



Research Article

Size shifts in late Middle Pleistocene to Early Holocene *Sus scrofa* (Suidae, Mammalia) from Apulia (southern Italy): ecomorphological adaptations?

Alessio IANNUCCI^{1,*}, Raffaele SARDELLA^{1,2}, Flavia STRANI^{1,2,3}, Beniamino MECOZZI¹¹Dipartimento di Scienze della Terra, Sapienza Università di Roma, PaleoFactory, p.le Aldo Moro 5, I-00185, Roma, Italy²Istituto Italiano di Paleontologia Umana, via U. Aldrovandi 18, I-00197 Roma, Italy³Departamento de Ciencias de la Tierra, Área de Paleontología, Universidad de Zaragoza, Pedro Cerbuna 12, S-50009 Zaragoza, Spain**Keywords:**Aurelian
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Abstract

The extant wild boar *Sus scrofa* has one of the largest geographical range of all mammals, and from its appearance in the late Early Pleistocene (Epivillafranchian) it is also widely represented in the European fossil record. Early forms of the species were larger than Late Pleistocene ones, but neither the chronology nor the causes of the size reduction have been thoroughly investigated. Here, we considered for the first time a large number of fossils from several late Middle Pleistocene to Early Holocene sites of the Apulian region (Italian Peninsula). In contrast to the supposed existence of a progressive trend towards small dimensions, morphometric comparisons and body mass estimates allow us to recognize several size oscillations during the late Middle Pleistocene–Early Holocene, with large forms occurring during interglacial stages and smaller ones during glacial stages. This suggests that fossil Apulian wild boar did not conform to Bergmann's rule, that predicts larger size in colder climates due to the selective pressure towards lower surface area to volume ratio. Climate recrudescence may have played an indirect role in reducing the availability of trophic resources and hence promoting the observed pattern.

Introduction

The extant wild boar (*Sus scrofa*) is one of the widest-ranging mammals in the world, occurring natively throughout the Palearctic, northern Africa, the Middle-East and part of South-East Asia (Groves, 1981). Accordingly, it displays a great morphological diversity, with a significant amount of variation explained by geographical clines (Albarella et al., 2009; Groves, 2007). The species originated in Asia during the Early Pleistocene and spread in Europe during the late Early Pleistocene (Epivillafranchian) (Iannucci et al., 2020; Cherin et al., 2018; Frantz et al., 2016; Bellucci et al., 2015; Martínez-Navarro et al., 2015). It is first recorded in Europe from the ~1.1 Ma site of Untermassfeld (Germany) (Guérin and Faure, 1997), and in Italy from the slightly younger Slivia at ~0.9–0.85 Ma (Petronio et al., 2011; Ambrosetti et al., 1979). Early forms of wild boars are often ascribed to a distinct subspecies, *S. scrofa priscus* (Goldfuss, 1823), characterized by low molar complexity and large size (Tsoukala and Guérin, 2016; Petronio et al., 2011; Guérin and Faure, 1997; Faure and Guérin, 1983; Hünemann, 1975, 1969). The validity of this taxon is often questioned, but there is a general consensus in recognizing the large dimensions of early wild boars (Made et al., 2017; Lister et al., 2010). Yet, the tempo and mode of the size reduction of this species have not been carefully investigated so far. The evolution of the wild boar is often depicted as a progressive trend towards smaller dimensions, and successively smaller

chronosubspecies are sometimes identified (Hünemann, 1969), eventually leading to the modern *S. s. scrofa* since the Late Pleistocene (Faure and Guérin, 1983). However, this scenario is in contradiction with the high adaptive plasticity exhibited by the species (Ballari and Barrios-García, 2014), which displays substantial variation in size and morphology throughout its geographic range (Albarella et al., 2009; Genov, 1999).

In Italy — an especially suitable territory for biochronological and paleoenvironmental studies of the Mediterranean area (Sardella et al., 2018a; Azzaroli, 1977) — Suidae fossils of large size are known from numerous Middle Pleistocene localities, such as Bristie 1 (Lugli and Sala, 2000), Cerè (Fabiani, 1919), La Polledrara di Cecanibbio (Anzidei et al., 2012), Malagrotta (Caloi and Palombo, 1979) and Torre del Pagliaccetto (Caloi and Palombo, 1978). Other scanty and/or poorly described remains come from several key localities of the Italian large mammal biochronological scale, for instance Ponte Galeria (Petronio and Sardella, 1999), Isernia La Pineta (Sala, 1996), Fontana Ranuccio (Strani et al., 2018) and Visogliano (Abbazzi et al., 2000). However, large specimens have also been recovered from Late Pleistocene sites of Italy (e.g. Minieri et al., 1995; Mirigliano, 1942; Del Campana, 1909), and more generally in Europe (e.g. Lister et al., 2010; Moigne et al., 2006; Faure and Guérin, 1983), thus challenging the hypothesis of a gradual size reduction.

The existence of ecological and dimensional clines over the extant *S. scrofa* geographical range, urges to investigate its evolution excluding the confounding factor of topographical distance, which is known to

*Corresponding author

Email address: alessio.iannucci@uniroma1.it (Alessio IANNUCCI)

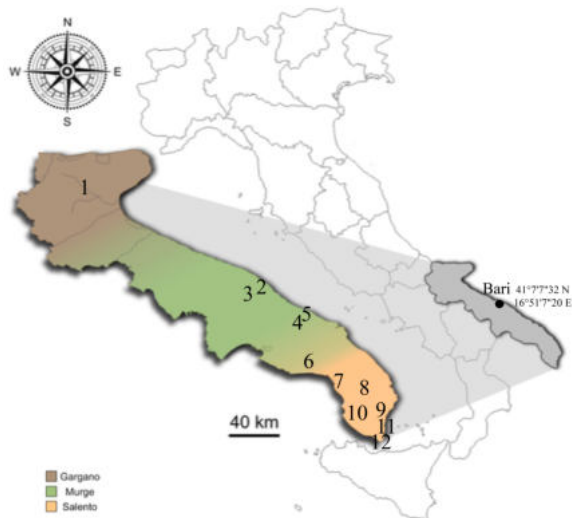


Figure 1 – Location of Apulia (grey area) along the Italian Peninsula. The Gargano, Murge and Salento areas are indicated. 1 – Grotta Paglicci; Murge: 2 – Grotta delle Mura; 3 – Grotta della Jena; 4 – Grotta Laceduzza; 5 – SMA-esterno; 6 – Avetrana; 7 – Grotta Mario Bernardini; Grotta Uluzzo C; 8 – Melpignano; San Sidero; 9 – Grotta delle Striare; Grotta Romanelli; Grotta Zinzulusa; 10 – Fondo Focone; 11 – Grotta delle Prazziche; 12 – Grotta dei Giganti; Grotta delle Tre Porte.

