiquus*). The presence of fallow deer at Porta Salaria is here reported for the first time. The deposition of the fossils from Porta Salaria spans approximately from 367 to 287 ka (Pandolfi and Marra 2015).

Prati Fiscali

The deposit of Prati Fiscali (=Monte Sacro; Rome, Latium) was located at about 1 km from the Ponte Nomentano bridge, along the Nomentana road, on the right bank of Aniene river. As in Batteria Nomentana, the sedimentary succession looked like that exposed at Sedia del Diavolo, but also in this case the site was destroyed or buried below anthropogenic deposits during the early decades of 1900. The fossil sample was collected above the Tufo Lionato deposit. From Prati Fiscali, several bovid crania were ascribed to *Bos primigenius* and *Bison* by Portis (1907), a cranium was attributed to *Panthera pardus* by Portis (1909), and revised by Kotsakis and Palombo (1979), whereas few rhino specimens were referred to *Stephanorhinus* sp. by Pandolfi and Marra (2015). A preliminary mammal list was provided by Di Stefano et al. (1998): *Ursus* sp., *Crocuta crocuta, Stephanorhinus* sp., *Stephanorhinus hemitoechus, Equus* sp., *Equus hydruntinus, Hippopotamus* sp., *Cervus elaphus, Dama dama* ssp. (*Dama dama tiberina* in Di Stefano and Petronio 1997), *Bos primigenius* and *Elephas antiquus*

(=*Palaeoloxodon antiquus*). According to Pandolfi and Marra (2015), the mammal remains of Prati Fiscali were deposed approximately between 367 to 287 ka.

Sedia del Diavolo

This historical locality is known from the end of 1800, with the first contribution reported by Terrigi (1881). A number of works were published by important Italian scientists (Blanc, Clerici, Meli, Ponzi, Portis, Taschini) focused on geological and palaeontological aspects (Palombo et al. 2004 and references therein). The stratigraphical succession of Sedia del Diavolo was exposed in a quarry located near the Aniene river (Rome, Latium). Fossils were found in two levels: the Tufo Lionato pyroclastic-flow in the lower part, and the fluvial gravel in the medial part of the succession. This lithified pyroclastic-flow level, erupted by the Colli Albani volcanic district, is an important marker for the chronostratigraphy of the urban area of Rome, dated approximately at 367 ± 4 ka (Marra et al. 2009). As other historical localities of the urban area of Rome, the outcropping was destroyed or buried by the intense urbanization process during the early 1900s. However, the fluvial gravel level was capped by a pumiceous ash flow deposit, which was dated by Palombo et al. (2004) at approximately 284 ka.

The fallow deer remains (*Dama dama*, *Dama* sp., *Dama* cf. *clactoniana*) were collected by the fluvial gravel level, referred to the Aurelian Formation (or PG6; Milli et al. 2004; Palombo et al. 2004). Other mammals by the fluvial gravel level were described by Caloi et al. (1980): *Canis* sp., *Dicerorhinus* sp. (=*Stephanorhinus* sp.), *Equus* sp., *Equus caballus* (=*Equus ferus*), *Equus hydruntinus*, *Elephas antiquus* (=*Palaeoloxodon antiquus*), *Sus scrofa*, *Hippopotamus amphibius*, *Cervus elaphus* and *Bos primigenius*.

Vigna San Carlo

The deposit of Vigna San Carlo was located along via Portuense, in the south sector of Rome, near the Tiber river (Rome, Latium). Unfortunately, this sedimentary deposit was destroyed or buried below anthropogenic deposits during the early decades of 1900. Mammal finds were found in the fluvial-lacustrine level, deposit that overlapped the Tufo Lionato pyroclastic-flow level (Marra et al. 2018). Di Stefano et al. (1998) reported the following taxa: *Ursus* sp., *Stephanorhinus* sp. (*Stephanorhinus hemitoechus* in Pandolfi and Marra, 2015), *Dama dama tiberina*, *Cervus elaphus*, *Bos primigenius* and *Elephas antiquus* (=*Palaeoloxodon antiquus*). According to Pandolfi and Marra (2015), the

mammal remains from Prati Fiscali were deposed approximately between 367 to 287 ka.

Vitinia

The fossiliferous deposit of Vitinia (also named Quartaccio) is located along the Cristoforo Colombo road (Rome, Latium). The stratigraphic succession and the fossil sample were described by Caloi et al. (1981), which recognised three main fossiliferous complexes all consisting in pebbles and sands: the lower level referred to the Ponte Galeria Formation (early Middle Pleistocene, MIS 16-15, 0.650-0.620 Ma); the middle level attributed to the Aurelia Formation (late Middle Pleistocene, MIS 9); the upper level referred to the Vitinia Formation (late Middle Pleistocene, MIS 7, ca. 0.248 Ma) (MIS and Ma from Caloi et al. 1998 and Pandolfi and Marra 2015). According to Caloi et al. (1981), the majority of the fossil remains were collected from the upper level, whereas a few specimens were recovered from the lower and middle levels. Three fossils from the lower level were attributed to *Dama* sp., whereas the other remains collected from middle and upper ones were ascribed to *Dama dama* (Caloi et al. 1981).

Caloi et al. (1981) give the following mammal assemblages: i) *Dicerorhinus* (=*Stephanorhinus*) cf. *hemitoechus*, *Equus* sp., *Cervus elaphus*, *Megaceros* (=*Praemegaceros*) *verticornis* and *Bos primigenius* (lower level); ii) *Equus caballus*, *Cervus elaphus* and *Bos primigenius* (middle level); iii) *Elephas* (=*Palaeoloxodon*) *antiquus*, *Dicerorhinus* (=*Stephanorhinus*) *hemitoechus*, *Equus caballus* (=*Equus ferus*), *Cervus elaphus*, *Bos primigenius* and *Canis lupus* (upper level).

Results

Late Early Pleistocene to late Middle Pleistocene medium-sized deer

'Pseudodama'

The sample from Pirro Nord here analysed, consists of several dental and postcranial specimens and a fragmented basal portion of antler (Figs. 2a-3a). The basal antler shows a strong basal tine resting directly on the burr and at a very open angle to the beam, both features shared between advanced '*Pseudodama*' and *Dama roberti*. The morphology of preserved teeth and postcranials falls in the variability of both the '*Pseudodama*' group and *Dama roberti*. As typical of '*Pseudodama*' (Breda 2015), the Pirro Nord sample confirms the presence of a mix of features detected in modern *Cervus elaphus* and *D. dama dama*, e.g.

the variability of the development of the radial and coronoid fossa (of equal size and barely divided in 5 specimens, but clearly divided in 3 specimens) and of the distolateral edge of the capitulum of the humerus (with a clear bulge in 3 specimens and a weak bulge in 5 specimens). The lack of complete antlers and the undescribed morphological variability of the postcranial elements in '*Pseudodama*', suggest a cautious attribution of this collection from Pirro Nord to '*Pseudodama*'. However, the presence of complete, unpalmated antlers in another batch of fallow specimens from coeval deposits at Pirro Nord (Breda, unpublished observations), strongly suggests that also the remains here analysed belong to '*Pseudodama*'.

Dama clactoniana

Fossils recovered from several Middle Pleistocene localities can be attributed to this taxon (Figs 2e-h-3c-d,f-j). Relevant samples are those from Riano and Ponte Molle, where complete antlers were found; their morphology is clearly indicative of *Dama clactoniana* (Leonardi and Petronio 1976; Mecozzi et al. 2021a). The analysis of anatomical features of the dental and mandibular remains improves the knowledge of the variability of *D. clactoniana*.

The best preserved specimen is the nearly complete skeleton from Riano, an adult male attributed to *D. clactoniana* by Leonardi and Petronio (1971, 1976) and known as Riano 6. It was retrieved together with six nearly complete skeletons of *Cervus elaphus* between 1960-1964, but no exact stratigraphic position or taphonomic information were provided. The skull and antlers of Riano 6 are badly deformed due to taphonomic processes (Fig. 4). The cranium is dorso-ventrally compressed, which makes its morphology quite difficult to be observed. The restoration work carried out in the 1960s masks several portion of the antler and some tines were incorrectly reconstructed: e.g. basal tine plus 1st and 2nd palmation tines of the right antler, all lacking in Figure 8 of Leonardi and Petronio (1976), have been reconstructed the former too straight, the latter two, with an unnatural medial bend. However, the morphology of the preserved portion is typical of the Clacton fallow deer, which leaves no doubt on its taxonomic attribution. Dental and postcranial morphological features of Riano 6 differ from both '*Pseudodama*' and *D. roberti* in the following traits: the bifurcate entostyle in the upper molars is absent and the lingual cingulum is weakly developed; the anterior hypoconid wing of P_4 is present and connected to the entoconid, the molarization is absent; the ectostylids and mesial cingulum in the lower molars are weakly developed; the step between the lingual walls of 2nd and 3rd lobes in M_3 is present and the additional stylid between hypoconid and talonid is absent. These dental features are therefore indicative of *D. clactoniana*.

The fauna from Ponte Molle includes the fallow deer skull originally described by Di Stefano and Petronio (1997) as *Dama dama tiberina,* and recently synonymised with *D. clactoniana* by Mecozzi et al. (2021a). The sample shows several dental features typically observed in the specimen of *D. clactoniana* from Riano, confirming Mecozzi et al.'s specific attribution (Fig. 3c).

Other records of *D. clactoniana* are those from Batteria Nomentana, Malagrotta, Prati Fiscali, Tor di Quinto, Vigna San Carlo and Vitinia.

Fragmentary antlers were found at Malagrotta (Fig. 2e), including the basal tine and part of the beam with the insertion of the second anterior tine, feature that allows to exclude its attribution to *D. roberti*. Therefore, the identification as *D. clactoniana* previously proposed by Caloi and Palombo (1979) can be confirmed.

The sample from Vigna San Carlo includes a partial antler and a fragment of humerus (Fig. 2g). The antler, MPUR 868, misses the basal portion (burr, basal tine and basal beam) and was indicated by Di Stefano and Petronio (1997) as paratype of *Dama dama tiberina.* Although this antler is quite peculiar for the strong development of two posterior palmation tines, no reliable differences with *D. clactoniana* can be recognised. The distal humerus possesses a radial fossa wider than the coronoid one, differently to the condition generally observed in *D. roberti*. Therefore, the sample from Vigna San Carlo can be tentatively referred to *D. clactoniana*.

The fossil material from Batteria Nomentana (Fig. 3d), Prati Fiscali (Fig. 3j) and Tor di Quinto (Fig. 3h) possess a dental morphology indicative of *D. clactoniana,* with features observed in Riano and Ponte Molle samples: absence of molarization of P_4; presence of the step between the lingual walls of 2nd and 3rd lobe; presence of the ecostylid between 1st and 2nd lobe; absence of the additional stylid between hypoconid and talonid in M_3.

The material from the upper level of Vitinia (Fig. 3f-g) was referred to *Dama dama* by Caloi et al. (1981). Nevertheless, the sample shows typical features clearly indicative of *D. clactoniana* (e.g. absence of molarization of P_4; presence of the step between the lingual walls of 2nd and 3rd lobe). This new identification is in accordance with the age of the deposits, attributed to MIS 7.

Dama-like deer

The sample from Saticula, attributed to *Axis eurygonos* by Russo Ermolli et al. (2010), includes a fragmented basal portion of antler (Fig. 2b) and a fragmented metatarsal. The morphology of the remains (e.g. large and oval foramen at the level of the distal epiphysis of the metatarsal in dorsal view) resembles '*Pseudodama*', but a reliable attribution cannot be attempted. The sample is therefore identified as *Dama*-like deer.

Fig. 2 Antlers of medium-sized deer from the Italian Peninsula: '*Pseudodama*' sp. from Pirro Nord (GP1; **a**); *Dama*-like deer from Saticula (SAGND08; **b**), Cava Alibrandi (NS84 13; **c**), Cava di Breccia - Casal Selce 1 (CS411; **d**); *Dama clactoniana* from Malagrotta (638b; **e**), Ponte Molle (MPUR 605, **f**), Vigna San Carlo (868, **g**), Tor di Quinto (629, **h**), Batteria Nomentana (674b, **i**); *Dama* sp. from Torre del Pagliaccetto (540, **j**), Sedia del Diavolo (SN901/LJ, **k**). Scale bar 3 cm

A partial cranium with fragmented antlers, lacking the distal portions (Figs. 2d, 3b1-3 and 5d), was recovered from the Cava di Breccia - Casal Selce 1 (Marra et al. 2014; Sardella et al. 2015). This specimen was assigned to *Axis* (=‘*Pseudodama*’) *eurygonos* by Marra et al. (2014) and Sardella et al. (2015).

