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Late Miocene to Quaternary European Suidae: Evolution and Biochronology

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Foreword

This thesis is based on a collection of original papers elaborated during the three years of the PhD program in Earth Sciences, Sapienza University of Rome:

1. Iannucci A., Begun D.R., 2022. Suidae (Mammalia, Artiodactyla) from the late Miocene hominoid locality of Alsótelekes (Hungary). Geobios 71. https://doi.org/10.1016/j.geobios.2022.01.002

2. Iannucci A., Cherin M., Sorbelli L., Sardella R., (2021). Suidae transition at the Miocene-Pliocene boundary: a reassessment of the taxonomy and chronology of *Propotamochoerus provincialis*. Journal of Mammalian Evolution 28:323–335. https://doi.org/10.1007/s10914-020-09521-w

3. Iannucci A., Bellucci L., Conti J., Mazzini I., Mecozzi B., Sardella R., Iurino D.A., (2022). Neurocranial anatomy of *Sus arvernensis* (Suidae, Mammalia) from Collepardo (Early Villafranchian; central Italy): taxonomic and biochronological implications. Historical Biology 34:108–120. https://doi.org/10.1080/08912963.2021.1902999

4. Iannucci A., Gasparik M., Sardella R., (2020). First report of *Sus strozzii* (Suidae, Mammalia) from the Early Pleistocene of Hungary (Dunaalmás) and species distinction based on deciduous teeth. The Science of Nature 107:5. https://doi.org/10.1007/s00114-019-1661-6

5. Iannucci A., in press. New results on suids from the Early Pleistocene site of Untermassfeld. In: Kahlke R.-D. (Ed.) The Pleistocene of Untermassfeld near Meiningen (Thüringen, Germany). Part 5. Monographien des Römisch-Germanischen Zentralmuseums 40, 5.

6. Strani F., Bellucci, L., **Iannucci A.**, Iurino D.A., Mecozzi B., Sardella R., (2022). 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 34:555–565. https://doi.org/10.1080/08912963.2021.1935920

7. Mecozzi B., **Iannucci A.**, Mancini M., Sardella R., (2021). Redefining Ponte Molle (Rome, central Italy): an important locality for Middle Pleistocene mammal assemblages of Europe. Alpine and Mediterranean Quaternary 34:131–154. https://doi.org/10.26382/AMQ.2021.09

8. 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 31:10–20. https://doi.org/10.4404/hystrix-00258-2019

9. Iannucci A., (2022). On the authorship, availability, and improper use of *Sus scrofa ferus* for referring to wild pigs. Taxonomy 2:91–98. https://doi.org/10.3390/taxonomy2010007

In the manuscripts in which I am the first author, I collected, analyzed, and interpreted most of the data, with the precious assistance and cooperation of the coauthors. In particular, I wish to acknowledge support on the geo-paleontological background sections (**Papers 1, 3, 4, 8**), analyses (**Papers 2, 3, 6**), and data collection (**Papers 3, 8**). In the manuscripts in which I am a coauthor (**Papers 6, 7**), I took care of part of data collection, analysis, and writing.

Abstract

Suidae (Mammalia, Artiodactyla) are a diverse group of large mammals, today widely distributed in Africa and Eurasia, but also including a heterogeneous array of extinct forms. Most extant suids are fast-breeding and highly adaptable species. This likely explains why several lineages experimented rapid (over the course of geological time) episodes of diversification which, in addition to the importance for the evolution of the group, are of great interest for biochronological correlations and paleoenvironmental reconstructions. These applications are especially developed in the African Neogene-Quaternary, where fossil suids assume a fundamental role in the relative dating of several key sites for human evolution. In Europe, this potential is relatively poorly exploited, partly due to inherent differences between species, but mostly, and somehow paradoxically, because historical recoveries often lack appropriate controls. Indeed, even though suids are of great possible value for many applications, a drawback of the overall plesiomorphic morphology and plastic adaptability of suids is that evolutionary changes need to be tested within well chronologically and geographically constrained settings.

In contributing to the general goal of resolving the evolutionary relationships and developing a biochronological scheme for Neogene-Quaternary suids of Europe, a collection of case studies is presented in this thesis, which are or will be soon published as a series of independent papers.

The results of this thesis confirm and discuss, at different chronological, geographical, and phylogenetic scales, the biochronolocical and paleoecological value of European suids. In particular for: 1) the so-called Vallesian crisis ~9.7 Ma; 2) the Miocene-Pliocene (Turolian-Ruscinian) transition ~5.3 Ma; 3) the late Early Pleistocene, in pre- and post-Epivillafranchian faunas ~1.2–0.8 Ma; 4) Middle to Late Pleistocene environmental and climatic fluctuations. Moreover, analyses on neurocranial anatomy and ecomorphology yielded unexpected results, opening promising lines for future research.

Riassunto

I Suidae (Mammalia, Artiodactyla), sono un diversificato gruppo di grandi mammiferi, oggi ampiamente distribuito in Africa e in Eurasia, che include anche un diversificato assortimento di forme estinte. La maggior parte delle specie attualmente viventi si riproducono velocemente e sono molto adattabili. Questo probabilmente spiega perché diverse linee evolutive abbiano sperimentato rapidi (nel corso del tempo geologico) momenti di diversificazione, i quali, oltre che per l'importanza nell'evoluzione del gruppo, rivestono grande interesse per correlazioni biocronologiche e ricostruzioni paleoambientali. Queste applicazioni sono specialmente sviluppate per il Neogene e il Quaternario dell'Africa, dove i suidi fossili assumono un ruolo fondamentale nella datazione relativa di diversi siti chiave dell'evoluzione umana. In Europa, questo potenziale è relativamente poco sfruttato, in parte per insite differenze tra le diverse specie, ma soprattutto, e in qualche modo paradossalmente, perché i ritrovamenti effettuati in tempi storici spesso mancano di un contesto affidabile. In effetti, anche se i suidi fossili sono potenzialmente di grande importanza per molte applicazioni, la generale plesiomorfia e plastica adattabilità di questo gruppo rende necessario valutare i cambiamenti evolutivi all'interno di contesti ben vincolati cronologicamente e geograficamente.

Nel contribuire al più ampio obiettivo di risolvere le relazioni evolutive e sviluppare uno schema biocronologico per i suidi neogenico-quaternari dell'Europa, una serie di casi di studio è presentata in questa tesi, che sono stati pubblicati o sono in corso di pubblicazione come articoli indipendenti.

I risultati di questa tesi confermano e discutono, a diverse scale cronologiche, geografiche e filogenetiche, il valore biocronologico e paleoecologico dei suidi europei. In particolare per: 1) la cosiddetta crisi del Vallesiano ~9.7 Ma; 2) la transizione Miocene-Pliocene (Turoliano-Rusciniano) ~5.3 Ma; 3) il Pleistocene Inferiore superiore, nelle faune pre- e post-Epivillafranchiano ~1.2–0.8 Ma; 4) le oscillazioni climatiche ed ambientali del Pleistocene Medio al Pleistocene superiore. Inoltre,

analisi di neuroanatomia del cranio ed ecomorfologia hanno restituito risultati inaspettati, aprendo promettenti linee di ricerca per studi futuri.

Di seguito i riassunti dei diversi articoli (**Capitoli 2–10**) presenti in questa tesi.

Capitolo 2

Vengono descritti i ritrovamenti di suidi provenienti dal Miocene superiore di Alsótelekes, nel nordest dell'Ungheria. I reperti vengono attribuiti a *Propotamochoerus palaeochoerus* (Suinae) e cf. *Parachleuastochoerus* (Tetraconodontinae). La copresenza di queste due specie è in accordo con l'attribuzione biocronologica al Vallesiano inferiore (MN 9) stimata in precedenza sulla base dei micromammiferi, e suggerisce la presenza di ambienti boschivi, con abbondanza di risorse trofiche nel substrato del terreno e accesso diretto all'acqua. Questo quadro combacia bene con la presenza di diversificate zone umide e foreste ripariali che caratterizzavano il lago Pannonico ~10 Ma, come documentato nel vicino sito di Rudabánya. Inoltre, si discute della contorta tassonomia dei Tetraconodontinae europei.

Capitolo 3

La transizione tra il Miocene e il Pliocene (Turoliano-Rusciniano), rappresenta un intervallo fondamentale nell'evoluzione delle paleocomunità euromediterranee. Infatti, i cambiamenti paleoambientali legati alla fine della crisi di salinità del Messiniano si riflettono in un grande rinnovamento degli insiemi faunistici a mammiferi. Un importante bioevento tra i grandi mammiferi terresti è la diffusione del genere *Sus*, che durante il Pliocene rimpiazzò la quasi totalità delle specie di suidi presenti precedentemente in Eurasia. Nonostante la sua possibile rilevanza biocronologica e paleoecologica, le correlazioni basate su questo bioevento sono indebolite dalla presunta persistenza delle ultime popolazioni di *Propotamochoerus provincialis*, una specie del Miocene superiore. In questo capitolo vengono revisionati i reperti del Miocene superiore del bacino del Casino (Toscana, Italia centrale), la cui attribuzione è rimasta controversa nel corso dei quasi 150 anni passati dalla loro scoperta. In seguito alla comparazione con altre specie euroasiatiche del Miocene, Pliocene e Pleistocene, i suidi del Casino vengono assegnati a *P. provincialis* e la diagnosi della specie viene emendata. Inoltre, viene riconosciuto come tutto il materiale europeo del Miocene superiore (Turoliano) di *Propotamochoerus* appartenga a *P. provincialis* e come non ci sia nessuna prova valida della presenza di questa specie al di là della transizione Turoliano-Rusciniano (MN 13-MN 14).

Capitolo 4

I reperti di suidi recuperati dal Pliocene superiore di Collepardo (Lazio, Italia centrale) sono descritti ed assegnati a *Sus arvernensis*, una specie di piccole dimensioni distribuita dal Rusciniano al Villafranchiano Inferiore (MN 14-MN 16a), supportando la recente revisione della cronologia del sito di Collepardo. Metodologie di tomografia computerizzata vengono utilizzate per estrarre virtualmente ed analizzare un neurocranio recentemente ritrovato, fornendo il contenuto per la prima descrizione dell'anatomia interna del cranio in un suide estinto. L'analisi rivela come *S. arvernensis* possedesse un telencefalo allungato anteroposteriormente e appiattito dorsoventralmente, simile nell'architettura generale a quello del suide asiatico *Babyrousa babyrussa* e del cinghiale gigante africano *Hylochoerus meinertzhageni*. Queste specie differiscono notevolmente nelle dimensioni e sono rappresentanti di due rami filogenetici ampiamente divergenti, escludendo interpretazioni relativamente semplici per la morfologia del cervello nei suidi, in senso evolutivo o allometrico.

Capitolo 5

Viene descritto un frammento di mandibola che preserva un quarto premolare deciduo (dp4) proveniente dalla località di Dunaalmás, Pleistocene Inferiore, che rappresenta la prima segnalazione confermata di *Sus strozzii* in Ungheria. La comparazione delle misure del dp4 supporta una distinzione statisticamente significativa tra *S. strozzii* e *S. scrofa*. Le due specie di sovrappongono cronologicamente durante il Pleistocene Inferiore superiore dell'Europa (Epivillafranchiano), sebbene i reperti di suidi di questo periodo sono raramente attribuiti ad una specie precisa. La corretta identificazione dei suidi epivillafranchiani, i quali sono spesso associati con evidenze della presenza di ominini, è di grande valore paleoambientale perché *S. scrofa* e *S. strozzii* hanno diverse necessità ecologiche.

Capitolo 6

Vengono descritti nuovi o già noti reperti di suidi recuperati da Untermassfeld (Turingia, Germania). Il sito di Untermassfeld, Pleistocene Inferiore superiore, ha restituito uno dei campioni più abbondanti di suidi epivillafranchiani, che eppure consta solo di un numero di minimo di 6 individui identificati. I suidi di Untermassfeld sono stati considerati in passato i primi rappresentanti dell'attuale cinghiale eurasiatico e attribuiti a *Sus scrofa priscus*, poi riassegnati a *Sus* sp. e infine a *Sus strozzii*. Quest'ultima attribuzione viene favorita in questo lavoro e alcune differenze tra i suidi di Untermassfeld e i tipici *S. strozzii* villafranchiani vengono evidenziate, che sembrano coerentemente presenti in altri campioni epivillafranchiani. Al momento non è possibile valutare se queste caratteristiche siano emerse repentinamente nelle popolazioni epivillafranchiane oppure furono il risultato di cambiamenti graduali non opportunamente documentati dallo scarso record fossile dei suidi europei successivo all'inversione paleomagnetica di Olduvai (~1.8 Ma).

Capitolo 7

L'area di Ponte Galeria, nella città di Roma, ha restituito numerose località fossilifere che rappresentano un punto di riferimento per lo studio degli ecosistemi europei del Pleistocene Medio. A Ponte Galeria, una ricca collezione di mammiferi fossili è stata portata alla luce dalla Cava di Breccia - Casal Selce 2, perciò il sito rappresenta un ottimo laboratorio per investigare i paleoambienti di un territorio ben definito durante il Pleistocene Medio. Abbiamo investigato le abitudini alimentare della comunità di ungulati di Cava di Breccia - Casal Selce 2 per ricostruire gli habitat del MIS 15 e inoltre comparare i dati con quelli del vicino sito di Fontana Ranuccio (MIS 11), che condivide una simile composizione faunistica con Cava di Breccia - Casal Selce 2, per valutare se gli ungulati occupassero le stesse nicchie durante due interglaciali differenti. Ambienti aperti e sparse zone boschive caratterizzavano l'area di Ponte Galeria durante il MIS 15, mentre la copertura forestale era più ampia durante il MIS 11 a Fontana Ranuccio. Gli ungulati mostrano diete simili in entrambe le località, suggerendo che i cervidi, i grandi bovidi e gli equidi adottarono simili strategie di ripartizione delle risorse trofiche durante entrambi gli interglaciali.

Capitolo 8

In questo lavoro è stato riconsiderato l'insieme faunistico a mammiferi proveniente dal Pleistocene Medio di Ponte Molle, una storica località fossilifera dell'area urbana di Roma. Congiuntamente è stata portata avanti una revisione della successione stratigrafica del deposito. Ciò ha permesso di ricostruire la provenienza del materiale fossile e di fornire vincoli cronologici, tramite la correlazione con unità litostratigrafiche e sintemiche della cartografia geologica nazionale e le unità aggradazionali, geocronologicamente vincolate, del Paleo-Tevere. Lo studio paleontologico assieme alla revisione geologica e stratigrafica hanno permesso di ridefinire il deposito di Ponte Molle e il suo insieme faunistico del Pleistocene Medio. In questa nuova veste, l'età a cui l'insieme faunistico di Ponte Molle può essere riferito si colloca in un intervallo tra 550 ka e 450 ka.

Capitolo 9

Il cinghiale, *Sus scrofa*, ha una delle più ampie distribuzioni geografiche tra tutti i mammiferi e dalla sua comparsa nel Pleistocene Inferiore superiore (Epivillafranchiano), è ampiamente rappresentato nel record fossile europeo. Le prime forme della specie erano più grandi di quelle del Pleistocene Superiore, ma né la cronologia né le cause di questa riduzione di taglia sono state investigate approfonditamente. In questo lavoro viene considerata per la prima volta un grande numero di fossili recuperati da diversi siti della Puglia (penisola italiana), datati tra il Pleistocene Medio superiore e l'Olocene Inferiore. In contrasto con la presunta esistenza di una progressiva tendenza evolutiva verso dimensioni più piccole, comparazioni biometriche e stime di massa corporea hanno permesso di riconoscere diverse oscillazioni tra il Pleistocene Medio superiore e l'Olocene Inferiore, con forme di grandi dimensioni presenti durante periodi interglaciali e forme piccole durante i periodi glaciali. Questo suggerisce che i cinghiali pugliesi del Pleistocene non aderissero alla regola di Bergmann, che predice dimensioni più grandi in climi freddi come risposta selettiva verso un minore rapporto tra la superficie e il volume corporeo. La recrudescenza climatica potrebbe aver giocato un ruolo indiretto nel ridurre la disponibilità di risorse trofiche e quindi promuovere lo schema osservato.

Capitolo 10

Il cinghiale, *Sus scrofa*, è uno dei grandi mammiferi di maggiore successo in termini di distribuzione geografica. Assieme al suo discendente domestico, il maiale, sono animali estremamente importanti per la conservazione, l'economia, il benessere e il sostentamento umano. Denominare i maiali selvatici e domestici in un modo che permetta di riferirsi a loro in maniera efficace e non ambigua è cruciale per un gran numero di studi in archeozoologia, biomedicina, genetica, epidemiologia, paleontologia e nella gestione della fauna selvatica. *Sus scrofa ferus* o, meno comunemente, *Sus ferus*, è sovente utilizzato per riferirsi a popolazioni selvatiche, frequentemente contrapposto a *S. scrofa domesticus* o *S. domesticus* in riferimento ai maiali domestici. In questo lavoro viene argomentato che *S. scrofa ferus* è disponibile per propositi nomenclaturali, ma non dovrebbe essere ritenuto valido da una prospettiva tassonomica. Gli autori dovrebbero riferire le popolazioni selvatiche a sottospecie valide, ad esempio *S. scrofa scrofa*, oppure a *S. scrofa* ssp., quando informazioni sullo stato sottospecifico delle popolazioni in studio non sono disponibili o rilevanti per le domande di ricerca considerate. Questa osservazione non rappresenta solo un mero chiarimento nomenclaturale, perché la potenziale identificazione di differenze tra i diversi taxa di cinghiale è spesso nascosta dietro una semplicistica ripartizione dicotomica tra forme selvatiche e domestiche.

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1. Introduction

Suids (Suidae, or simply the pigs) are a diverse group of even-toed ungulate large mammals, natively distributed throughout the Old World. Over the last couple of decades, a paradigmatic shift in our comprehension of the relationships within Artiodactyla occurred. The traditionally recognized suborder Suiformes (suids, peccaries, and hippos) has long been considered the sister-group of Ruminatia (including all other artiodactyls), but the taxonomic arrangement derived from recent molecular advancements is quite different. It is unclear whether extant Suoidea (suids and peccaries) or Tylopoda (camelids) are sister-group of all other artiodactyls, but hippos and Cetacea are consistently recovered as forming a monophyletic group (Graur and Higgins 1994; Irwin and Árnason 1994; Gatesy et al. 1996; Montgelard et al. 1997; Waddell et al. 1999; Spaulding et al. 2009; Zurano et al. 2019). The latter point deeply impacted collective imagination even outside the scientific community, to the extent that the usage of "Cetartiodactyla" (for the clade Cetacea + Artiodactyla) became widespread, despite being formally unnecessary and potentially misleading, as Cetacea are nested within Artiodactyla (Archibald 2003; Helgen 2003; Asher and Helgen 2010; Prothero et al. 2021).

In any case, if not the most primitive among extant artiodactyls, suoids are for sure the most "primitive-looking", retaining a series of anatomical features absent in other artiodactyls, as for instance bunodont and brachydont (in most species) dentition, unfused metapodials, and a simple (non-ruminant) stomach. Suids are evidently divergent from their closest living relatives, peccaries (Tayassuidae), especially in the variety of forms and shapes exhibited by their sexually dimorphic male canines (e.g., Stehlin 1899–1900; Cooke and Ewer 1972; Hardjasasmita 1987; Orliac et al. 2010; Macdonald and Shaw 2018). Nevertheless, different suid lineages evolved roughly convergent morphologies and others retained relatively small canines. By coupling this fact with the overall plesiomorphic anatomy of suids and the patchy fossil evidence in certain chronological intervals, it appears evident why several aspects of their evolution are still unsolved. For instance, there are several putative Eocene evidence of suids but the material is quite scanty and the relationships between early suoids are unclear and controverse, indeed suid diversity only rise during the Miocene (Ducrocq et al. 1998; Liu 2001; van der Made 2010, 2020).

Today, there are at least 17 suid species, subdivided into 6 genera. This is the number recognized by the IUCN, but there are proposals to raise several subspecies to a full species rank (Groves and Grubb 2011; Melletti and Meijaard 2017). The number of taxa increased slowly but steadily over the years, and it is likely that the trend will continue with the gathering of further morphological and genetic data (Groves 1981, 2007; Oliver 1995; Groves and Grubb 1993, 2011; Melletti and Meijaard 2017).

At a coarse scale, the phylogenetic relationships between extant suids are well resolved (Gongora et al. 2011; Darfour-Oduro et al. 2015; Frantz et al. 2016). Babirusas (*Babyrousa*) were the first lineage to split and accordingly evolved some peculiar anatomical features. For instance, maxillary canines that in males protrude upwards and towards the rear of the cranium, and a complex and elongated stomach (Leus et al. 1999; Macdonald and Shaw 2018). Remaining Eurasian suids (*Porcula* and *Sus*) and African species (*Hylochoerus*, *Phacochoerus*, *Potamochoerus*) form two long diverging and different clades. At a finer scale, resolving the relationships between taxa is more difficult due to the inadequate sampling of some species, especially in Asia, and the common retention of plesiomorphic characters which complicates morphological studies. For example, *Potamochoerus* has often been aligned to *Sus* due to its morphology, and the initially proposed generic distinction of the pygmy hog (*Porcula salvania*) has only recently regained credit (Funk et al. 2007; Frantz et al. 2016; Cherin et al. 2018).

Most suids species treated in this thesis belong to Suinae, as this subfamily originated in the late Miocene and soon became dominant in Africa and Eurasia.

Here, in contributing to the general goal of resolving the evolutionary relationships and developing a biochronological scheme for Neogene-Quaternary suids of Europe, a collection of case studies is presented. This thesis explores, at different chronological, geographical, and phylogenetic scales, the biochronolocical and paleoecological value of European suids. In particular for: 1) the so-called

Vallesian crisis ~9.7 Ma; 2) the Miocene-Pliocene (Turolian-Ruscinian) transition ~5.3 Ma; 3) the late Early Pleistocene, in pre- and post-Epivillafranchian faunas ~1.2–0.8 Ma; 4) Middle to Late Pleistocene environmental and climatic fluctuations. Moreover, analyses are conducted on neurocranial anatomy and ecomorphology, and some nomenclatural issues are also addressed.

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2. Paper 1

Suidae (Mammalia, Artiodactyla) from the late Miocene hominoid locality of Alsótelekes (Hungary)

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Abstract

The Suidae from the late Miocene of Alsótelekes (northeastern Hungary, Borsod-Abaúj-Zemplén county) are described and assigned to *Propotamochoerus palaeochoerus* (Suinae) and cf. *Parachleuastochoerus* (Tetraconodontinae). The co-occurrence of these species agrees with a reference to the early Vallesian (MN 9), as previously indicated from biochronologic correlation of the small mammal fauna, and suggests the presence of woodland environments, with abundance of below-ground resources and direct access to water. This fits well with the diverse wetlands and riparian forests that characterized Lake Pannon ~10 Ma, as documented in the geographically close site of Rudabánya. The convoluted taxonomy of European Tetraconodontinae is discussed.

Keywords: Large mammals; primates; Vallesian Crisis; faunal turnover; climate change; Europe

2.1. Introduction

Suidae are a successful group of even-toed ungulates (Artiodactyla) native to and widespread in Africa and Eurasia (Melletti and Meijaard 2017). Their past diversity was even greater than today (Harris and White 1979; Pickford 1988; Van der Made and Moyà-Solà 1989; Orliac et al. 2010a). Fossils of the group are known since the Oligocene of Pakistan (Orliac et al. 2010b), with several putative earlier occurrences from East Asia (Ducrocq et al. 1998; Liu 2001). During the Miocene suids dispersed and diversified throughout the Old World, providing a valuable source of information for biochronological correlations and paleoecological inference (White and Harris 1977; Cooke and Wilkinson 1978; Fortelius et al. 1996a; Souron 2017). Hungary has yielded an abundant record of Miocene to Pleistocene extinct species (Kormos 1913; Mottl 1939; Kretzoi 1952a, b; Bernor and Fessaha 2000; Fortelius et al. 2005; Iannucci et al. 2020a).

The early late Miocene (early Vallesian, MN 9, ~11.2–9.7 Ma) represented an optimum of diversity for suids and more generally for mammalian paleocommunities of Europe, with a high number of species adapted to forested environments (Begun et al. 2012; Agustí et al. 2013). This richness notably stands out when compared with the severe impoverishment that occurred soon after, i.e., the demise of woodland-adapted faunas often referred to as the (mid-)Vallesian Crisis (Agustí and Moyà-Solà 1990; Fortelius et al. 1996a, 1996b; Agustí et al. 2013), even though the scope, magnitude, and pace of this event are debated (e.g., Koufos 2006; Casanovas-Vilar et al. 2014; Daxner-Höck et al. 2016). One of the key MN 9 localities is Rudabánya (~10 Ma), in northeastern Hungary, which provides an important window on the diverse early Vallesian ecosystems of central Europe. Alsótelekes is geographically and chronologically close to Rudabánya, and has yielded an abundant and diversified fauna not yet described, including crustaceans, fishes, turtles, snakes, amphibians, rhinos, equids (*Hippotherium*), bovids, cervids, moschids, sciurids, beavers and other rodents, eulipotyphlans, hominoids (*Rudapithecus*) and pliopithecoids (*Anapithecus*). Rudabánya and Alsótelekes are the only sites where the dryopithecin great ape *Rudapithecus hungaricus* is documented (Kretzoi et al. 1974; Kordos and Begun 2002; Bernor et al. 2004b; Eastham et al. 2016, 2017; de Bonis et al. 2017). Rudabánya and Alsótelekes are also among the rare co-occurrences of a great ape and a pliopithecoid (Kordos and Begun 2001; Sukselainen et al. 2015; Gilbert et al. 2020). The description of new sites and fossils from this timespan are of crucial relevance for gaining further insights on faunal and paleoenvironmental dynamics, including those related to the evolution and extinction of *Rudapithecus* and other dryopithecins, pliopithecoids, and their replacement with cercopithecoids (Begun 2015).

Here, as a first contribution to the study of the large mammal fauna recovered from Alsótelekes, we present the suid remains recovered from the site, discussing their systematic placement as well as the biochronological and paleoecological significance of the species identified.

2.2. The locality of Alsótelekes

Alsótelekes is a village in Borsod-Abauj-Zemplen county, at the southwestern edge of the Rudabánya mountains, an elongated chain of SW-NE striking bluffs in northeastern Hungary (Figure 1). Quarrying at the nearby still active Triassic gypsum quarry (Zelenka et al. 2005), has led to the exposure of the overlying late Miocene fluvio-lacustrine sediments. In the early 1990s a small "*Hipparion*" fauna was recovered from surface collecting and screen washing (Kordos 1997). Some still undescribed large mammals were recovered at that time along with a small sample of eulipotyphlans and an unspecified number of *Anapithecus* specimens (Kordos 1997). The insectivores were briefly described and attributed to MN 9, leading to the conclusion that Alsótelekes is close in age to, but possibly slightly older than the nearby rich late Miocene site of Rudabánya (Mészáros 1999). Mészáros (1999) also concluded that the damage to the insectivore teeth suggests transport to some distance prior to deposition. Other fossils, including the suid described here as well as the *Rudapithecus* fossils, suggest minimal transport. Work is underway to analyze the geology and taphonomy of the Alsótelekes locality.

In 2015, 2016, and 2018 systematic excavations were undertaken following renewed surface collections by DRB at the edge of the quarry. Three localities have been identified at Alsótelekes. The main locality, Alsótelekes 2 (GPS coordinates: 48°25'23"N 20°39'30"E), has yielded the vast majority of the fossils, including all the hominids and the suids describe here. It occurs on a narrow ledge onto which a 4 x 21 meters grid was mapped. All specimens recovered from these excavations are documented to within a centimeter horizontally and vertically, within their 1 x 1 meter map square. The sediments are similar to the hominoid bearing R. II locality at Rudabánya, with alternating lignite and clay. The clay sediments are richer in terrestrial and lacustrine gastropods than R. II and the clay is less calcareous. The presence of fish and crustacean fossils also distinguishes Alsótelekes from Rudabánya. To date we have only recovered fauna from a single clay layer in the sequence, suggesting a relatively short time of accumulation.

Figure 1 - Outline of Hungary and geographical location of the late Miocene vertebrate locality of Alsótelekes.

2.3. Material and methods

The Suidae remains recovered from Alsótelekes are housed in the Geological Museum of the Mining and Geological Survey of Hungary in Budapest. The studied sample was compared with other remains stored in the same museum and in other institutions (see abbreviations below).

Measurements were taken using a digital caliper to the nearest 0.1 mm and are provided in Table 1. Dental terminology and measurements mainly follow Van der Made (1996). Upper and lower teeth are in upper and lower case, respectively, and a "d" precedes deciduous teeth (e.g., P3 = upper third premolar; di2 = lower second deciduous incisor). Dental rows are measured along the alveoli on the buccal side. Measurements of dental rows are inclusive of the indicated teeth (e.g., m1-m3 is the length of the lower molar row).

Synonymy between Suinae genera follows Iannucci et al. (2021b), while the convoluted taxonomy of the European Tetraconodontinae is discussed more extensively where appropriate throughout the text. *Parachleuastochoerus* is abbreviated to *Pa.* and *Propotamochoerus* to *Pr.*, to avoid confusion when referring to different species.

Institutional abbreviations: AFS: Museum of Natural History, Accademia dei Fisiocritici, Siena; HNHM: Hungarian Natural History Museum, Budapest; IGF: Natural History Museum of the University of Florence, section of Geology and Paleontology; MBFSZ: Geological Museum of the Mining and Geological Survey of Hungary, Budapest; MNCN: National Museum of Natural Sciences, Madrid; NMB: Natural History Museum, Basel; NHMMZ: Mainz Natural History Museum/State Collection of Natural History of Rhineland-Palatinate.

Measurements abbreviations: BLD: buccolingual diameter in incisors; MDD: mesiodistal diameter in incisors; ID-MP: Infradentale-mental prominence (length of the mandibular symphysis); HMm1: height of the mandible in front of m1; WMm1: width of the mandible in front of m1; L: length; W: width (-m: mesial; -d: distal/second lobe in a molar; -t: third lobe in a molar); cLa: length of the labial side in c; cLi: length of the lingual side in c; cD: length of the distal side in c.