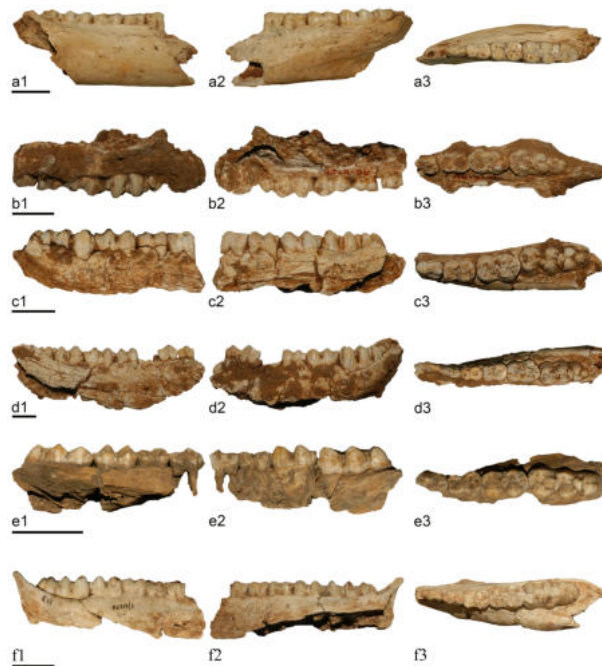


Figure 2 – Fossil specimens from Apulian sites: a – MPND683, right hemimandible from Melpignano; b – A8-II-205, left maxillary from Avetrana; c – AND1694, left hemimandible from Avetrana; d – AND1695, right hemimandible from Avetrana; e – ISIPU-GZ482, right hemimandible from Grotta Zinzulusa; f – MUCIV-GR3499, left hemimandible from Grotta Romanelli. Fossils are figured in labial (l), lingual (l), and occlusal (o) view. Scale bars 3 cm.

affect the morphology of the species (Iannucci et al., 2020; Albarella et al., 2009; Groves, 2007, 1981; Guérin and Faure, 1997).

In this work, a comprehensive account of wild boar material from the Apulian region, in many cases reported but not described, is presented (e.g. Grotta del Cavallo, Sarti et al., 1998; Grotta Uluzzo C, Borzatti von Löwenstern and Magaldi, 1969; Grotta dei Giganti, Blanc, 1958). Apulia is a geographically well-constrained setting, with a rich fossil record and a long research tradition, hence represents an optimal case study to test *S. scrofa* body size variability during the late Mid-

dle Pleistocene-Early Holocene. The existence of evolutionary trends is investigated by performing tooth and postcranial measurements and body mass estimates.

Table 1 – Fossil material of *Sus scrofa* from the late Middle Pleistocene-Early Holocene of the Apulian Peninsula: 1 – San Sidero (1a - Cava L, 1b - fessura I); 2 – Melpignano (2a - Cava Bianco, 2b - Cava Nuzzo, 2c - Collezione Mirigliano); 3 – Grotta delle Striare; 4 – Grotta delle Tre Porte (Antro del Bambino, level F); 5 – Avetrana (5a - beds 2–7, 5b - bed 8); 6 – Grotta Mario Bernardini (6a - levels B3–4, 6b - level A8); 7 – Grotta Uluzzo C (7a - level G, 7b - level F, 7c - level E); 8 – Grotta dei Giganti (levels 3f–3c); 9 – Grotta Laceduzza; 10 – Grotta Zinzulusa (10a - level B6, 10b - levels B5–3); 11 – SMA-esterno (11a - level 8, 11b - levels 6A–4C); 12 – Fondo Focone; 13 – Grotta Romanelli (levels E–A); 14 – Grotta della Jena; 15 – Grotta delle Prazziche.

Anatomical portion	Site																								
	1a	1b	2a	2b	2c	3	4	5a	5b	6a	6b	7a	7b	7c	8	9	10a	10b	11a	11b	12	13	14	15	
Cranium									1										1			10			
Maxillary									1								1			1		2		8	
Upper tooth	1		1	1			2	3	8		1		1				2	2	1	1	1	6		7	
Hemimandible			5	1	1				5		1		1						2		1	5		9	
Lower tooth	1	2	2	3	1	1	3	2	8			1	2	1	2	4	3	4	1	1	3	10	1	16	
Scapula																							2		
Vertebra				15																			2		
Rib				1																					
Pelvis	2		5																						
Humerus		1							2		1								2					1	
Radius		1			1																	1		1	
Ulna			2						1															1	
Metacarpal			1	1				1																4	
Carpal									5																
Femur				1					2													1			
Tibia			3	1					1																
Fibula																								2	
Metatarsal			2									1	1											5	
Metapodial								1	4											1				3	
Calcaneus					1				3																
Talus			3						3																
Tarsal									2															1	
I Phalanx	1							2	2											3				3	
II Phalanx	1								5	1	1													2	
III Phalanx									3																3
Total	6		43	8	3		5	8	57	1	4	2	5	1	2	4	6	6	14	3	6	64	1	40	

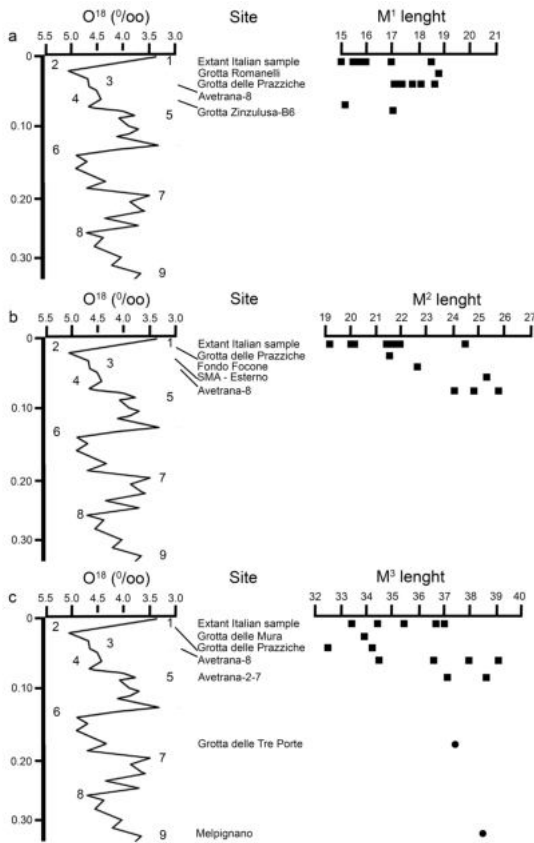


Figure 3 – The variation in size in *Sus scrofa*, as indicated by the length of the upper first (a), second (b), and third (c) molar. Age in millions of years (vertical axis) and oxygen isotope curves (horizontal axis; after Shackleton, 1995) on the left, followed by the fossiliferous sites and their suggested ages. Symbol: circle – Middle Pleistocene; square – Late Pleistocene-Holocene.