It matches both late ‘*Pseudodama*’ species and *D. roberti* in the obtuse angle between beam and first (basal) tine, the position of the basal tine with respect to the burr and the length of the basal tine (Fig. 5). The overall morphology differs from that of *D. clactoniana* in several features, among

which a sigmoidal profile of the beam, the lack of a second anterior tine, and the development of the basal tine which is forward directed at its basis and then bends upward forming an almost right angle. Considering its strong similarity with both late ‘*Pseudodama*’ and *D. roberti*, the fossil from the Cava di Breccia - Casal Selce 1 is generically attributed to a *Dama*-like deer.

The sample from Cava Alibrandi consists in a fragment of pedicle of an adult individual with very basal part of the antler (the burr and just stumps of beam and basal tine - Fig. 2c) and a fragmented antler of a juvenile. The incompleteness of

Fig. 3 Hemimandibles and dental remains of medium-sized deer from the Italian Peninsula: '*Pseudodama*' sp. from Pirro Nord (GP3; **a1-3**); *Dama*-like deer from Cava di Breccia di Casal Selce 1 (CS2004, **b1-3**); *Dama clactoniana* from Ponte Molle (615A, **c1-3**), Batteria Nomentana (689, **d1-3**), Vitinia – Upper level (MPUR9/10, **f1-3**), Vitinia – Upper level (MPUR 9/41, **g1-3**), Tor di Quinto (664, **h1-3**), Riano (Riano 6, **i1-3**), Prati Fiscali (672, **j1-3**); *Dama* sp. from Porta Salaria (677, **e1-3**). Specimens figured in labial (**1**), lingual (**2**) and occlusal (**3**) views. Scale bar 3 cm

the adult specimen prevents even a generic attribution, and therefore the remains from Cava Alibrandi are considered here as *Dama*-like deer.

A rich fallow deer sample was collected from Cava di Breccia - Casal Selce 2. The dental remains possess some features suggestive of '*Pseudodama*' and *D. roberti,* such

Fig. 4 Complete skeleton (Riano 6) from the Middle Pleistocene of Riano on display at Museo Universitario di Scienze della Terra, Sapienza University of Rome (MUST; University Museum of Earth Science, Sapienza University of Rome), in frontal (**a**) and right lateral (**b**) views

as the presence of a strong mesial cingulum and a strongly developed bifurcate entostyle in the upper molars, and the lack of a step between the lingual walls of 2nd and 3rd lobe, a strong ecostylid between 1st and 2nd lobe and the presence of an additional stylid between hypoconid and talonid in M$_3$ (Fig. 3b). Postcranial elements recovered in the same level possesses a mosaic of features where *Dama*-like characters dominate: the shape of the glenoid cavity of the scapula in proximal view (circular in 2 specimens and mildly flattened in 3 specimens; character 1 in Lister 1996), a convex dorsal edge of the articular surface to the medial carpal element and a ridge on the dorsal epiphysis of the distal radius (characters 1 and 5 in Lister 1996), and a smooth tuberosity on the dorsal epiphysis of the proximal metacarpal (character 5 in Lister 1996). *Cervus*-like characters are less abundant but can be observed in the scapula (a squared acromial process in lateral view; character 2 in Lister 1996), radius (smoother medial edge of the articular surface to the medial carpal element; character 2 in Lister, 1996), metacarpal (a split between distal epiphyses of 3rd and 4th metacarpal; character 6 in Lister 1996), and tibia (L-shaped profile of the edge joining the

medial malleolus to the body of the distal epiphysis; character 5 in Lister 1996). As for to the partial cranium with fragmented antlers recovered from the Cava di Breccia - Casal Selce 1, the lack of clear diagnostic characters of the sample from the upper level of the same locality prevents a generic taxonomic attribution, and therefore the material is here considered *Dama*-like deer.

The mandibular fragment of a juvenile specimen from G.R.A. Km2, in the lack of diagnostic characters for young individuals, is identified as *Dama* sp., as previously suggested by Caloi and Palombo (1986).

Fossils from Cretone were ascribed to *Dama* cf. *clactoniana* by Di Canzio et al. (2003). The sample includes a fragmentary antler, a fragment of the left tibia and a nearly complete calcaneus. Unfortunately, none of these specimens has features useful for a taxonomic identification, and they are thus attributed to *Dama*-like deer.

The sample from the lower level of Torre del Pagliaccetto includes only four specimens, among which an isolated lower molar. This tooth possesses clear features of *Dama* as a little developed mesial cingulum, a little developed ectostylid, and an antero-posteriorly separated protoconid and hypoconid.
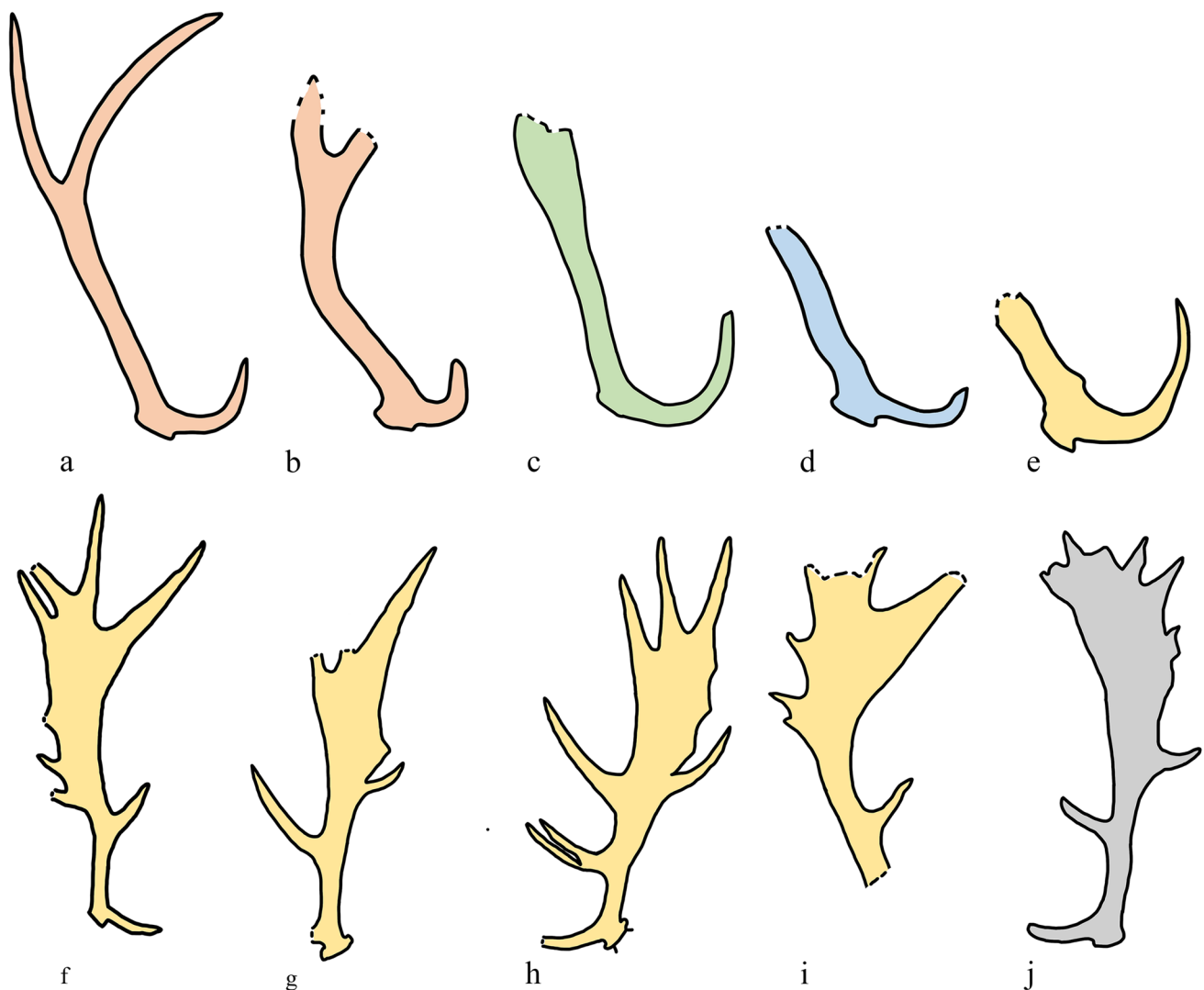
Fig. 5 Antlers of fallow deer: representative of '*Pseudodama*' (Breda 2015, **a**); IQW 2003/28 185 (Mei. 27 347) from Untermassfeld (de Lumley et al. 1988, **b**); NCM 2004.831.12-14 from Pakefield (Breda and Lister 2013, **c**); CS411 from Cava di Breccia - Casal Selce 1 (**d**); F13.FEJ12.341 from Caune de l'Arago (Magniez et al. 2013, **e**); MPUR 605 from Ponte Molle (**f**); Riano 6 from Riano (**g**); 16349 from Swanscombe (Leonardi and Petronio 1976, **h**); FR56539 from Fontana Ranuccio (Cassoli and Segre Naldini 1993, **i**); no catalogue number of extant Italian specimen of *D. dama dama* (Di Stefano and Petronio 1993, **j**). *Pink: 'Pseudodama'; Green*: *Dama roberti*; *Blue: Dama*-like deer; *Orange*: *Dama clactoniana*; *Grey*: extant *Dama dama dama*. The images are not in scale

But diagnostic characters for a specific attribution lack, and therefore the sample is referred to *Dama* sp.

Caloi et al. (1981) attributed two upper third molars to *Dama dama* collected in the middle level of Vitinia. These two teeth show the typical characters of *Dama* (e.g. buccal cones and styles less developed, moderate ectostylids), but not enough for a specific attribution, and therefore we referred them to *Dama* sp.

An isolated hemimandible from Porta Salaria (Fig. 3e) can only be attributed to *Dama*-like deer because of the advanced wear of the teeth.

The sample from Sedia del Diavolo was attributed to *Dama dama*, *Dama* sp. and *Dama* cf. *clactoniana* (Caloi et al. 1980). The fallow deer sample includes mainly post-cranial bones, and a single upper molar. The humerus shows a radial fossa wider than the coronoid fossa, with the two fossae clearly divided. This feature suggests an attribution to the genus *Dama,* but the lack of other diagnostic features prevents a specific identification.

Finally, the specimens from the upper level of Torre del Pagliaccetto are also referred to *Dama* sp. The lower molar has a scarcely developed mesial cingulum, a little ectostylid and antero-posteriorly separated protoconid and hypoconid; the humerus shows a radial fossa wider than the coronoid fossa, with the two fossae clearly divided. These features, however, prevents a reliable specific attribution.

Body size and height at withers

Calculating the body size of fossil mammals could represent an important proxy to evaluate possible ecological niche differentiation during the late Early to Late Pleistocene terrestrial ecosystem. Several works provide a series of predictive equations for different groups of mammals, the most quoted for herbivorous species being those of Damuth (1990). However, since Damuth's (1990) formulas are based on dental measurements, we believe that they ignore the sexual dimorphism, that instead is quite marked in several extant mammals, among which cervids. As a matter of fact, in extant populations of *Dama dama dama*, males are generally larger (58-85 kg) than females (35-53 kg; Carpaneto 2003) although the weight fluctuates considerably during the year; in males for example, the weight reduces progressively of as much as 20 kg during the breeding season (January to March; Carpaneto 2003). On the contrary, sexual size dimorphism in fallow deer mandible and teeth is insignificant (Chapman and Chapman 1969; Nugent and Frampton 1994) probably because teeth size is linked to energy requirements and, although a female is quite smaller than a male and should thus have smaller teeth, she must account for the much increased energetical needs during pregnancy and milk feeding.