Upper teeth	MBFSZ V 2019.15.1.	**Lower teeth**	MBFSZ V 2017.21.1.
P3 L	15.2	i1 MDD	6.9
P3 Wm	11.0	i1 BLD	9.6
P3 Wd	14.1	i2 MDD	8.6
P4 L	13.9	i2 BLD	10.5
P4 W	16.3	c L	9.2
M1 L	16.5	c W	7.3
M1 Wm	15.7	cLi	8.9
M1 Wd	14.8	cLa	8.8
M2 L	21.7	cD	5.1
M2 Wm	18.7	p1 L	10.4
M2 Wd	17.9	p1 W	5.3
P3-M2	63.4	p2 L	12.4
P3-P4	29.2	p2 Wm	5.2
		p2 Wd	5.5
	MBFSZ V 2017.127.1.	p3 L	13.9
dP4 Wm	11.8	p3 Wm	7.3
		p3 Wd	7.5
		p4 L	15.8
		p4 Wm	10.6
		p4 Wd	12.2
		m1 L	18.1
		m1 Wm	12.1
		m1 Wd	12.8
		m2 L	21.4
		m2 Wm	14.7
		m2 Wd	15.1
		m3 L	28.4
		m3 Wm	14.7
		m3 Wd	14.0
		m3 Wt	11.3
		ID-m3	167.1
		c-m3	139.7
		ID-MP	53.1
		p1-p4	65.7
		p2-p4	43.4
		p1-m3	135.8
		p2-m3	114.8
		m1-m3	68.3
		HMm1	38.8
		WMm1	28.9

Table 1 - Tooth measurements (in mm) of *Propotamochoerus palaeochoerus* from Alsótelekes, Hungary (see material and methods for abbreviations).

2.4. Systematic paleontology

Class Mammalia Linnaeus, 1758
Order Artiodactyla Owen, 1848
Family Suidae Gray, 1821
Subfamily Suinae Gray, 1821
Tribe Dicoryphochoerini Schmidt-Kittler, 1971
Genus *Propotamochoerus* Pilgrim, 1925

Type species: *Propotamochoerus hysudricus* (Falconer and Cautley, 1847)

Propotamochoerus palaeochoerus (Kaup, 1833)

Type specimen: Din 3, right mandible with p3-m3, housed in Darmstadt (Hessisches Landesmuseum). First described by Kaup (1833), selected as the lectotype of the species by Hünermann (1968).

Type locality: Eppelsheim, Dinotheriensande (Germany).

Age of the type locality: Late Miocene, early Vallesian, MN 9 (but see Böhme et al. 2012).

Referred material from Alsótelekes: MBFSZ V 2019.15.1., left fragmentary maxilla with P3-M2 (Figure 2A); MBFSZ V 2017.127.1., fragment of left dP4 (Figure 2B); MBFSZ V 2017.103.1., fragment of right P2 (Figure 2C); MBFSZ V 2017.21.1., almost complete female mandible (Figure 2D); MBFSZ V 2019.78.1.; fragment of m3 (Figure 2E); MBFSZ V 2017.78.1., fragment of left di2 (Figure 2F).

Measurements: See Table 1

Diagnosis: (mainly based on personal observations and on Mottl 1966 and Van der Made 1999): *Propotamochoerus* species smaller than *Pr. provincialis* and *Pr. hyotherioides*, larger than *Pr. wui*; parietal lines meet to form a sagittal crest; P2 smaller than P3; M3/m3 relatively poorly elongated; lower male canines with all three sides convex; p3 usually relatively slender (low Wd); mesial cingulum in m3 usually well-developed.

Description:

<u>Maxilla and upper dentition.</u> *MBFSZ V 2019.15.1.* (Figure 2A). The specimen is a fragmentary left maxilla that preserves P3-M2 and a small portion of the palatal area. The P3 has a pointed main cusp (paracone), a smaller one located distally along the same mesiodistal axis (metacone), and a well-developed distolingual protocone, separated from the rest of the tooth by a valley (protofossa). In the P4, the two buccal cusps are closer in dimension, though the paracone is larger in this tooth as well. The protocone is placed more forward than in P3, and the protofossa is filled by accessory developments of the main cusps, giving a more molariform appearance to this tooth. M1 and M2 share the same general structure: they are bilobed teeth with two main cusps in each lobe, and accessory cusplets placed medially along the mesiodistal axis of the tooth. The central accessory cusplet (tetrapreconule), situated in the valley between the two lobes, is relatively isolated, while the mesial and distal ones are part of the mesial and distal cingula, respectively.

MBFSZ V 2017.103.1. (Figure 2C). The specimen is a fragment of a right P2. Only part of the distal portion of the tooth is preserved, including part of the lingually developed protocone. The specimen is not very informative, but it fits with an attribution to *Pr. palaeochoerus*.

MBFSZ V 2017.127.1. (Figure 2B). The specimen is a tooth germ of a left dP4, damaged distally. The tooth is molariform and resembles a permanent M1, but the mesial cingulum is oblique to the medial axis of the tooth. Its mesial width is 11.8 mm, which is in the lower part of the dimensional range of dP4 from Rudabánya (N = 14, min = 11.2 mm, mean = 13.1 mm, max = 14.4 mm; Fortelius et al. 2005).

<u>Mandible and lower dentition.</u> *MBFSZ V 2017.21.1.* (Figure 2D). This is an almost complete female mandible, lacking the ascending rami but preserving all teeth on both sides, apart from i3. It belonged to a young adult, considering the limited wear on the teeth. Preserved incisors, i1 and i2, have a similar morphology, with two mesiodistal ridges and valleys between each of them; they do differ in the orientation of these structures, which are more asymmetric in i2, the buccodistal side being longer. All incisors together form a protruding, shovel-like structure that is employed in suids in their most

distinctive feeding activity, rooting. Canines are different from those of male representatives of the species in that they are smaller, they have a groove on their enamel-covered distal facet, and they are oriented more vertically (those of male point outwards). Sexual differences are also evident in the symphysis, which is markedly shorter and less wide than in males (e.g., ID-MP inMBFSZ V 2017.21.1. is 53.1 mm, while in the male mandible MBFSZ V 2021.1.1. from Rudabánya it is 75.3 mm). The p1 has two roots. In p1 there is a main cuspid (protoconid) that is placed forward, which is connected by a ridge to the small precristid. Other premolars have the protoconid placed more centrally, the mesial precristid more developed, and a distinct second cuspid (metaconid) distally to the protoconid. In p2 and p3 the two principal cuspids are almost located along the same mesiodistal axis, while in p4 they are shifted, with the metconid projecting lingually. Premolars also have a talonid that hosts the hypoconid, which becomes more developed and separated in p4. All premolars but p4 have a slight concavity on their lingual side. Lower molars have the same general morphology of their upper counterparts, but in comparison they are more symmetric and elongated. The m3 has three lobes, the distal one possessing only one main additional cuspid placed mediodistally, and smaller accessory developments at its sides. The p1 is separated by a small diastema (~5 mm) from the canine, and by a larger one (~15 mm) from the p2. Two mental foramina are present on the horizontal rami below the p1-p2 diastema and p3, respectively, the former being substantially larger. Three pairs of small openings also occur on the ventral portion of the symphysis. The mesial extremity of the mandible is fragmented but its ventral side is partly preserved.

MBFSZ V 2017.78.1. (Figure 2F). It is a fragment of a left di2, lacking most of the root and the occlusal surface in an advanced wear stage, precluding a description of finer morphological details. The mesial side is almost devoid of enamel, and at its tip there is a marked interstitial facet evidencing the contact surface with di1.

MBFSZ V 2019.78.1. (Figure 2E). A distal fragment of m3, only part of the third lobe of the tooth is preserved, possessing a mediodistal cuspid. The specimen is not very informative, but in its morphology and size is very close to m3 preserved on *MBFSZ V 2017.21.1.*

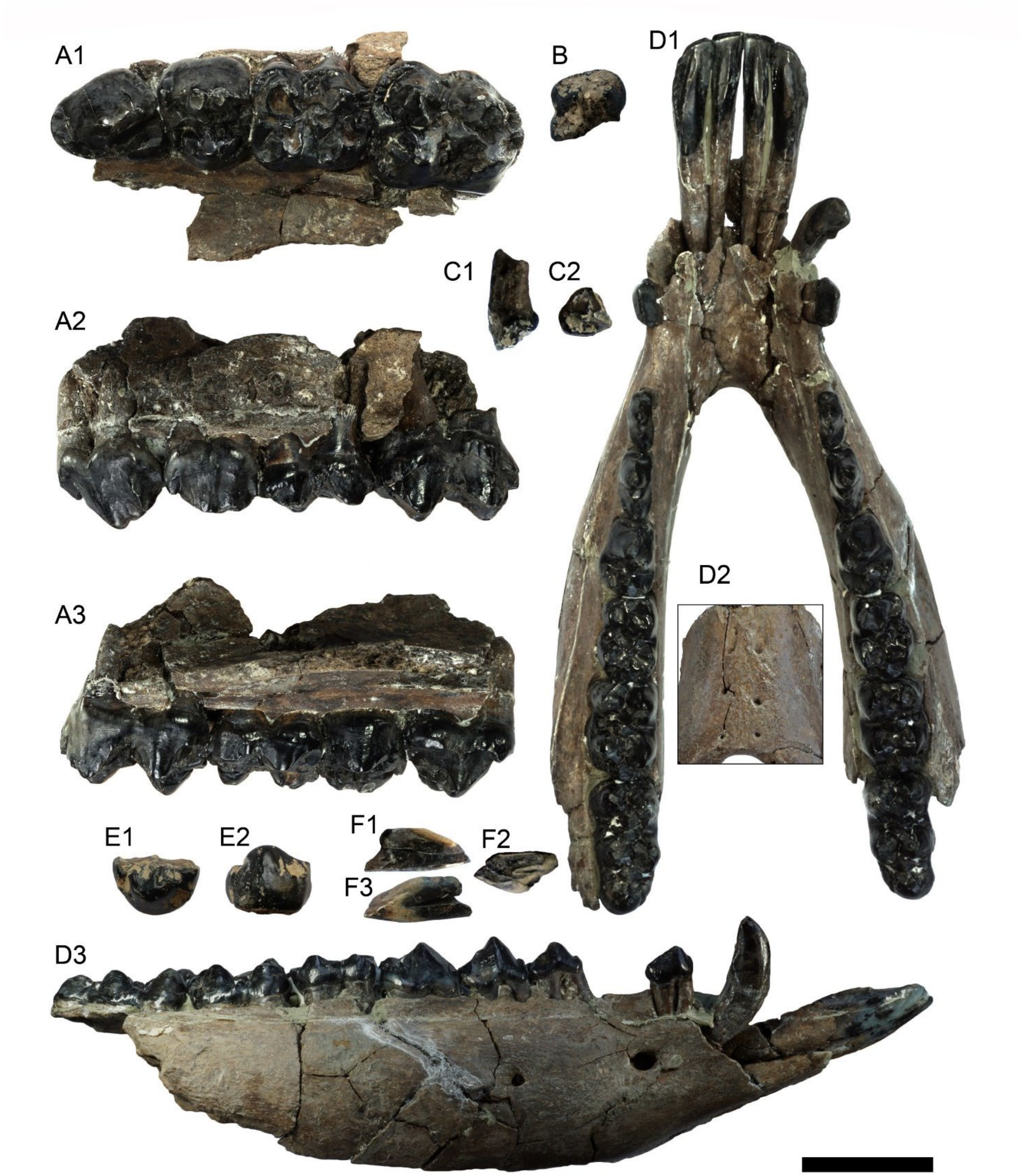

Figure 2 - *Propotamochoerus palaeochoerus* from Alsótelekes (Hungary). **A.** Left maxilla with P3-M2 (MBFSZ V 2019.15.1.) in occlusal (1), buccal (2), and lingual (3) views. **B.** Left dP4 fragment in occlusal view (MBFSZ V 2017.127.1.). **C.** Right P2 fragment (MBFSZ V 2017.103.1.) in lingual (1) and occlusal (2) views. **D.** Almost complete female mandible (MBFSZ V 2017.21.1.) in occlusal view (1), detail of the symphysis in ventral view (2), and right buccal view (3). **E.** m3 fragment (MBFSZ V 2019.78.1.) in occlusal (1) and distal (2) views. **F.** Left di2 fragment (MBFSZ V 2017.78.1.) in mesial (1), occlusal (2), and distal (3) views. Scale bar = 20 mm.

Remarks: MBFSZ V 2017.21.1. from Alsótelekes is compared with other European mandibles of *Propotamochoerus* and *Sus arvernensis* that preserve the p2-m3 series using a log-ratio diagram (Figure 3). The standard is the mean value of specimens 22-1067 and 22-1068 of *Pr. palaeochoerus* from Grytsiv (Van der Made et al. 1999), whose teeth are in a stage of wear intermediate between other specimens of *Pr. palaeochoerus* considered herein (MBFSZ V 2017.21.1. from Alsótelekes and MBFSZ V 2021.1.1. from Rudabánya, locality II). It would be desirable to focus the comparison only on remains of similar wear (Zeder and Lemoine 2020), but the fossil record of these species is too limited to allow it. The diagram shows that *Pr. palaeochoerus* is smaller than *Pr. provincialis* and larger than *S. arvernensis*, but there is overlap or little difference in several measurements. Within *Pr. palaeochoerus*, the female mandible from Alsótelekes is smaller than the male mandible from Rudabánya, although differences are not marked, aligning with the low sexual size dimorphism observed in tooth measurements of extant suid species (Iannucci et al. 2020b). On the other hand, as previously noted sexual differences in the symphysis are pronounced, as in other suid species (Souron 2012; Boisserie et al. 2014). Distal widths of p2 and p3 are quite variable, but larger in *Pr. provincialis*, while p4 proportions are more similar between the different species compared. Differences in measurements of m1, especially m1 L, vary more in relation to wear stage than to taxonomy. Wear influences m2 variation as well, but the tooth is a more consistent indicator of the size differences between taxa. In m3, proportions of the different species seem generally similar, even if with fluctuations in the relative development of widths, especially m3 Wt. Considering differences in proportions along the dental row, it can be stressed that *S. arvernensis* has a relatively large m3, while *Pr. palaeochoerus* has proportionally larger premolars. Comparing the p4 L/m3 L ratio this characteristic becomes evident (Figure 4). Moreover, it is worth noting that despite differences in size, this ratio aligns *Pr. provincialis* with *S. arvernensis*, allowing a separation from *Pr. palaeochoerus* that has p4 at least as long as half of m3 (i.e., p4 L/m3 L > 0.5). The individual from Alsótelekes falls close to the mean values of other samples of *Pr. palaeochoerus*.

The attribution of the Alsótelekes suine to *Pr. palaeochoerus* is strongly supported by the diagnostic morphology and dental proportions of the recovered specimens, showing e.g., large p4 with protoconid and metaconid not aligned along the same mesiodistal axis; slender p3; m3 relatively poorly elongated, with a pronounced mesial cingulum.

Propotamochoerus is a Eurasian genus with at least five recognized species: *Pr. hyotherioides*, *Pr. hysudricus*, *Pr. palaeochoerus*, *Pr. provincialis*, and *Pr. wui* (Hünermann 1968; Schmidt-Kittler 1971; Pickford 1988, 2013; Van der Made and Moyà-Solà 1989; Van der Made and Han 1994; Fortelius et al. 1996a; Van der Made et al. 1999; Geraads et al. 2008; Sein et al. 2009; Hou et al. 2019; Iannucci et al. 2021). Isolated teeth of these species are of similar morphology and partly overlap in size, and hence they are often difficult to identify. For completeness it is worth mentioning that, in some cases, the same applies to remains of the Pliocene *S. arvernensis* (Azzaroli 1952; Iannucci et al. 2022). For instance, Suidae from the early Pliocene of Alcoy (Spain) have been reported either as *Pr. palaeochoerus* (Gervais 1853; Van der Made and Belinchón 1991) or *S. arvernensis* (Crusafont and de Villalta 1955; Hünermann 1971) – in the former case substantially extending the chronological range of the species (Van der Made and Moyà-Solà 1989). Eventually this material was assigned to *S. arvernensis* after the description of more diagnostic elements (Montoya et al. 2006). A specimen of *S. arvernensis* from Collepardo (Italy) displays a weak sagittal crest, but this trait is not as pronounced as the condition observed in *Pr. palaeochoerus*, and the morphology of the neurocranium differs in many respects (Iannucci et al. 2022). Another presumed late occurrence of *Pr. palaeochoerus*, from the latest Miocene of Maramena (Greece, Hellmund 1995), was based on material first reassigned to *Propotamochoerus* sp. (Van der Made 1999; Geraads et al. 2008) and then to *Pr. provincialis* (Iannucci et al. 2021). Once excluded the putative late records, the chronological distribution of *Pr. palaeochoerus* appears mainly limited to MN 9, with a few earlier (MN 7+8, Sant Quirze, Saint Gaudens) and a tentative later (MN 10, Can Jofresa) reports (Ginsburg 1974; Van der Made and Moyà-Solà 1989; Van der Made 1990). *Propotamochoerus* *palaeochoerus* is the only of the aforementioned species of Suinae present in the Vallesian of Europe (Hünermann 1968).

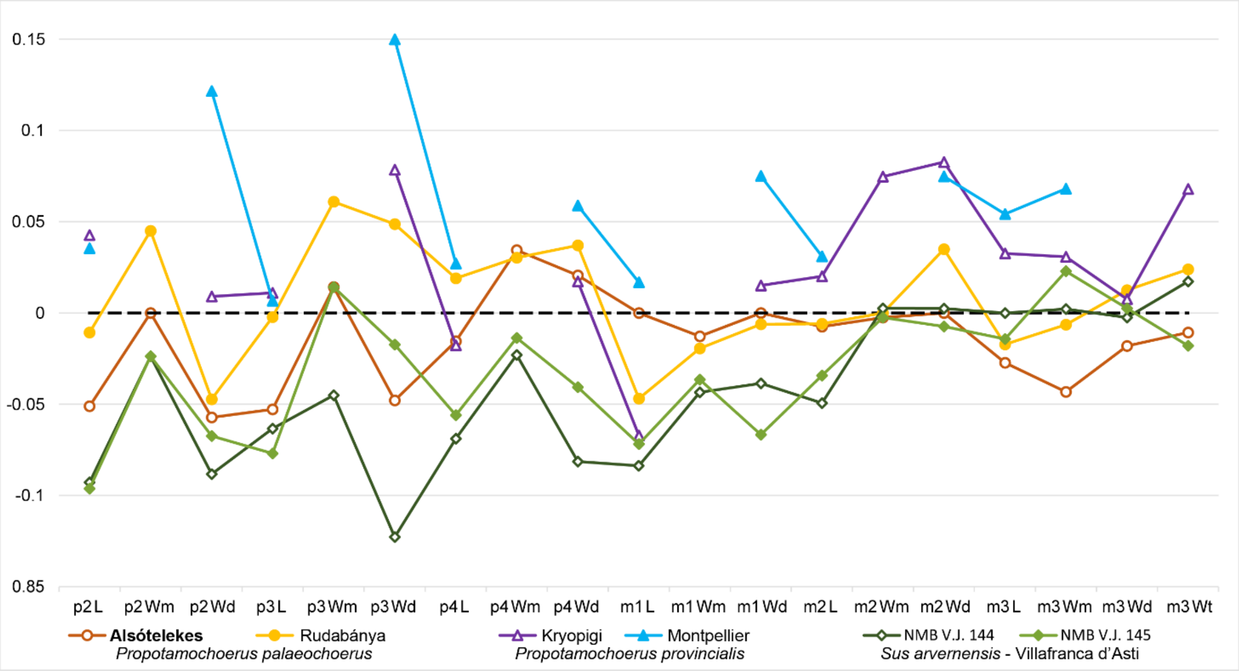

Figure 3 - Log-ratio diagram of *Propotamochoerus palaeochoerus* from Alsótelekes (MBFSZ V 2017.21.1.) and Rudabánya, locality II (MBFSZ V 2021.1.1.); *Pr. provincialis* from Kryopigi (KRY1094; Lazaridis, 2015) and Montpellier (FSL 40 072; Pickford, 2013); *Sus arvernensis* from Villafranca d'Asti (NMB V.J. 144, NMB V.J. 145). The standard is the mean value of specimens 22-1067 and 22-1068 of *Pr. palaeochoerus* from Grytsiv (Van der Made et al. 1999).

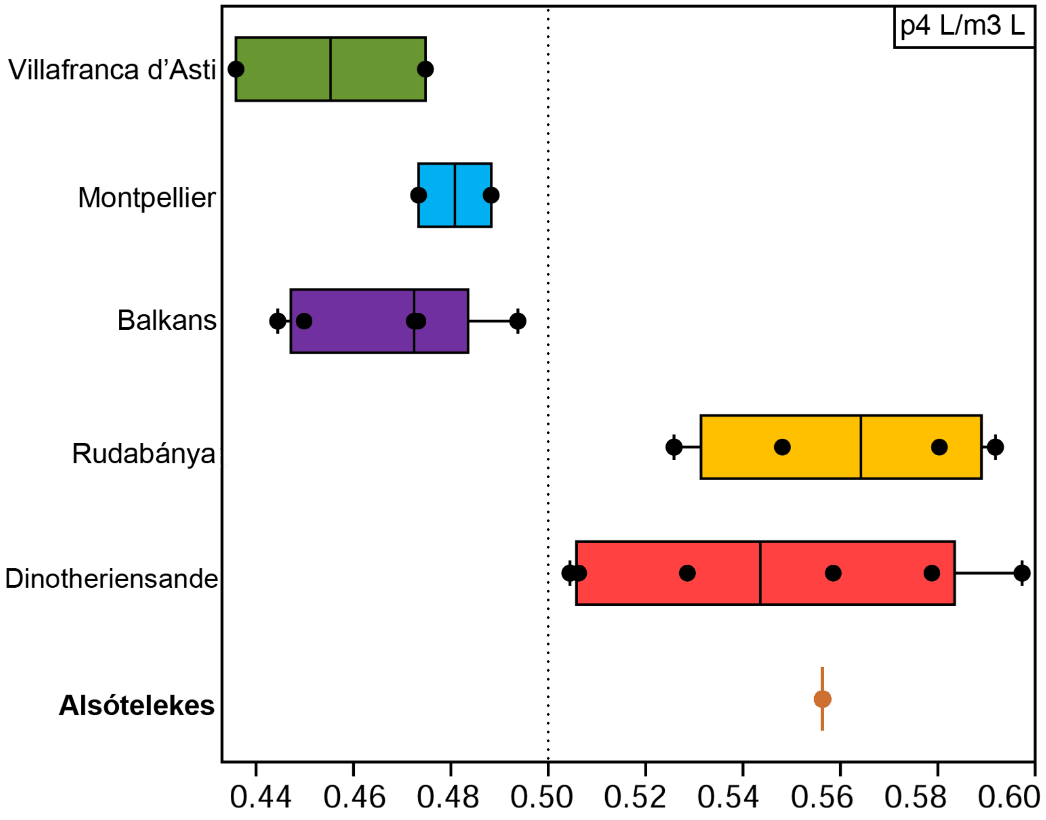

Figure 4 - Boxplot (whiskers from minimum to maximum values) of the p4 L/m3 L ratio of *Propotamochoerus palaeochoerus* from Alsótelekes (MBFSZ V 2017.21.1.), Rudabánya, locality II (MBFSZ; Fortelius et al., 2005), Dinotheriensande (NHMMZ; Hünermann, 1968), *Pr. provincialis* from the Balkans (Geraads et al., 2008; Lazaridis, 2015) and Montpellier (Pickford, 2013), and *Sus arvernensis* from Villafranca d'Asti (NMB).

Subfamily Tetraconodontinae Lydekker, 1876

Tribe Parachleuastochoerini Van der Made, 1999

Genus *Parachleuastochoerus* Golpe-Posse, 1972

Type species: *Parachleuastochoerus crusafonti* Golpe-Posse, 1972.

Type locality: Can Llobateres (Spain).

Age of the type locality: Late Miocene, early Vallesian, MN 9.

cf. *Parachleuastochoerus*

Referred material from Alsótelekes: MBFSZ V 2017.13.1., fragment of left I2 (Figure 5A).

Description: The only specimen attributed to cf. *Parachleuastochoerus* is a fragment of a left I2. The crown is preserved but it lacks almost all the root. The tooth is moderately worn but details of crown morphology are still observable. In occlusal view, it has an oval outline, with a small concavity on the lingual side. This concavity divides the tooth into two, while in *Pr. palaeochoerus* the mesial part is about one third of the whole occlusal surface. In fact, in comparison with I2 of *Pr. palaeochoerus*, this specimen is less elongated, especially distally (postcrista). Moreover, the buccomesial wear facet is orientated more outwards in MBFSZ V 2017.13.1., suggesting a slightly different occlusion with i2.

Figure 5 - A. cf. *Parachleuastochoerus* from Alsótelekes (Hungary), left I2 fragment (MBFSZ V 2017.13.1.). **B.** *Propotamochoerus palaeochoerus* from Rudabánya, locality II (Hungary), left I2 (MBFSZ V.21162). Both specimens in buccal (1), lingual (2), and occlusal (3) views. Scale bar = 10 mm.

Remarks: The I2 recovered from Alsótelekes differs biometrically from those of the other suid present at the site, *Pr. palaeochoerus*: MBFSZ V 2017.13.1. MDD x BLD = 12.8 x 7.2 mm; *Pr. palaeochoerus* from Rudabánya (N = 7) MDD x BLD: min = 15.1 x 7.2 mm, mean = 15.7 x 7.5 mm, max = 16.8 x 7.8 mm (Fortelius et al. 2005); *Pr. palaeochoerus* from Gau-Weinheim (Dinotheriensande, NHMMZ; N = 5) MDD x BLD: min = 15.4 x 6.2 mm, mean = 16.7 x 7.5 mm, max = 18 x 8.7 mm. Considering other European Miocene species, Suinae have larger and/or more elongated I2, and Listriodontinae are markedly divergent (Van der Made et al. 2014). Compared with Tetraconodontinae, a subfamily whose taxonomy remains controversial (see below), the specimen is larger than I2 of *Pa. crusafonti* (Pickford 1981) and smaller than I2 assigned to *C. simorrensis* and *Pa. steinheimensis* (Van der Made et al. 2014).

Measurements and morphology of the I2 MBFSZ V 2017.13.1. are compatible with those of a relatively small tetraconodont suid, smaller than *C. simorrensis* and *Pa. steinheimensis* and larger than *Pa. crusafonti* (Pickford 1981; Van der Made et al. 2014). An attribution to

Parachleuastochoerus seems the most reasonable, but considering the paucity of available comparative material we favor an open nomenclature, assigning MBFSZ V 2017.13.1. to cf. *Parachleuastochoerus*.

The name *Parachleuastochoerus* was coined by Golpe-Posse (1972) for the small-sized *Pa. crusafonti* from Can Llobateres, envisioning affinities with the Asian *Chleuastochoerus* Pearson, 1928 (hence the name). Pickford (1981) recognized that the species instead belongs to Tetraconodontinae.

The taxonomy of European Tetraconodontinae has been the subject of intense debate over the last couple of decades, with radically different classifications proposed (Bernor et al. 2004a; Fortelius et al. 2005; Daxner-Höck and Bernor 2009; Pickford 2014, 2016; Pickford and Laurent 2014; Van der Made et al. 2014; Van der Made 2020). Historically, most samples have been included within *Conohyus simorrensis* (Lartet, 1851), occasionally evidencing differences from *C. steinheimensis* (Fraas, 1870) (Stehlin 1899-1900; Thenius 1952); it is only after Chen (1984) that the separation of the two forms has been widely accepted. The main divergent feature supporting the identification of two species is the presence of relatively smaller P3/p3 and P4/p4 in *C. steinheimensis* (Stehlin 1899-1900; Thenius 1952; Chen 1984).

Heissig (1989) named *C. huenermanni* based on a fragmentary mandible from Breitenbrunn, seeing it as evolving through size reduction from the line of *C. steinheimensis*. He also considered the species present within the material from the Dinotheriensande described by Hünermann (1968), although doubting a Vallesian age for Breitenbrunn. Several authors accordingly referred Breitenbrunn to the late MN 7+8 (e.g., Van der Made 1999; Eronen and Rössner 2007; Seehuber 2008), although references to MN 6 (Pickford 2014, 2016) or to MN 9 (Bernor et al. 2004a) have also been suggested. Van der Made (1990) transferred *C. huenermanni* into *Parachleuastochoerus*, assigned to the species all the material previously attributed to *Pa. crusafonti* (Golpe-Posse 1972; Pickford 1981) apart from that from Can Llobateres and La Tarumba (MN 10), and stressed the biochronological importance of the size reduction in the *Pa. huenermanni*–*Pa. crusafonti* lineage. Pickford (1993) agreed on the identification of two species within *Parachleuastochoerus*, emphasizing their full specific status and underlining again their potential value for correlations. Van der Made (1990) still placed *Pa. steinheimensis* within *Conohyus* but suggested an inclusion of the species in *Parachleuastochoerus*, eventually formalized by Fortelius et al. (1996a). Van der Made (1999) provided a biometric review of Tetraconodontinae, detailing dimensional trends within *Conohyus* and *Parachleuastochoerus* and using them for diagnosing different species.

Bernor et al. (2004a) named *Conohyus olujici* from the early Miocene of Lučane and reassigned the species *C. huenermanni* and *C. steinheimensis* to *Conohyus*, while retaining in *Parachleuastochoerus* only *Pa. crusafonti* and the sample from Rudabánya, soon after named *Pa. kretzoii* by Fortelius et al. (2005). Daxner-Höck and Bernor (2009) followed the same scheme and assigned the material from Atzelsdorf to *Pa. kretzoii*, expanding the chronological range of the species to the early MN 9 (~11.2 Ma).

Van der Made et al. (2014) retained three species within *Parachleuastochoerus*, namely *Pa. steinheimensis*, *Pa. huenermanni*, and *Pa. crusafonti*, further developing the interpretation of the lineage *Pa. huenermanni*–*Pa. crusafonti* as an offshoot that progressively acquired smaller dimensions, while *Pa. steinheimensis* evolved towards a larger size (Van der Made 1990, 1999; Fortelius et al. 1996a). Van der Made et al. (2014) also rejected the validity of *C. olujici* and *Pa. kretzoii*, synonymizing them with *Pa. steinheimensis* and *Pa. huenermanni*, respectively.

Pickford (2014, 2016) and Pickford and Laurent (2014) adopted a splitter approach, partly separating *Parachleuastochoerus* into the newly named *Versoporcus* and recognizing a total of six species: *V. grivensis* (Gaillard, 1889), *V. steinheimensis*, *Pa. crusafonti*, *Pa. huenermanni*, and *Pa. valentini* (Filhol, 1882). Contrary to what this plethora of names would suggest, separations are still mainly based on biometry. The only cranial features highlighted as distinctive between *Parachleuastochoerus* and *Versoporcus* are the position of the root of the zygomatic arch, departing from the maxilla above M2 in *Parachleuastochoerus*, while above P4 in *Versoporcus*; and the position of the posterior choanae on the palate, far behind M3 in *Parachleuastochoerus*, while in line with the distal end of M3 in *Versoporcus* (Pickford 2014, 2016). However, these characters are based on MNHN HGP17 from Le Fousseret or St. Gaudens (see Van der Made 2020, for discussion) for *Pa. valentini* and SMNS M 20223 from Steinheim (Chen 1984; Pickford 2014) for *V. steinheimensis*. Considering that *Pa. valentini* is included in *C. simorrensis* by Van der Made (2020), the morphology underlined as diagnostic for *Versoporcus* by Pickford (2014, 2016) would apply to *Parachleuastochoerus* according to Van der Made (2020), while that of *Parachleuastochoerus* (*sensu* Pickford 2014, 2016) would apply to *Conohyus* (*sensu* Van der Made 2020). No adequately preserved remains of the species named *C. huenermanni*, *Pa. kretzoii*, and *Pa. crusafonti* are known that allow to observe these features.