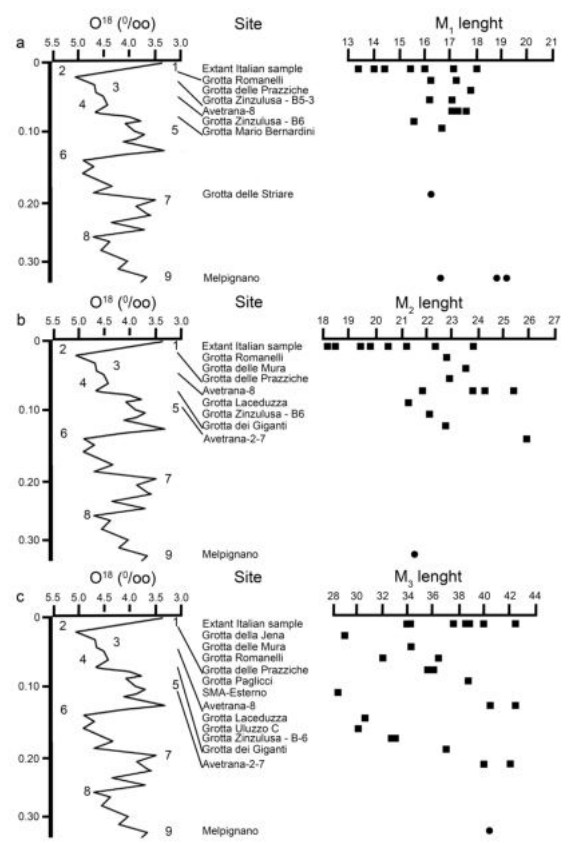


Figure 4 – The variation in size in *Sus scrofa*, as indicated by the length of the lower first (a), second (b), and third (c) molar. Age in millions of years (vertical axis) and oxygen isotope curves (horizontal axis; after Shackleton, 1995) on the left, followed by the fossiliferous sites and their suggested ages. Symbol: circle – Middle Pleistocene; square – Late Pleistocene-Holocene.

Confounding factors of variations

Body size may be influenced by several factors which are not related to ecomorphological adaptations and may introduce a bias in our analysis. Here they are briefly discussed.

Although wild boars are sexually dimorphic animals with males larger than females, the sex determination of isolated remains is possible only for a few anatomical elements, namely canines and related cranial regions (e.g. mandibular symphysis, canine flanges). However, sexual size dimorphism is very low in cheek tooth measurements in *S. scrofa* (2–7%, Kuşatman, 1991; 3%, Made, 1991), and similar values occur in other extant suid species (2–5%, Made, 1991), whereas differences in the postcranial skeleton of *S. scrofa* are more variable and pronounced (1–16%, Kuşatman, 1991). A divergence between sexes

arises during growth, with females gaining relatively less weight than males from the age of ~18–24 months, mainly as a result of the pregnancy effort (Gallo-Orsi et al., 1995).

Human populations may have played a role in the prey selection, for instance preferably hunting wild boar juveniles, as reported for the *terre brune* of Grotta Romanelli (Tagliacozzo, 2003). However, a high percentage of young individuals also occurs in sites not associated with evidence of human presence (e.g. Melpignano, 16.3%), and it more likely reflects a natural fallout of the r-strategy adopted by the species (peak in juveniles mortality, Martínez-Navarro et al., 2015; Gaillard et al., 1989).

Similarly, hunting and predatory pressure have been demonstrated to be secondary factors in limiting the population density (strictly related to body mass) of extant wild boars, in comparison with temperature and trophic resource availability (Frauendorf et al., 2016; Nores et al., 2008; Okarma et al., 1995).

Therefore, even though it is not possible to completely exclude an influence of the aforementioned factors on body size shifts, the selective pressures of the physical environment have surely played a much more important role.

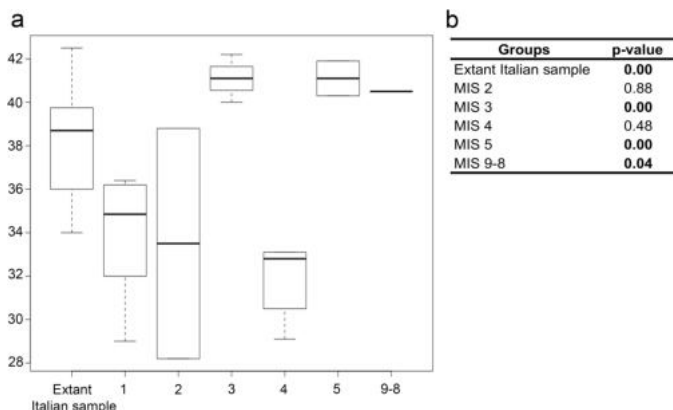


Figure 5 – (a) Boxplot of M_3L from the late Middle Pleistocene-Early Holocene sites grouped for chronology (MIS) (see Tab. 2); (b) Table of p -values for the linear model.

The Apulian region

The Italian territory represents a crossroads in the Mediterranean area, playing a pivotal role in our comprehension of palaeoenvironmental dynamics during the Quaternary (Sardella et al., 2018a). Its vast latitudinal extension causes a strong climatic gradient, which in turn produces regional differences in palaeontological faunal assemblages (Petronio et al., 2007; Sala and Masini, 2007; Bedetti et al., 2001; Gliozzi et al., 1997; Sala et al., 1992; Masini et al., 1990). In this context, the Apulian region (southern Italy), spanning more than 350 km from the Northwest to Southeast extremities, and with a least extension of 30 km along the

Table 2 – Chronology of the fossil material of *Sus scrofa* from the late Middle Pleistocene-Early Holocene of the Apulian Peninsula.