In order to test this hypothesis, we apply Damuth's (1990) equation to extant specimens of *D. dama dama* using the length of the lower second molar (M_2L) which, as discussed by Iannucci et al. (2020), represents the most reliable tooth for body mass estimation in large mammalian herbivores. Following Damuth (1990), values of slope and intercept of the regression equations for the M_2L in "All ungulates" version are 3.07 and 1.07 respectively. Results of this estimation based on 10 specimens provide a mean value of 53.7 Kg, with a range of 50.2 Kg – 57.8 Kg (see Table SD2) and so exactly in between the weight range of males and females. These values demonstrate as the application of these equations cannot be reliable, since they underestimate the large sexual dimorphism of the extant specimens (see above). For these reasons, we choose to not apply the body size estimation to fossil remains of *Dama*-like deer.

Another possibility to reconstruct the body mass of fossil *Dama*-like deer could be based on astragalus, as reported by Martinez and Sudre (1995). Nevertheless, the astragalus sample available in this study is too limited to draw significant considerations (astragali are recorded only at Pirro Nord, Casal Selce 2, and upper levels of both Torre del Pagliaccetto and Vitinia).

The estimation of the height at the withers represents instead an interesting tool to investigate possible size differences among the fossil cervid taxa. These formulas were provided and summarised by von den Driesch and Boessneck (1974). The height can be calculated based on the total length of the cranial or postcranial remains, and therefore complete specimens are needed. Unfortunately, the fragmentary condition of the long bones and the lack of complete crania in our sample prevent the application of these equations to the late Early-Middle Pleistocene deer under investigation.

Biometric comparison of the M_3L

Firstly, we used the Shapiro-Wilk test to assess the normal distribution of M_3 length of the fallow deer samples. The result was negative, therefore we performed a Kruskal-Wallis test (not parametric test) (Table 2). The biometric analysis on M_3L revealed a difference in size between the Early to Middle Pleistocene samples, as reported in Figure 6. '*Pseudodama*' sp. from Pirro Nord is smaller than the three considered species of the genus *Dama*. *Dama roberti* displays a wide variability, with an extremely large M_3 from Valdemino cave and small specimens from Contrada Monticelli, which are respectively the largest and the smallest of the genus *Dama* in our graph. Also *D. clactoniana* is quite variable with relatively small specimens at Tor di Quinto and Ponte Molle. Extant *D. dama* is smaller than most of the *D. clactoniana* record, whereas it falls within the range of *D. roberti* (smaller than the specimen from Valdemino cave but larger than those from Contrada Monticelli).

Statistically speaking, the result of the Kruskall Wallis test reveals a weak difference among the considered groups. Extant sample of *D. dama*, chosen as reference, differs from the samples of Pirro Nord, Slivia, Valdemino, Notarchirico, Fontana Ranuccio, Riano and Prati Fiscali (p-value < 0.05). Other samples probably show no statistical difference due to the limited number of available specimens (Cava di Breccia – Casal Selce 2, Visogliano, Batteria Nomentana; p-value > 0.05).

Discussion

Taxonomy of fallow-like deer

Taxonomy of Plio-Pleistocene deer rests mainly on the antler morphology, with different opinions on their generic and specific attribution (e.g. Di Stefano and Petronio 1998, 2002; Pfeiffer 1999; van der Made 1999; Croitor 2006; Lister et al. 2010, Breda and Lister 2013). Morphological features of craniodental and postcranial elements have been mainly neglected in literature, which complicates the identification whenever antlers are lacking or incomplete. Detailed description of craniodental features

Table 2 Table of p-values for the Kruskall Wallis test. *Pink*: 'Pseudodama' sp.; *Green: Dama roberti*; *Orange: Dama clactoniana*; *Blue: Dama-like deer*

Species	Site	Abbreviations	Age	Number of specimens	p-values
Pseudodama sp.	Pirro Nord	PN	Early Pleistocene	2	**0.04**
Dama sp.	Slivia	Sl	Early Pleistocene	2	**0.04**
Dama sp.	Notarchirico	No	Middle Pleistocene	9	**0.00**
Dama cf. *roberti*	Contrada Monticelli	CM	Middle Pleistocene	2	0.33
Dama roberti	Valdemino	Va	Middle Pleistocene	1	**0.01**
Dama-like deer	Cava di Breccia - Casal Selce 2	CS	Middle Pleistocene	1	0.41
Dama clactoniana	Ponte Molle	PM	Middle Pleistocene	7	0.21
Dama clactoniana	Tor di Quinto	TQ	Middle Pleistocene	4	0.29
Dama clactoniana	Visogliano	Vi	Middle Pleistocene	1	0.16
Dama clactoniana	Fontana Ranuccio	FR	Middle Pleistocene	5	**0.00**
Dama clactoniana	Riano	Ri	Middle Pleistocene	1	**0.03**
Dama clactoniana	Batteria Nomentana	BN	Middle Pleistocene	1	0.24
Dama clactoniana	Prati Fiscali	PF	Middle Pleistocene	1	**0.03**
Dama clactoniana	Vitinia - Upper levels	VU	Middle Pleistocene	3	0.09
Extant *Dama dama*		Ex		4	

of '*Pseudodama*' *vallonnetensis* was recently carried out by Breda et al. (2020), based on a rich sample from the iconic European Pleistocene site of Untermassfeld (Germany). The morphology of '*Pseudodama*' postcranials has been attempted by Pfeiffer (1999), Croitor (2006), and Breda (2015), but the results are not conclusive.

The analysis of the sample from Pirro Nord allows a description of dental and postcranial remains of '*Pseudodama*'. The morphological characters of the Pirro Nord fallow deer confirm the presence of a mix of features proper to modern *Cervus elaphus* and *D. dama dama* as suggested by Breda and Lister (2013) and Breda (2015) for this group.

Fig. 6 Boxplot of the length of the M$_3$ of the chronologically arranged *Dama*-like deer from the Italian Peninsula and of extant *Dama dama* specimens. '*Pseudodama*' sp. from Pirro Nord (*PN*); *Dama*-like deer from Slivia (*Sl*), Notarchirico (*No*), Cava di Breccia - Casal Selce 1 (*CS*); *Dama roberti* from Contrada Monticelli (*CM*), Valdemino (*Va*); *Dama clactoniana* from Ponte Molle (*PM*), Tor di Quinto (*TQ*), Visogliano (*Vi*), Fontana Ranuccio (*FR*), Riano (*Ri*), Batteria Nomentana (*BN*), Prati Fiscali (*PF*), Vitinia - upper level (*VU*); extant *Dama dama* (*Ex*)
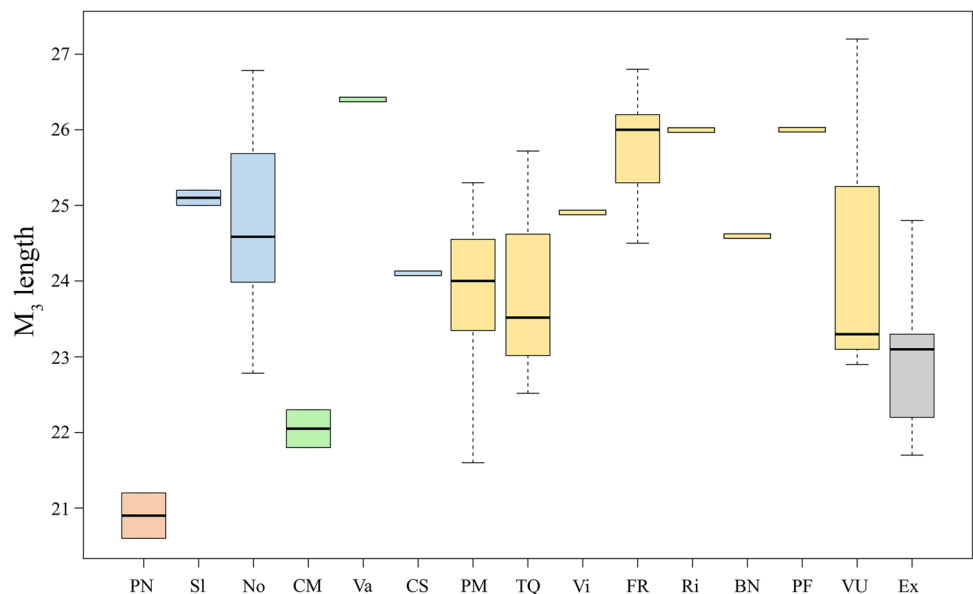
Due to the lack of diagnostic morphological criteria and to the incompleteness of the remains, identifications of fallow deer material from Italian sites of the late Early to early Middle Pleistocene have been mostly limited to a generic *Dama* sp. This is the case of Cava Alibrandi (Capasso Barbato and Petronio 1983), Cava Zanola (Bona and Sardella 2014), Pagliare di Sassa (Palombo et al. 2001), Vitinia – lower level (Caloi et al. 1981), Slivia (Ambrosetti et al. 1979), and localities of the Cretone basin (Camporioccio, Fosso Casa Cotta, Fosso delle Bufala, Osteria Moricone and Sferracavallo; Marra et al. 2016).

The presence of fallow deer in the Middle Pleistocene levels of the Ponte Galeria area was firstly reported by Ambrosetti (1967), who described three basal fragments of antler with pedicle and part of the basal tine. The author considered a number of fossiliferous deposits (see Figure 1 in Ambrosetti 1967), but provided no information about the locality of provenance of the fallow deer remains. Reliable records of medium-sized deer in the Ponte Galeria area were retrieved at Cava Alibrandi and Cava di Breccia di Casal Selce 1 and 2, and are here generically referred to *Dama*-like deer. Marra et al. (2014) considered the fossil sample described by Ambrosetti (1967) as collected from a single quarry located at km 11 of Portuense road, Cava Arnolfi. However, Ambrosetti (1967) had referred to Cava Arnolfi only a nearly complete hemimandible of *Bos primigenius* (later referred to *Bison* sp. by Sala 1986). The presence of other mammal remains from Cava Arnolfi was pointed out by Bonadonna (1965), who, in addition to a lower canine of *Hippopotamus amphibius*, reported bones of *Bos* and *Cervus* and tusks of *Elephas.* Thus, the exact geographical provenance of the three antler fragments listed by Ambrosetti (1967) remains unknown.

The wide intraspecific variability and, by contrast, the superposition of morphologies between advanced '*Pseudodama*' and early *Dama*, make a precise identification often not possible in small samples. In particular, with respect to *Dama*, '*Pseudodama*' is characterised by some plesiomorphic features that approach it morphologically to *Cervus* (Breda and Lister 2013; Breda 2015; Cherin et al. 2022). The apomorphic *Dama* features develop little by little in progressively more advanced representatives of the '*Pseudodama*' group and are not fixed yet in the most primitive *Dama*, i.e. *D. roberti* (Breda and Lister 2013; Breda et al. 2015). Thus both late '*Pseudodama*' and early *Dama* are often polymorphic in several features, making the identification of small samples unreliable.

Indeed, our morphological analysis of the considered fallow deer specimens confirms as the late Early and early Middle Pleistocene populations possess a mosaic of characters, with dominant *Dama*-like features, and a minor part of *Cervus*-like features (see chapther 4.1).

The amount of *Cervus*-like features decreases from the Early Pleistocene (e.g. Pirro Nord), where unpalmated antlers attributed to '*Pseudodama*' are recorded, to the early Middle Pleistocene (e.g. Cava di Breccia – Casal Selce 2), when the earliest palmated antlers are retrieved at Pakefield and West Runton (UK, Breda and Lister 2013). In this interim period, the presence of both *Dama*-like and *Cervus*-like features prevents a clear taxonomic identification in small samples lacking reasonably complete antlers.