It is predictable that with the recovery and description of new material our comprehension of the evolution and systematics of European Tetraconodontinae will improve, but up to now most of the samples are represented by isolated teeth, with few localities yielding abundant remains and having robust independent age constraints (Van der Made et al. 2014; Pickford 2016). From a biometric perspective the long recognized relative enlargement of third and fourth premolars is still the best distinction criterion for separating species of the subfamily (Stehlin 1899-1900; Thenius 1952; Chen 1984). This led to the identification of two groups, one including the "classical" samples of *C. simorrensis* (e.g., Göriach; Thenius 1956), the other *Pa. steinheimensis* and the type species of *Parachleuastochoerus*, *Pa. crusafonti* (Pickford 2014; Van der Made et al. 2014). Accordingly, these two clusters can be referred to as *Conohyus* (relatively larger third and fourth premolars) and *Parachleuastochoerus* (same teeth relatively smaller). Within both genera, different species are recognized, mainly separated due to their size (Pickford 2014, 2016; Van der Made 2020). Envisioning gradually evolving lineages, the delimitation of chrono(sub)species is a rather subjective exercise, but for a subdivision to be valid and useful, it is at least necessary that named taxa allow an effective allocation. As for *Parachleuastochoerus*, the samples from Steinheim (early MN 7+8) and Can Llobateres (late MN 9) include abundant remains from two reference localities for the European biochronological framework (Mein 1990; de Bruijn et al. 1992), providing convincing evidence of the biometric and chronological separation between *Pa. steinheimensis* and *Pa. crusafonti*. The attribution of the samples of intermediate dimension and age remains open to controversy. The material from Breitenbrunn is limited to the holotype mandible of *Pa. huenermanni*, whose presence has been stressed for correlating the deposit to the late MN 7+8 (Seehuber 2008). There is a clear risk of circularity in this reasoning, and the other few species reported from Breitenbrunn do not provide further chronological constraints (Seehuber 2008). Even assuming that the chronology of the site is correct, it is worth noting that measurements of *Pa. huenermanni* from Breitenbrunn fall in the lower part of the dimensional range of *Pa. steinheimensis* (Van der Made et al. 2014). The most important morphological feature underlined by Heissig (1989) in separating *Pa. huenermanni* from *Pa. steinheimensis* was the presence of three roots in p3 instead of two as in *C. simorrensis*. However, as pointed out by Fortelius et al. (1996a), there is variability in the degree of fusion of the roots when large samples are considered. Therefore, it cannot be ruled out that the material from Breitenbrunn belongs to a small individual of *Pa. steinheimensis* and it seems necessary to consider *Pa. huenermanni* a *nomen dubium* (*nomen vanum*, *sensu* Mones 1989) that should be restricted to the holotype.

2.5. Discussion

2.5.1. Biochronology

The suid remains recovered from Alsótelekes are ascribed to cf. *Parachleuastochoerus* and *Pr. palaeochoerus*. These suids co-occur in several early Vallesian (MN 9) localities (e.g., Can Llobateres, Castell de Barberà, and Rudabánya), thus supporting previous biochronological correlations for Alsótelekes (Mészáros 1999). Although scanty, the material of cf. *Parachleuastochoerus* from Alsótelekes is substantially larger than that of *Pa. crusafonti* from Can Llobateres (Golpe-Posse 1972; Pickford 1981). It is often assumed that *Pa. crusafonti* is the endmember of a lineage that reduced its size through time (Van der Made 1990; 1999; Pickford 1993;

Van der Made et al. 2014). This suggests that Alsótelekes – and Rudabánya – predate the latest occurrences of *Parachleuastochoerus*. However, Can Llobateres and Rudabánya are both correlated with the upper part of MN 9 (~10 Ma; Kordos and Begun 2002; Bernor et al. 2004b; Casanovas-Vilar et al. 2011). The observed biometric differences may therefore partly reflect geographical differences (e.g., due to differences in climate, trophic resources, competition with other sympatric species). For instance, dryopithecins from the same localities are represented by the two related and yet different genera, *Hispanopithecus laietanus* and *Rudapithecus hungaricus* (Begun 2015; Urciuoli et al. 2021). *Rudapithecus* is also somewhat larger than *Hispanopithecus*, judging from craniodental fossils (Begun 2002). Van der Made et al. (2014) and Van der Made (2020) assigned the Suidae material from Can Llobateres to four species, namely *Listriodon splendens*, *Pr. palaeochoerus*, *Pa. steinheimensis*, and *Pa. crusafonti*, while only two suids are present in Alsótelekes and Rudabánya. During the late Miocene, regional differences in climate are documented (Jímenez-Moreno et al. 2010), which were conceivably responsible for promoting differential responses of mammalian faunas even at a short geographical scale, as recorded between inland and coastland areas of the Iberian Peninsula (Madern et al. 2018). A study focused on a well-constrained geographical region in southern Italy during the Late Pleistocene revealed pronounced fluctuations in size in the extant wild boar, *Sus scrofa*, between glacial and interglacial stages, accounting for more than 20% variation in m3 L (Iannucci et al. 2020b). It cannot be assumed that extinct species were similarly prone to ecomorphological adaptations to cope with environmental changes, but this possibility should not be ruled out. Differences in m3 L between *Pa. steinheimensis* and *Pa. crusafonti* from their type localities are 27.3%, but both differ less than 20% from *Pa. kretzoii* from Rudabánya (data from Pickford 1981, 2016; Fortelius et al. 2005). We refrain from attributing the Alsótelekes cf. *Parachleuastochoerus* material to a precise species and we remark that European Tetraconodontinae need an in-depth revision. Given that the assignments are mainly based on quantitative criteria, samples from localities with inadequate sample sizes are difficult to incorporate into current analyses. More effort needs to be done to compare these suid taxa using qualitative morphological criteria.

2.5.2. Paleoecology

The co-occurrence of cf. *Parachleuastochoerus* and *Propotamochoerus* also provides some paleoecological insights on Alsótelekes environment. Stable carbon and oxygen isotope compositions of tooth enamel of *Pr. palaeochoerus* and *Pa. kretzoii* from Rudabánya were analyzed by Eastham et al. (2016), revealing relatively high $\delta^{13}C$ and relatively low $\delta^{18}O$ values for both species. The recorded values of $\delta^{13}C$ were interpreted as suggestive of a consumption of C_3 plants in relatively open canopy environments (Eastham et al. 2016), although the variable feeding behavior of suids precludes easy interpretations (Souron 2017). In any case, Alsótelekes and Rudabánya deposits accumulated during a period of high precipitation and humidity along the shoreline of Lake Pannon (Magyar et al. 1999; Harzhauser et al. 2007). The low oxygen isotope values observed for suids have been considered indicative of a frequent engagement in rooting (Eastham et al. 2016), as belowground resources such as tubers and rhizomes are lower in ^{18}O compared to leaf or fruit water (Dunbar and Wilson 1983; Yakir 1992), but the obligate drinking behavior of suids likely played an important role in influencing these observations (Kohn 1996; Levin et al. 2006). For instance, low oxygen isotope values are also recorded in *Hylochoerus* (the extant African giant forest hog), a suid whose rooting activity is relatively limited (Lazagabaster et al. 2021). In any case, the consumption of underground resources by suids at Rudabánya is supported by the analysis of enamel strontium/calcium ratios (Eastham et al. 2017). *Propotamochoerus palaeochoerus* displayed the highest $\delta^{13}C$ values among the ungulate species compared by Eastham et al. (2016), higher than those of *Parachleuastochoerus* from the same locality and other sites (Aiglstorfer et al. 2014). This suggests that *Parachleuastochoerus* relied more heavily on below-ground resources, while *Pr. palaeochoerus* exhibited a more flexible feeding behavior, consuming a larger proportion of leaves and fruits (Aiglstorfer et al. 2014; Eastham et al. 2016). This is seemingly in contrast with the development of morphological traits, especially the elongation of the incisors, which indicate a better developed rooting behavior in *Pr. palaeochoerus* (Van der Made et al. 2014). It is possible that *Pr. palaeochoerus* accessed below-ground resources proportionally less but more effectively than *Parachleuastochoerus*. Being better adapted to rooting could have been helpful in coping with fluctuations in the availability of different trophic resources, or in allowing feeding in suboptimal conditions or areas. Rooting should not have been too demanding in the soft substrates surrounding Lake Pannon, and it is conceivable that *Parachleuastochoerus* moved over significant distances when feeding, as $^{87}Sr/^{86}Sr$ isotope composition of *Pa. steinheimensis* from Gratkorn indicates that the species was not a permanent resident but inhabited a wide area (Aiglstorfer et al. 2014). Data on $\delta^{13}C$ and $\delta^{18}O$ as well as on trace element analysis for *C. simorrensis* from the middle Miocene of Somosaguas revealed heterogeneous values which were considered indicative of a certain degree of omnivory (Domingo et al. 2009, 2012). Reconstructing the environmental preferences of adaptable omnivores such as suids from isotope proxies is complicated by several confounding factors whose impact is difficult to properly evaluate, for instance the obligate drinking behavior of the group (Kohn 1996; Levin et al. 2006), or the consumption of animal matter and aquatic plants (both of which may vary substantially in $\delta^{13}C$ values; Souron 2017), but the coexistence of cf. *Parachleuastochoerus* and *Propotamochoerus* at Alsótelekes is in any case suggestive of woodland environments with abundance of belowground resources and direct access to water. This fits well with the diverse wetlands and riparian forests that characterized Lake Pannon ~10 Ma (Magyar et al. 1999; Harzhauser et al. 2007; Eastham et al. 2016).

At a coarse scale, during the early late Miocene, the climate was particularly humid and warm, supporting subtropical evergreen forests and generally high levels of biodiversity (Van Dam 2006; Harzhauser et al. 2007; Böhme et al. 2008, 2011; Pound et al. 2011; Begun et al. 2012; Agustí et al. 2013; Utescher et al. 2017). Alsótelekes and Rudabánya offer one of the few windows on the diverse ecosystems of central Europe before the Vallesian Crisis. This event, around 9.7 Ma, was associated with increased seasonality and lower precipitations and humidity which led to the spread of deciduous woodlands and faunas adapted to more open environments (Fortelius 1996b; Van Dam 2006; Domingo et al. 2013), although the Vallesian Crisis likely did not occur so abruptly as often portrayed and affected different regions heterogeneously (Agustí and Moyà-Solà 1990; Fortelius et al. 1996b;

Casanovas-Vilar et al. 2014; Daxner-Höck et al. 2016; Madern et al. 2018; Butiseacă et al. 2021). The sharpness of the turnover event may have been exacerbated by the uneven quality of the fossil record between different areas of Europe, by the overidentification of fragmentary remains based on contextual data, and/or by the biochronological attributions of localities that lack independent age constraints (Casanovas-Vilar et al. 2014; Madern et al. 2018), caveats especially relevant considering the case of the Dinotheriensande, one of the most important early Vallesian (MN 9) localities that also contains reworked sediments and fauna (Böhme et al. 2012). Abrupt or gradual, there was nonetheless an evident turnover of mammalian faunas during the late Miocene, which preferentially affected forest-adapted taxa, including suids and hominoids (Agustí and Moyà-Solà 1990; Fortelius et al. 1996a, 1996b; Begun et al. 2012). A few remains of *Pa. crusafonti* were reported from the late Vallesian (MN 10) of La Tarumba (Van der Made 1990; Van der Made et al. 2014), but both *Parachleuastochoerus* and *Pr. palaeochoerus* as well as the folivore listriodonts went extinct during the second half of the Vallesian (MN 10). After that, probably taking advantage of the concurrent environmental changes, Suinae became dominant and new species of *Propotamochoerus* and *Hippopotamodon* characterized Turolian (MN 11–MN 13; ~8.9–5.3 Ma) assemblages of Europe (Fortelius et al. 1996a; Iannucci et al. 2021).

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3. Paper 2

Suidae transition at the Miocene-Pliocene boundary: a reassessment of the taxonomy and chronology of *Propotamochoerus provincialis*

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Abstract

The Miocene-Pliocene (Turolian-Ruscinian) transition represents a fundamental interval in the evolution of Euro-Mediterranean paleocommunities. In fact, the paleoenvironmental changes connected with the end of the Messinian salinity crisis are reflected by a major renewal in mammal faunal assemblages. An important bioevent among terrestrial large mammals is the dispersal of the genus *Sus*, which replaced all other suid species during the Pliocene. Despite its possible paleoecological and biochronological relevance, correlations based on this bioevent are undermined by the supposed persistence of the late surviving late Miocene *Propotamochoerus provincialis*. However, a recent revision of the type material of this species revealed an admixture with remains of *Sus strozzii*, an early Pleistocene (Middle Villafranchian to Epivillafranchian) suid, questioning both the diagnosis and chronological range of *P. provincialis*. Here we review the late Miocene Suidae sample recovered from the Casino Basin (Tuscany, central Italy), whose taxonomic attribution has been controversial over the nearly 150 years since its discovery. Following a comparison with other Miocene, Pliocene, and Pleistocene Eurasian species, the Casino Suidae are assigned to *P. provincialis* and the species diagnosis is emended. Moreover, it is recognized that all the late Miocene (Turolian) European *Propotamochoerus* material belongs to *P. provincialis* and that there is no compelling evidence of the occurrence of this species beyond the Turolian-Ruscinian transition (MN13-MN14).

Keywords: Large mammals; Faunal turnover; Euro-Mediterranean; Latest Miocene; Messinian; Ruscinian

3.1. Introduction

The late Miocene was a period of dramatic changes at a global scale (Cerling et al. 1997; Herbert et al. 2016), which also led to the physiographic separation of the Mediterranean Sea from the Atlantic Ocean (Krijgsman et al. 1999). At the Miocene-Pliocene boundary, the Messinian salinity crisis reached its acme and after that ended with an abrupt —if not properly catastrophic (Garcia-Castellanos et al. 2009)— restoration of the basin-ocean connection (Hsü et al. 1977; Meijer and Krijgsman 2005). Undoubtedly, the resulting environmental upheaval put strong pressure on continental ecosystems (Eronen et al. 2009; Carnevale et al. 2019). Indeed, this episode roughly corresponds with the Turolian-Ruscinian transition —zones MN13–14 of the European mammal biochronological scale (Mein 1975)— a significant reorganization of the mammalian paleocommunities (de Bruijn et al. 1992; Agustí et al. 2001; Hordijk and de Bruijn 2009; Hilgen et al. 2012).

The impact of this transition was particularly strong on the carnivoran guild, featuring the extinction of more than 90% of the species (Werdelin and Turner 1996), but was also significant among ungulates. For instance, the Pikermian fauna (Bernor et al. 1979), adapted to dry and open environmental conditions, disappeared (Fortelius et al. 2006; Eronen et al. 2009; Kaya et al. 2018). *Sus arvernensis* (Croizet and Jobert, 1828), was one of the few species capable of taking advantage of the change. It represents the earliest member of a very successful genus that replaced all other suine species during the Pliocene (Frantz et al. 2016).

The role of *S. arvernensis* as a Pliocene (Ruscinian) biochronological marker has been recognized by several authors (van der Made 1990; Agustí et al. 2001). However, correlations based on the "*Sus* event" have been weakened by: 1) the supposed persistence of the last-surviving late Miocene *Propotamochoerus provincialis* (Blainville, 1847), and 2) the uncertain attribution of fossil Suidae close to the Miocene-Pliocene boundary. Controversy arose mainly from the heterogeneous nature of the type material of *P. provincialis* from Montpellier (Blainville 1847; Gervais 1850; Stehlin 1900).

Indeed, early researchers described under the same name an ensemble constituted by different species, which has been only recently reassessed (Pickford 2013). In particular, some remains previously assigned to *P. provincialis* actually belong to *Sus strozzii* Forsyth Major, 1881, a large-sized early Pleistocene (Middle Villafranchian to Epivillafranchian) suid (Azzaroli 1952; Cherin et al. 2018, 2020; Iannucci et al. 2020a).

The occurrence of Suidae remains in the Casino Basin (Tuscany, central Italy) has been reported by Forsyth Major (1875), and briefly discussed by Pantanelli (1879) and Stehlin (1900). Subsequent studies have proposed various interpretations of the taxonomy of these fossils, but they did not provide a thorough revision of the sample (van der Made and Belinchón 1991; Montoya et al. 2006; Guérin and Tsoukala 2013; Pickford and Obada 2016).

In spite of their convoluted taxonomic history, the Casino Suidae are relatively abundant, well preserved, and chronologically well constrained. Herein, we offer a description, review, and an analysis of the biochronological framework of this material, in a comparative study with other Miocene, Pliocene, and Pleistocene Eurasian Suinae.

3.2. The Casino Basin Fossil Locality

The Casino fluvio-lacustrine (sub-)basin is located in the northern part of the Siena Basin, a NNW-SSE oriented tectonic depression with a complex internal architecture (Tuscany, central Italy; Figure 1). The deposition of the Neogene sedimentary succession is related to an extensional tectonic phase started in the middle Miocene. The basin records two Miocene sedimentary cycles, respectively dated to the Tortonian-early Messinian and the end of the Messinian (Lazzarotto and Sandrelli 1977; Bossio et al. 2002; Abbazzi et al. 2008; Brogi 2011).

Ambrogio Soldani (1736–1808) was the first to report the occurrence of fossil remains in the lignite outcrops of the Casino Basin (Soldani 1789: 194), but a mammalian fauna was recovered only during the 1870s, from lignite beds deposited during the second fluvio-lacustrine sedimentary cycle (Forsyth Major 1875; Pantanelli 1879).

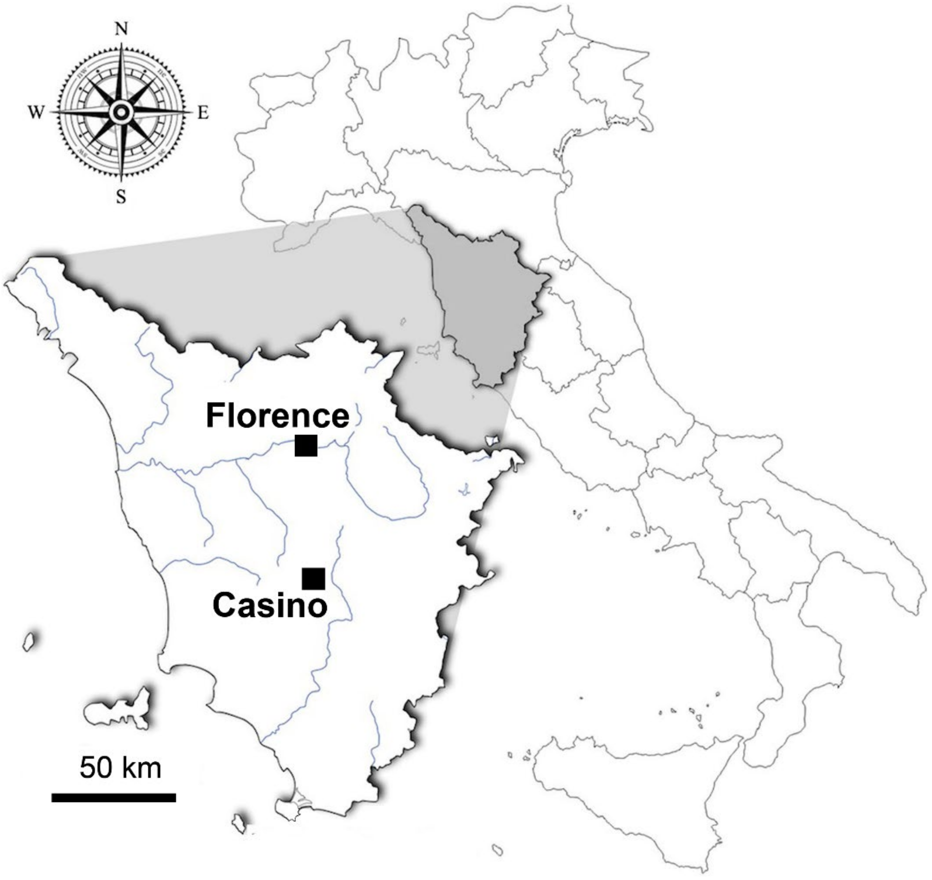

Figure 1 - Location of the Casino Basin fossil locality.

The assemblage is referred to MN13 and includes *Eucyon* sp., *Thalassictis* cf. *T. hipparionum*, *Mesopithecus pentelicus, Tapirus arvernensis*, an hipparionine (likely *Hippotherium malpassii*; Rook and Bernor 2013), *Hexaprotodon*? *pantanellii*, *Parabos* sp., and *Dipoides problematicus* (Rook et al. 1999).

The taphonomic analysis of the remains has revealed an overall homogeneity and a short time-averaged accumulation of the fossil assemblage, with the exception of some allochthonous remains among which there are no Suidae (Gallai 2005).

3.3. Materials and Methods

The Suidae remains from the Casino Basin are housed in the Accademia dei Fisiocritici di Siena (AFS) and in the Natural History Museum of the University of Florence, Section of Geology and

Paleontology (IGF). Measurements were taken to the nearest 0.1 mm with a digital calliper and are provided in Table 1. The studied sample was compared with other remains housed in the same institutions, in the Hungarian Natural History Museum, Budapest (HNHM), in the Museum of the Geological and Mineralogical Survey of Hungary, Budapest (MAFI), in the Natural History Museum, Mainz (NMM), and in the Department of Earth Sciences, Utrecht University (IVAU), as well as with data from the literature (Table 2). Upper and lower teeth are in upper and lower case, respectively (e.g., P2 = upper second premolar; m3 = lower third molar). "D" denotes deciduous teeth. Measurements and terminology mainly follow van der Made (1996).

Over the years, several of the species included in the analysis have been assigned to different genera and some of them have been considered synonyms. Here we accept the synonymy between *Propotamochoerus* Pilgrim, 1925, and *Korynochoerus* Schmidt-Kittler, 1971 (Fortelius et al. 1996), and between *Hippopotamodon* Lydekker, 1877, and *Microstonyx* Pilgrim, 1925 (Pickford 2015). In both cases the former genus has the priority. We conservatively treated as separated *Hippopotamodon major* (Kaup, 1833) and *Hippopotamodon erymanthius* (Roth and Wagner, 1854), even though the two taxa overlap in size and may represent the same species. Finally, some authors resurrected the genus *Dasychoerus* Gray, 1873, to include extinct and extant verrucosic warty pigs (Berdondini 1992, as a subgenus; Pickford 2012). However, the monophyly of this group is not adequately supported (Frantz et al. 2016; Cherin et al. 2018) and therefore we refer these species to *Sus*.

We performed a Principal Component Analysis (PCA) on the variance-covariance matrix of tooth length and width values of the maxillaries bearing P3-M3 of several Suinae species (*Hippopotamodon sivalense*, *H. major*, *H. erymanthius*, *Propotamochoerus palaeochoerus*, *Propotamochoerus wui*, *P. provincialis*, *S. arvernensis*, *S. strozzii*) in order to undertake a thorough comparison of the material from Casino and explore the variability of the fossil sample. Following previous studies (Geraads et al. 2008; Lazaridis 2015), we excluded M1 and M2 measurements because they may vary substantially due to the wear stage. To evaluate differences related to the effect of size, we conducted two analyses, one considering unstandardized variables and one considering standardized variables.

The variables in the latter were calculated by dividing raw measurements by the geometric mean of all variables (Mosimann 1970). The software PAST (Hammer et al. 2001) was used for the analysis. We further investigated the biometric variability of the fossil sample by using bivariate diagrams. All data generated or analyzed during this study are included in this published article.

Specimen Id.	Side	Tooth	L	Wm	Wd	Wt
AFS 2840	Sn	I1	17	9.5		
AFS 2865	Sn	M1	18.6	17.1	17.1	
AFS 2865	Sn	M2		22.4		
AFS 2868	Dx	D4	15.9	13.2	13.3	
AFS 2868	Dx	M1	20.8	16.6	15.4	
AFS 2869a	Sn	m3	36.8	19.8	18.3	15.4
AFS 2869b	Sn	P3	14.8	11.7	13.6	
AFS 2869c	Dx	p4	16.1	10.1	11.3	
AFS 2869d	Sn	P2	17.4	8.3	10.6	
AFS 2869e	Sn	p3	17.4	9.1	9.9	
AFS 2869f	Sn	P2	16.3	8.1	8.3	
IGF 5913Va	Dx	P4	13.2		15.5	
IGF 5913Vb	Dx	M3		25.3		
IGF 5913Vc	Dx	P3	15.3	11.4	12.6	
IGF 5913Vd	Sn	P3	15.2	10.9	11.1	

Table 1 - *Propotamochoerus provincialis* (Blainville 1847) from Casino Basin, measurements of the teeth (mm). Dx = right; Sn = left; L = length (mesiodistal diameter in incisors); Wm = mesial width (buccolingual diameter in incisors); Wd = distal width (second lobe in a molar); Wt = width of the third lobe in a molar

Specimen Id.	Species	Locality	Reference	P3L	P3W	P4L	P4W	M3L	M3W
GSP 3789	*H. sivalense*	Loc. 106 (India)	Pickford (1988)	21	20.3	19.4	23.6	53.2	31.8
IPUW 4059	*H. erymanthius*	Pikermi (Greece)	Pickford (2015)	17.3	14.9	15.8	17.8	40.6	27.3
IPUW 5310	*H. erymanthius*	Pikermi (Greece)	Pickford (2015)	17.7	15.7	16.3	19.3	39.2	26.5
MNHN PIK 763	*H. erymanthius*	Pikermi (Greece)	Pickford (2015)	17.1	15.7	16.3	18.9	41.1	27
MNHN PIK 764	*H. erymanthius*	Pikermi (Greece)	Pickford (2015)	18	15.8	17.1	19.9	42.9	28.1
MNHN PIK 780	*H. erymanthius*	Pikermi (Greece)	Pickford (2015)	19	16.5	16.2	19.4	43.5	27.5
NHML M 9053	*H. erymanthius*	Pikermi (Greece)	Pickford (2015)	17.6	13.5	15.3	17.9	40.6	26
PIMUZ A/V 2371	*H. erymanthius*	Gulpinar (Turkey)	Pickford (2015)	18.4	15	17	19.2	42	24.9
PIMUZ A/V 2355	*H. erymanthius*	Karakai (Turkey)	Pickford (2015)	19.7	18.5	18.6	20.6	45.3	27.5
IPUW (Krahuletz Museum)	*H. major*	Sträzing bei Krems (Austria)	Pickford (2015)	18.4	16.9	16	21.6	44	28.4
Pk-5265	*H. major*	Petrelik (Bulgaria)	Kostopoulos et al. (2001)	17.8	17.2	15.8	19.3	44.1	29.2
FM-2801	*H. major*	Strumyani-2 (Bulgaria)	Geraads et al. (2011)	19.9	15.9	15.9	19.6	45.4	30.8
MNHN LUB 660	*H. major*	Luberon, Cucuron (France)	Pickford (2015)	18.5	17.2	18.2	21.3	45.4	31.3
MR 303442	*H. major*	Luberon, Cucuron (France)	Pickford (2015)	18	18.5	19	22.3	45.5	31.8
CCECL AA 114	*H. major*	Soblay (France)	Pickford (2015)	17	16.7	15	19.3	38.8	26.5
Tbilisi	*H. major*	Bazaleti (Georgia)	Pickford (2015)	18.5	17	18.1	20.2	44	29.8
NMT 343-13	*H. major*	Udabno (Georgia)	Pickford (2015)	20.7	20.4	17.6	22.6	50.5	31
NKT-68	*H. major*	Nikiti (Greece)	Kostopoulos (1994)	18	17.3	17.1	19.8	43.5	27.8
MNHN SLQ 1075	*H. major*	Salonique (Greece)	Pickford (2015)	18.4	15	16.3	18	40.9	26
MNHN SLQ 913	*H. major*	Salonique (Greece)	Pickford (2015)	16.2	16.8	17	18.8	40.6	26

AMNH 20653-Q5	*H. major*	Samos (Greece)	Sylvestrou and Kostopoulos (2009)	16.9	13.9	15.7	18.1	36.7	25.8
AMNH 20795-Q5	*H. major*	Samos (Greece)	Sylvestrou and Kostopoulos (2009)	18.6	15.5	15.3	19.5	39.3	27.5
MTLA-537	*H. major*	Samos (Greece)	Sylvestrou and Kostopoulos (2009)	19.8	14.9	16.8	19.3	43.4	27.2
MAFI Ob. 2784	*H. major*	Polgárdi (Hungary)	This work	18.4	16.1	16.7	19.1	45.3	29.4
MNCN BAT 1014 E346	*H. major*	Batallones (Spain)	Pickford (2015)	19.6	17.9	17.2	20.1	44.1	28.4
DT Ro 2992	*H. major*	La Roma 2 (Spain)	Pickford (2015)	17.2	16.1	16.6	19.4	42.2	26.8
IPS 2002	*H. major*	Piera (Spain)	van der Made et al. (1992)	17.9	19.5	18.5	23.3	48.7	31.6
IPS 9761	*H. major*	Terrasa (Spain)	Pickford (2015)	19.2	18	19.2	22.8	46.7	31.2
58-HAY-2/45	*H. major*	Sivas (Turkey)	van der Made et al. (2013)	17.7	15.9	16.7	19.9	43.8	27.6
LJG 60.258	*P. palaeochoerus*	Johnsdorf, Ost-Steiermark (Austria)	Hellmund (1995)	14.8	12.8	13.3	15.3	26	20.6
1956/520 (b-f)	*P. palaeochoerus*	Gauweinheim, Wissberg (Germany)	Hellmund (1995)	16.3	14.1	13.3	16.2	30.5	20.4
BSP AS 103	*P. palaeochoerus*	Münchener Flinz (Germany)	Hellmund (1995)	16.9	12.4	13.5	17	24.1	20.9
Vozarci-271	*P. provincialis*	Vozarci (Bulgaria)	Geraads et al. (2008)	14.5	13.1	13.2	16.6	29.5	21.1
KRY3820	*P. provincialis*	Kryopigi (Greece)	Lazaridis (2015)	14.5	13.8	13.1	17.2	33.5	24.8
AMGP-MA 501	*P. provincialis*	Maramena (Greece)	Hellmund (1995)	16.8	13	14	15.4	32	20.8
AMGP-MA 502	*P. provincialis*	Maramena (Greece)	Hellmund (1995)	15.4	12.3	14.8	15.7	32.4	21
AFS 2865	*P. provincialis*	Bacino del Casino (Italy)	This work	15	13.2	13.4	17	33.5	23.1
VM 628	*P. provincialis*	Venta del Moro (Spain)	Morales (1984)	17	14.1	15.1	16.8	34.1	23.6

No id.	*P. wui*	Lufeng (China)	van der Made and Han (1994)	11	9.7	10.1	11.9	25.2	16.3
No id.	*P. wui*	Lufeng (China)	van der Made and Han (1994)	10.8	10.3	9.6	12.9	25.9	18.5
FSL 40 073	*S. strozzii*	Montpellier (France)	Pickford (2013)	17.5	14	14.6	18	37	26
GER-51	*S. strozzii*	Gerakarou (Greece)	Koufos (1986)	12.7	11.5	13.2	15.2	37.1	24.4
IGF 424	*S. strozzii*	Upper Valdarno (Italy)	This work	13.2	14.2	13.6	17	42.5	26.2
FP1-2001-0251	*S. strozzii*	Fonelas P-1 (Spain)	Arribas and Garrido (2008)	15	13.9	15	18.1	42.8	26.5
IPS 107041a	*S. strozzii*	Vallparadís Estació EVT7 (Spain)	Cherin et al. (2020)	13.1	12	12.9	15.7	38.2	24.1
NHMB Perp	*S. arvernensis*	Perpignan (France)	Pickford and Obada (2016)	13.3	10.8	12	14.6	26.6	17.5
CCECL Pp 198	*S. arvernensis*	Perpignan, Citadelle (France)	Pickford and Obada (2016)	13.4	10	11	12.7	25.6	17.6
NHMB Rss 70	*S. arvernensis*	Perpignan, Roussillon (France)	Pickford and Obada (2016)	14	11	12	14	28	18
CCECL Br 87	*S. arvernensis*	Trévoux, Reyrieux (France)	Pickford and Obada (2016)	13.3	10.7	11.6	14.5	28.7	20.2
NHMB VI 1	*S. arvernensis*	Villafranca D'Asti (Italy)	Pickford and Obada (2016)	12.2	13.3	11	16.3	28	20.4
NHMB VI 144	*S. arvernensis*	Villafranca D'Asti (Italy)	Pickford and Obada (2016)	13	10.4	11	13.9	26.5	19.8

NHMB VI 146	*S. arvernensis*	Villafranca D'Asti (Italy)	Pickford and Obada (2016)	12.6	12.6	11.6	15.4	26	20
NMENHM	*S. arvernensis*	Musaitu (Moldova)	Pickford and Obada (2016)	14	11.5	11.8	14.6	27	20
Piedrabuena	*S. arvernensis*	Piedrabuena (Spain)	Pickford and Obada (2016)	14	9.5	10.3	14	27	18.5

Table 2 - Measurements (mm) of the specimens included in the statistical analysis.