Site	Reference	MIS	Date
San Sidero	Mecozzi et al., 2019a; Sala et al., 1992; This work	?9–8	Biochronology
Melpignano	Mecozzi et al., 2019a; Sala et al., 1992; This work	?9–8	Biochronology
Grotta delle Striare	Maviglia, 1955; Cigna and Orlandi, 1954; This work	?7-5	Biochronology
Grotta delle Tre Porte	Blanc, 1958; This work	?7-5	Biochronology
Avetrana beds 2–7	Petronio et al., 2008; Sardella et al., 2005	5	Biochronology
Grotta dei Giganti	Aureli and Ronchitelli, 2018; Blanc, 1958	4	Biochronology and Chrono-cultural
Grotta Zinzulusa - B6	Blanc, 1962; Cardini, 1962	4	Biochronology and Chrono-cultural
Grotta Mario Bernardini	Aureli and Ronchitelli, 2018; This work	4	Stratigraphy and Chrono-cultural
Grotta Uluzzo C	Aureli and Ronchitelli, 2018; This work	4	Stratigraphy and Chrono-cultural
Grotta Laceduzza	Mecozzi et al., 2019b	4	Biochronology and Chrono-cultural
Avetrana bed 8	Salari et al., 2019; Mecozzi and Bartolini Lucenti, 2018	3	Biochronology
Fondo Focone	Cancellieri, 2017	2	Biochronology and Chrono-cultural
Grotta Zinzulusa - B5–3	Blanc, 1962; Cardini, 1962	2	Biochronology and Chrono-cultural
Grotta Paglicci	Boscato, 1994	2	Radiometric data
SMA-esterno	Coppola et al., 2017; Baills, 2015	2	Radiometric data
Grotta Romanelli	Calcagnile et al., 2019; Sardella et al., 2018b	1	Radiometric data
Grotta della Jena	Anelli, 1956; This work	1	Biochronology and Stratigraphy
Grotta delle Mura	Bon and Boscato, 1993	1	Radiometric data
Grotta delle Prazziche	Borzatti von Löwenstern, 1969, 1966	1	Stratigraphy and Chrono-cultural

Southwest-Northeast axis, represents a noteworthy case, a peninsula in the peninsula (Fig. 1).

Moreover, this territory is rich in mammal remains often associated to Mousterian technoculture (Middle Palaeolithic) and Neanderthal fossils (e.g. Fondo Cattiè, Corridi, 1989; Grotta delle Tre Porte, Blanc, 1962; see also Romandini et al., 2019). The human occupation of the region is also documented through the whole Upper Palaeolithic, with bone and lithic industry, mobiliary and rock art, and fossils of *Homo sapiens* (e.g. Grotta Romanelli, Sardella et al., 2019; Grotta Paglicci, Berto et al., 2017).

Since the end of 1800s Apulia represents a key region to study the mammal fauna evolution and the climatic changes that took place during the Quaternary in the Mediterranean area (e.g. Blanc, 1920; Botti, 1890, 1874a,b). Indeed, several Apulian fossiliferous localities are a reference point for the Italian large mammal biochronological scale, especially for the late Middle Pleistocene-Late Pleistocene transition (Petronio et al., 2007; Bedetti et al., 2001; Sala et al., 1992; among others). However, due to their complex depositional settings (inland karst systems and coastal caves), only a few Apulian sites have been recently radiometrically dated (e.g. Grotta del Cavallo, Zanchetta et al., 2018; Grotta Paglicci, Berto et al., 2017; Boscato, 1994). The earliest Apulian sites considered herein have long been chronologically attributed to the early Late Pleistocene (Sardella et al., 2005; Bologna et al., 1994; Sala et al., 1992), even though the ongoing revision of the stratigraphic and fossil data does not exclude an even older age (see Sardella et al., 2018b for discussion). For instance, the large mammal assemblage from the *terre rosse* of Melpignano was chronologically referred to the early Late Pleistocene (MIS 5). Nevertheless, the revision of the old fossil collections and the description of the new ones led to extend the biochronological time-span of this locality to the late Middle Pleistocene (Mecozzi et al., 2019a). Another Apulian site of debated chronology is Avetrana. The entire faunal assemblage has been firstly attributed to the early Late Pleistocene (MIS 5) (Pandolfi et al., 2013, 2011; Petronio et al., 2008). Later, the revision of the material from the uppermost fossiliferous layer of the succession (bed 8) led to refer this level to MIS 3 (Salari et al., 2019; Mecozzi and Bartolini Lucenti, 2018). However, there is neither a radiometric age for the deposit, nor a certain stratigraphic provenience for all the remains. If the revision of the material from bed 8 proposed a younger age for the upper part of the succession, on the other hand, the study in progress on the faunal remains from the lower part of the deposit would suggest an older age, probably referable to the late Middle Pleistocene.

Finally, the Apulian region has also been regarded as a refuge area for several mammals adapted to warm conditions, especially during MIS

4, even though the debate on this matter still goes on (Sardella et al., 2018b; Mecozzi et al., 2018; Pandolfi and Petronio, 2015; Braun and Palombo, 2012; among others).

Materials and methods

The sample of Suidae analysed herein is housed in several Italian institutions and museums (Tab. 1 and online resource Supplemental S1). We built our dataset by considering the available studies on specimens from the late Middle Pleistocene to the Early Holocene of the Apulian region (Tab. 2 and online resource Supplemental S1). We compared the fossil remains with a sample of extant Italian wild boars stored in the Comparative Anatomy Museum “Battista Grassi”, Sapienza University of Rome (MACUS), as well as literature data from Kuşatman (1991). Measurements of the specimens considered in this study are provided in Tab. 3 (upper teeth), Tab. 4 (lower teeth), and Tab. 5 (postcranial). Craniodental and postcranial measurements were taken to the nearest 0.1 mm with a digital caliper, as reported by Driesch (1976).

We also performed body mass estimates (Tab. 5 and 6) of the fossil and extant samples following regression equations based on the length of each molar (Damuth, 1990), on the antero-posterior distal diameter (Bd) of humerus and radius (Scott, 1990), and on the greatest length (GLI) of the talus (Tsubamoto, 2014). Slope and intercept values are given in Tab. 7. Since in our sample males and females are treated together, the estimated body masses should be regarded as approximate mean values between sexes.

We further assessed the degree of intergroup affinity of the Apulian wild boar by conducting statistical analysis on the length of the lower third molar (M_3L), which is the best represented tooth in our sample and the least affected by wear, thus the most reliable for comparisons. The dataset has been grouped according to the chronology (MIS) in order to assess the correlation between climate and size. We acknowledge that during an isotope stage several climatic oscillations may occur, but due to the lack of radiometric data the representativeness of MIS groups is usually considered an acceptable assumption, common to several studies focused on intraspecific size comparisons in the Pleistocene (e.g. Marciszak et al., 2019; Mazza and Bertini, 2013; Asperen, 2010). Moreover, this resolution is at a finer scale than what adopted in previous works on *S. scrofa* (Tsoukala and Guérin, 2016; Guérin and Faure, 1997; Faure and Guérin, 1983). MIS 1 is technically an interglacial stage, but the sites considered herein actually date to the early part of the Holocene, before the onset of the present-day climate regime (Giustini et al., 2018; Martrat et al., 2014; Sadori and Narcisi, 2001). Therefore, we refer to interglacial periods (MIS 5 and MIS 3) and Early Holocene (MIS 1) separately. We evaluated differences in M_3L in the

Table 3 – Measurements (mm) of the upper teeth of *Sus scrofa* from the late Middle Pleistocene-Early Holocene sites of Apulia and the extant Italian wild boar.