Up to now, no complete antlers of *D. roberti* have been retrieved in the Italian Peninsula, but specimens from Cesi (Breda and Lister 2013), Contrada Monticelli (Stefanelli et al. 2021), Isernia La Pineta (Breda et al. 2015) and Valdemino cave (Breda 2015) have been tentatively referred to this species. As aforementioned, many postcranial morphologies are shared between *D. clactoniana* and *D. roberti,* with the exception of a few features as, for example, the development of the radial and coronoid fossa of the humerus, with the former generally larger than the latter in the Clacton fallow deer but equal in *D. roberti*. Some differences between these two taxa are recognised in dental remains as well: *D. roberti* generally shows a strong entostyle bifurcated at its base and a lingual cingulum in the upper molars, a clear molarization of the P_4, the absence of the step between the lingual walls of the 2nd and 3rd lobes of M_3 and the presence of the ectostylid between the 1st and 2nd lobes in the same tooth (Breda and Lister 2013; Breda 2015; Breda et al. 2015; Stefanelli et al. 2021). The samples from Riano and Ponte Molle suggest that *Dama clactoniana* rather shares the state of these features with modern *D. dama*.

In conclusion, in addition to the more conspicuous antler characters, some dental morphologies allow a specific attribution of the different *Dama* species, while for postcranial bones the intra- and infra-specific variabilities overlap more. However, both *D. roberti* and *D. clactoniana* approach modern *Dama* postcranial morphology more than '*Pseudodama*' which sports more *Cervus*-like (plesiomorphic) features.

Biochronology of the late Early to late Middle Pleistocene Dama-like deer

The late Villafranchian and Epivillafranchian fallow-like deer with un-palmated antlers are universally assigned to '*Pseudodama*' or to those species that in the intent of Azzaroli (1992) belong to this genus. The extremely rich collections from Untermassfeld (Thuringia - Breda et al. 2020) and from Vallparadís (Catalonia - under study) only recently yielded clearly un-palmated antlers that allow the positioning of the described species "*vallonnetensis*" in

'*Pseudodama*' (Breda et al. 2020) thus extending the presence of this group to the Epivillafranchian.

Fallow-like deer with palmated antlers from the start of the late Middle Pleistocene (MIS 13-11) are universally assigned to *Dama*, with the species *D. clactoniana* (=*D. dama clactoniana* for some authors). The interim period, the early Middle Pleistocene, corresponding to the first part of the Galerian (Ponte Galeria and Isernia Fauna Units) and to the English Cromerian (Pakefiled Rootlet Bed and West Runton Upper Fresh Water Bed), for a long time have been pour in fallow-like remains. This brought to the common usage of attributing the fallow-like remains from this time span either to a late '*Pseudodama*' (e.g. Sardella et al. 1998 for Italian sites; Kahlke et al. 2011 for Italian and Iberian Peninsulas) or to *D. clactoniana* (e.g. Azzaroli 1953 for the English Forest Bed; Abbazzi 1995 for Valdemino; Abbazzi and Masini 1997 for Isernia; Abbazzi and Lacombat 2005 for Soleilhac). The issue was partially solved only a decade ago with the description of *D. roberti*, the earliest palmated fallow deer, from the early Middle Pleistocene of western Europe (Breda and Lister 2013).

The many records of medium-sized deer from Italian localities of the late Early Pleistocene (end of the Late Villafranchian and Jaramillo subchron) can confidently be assigned to advanced forms of '*Pseudodama*', i.e. forms with the basal tine inserted very close to the burr and at an open angle to the beam (disregarding the specific epithet, either *farnetensis* or *vallonnetensis*, assigned to this morphotype). These late Early Pleistocene remains are recorded from the following Italian localities: Pirro Nord (*Axis eurygonos* in Petronio et al. 2013); Capena (*Dama nesti eurygonos* in Petronio 1979), Colle Curti (or Collecurti, *Pseudodama* ex gr. *nestii* in Mazza and Ventra 2011), Monte Peglia (*Axis eurygonos* in Petronio et al. 2020), "Frantoio" (*Pseudodama farnetensis* in Bona and Sala 2016), Imola (*Cervus* sp. in Azzaroli and Berzi 1970), and undefined deposits at Scoppito (*Axis eurygonos* in Mancini et al. 2012) (Fig. 7).

Dama roberti appears in the European record during the early Middle Pleistocene, as documented at Pakefiled (0.7 Ma; Stuart and Lister 2010; Parfitt et al. 2005), West Runton (0.7-0.6 Ma; Stuart and Lister 2010) and Soleilhac (0.7-0.6 Ma; Lacombat 2005) and still occurs in the later sites of Boxgrove and Westbury (0.5 Ma; Preece and Parfitt 2000). In the Italian Peninsula, samples tentatively referred to *D. roberti* were recovered from Cesi, Contrada Monticelli, Isernia La Pineta and Valdemino cave (Fig. 7). Tempo and mode of the early dispersal of this taxon in Europe are still unknown and would require the taxonomical revision of the fallow deer remains from late Early to early Middle Pleistocene localities in western Europe. Examples are the remains from the Sierra de Atapuerca (Gran Dolina, Penal, Sima del Elefante, Trinchera Galerìa, van der Made 1998, 1999, 2001, 2013, 2015; van der Made et al. 2003, 2017), the complex

moyen II at the Caune de l'Arago (France; Magniez et al. 2013) or the Italian remains of Cava Redicicoli (Caloi et al. 1979), Pagliare di Sassa (Palombo et al. 2001) and Slivia (Ambrosetti et al. 1979).

The earliest appearance of *D. clactoniana* is generally accepted from several Italian, French, Spanish and British localities during MIS 11 (Breda and Lister 2013). An earlier occurrence of this taxon was reported for Ponte Molle, where a recent revision of the chronostratigraphic framework revealed an age between 540 to 460 ka (Mecozzi et al. 2021a) (Fig. 7). This earliest dispersal is also supported by the sample from Tor di Quinto, another site which age is similar to Ponte Molle (540 to 460 ka). Of difficult interpretation is instead the sample of *D. clactoniana* recovered from the levels alfa and a of Notarchirico. Dating carried out in this deposit provide an age of 658 ± 9 and 612 ± 5 ka respectively for the levels alfa and a (Moncel et al. 2020). The faunal assemblage of the levels alfa and a of Notarchirico includes *Lepus* cf. *europaeus*, Elephantidae, *Sus scrofa*, *D. clactoniana*, *Cervus elaphus, Megaceroides* sp., *Bos primigenius* and *Bison* sp. (Cassoli et al. 1999). Uncertainty persists on the age of the faunal assemblage of the upper levels of Notarchirico; *B. primigenius* and *D. clactoniana* for example would suggest a younger age, more consistent with an attribution to the Fontana Ranuccio F.U. than to the Isernia F.U.. Further studies on these remains are needed to confirm the identification made by Cassoli et al. (1999) and clarify the biochronological attribution of the faunal assemblage of the upper levels. Pending a proper palaeontological revision, the fossils of levels alfa and a of Notarchirico are referred to *Dama* sp.

The presence of *D. clactoniana* is recognised in several Middle Pleistocene sites of the Italian Peninsula, that confirms as this cervid was one of the most common species in the late Galerian and early Aurelian terrestrial ecosystems (Fig. 7). Recently, *D. clactoniana* was also identified in karst infilling deposit of Cava Bianco (Melpignano area) referred to late Middle Pleistocene (Mecozzi et al. 2021b). However, its last occurrence in the Italian record is in the upper levels of the late Middle Pleistocene site of Vitinia. Similarly to what observed for '*Pseudodama*' – *Dama roberti* replacement, also the latest occurrences of *Dama clactoniana* and the first dispersal of *Dama dama* is still uncertain. This transition possibly took place during the late Middle Pleistocene, but only the revision of fossils from several key European sites (e.g. Bolomor Cave, Grotta Romanelli, Grotte du Lazaret, Lunel Viel, Steinheim) will allow to get data on this important bioevent. In Italy, samples that need to be revised are those from the late Middle Pleistocene sites of Bucine, Casal de' Pazzi, Castel di Guido, Cerveteri, Monte delle Gioie, Monte Li Pozzi, Poggetti Vecchi and Ponte Mammolo.
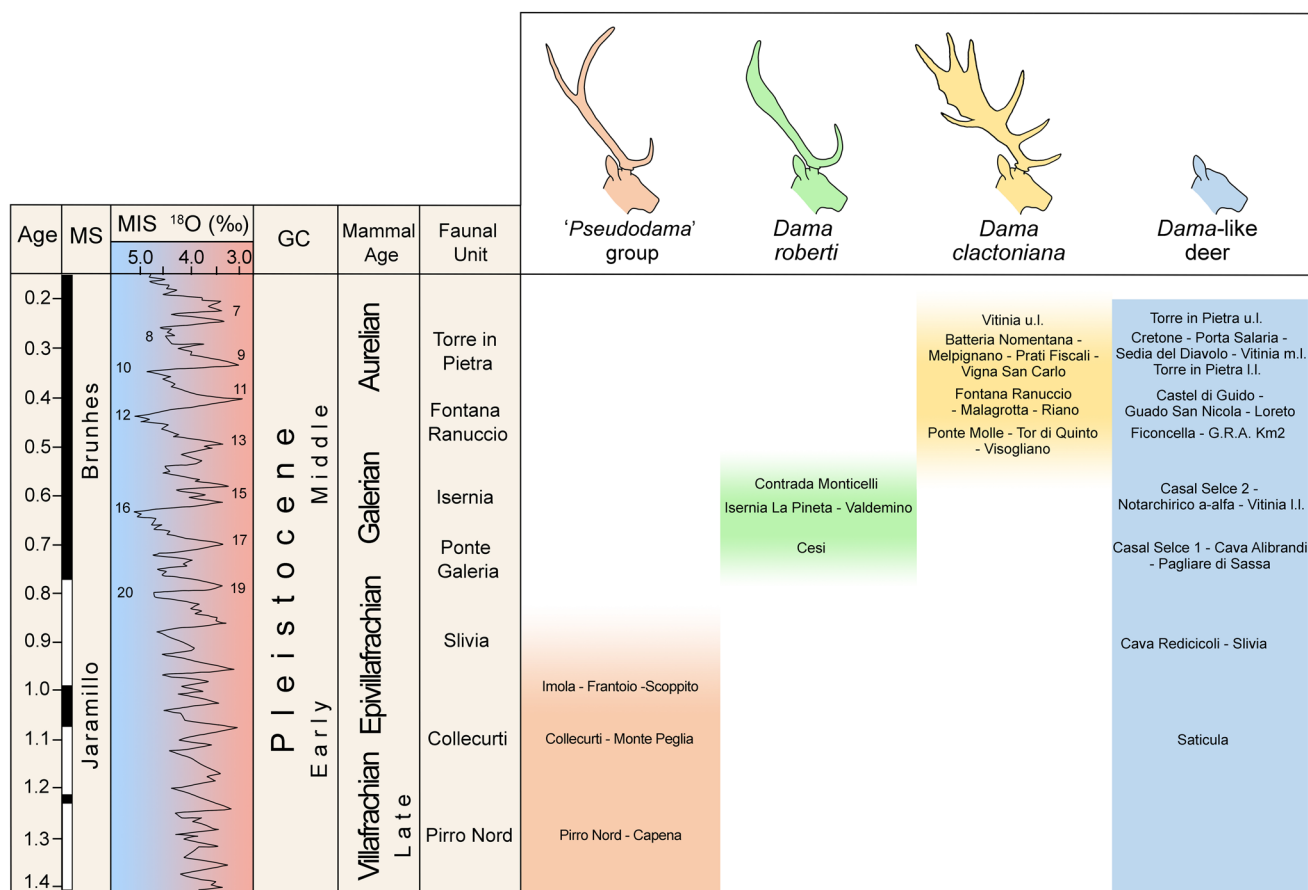
Fig. 7 Quaternary time scale, biochronological scheme with selected Italian localities mentioned in the text. Abbreviations: *MG* Magnetostratigraphy; *GC* Geochronology; *MIS* Marine Isotope Scale

Size variability

Size variations in large mammals during the Quaternary could represent an important proxy to investigate the effect of climate changes on terrestrial ecosystems or the response of different taxa to climatic oscillations. The starting point of these research is the study of the modern mammals and their adaptations to different climates. There is broad consensus that most modern taxa follow the Bergmann's ecogeographical rule (Bergmann 1847) (e.g. Faure and Guérin 1983; Dayan et al. 2002; Meiri and Dayan 2003; Meiri et al. 2007; Albarella et al. 2009), which postulates a strong relationship between temperature and body size, predicting larger dimension in colder climates. Nevertheless, several works demonstrated as this general rule is not universally valid for modern species, highlighting the contribution of other factors in causing size fluctuations (Huston and Wolverton 2011; McNab 2010; Meiri et al. 2007: Yom-Tov and Geffen 2006). Examples not matching the Bergmann's rule have been reported also for European Quaternary mammals (e.g. van Asperen 2010; Mazza and Bertini 2013; Iannucci et al. 2020), with large-sized specimens found in warm stages.