3.4. Statistical Analysis

The scatter diagram of the first two axes of the unstandardized PCA (97.4% of the total variance) reveals almost no overlap between the compared species, apart from *H. erymanthius* and *H. major* (Figure 2a). The first component accounts for 94.4% of the total variance and all the variables positively contribute to it, with a major influence of M3 L (Figure 2b). This axis evidences the size differences in the sample, allowing a separation between small-sized (*Propotamochoerus* and *S. arvernensis*) and large-sized (*Hippopotamodon* and *S. strozzii*) suids, and with less support even between each species. The second component explains 3.0% of the total variance and it is mainly influenced by the opposite contributions of M3 L and premolar measurements (Figure 2c). The separation along the vertical axis is clear between species with relatively longer M3 (*P. wui* and *S. strozzii*) and *P. palaeochoerus*, showing relatively larger premolars, whereas the other species overlap, having similar proportions.

The first two axes of the standardized PCA account for 85.6% of the total variance, of which 73.0% is explained by the first component and 12.6% by the second (Figure 3a). Along the PC1 axis, M3 L is the most influential variable, separating species with proportionally small (*P. palaeochoerus*) and proportionally large (*S. strozzii*) third molars. This is similar to the second component of the unstandardized PCA, but results differ in that both M3 measurements (length and width) contribute on the same direction and M3 L is relatively more important than premolar measurements (Figure 3b). Along the PC2 axis, none of the species considered is clearly separated and only *S. strozzii* occupies a relatively small area, mainly in the first quadrant. As the second component is influenced by the opposite contributions of width and length values (Figure 3c), this indicates that only *S. strozzii* possesses, on average, relatively wider teeth.

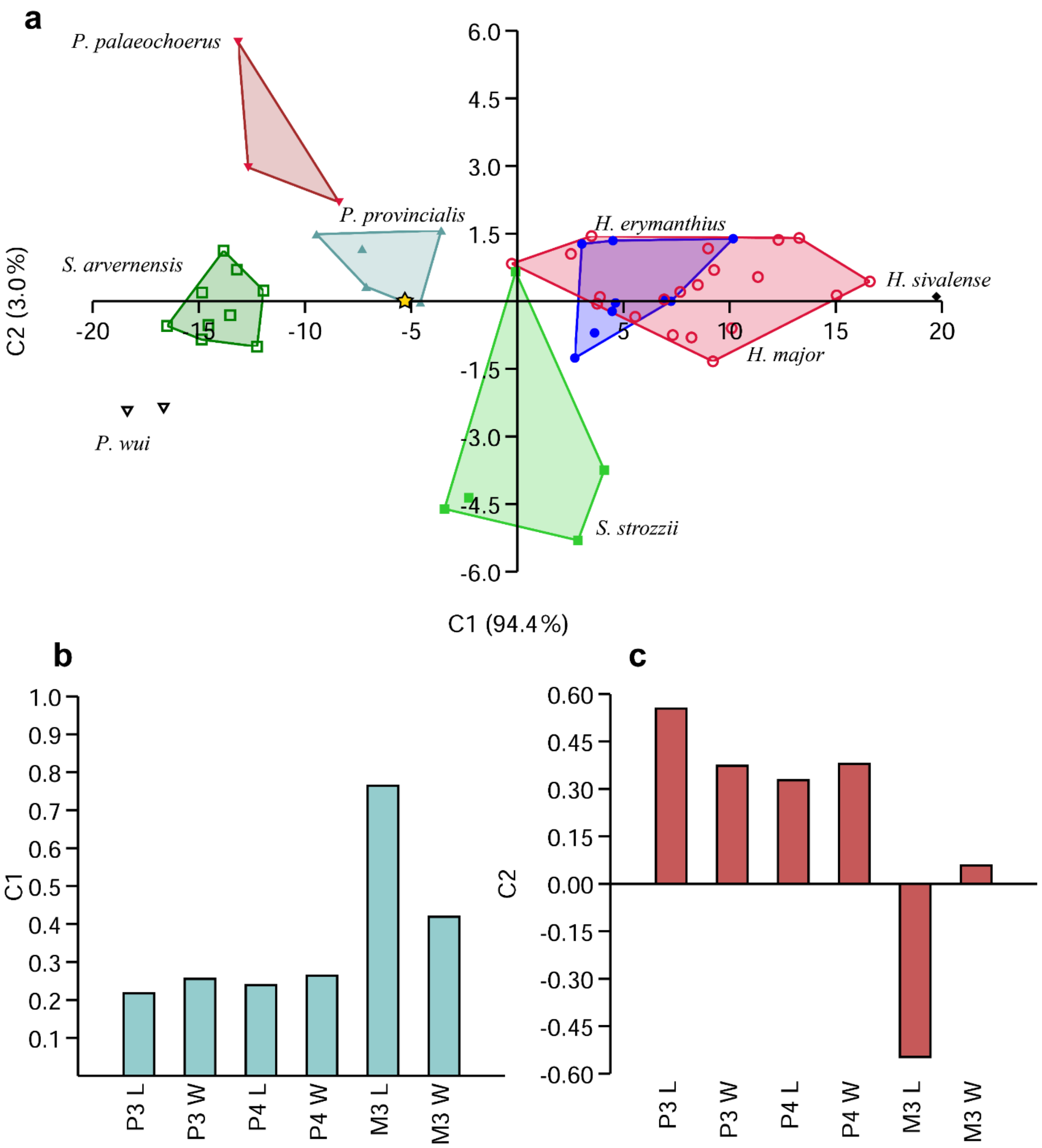

Figure 2 - PCA (unstandardized) of the compared Suinae species (*H. sivalense*, *H. major*, *H. erymanthius*, *P. palaeochoerus*, *P. provincialis*, *P. wui*, *S. arvernensis*, *S. strozzii*); scatter diagram (**a**) and loadings of the first (**b**) and second (**c**) components. The star indicates AFS 2865 from Casino. Raw data are in Table 1.

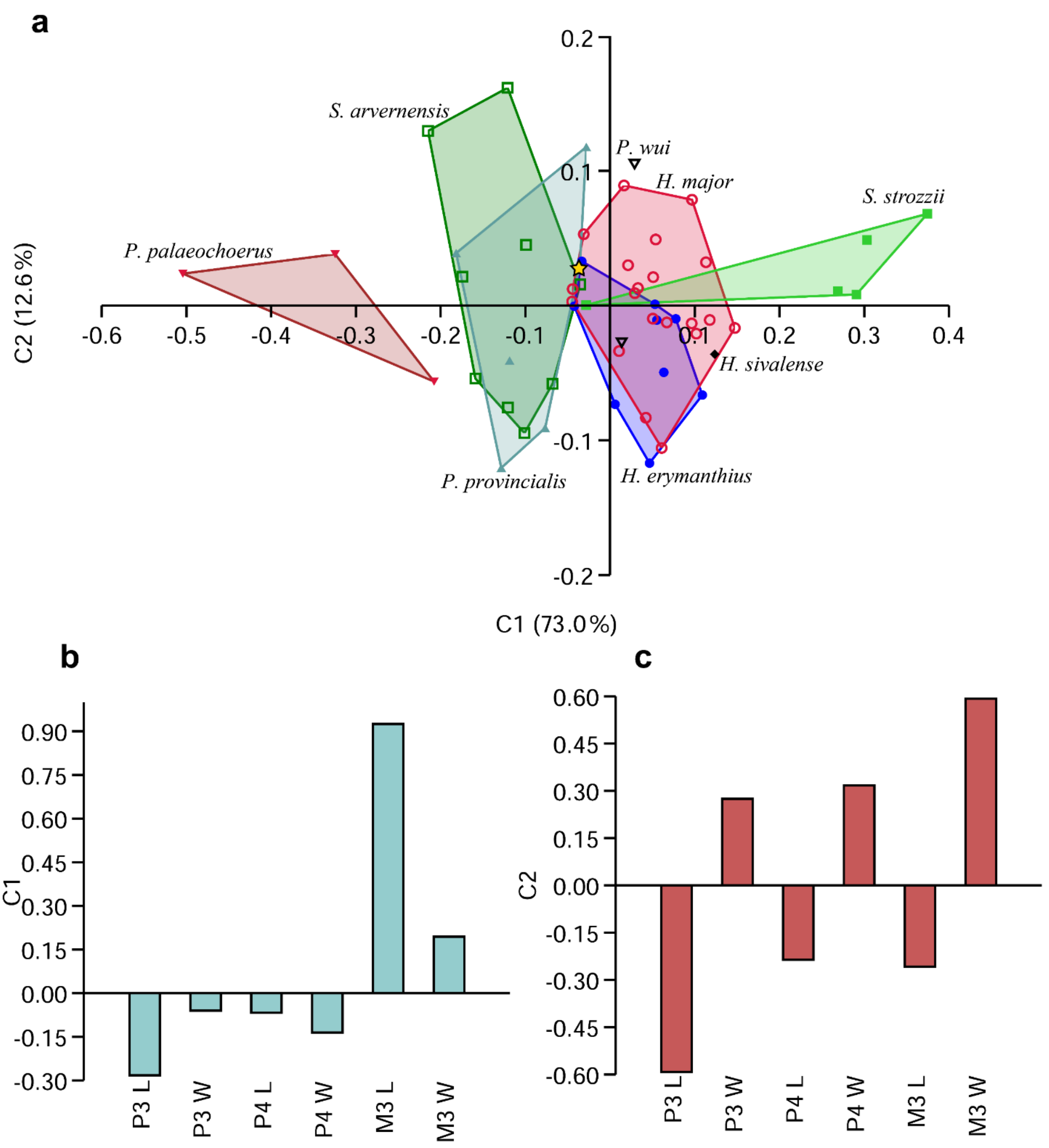

Figure 3 - PCA (standardized) of the compared Suinae species (*H. sivalense*, *H. major*, *H. erymanthius*, *P. palaeochoerus*, *P. provincialis*, *P. wui*, *S. arvernensis*, *S. strozzii*); scatter diagram (**a**) and loadings of the first (**b**) and second (**c**) components. The star indicates AFS 2865 from Casino. Raw data are in Table 1.

3.5. Systematic Paleontology

Order Artiodactyla Owen, 1848

Family Suidae Gray, 1821

Subfamily Suinae Gray, 1821

Tribe Dicoryphochoerini Schmidt-Kittler, 1971

Genus *Propotamochoerus* Pilgrim, 1925

Propotamochoerus provincialis (Blainville, 1847)

3.5.1. Selected Synonymy List

Sus different from *Sus choeroides* and *Sus strozzii* Forsyth Major, 1875

Sus erymanthius var. minor Pantanelli, 1879

Sus cfr. *S. palaeochoerus* Stehlin, 1900

Sus minor De Giuli et al., 1983

Korynochoerus provincialis van der Made and Belinchón, 1991

Sus cf. *S. minor* Rook, 1992

Korynochoerus cf. *K. provincialis* Gallai, 2005

Propotamochoerus provincialis Gallai, 2006

Propotamochoerus provincialis Montoya et al., 2006

Sus arvernensis Guérin and Tsoukala, 2013

3.5.2. Emended Diagnosis

Propotamochoerus species larger than *S. arvernensis*, *P. wui*, and *P. palaeochoerus*; smaller than *S. strozzii* and *Hippopotamodon*. Parietal lines do not meet to form a sagittal crest. The angle enclosed between the maxilla and the zygoma ranges from 90° to 130°. P2 usually larger than P3. The mesial cingulum in m3 has a limited development. Modified and expanded after Pickford (2013).

3.5.3. Type Specimen

UM SM 460, right M3 from the "Sables marins" of Montpellier, designed as lectotype by Pickford (2013) after the description of Blainville (1847: 208, pl. 9; but not the m2-m3, which belong to *S. strozzii*).

3.5.4. Stratigraphic Range

Late Miocene (Turolian, MN11-MN13).

3.5.5. Referred Material from the Casino Basin

AFS 2840: two I1 of the same individual (Figure 4b); AFS 2865: fragment of left maxilla with P3-M3 (Figure 4a); AFS 2867: upper right female canine (Figure 4c); AFS 2868: fragment of right maxilla with D4-M1 (Figure 4l); AFS 2869a-f: six isolated teeth, left m3 associated with AFS 2865 (Figure 4e), left P3 (Figure 4k), right p4 (Figure 4f), left P2 (Figure 4n), left p3 (Figure 4g), left P2 (Figure 4m); IGF 5913Va-d: four isolated teeth: right P4 (Figure 4h); fragment of right M3 (Figure 4d); right P3 (Figure 4i); left P3 (Figure 4j).

3.5.6. Description

The studied sample is mainly composed of isolated, brown/dark-colored teeth, in good state of preservation and with no significant taphonomic modifications, except for the M1 of AFS 2868, which bears evident root-etching marks on its lingual side (Figure 4l3). The specimen is also slightly deformed, displaying an artificial diastema between D4 and M1.

AFS 2865 preserves part of the malar bone of the zygomatic arch, which departs from the maxilla spanning an angle of ~110° (Figure 4a3).

The I1 is represented by the two antimere elements that belong to a single individual (AFS 2840), as is revealed by the coinciding interstitial facets on the mesial tip of the incisors (Figure 4b).

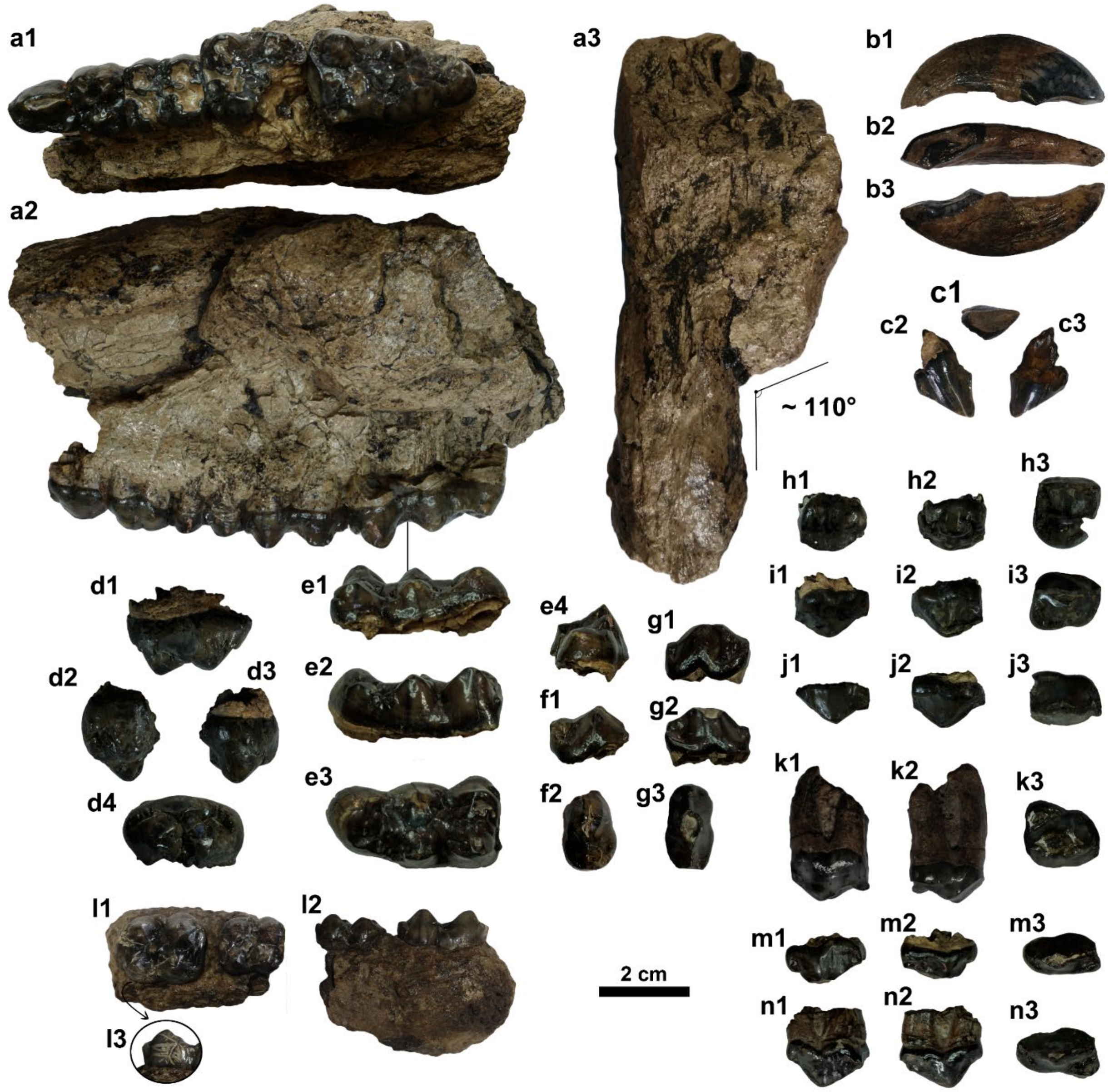

Figure 4 - *Propotamochoerus provincialis* from Casino: **a** - left maxillary with P3-M3 in occlusal (1), buccal (2), and dorsal (3) views (AFS 2865); **b** - left I1 in buccal (1), occlusal (2), and mesial (3) views (AFS 2840); **c** - right upper female canine in occlusal (1), lingual (2), and buccal (3) views (AFS 2867); **d** - right M3 fragment in mesial (1), lingual (2), buccal (3), and occlusal (4) views (IGF 5913Vb); **e** - left m3 in buccal (1), lingual (2), occlusal (3), and distal (4) views (AFS 2869a, associated with AFS 2865); **f** - right p4 in buccal (1) and occlusal (2) views (AFS 2869c); **g** - left p3 in buccal (1), lingual (2), and occlusal (3) views (AFS 2869e); **h** - right P4 in buccal (1), lingual (2), and occlusal (3) views (IGF 5913Va); **i** - right P3 in buccal (1), lingual (2), and occlusal (3) views (IGF 5913Vc); **j** - left P3 in buccal (1), lingual (2), and occlusal (3) views (IGF 5913Vd); **k** - left P3 in buccal (1), lingual (2), and occlusal (3) views (AFS 2869b); **l** - right maxillary with D4-M1 in occlusal (1) and buccal (2) views, and particular of the lingual view (3) (AFS 2868); **m** - left P2 in buccal (1), lingual (2), and occlusal (3) views (AFS 2869f); **n** - left P2 in buccal (1), lingual (2), and occlusal (3) views (AFS 2869d).

The teeth are mesiodistally elongated, concave on the lingual side. Both are well preserved, but the moderate wear prevents description of the finer details of their morphology.

The fragment of upper canine (AFS 2867) has a triangular occlusal section (Figure 4c), with a rounded development on the lingual side. Its reduced development allows us to hypothesize that it belonged to a female individual.

The two P2s in our sample (AFS 2869df) differ greatly in the development of the protocone. In AFS 2869d (Figure 4n) the cusp is markedly pronounced, while it is very poorly developed in AFS 2869f (Figure 4m).

The P3 is a stouter version of the P2, slightly shorter and with a major development of the protocone (Figure 4a, i-k).

The P4 is a trapezoidal-shaped tooth, broader than it is long (Figure 4a, h). It is the most molarized premolar of the series. The three main cusps have approximately the same dimensions, with the protocone slightly shifted distally. The sagittal valley (protofossa) is filled by accessory cusplets, which develop lingually to the labial main cusps.

Molars from Casino, and the D4, are bunodont teeth with two (D4, M1, M2) or three (M3, m3) lobes, each possessing a pair of main cusps/cuspids and accessory cusplets located along the medial axis. In each pair, the buccal main cusp is higher in the upper molars, while the opposite condition occurs in the m3. There is a mesial cingulum bearing one of the accessory cusplets, which is perpendicular to the medial axis of the teeth. Bilobated molars are hardly different from one another, except for their size.

In the upper molars the lingual cusps are translated distally in comparison to the buccal ones, especially in the M3 (AFS 2865; Figure 4a). The tooth has an asymmetric talon with a slightly lingually placed pentacone.

In the preserved p3 (AFS 2869; Figure 4g), the protoconid and metaconid are merged in a single dentine islet due to the moderately advanced wear stage, resembling a single massive cuspid.

The p4 (AFS 2869) is of the Dicoryphochoerini type (Schmidt-Kittler 1971), with the two main cuspids not placed on the same mesiodistal axis, but shifted. The talonid is low. The tooth is well preserved but slightly damaged mesiolingually.

The m3 (AFS 2869a) perfectly occludes with the M3 of AFS 2865, suggesting that they belong to the same individual (Figure 4e). The development of the mesial cingulum is limited to the mesial part of the tooth. In the third lobe there are two prominent cuspids, pentaconid and pentapreconid, which are aligned mesiodistally. The tooth is curved along the mesiodistal axis.

3.6. Comparative Discussion

The Suidae from Casino belong to the subfamily Suinae, as revealed by the occurrence of a closed sagittal valley (protofossa) in the P4 (Pickford 1988). The p4, with the two main cusps not placed along the same mesiodistal axis, allows reference of the sample to the tribe Dicoryphochoerini (Schmidt-Kittler 1971). Moreover, the zygomatic of AFS 2865 is inflated and abruptly departing from the maxilla, whereas this bone is gently receding in *Sus* (Azzaroli 1975; van der Made and Moyà-Solà 1989; Hellmund 1995). European late Miocene Dicoryphochoerini —with the exception of *Eumaiochoerus etruscus* (Michelotti, 1861), endemic of the Tusco-Sardinian paleobioprovince (Hürzeler 1982; Mazza and Rustioni 1997)— are referred to *Propotamochoerus* (= *Korynochoerus*) or *Hippopotamodon* (= *Microstonyx*). *Propotamochoerus* is characterized by a substantially smaller size, comparable with that of the Casino specimens.

At least five species of *Propotamochoerus* are recognized: *P. provincialis*, *P. palaeochoerus*, *P. hyotherioides*, *P. hysudricus*, and *P. wui* (Pickford 1988, 2013; van der Made and Moyà-Solà 1989; van der Made and Han 1994; Fortelius et al. 1996; van der Made et al. 1999; Geraads et al. 2008; Sein et al. 2009; Hou et al. 2019). The first two species are represented in the European fossil record. However, the existence of a third European species of *Propotamochoerus* replacing the Vallesian *P. palaeochoerus* in the Turolian assemblages (MN11–13) has long been suggested in the literature

(Fortelius et al. 1996; van der Made et al. 1999; Geraads et al. 2008; Gallai and Rook 2011). Fortelius et al. (1996) considered the *Propotamochoerus* sp. remains from Baccinello V3 (MN13, Italy; Rook 2016) as representatives of this taxon, suggesting a close relationship with *P. hyotherioides* from Lufeng (China; van der Made and Han 1994). Van der Made et al. (1999) went a step further by also including in the MN11-MN13 *Propotamochoerus* the remains recovered from the Greek localities of Samos (Thenius 1950), Maramena (Hellmund 1995), and Ravin des Zouaves-5 (de Bonis and Bouvrain 1996), remarking the similarities between this group, *P. provincialis*, and *P. hyotherioides*. Geraads et al. (2008) described as *Propotamochoerus* sp. several remains from the late Miocene of the Balkans (Macedonia and Bulgaria), arguing that they may represent an Aegean species distinct from other European (*P. palaeochoerus* and *P. provincialis*) and Asian (*P. hysudricus* and *P. hyotherioides*) forms. Lazaridis (2015) eventually named this species *Propotamochoerus aegaeus*, describing a cranium and associated mandible from Kryopigi (Greece). The author included in the hypodigm of the species the *Propotamochoerus* remains recovered from Ravin des Zouaves-5, Samos, and Thermopigi (Greece), Vozarci and Kalnitsa (Macedonia), Kalimantsi (Bulgaria), and Salihpaşalar (Turkey), but not from Maramena and Baccinello V3. According to the original diagnosis, *P. aegaeus* should differ from *P. provincialis* in the following features: 1) smaller dimensions; 2) presence of diastemata between C, P1, and P2 (albeit it should be noticed that not all the fossils ascribed to the species possess a diastema between P1 and P2); 3) P1 with two roots; 4) P2 longer than P3. However, these supposed differences are based upon the comparison with remains that do not belong to *P. provincialis*. In fact, Pickford (2013) convincingly exposed how the type material of *P. provincialis* (Blainville, 1847) was a “chimera,” including specimens actually referable to *S. strozzii*. Moreover, the type locality also yielded remains of *S. arvernensis* and an M3 similar to the form occurring in Kvabebi (Georgia) —an enigmatic suid biometrically close to *P. provincialis*, but morphologically closer to *Sus arvernensis* (Vekua 1972; Azzaroli 1975; see Pickford and Obada 2016 for a discussion).

In particular, FSL 40073, a snout of *S. strozzii* from Montpellier, has long been regarded as one of the few cranial remains of *P. provincialis* (Geraads et al. 2008). This specimen displays a single-rooted P1 and no diastemata in the tooth row, and it is the source of the incorrect attribution of these features to *P. provincialis* (Pickford 2013). Furthermore, once the *S. strozzii* material is excluded from the comparison, there are no significant size differences between Aegean and non-Aegean *P. provincialis* (Figures 2a, 5). Indeed, the PCA and the bivariate diagrams reveal that the Aegean group clusters with the specimens from Casino, Venta del Moro (Spain; Morales 1984), and Maramena (Figures 2a, 5). This group is characterized by a size intermediate between the smaller *S. arvernensis*, *P. palaeochoerus*, and *P. wui*, and the larger *Hippopotamodon* and *S. strozzii*. Moreover, the teeth in the cranium from Kryopigi are in advanced stage of wear (Lazaridis 2015, fig. 27), implying that the actual size of the specimens is even underestimated.

Measurements of p4 reveal a certain degree of separation between Aegean and non-Aegean *P. provincialis* (Figure 5d), the latter group being slightly larger. However, these are trivial differences (~1.5 mm in length on average), which are also partly biased by the more advanced wear stage of several Aegean remains (Geraads et al. 2008; Lazaridis 2015). Moreover, size differences can also be related to ecomorphological adaptations occurring in the same species, as it is common in fossil and recent wild boar (Albarella et al. 2009; Lister et al. 2010; Iannucci et al. 2020b) and other mammalian taxa (e.g., van Asperen 2010). In fact, the genus *Propotamochoerus* has typically been regarded as adapted to warm-temperate or subtropical environments (Bernor and Fessaha 2000), whereas several of the Balkan sites where it occurs were characterized by more open and drier conditions (Koufos 2003; Fortelius et al. 2006; Lazaridis 2015; Koufos and Vasileiadou 2015). This suggests that *P. provincialis* was endowed with a wider ecological tolerance than assumed, and hence it is conceivable that the species displayed morphological and biometric differences accordingly.