Site	Reference	MIS	P ³ L	P ³ W	P ⁴ L	P ⁴ W	M ¹ L	M ¹ W	M ² L	M ² W	M ³ L	M ³ W
Melpignano	Bologna, 1992	79–8									38.5	19.0
Grotta delle Tre Porte	This work	77–5									37.4	21.9
Avetrana 2–7	This work	5									37.8 (min=37.1- max=38.6)	20.5 (min=19.0- max=22.0)
Grotta Zinzulusa - B6	This work	4					17.1	13.8				
Avetrana 8	This work	3	13.0 (min=12.2- max=13.9)	13.4 (min=12.7- max=14.1)			15.6	14.6	24.8 (min=24.0- max=25.7)	18.1 (min=16.7- max=19.6)	37.0 (min=34.5- max=39.1)	21.0 (min=19.0- max=22.0)
Fondo Focone	This work	2							22.6	19.4		
SMA-esterno - Gravettian	This work	2							25.5	17.2		
SMA-esterno - Epigravettian	This work	2	13.3	13.6								
Grotta Romanelli	This work	1	14.9	10.5			18.9	13.9				
Grotta delle Mura	Bon and Boscato, 1993	1									33.9	18.5
Grotta delle Prazziche	This work	1	14.4	14.5			17.7 (min=17.1- max=18.6)	14.2 (min=13.8- max=15.1)	21.5	16.4	33.3 (min=32.5- max=34.2)	18.8 (min=18.7- max=19.0)
Extant <i>Sus scrofa</i>	Kuşatman, 1991; This work		14.5	10.9	14.2	14.6	16.4 (min=15- max=18.6)	14.7 (min=13.8- max=13.5)	21.3 (min=19.1- max=24.5)	17.9 (min=16.5- max=19.2)	35.6 (min=33.4- max=37)	20.5 (min=19- max=21.8)

late Middle Pleistocene, Late Pleistocene, Early Holocene, and extant Italian samples, using linear model with corner point parameterization testing the null hypothesis of no-differences between the mean of the reference sample (MIS 1) and the other populations ($p>0.05$). Sites of uncertain age are not included in the analysis. The statistical analysis was performed using the R software (R Core Team, 2019).

Institutional abbreviations

IGF: Museum of Natural History of the University of Florence, section of Geology and Paleontology. IIPP: Italian Institute of Prehistory and Protohistory. IsIPU: Italian Institute of Human Paleontology. ITCGC: Commercial Technical Institute “Galilei-Costa”. MACUS: Comparative Anatomy Museum “Battista Grassi”, Sapienza University of Rome. MGP: Museum of Geology and Paleontology of Turin. MPCCSM: Museum of Pre-Classical Civilizations of Southern Murgia. MPUN: Paleontological Museum of the University of Naples Federico II. MUCIV: Archaeozoology laboratory of the Museum of Civilizations (includes the National Prehistoric Ethnographic Museum “Luigi Pigorini”). MUST: University Museum of Earth Sciences, Sapienza University of Rome (includes the Museum of Paleontology, MPUR). PF: PaleoFactory Laboratory, Sapienza University of Rome. SMCC: Speleological Museum of Castellana Caves “Franco Anelli”.

Results and discussion

Morphometry

Suidae from the late Middle-Late Pleistocene of Apulia display a huge dental variability (Fig. 2, 3, and 4). Nevertheless, the statistical analysis of M₃L supports a significant separation between a large-sized interglacial group and a small-sized glacial + Early Holocene one. In fact, the MIS 1 reference sample is classified as distinct from the interglacial samples (MIS 3 and MIS 5), Melpignano, and the extant Italian population, but not from glacial groups (MIS 2 and MIS 4) (Fig. 5).

Lower third molars are larger in Melpignano (M₃L 40.5 mm) and interglacial specimens (Avetrana 2–7: M₃L mean 41.1 mm, min 40.3 mm, max 41.9 mm; Avetrana 8: M₃L mean 41.1 mm, min 40.0 mm, max 42.2 mm) than in the glacial ones (the longest specimen is from Grotta Paglicci: M₃L 38.8 mm) and extant wild boar (M₃L mean 38.2 mm, min 34.0 mm, max 42.5 mm) (Tab. 4, Fig. 4). These values significantly exceed the 2–7% range of sex-related differences observed in previous studies (Made, 1991; Kuşatman, 1991). Indeed, the average interglacial (MIS 3 and MIS 5) M₃L of 41.1 mm is 20.2% larger than the average glacial length of 32.8 mm, with no overlap in measurement (Tab. 4, Fig. 5). Judging by their size, interglacial suids from Apulia are closer to the Italian Middle Pleistocene remains than to the others Apulian Late Pleistocene ones. Particularly, M₃L from Avetrana are comparable to Bristie 1 (Trieste) (M₃L mean 42.3 mm, min 39.6 mm, max 44.1 mm; M₃W mean 18.9 mm, min 18.0 mm, max 19.7 mm), Cerè (M₃L 41.5.0 mm, M₃W 17.5 mm) and the upper levels of Torre del Pagliaccetto (Rome) (Id. n.399: M₃L 47.0 mm, M₃W 20.0 mm; Id. n.624: M₃L 41.0 mm M₃W 19.0 mm) chronologically referred to the Middle Pleistocene (Ghezzo et al., 2014; Lugli and Sala, 2000; Caloi and Palombo, 1978; Fabiani, 1919). Conversely, small-sized *S. scrofa* is reported from Grotta della Cala (Salerno) levels dated to 26.380 ± 260 ¹⁴C yr BP and 26.680 ± 320 ¹⁴C yr BP (MIS 2) (M₃L 30.1 mm, M₃W 17.6 mm; M₂L 25.2 mm, M₂W 17.0 mm; M₃L 27.5 mm, M₃W 15.6 mm) (Boscato et al., 1997). Second molar measurements are consistent with these results (interglacial-glacial divergence: M²L 3.2%, M₂L 9.24%), with late Middle Pleistocene and interglacial specimens of larger size than the rest of the fossil material, whereas first molars do not evidence a clear pattern (Tab. 3 and 4, Fig. 3 and 4).