One of the main factors influencing mammal size variation is food availability, which is in turn influenced by inter- and intra-specific competition and by vegetation cover, hence by the climatic conditions (Calder 1984; Schmidt-Nielsen 1984; Damuth and MacFadden 1990; Weinstock 2006). Thus, the climate can affect the size directly, as predicted by Bergmann's rule (Bergmann 1847), but also indirectly, influencing the environment and the trophic availability.

The size of modern and fossil *Cervus elaphus* mostly follows Bergmann's rule, with largest modern populations found at Northern latitudes and the largest fossil populations recovered from glacial stages (e.g. Prat and Suire 1971; Steele 2002; Di Stefano et al. 2015; Di Stefano and Petronio 2021). However, for the reindeer, *Rangifer tarandus*, the largest dimension is recorded during the Late Glacial (Weinstock 1997, 2006; Magniez 2010), but the size variation in extant populations does not follow Bergmann's rule (Geist 1987). Size variability of modern reindeer populations has been associated to availability of trophic resources, topography of the landscape, population density and behaviour strategies (Klein 1968; Klein et al. 1987; Skogland 1989; Geist 1999). Modern *Dama dama*

is a generalist herbivore, with a large adaptability to thrive in different ecosystems and with a vast spectrum of food preferences (Esattore et al. 2022 and reference therein). This species is found from wooded habitats to steppe, with a wide range of plant species, including grass, graminoids, herbs, and leaves of various trees fruits and crops (Jackson 1977; Bruno and Apollonio 1991; Mertzanidou and Legakis 2004; Truv and Cederlund 2005; Jackowiak et al. 2017). Size variation in modern populations show no latitudinal gradient, so *D. dama* is one of the modern species that does not follow Bergmann's ecogeographical rule (Davis 1981).

As a matter of fact, the results of our biometric comparison show that no clear size trend can be detected among the late Early to late Middle Pleistocene fallow deer. The boxplot in Fig. 6, in which the localities are arranged in chronological order, highlights a high size variability for *D. roberti* and the *Dama*-like deer from the same time span, while an initial slight size increase and then decrease, might be spotted in *D clactoniana*. It is unclear whether this mild size trend in *D. clactoniana* is real or due to the small sample size. However, if it was present, it was not linked to the global temperature variation depicted by the oxygen isotope curve. This means that the size fluctuation, if present, is not driven by local climate. Infact, although possibly hampered by the reduced number of specimens available, our analysis reveals that fossil *Dama*-like deer disagree with Bergmann's ecogeographical rule, as observed in modern populations (Davis 1981). The smallest size is recorded in two sites of the Apulia (southern Italy), Pirro Nord and Contrada Monticelli: these sites represent the southernmost record of '*Pseudodama*' and *D.* cf. *roberti* respectively. The three coeval sites where *D. roberti* is recorded, Contrada Monticelli, Isernia and Valdemino, are chronologically referred to about 0.6 Ma and so to the warm MIS 15. Both Contrada Monticelli and Isernia yielded straight tusked elephant, Hundsheim rhinoceros and woodland bison (Sala 1986; Ballatore and Breda 2013; Mecozzi et al. 2017; Stefanelli et al. 2021; Mecozzi, unpublished data). At Valdemino cave, forest rhinoceros and barbary macaque were associated to aurochs, Hermann's tortoise and other elements of warm significance, the only exception being the steppe mammoth (Sala 1992). These deposits have approximately a similar age, but the size of the fallow M_3 largely differs with the Valdemino specimen much larger than the Contrada Monticelli ones (unfortunately there are no M_3s from Isernia to check their size). However, given the warmer climatic meaning of Valdemino fauna with respect to Contrada Monticelli and Isernia, Bergmann's rule would have suggested a larger fallow in the latter two, which is not the case. Clearly, this in a way unexpected result, could be hampered by the extremely low number of individuals from the two localities.

At Casal Selce, the palaeoenvironmental reconstruction indicated the dominance of open habitats and scattered woodlands (Strani et al. 2021). The faunal assemblage includes wild boars, hippopotamuses, bovids, equids, cervids, rhinoceroses and barbary macaques. The lower third molar size of *Dama*-like deer is intermediate between Valdemino and Contrada Monticelli.

For *D. clactoniana,* a large size variation can be observed, with the smallest samples from Ponte Molle, Tor di Quinto and Vitina. One of the samples of *D. clactoniana* with the longest teeth is that of Fontana Ranuccio. At Fontana Ranuccio, the palaeoenvironment consisted of grasslands and, more represented, wooded habitats (Strani et al. 2018). The mammal fauna includes straight tusked elephant, hippopotamuses, cervids, bovids, rhinoceroses, equids, wild boars and barbary macaques.

The scenario suggested by our analysis appears complex and articulated, prompting a better understanding of the causes of size-changes in extant fallow deer, in order to be able to interpret the size changes in past populations.

Conclusion

The taxonomical attribution of the late Early to late Middle Pleistocene medium sized deer rests on antler morphology, with a few diagnostic features identified in craniodental elements. Specific attribution is commonly based on chronological ground, reflecting the current limited availability of data on the morphology and size variability of this group.

This work attempts an identification of the fallow deer remains from selected Italian sites from the late Early Pleistocene to the late Middle Pleistocene based on craniodental and postcranial morphology. In addition to the antler characters, few morphological craniodental features, especially of the lower teeth, are here suggested to be useful for the distinction among the *"Pseudodama"* group, *Dama clactoniana* and *D. roberti.*

Postcranial morphologies allowing a clear taxonomical identification within the fallow deer group have not been spotted, with the apparent exception of a feature of the distal humerus (a different development of the coronoid and radial fossa). This is partly due to the extremely low number of available specimens for each bony element, and partly to the wide intraspecific morphological variation that, in postcranial elements, appears to overlap the interspecific variation.

The analysis of the material from the considered localities allows to confirm that '*Pseudodama*' sports a higher number of *Cervus*-like features or, in other words, it is more plesiomorphic, as already suggested by Breda (2015) and by Cherin et al. (2022). *Dama roberti* and *D. clactoniana*, are instead morphologically closer to modern *D. dama*. Within the *Dama* group, the morphology of the postcranial bones

is quite constant, with the only useful character observed in the development of the radial and coronoid fossa in the distal epiphysis of the humerus, a feature used by Lister (1996) in the distinction *Dama dama-Cervus elaphus*.

From a biochronological point of view, the disappearance of *'Pseudodama'* from the European record is still imperfectly unknown. The earliest presences of *Dama roberti* attested during the early Middle Pleistocene however suggest that the replacement took place during the early Middle Pleistocene Transition, when one of the major faunal renewal recognised in the European fossil record occurred. Doubts instead persist on the earliest dispersal of *Dama clactoniana* and, later, of *Dama dama*.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12549-023-00583-1.

Data availability All data generated or analysed during this study are included in this published article.

Declarations

Conflict of Interest The authors have no conflict of interest to declare.

References

Abbazzi, L. (1995). *Variazioni nei popolamenti di cervidi durante il Pleistocene italiano*. PhD thesis (pp. 135), University of Modena.

Abbazzi, L., & Lacombat, F. (2005). *Dama clactoniana*—Soleilhac. In Lacombat, F. (Ed.), *Les grands mammifères fossiles du Velay : les collections paléontologiques du Plio-Pléistocène du Musée Crozatier, Le Puy-en-Velay* (pp. 122). Le Puy-en-Velay: Annales des Amis du Musée Crozatier.

Abbazzi, L., & Masini, F. (1997). *Megaceroides solilhacus* and other deer from the middle Pleistocene site of Isernia La Pineta (Molise, Italy). *Bollettino Societa Paleontologica Italiana*, *35*, 213–227.

Abbazzi, L., Benvenuti, M., Boschian, G., Dominici, S., Masini, F., Mezzabotta, C., Rook, L., Valleri, G., & Torre, D. (1996). The Neogene and Pleistocene succession, and the mammal faunal assemblages of an area between Apricena and Poggio Imperiale (Foggia, Italy). *Memoir Società Geologica Italiana*, *51*, 383–402.

Accordi, B., & Maccagno, A.M. (1962). Researches in the Pleistocene of Riano (Roma). *Geologica Romana, 1*, 25–32.

Albarella, U., Dobney, K., & Rowley-Conwy, P. (2009). Size and shape of the Eurasian wild boar (*Sus scrofa*), with a view to the reconstruction of its Holocene history. *Environmental Archaeology, 14*, 103–136.

Ambrosetti, P. (1967). Cromerian fauna of the Rome area. *Quaternaria, 9*, 267–283.

Ambrosetti, P., Bartolomei, G., De Giuli, C., Ficcarelli, G., & Torre, D. (1979). La breccia ossifera di Slivia (Aurisina-Sistiana) nel Carso di Trieste. *Bollettino della Società Paleontologica Italiana, 18*, 207–220.

Arzarello, M., Marcolini, F., Pavia, G., Pavia, M., Petronio, C., Petrucci, M., Rook, L., & Sardella, R. (2009). L'industrie lithique du site Plèistocène inferieur de Pirro Nord (Apricena, Italie du sud): une occupation humaine entre 1,3 et 1,7 Ma. *L'Anthropologie, 113*, 47–58.

Arzarello, M., Pavia, G., Peretto, C., Petronio, C., & Sardella, R. (2012). Evidence of an early Pleistocene hominin presence at Pirro Nord (Apricena, Foggia, southern Italy): P13 site. *Quaternary International, 267*, 56–61.

Asperen, E.N. van (2010). Ecomorphological adaptations to climate and substrate in late Middle Pleistocene caballoid horses. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 297, 584–596.

Aureli, D., Rocca, R., Lemorini, C., Modesti, V., Scaramucci, S., Milli, S., Giaccio, B., Marano, F., Palombo, M.R., & Contardi, A. (2016). Mode 1 or mode 2? "Small tools" in the technical variability of the European Lower Palaeolithic: The site of Ficoncella (Tarquinia, Lazio, central Italy). *Quaternary International, 393*, 169–184.

Azzaroli, A. (1953). The deer of the Weybourne Crag and Forest bed of Norfolk. *Bulletin of the British Museum (Natural History) (A. Geology)*, *2*, 3–96.

Azzaroli, A. (1992). The cervid genus *Pseudodama* n.g. in the Villafranchian of Tuscany. *Palaeontographica Italica, 79*, 1–41.

Azzaroli, A., & Berzi, A. (1970). On an upper Villafranchian fauna at Imola, northern Italy, and its correlation with the marine pleistocene sequence of the Po plain. *Paleontographia Italica, 66*, 1–12.

Ballatore, M., & Breda, M. (2013). *Stephanorhinus hundsheimensis* (Rhinocerontidae, Mammalia) teeth from the early Middle Pleistocene of Isernia La Pineta (Molise, Italy) and comparison with coeval British material. *Quaternary International*. https://doi.org/10.1016/j.quaint.2013.02.002.

Bergmann, C. (1847). *Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse*. Göttinger Studien.

Bertini, A., Ciaranfi, N., Marino, M., & Palombo, M.R. (2010). Proposal for Pliocene and Pleistocene land-sea correlation in the Italian area. *Quaternary International 219*, 95–108.

Bon, M., Piccoli, G., & Sala, B. (1992). La fauna pleistocenica della breccia di Slivia (Carso triestino) nella collezione del Museo Civico di Storia Naturale di Trieste. *Atti del Museo Civico Storia Naturale, Trieste, 44*, 33–51.

Bona, F., & Sala, B. (2016). Villafranchian-Galerian mammal faunas transition in South-western Europe. The case of the late early Pleistocene mammal fauna of the Frantoio locality, Arda River (Castell'Arquato, Piacenza, northern Italy). *Geobios, 49*(5)*,* 329–347.