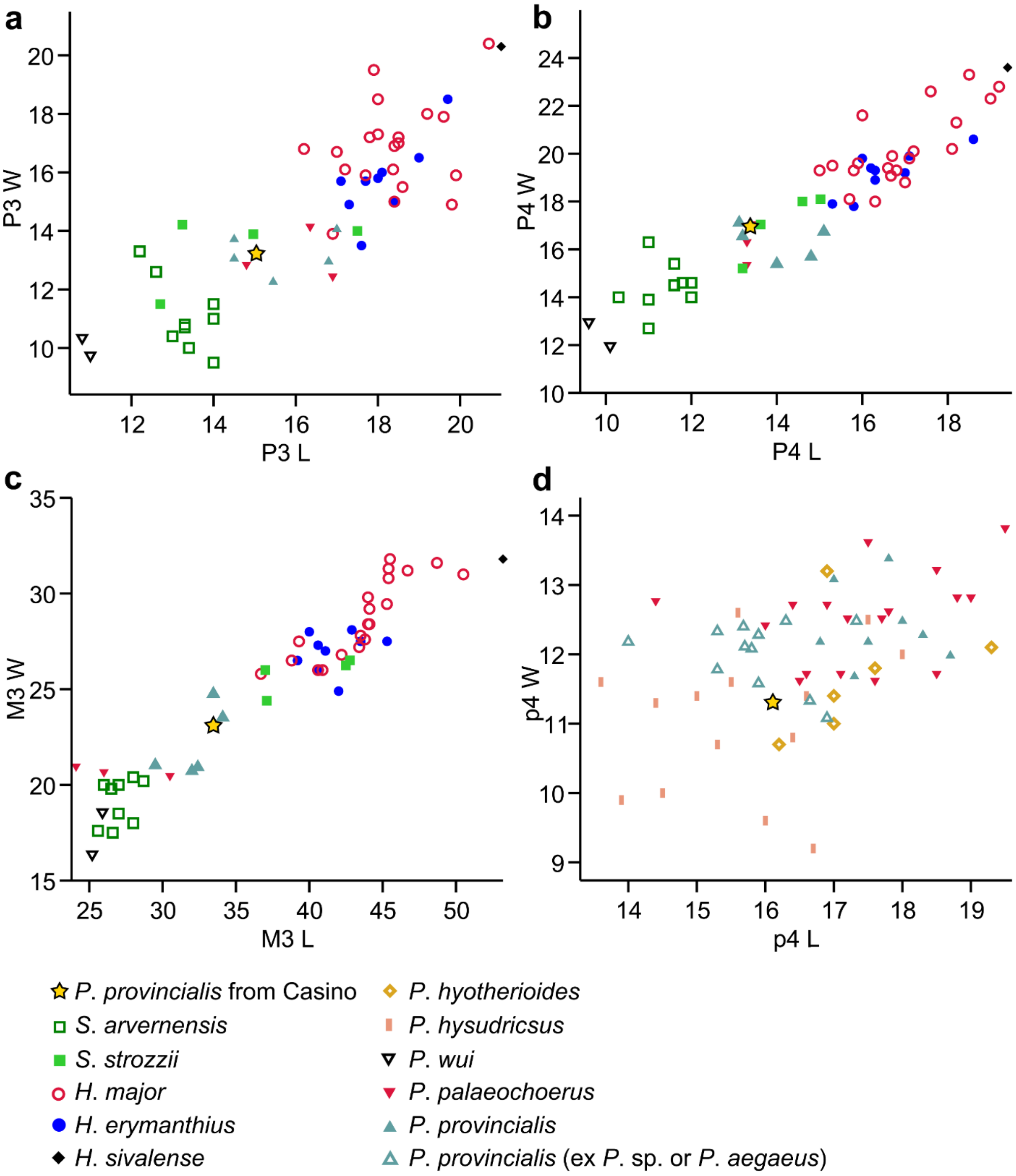

Figure 5 - Bivariate diagrams (L x W; in mm) of P3 (**a**), P4 (**b**), and M3 (**c**) of the specimens included in the statistical analysis; p4 (**d**) of *Propotamochoerus* species. Data from Thenius (1950); Hünermann (1968); van der Made and Han (1994); Hellmund (1995); de Bonis and Bouvrain (1996); Gallai (2006); Pickford (1988, 2013); Geraads et al. (2008); Lazaridis (2015); Hou et al. (2019).

3.7. Biochronology

The Miocene-Pliocene transition (MN13-MN14) records a return to more humid conditions after the trend of increasing aridity that took place in the late Miocene (Zachos et al. 2001; Fortelius et al. 2006). This is reflected in a faunal impoverishment, which is related to the disappearance of the open-adapted Pikermian assemblages (Bernor et al. 1979; Eronen et al. 2009; Kaya et al. 2018).

Propotamochoerus provincialis has long been considered the only species of the genus to survive beyond the Miocene-Pliocene boundary, usually regarded as a typical element of MN13 to MN15 faunal assemblages (van der Made and Moyà-Solà 1989; van der Made 1990; Fortelius et al. 1996; Gallai and Rook 2011). Guérin and Tsoukala (2013) even considered the species exclusively Ruscinian and placed it in the genus *Potamochoerus* Gray, 1854. However, this stratigraphic range is based on the supposed age of the type locality of the "Sables marins" of Montpellier (Faure and Guérin 1982; Guérin and Faure 1985), which is actually unknown (Pickford 2013). In fact, the historical collection from Montpellier is an artificial ensemble, including typical late Miocene (*P. provincialis*) to early Pleistocene (*S. strozzii*) suid taxa.

The other Pliocene remains tentatively ascribed to *P. provincialis* do not provide convincing evidence for this attribution. Suidae from the Ruscinian of Măluşteni (Romania) have been assigned to *P.* cf. *P. provincialis* due to their relatively large size (Simionescu 1930; Radulescu et al. 2003), similar to those recovered from Kvabebi (Vekua 1972). Nevertheless, as discussed above, the attributions based only on differences in size should be treated with caution, especially taking into account the huge morphological variability of the extant species of Suinae (Albarella et al. 2009; Lister et al. 2010; Boisserie et al. 2014; Iannucci et al. 2020b). Indeed, at least for the Kvabebi sample, subsequent studies have pointed out that the morphology is not consistent with an attribution to *Propotamochoerus*. Azzaroli (1975) ascribed the Kvabebi Suidae to *Sus minor* (= *S. arvernensis*), remarking the similarities with the cranium NHMB Rss 70 from Perpignan (France), while Pickford and Obada (2016) considered it closely related to *Dasychoerus* (= *Sus*) *arvernensis*, but preferred not to stress the classification beyond genus level.

Finally, remains assigned to "*Propotamochoerus*" *provincialis* from the intramontane Florina-Ptolemais-Servia Basin in Greece were referred to MN15 (van der Made and Moyà-Solà 1989), but the specimens were collected from the locality of Kardia (van de Weerd 1979), which is now finely correlated with the earliest MN14 at 5.2 Ma (Hordijk and de Bruijn 2009). The most significant specimen is a crushed skull, extremely compressed mediolaterally, which does not allow a secure attribution. However, the cranium has a relatively short snout and high occipital region, with a small and not inflated anterior portion of the zygomatic arch, features that align it to the genus *Sus* and not to *Propotamochoerus*, although an in-depth study of this specimen is needed to clarify its taxonomy. In brief, there is no compelling evidence of Ruscinian *P. provincialis* and the stratigraphic range of the species should be regarded as restricted to MN11-MN13 (Figure 6). In turn, this strengthens the biochronological value of the *Sus* dispersal bioevent at the Miocene-Pliocene boundary.

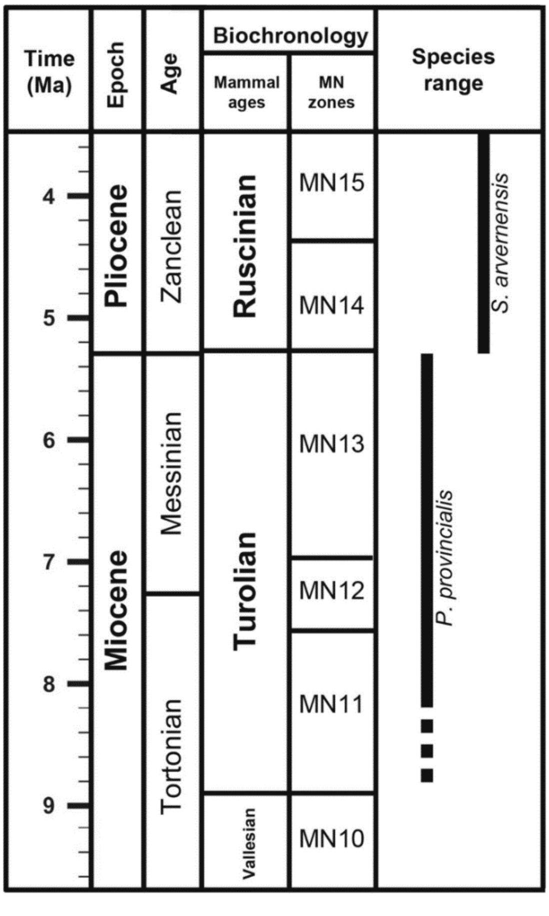

Figure 6 - European mammal biochronological scale, with the ranges of *Propotamochoerus provincialis* and *Sus arvernensis*. Subdivisions are after Hilgen et al. (2012).

3.8. Conclusions

The Suidae from the Casino Basin are attributed to *Propotamochoerus provincialis*. Differences within the European late Miocene (Turolian) *Propotamochoerus* sample are subtle and do not justify the identification of more than one species.

Early Pliocene (Ruscinian) assemblages are characterized by the occurrence of a newcomer from Asia, *Sus arvernensis*, which replaced *P. provincialis* at the Miocene-Pliocene transition. Therefore, the *Sus* dispersal bioevent is here confirmed to be a significant biochronological marker of the Ruscinian (MN 14).

We are confident that our results will prompt renewed studies on *Propotamochoerus* and related taxa. In particular, we expect our taxonomic revision of *P. provincialis* to serve as the basis for new phylogenetic reconstructions, in order to clarify relationships with other taxa from Eurasia (e.g., *Hippopotamodon*) and even Africa (e.g., *Metridiochoerus*, for which phylogenetic relationships with *Propotamochoerus* have been hypothesized by Pickford 2012, but should be carefully tested).

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4. Paper 3

Neurocranial anatomy of *Sus arvernensis* (Suidae, Mammalia) from Collepardo (Early Villafranchian; central Italy): taxonomic and biochronological implications

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Abstract

Suidae remains recovered from the late Pliocene site of Collepardo (Latium, central Italy) are described and assigned to *Sus arvernensis*, a small-sized Ruscinian to Early Villafranchian (MN14-MN16a) species. In Italy, *S. arvernensis* only occurs in the Triversa Faunal Unit (MN16a), supporting the recently revised chronology of Collepardo. CT-scan methods are used to virtually extract and analyse a newly discovered neurocranium, providing the content for the first inner cranial description carried out on an extinct Suidae. Our analysis reveals that *S. arvernensis* has an anteroposteriorly elongated and dorsoventrally flat cerebrum, similar to that of the Asian *Babyrousa babyrussa* and the African *Hylochoerus meinertzhageni*. These species substantially differ in size and are representatives of two widely diverging phylogenetic clades, excluding relatively simple evolutionary or allometric explanations for brain morphology in Suidae.

Keywords: CT-scanning; endocast; palaeoneurology; paranasal sinuses; Ruscinian; Pliocene

4.1. Introduction

The evolutionary history of the Suidae in Eurasia was characterised by several events of dispersal and radiation of new taxa. Three events were of special relevance: the appearance of the subfamily Suinae in the late Miocene, of the genus *Sus* in the Pliocene, and of *Sus scrofa* (the wild boar) in the Pleistocene. Yet, the tempo and mode of these events are still debated, and have recently generated growing interest (van der Made et al. 2006; Orliac et al. 2010; Martínez-Navarro et al. 2015; Frantz et al. 2016; Pickford and Obada 2016; Cherin et al. 2020; Iannucci et al. 2020a, 2020b)

Sus arvernensis (Croizet and Jobert, 1828) is the earliest representative of its genus, a successful species whose dispersal into Europe marks the beginning of the Ruscinian Mammal Age (MN14) at the onset of the Pliocene (Agustí et al. 2001; Iannucci et al. 2020a). Its fossil remains have been recovered from Europe (Azzaroli 1952, 1975), Anatolia (Hünermann 1975; Guérin et al. 1998), China (Berdondini 1992), and Africa (Hünermann 1971; Pickford and Obada 2016), even though some of the extra-European findings may need to be revaluated (Cherin et al. 2018a). *Sus arvernensis* is considered the ancestor of the Middle Villafranchian to Epivillafranchian *Sus strozzii* Forsyth Major, 1881 (Azzaroli 1952), and suggested to be close to the ancestor of the Sardinian dwarf *Sus sondaari* van der Made, 1999 and of the African *Kolpochoerus* van Hoepen and van Hoepen, 1932 (Pickford and Obada 2016; but see Cherin et al. 2018a).

Despite its putative wide geographic distribution and key phylogenetic position, the distinction among *S. arvernensis*, the late Miocene *Propotamochoerus provincialis* (Blainville, 1847), and the Early Pleistocene *S. strozzii* is often almost exclusively based on size (Vekua 1972; Radulescu et al. 2003). For instance, Pickford (2013), in redescribing the original hypodigm of ‘*Sus*’ *provincialis* Blainville, 1847, remarked only that the species is larger than *S. arvernensis* and smaller than *S. strozzii*, even questioning the generic attribution (hence ‘*Sus*’). Iannucci et al. (2020a) recently emended the diagnosis of *P. provincialis* and reconsidered the chronological distribution of the species, confirming its generic attribution and enhancing morphological and biometric distinctive features from other Eurasian Suinae, *S. arvernensis* included. However, most of the available data and comparisons rely on teeth, with relatively limited support from cranial anatomy. Indeed, there are just a few localities that have yielded cranial remains of *S. arvernensis* (Azzaroli 1975; Pickford and Obada 2016). In Italy, apart from the sample of Villafranca d'Asti, the species is documented in a few localities all referred to the Triversa Faunal Unit (FU), MN16a, corresponding to the beginning of the Villafranchian Mammal Age (Azzaroli1975; Berdondini 1992; Gliozzi et al. 1997).

Recent field surveys at the site of Collepardo (Latium, central Italy) led to the discovery of new faunal remains, including a Suidae neurocranium (Bellucci et al. 2019). This finding prompted the herein presented revision of the Suidae collection from this site, occasionally mentioned in several publications but never described in detail (e.g., Segre Naldini and Valli 2004; Guérin and Tsoukala 2013). Since the recovered neurocranium is embedded in a travertine block, we used CT-scan methods to virtually extract and analyse it (Cherin et al. 2018b; Bellucci et al. 2019), providing the content for the first inner cranial description (i.e., paranasal sinuses and brain endocast) carried out on an extinct Suidae.

4.2. Geological and Palaeontological background

In the early 1980s some fossil vertebrate remains were discovered by archaeologists of the 'Gruppo Archeologico Volsco di Ceccano' in travertine and breccia deposits on the slopes of the Ernici Mountains in the surroundings of the village of Collepardo (Frosinone), about 100 km southeast of Rome (Figure 1a). Immediately after, researchers of the Italian Institute of Human Paleontology (IsIPU) carried out new surveys and recovered a diversified mammal assemblage. A first faunal list was included in the biochronological synthesis of Gliozzi et al. (1997), and then updated by Segre Naldini and Valli (2004), who focused on the study of cervid remains. The following taxa were reported: *Stephanorhinus* cf. *jeanvireti, Equus stenonis, Sus* sp. (of a small size), *Leptobos* sp., *Hemitragus stehlini, Croizetoceros* sp., '*Pseudodama*' *lyra, Nyctereutes megamastoides, Acinonyx* *pardinensis* and *Megantereon cultridens*. The Collepardo assemblage was initially referred to the Saint Vallier FU, intermediate between the Montopoli (~2.6 Ma) and the Coste San Giacomo (~2.1 Ma) FUs (Gliozzi et al. 1997). Subsequent studies agreed upon this interpretation (Sardella et al. 1998; Petronio et al. 2002) or argued that a slightly older attribution (?Montopoli FU) could not be ruled out (Palombo et al. 2002; Segre Naldini and Valli 2004). Guérin et al. (2004), reviewing the fauna of Saint Vallier, remarked that the occurrence of *Dicerorhinus* (=*Stephanorhinus*) *etruscus* and *S. strozzii* in this French site allowed a chronological distinction with the site of Collepardo where *S.* cf. *jeanvireti* and *S. arvernensis* occur instead. The assemblages of Saint Vallier and Collepardo were correlated with MN17 and MN16b (equivalent to Montopoli FU), respectively.

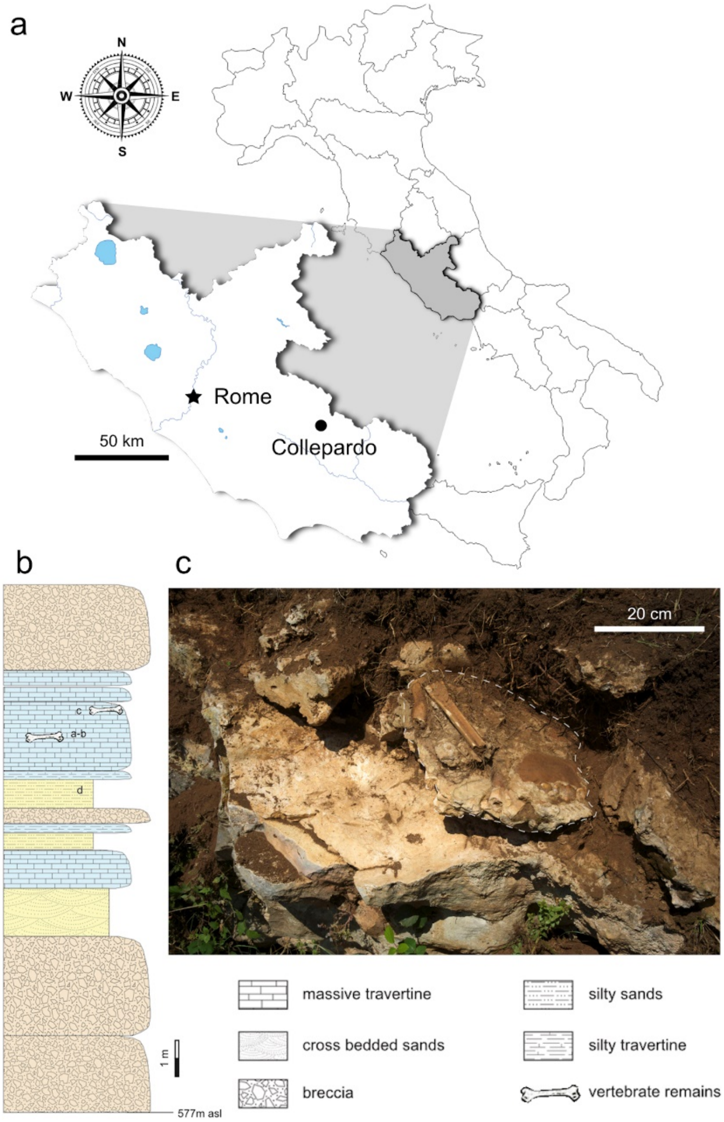


Figure 1 - Location of the Pliocene site of Collepardo (central Italy) (a), with schematic log of the section (modified from Bellucci et al. 2019) (b), and photographic detail of the massive travertine outcrop with the block containing the specimen CP 02-15 (c).

In 2015, the Department of Earth Sciences of Sapienza University of Rome, the Institute of Environmental Geology and Geoengineering of the National Research Council of Italy (IGAG CNR) and the Italian Institute of Human Paleontology (IsIPU) started a new project, carriying out several field surveys aimed at a better definition of the geological framework of Collepardo.

These activities clarified that fossils occur within the Upper travertine deposit (UD) (Figure 1b-c), representing a carbonate layer of about 4.5 m of thickness, cropping out in few sites. UD consists of laminated and crypto-laminated (at the millimetre scale) travertine of pinkish colour, including fossil remains of mammals, silty sands and silty travertine layers (Bellucci et al. 2019). This deposit is embedded within the breccia that crops out extensively in the area. At Collepardo, the breccia lies unconformably on the upper Messinian units and the upper Tortonian *Orbulina* marls, and is covered by the Early Pleistocene-Holocene Collepardo Breccia (Bellucci et al. 2019 and references therein). The Collepardo travertine deposited in a low-energy, shallow water pond. Such environment provided an excellent medium for fossils preservation; the calcareous matrix and probably the rapid depositional rate allowed a fast burial, whereas the reduced turbulence avoided abrasion and reworking of the fossil remains. The results of isotope analyses performed on the travertine are indicative of a relatively cold climate and humid environment (Bellucci et al. 2019).

Among the new findings, of considerable interest is a hemimandible of the large, short-faced bear *Agriotherium*, a Carnivora never reported before from Italy and very rare in the European fossil record (Bellucci et al. 2019). The occurrence of *Agriotherium* drove a reassessment of the age of the deposit, since this taxon is documented in late Miocene to early Pliocene localities (Morales 1984; Montoya et al. 2006). Taking also into account the occurrence of '*Pseudodama*' *lyra* and the possible presence of *S. arvernensis*, an Early Villafranchian age (Triversa FU, MN16a) for the Collepardo assemblage has been suggested (Bellucci et al. 2019).

4.3. Institutional abbreviations

AFS: Museum of Natural History, Accademia dei Fisiocritici, Siena

HNHM: Hungarian Natural History Museum, Budapest

IGF: Natural History Museum of the University of Florence, section of Geology and Paleontology

IsIPU: Italian Institute of Human Paleontology, Anagni

MACUS: Comparative Anatomy Museum 'Battista Grassi', Sapienza University of Rome

MAFI: Museum of the Geological and Mineralogical Survey of Hungary, Budapest

MNHN: Muséum National d'Histoire Naturelle, Paris

MPM: Paleontological Museum, Accademia Valdarnese del Poggio, Montevarchi

MUST: University Museum of Earth Sciences, Sapienza University of Rome

NMB: Natural History Museum, Basel

NMM: Natural History Museum, Mainz

PF: PaleoFactory Laboratory, Department of Earth Sciences, Sapienza University of Rome

4.4. Materials and methods

An isolated and fragmented right deciduous first incisor (CP '81-41) is part of the collection gathered in the 1980s (housed in IsiPU). A second specimen, an incomplete neurocranium (CP 02-15), is embedded in a travertine block together with a hemimandible of *Agriotherium* and other faunal remains as described by Bellucci et al. (2019). This material is provisionally stored in PF. The studied sample was compared both with specimens stored in several institutions (see Institutional abbreviations) and with data from the literature (Table 1). Measurements were taken to the nearest 0.1 mm with a digital calliper for the isolated tooth, and with the digital measuring tool available in Mimics for the 3D model of CP 02-15. Dental terminology follows van der Made (1996). Synonymy between suid genera follows Iannucci et al. (2020a). Teeth are abbreviated to their initial letter, with superscript and subscript referring to upper and lower teeth, respectively (e.g., M^3 = upper third molar). A 'd' indicates deciduous teeth.

The height of the Collepardo cranium (Akrokranion-Basion) was compared with that of *S. strozzii* ($n = 4$) and those of the Dicoryphochoerini species *Propotamochoerus* (due to the paucity of the fossil record, this taxon was analysed at the genus level, $n = 3$) and *Hippopotamodon major* ($n = 6$) (Table 1). To evaluate size-related differences, absolute and standardised measurements were used. In the latter case, we normalised the absolute measurements with the mean length of M^2 of the respective taxon. M^2 is considered the tooth least affected by relative differences between taxa and hence the most reliable for an independent size comparison (Fortelius et al. 1996; Iannucci et al. 2020c). For the Collepardo cranium, due to the lack of M^2, we used the mean value (19.5 mm) of a *S. arvernensis* sample from the literature (Montoya et al. 2006; Guérin and Tsoukala 2013; Pickford and Obada 2016) and personal observations ($n = 15$). Boxplots were used to investigate the biometric variability of the fossil sample.

The palaeoneurological comparison was carried out using a complete digital brain endocast of an extant *S. scrofa* and literature data on *Babyrousa babyrussa* (Linnaeus, 1758), *Hylochoerus meinertzhageni* Thomas, 1904, *Phacochoerus aethiopicus* (Pallas, 1766), *Potamochoerus porcus* (Linnaeus, 1758), *Porcula salvania* Hodgson, 1847, and *Pecari tajacu* (Linnaeus, 1758), from Kruska (1970, 1982).

4.4.1. Computed tomography

Tomographic images of CP 02-15 were taken using a Philips Brilliance CT 64-channel scanner at 'M.G. Vannini' Hospital (Rome). The digital model of the block containing the specimen results in 796 slices with an interslice thickness of 0.80 mm. The voxel size is 0.681641 × 0.681641 × 0.4 mm. The CT images of *S. scrofa* were downloaded from DigiMorph (DigiMorph Staff 2005) and result in 606 slices with an interslice thickness of 0.45 mm. The segmentation process of the CT images was carried out with Mimics 20.0, allowing the virtual extraction of the Suidae braincase from the travertine block and the acquisition of its biometric and morphological data. Terminology of the inner cranial anatomy follows Barone (2006a, 2006b). The final editing of the 3D images and videos (i.e., colouring, transparency effect and rendering process) was performed in ZBrush 4R6.

4.5. Systematic Palaeontology

Order Artiodactyla Owen, 1848

Family Suidae Gray, 1821

Subfamily Suinae Gray, 1821

Genus *Sus* Linnaeus, 1758

Sus arvernensis (Croizet and Jobert, 1828)

4.5.1. Previous attributions

Suidae from Collepardo were never described so far, therefore, the following list includes plain reports present in the literature. The only descriptive feature of the sample mentioned over the years, i.e., its small size, is reported within brackets if authors referred to it.

Sus sp. (of a small size) (Gliozzi et al. 1997)

Sus sp. (small size) (Petronio et al. 2002)

Sus minor (=*S. arvernensis*) (Palombo et al. 2002)

Sus sp. (Segre Naldini and Valli 2004)

Sus arvernensis (probablement *S. arvernensis* du fait de sa taille) (Guérin et al. 2004)

Sus arvernensis (probably *S. arvernensis* because of its size) (Guérin and Tsoukala 2013)

Sus arvernensis (small size) (Bellucci et al. 2019)

Specimen Id.	Locality	Nation	Species	Reference	H	M^2L
AM 101203	Dhok Pathan	Pakistan	*P. hysudricus*	Pickford (1988)	111	-
LJG 60.258	Johnsdorf, Ost-Steirmark	Austria	*P. palaeochoerus*	Mottl (1966)	126	20.2
KRY3820	Kryopigi	Greece	*P. provincialis*	Lazaridis (2015)	112.5	20.7
MTLA 537	Samos	Greece	*H. major*	Sylvestrou and Kostopoulos (2009)	212.2	30.1
NKT-68	Nikiti	Greece	*H. major*	Kostopoulos (1994)	150	29.7
NHML M9048	Pikermi	Greece	*H. major*	Sylvestrou and Kostopoulos (2009)	184	-
MOGU-2641	Taraklija	Moldova	*H. major*	Sylvestrou and Kostopoulos (2009)	233	-
MGRI-1781	Grebeniki	Ukraine	*H. major*	Sylvestrou and Kostopoulos (2009)	197	-
MOGU-2642	Grebeniki	Ukraine	*H. major*	Sylvestrou and Kostopoulos (2009)	215	-
CP 02-15	Collepardo	Italy	*S. arvernensis*	This work	77.6	-
IGF 423	Upper Valdarno	Italy	*S. strozzii*	This work	143.8	27.8
IGF 424	Upper Valdarno	Italy	*S. strozzii*	This work	145	28.7
IGF 441	Upper Valdarno	Italy	*S. strozzii*	This work	154.6	29.6
MPM 936	Upper Valdarno	Italy	*S. strozzii*	This work	140.6	27.3

Table 1 - Comparative height of the cranium (H; Akrokranion-Basion) and of the length of the upper second molar (M^2L) of *Propotamochoerus, Hippopotamodon*, and *Sus* species. Measurements in mm.

4.5.2. Diagnosis

Sus of small size, with a low cranium in relation to its size; gently rounded distal cranial profile and narrow cranial table, with parietal lines very close to each other or even forming a weak sagittal crest; dovetail-shaped occiput in dorsal view; laterally expanded nasals; widely diverging zygomatic arches, pronounced in the middle though not inflated as in *S. strozzii*; P_2 markedly smaller than P_3; P_4 with a small metaconid almost aligned along the same mesiodistal axis of the protoconid. In male individuals: large verrucosic (i.e., with a triangular cross-section, lateral sides almost equal in length and posterior facet smaller) lower canines; pachyostotic mandibles (i.e., with a longitudinal thickening of the horizontal branch near M_1 or M_2); supracanine flanges well developed and rugose. Mainly based on this work and on Azzaroli (1952), considering subsequent descriptions of other material (Azzaroli1975; Berdondini 1992; Pickford and Obada 2016).

4.5.3. Holotype

MNHN.F.PET2005, from the Early Villafranchian of Étouaires (Croizet and Jobert 1828; Heintz 1970). The holotype is represented by three fragments of a juvenile male individual, including part of left maxillary with dP^2-dP^4 and M^1; left hemimandible with dP_2-dP_4 and M_1 (and P_4 and M_2 in crypt) and symphysis with I_1 on both sides, left I_2, and fragmented canines; right hemimandible with dP_2-dP_4 and M_1. Figured in detail by Pickford and Obada (2016).

4.5.4. Stratigraphic range

Pliocene (Ruscinian to Early Villafranchian, MN14-MN16a).

4.5.5. Referred material from Collepardo

Fragmented right dI_1 (CP ’81-41) (Figure 2a-d); incomplete neurocranium embedded in a travertine block (CP 02-15) (Figure 3a-h, Supplementary video 1, 2).

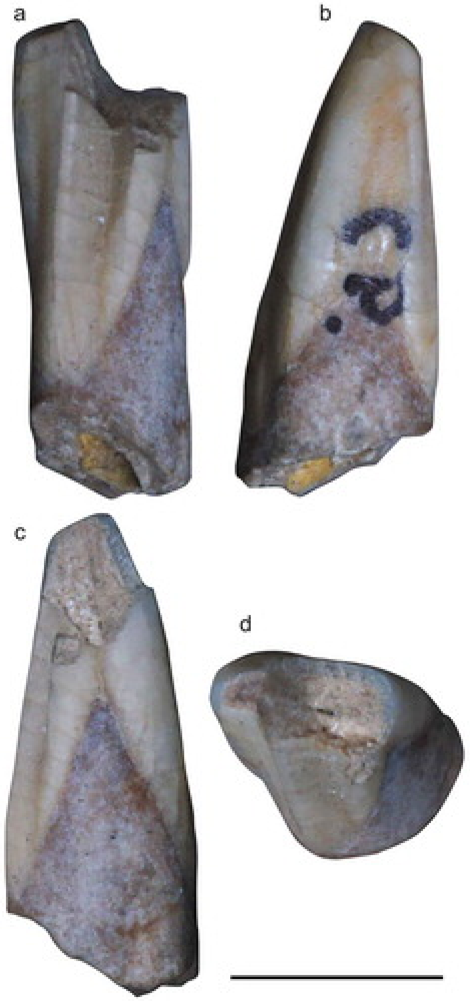


Figure 2 - Right dI_1 of *Sus arvernensis* CP ’81-41 in lingual (a), mesial (b), distal (c), and occlusal (d) views. Scale bar 5 mm.