The postcranial sample is too limited to draw significant considerations, nevertheless interglacial specimens from Avetrana are larger than the other specimens (Humerus Bd: 50.4 mm, 52 mm; Talus length: 57.1 mm; 60.8 mm) and close to the Middle Pleistocene Bristie 1 (Humerus Bd: 49.5 mm; 52.3 mm) or even larger (Talus length:

Table 4 – Measurements (mm) of the lower teeth of *Sus scrofa* from the late Middle Pleistocene-Early Holocene sites of Apulia and the extant Italian wild boar.

Site	Reference	MIS	P ² L	P ² W	P ³ L	P ³ W	P ⁴ L	P ⁴ W	M ¹ L	M ¹ W	M ² L	M ² W	M ³ L	M ³ W
Melpignano	This work	79-8					13.8	8.5	18.3 (min=16.8- max=19.2)	10.8 (min=9.2- max=11.7)	21.5	15.1	40.5	16.4
Grotta delle Striare	This work	77-5							16.2	11.8	25.9	17.5	41.1	17.7
Averana 2-7	This work	5											(min=40.3- max=41.9)	(min=17.5- max=17.9)
Grotta dei Giganti	This work	4	13.2	7.6			15.3	9.0	15.6	10.6	22.8	15.1	37.1	16.7
Grotta Zinzulusa - B6	This work	4									22.1	14.5	33.0	15.9
Grotta Mario Bernardini	This work	4											(min=32.8- max=33.1)	(min=15.2- max=16.6)
Grotta Uluzzo C	This work	4					13.8	9.7	16.6	12.6	21.2	12.7	29.1	15.4
Grotta Laceduzza	This work	4							17.3	12.7	23.8	16.6	30.5	14.6
Averana 8	This work	3	12.2	4.7	14.6 (min=14.4- max=14.8)	6.7 (min=6.4- max=7.1)	15.6 (min=15.1- max=16.1)	9.4 (min=9.0- max=9.9)	17.3 (min=17.1- max=17.5)	12.7 (min=11.9- max=13.7)	21.2 (min=21.9- max=25.4)	16.6 (min=16.4- max=16.9)	41.1 (min=40.0- max=42.2)	17.9 (min=17.4- max=18.3)
Fondo Focone	This work	2	11.6	6.8					16.7	11.3)				
Grotta Zinzulusa - B5-3	This work	2							(min=16.2- max=17.1)	(min=11.1- max=11.4)				
Grotta Paglicci	Boscatto, 1994	2							16.7	11.5)			38.8	17.8
SMA-esterno - Epigravettian	This work	2							16.7	11.5	22.9	15.0	28.2	14.8
Grotta Romanelli	This work	1			13.9	8.2	13.9	9.7	16.7 (min=16.2- max=17.2)	11.5 (min=10.9- max=12.0)	22.9 (min=14.6- max=32.0)	15.0 (min=15.3)	34.2 (min=14.7- max=36.4)	15.9 (min=17.1)
Grotta della Jena	This work	1											29.0	14.6
Grotta delle Mura	Bon and Boscatto, 1993	1							17.8	13.2	23.7	14.0	34.0	16.7
Grotta delle Prazziche	This work	1			12.1	7.0					22.9	15.7	35.9	16.0
Extant <i>Sus scrofa</i>	Krusáman, 1991; This work		11.5	5.3	14.2	7.4	14.7	9.3	15.5 (min=14.2- max=15.6)	11.9 (min=11.5- max=12.5)	20.7 (min=18.2- max=23.8)	14.9 (min=13- max=16.7)	38.2 (min=34- max=42.5)	17.0 (min=15.5- max=18.6)

Table 5 – Measurements (mm) of postcranial remains and associated body mass estimates (Kg) of *Sus scrofa* from the late Middle Pleistocene-Early Holocene sites of Apulia.

Site	Reference	MIS	Humerus Bd	Humerus estimate	Radius Bd	Radius estimate	Talus GL1	Talus estimate
Melpignano	This work	79–8			37.4	111.4		
Grotta Mario Bernardini	This work	4	47.7	159.1				
Avetrana 8	This work	3	51.2	198.2			58.9	289.6
			(min=50.4- max=52)	(min=188.7- max=207.7)			(min=57.1- max=60.8)	(min=261.3- max=317.9)
Fondo Focone	This work	2			34.3	89.8		
Grotta Paglicci	Boscato, 1994	2			41.7	145.7	49.2	166.3
							(min=46- max=52.4)	(min=132.9- max=199.8)
Grotta Romanelli	This work	1	45.3	137.1				

51 mm; 54 mm; 57.5 mm) (Tab. 5). Moreover, at least for the talus, glacial-interglacial differences (16.5%) slightly exceed the range of sexual variability of modern wild boar (Kuşatman, 1991).

The large size of Middle Pleistocene European wild boar is widely recognized among researchers (Lister et al., 2010; Guérin and Faure, 1997), but no agreement exists on the time and mode of the size reduction. Our results reveal that in the late Middle-Late Pleistocene there is no progressive trend towards small dimensions, as assumed in previous studies (e.g. Guérin and Faure, 1997; Faure and Guérin, 1983; Hünermann, 1975, 1969). Conversely, we observe several shifts in size, related to interglacial-glacial cycles. The only apparent discrepancy is the interglacial but small-sized MIS 1 sample (Grotta Romanelli, Grotta della Jena, Grotta delle Mura, Grotta delle Prazziche). However, the Early Holocene was characterized by a cold and dry environment (Giustini et al., 2018; Martrat et al., 2014; Sadori and Narcisi, 2001), hence this exception actually proves the general pattern observed in this study (smaller size in colder settings). The sample from MIS 2 displays wide amplitude of M₃L (min 28.2 mm; max 38.8 mm). The variability of this group, unfortunately represented by only two specimens (Tab. 4), exceeds that of the extant sample, even if it does not overlap with MIS 3 and MIS 5 specimens.

Body mass

Predicted values vary greatly between different measured elements (teeth: M¹L min estimate: 49.4 kg; M₃L max estimate: 127 kg; Humerus Bd min estimate: 137.1 kg; max estimate: 207.7 kg; Tab. 5 and 6). Therefore, it is not possible to use body mass as a common currency to compare different morphometric measurements. Suidae are generalist mammals that retain primitive anatomical features (e.g. bunodont dentition, four-toes foot), and the difficulties in reconstructing the body mass of this group of animals are well known in the literature (Fortelius et al., 1996; Janis, 1990; Scott, 1990). For the same reason, we would have expected more reliable predictions based on the talus length, being the equations provided by Tsubamoto (2014) developed with the aim of reconstruct the body mass of Palaeogene mammals with difficult systematics affinities. However, this is not the case either. In fact, talus-based results are clearly overestimated (Avetrana max estimate: 317.9 kg), predicting body masses comparable only to the largest living wild boars from the Russian Far East (Heptner et al., 1988).