Bona, F., & Sardella, R. (2014). Co-occurrence of a sabertoothed cat (*Homotherium* sp.) with a large lion-like ca (*Panthera* sp.) in the Middle Pleistocene karst infill from nuova «Cava Zanola» (Paitone, Brescia, Lombardy, Northern Italy). *Bollettino della Società Paleontologica Italiana, 53*(2), 81–88.

Bonadonna, P. (1965). Resti di *Hippopotamus amphibius* Linnè nei sedimenti del Pleistocene medio-inferiore della via Portuense, Roma. *Bollettino della Società Geologica Italiana, 84*, 29–39.

Breda, M. (2015). The early Middle Pleistocene fallow deer *Dama roberti*: new insight on species morphology from a complete postcranial skeleton from Valdemino (northwestern Italy). *Geological Journal, 50*. https://doi.org/10.1002/gj2624.

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

Breda, M., Thun-Hohenstein, U., & Peretto, C. (2015). The deer from the early Middle Pleistocene site of Isernia La Pineta (Molise, Italy): revised identifications and new remains from the last 10 years of excavation. *Geological Journal, 50,* 290–305.

Breda, M., Kahlke, R.-D., & Lister, A.M. (2020). New results on cervids from the Early Pleistocene site of Untermassfeld. In R.-D. Kahlke (Ed.), *The Pleistocene of Untermassfeld near Meiningen (Thüringen, Germany) PART 4*, (pp. 1197-1250). Germany, Beltz Grafische Betriebe GmbH, Bad Langensalza press.

Bruno, E., & Apollonio, M (1991). Seasonal variations in the diet of adult male fallow deer in a submediterranean coastal area. *Revue d'écologie, Terre et Vie, 46*(4), 349–362.

Calder, W.A. (1984). *Size, Function and Life Hisotry. Cambridge*. Massachusetts: Harvard University Press.

Caloi, L., & Palombo, M.R. (1978). Anfibi, rettili e mammiferi di Torre del Pagliaccetto (Torre in Pietra, Roma). In A. Malatesta (Ed.), *Torre in Pietra, Roma* (pp. 315–428). *Quaternaria, 20*.

Caloi, L., & Palombo, P. (1979). Resti di mammiferi del Pleistocene Medio di Malagrotta (Roma). *Bollettino del Servizio Geologico d'Italia, 100*, 141–188.

Caloi, L., & Palombo, M.R. (1980). Resti di mammiferi del Pleistocene medio di Malagrotta (Roma). *Bollettino del Servizio Geologico Italiano, 100*, 141–188.

Caloi, L., & Palombo, M.R. (1986). Resti di mammiferi in livelli del Pleistocene medio inferiore affioranti al Km 2 del G.R.A. (Roma). *Bollettino del Servizio Geologico d'Italia, 104*, 141–156.

Caloi, L., Palombo, M.R., & Petronio, C. (1979). Cenni preliminari sulla fauna di Cava Redicicoli (Roma). *Bollettino del Servizio Geologico d'Italia, 100*, 189–198.

Caloi, L., Palombo, M.R., & Petronio, C. (1980). La fauna quaternaria di Sedia del Diavolo (Roma). *Quaternaria, 22,* 177–209.

Caloi, L., Cuggiani, M.C., Palmarelli, A., & Palombo, M.R. (1981). La fauna a Vertebrati del Pleistocene medio e superiore di Vitinia (Roma). *Bollettino del Servizio Geologico d'Italia, 102*, 41–76.

Caloi, L., Palombo, M.R, & Zarlenga, F. (1998). Late-Middle Pleistocene mammal faunas of Latium (central Italy): stratigraphy and environment. *Quaternary International, 47/48*, 77–86.

Capasso Barbato, L., & Petronio, C. (1981). La mammalofauna pleistocenica di Castel di Guido (Roma). *Bollettino del Servizio Geologico d'Italia, 102*, 95–108.

Capasso Barbato, L., & Petronio, C. (1983). Nuovi resti di mammiferi del Pleistocene medio-inferiore di Ponte Galeria (Roma). *Bollettino del Servizio Geologico d'Italia, 104*, 157–176.

Carpaneto, G.M. (2003). *Dama dama* (Linnaeus, 1758). In L. Boitani, S. Lovari, & A. Vigna Taglianti (Eds.), *Fauna d'Italia. Mammalia III. Carnivora-Artiodactyla* (pp 261–271). Bologna: Calderini press.

Cassoli, P.F., & Segre Naldini, E. (1993). Le faune di Costa S. Giacomo e Fontana Ranuccio. (pp. 30–38). In S. Gatti (Ed.), *Dives Anagnia. Archeologia nella Valle del Sacco*. Roma: L'Erma.

Cassoli, P.F., Di Stefano, G., & Tagliacozzo, A. (1999). I vertebrati dei livelli superiori (A e Alfa) della serie stratigrafica di Notarchirico. In Piperno, M. (Ed.), *Notarchirico. Un sito del Pleistocene medio-iniziale nel bacino di Venosa (Basilicata)* (pp. 361–438). Venosa: Osanna.

Chapman, D., & Chapman, N, (1969). Geographical Variation in Fallow deer (*Dama dama* L.). *Nature, 221*, 59–60.

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

Coltorti, M., Cremaschi, M., Delitala, M.C., Esu, D., Fornaseri, M., McPherron, A., Nicoletti, M., Otterloo, R. Van, Peretto, C., Sala, B., Schmidt, V., & Sevink, J. (1982). Reversed magnetic polarity at an early Lower Palaeolithic site in Central Italy. *Nature, 300*, 173–176.

Coltorti, M., Feraud, G., Marzoli, A., Peretto, C., Ton-That, Y., Voinchet, P., Bahain, J.J., Minelli, A., & Thun Hohenstein, U. (2005). New40Ar/39Ar, stratigraphic and palaeoclimatic data on the Isernia La Pineta Lower Palaeolithic site, Molise, Italy. *Quaternary International, 131*, 11–22.

Croitor, R. (2006). Early Pleistocene small-sized deer of Europe. *Hellenic Journal of Geoscience, 41*, 89–117.

Croitor, R. (2014). Deer from Late Miocene to Pleistocene of Western Palearctic: matching fossil record and molecular phylogeny data. *Zitteliana B*, *32*, 115–153.

Croitor, R., Sanz, M., & Daura, J. (2019). Deer remains from the Middle Pleistocene site of Gruta da Aroeira (Portugal): Iberian faunal endemism and implications for hominin paleobiogeography. *Quaternary Science Reviews, 225*, 106022.

Damuth, J. (1990). Problems in estimating body masses of archaic ungulates using dental measurements. In J. Damuth, B. J. MacFadden (Eds.), *Body Size in Mammalian Paleobiology: Estimation and Biological Implications* (pp. 229–254). Cambridge: University Press.

Damuth, J., & MacFadden, B.J., (1990). Introduction: body size and its estimation. In J. Damuth, & B. J. MacFadden (Eds.), *Body Size in Mammalian Paleobiology: Estimation and Biological Implication*s (pp. 1–10). Cambridge: University Press.

Davis, S.J.M. (1981). The effect of temperature change and domestication on the body size of late Pleistocene to Holocene mammals of Israel. *Paleobiology*, *7*, 101-114.

Dayan, T., Wool, D., & Simberloff, D. (2002). Variation and covariation of skulls and teeth: modern carnivores and the interpretation of fossil mammals. *Paleobiology*, *28*(4), 508–526.

Di Canzio, E., Bedetti, C., Petronio, C., & Sardella, R. (2003). Middle Pleistocene fauna from Cretone (Sabina, Latium). *Bollettino della Società Paleontologica Italiana, 42*, 129–132.

Di Stefano, G., (1994). *Il daino pleistocenico dell'Eurasia*. PhD Thesis (pp. 270), Sapienza, University of Rome.

Di Stefano, G. (1996). Identification of fallow deer remains on the basis of its skeletal features: taxonomical considerations. *Bollettino della Società Paleontologica Italiana, 34*(3), 323–331.

Di Stefano, G., & Petronio, C. (1993). A new *Cervus elaphus* of Middle Pleistocene age. *Neues Jahrbuch für Geologie und Paläontologie (Abh.), 190*, 1–18.

Di Stefano, G., & Petronio, C. (1997). Origin and evolution of the European fallow deer (*Dama*, Pleistocene). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 203*(1), 57–75.

Di Stefano, G., & Petronio, C. (1998). Origin and relantionship among *Dama*-like cervids in Europe. *Neues Jarbuch für Geologie und Paläeontologie Abhandlungen*, *207*, 37-55.

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

Di Stefano, G., & Petronio, C. (2021). Importance of the morphological plasticity of *Cervus elaphus* in the biochronology of the Middle and Late Pleistocene of the Italian peninsula. *The Science of Nature, 108*(5), 1–12

Di Stefano G., Petronio, C., & Sardella, R. (1998). Biochronology of Pleistocene mammal faunas from Rome urban area. *Il Quaternario, 11*, 191–199.

Di Stefano, G., Pandolfi, L., Petronio, C., & Salari, L. (2015). The morphometry and the occurrence of *Cervus elaphus* (Mammalia, Cervidae) from the Late Pleistocene of the Italian Peninsula. *Rivista Italiana di Paleontologia e Stratigrafia, 121*(1), 103–120.

Driesch, A. von den (1976). A guide to the measurement of animal bones from archaeological sites. *Peabody Museum Bulletin, 1*(3-4), 1–137.

Driesch, A., von den, & Boessneck, J. (1974). Kritische Anmerkungen zur Widerristhöhenberechnung aus Langenmassen vor- und frühgeschichtlicher Tierknochen. *Saugetierkundliche Mitteilungen, 22*, 325–348.

Esattore, B., Saggiomo, L., Sensi, M., Francia, V., & Cherin, M. (2022). Tell me what you eat and I'll tell you…where you live: an updated review of the worldwide distribution and foraging ecology of the fallow deer (*Dama dama*). *Mammalian Biology*, https://doi.org/10.1007/s42991-022-00250-6.

Falconer, H. (1868). On the European Pliocene and Postpliocene species of the genus *Rhinoceros*. *Paleontological Memoirs, 2*, 309–403.

Falguères, C., Bahain, J.J., Tozzi, C., Boschian, G., Dolo, J. M., Mercier, N., Valladas, H., & Yokoyama, Y. (2008). ESR/U-series chronology of the Lower Palaeolithic palaeoanthropological site of Visogliano, Trieste, Italy. *Quaternary Geochronology, 3*(4), 390–398.

Faure, M., & Guérin, C. (1983). Le *Sus scrofa* (Mammalia, Artiodactyla, Suidae) du gisement Pléistocène superieur de Jaurens à Nespouls, Corrèze, France. *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon, 21*, 45–63.

Ficcarelli, G., Abbazzi, L., Albianelli, A., Bertini, A., Coltorti, M., Magnatti, M., Masini, F., Mazza, P., Mezzabotta, C., Napoleone, G., Rook, L., Rustioni, M., & Torre, D., 1997. Cesi, and early Middle Pleistocene site in Colfiorito Basin (Umbro-Marchean Apennine), central Italy. *Journal of Quaternary Science, 12*(6), 507–518.

Geist, V. (1987). Bergmann's rule is invalid. *Canadian Journal of Zoology, 65*, 1035–1038.

Geist, V. (1999). *Deer of the World: Their Evolution, Behavior, and Ecology* (pp. 421). England, Swan Hill Press.

Huston, M.A., & Wolverton, S. (2011). Regulation of animal size by eNPP, Bergmann's rule, and related phenomena. *Ecological Monographs, 81*, 349–405.

Iannucci, A., Sardella, R., Strani, F., & Mecozzi, B. (2020). Size shifts in late Middle Pleistocene to Early Holocene *Sus scrofa* (Suidae, Mammalia) from Apulia (southern Italy): ecomorphological adaptations? *Hystrix, the Italian Journal of Mammalogy, 31*(1), 10–20.

Iannucci, A., Mecozzi, B., Sardella, R., & Iurino, D.A. (2021). The extinction of the giant hyena *Pachycrocuta brevirostris* and a reappraisal of the Epivillafranchian and Galerian Hyaenidae in Europe: Faunal turnover during the EarlyeMiddle Pleistocene Transition. *Quaternary Science Reviews, 272,* 107240.