4.6. Description

4.6.1. CP ’81-41

The dI_1 CP ’81-41 (Figure 2a-d) is represented by a fragment of the right antimere. The tooth is broken just below the cementoenamel junction and the rest of the root is missing. The specimen is also damaged at the tip. The enamel is pale yellow to pink in colour and the root is grey with a pink tinge. There is a prominent central ridge, the endocristid, and two others at its sides, precristid and postcristid, which are separated by small grooves. The endocrisitd and postcristid converge near the root, whereas the precristid remains distinct, so that the tooth is slightly asymmetric. The cross-section of the broken root is oval to piriform in shape, dorsally elongated as a continuation of the endocristid-postcristid convergence.

4.6.2. CP 02-15 – outer cranial anatomy

The neurocranium CP 02-15 (Figure 3c-h) is in a good state of preservation and preserves the posterior bases of the zygomatic arches, the cranial roof, and the occipital region. Most of the basicranium is missing, but the foramen magnum and the occipital condyles are preserved. The specimen is slightly compressed laterally, and a little dorsal deformation is present only in the most anterior preserved portion. The CT-scan revealed the presence of some fractures and missing bone fragments, especially on the ventral side of the neurocranium. The sharp edges of the fractures and the lack of newly formed bone tissue indicate a *post mortem* origin of these lesions due to taphonomic processes. No bitemarks or pathologies have been detected on the braincase.

The cranial table is broad anteriorly (in the frontal area) and narrow posteriorly (in the parietal area). Here, the parietal lines meet along the sagittal plane forming a weak crest (Figure 3c-e). The preserved part of the frontal ends anteriorly to the orbits. The supraorbital foramina open approximately dorsally to this point. The parietal is anteroposteriorly convex, and the occipital is concave. The completely fused sutures of the braincase indicate an adult age of the individual.

4.6.3. CP 02-15 – paranasal sinuses

Paranasal sinuses are air-filled chambers that form inside the cranial bones of many vertebrates and are connected to the nasal cavity (Farke2010; Iurino et al. 2020; Boscaini et al. 2020b). They are typically found within the frontal and sphenoidal bones but, in several mammals, they extend into other cranial bones, forming in some cases large and complex pneumatic systems (Boscaini et al. 2020b). Their development can also vary according to sexual dimorphism and the age of the individuals, reaching their maximum extent in adult specimens (Boscaini et al. 2020b). In CP 02-15 the neurocranial pneumatisation is so developed that mirrors the external shape of the cranium with a complex system of sinuses not divided into well-defined chambers (Figure 4a1-a6). The pneumatisation is almost symmetrical along the median plane of the braincase and involves the

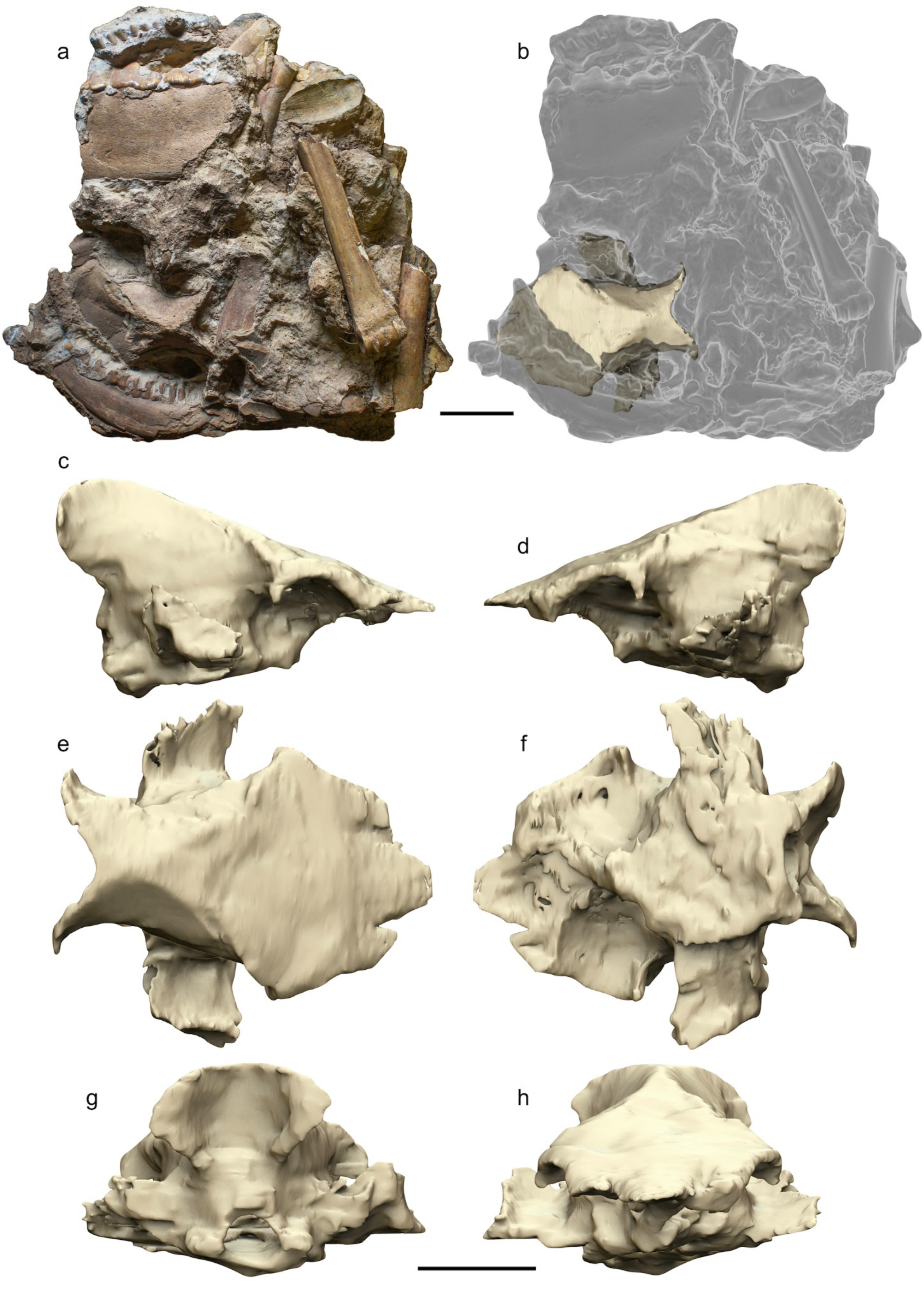

a
b
c
d
e
f
g
h

Figure 3 - (previous page) Travertine block from Collepardo before (a) (from Bellucci et al. 2019) and after (b) the CT images processing, with the embedded cranium of *Sus arvernensis* CP 02-15 in right lateral (c), left lateral (d), dorsal (e), ventral (f), posterior (g), and anterior (h) views. Scale bars 50 mm.

frontal, parietal, temporal, and occipital bones. Unfortunately, due to the breakage of the anterior portion of CP 02-15, the maxillary sinuses cannot be observed. In dorsal view, the 3D model of the sinuses starts from the anterior potion of the frontal, right at the fracture line, reaching its maximum width in correspondence of the zygomatic processes of the frontal. The left side of the frontal sinuses is less complete than the right one and some empty areas are visible on the 3D model where the preservation conditions of the specimen are poor. The parietals show a high level of pneumatisation with extensive sinuses extending from their anterior to posterior edges, representing a considerable portion of the total volume of the bone. On the dorsal part of the 3D model, in correspondence of the sagittal suture, a deep groove divides the parietal sinuses into two symmetrical portions. Both parts perfectly cover the dorsal area of the brain cavity reaching the temporoparietal suture. The uppermost portion of the temporal bone is not pneumatised, whereas in correspondence of the right squamosal the bone is partially occupied by sinuses that invade the tip of the zygomatic process. The neurocranial pneumatisations reach the occipital bone where they end at the sagittal crest, assuming a characteristic dovetail shape, evident in dorsal view.

4.6.4. CP 02-15 – brain

The brain endocast of CP 02-15 (Figure 4a5, a6) only misses the olfactory bulbs. It consists of an elongated and dorsoventrally compressed cerebrum, a prominent cerebellum, and the posterior part of the medulla oblongata. The external surface is badly preserved and only a few of the main gyri and sulci are identified (Figure 4a5, a6). In dorsal view, a poorly marked longitudinal fissure divides the telencephalon into two cerebral hemispheres with almost symmetrical convolutions represented, from front to back, by the precruciate, orbitofrontal, lateral, suprasylvian, sylvian, and occipital gyri. The precruciate gyri are lyre-shaped and are divided from the orbitofrontal ones by

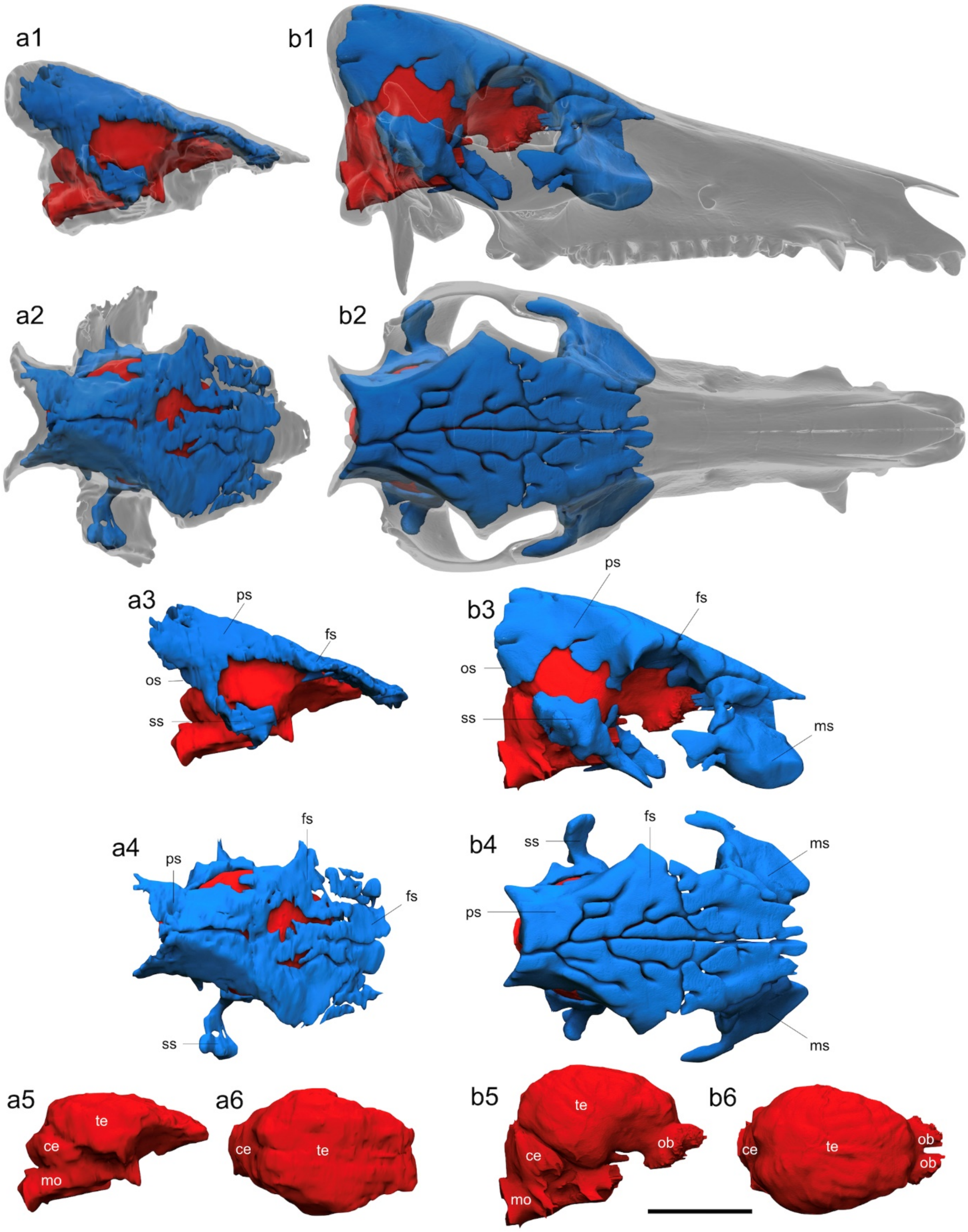


Figure 4 - Digital reconstruction of the inner cranial anatomy of *Sus arvernensis* CP 02-15 (a1-a6) and extant *Sus scrofa* (b1-b6). Crania in right lateral (a1, b1) and dorsal (a2, b2) views, paranasal sinuses and brain endocasts in right lateral (a3, b3), and dorsal (a4, b4) views, brain endocasts in right lateral (a5, b5) and dorsal (a6, b6) views. Cerebellum (**ce**), frontal sinuses (**fs**), medulla oblongata (**mo**), maxillary sinuses (**ms**), olfactory bulb (**ob**), occipital sinuses (**os**), parietal sinuses (**ps**), squamosal sinuses (**ss**), and telencephalon (**te**). Scale bar 50 mm.

the cruciate sulci. The ansate sulcus divides the cerebrum into two halves along the coronal plane approximately in correspondence of the frontoparietal suture. The lateral, suprasylvian, and sylvian gyri are separated by the lateral and suprasylvian sulci, respectively. The occipital gyri are mediolaterally oriented and are divided from the cerebellum by a long transverse fissure, which appears not very deep due to the lack of the tentorium. In lateral view, the rhinal and sylvian fissures are recognisable as well as the proximal portion of the optic nerve. The cerebellum is separated into two cerebellar hemispheres by a little-pronounced vermis. Due to damage of the ventral area of the CP 02-15 neurocranium, the basal portion of the brain does not preserve anatomical details, except for the optic nerves and the medulla oblongata.

4.7. Comparisons

4.7.1. CP ’81-41

The overall morphology of dI_1 is compatible either with a permanent or deciduous lower first incisor of many Suinae, but the small size (measuring approximately 4 mm mesiodistally and 7 mm buccolingually) suggests an attribution to a deciduous of a small-sized species. Guérin et al. (2004) considered this species *S. arvernensis*, but an assignment to *Propotamochoerus* cannot be ruled out.

4.7.2. CP 02-15 – outer cranial anatomy

The neurocranium has a convex, gently rounded dorsal cranial profile, terminating posteriorly in a relatively low occipital region. This morphology is shared within the genus *Sus*, whereas in *Propotamochoerus* and *Hippopotamodon* the occiput is markedly overhanging. CP 02-15 differs from *S. scrofa* in its more pronounced postorbital constriction and caudally projected nuchal crests, and from *S. strozzii* in its diminutive size and narrow parietal region. The latter trait distinguishes CP 02-15 from most living Suidae, apart for *B. babyrussa* and *Sus barbatus* Müller, 1838. However, in *B. babyrussa* the narrowing of the parietals is more pronounced, properly forming a sagittal crest, the frontals are less wide, the supraorbital foramina open more anteriorly and in more divergent position. CP 02-15 also differs from *S. barbatus*, which is larger and possesses a more elongated cranium. CP 02-15 is very similar in size and proportions to specimens of *S. arvernensis*, such as NMB Rss 70 from Perpignan (France), apart for the presence of a weak sagittal crest. Nevertheless, all the few crania of *S. arvernensis* known so far have a narrow posterior cranial table, almost approaching the condition observed in CP 02-15 (Azzaroli 1952; Pickford and Obada 2016). Therefore, the suid from Collepardo is attributed to *S. arvernensis*. This species is not only small, as evident from comparing the height of the cranium with other species (Figure 5a), but it also has the lowest cranium in relation to its size (Figure 5b).

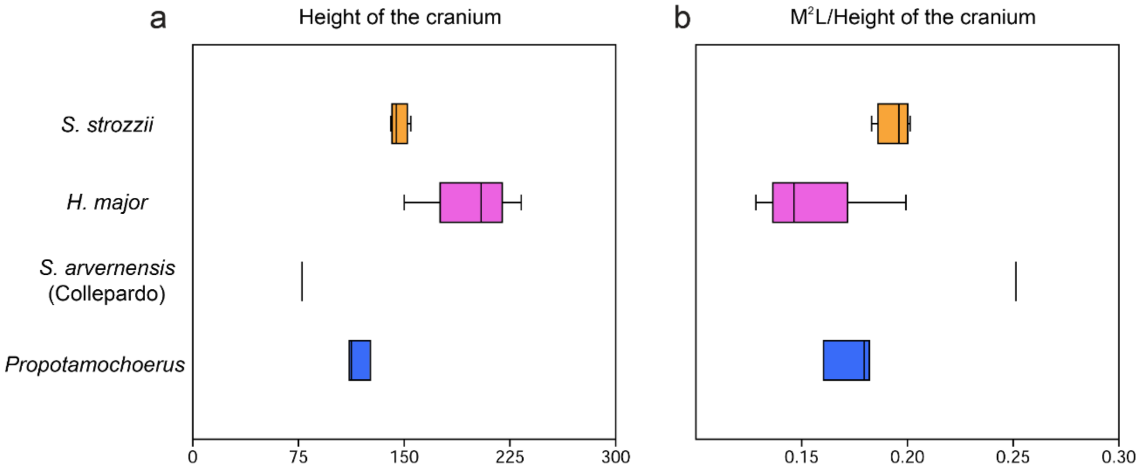


Figure 5 - Boxplot of the height of the cranium (a) and of M^2L/height of the cranium ratio (b) of *Propotamochoerus, Hippopotamodon*, and *Sus*. Measurements in mm.

4.7.3. CP 02-15 – paranasal sinuses

Comparative CT analysis of *S. arvernensis* from Collepardo evidenced a similar arrangement and a strong morphological resemblance of the neurocranial pneumatisation between CP 02-15 and the extant *S. scrofa* (Figure 4a1-b6). In fact, in dorsal and lateral views the sinuses silhouettes of these species are virtually overlapping. Dorsally, the frontal sinuses assume a rhomboidal shape with a maximum width of 83.3 mm in CP 02-15 and 87.8 mm in *S. scrofa*, the squamosal sinuses are laterally elongated, occupying the posteriormost portion of the bone, while the parietal pneumatisation shows a quite different development between the two species. In lateral view, the posteriormost portion of the parietal sinuses of CP 02-15 is posteriorly elongated and extends beyond the foramen magnum, whereas in *S. scrofa* it is shorter, more compacted and aligned on the same plane of the foramen magnum. In dorsal view, the sinuses of *S. scrofa* are completely flat over the entire length of the neurocranium, from the frontal to the occipital. Conversely, in *S. arvernensis* the parietal sinuses converge at the sagittal suture, forming a marked bump that is the counterpart of the external occipital protuberance. In CP 02-15, the pattern of deep root-shaped grooves observable on the dorsal surface of the temporal and parietal sinuses in *S. scrofa* is missing, due to the taphonomic damage suffered by the bone tissue.

Considering the fossil remains of *S. arvernensis*, the only specimen currently known with exposed and partially preserved cranial pneumatisation is the strongly damaged cranium AFS 4947 (Figure 6a-c) probably recovered from the Pliocene locality of Val di Pugna (Siena, Italy) (Azzaroli 1975; Berdondini 1992). AFS 4947 and CP 02-15 apparently share a similar arrangement of the paranasal sinuses. For instance, the fragmented zygomatic arches of AFS 4947 expose large squamosal sinuses that seem more expanded and lobed than those of *S. scrofa*, resembling the condition observable in CP 02-15 (Figure 4a4). The pneumatic cavities detectable on the frontoparietal and occipital region of AFS 4947 (Figure 6b, c), some of which are partially filled by sediment, indicate that the lower portion of the occipital sinuses reaches the upper part of the cerebellum, while the parietal sinuses cover the upper half of the temporal lobes of the brain. This arrangement is comparable to what observed in CP 02-15 and *S. scrofa*. Moreover, both maxillae of the specimen from Siena are broken, exposing a limited portion of the maxillary sinuses which is missing in CP 02-15. Unfortunately, their partial exposure prevents a more accurate comparison with those of *S. scrofa*.

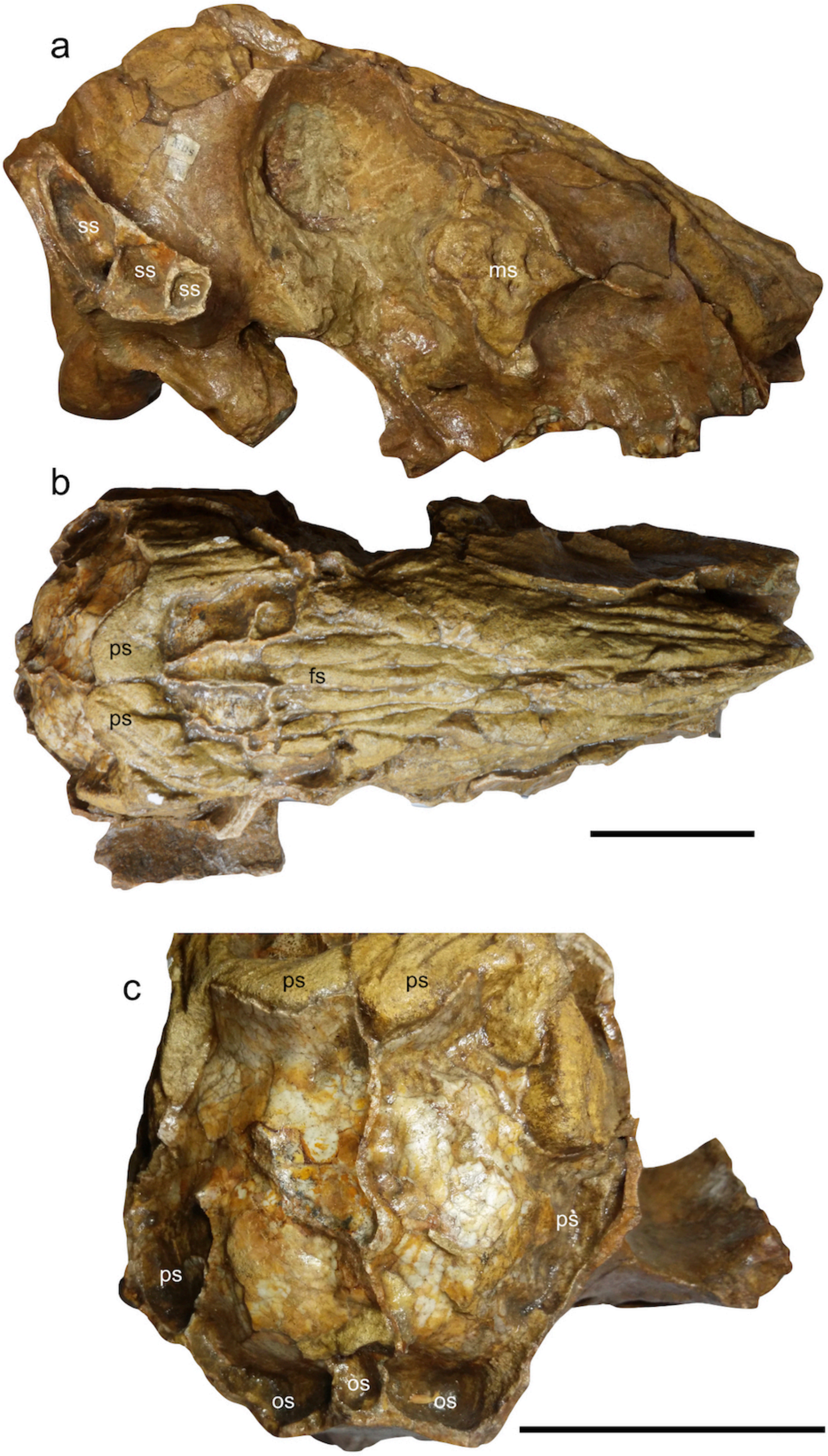
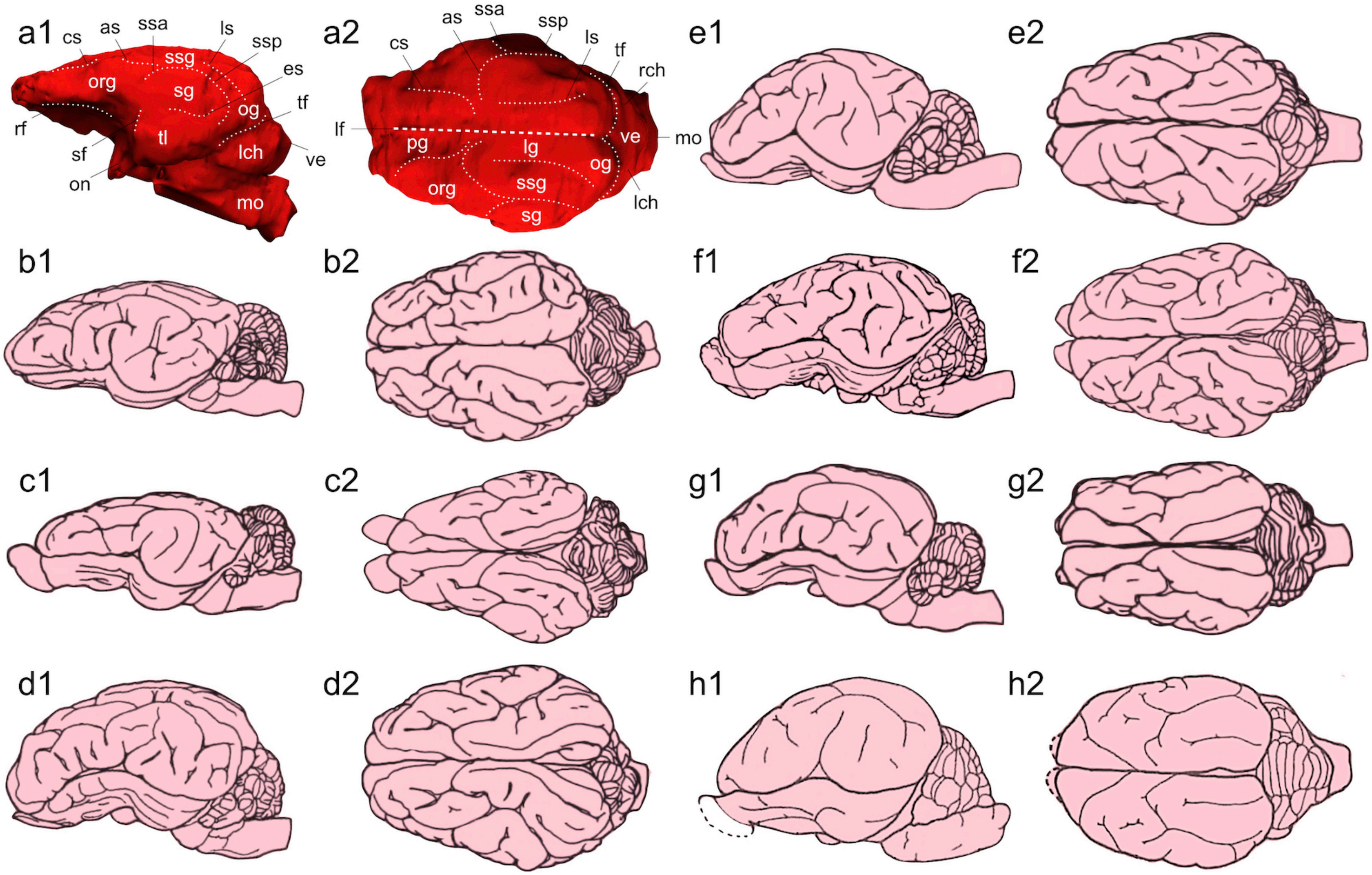


Figure 6 - *Sus arvernensis* AFS 4947 from the Pliocene locality of Val di Pugna (Siena, Italy) in right lateral (a) and dorsal (b) views. Braincase magnification in dorsal view (c). Squamosal sinuses (**ss**), maxillary sinuses (**ms**), parietal sinuses (**ps**), frontal sinuses (**fs**), and occipital sinuses (**os**). Scale bars 50 mm.

4.7.4. CP 02-15 – brain

Comparison of the CP 02-15 endocast with brains of living species of Suidae and Tayassuidae (Figures 4a5-b6, 7a1-h2, Table 2) reveals a certain variability in size and morphology albeit a common pattern of convolutions is detectable in all the sample. *Sus arvernensis, H. meinertzhageni* and *B. babyrussa* share an anteroposteriorly elongated and dorsoventrally flat cerebrum (Figure 7a1-c2). In lateral view, the lower portion of the cerebellum of these species is aligned or positioned above the lower margin of the parietal lobe, while the upper edge of the cerebellum reaches the roof of the telencephalon, except in CP 02-15. In *Phacochoerus aethiopicus, Potamochoerus porcus, S. scrofa, Pecari tajacu*, and *Porcula salvania* the cerebrum is more globose and dorsally arched, the lower portion of the cerebellum is positioned below the lower margin of the parietal lobe (Figure 7d1-h2) and the upper edge of the cerebellum never reaches the roof of the telencephalon. In dorsal view, the cerebrum is narrower at the frontal lobe and rather enlarged in correspondence of the parietal lobes where the maximum width of the brain is detected in all specimens (Table 2). This constriction is placed at the level of the ansate sulci and is particularly evident in *B. babyrussa*, whereas it is scarcely marked in *Porcula salvania*. The brain volume has been obtained using the digitalised specimens (as they are represented in Figure 4a5-b6) and is 79.08 cm^3 for *S. arvernensis* and 131.7 cm^3 for *S. scrofa*.

Figure 7 - (next page) Morphological comparison between the brains of *Sus arvernensis* CP 02-15 (a1, a2), *Hylochoerus meinertzhageni* (b1, b2), *Babyrousa babyrussa* (c1, c2), *Phacochoerus aethiopicus* (d1, d2), *Potamochoerus porcus* (e1, e2), *Sus scrofa* (f1, f2), *Pecari tajacu* (g1, g2), and *Porcula salvania* (h1, h2). The brains are shown in left lateral (a1-h1) and dorsal (a2-h2) views. Ansate sulcus (**as**), cruciate sulcus (**cs**), ectosylvian sulcus (**es**), left cerebellar hemisphere (**lch**), longitudinal fissure (**lf**), lateral gyrus (**lg**), lateral sulcus (**ls**), medulla oblongata (**mo**), occipital gyrus (**og**), optic nerve (**on**), orbitofrontal gyrus (**org**), precruciate gyrus (**pg**), right cerebellar hemisphere (**rch**), rhinal fissure (**rf**), sylvian fissure (**sf**), sylvian gyrus (**sg**), anterior suprasylvian sulcus (**ssa**), suprasylvian gyrus (**ssg**), posterior suprasylvian sulcus (**ssp**), transverse fissure (**tf**), temporal lobe (**tl**), vermis (**ve**). The brains (b1-h2) are redrawn from Kruska (1970, 1982). All the images are normalized.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b1
b2
f1
f2
c1
c2
g1
g2
d1
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h1
h2

Taxon	HL	HB	HH
Bb	76	34	36
Bb	69	27	32
Hm	87	36	45
Pa	83	35	42
Pa	73	32	35
Pa	77	33	39
Pa	82	33	40
Pa	78	36	39
Pa	72	33	40
Pp	76	33	41
Pp	60	27	30
Ps	45.3	19.3	22.7
Ps	42	22.7	20
Ss	91	37	48
Ss	85	37	48
Ss	83	36	42
Ss	81	35	45
Ss	86	36	47
Ss	**72**	**28**	**47**
Sa	**68**	**27**	**32**

Table 2 - Comparative length (HL), breadth of a single hemisphere (HB) and height (HH) of the cerebrum of *Babyrousa babyrussa* (Bb), *Hylochoerus meinertzhageni* (Hm), *Phacochoerus aethiopicus* (Pa), *Potamochoerus porcus* (Pp), *Sus scrofa* (Ss), and *Sus arvernensis* (Sa). The data are from Kruska (1970) except those in bold (this work). Measurements in mm.