Comparing the outcomes obtained for the extant Italian sample with values directly measured on living animals — between 58.9 Kg and 85.6 Kg (Apollonio, 2003) — it can be supported that second molars provide the most reliable results — being between 56.9 kg and 75.3 kg — in agreement with previous studies (Fortelius et al., 1996; Janis, 1990). For what concerns the other teeth, first and third molars estimates are quite divergent. Precisely, first molars underestimate the individual body mass, whereas third molars overestimate it. Only the latter case has an explanation from the literature, as a limitation of using ungulate-fitted equations for omnivores, which possess proportionally longer teeth (Janis, 1990).

According to second molar predictions, the heaviest wild boars occurred during interglacial stages, with estimated mean values in each case above the ones predicted for the glacial and extant samples (Tab. 4). In fact, M²L predicts an average body mass of 76.3 kg for the interglacial sample (MIS 5 and MIS 3), whereas average values are 73.9 kg for the glacial one (MIS 4 and MIS 2) and 65.7 kg for the extant population. M₂L provides similar results, 75.5 kg during interglacial periods, whereas average glacial, early Holocene and extant values are respectively 68.7 kg, 72.2 kg, and 64.5 kg. M₁L, M³L, and M₃L estimates are consistent with these results, even though they provide less reliable absolute values. The only exception are M¹L estimates, which are biased, however, by the poor representativeness of the first upper molar in the interglacial sample (only one specimen) and by the high percentage of young individuals — thus with relatively longer teeth, being less affected by wear — in the Early Holocene sample.

Ecomorphological adaptations

Many generalist, wide-ranging large mammal species, display several ecomorphological adaptations in accordance with the environmental variations encountered throughout their geographic range. The extant wild boar roughly follows Bergmann's ecogeographical rule (Bergmann, 1847), that predicts larger size in colder climates (Albarella et al., 2009; Faure and Guérin, 1983). This pattern has been suggested to be valid even through time for other species, with large-sized *Crocota crocota* (Klein and Scott, 1989), *Bos primigenius* (Wright, 2013; Cerilli and Petronio, 1992) and *Canis lupus* (Mecozzi and Bartolini Lucenti, 2018; Sansalone et al., 2015) reported from glacial stages. However, in fossil *S. scrofa* from Apulia large dimensions are, conversely, associated with interglacial stages, and this study focuses on a well-constrained region, hence excluding a geographical-driven explanation for the observed values.

Moreover, several studies have casted doubt on the generality of Bergmann's rule (e.g. Huston and Wolverson, 2011; McNab, 2010; Meiri et al., 2007; Yom-Tov and Geffen, 2006; Ashton et al., 2000; Dayan et al., 1991; Demment and Van Soest, 1985). Indeed, contrary to the rule predictions, several fossil mammals underwent drops in size in colder climatic conditions (Lister et al., 2010; Collinge, 2001; Kurtén, 1968) or exhibited a series of size fluctuations for which climate is hardly the solely responsible (Marciszak et al., 2019; Made et al., 2014). Asperen (2010) examined late Middle Pleistocene caballoid horses from Europe and concluded that the glacial specimens were in general smaller than the interglacial ones, interpreting this evidence as the result of an adaptive response to the open-environments degradation and the consequently lower environmental productivity. Similarly, Mazza and Bertini (2013) observed evidence of climate-driven body size changes in Pleistocene hippopotamuses, with larger specimens found in warmer intervals and smaller individuals in colder settings. The authors argued for the combined importance of the short-term Pleistocene climatic cycling (recurrent stresses) and the long-term Quaternary habitat fragmentation (general deterioration), in promoting less favourable environmental conditions.

Table 6 – Body mass estimates (Kg) derived from the molars of *Sus scrofa* from the late Middle Pleistocene-Early Holocene sites of Apulia and the extant Italian wild boar.

Site	Reference	MIS	M ¹ L	M ² L	M ³ L	M ₁ L	M ₂ L	M ₃ L
Melpignano	This work	?9–8			109.5	58.1 (min=53.5- max=60.9)	67.1	121.9
Grotta delle Striare	This work	?7–5				51.6		
Grotta delle Tre Porte	This work	?7–5		106.4				
Avetrana 2–7	This work	5			107.5 (min=105.5- max=109.8)		80.6	123.7 (min=121.3- max=126.1)
Grotta dei Giganti	This work	4					71.1	111.7
Grotta Zinzulusa - B6	This work	4	54.0			49.8	68.9	99.3 (min=98.7- max=99.8)
Grotta Mario Bernardini	This work	4				52.9		
Grotta Uluzzo C	This work	4						87.8
Grotta Laceduzza	This work	4					66.1	92.0
Avetrana 8	This work	3	49.4	76.3 (min=73.8- max=78.9)	105.3 (min=98.2- max=111.2)	55.0 (min=54.4- max=55.7)	74.1 (min=68.3- max=79.0)	123.7 (min=120.4- max=127.0)
Fondo Focone	This work	2		69.5				
Grotta Paglicci	Boscatto, 1994	2						116.8
Grotta Zinzulusa - B5–3	This work	2				53.2 (min=51.6- max=54.4)		
SMA-esterno - Gravettian	This work	2			78.3			
SMA-esterno - Epigravettian	This work	2						85.1
Grotta Romanelli	This work	1	59.6			53.2 (min=51.6- max=54.7)	71.3	103.0 (min=96.5- max=109.6)
Grotta della Jena	This work	1						87.5
Grotta delle Mura	Bon and Boscatto, 1993	1			96.5		73.8	102.5
Grotta delle Prazziche	This work	1	55.9 (min=54.0- max=58.7)	66.2	94.9 (min=92.6- max=97.4)	56.6	71.4	108.1 (min=107.5- max=109.0)
Extant <i>Sus scrofa</i>	Kuşatman, 1991; This work		51.7 (min=47.5- max=58.7)	65.7 (min=58.9- max=75.3)	101.4 (min=95.1- max=105.3)	49.4 (min=43.2- max=57.2)	64.5 (min=56.9- max=74.1)	114.9 (min=102.5- max=127.9)

During glacial periods, in the Mediterranean area the reduced availability of trophic resources was pronounced, with generally open palaeoenvironments dominant (steppe and/or grasslands) (Renault-Miskovsky et al., 2015, 2011; Allen and Huntley, 2009; among others). Moreover, Apulia is a relatively isolated peninsula, whose geographical setting may have exacerbated the patchiness of the environment in cooler and drier stages. Therefore, a great deterioration and fragmentation of the forest, and consequently the decrease of the available trophic resources and the increase of the competition, might have promoted the observed size reductions in *S. scrofa* during the glacial stages.