Jackowiak, H., Skubis, J., Łakomy, P., Nasiadka, P., & Godynicki, S. (2017). Anatomy of the tongue and microstructure of the lingual papillae in the fallow deer *Dama dama* (Linnaeus, 1758). *Mammalian Bioliogy, 85,* 14–23.

Jackson, J. (1977). The annual diet of the fallow deer (*Dama dama*) in the New Forest, Hampshire, as determined by rumen content analysis. *Journal of Zoolpgy, 181,* 465–473.

Kahlke, R.-D., García, N., Kostopoulos, D.S., Lacombat, F., Lister, A. M., Mazza, P.A., Spassov, N., & Titov, V.V. (2011). Western Palaearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe. *Quaternary Science Reviews, 30*, 1368–1395.

Klein, D.R. (1968). The introduction, increase, and crash of reindeer on St. Matthew Island. *Journal of Wildlife Management, 32*(2), 350, 421–467.

Klein, D.R., Meldgaars, M., & Fancy, S.G. (1987). Factors determining leg length in *Rangifer tarandus*. *Journal of Mammalogy, 68*(3), 642–655.

Kotaskis, T., & Palombo, M.R. (1979). Un cranio di *Panthera pardus* (L.) del Pleistocene Medio Superiore di Monte Sacro (Roma). *Geologica Romana, 18*, 137–155.

Lacombat, F. (2005). *Les grands mammifères fossiles du Velay: les collections paléontologiques du Plio-Pléistocène du musée Crozatier, Le Puy-en-Velay*. Le Puy-en-Velay: Annales des Amis du Musée Crozatier.

Leonardi, G., & Petronio, C. (1971). I Cervi Pleistocenici del bacino diamotico di Riano (Roma). *Atti dell'Accademia Nazionale dei Lincei, 12*, 9–208.

Leonardi, G., & Petronio, C. (1976). The fallow deer of European Pleistocene. *Geologica Romana, 25*, 1–67.

Lister, A.M. (1996). The morphological distinction between bones and teeth of fallow deer (*Dama dama*) and red deer (*Cervus elaphus*). *International Journal of Osteoarchaeology, 6,* 119–143.

Lister, A.M., Parfitt, S.A., Owen, F.J., Collinge, S.E., & Breda, M. (2010). Metric analysis of ungulate mammals in the early Middle Pleistocene of Britain, in relation to taxonomy and biostratigraphy. II: Cervidae, Equidae and Suidae. *Quaternary International, 228,* 157–179.

Lumley, H. de, Kahlke, H.-D., Moigne, A.-M., & Moullé, P.-E. (1988). Les faunes des grands Mammifères de la Grotte du Vallonnet, Roquebrune-Cap-Martin, Alpes-Maritimes. *L'Anthropologie, 92*, 465–496.

Made, J. van der (1998). Ungulates from Gran Dolina (Atapuerca, Burgos, Spain) [La faune des ongulés de la séquence de Gran Dolina (Atapuerca, Burgos, Espagne)]. *Quaternaire, 9*(4), 267–281.

Made, J. van der (1999). Artiodactylia del yacimiento mesopleistoceno de Galería (Sierra de Atapuerca). In E. Carbonell Roura, A. Rosas González, J. C. Díez Fernández-Lomana (Eds.), *Atapuerca: ocupaciones humanas y paleoecología del yacimiento de Galería, Consejería de Educación y Cultura* (pp. 143–167). Zamora: Heraldo de Zamore.

Made, J. van der (2001). Les Ongulés d'Atapuerca. Stratigraphie et biogéographie. *L'Anthropologie, 105,* 95–113.

Made, J. van der (2013). First description of the large mammals from the locality of Penal, and updated faunal lists for the Atapuerca ungulates - *Equus altidens, Bison* and human dispersal into Western Europe. *Quaternary International, 295*, 36–47.

Made, J. van der (2015). The latest Early Pleistocene giant deer *Megaloceros novocarthaginiensis* n. sp. and the fallow deer

Dama cf. *vallonnetensis* from Cueva Victoria (Murcia, Spain). *Mastia, 10*, 269–323.

Made, J. van der, Aguirre, E., Bastir, M., Fernández Jalvo, Y., Huguet, R., Laplana, C., Marquez, B., Martínez, C., Martinón, M., Rosas, A., Rodríguez, J., Sánchez, A., Sarmiento, S., & Bermúdez de Castro, J.M. (2003). El registro paleontológico y arqueológico de los yacimientos de la Trinchera del Ferrocarril en la Sierra de Atapuerca. *Coloquios de Paleontología, volumen extraordinario, 1,* 345–372.

Made, J. van der, Rosell, J., & Blasco, R. (2017). Faunas from Atapuerca at the Early-Middle Pleistocene limit: The ungulates from level TD8 in the context of climatic change. *Quaternary International, 433*, 296–346.

Magniez, P. (2010). Incidence des fluctuations climatiques sur la taille du renne (*Rangifer tarandus*) au Pléistocène supérieur. *Quaternaire, 21*(3), 259–279.

Magniez, P., Moigne, A.-M., Testu, A., & de Lumley, H. (2013). Biochronology of Quaternary Mammals. New insights on the Cervidae of the Middle Pleistocene site of the Caune de l'Arago (Tautavel, Pyrénées-orientales, France). *Quaternaire, 24*, 477–502.

Mancini, M., Cavuoto, G., Pandolfi, L., Petronio, C., Salari, L., & Sardella, R. (2012). Coupling basin infill history and mammal biochronology in a Pleistocene intramontane basin: The case of western L'Aquila Basin (central Apennines, Italy). *Quaternary International, 267*, 62–77.

Marra, F., & Rosa, C. (1995). Stratigrafia e assetto geologico dell'area romana. *Memorie Descrittive della Carta Geologica d'Italia, 50*, 49–118.

Marra, F., Karner, D.B., Freda, C., Gaeta, M., & Renne, P.R. (2009). Large mafic eruptions at the Alban Hills Volcanic District (Central Italy): chronostratigraphy, petrography and eruptive behavior. *Journal of Volcanology and Geothermal Research, 179,* 217–232.

Marra, F., Pandolfi, L., Petronio, C., Di Stefano, G., Gaeta, M., & Salari, L. (2014). Reassessing the sedimentary deposits and vertebrate assemblages from Ponte Galeria area (Rome, central Italy): An archive for the Middle Pleistocene faunas of Europe. *Earth- Science Reviews, 139*, 104–122.

Marra, F., Ceruleo, P., Jichac, B., Pandolfi, L., Petronio, C., Salari, L., Giaccio, B., & Sottili, G. (2016). Glacio-eustatic and tectonic forcing on the lacustrine succession of the Cretone basin: chronostratigraphic constraints to Acheulian industry and Middle Pleistocene faunal assemblages of Latium (central Italy). *Journal of Quaternary Science, 31*, 641–658.

Marra, F., Nomade, S., Pereira, A., Petronio, C., Salari, L., Sottili, G., Bahain, J.J., Boschian, G., Di Stefano, G., Falguerès, C., Florindo, F., Gaeta, M., Giaccio, B., & Masotta, M. (2018). A review of the geologic sections and the faunal assemblages of Aurelian Mammal Age of Latium (Italy) in the light of a new chronostratigraphic framework. *Quaternary Sciences Reviews, 181*, 173–199.

Martinez, J.-N., & Sudre, J. (1995). The astragalus of Paleogene artiodactyls: comparative morphology, variability and prediction of body mass. *Lethaia, 28*, 198–209.

Martinez-Navarro, B., & Palombo, M.R. (2004). Occurrence of the Indian genus *Hemibos* (Bovini, Bovidae, Mammalia) at the Early–Middle Pleistocene transition in Italy. *Quaternary Research, 61,* 314–317.

Masini, F., & Sala, B. (2007). Large and small-mammal distribution patterns and chronostratigraphic boundaries from the Late Pliocene to the Middle Pleistocene of the Italian peninsula. *Quaternary International, 160*, 43–56.

Mazza, P.P.A., & Bertini, A. (2013). Were Pleistocene hippopotamuses exposed to climate driven body size changes? *Boreas 42,* 194–209.

Mazza, P.P.A., & Ventra, D. (2011). Pleistocene debris-flow deposition of the hippopotamus-bearing Collecurti bonebed (Macerata, Central Italy): Taphonomic and paleoenvironmental analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology, 310*(3-4), 296–314.

McNab, B.K. (2010). Geographic and temporal correlations of mammalian size reconsidered: a resource rule. *Oecologia, 164*, 13–23.

Mecozzi, B. (2021). *Meles meles* from Middle Pleistocene to Early Holocene of the Italian Peninsula within the evolution of European badgers in the Quaternary of Eurasia. *Palaeontographica, Abt. A.: Palaeozoology – Stratigraphy*, https://doi.org/10.1127/pala/2021/0100.

Mecozzi, B., Iurino, D.A., Berte, D.F., & Sardella, R. (2017). *Canis mosbachensis* (Canidae, Mammalia) from the Middle Pleistocene of Contrada Monticelli (Putignano, Apulia, southern Italy). *Bollettino della Società Paleontologica Italiana, 56,* 71–78.

Mecozzi, B., Iannucci, A., Mancini, M., & Sardella, R. (2021a). Redefining Ponte Molle (Rome, central Italy): an important locality for Middle Pleistocene mammal assemblages of Europe. *Alpine and Mediterranean Quaternary, 34*(1), 131–154.

Mecozzi, B., Bellucci, L., Giustini, F., Iannucci, A., Iurino, D.A., Mazzini, I., Strani, F., & Sardella, R. (2021b). A reappraisal of the Pleistocene mammals from the karst infilling deposits of the Maglie Area (Lecce, Apulia, Southern Italy). *Rivista Italiana di Paleontologia e Stratigrafia, 127*(2), 355–382.

Meiri, S., & Dayan, T. (2003). On the validity of Bergmann's rule. *Journal of Biogeography, 30,* 331–351.

Meiri, S., Yom-Tov, Y., & Geffen, E. (2007). What determines conformity to Bergmann's rule? *Global Ecology and Biogeography, 16*, 788–794.

Meli, R. (1886). Sopra alcune ossa fossili rinvenute nelle ghiaie allivionali presso la via Nomentana, al 3° chilom. da Roma. *Bollettino del Regio Comitato Geologico d'Italia, 17*, 265–280.

Mertzanidou D., & Legakis A. (2004). *Fallow deer distribution and habitat in the Mediterranean landscape of Rhodes islands as determined by a track survey: preliminary data*. (pp. 1-3). In M. Arianoutsou, & V. P. Papanastis (Eds.), Proceedings 10th MEDECOS conference, April 25 – May 1 2004.

Milli, S., Palombo, M.R., Petronio, C., & Sardella, R. (2004). The Middle Pleistocene deposits of the Roman Basin (Latium, Italy). An integral approach of Mammal Biochronology and sequence Stratigraphy. *Rivista Italiana di Paleontologia e Stratigrafia, 110*, 559–565.

Moncel, M.H., Santagata, C., Pereira, A., Nomade, S., Voinchet, P., Bahain, J.J., Daujeard, C., Curci, A., Lemorini, C., Hardy, B., Eramo, G., Berto, C., Raynal, J.P., Arzarello, M., Mecozzi, B., Iannucci, A., Sardella, R., Allegretta, I., Delluniversità, E., Terzano, R., Dugas, P., Jouanic, G., Queffelec, A., d'Andrea, A., Valentini, R., Minucci, E., Carpentiero, L., & Piperno, M. (2020). The origin of early Acheulean expansion in Europe 700 ka ago: new findings at Notarchirico (Italy). *Scientific reports, 10*(1), 1–16.

Moullé, P.E., Lacombat, F., & Echassoux, A. (2006). Apport des grands mammifères de la grotte du Vallonnet (Roquebrune-Cap-Martin, Alpes-Maritimes, France) à la connaissance du cadre biochronologique de la seconde moitié du Pléistocène inférieur d'Europe. *L'Anthropologie, 110*, 837–849.

Muttoni, G., Scardia, G., Kent, D.V., Morsiani, E., Tremolada, F., Cremaschi, M., & Peretto, C. (2011). First dated human occupation of Italy at ~ 0.85 Ma during the late Early Pleistocene climate transition. *Earth Planetary Science Letter, 307*, 241–252.