4.8. Discussion

Although the Suidae material from Collepardo was never described and/or figured, it was firstly referred to *Sus* sp. (Gliozzi et al. 1997; Segre Naldini and Valli 2004) and subsequently to *S. arvernensis* exclusively on the basis of its small size (Guérin et al. 2004; Guérin and Tsoukala 2013). This attribution played an important role in the relative biochronological placement of Collepardo and Saint Vallier, considering the reported presence of *S. strozzii* from the French site (Guérin et al. 2004). It is worth mentioning that *S. strozzii* at Saint Vallier is solely represented by a fragmented dP$_4$, which is also relatively wider than other remains of the species (Faure 2004; Iannucci et al. 2020b). The Suidae from the old collection of Collepardo only consist of a single specimen, an isolated and fragmented dI$_1$ (CP ’81-41). Relying on the reported small size of the Suidae from Collepardo (Gliozzi et al. 1997), Guérin et al. (2004) hypothesised that it represented *S. arvernensis* instead of the large-sized *S. strozzii*. However, the size alone, especially for a fragmented deciduous tooth, would not be enough to exclude an attribution to *P. provincialis*, until recently considered the only member of its genus to have survived beyond the Miocene-Pliocene boundary (Iannucci et al. 2020a). The hypothesis of Guérin et al. (2004) was nonetheless correct, as the recently recovered neurocranium CP 02-15 shows morphological and biometric features that consistently align it to *S. arvernensis* and not to *P. provincialis*. Specifically, the cranium is smaller than in the latter taxon, its height is relatively reduced, and its profile gently rounded instead of protruding upward (Mottl 1966; Azzaroli 1975; Pickford 1988). Being the only fossil of *S. arvernensis* that preserves the entire occipital region (Azzaroli 1952; Pickford and Obada 2016), it allowed us to perform a detailed quantitative comparison, revealing that the species is not just smaller than *Propotamochoerus, Hippopotamodon*, and *S. strozzii*, but that it also possesses a relatively low cranium in relation to its size. Of course, further remains are needed to explore the allometric scaling of this relationship, and in this respect differences between *S. arvernensis* and *S. strozzii*, or within the genus *Sus* in general may be less important (Azzaroli 1952). The differences between *Sus* and Dicoryphochoerini

(*Propotamochoerus* and *Hippopotamodon*) are morphologically and biometrically supported and of particular interest in this comparison is the relative position of *Propotamochoerus*: similar to *S. arvernensis* considering its absolute size (Figure 5a); similar to *H. major* and markedly distinct from *S. arvernensis* when size is normalised (Figure 5b). Another interesting feature is the presence of a sagittal crest in CP 02-15, though weakly expressed, which slightly expands the known morphological variation of the species.

The ongoing reassessment of the Collepardo assemblage highlights that the fauna should be referred to the Triversa FU (Bellucci et al. 2019). In Italy, *S. arvernensis* is only reported from localities attributed to this FU (Azzaroli 1975; Gliozzi et al. 1997) and thus its occurrence at Collepardo supports this new chronology, even though the *Sus* dispersal event is a Ruscinian (MN14) biochronological marker and it would not preclude a slightly earlier age (Agustí et al. 2001; Iannucci et al. 2020a).

The site of Collepardo provides a challenging but exciting opportunity to refine practices of virtual extraction of fossil remains, as many fossils occur deeply embedded in the travertine deposit and are also internally fractured, limiting classical excavation procedures. In this framework, the Suidae specimen from Collepardo represents a valuable case study, as its description and comparative palaeoneurological analysis have been only possible after the digital processing of the travertine block and its content.

4.8.1. Inner cranial anatomy

Non-invasive CT methods allow us to virtually extract the 3D model of the braincase from the travertine block and successively those of the paranasal sinuses and brain.

In CP 02-15, the dorsal flattening of the brain and paranasal sinuses, as well as the posterior development of parietal pneumatisation, perfectly mirrors the external neurocranial morphology, which does not appear to be markedly affected by taphonomic processes, if not for a slight lateral compression. This suggests that the endocranial anatomy of the Collepardo braincase reflects the condition *ante mortem*, allowing us to make the first description of the endocranial anatomy of the late Pliocene *S. arvernensis* and, more generally, of a fossil Suidae.

Comparisons with extant *S. scrofa* evidenced a strong morphological resemblance in the cranial pneumatisation, except for the posterior and dorsal portions of the parietal sinuses, which appear caudally projected and dorsally pointed in *S. arvernensis*. The morphology of the brain endocasts is more divergent between the two species, as CP 02-15 is dorsally flat with a more prominent cerebellum, while the opposite condition is observed in *S. scrofa*. Extending the comparisons to a selected sample of extant taxa reported by Kruska (1970, 1982), the morphological variability of the brain in Suidae and Tayassuidae became evident (Figure 7a1-h2, Table 2). The flattening of the brain of *S. arvernensis* is a feature shared with the extant Asian *B. babyrussa* and the African *H. meinertzhageni*. These species are representatives of two widely diverging phylogenetic clades (Gongora et al. 2011; Frantz et al. 2016), and *H. meinertzhageni* (commonly known as the 'giant forest hog') is also characterised by a very large size. Considering this, although caution is needed given the paucity of the sample, among Suidae the shape of the brain would appear to be independent from body size and phylogeny. Indeed, paranasal sinuses and even more brain endocasts are related to several morphofunctional and eco-ethological aspects, and therefore are widely investigated for inferring these characteristics in extinct species (Sakai et al. 2011; Vinuesa et al. 2016; Iurino et al. 2020; Pérez-Ramos et al. 2020; Boscaini et al. 2020a). In a recent work (Bhagwandin et al. 2017), the differences in brain morphology of the extant rhinoceros *Diceros bicornis* (Linnaeus, 1758) and *Ceratotherium simum* (Burchell, 1817) have been related to diet. According to the authors, the shape of the brains reflects the overall architecture of the skulls, which in turn is related to the behaviour and feeding habits of the two species, browsing for the black rhinoceros, and grazing for the white rhinoceros (Bhagwandin et al. 2017). More recently, Iurino et al. (2020) using CT analyses, confirmed the morphological differences in the brain endocasts of *D. bicornis* and *C. simum*, and documented a similar arrangement of the cranial pneumatisation in both species. Similarly, *S.*

arvernensis and *S. scrofa* share similar paranasal sinuses and differently shaped brains. The current knowledge does not allow detailed considerations, but future studies on brain and paranasal sinuses may provide content for taxonomic and/or adaptive inferences in Suidae.

4.8.2. Geographical and chronological distribution of *Sus arvernensis*

Sus arvernensis is recognised as a typical species of the Ruscinian (MN14-MN15) and Early Villafranchian (MN16) assemblages of Europe and Anatolia (Hünermann 1971, 1975; Azzaroli 1975; Gliozzi et al. 1997; Guérin et al. 1998), whereas other findings from China (Berdondini 1992) and Africa (Hünermann 1971; Pickford 2012) are more doubtful (Cherin et al. 2018a).

4.8.2.1. Geographical distribution

Berdondini (1992) assigned to *S. minor* (=*S. arvernensis*) a fragmented cranium from the Nanzhuanggou (or Nan Zhuang Gou) valley (Yushe Basin, Chinese province of Shanxi), which preserves the anterior portions of the snout and of the zygomatic arches, and part of the cranial vault. This specimen was recovered from the upper part of the Gaozhuang Formation, which crops out in the north-western part of the valley (Berdondini 1992), implying an age bracketed between 4.5 and 4.2 Ma for this Chinese occurrence (Flynn and Qiu 2013; Opdyke et al. 2013). The attribution to *S. arvernensis* was accepted by Pickford (2012), while Cherin et al. (2018a) suggested a revision of the material to verify its taxonomic position. The cranium has gently receding zygomatic arches, which are widely diverging but not markedly inflated; the nasal bones are laterally expanded, and the supracanine flanges are relatively developed and rugose. All these features align it with a *Sus* of the '*Sus verrucosus* group' (*sensu* Azzaroli 1952) and are very similar to those of crania of *S. arvernensis* (Azzaroli 1975; Pickford and Obada 2016). It is likely that it does represent this species, or a closely related form. Nonetheless, most of the roughly coeval Asian material of Suinae still awaits to be described, which clearly complicates systematic assignments (Wang et al. 2013).

Andrews (1902) described a fragmented lower third molar of *Sus* sp. from Wadi-Natrun, in Egypt, considering it similar to *Sus hysudricus* Falconer and Cautley, 1847 from the Siwalik, but smaller. Tobien (1936) reported three other molars from the same locality and assigned them, as well as Andrew's specimen, to Suidae gen. et sp. indet., leaving open the possibility that they belonged to another form of European affinities. Hünermann (1971), referring to Tobien's work, listed these remains as the only evidence of *S. minor* (=*S. arvernensis*) in Africa, but without further discussion. Pickford (2012) established a new species on the sample of Wadi-Natrun, *Dasychoerus* (=*Sus*) *natrunensis*, which he considered different from *S. arvernensis* only in having smaller third molars, suggesting close affinities between the two species. Up to now, the sample of small Suidae from Wadi-Natrun only consists of six isolated molars, in particular only three third molars (one upper and two lower), which in our opinion does not allow to solve its systematic placement. Pickford (2012) also synonymised *Kolpochoerus deheinzelini* Brunet and White, 2001 from Aramis (Middle Awash, Ethiopia) and other Pliocene African sites with *S. arvernensis*, considering them 'morphometrically indistinguishable' (Pickford 2012, p. 24). According to this hypothesis, *S. arvernensis* would be ancestral to the African *Kolpochoerus*, as *K. deheinzelini* is the earliest representative of the genus (Pickford and Obada 2016). Indeed, the material of *K. deheinzelini* is close in size and dental proportions to *S. arvernensis*, and its morphology is different from *Propotamochoerus* (Iannucci et al. 2020a), to which it was initially tentatively related (Brunet and White 2001). However, envisioning a derivation of *Kolpochoerus* from *S. arvernensis* is hardly reconcilable with morphological (Cherin et al. 2018a) and molecular (Gongora et al. 2011) phylogenetic analyses. Such analyses consistently point to African Suinae as a monophyletic clade with estimated divergence times from their Eurasian relatives (~10-11 Ma) predating the early Pliocene occurrence of *K. deheinzelini* in the continent (Brunet and White 2001). Following this, the similarities between *S. arvernensis* and *K. deheinzelini* could be due to retention of plesiomorphic features and should be carefully tested in a broader phylogenetic framework.

4.8.2.2. Chronology

The earliest record of *S. arvernensis* may be represented by a crushed skull from Kardia (Greece, ~5.2 Ma, MN14) (Iannucci et al. 2020a), and several other occurrences are reported from Ruscinian localities (Hünermann 1971; Azzaroli 1975; van der Made and Moyà-Solà 1989; Guérin et al. 1998; Pickford and Obada 2016). Arguably, the best-known findings are those from early Villafranchian localities in southern France (Pickford and Obada 2016) and northern Italy (Berdondini 1992). However, most of these specimens were recovered long ago and lack precise chronological constraints (e.g., Croizet and Jobert 1828; Depéret 1885). For instance, the mammal fauna of Étouaires, type locality of *S. arvernensis*, is a chronologically averaged ensemble that includes Early to Middle Villafranchian species (Heintz 1970; Ballatore and Breda 2019). In Italy, *S. arvernensis* is reported from several localities referred to the Triversa FU, which is usually referred to ~3.2 Ma (Gliozzi et al. 1997). A fossiliferous level of the Santa Barbara quarry in central Italy has been palaeomagnetically calibrated with the Kaena reversed interval within the Gauss Chron (C2An.1 r) at ~3.07 Ma (Albianelli et al. 1997). The scarce faunal assemblage recovered from this site contains typical elements of the Triversa FU, but *S. arvernensis* is not recorded among them (Albianelli et al. 1997).

Considering these uncertainties, the last known occurrence of *S. arvernensis* is likely from Kvabebi, in Georgia. This site, which is also palaeomagnetically calibrated with the Kaena subchron at ~3.07 Ma (Agustí et al. 2009), has yielded remains initially ascribed to *P. provincialis* by Vekua (1972), but soon reassigned to *S. minor* (=*S. arvernensis*) by Azzaroli (1975). Recently, Pickford (2013) and Pickford and Obada (2016) argued for a more conservative attribution to *Dasychoerus* (=*Sus*) sp. for the Georgian sample, due to its size slightly larger than typical *S. arvernensis*. These size differences are not pronounced, especially considering the variability of extant Suinae (Souron2012; Cherin et al. 2020; Iannucci et al. 2020b), and they may be related to other factors, such as ecomorphological adaptations within the same species (Iannucci et al. 2020c). In this respect, it is worth remarking that most findings of *S. arvernensis* are concentrated within geographically close localities of southwestern Europe (Pickford and Obada 2016; Iannucci et al. 2020a), potentially biasing our perception of the variability of the species. Pending a redescription of the sample from Kvabebi, an attribution to *S. arvernensis* seems at the moment the most parsimonious.

4.9. Conclusions

Suidae remains from Collepardo are here assigned to *S. arvernensis*, a small-sized Ruscinian to Early Villafranchian (MN14-MN16a) species. In Italy, the chronological range of *S. arvernensis* seems to be limited to the Triversa FU (MN16a), hence agreeing with the recently revised chronology of the Collepardo site (Bellucci et al. 2019), despite a Ruscinian age cannot be ruled out. *Sus arvernensis* is usually regarded as a species of subtropical affinities (e.g., Pickford and Obada 2016). The results of isotope analyses performed on the travertine at Collepardo are indicative of a humid but relatively cold climate environment (Bellucci et al. 2019), supporting the hypothesis that *S. arvernensis* inhabited humid environments, but suggesting also that slightly cooler conditions were not a limiting factor for the species.

The virtually extracted neurocranium from Collepardo (CP 02-15) is the only remain of an adult *S. arvernensis* that preserves the entire occipital region. In *S. arvernensis* the cranium is low, and its dorsal profile is gently rounded; it differs markedly from the high and protruding occiput of *Propotamochoerus* and *Hippopotamodon*.

The first inner cranial description carried out herein on *S. arvernensis*, and more broadly on an extinct Suidae, revealed that the neurocranial sinuses are extensively developed and mirror the outer morphology of the braincase, with a general resemblance to *S. scrofa*, apart for the occipital region. The brain endocast is quite distinct between the two species, with *S. scrofa* having a larger and more globular brain and *S. arvernensis* showing a flattened brain similar to those of the Asian *B. babyrussa* and the African *H. meinertzhageni*. These two species substantially differ in size and belong to widely diverging phylogenetic clades (Frantz et al. 2016), excluding relatively simple evolutionary or allometric interpretations. The relationship between brain morphology, cranial pneumatisation, and ecology have provided insights on several mammal species (Sakai et al. 2011; Vinuesa et al. 2016; Iurino et al. 2020; Pérez-Ramos et al. 2020; Boscaini et al. 2020a) but it is still an unexplored issue in Suidae. Future studies should evaluate the significance of inner cranial anatomy in inferring several palaeobiological aspects (e.g., sensory-perceptual abilities, sociality, feeding behaviour) of this important clade of mammals.

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Supplementary material

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5. Paper 4

First report of *Sus strozzii* (Suidae, Mammalia) from the Early Pleistocene of Hungary (Dunaalmás) and species distinction based on deciduous teeth

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Abstract

Herein we describe a fragment of a mandible with a deciduous fourth premolar (dp4) from the Early Pleistocene locality of Dunaalmás, representing the first confirmed report of *Sus strozzii* from Hungary. The comparison of dp4 measurements supports a statistically significant distinction between *S. strozzii* and *Sus scrofa*. The two species overlap in time during the late Early Pleistocene of Europe (Epivillafranchian), but suid remains of this time-span are seldom classified at a species level. The correct taxonomic identification of the Epivillafranchian suids, which are often associated with evidence of hominin presence, is of great palaeoenvironmental value because *S. scrofa* and *S. strozzii* possess different ecological requirements.

Keywords: Villafranchian; Epivillafranchian; Villanyian; Quaternary; Europe; wild boar

5.1. Introduction

Suidae are even-toed ungulates (Artiodactyla) that retain primitive anatomical features, such as a four-toe foot, simple stomach, and bunodont dentition (Simpson 1945; Groves 1981; Montgelard et al. 1998).

Nowadays the wild boar *Sus scrofa* Linnaeus, 1758 is the only species inhabiting continental Eurasia —with the exception of the peculiar pigmy hog *Porcula salvania* Hodgson, 1847, whose distribution is very limited (Oliver 1980)— but in the past several species contributed to the diversity of the group (van der Made and Moyà-Solà 1989; Pickford 1993; Fortelius et al. 1996).

Sus strozzii Forsyth Major, 1881 was a typical element of the Villafranchian fauna (Early Pleistocene) (Azzaroli 1977; Gliozzi et al. 1997; Rook and Martínez-Navarro 2010), which is considered phylogenetically close to several extinct and extant pigs from Island South East Asia (Azzaroli 1952; Berdondini 1992; Cherin et al. 2018). This species also shares several morphological similarities with the extant African river hog, *Potamochoerus* Gray, 1854, suggesting a convergent adaptation to humid environments (Azzaroli 1952; Faure and Guerin 1984).

S. strozzii underwent a severe demographic reduction at the end of the Gelasian, since there are no or doubt suid remains in Europe between 1.8 and 1.2 Ma (Martínez-Navarro et al. 2015; Cherin et al. 2018; but see van der Made et al. 2017). However, *S. strozzii* persists in Europe at least until the end of the Jaramillo magnetosubchron, as recently confirmed by its occurrence from Frantoio (Arda river) approximately dated to ~0.99 Ma (Bona and Sala 2016), thus overlapping in time with the early representatives of *S. scrofa* (Guérin and Faure 1997; Bellucci et al. 2015).

The replacement of the humid-specialized *S. strozzii* with the adaptable *S. scrofa* is a bioevent of high palaeoecological significance (Faure and Guerin 1984). Moreover, it takes place in a time-span of great interest in the context of early hominins diffusions from Africa to Europe (Carbonell et al. 2008; Madurell-Malapeira et al. 2010; Manzi et al. 2011; Michel et al. 2017; Sardella et al. 2018). However, even though *S. scrofa* and *S. strozzii* are clearly distinguishable from several anatomical features, detailed comparative analysis of the species is still lacking and consequently the taxonomic attribution of the European Epivillafranchian suines is still unsolved (Table 1).

The deciduous teeth are rare in the fossil record and seldom compared, even though remains ascribed to *S. strozzii* have been recovered from several localities (Figure 1).

Herein, we described a fragment of mandible with a deciduous fourth premolar (dp4) from the Early Pleistocene locality of Dunaalmás, and we carried out a morphological and biometric comparison of homologous teeth of *S. scrofa* (including fossil and recent specimens from Asia and Europe) and *S. strozzii* (including the type locality and all the published remains assigned to the species). We also performed a statistical analysis to test the reliability of the observed differences.

The suid from Dunaalmás is the first confirmed *S. strozzii* from Hungary and one of the most continental occurrences of the species.

Locality	Nation	Attribution	Reference
Sima del Elefante (Atapuerca)	Spain	*Sus* sp.	Carbonell et al. 2008
Vallparadís Estacio	Spain	*Sus* sp.	Madurell-Malapeira et al. 2010
Le Vallonnet	France	*Sus* sp.	Moullé et al. 2006
Castagnone	Italy	*Sus* sp.	Siori and Sala 2007
Madonna della Strada	Italy	*Sus* sp.	Maccagno 1962
Somssich Hill 2	Hungary	*Sus* sp.	Gasparik and Pazonyi 2018
Kozarnika	Bulgaria	*Sus* sp.	Sirakov et al. 2010
Frantoio	Italy	*Sus strozzii*	Bona and Sala 2016
Barranc de la Boella	Spain	*Sus strozzii*	Vallverdù et al. 2014
Untermassfeld	Germany	*Sus scrofa priscus*	Guérin and Faure 1997
Slivia	Italy	*Sus* cf. *scrofa*	Ambrosetti et al. 1979
Gran Dolina (Atapuerca)	Spain	*Sus scrofa*	Made et al. 2017

Table 1 - Epivillafranchian (~1.2–0.8 Ma) localities with suid remains.

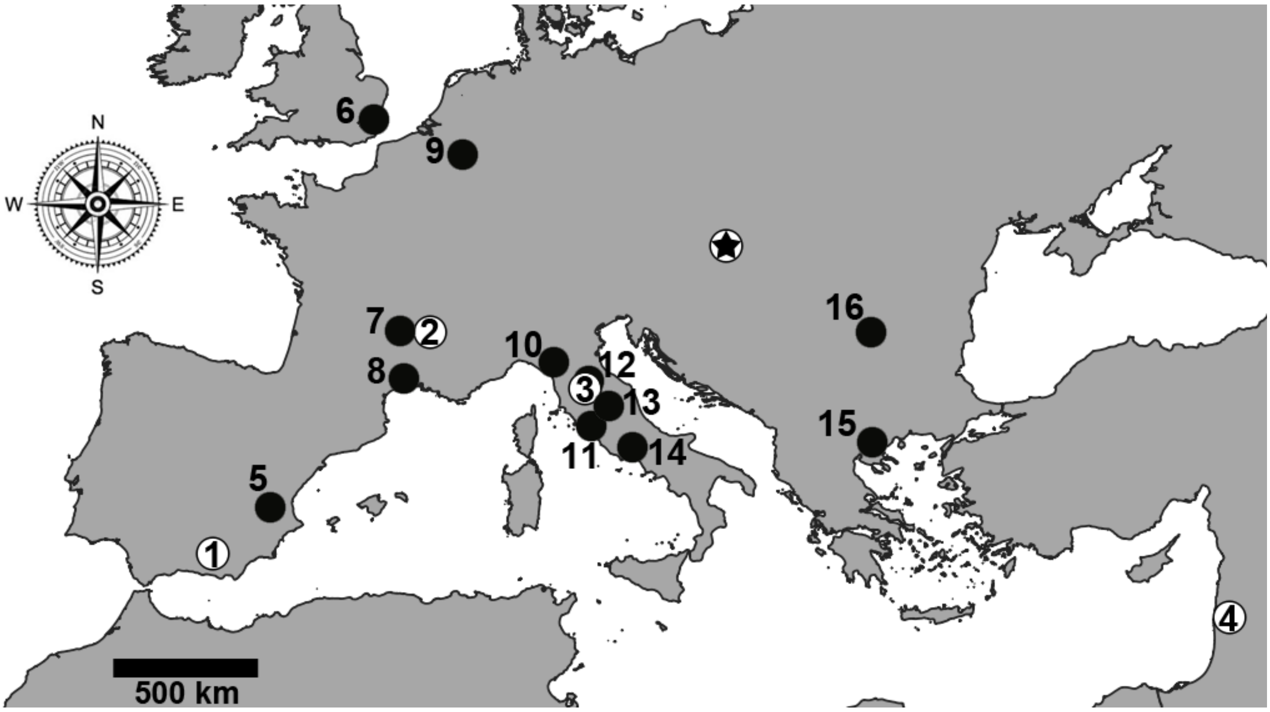


Figure 1 - *Sus strozzii* in the Villafranchian of Europe. Localities with lower fourth deciduous premolars are marked with open dots: star, Dunaalmás; 1, Fonelas P-1 (*Potamochoerus magnus* in Arribas and Garrido 2008); 2, Saint Vallier; 3, Upper Valdarno; 4 Ubeidiya (*Sus* sp.); 5, Valdeganga; 6, Red Crag; 7, Senèze; 8, Montpellier; 9, Tegelen; 10,Olivola; 11, Monte Riccio; 12, Mugello; 13, Pantalla, Santa Sabina, Torre Picchio, Villa San Faustino; 14, Coste San Giacomo; 15, Gerakarou, Vassiloudi; 16, Valea Grăunceanului.

5.2. The locality of Dunaalmás

The locality of Dunaalmás (Figure 1), in the Komárom-Esztergom county (Hungary), has yielded several Early Pleistocene fossil remains coming from a few palaeontological sites and sporadic collecting. The oldest Quaternary vertebrate remains —among others *Anancus arvernensis* Croizet and Jobert, 1828 and *Mammuthus meridionalis* Nesti, 1825— have been recovered from the freshwater limestones of the so-called Süttő-Dunaalmás Travertine Complex, their age is estimated as earliest Pleistocene (Middle Villafranchian) (Jánossy 1986). Three molars of *M. meridionalis* from the freshwater limestone of Les-hegy (Les Hill) are also dated to the earliest Pleistocene (Virág and Gasparik 2012).

The richest assemblage has been recovered from the freshwater limestone quarry of Dunaalmás 4 locality. Terrace geomorphology and micromammals biochronology —in particular the occurrences of *Episoriculus gibberodon* (Petényi 1864), *Prospalax priscus* (Nehring 1897), and *Mimomys pitymyoides* Jánossy and Meulen, 1975— allow to refer the fauna to the Late Villanyian (late Middle to early Late Villafranchian) with an estimated age of ~2.0 Ma (Kretzoi and Pécsi 1979; Jánossy 1986) or slightly older, ~2.4 Ma (Kordos 1994). Dunaalmás 4 has been also calibrated by means of magnetostratigraphic correlations, which consistently constrain the site between 2.0 and 2.4 Ma (Lantos 2004).

In 2000, an upper molar fragment of *M. meridionalis* was collected from Dunaalmás Bethlehem Quarry, which exposes a sequence of freshwater limestone and sandy or gravelly sediments. The specimen was found in the lower sandy gravel layers containing small blocks of freshwater limestone (Viczián 2013). Considering its characteristics (lamellar frequency, 5; average enamel thickness, 3.4 mm), its age is probably between 2.0 and 1.5 Ma or a bit younger (see fig. 3 of Virág and Gasparik 2012).

The Dunaalmás suid specimen was probably a sporadic find, and according to the old inventory label, it was bought from József Radok in 1897. It preserves a very small amount of calcified sandy sediment that strongly resembles the one previously described, and we can assume that the specimen originated from a similar sequence.

According to all of the above mentioned data and characteristics, we refer the Dunaalmás suid to the Late Villafranchian, with an estimated age of ~2.0–1.5 Ma.

5.3. Materials and methods

The specimen from Dunaalmás (HNHM V. 60. 609) is housed in the Hungarian Natural History Museum (HNHM). We built a comparison dataset including remains stored in the Montevarchi Paleontological Museum (MPM; id. numbers 941 and 943) and in the Museum of Natural History of the University of Florence, section of Geology and Paleontology (IGF; id. numbers 418, 435, 436, and 4692; Table 2) as well as literature data (Geraads et al. 1986; Kuşatman 1991; Guérin and Faure

1997; Fujita et al. 2000; Faure 2004; Arribas and Garrido 2008) for a total of 148 specimens: *Sus strozzii* (*n* = 12), fossil *Sus scrofa* (Sf; *n* = 7), recent *S. scrofa* from East continental Asia (ECA; *n* = 8), and Germany (*n* = 121).

The specimens from Ubeidiya currently ascribed to *S. strozzii* are markedly outliers compared to the other remains of the species, being substantially smaller. Moreover, the *Sus* recovered from this locality retains the upper third incisor (Geraads et al. 1986), whereas this tooth has been lost in *S. strozzii* (Azzaroli 1952). Therefore, the remains from Ubeidiya have been excluded from the statistical analysis, pending a taxonomic revision of this sample. *Potamochoerus magnus* from Fonelas P-1 (Arribas and Garrido 2008) is here considered a later synonym of *S. strozzii*, in agreement with other authors (Pickford and Obada 2016; Cherin et al. 2018).

Four tooth measurements have been taken to the nearest 0.01 mm with a digital caliper: length, i.e., anteroposterior diameter (L), widths, transverse diameter of the anterior (Wa), middle (Wm), and posterior (Wp) lobes. Measurements and terminology follow van der Made (1996).

To evaluate the statistical significance of the observed differences, we performed a non-parametric Wilcoxon test for equality of medians between each possible pair of populations. The statistical analysis was conducted in the R environment (R core Team 2000).

Specimen Id.	Locality	dp4 L	dp4 Wa	dp4 Wm	dp4 Wp
HNHM V. 60. 609	Dunaalmás	25.22	9.52	10.26	12.36
IGF 418	Upper Valdarno	23.02	8.48	9.51	11.11
MPM 943	Upper Valdarno	24.31	8.6	10.36	11.61
IGF 435	Upper Valdarno	24.54	9.06	10.43	12.21
IGF 436	Upper Valdarno	24.2	9.01	9.48	12.02
MPM 941	Upper Valdarno	22.72	8.55	10.63	12.18

Table 2 - Lower deciduous fourth premolar measurements (mm) of *Sus strozzii.*

5.4. Systematic paleontology

Order Artiodactyla Owen, 1848

Family Suidae Gray, 1821

Subfamily Suinae Gray, 1821

Genus *Sus* Linnaeus, 1758

Sus strozzii Forsyth Major, 1881

5.4.1. Material

HNHM V. 60. 609, left fragment of hemimandible of a juvenile with dp4 and alveolar traces of m1 and dp3 (only the distal root).

5.4.2. Description

The specimen preserves a fragment of the distal root of dp3 (Figure 2, 1b) and traces of m1 at the alveolar level. The latter tooth was not yet in line with dp4 at the age of death, similarly to the eruption state of IGF 418 (Figure 2, 2). Comparing the tooth eruption state and its wear stage with schemes developed for extant wild boars, the age at the time of death is estimated ~1 year (between 6 and 15 months) (Matschke 1967; Kuşatman 1991).