Indeed, in the low trophic Mediterranean area, extant wild boars from Andalusia (southern Spain), Corsica (France), and Sardinia (Italy) are usually grouped in the subspecies *S. scrofa meridionalis*, whose small size is the most distinctive trait (Groves, 2007). However, Corsica and Sardinia are islands whereas Andalusia is a low trophic, but continental, region, similarly to Apulia.

These examples testify that “rules” alternative to Bergmann’s thermoregulatory principle better explain the wild boar geographic size pattern, such as the “resource rule” (resource availability; McNab, 2010) or the “eNPP rule” (amount of ecologically and evolutionarily relevant net primary productivity; Huston and Wolverton, 2011). Indeed, several empirical studies that have evaluated the adherence of different species to Bergmann’s principle (Freckleton et al., 2003; Meiri and Dayan, 2003; Ashton et al., 2000), have also denoted a dissimilar attitude to follow the rule in large and small mammals, with no or different patterns more common in smaller species (e.g. adherence to the

rule: >85% in species larger than 5 kg; <50% in species smaller than 0.5 kg; Meiri and Dayan, 2003). However, on a theoretical ground this differential response is in contrast with Bergmann’s thermoregulatory explanation, since small mammals are supposed to display a stricter adherence to the rule, being affected by a higher rate of heat dispersion (Ashton et al., 2000; Studel et al., 1994). The paradox is solved if another underlying principle is proposed to describe the observed pattern: the availability of trophic resources (Huston and Wolverton, 2011; McNab, 2010). In fact, in this case the differences between large and small mammals can be interpreted as differences between, respectively, K- and r-selected species (which differ in terms of productivity and efficiency of reproduction), the latter being more prone to evolve faster adaptations to cope with resources oscillations (Tuomi, 1980; Pianka, 1970). Palaeontologists are well aware of the dissimilar rate of change in small and large mammals, which enhance the importance of integrated biochronological scales (Masini and Sala, 2007; Gliozzi et al., 1997).

Of course, the dichotomy between r and K strategy is an empirical generalization and species are distributed along an ecological continuum (Tuomi, 1980; Pianka, 1970). Indeed, despite being large mammals, suids are relatively r-selected species (Martínez-Navarro et al., 2015) and this is reflected in the great biochronological value of this group (e.g. White and Harris, 1977). The wild boar, in particular, can be considered the most r-selected extant large mammal, being the ungulate species with the highest reproductive potential in relation to its body mass (Bieber and Ruf, 2005).

Table 7 – Regression equations used for estimating the body mass of *Sus scrofa* from the late Middle Pleistocene-Early Holocene sites of Apulia and the extant Italian wild boar.

Equation	Reference	Measure (a)	Slope (b)	Intercept (c)
Body mass=axb+c	Damuth, 1990	M ¹ L	3.09	1.21
Body mass=axb+c	Damuth, 1990	M ² L	3.03	1.06
Body mass=axb+c	Damuth, 1990	M ³ L	2.81	1.29
Body mass=axb+c	Damuth, 1990	M ₁ L	3.11	1.24
Body mass=axb+c	Damuth, 1990	M ₂ L	3.07	1.07
Body mass=axb+c	Damuth, 1990	M ₃ L	2.99	0.80
Log ₁₀ (Body mass)=Log ₁₀ (a)xb+c	Scott, 1990	Humerus Bd	3.09	0.02
Log ₁₀ (Body mass)=Log ₁₀ (a)xb+c	Scott, 1990	Radius Bd	2.48	1.14
(Ln(Body mass)=Ln(a)xb+c)x1.345	Tsubamoto, 2014	Talus GLI	3.12	-0.46

This perspective provides further support for the evolutionary scenario reconstructed for the late Middle Pleistocene-Early Holocene *S. scrofa* in Apulia and challenges the supposed conformity of the species to Bergmann's rule. In fact, the ecological strategy adopted by the species is in contrast with an adherence to the rule, but explains how the wild boar managed to cope with the severe resource fluctuations occurred during glacial stages with a size reduction pattern, whereas other large mammals reacted by modifying their range or went extinct (see online resource Supplemental S1).

Conclusion

The wild boar is one of the most common species in the Middle-Late Pleistocene fossil record of Italy and Europe. Nevertheless, most of the material has never been described or figured, as in the case of several Italian localities assuming a key role for the Italian large mammal biochronological scale, such as Ponte Galeria, Isernia La Pineta, and Fontana Ranuccio.

The fossils from several late Middle Pleistocene to Early Holocene sites from the Apulian Peninsula are here considered for the first time. Our data give no support to the hypothesis of a progressive trend towards small dimension, as sometimes assumed in previous studies. Conversely, morphometric comparisons, body mass estimates and statistical analysis identify two distinct groups of wild boars: large-sized from interglacial stages; small-sized from glacial ones and the cold Early Holocene. The interglacial group is 20.2% larger in M₃L than both glacial and Early Holocene specimens, with no overlap in measurements. Moreover, this divergence markedly exceeds the range of sexual size dimorphism in extant wild boars (2–7%). M²L, M₂L, and M³L are consistent with these results, even though differences are less pronounced for second molars and we lack M³ from glacial sites. First molars and postcranial remains are too limited to draw significant considerations.

In the first cold Late Pleistocene stage, the straight-tusked elephant and hippo disappeared from Italy. This clearly indicates an early climatic recrudescence, which affected the composition of the large mammal fauna. The results of this work suggest that the wild boar apparently responded to strong climatic fluctuations with a size reduction pattern, whereas other large mammals reacted by modifying their range or went extinct. Moreover, climate could have played an indirect role in leading to the onset of a typical Mediterranean environment, reducing the availability of trophic resources. This pattern is in contrast with the supposed adherence of *S. scrofa* to Bergmann's rule, but in agreement with the r-strategy adopted by the species.

Finally, in order to provide a more articulated framework of the climate-terrestrial ecosystems interactions during the late Quaternary, the comparison to Peninsular Italy and other region of the Euro-Mediterranean area is needed. ☞

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Supplement S1 Late Middle Pleistocene-Early Holocene Apulian fossil Suidae.