Nomade, S., & Pereira, A. (2014). Datation ^{40}Ar/^{39}Ar Du site de Guado San Nicola. In B. Muttillo, G. Lembo, & C. Peretto (Eds.), *L'insediamento a bifacciali di Guado San Nicola, Monteroduni, Molise, Italia* (pp. 59-78.). Ferrara: Annali dell'Università degli

Studi di Ferrara, Sez. Museologia Scientifica e Naturalistica, Volume 10/1A, Università degli Studi di Ferrara.

Nugent, G., & Frampton, C. (1994). Microgeographic and temporal variation in mandible size within a New Zealand fallow deer (*Dama dama*) population. *Journal of Applied Ecology, 31*, 253–262.

Palombo, M.R., Abbazzi, L., Agostini, S., Mazza, P.P.A., & Mussi, M. (2001). Middle Pleistocene fauna and lithic implements from Pagliare di Sassa (L'Aquila, Central Italy). In G. Cavarretta, P. Gioia, M. Mussi, & M. R. Palombo (Eds.), *The world of Elephants* (pp. 224–229). Roma: Consiglio Nazionale delle Ricerche.

Palombo, M.R., Azanza, B., & Alberdi, M.T. (2002). Italian mammal biochronlogy from the latest Miocene to the Middle Pleistocene: a multivariate approach. *Geologica Romana, 36*, 335–368.

Palombo M.R., Milli S., & Rosa C. (2004). Remarks on the biochronology of the late Middle Pleistocene mammalian faunal complexes of the Campagna Romana (Latium, Italy) *Geologica Romana, 37*(2003-2004), 135–143.

Pandolfi, L., & Marra, F. (2015). Rhinocerotidae (Mammalia, Perissodactyla) from the chrono-stratigraphically constrained Pleistocene deposits of the urban area of Rome (Central Italy). *Geobios, 48*(2), 147–167.

Parfitt, S.A., Barendregt, R.W., Breda, M., Candy, I., Collins, M.J., Coope, G.R., Durbidge, P., Field, M.H., Lee, J.R., Lister, A.M., Mutch, R., Penkman, K.E.H., Preece, R.C., Rose, J., Stringer, C.B., Symmons, R., Whittaker, J.E., Wymer, J.J. & Stuart, A.J. (2005). The earliest record of human activity in northern Europe. *Nature, 438*, 1008–1012.

Pavia, G., Bertok, C., Ciampo, G., Di Donato, V., Martire, L., Masini, F., Pavia, M., Santangelo, N., Taddei Ruggiero, E., & Zunino, M. (2010). Tectono-sedimentary evolution of the Pliocene to lower Pleistoceine succession of the Apricena- Lesina-Poggio Imperiale quarrying district (western Gargano, southern Italy). *Bollettino della Società Geologica Italiana, 129*, 132–155.

Petronio, C. (1979). *Dama nestii eurygonos* Azz. di Capena (Roma). *Geologica Romana, 18*, 105–125.

Petronio, C., & Sardella, R. (1998). *Bos galerianus* n. sp. (Bovidae, Mammalia) from the Ponte Galeria Frmation (Rome, Italy). *Neues Jahrbuch für Geologie und Paläontologie, 5*, 269–284.

Petronio, C., & Sardella, R. (1999). Biochronology of the Pleistocene mammal fauna from Ponte Galeria (Rome) and remarks on the Middle Galerian faunas. *Rivista Italiana di Paleontologia e Stratigrafia, 105*, 155–164.

Petronio, C., Argenti, P., Caloi, L., Esu, D., Girotti, E., & Sardella, R. (2002). Updating Villafranchian mollusc and mammal fauna of Umbria and Latium (Central Italy) *Geologica Romana, 36*, 369–387.

Petronio, C., Bellucci, L., & Di Stefano, G. (2013). *Axis eurygonos* from Pirro Nord (Apricena, Southern Italy). *Palaeontographica Abt. B, 298*, 169–181.

Petronio, C., Angelone, C., Atzori, P., Famiani, F., Kotsakis, T, & Salari, L. (2020). Review and new data of the fossil remains from Monte Peglia (late Early Pleistocene, central Italy). *Rivista Italiana di Paleontologia e Stratigrafia (Research in Paleontology and Stratigraphy), 126*(3), 791–819.

Pfeiffer, T. (1998). Die fossilen Damhirsche von Neumark-Nord (Sachsen-Anhalt) — *Dama dama geiselana* n. ssp. *Eiszeitalter und Gegenwart, 48*, 72–86.

Pfeiffer, T. (1999). Die Stellung von *Dama* (Cervidae, Mammalia) im System plesiometacarpaler Hirsche des Pleistozäns. *Courier Forschungsinstitut Senckenberg, 211*, 1–218.

Pfeiffer-Deml, T. (2018). The fossil fallow deer *Dama geiselana* (Cervidae, Mammalia, upgrade to species level) in the context of migration and local extinctions of fallow deer in the Late and Middle Pleistocene in Europe. *PalZ, 92*, 681–713.

Portis, A. (1893). *Storia fisica del bacino di Roma e studi sopra l'estensione da darsi al Pliocene Superiore.* Volume 1. Roma-Torino: Roux e C.L. press.

Portis, A. (1907). Di alcuni avanzi fossili di grandi ruminanti principalmente della provincia di Roma. *Palaeontolographia italica, 13*, 141–198.

Portis, A. (1909). Avanzi di Canidi fossili dai terreni sedimento-tufacei di Roma. *Bollettino della Società Geologica Italiana, 28*, 203–244.

Prat, F., & Suire, C. (1971). Remarques sur les cerfs comtemporains des deux stades würmiens. *Bulletin de la Société préhistorique française, 68*, 75–79.

Preece, R.C., & Parfitt, S.A. (2000). The Cromer Forest-bed Formation: new thoughts on an old problem. In S. G.Lewis, C. A. Whiteman, & R. C. Preece (Eds.), *The Quaternary of Norfolk and Suffolk: Field Guide* (pp. 1–27). London: Quaternary Research Association.

Russo Ermolli, E. R., Sardella, R., Di Maio, G., Petronio, C., & Santangelo, N. (2010). Pollen and mammals from the late Early Pleistocene site of Saticula (Sant'Agata de'Goti, Benevento, Italy). *Quaternary International, 225*(1), 128–137.

Sala, B. (1986). *Bison schoetensacki* Freud. from Isernia la Pineta (early Mid-Pleistocene, Italy) and revision of the European species of bison. *Palaeontographia Italica, 74*, 113–170.

Sala, B. (1992). I mammiferi del Quaternario italia no. In C. Tugnoli (Ed.), *I segni del tempo— Memoria delle origini ed icone del primordiale* (pp. 209–227). Trento: Atti corso agg. per personale docente.

Sala, B., & Masini, F. (2007). The late Pliocene and Pleistocene small mammal chronology in the Italian peninsula. *Quaternary International, 160*, 4–16.

Sala, B., Boulbes, N., Moigne, A.-M., & Thun Hohenstein U. (2014). L'insieme faunistico del Giacimento. In B. Muttillo, G. Lembo & C. Peretto (Eds.), *L'insediamento a bifacciali di Guado San Nicola, Monteroduni, Molise, Italia* (pp. 59-78). Ferrara: Annali dell'Università degli Studi di Ferrara, Sez. Museologia Scientifica e Naturalistica, Volume 10/1A, Università degli Studi di Ferrara.

Sardella, R., & Petrucci, M. (2012). The earliest Middle Pleistocene *Crocuta crocuta* (Erxleben, 1777) at Casal Selce (Rome, Italy). *Quaternary International, 267*, 103–110.

Sardella, R., Abbazzi, L., Argenti, P., Azzaroli, A., Caloi, L., Capasso Barbato, L., Di Stefano, G., Ficcarelli, G., Gliozzi, E., Kotzakis, T., Masini, F., Mazza, P., Mezzabotta, C., Palombo, M.R., Petronio, C., Rook, L., Sala, B., & Torre, D. (1998). Mammal faunal turnover in Italy from the Middle Pliocene to the Holocene. *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO, 60*, 499-512.

Sardella, R., Bedetti, C., Iurino, D. A., Pavia, M., & Bellucci, L. (2015). Comment on "Reassessing the sedimentary deposits and vertebrate assemblages from Ponte Galeria area (Rome, central Italy): an archive for the middle pleistocene faunas of Europe" by Marra, F., Pandolfi, L., Petronio, C., Di Stefano, G., Gaeta, M., & Salari, L. [*Earth-Science Reviews, 139* (2014), 104–122]. *Earth-Science Reviews, 147*, 201–203.

Schmidt-Nielsen, K. (1984). *Scaling*. Cambridge: University Press.

Steele, T.E. (2002). Red deer: their ecology and how they were hunted by Late Pleistocene hominids in western Europe. *Phd Thesis* (pp. 1-274), Stanford University.

Stefanelli, D., Mecozzi, B., Francescangeli, R., Girone, A., Marino, M., Montenegro, V., Sardella, R., & Breda M. (2021). The Fallow deer from Contrada Monticelli (Bari, Southern Italy): the southernmost occurrence of a large *Dama* of the early Middle Pleistocene. *Bollettino della Società Paleontologica Italiana, 60*(1), 55–60.

Strani, F., Demiguel, D., Bona, F., Sardella, R., Biddittu, I., Bruni, L., De Castro, A., Guadagnoli, F., & Bellucci, L. (2018). Ungulate

dietary adaptations and palaeoecology of the Middle Pleistocene site of Fontana Ranuccio (Anagni, Central Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology, 496*, 238–247.

Strani, F., Bellucci, L., Iannucci, A., Iurino D.A., Mecozzi, B., & Sardella, R. (2021). Palaeoenvironments of the MIS 15 site of Cava di Breccia - Casal Selce 2 (central Italian Peninsula) and niche occupation of fossil ungulates during Middle Pleistocene interglacials. *Historical Biology, 34*(3), 555–565.

Stuart, A.J., & Lister, A.M. (2010). The West Runton Freshwater Bed and the West Runton Mammoth. *Quaternary International, 228*, 12–48.

Skogland, T. (1989). Comparative social organization of wild reindeer in relation to food, mates and predator avoidance. *Advances in Ethology*, *29*, Berlin: Pual Parey.

R Core Team (2019). *R language definition*. Vienna, Austria: R foundation for statistical computing.

Terrigi, G. (1881). Le formazioni vulcaniche del bacino Romano considerate nella loro fisica costituzione e giacitura. *Atti della Regia Accademia dei Lincei*, *10*, 389–419.

Truv, J., & Cederlund, G. (2005). *Mammals in the areas adjacent to Forsmark and Oskarshamn. Population density, ecological data and carbon budget*. Swedish Nuclear Fuel and Waste Management Co.

Villa, P., Soriano, S., Grün, R., Marra, F., Nomade, S., Pereira, A., Boschian, G., Pollarolo, L., Fang, F., & Bahain, J.-J. (2016). The Acheulian and Early Middle Paleolithic in Latium (Italy): Stability and Innovation. *PLoS One 11*, e0160516.

Villa, P., Boschian, G., Pollarolo, L., Saccà, D., Marra, F., Nomade, S., & Pereira, A. (2021). Elephant bones for the Middle Pleistocene toolmaker. *PloS one, 16*(8), e0256090. https://doi.org/10.1371/journal.pone.0256090

Vos J. de, Mol, D., & Reumer J.W.F. (1995). Early Pleistocene Cervidae (Mammalia, Artyodactyla) from the Oosterschelde (the Netherlands), with a revision of the cervid genus *Eucladoceros* Falconer, 1868. *Deinsea, 2*, 95–121.

Weinstock, J. (1997). The relationship between body size and environment the case of Late Pleistocene reindeer (*Rangifer tarandus*). *Archeofauna, 6*, 123–135.

Weinstock, J. (2006). Environment, body size and sexual dimorphism in Late Glacial reindeer. In D. Ruscillo (Ed.), *Recent Advances in Ageing and Sexing Animal Bones* (pp. 246–252). Barnsley: Oxbow Books.

Yom-Tov, Y., & Geffen, E. (2006). Geographic variation in body size: the effects of ambient temperature and precipitation. *Oecologia, 148*, 213–218.