The dp4 is well preserved, only slightly damaged bucco-distally. The tooth has a trilobated structure, with each lobe possessing a pair of main cusps (respectively, paraconid and primoconid, protoconid and metaconid, hypoconid and entoconid). The mesial lobe is the narrowest, and the distal lobe is the widest, with a major development especially on the buccal side. The lingual cusps are slightly higher than their labial homologous. The first pair of cusps is clearly divided by a shallow furrow, while in the second lobe, the cusps areas are merging together due to the advancement of the wear stage, and in the third lobe, only the entoconid is still isolated. In fact, the hypoconid is merging with the most evident accessory cusplets: the hypopreconulid, which occupies the transverse valley between the second and the third lobe, and the pentaconid, which protrudes distally. The overall morphology of the tooth is similar in *S. scrofa* and *S. strozzii*, but the Dunaalmás suid more closely resembles the specimens from the type locality of the latter species (Figure 2), especially in the wider development of the posterior lobe.

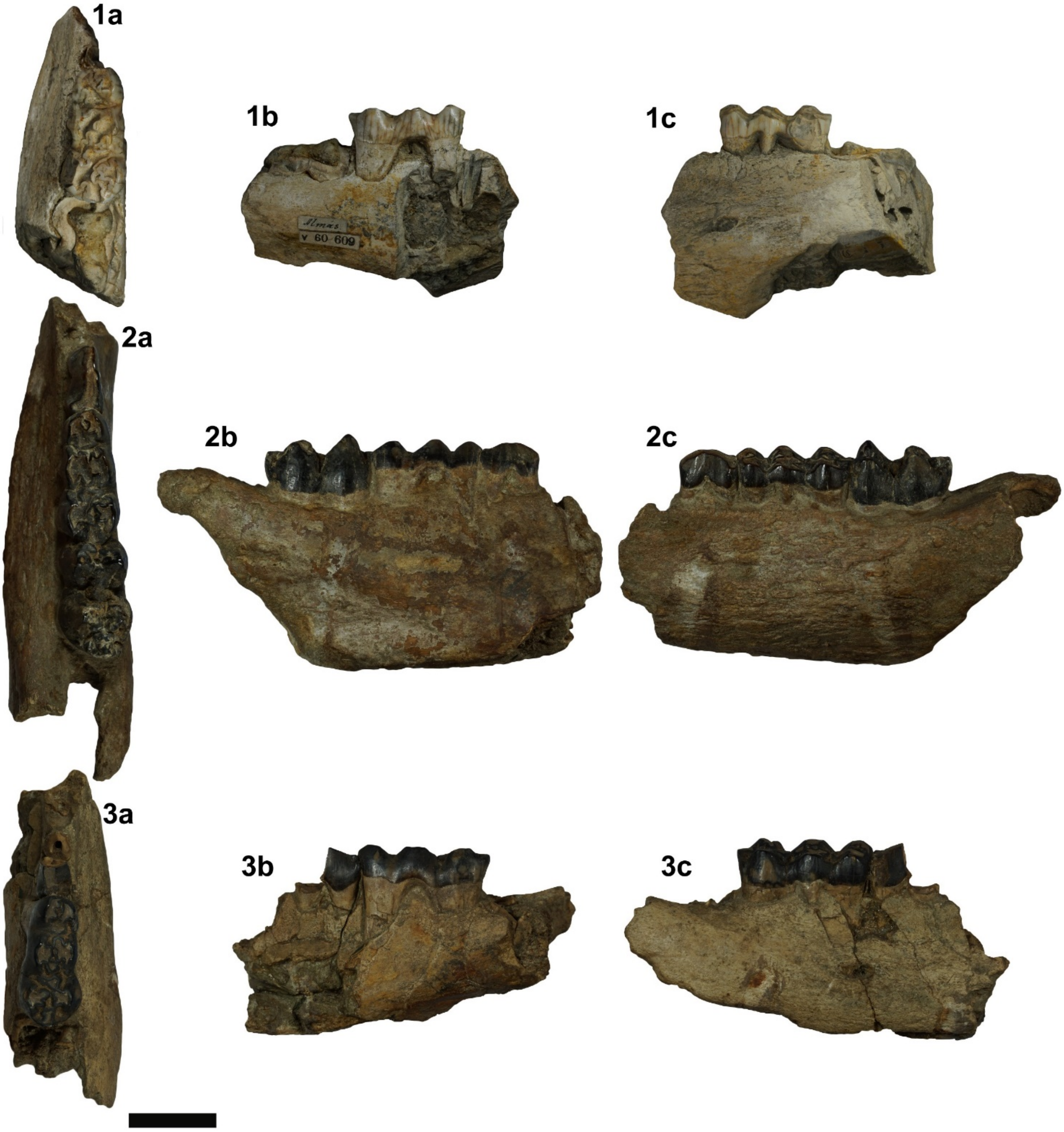


Figure 2 - *Sus strozzii* from: Dunaalmás (HNHM V. 60. 609), 1, left hemimandible with dp4 and fragments of dp3 and m1; and Upper Valdarno (IGF 418), 2, left hemimandible with dp3, dp4, m1; (IGF 436), 3, right hemimandible with dp4. Occlusal **(a)**, lingual **(b)**, and buccal **(c)** views. Scale bar 2 cm.

5.5. Results

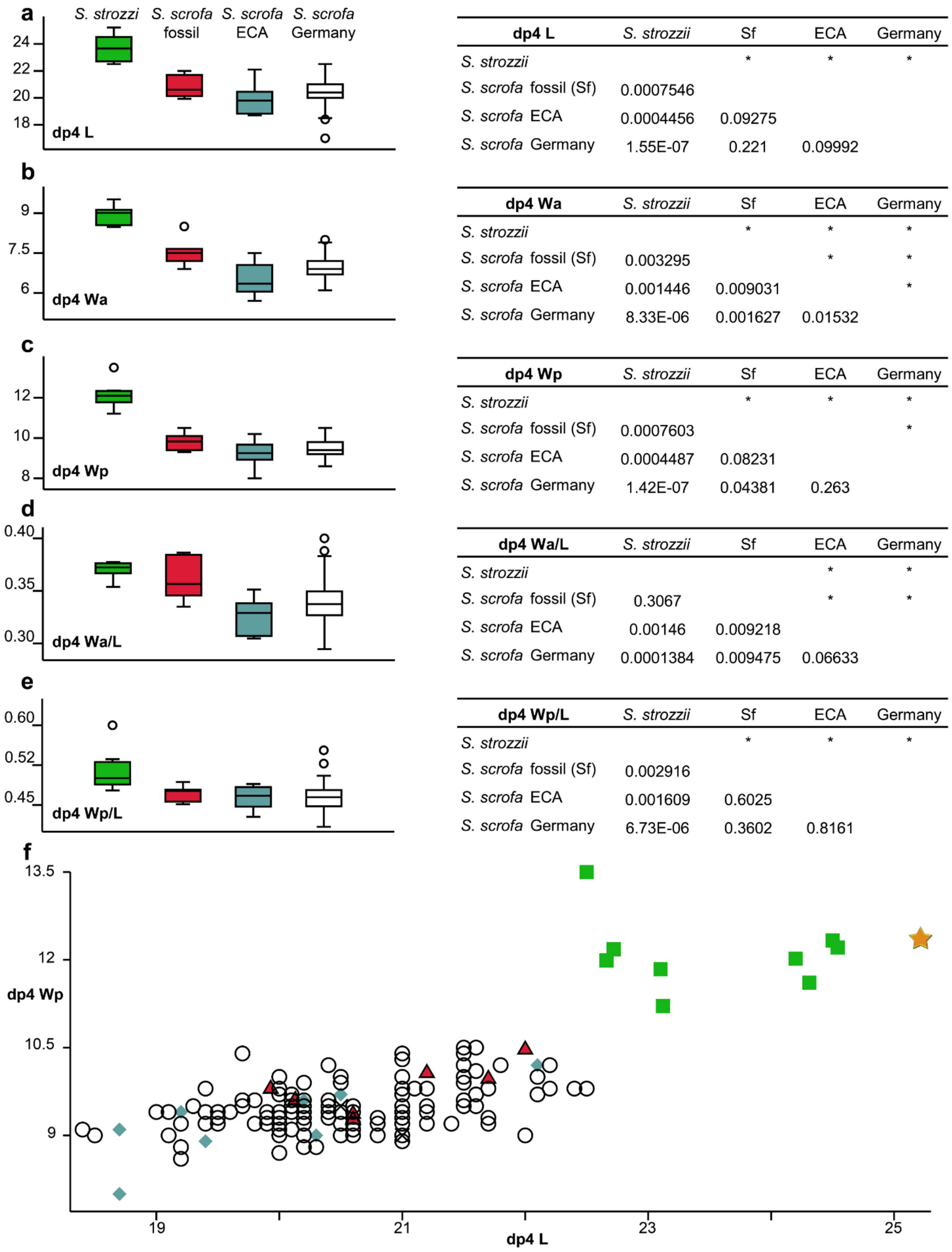
The statistical analysis supports a significant separation between *S. strozzii* and *S. scrofa*, the former species has larger and proportionally wider teeth than the latter. The only exception is the Wa/L ratio (Figure 3d), which is similar between *S. strozzii* and the *S. scrofa* fossil (Sf) group and between the two extant samples (ECA and Germany). All groups are separated by means of their anterior width (Figure 3b). Sf is also posteriorly wider than the others *S. scrofa* (Figure 3c). For what concerns L and Wp/L, no group of *S. scrofa* is different from one another (Figure 3a, e).

The Dunaalmás suid is far outside the range of variability of *S. scrofa* (Figure 3f).

5.6. Discussion

The results of this work clearly indicate that *S. strozzii* possesses longer, broader, and also proportionally wider teeth than *S. scrofa*. The larger dimensions of the former species are commonly recognized in the literature (Ambrosetti et al. 1979; van der Made et al. 2017; Cherin et al. 2018), but quantitative analyses that allow a thorough comparison of isolated remains are actually scanty. Moreover, the wild boar *S. scrofa* displays a huge morphological variability, and it is known that several fossil and recent specimens have reached even larger proportions than *S. strozzii* (Groves 1981; Guérin and Faure 1997). The deciduous teeth may be more conservative than the permanent dentition and retain phylogenetically relevant information (Guanfang and Schmidt-Kittler 1983; Pickford 2018).

The only exception to the clear separation between the two species is the Wa/L ratio, which does not discriminate *S. strozzii* from fossil *S. scrofa*. The latter group is indeed slightly larger, on average, than the others *S. scrofa*. However, this ambiguity is mostly due to a single specimen from Untermassfeld (the outlier in Figure 2b), which has a very wider mesial lobe.



dp4 L	*S. strozzii*	Sf	ECA	Germany
S. strozzii		*	*	*
S. scrofa fossil (Sf)	0.0007546			
S. scrofa ECA	0.0004456	0.09275		
S. scrofa Germany	1.55E-07	0.221	0.09992	

dp4 Wa	*S. strozzii*	Sf	ECA	Germany
S. strozzii		*	*	*
S. scrofa fossil (Sf)	0.003295		*	*
S. scrofa ECA	0.001446	0.009031		*
S. scrofa Germany	8.33E-06	0.001627	0.01532	

dp4 Wp	*S. strozzii*	Sf	ECA	Germany
S. strozzii		*	*	*
S. scrofa fossil (Sf)	0.0007603			*
S. scrofa ECA	0.0004487	0.08231		
S. scrofa Germany	1.42E-07	0.04381	0.263	

dp4 Wa/L	*S. strozzii*	Sf	ECA	Germany
S. strozzii			*	*
S. scrofa fossil (Sf)	0.3067		*	*
S. scrofa ECA	0.00146	0.009218		
S. scrofa Germany	0.0001384	0.009475	0.06633	

dp4 Wp/L	*S. strozzii*	Sf	ECA	Germany
S. strozzii		*	*	*
S. scrofa fossil (Sf)	0.002916			
S. scrofa ECA	0.001609	0.6025		
S. scrofa Germany	6.73E-06	0.3602	0.8161	

Figure 3 - Boxplots of dp4 measurements (on the left) and their respective *p* values for the Wilcoxon test (on the right): **(a)** dp4 L, **(b)** dp4 Wa, **(c)** dp4 Wp, **(d)** dp4 Wa/L, **(e)** dp4 Wp/L, significance with α = 0.05 is marked (*), **(f)** bivariate diagram of dp4 L x Wp. Star, Dunaalmás; Square, *Sus strozzii*; triangle, *Sus scrofa* fossil; diamond, *S. scrofa* ECA; dot, *S. scrofa* Germany (for abbreviations, see Materials and methods).

The differences between the groups of *S. scrofa* are more subtle than those that occur between *S. scrofa* and *S. strozzi* and although in some cases they are statistically significant, a broader and more detailed study is needed to test and eventually clarify their actual biological meaning.

Sus strozzii is usually considered a species adapted to very humid, even swampy environments (Faure and Guerin 1984). Specifically, it is characterized by an even stouter appearance than *S. scrofa*, with metapodials proportionally shorter than the whole limbs, limbs proportionally shorter than the trunk, an enlarged articular surface of the carpus, and other similarities with the extant genus *Potamochoerus* in the morphology of the cervical vertebrae, the humerus, and the femur (Azzaroli 1952). These palaeoecological considerations are strengthened by the severe rarefaction experienced by the species in the post-Olduvai pre-Jaramillo Early Pleistocene (~1.8–1.2 Ma) (Martínez-Navarro et al. 2015; Cherin et al. 2018).

The presence of *S. strozzii* from the Early Pleistocene of Dunaalmás is in agreement with the biochronological and palaeoenvironmental context depicted by the faunal assemblages recovered from the area (Jánossy 1986; Virág and Gasparik 2012; Viczián 2013), as well as with the widespread distribution of the species in the Villafranchian of Europe (Azzaroli 1952; Koufos 1986; Gliozzi et al. 1997; Martínez-Navarro et al. 2015; van der Made et al. 2017; Cherin et al. 2018). However, this is the first confirmed record of *S. strozzii* from Hungary. In fact, even though Jánossy (1986) listed "*Sus strozzii* group" among the taxa recorded from Osztramos locality number 3, suid remains are neither mentioned in previous works on the site (Jánossy 1969, 1970), nor there are any specimens stored in HNHM, where the material should eventually be housed.

Conversely to *S. strozzii*, *S. scrofa* is an opportunistic animal capable of living in a wide range of environments, as it is reflected by the vast geographic range occupied by the extant populations of the species (Groves 1981). The arrival of the extant wild boar in Europe can be related to a profound change in the ecosystems and in the Earth's climate system (Head and Gibbard 2005; Maslin and Ridgwell 2005; Suc and Popescu 2005; Tzedakis 2007; Kahlke et al. 2011), which eventually led to a more stable human presence in Europe during the Middle Pleistocene (Oms et al. 2000; Wagner et al. 2010; Moncel et al. 2018). However, the tempo and mode of the earliest hominins diffusion from Africa to Europe engenders lively discussions (Roebroeks 2001; Martínez-Navarro 2010; Dennell et al. 2010; Muttoni et al. 2010; Lordkipanidze et al. 2013; among others). The correct taxonomic identification of the Epivillafranchian suid remains will therefore provide new palaeoecological and biochronological insights to this stimulating debate.

5.7. Conclusion

The here described fragment of mandible from Dunaalmás is the first confirmed record of *Sus strozzii* from Hungary. It expands our knowledge on the distribution of the species and emphasizes the usefulness of deciduous teeth in the distinction between *S. strozzii* and *S. scrofa*. The two species possess different ecological requirements and are part of the Epivillafranchian fauna associated with early hominins diffusion from Africa to Europe (Madurell-Malapeira et al. 2010; Sirakov et al. 2010; Michel et al. 2017). In particular, unidentified deciduous suid teeth have been found together to the earliest direct evidence of hominins presence in Europe (Carbonell et al. 2008). New morphometric investigations on Epivillafranchian suids are needed to clarify their taxonomic identity and gain new insights on the palaeoenvironmental context of the late Early Pleistocene European faunal renewal.

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6. Paper 5

New results on suids from the Early Pleistocene site of Untermassfeld

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Abstract

New and previously discussed suid remains recovered from Untermassfeld (Thuringia, Germany) are described. The late Early Pleistocene site of Untermassfeld yielded one of the most abundant samples of Epivillafranchian suids, and yet only a minimum number of 6 individuals has been identified. Untermassfeld suids have been considered the first representatives of the extant wild boar and ascribed to *Sus scrofa priscus*, then reassigned to *Sus* sp., and eventually to *Sus strozzii*. The latter attribution is favoured herein and some morphological differences from typical Villafranchian *S. strozzii* are noticed, which seem to be consistently present in other Epivillafranchian samples. At the moment it is not possible to evaluate whether these traits emerged abruptly in Epivillafranchian populations or were the result of gradual changes not recorded in the scanty post-Olduvai (~1.8 Ma) European suid record.

6.1. Introduction

Suids represent not but a fraction of the mammalian remains recovered from the late Early Pleistocene site of Untermassfeld (Thuringia, Germany), the minimum number of individuals (MNI) being only 6, including 3 juveniles and 3 adults (Kahlke 2006; in this volume), accounting for only 1.3% of all large mammals. Yet they played an important role in shaping the palaeobiological thought on the dispersal of the extant wild boar, *Sus scrofa* Linnaeus, 1758, into Europe. Indeed, Untermassfeld suids were described as the earliest fossil evidence of *S. scrofa* and assigned to *S. scrofa priscus* Goldfuss, 1823 (Guérin and Faure 1997), culminating the hypothesis of a progressive trend towards smaller dimension and more complex molar morphology in the evolution of the species (Hünermann 1965, 1969, 1975; Faure and Guérin 1983; Guérin and Faure 1997). Guérin and Faure (1997) suggested that the first representatives of *S. scrofa* coexisted with the last populations of *Sus strozzii* Forsyth Major, 1881, a typical suid of European Villafranchian faunas (Azzaroli 1952; Faure and Guérin 1984; Cherin et al. 2018; Iannucci et al. 2020a). The attribution of Epivillafranchian suids engendered controversy and debate, with different samples assigned to *S. scrofa*, *S. strozzii*, or *Sus* sp. (Iannucci et al. 2020a). Martínez-Navarro et al. (2015) argued that suids are basically absent from European localities dated between ~1.8 and 1.2 Ma and interpreted the whole Epivillafranchian contingent as *S.* gr. *scrofa*, i.e., as the arrival of a species phylogenetically related to the extant wild boar. According to this hypothesis, the wild boar dispersal would be approximately concurrent with other faunal events chosen to denote the beginning of the Epivillafranchian at ~1.2 Ma (Kahlke 2006, 2007, 2009; Bellucci et al. 2015), and hence of great biochronological value. However, an almost complete mandible of *S. strozzii* was described from the post-Jaramillo (~0.99 Ma) locality of Frantoio (Bona and Sala 2016). Indeed, van der Made et al. (2017) did not recognize any gap in the ~1.8–1.2 Ma European suid fossil record, but classified the latest Early Pleistocene specimens as *Sus* sp., including the sample from Untermassfeld. Eventually, Cherin et al. (2020) argued that Epivillafranchian suids should be ascribed to *S. strozzii*, remarking that all lower male canines known from Epivillafranchian localities show a verrucosic section (i.e., with the two lateral sides almost equal in length and larger than the distal facet), different from the scrofic section of *S. scrofa* (i.e., with the lingual side shorter than the distal facet). In suids, canines are sexually dimorphic and in male individuals they project outwards and often upwards from the skull, with a variety of forms and shapes exhibited by extant and extinct species (e.g., Stehlin 1899–1900; Cooke and Ewer 1972; Hardjasasmita 1987; Orliac et al. 2010; Macdonald and Shaw 2018). The dichotomy between scrofic and verrucosic canines is of great relevance within *Sus*, although several authors recognised intermediate morphologies (e.g., Fujita et al. 2000; Dong 2008; Sun et al. 2021). The suid canines from Untermassfeld were described as scrofic (Guérin and Faure 1997), but later reconsidered as verrucosic (van der Made et al. 2017; Cherin et al. 2020). However, van der Made et al. (2017) did not provide further details, while Cherin et al. (2020) only rediscussed one previously published canine (Guérin and Faure 1997).

The suid material from Untermassfeld is redescribed herein and its taxonomic status is reviewed, also considering previously unpublished specimens.

6.2. Material and methods

The suid material described in this work is part of the Untermassfeld collection housed in the Senckenberg Research Station of Quaternary Palaeontology Weimar (IQW) in Germany. Most fossils were recovered from the south-eastern part of the excavation area, accordingly nicknamed "Schweineecke", i.e., the "pig corner" (Ellenberg and Kahlke 1997).

Comparative material of *S. scrofa* and *S. strozzii* has been studied in the following institutions: CMNH: Civic Museum of Natural History, Trieste (Italy); HNHM: Hungarian Natural History Museum, Budapest (Hungary); IGF: Natural History Museum of Florence, section of Geology and Paleontology (Italy); IsIPU: Italian Institute of Human Paleontology, Anagni (Italy); MACUS: Comparative Anatomy Museum "Battista Grassi", Sapienza University of Rome (Italy); MANA: Civic Archaeological-Naturalistic Museum "Adolfo Klitsche de la Grange", Allumiere (Italy);

MNCN: National Museum of Natural Sciences, Madrid (Spain); MPM: Paleontological Museum, Accademia Valdarnese del Poggio, Montevarchi (Italy); MUST: University Museum of Earth Sciences (including the former MPUR: Museum of Paleontology), Department of Earth Sciences, Sapienza University of Rome (Italy); NMB: Natural History Museum, Basel (Switzerland); NMM: Natural History Museum, Mainz (Germany); NWHCM: Norwich Castle Museum (UK); PF: PaleoFactory Laboratory, Department of Earth Sciences, Sapienza University of Rome (Italy).

The expression "typical *S. strozzii*" is used throughout the text for referring to samples from localities customarily dated at ~2.0–1.8 Ma, from which most fossils of the species have been recovered (Azzaroli 1952; Cherin et al. 2018; Iannucci et al. 2020a).

Measurements were taken with a digital calliper to the nearest 0.1 mm, mainly following Driesch (1976) and van der Made (1996). The latter work is also the reference for the dental nomenclature used herein. When feasible, measurements were taken on both sides and the mean of measured values is used. When referring to canines a superscript (for upper teeth) or subscript (for lower teeth) letter is used to denote males (m) or females (f) specimens (e.g., C_f = lower female canine). Measurements abbreviations are as follows: LLD: labio-lingual diameter in incisors; MDD: mesio-distal diameter in incisors (maximum diameter of the crown in I_3); ID-MP: Infradentale-mental prominence (length of the mandibular symphysis); WMM_1: width of the mandible in front of m1; L: length; W: width (-m: mesial; -d: distal/second lobe; -t: third lobe); cLi: length of the lingual side in C_x; cLa: length of the labial side in C_x; cD: length of the distal side in C_x.

6.3. Description

6.3.1. Cranium and mandible

IQW 1985/20 509 (Mei. 20 028) is a juvenile cranium with both tooth series preserved, inclusive of DI^1-DI^3, P^1, DP^2-DP^4, M^1, and the germ of M^2 (Figure 1, Table 1). Although fragmented, especially at the level of the maxilla, the preserved portion of the specimen is almost undeformed. In lateral view the vault of the cranium is dorsally convex and gently curved (Figure 1c). The lacrimal bone has a sub-rectangular shape and preserves a lacrimal foramen. The orbit is wide, and its anterior margin ends above the distal margin of the germ of M^2. It preserves the opening of the supraorbital canal. In dorsal view the zygomatic arches are gradually departing from the maxilla, their anterior (maxillary) portion ends above DP^4, while the malar bone departs from the maxilla roughly above M^1. The parietal lines are well separated, the minimum distance between them being 33.2 mm (Figure 1d). Since the cranium belongs to a juvenile individual, most of these characters differs from the adult condition.

The juvenile mandible IQW 1980/16 539 (Mei. 16 060) belongs to the same individual of IQW 1985/20 509 (Mei. 20 028). It preserves part of the left ascending ramus, a good portion of both mandibular corpi, the symphysis, left and right DI_1-DI_2, germ of I_3, and DP_2-M_1 (Figure 2, Table 2). Germs of the left M_2 and both P_4 are also present, although their morphology is not observable. The mandible is slender, and the symphysis is neither deep nor wide. In lateral view several small openings are evident, the most important being the main mental foramen below the P^1-DP^2 diastema (Figure 2c–d).

The dentition of the individual provides information on its sex and age at death. In the well-preserved alveolus of the missing lower right permanent canine the lingual side is slightly larger than the labial facet and both have rounded margins, while the distal side is substantially smaller and has a small notch. This morphology suggests that it probably belonged to a female. Aging wild boars by dentition eruption stage is a consolidate practice in wildlife management (e.g., Matschke 1967; Clarke et al. 1992). P^1/P_1 and M^1/M_1 erupt approximately at the same time, followed by I^3/I_3 and canines, then by M^2/M_2, and so on. In IQW 1980/16 539 (Mei. 16 060) at least C_f is erupting (it should be considered that teeth classified as "erupting" in living animals are only those that protrude from the gum, while the alveolar opening in the bone is observable slightly earlier), while M_2 is still enclosed in the alveolus. In *S. scrofa* this would correspond to an age between 7 and 12 months, probably closer to 7 than 12, considering that I_3 is almost erupting but DI^3 is still present. Indeed, in *S. scrofa* upper teeth erupt slightly later than their lower counterparts (Kuşatman 1991).

Figure 1 - *Sus strozzii* Forsyth Major, Untermassfeld. – **a–d** Juvenile cranium IQW 1985/20 509 (Mei. 20 028) with left and right DI^1-DI^3, P^1, DP^2-DP^4, M^1, germ of M^2, left occlusal, right occlusal, left lateral, dorsal views. – Scale: 30 mm.

	IQW 1985/20 509 (Mei. 20 028)	IQW 1985/20 709 (Mei. 20 228)
DI^1 MDD	8.7	
DI^1 LLD	4.8	
DI^2 MDD	13.9	
DI^2 LLD	4.2	
DI^3 L	4.5	
DI^3 W	2.5	
DP^2 L	12.0	
DP^2 Wm	5.5	
DP^2 Wd	7.6	
DP^3 L	14.4	
DP^3 Wm	6.9	
DP^3 Wd	10.9	
DP^4 L	15.9	
DP^4 Wm	13.9	
DP^4 Wd	14.4	
P^1 L	11.5	
P^1 W	5.3	
P^3 L		14.2
P^4 L		13.9
P^4 W		15.1
M^1 L	20.4	
M^1 Wm	17.7	
M^1 Wd	18.4	
M^2 L	27.1	
M^2 Wm	22.1	
M^2 Wd	20.0	
DP^2-DP^4	40.9	
DP^4-M^1	31.6	

Table 1 *Sus strozzii* Forsyth Major, measurements (mm) of cranial remains and upper teeth, Untermassfeld. For abbreviations see section 2.

Figure 2 - *Sus strozzii* Forsyth Major, Untermassfeld. – **a–d** Juvenile mandible IQW 1980/16 539 (Mei. 16 060) with left and right DI$_1$-DI$_2$, germ of I$_3$, DP$_2$-M$_1$, right occlusal, left occlusal, left lateral, right lateral views. – Scale: 30 mm.

	IQW 1980/16 539 (Mei. 16 060)	IQW 1984/20 309 (Mei. 19 829) + IQW 1984/20 310 (Mei. 19 830)
DI_1 MDD	3.4	
DI_1 LLD	6.7	
DI_2 MDD	4.3	
DI_2 LLD	8.2	
DP_2 L	11.2	
DP_2 Wm	3.7	
DP_2 Wd	4.7	
DP_3 L	12.7	
DP_3 Wm	5.1	
DP_3 Wd	6.1	
DP_4 L	21.8	
DP_4 Wm	8.3	
DP_4 Wd	9.0	
DP_4 Wt	10.6	
P_2 L		14.0
P_2 Wm		5.7
P_2 Wd		6.3
P_3 Wd		9.7
P_4 L		15.8
P_4 Wm		10.3
P_4 Wd		12.4
M_1 L	20.2	17.6
M_1 Wm	13.0	12.7
M_1 Wd	14.5	14.6
DP_2-DP_4	45.5	
ID-MP	54.6	
WMM_1	22.3	

Table 2 - *Sus strozzii* Forsyth Major, measurements (mm) of mandibles and lower teeth, Untermassfeld. For abbreviations see section 2.

6.3.2. Dentition

6.3.2.1. Deciduous dentition

Some deciduous teeth are preserved in the cranium IQW 1985/20 509 (Mei. 20 028) (Figure 1) and in the mandible IQW 1980/16 539 (Mei. 16 060) (Figure 2). DI^{1-2}/DI_{1-2} are similar to but smaller than their respective successional tooth. Unfortunately, they are severely worn, and hence details of crown morphology are not observable. DI^3 is a small peg with an oval occlusal outline. Its root is implanted in the premaxilla at an angle opposite to that of the other incisors, i.e., projecting distally rather than mesially.

DP^2 has a prominent central cusp, which separates two lower areas. The disto-lingual side of the tooth is enlarged and hosts a protocone. DP^3 is severely worn but preserves a characteristic piriform shape in occlusal view, with a separation between the mesial and distal sides of the tooth less marked than that of DP^2. DP^4 has a bilobed structure like that of a permanent molar, but its mesial side is oblique rather than perpendicular to the major axis of the tooth. DP_2 has a structure similar to that of P_2 but appears smaller and slenderer. DP_3 is severely worn. DP_4 is a trilobate tooth whose lobes are arranged in an opposite dimensional sorting than that of M_3, i.e., the mesial lobe is the narrowest and the distal lobe is the widest.

Data on deciduous dentition are in most cases too limited to provide useful comparative information, and Untermassfeld teeth are also severely worn. Nonetheless, in a study focused on DP_4 Iannucci et al. (2020a) recognised biometric differences between *S. scrofa* and *S. strozzii* comparable to those observable in the permanent dentition, i.e., with *S. strozzii* possessing proportionally wider teeth than those of *S. scrofa*. On that occasion Untermassfeld suids were treated as fossil *S. scrofa*, following Guérin and Faure (1997), but resulted outliers due to their large DP_4 Wm.

6.3.2.2. Upper permanent dentition

Isolated suid teeth from Untermassfeld are solely represented by permanent teeth and include several incisors and canines, and a few premolars and molars (Figure 3, Tables 3–5). Upper incisors comprise a I^1, IQW 1986/21 130 (Mei. 20 749) (Guérin and Faure 1997, fig. 5, pl. 67) and a I^2, IQW 1984/20

307 (Mei. 19 827) (Figure 3a). I^1 is covered by a cingulum-like development of the enamel along the border of its occlusal area, apart from the mesio-lingual portion. The cingulum is particularly pronounced on the disto-lingual portion, which is also its lowest point below the occlusal level. In I^2 the lingual cingulum develops in parallel to the mesio-distal axis and covers about two-thirds of the length of the tooth. The cingulum is clearly on a lower plane than the rest of the incisor. The labial side of I^2 hosts a series of three protruding structures and an elevated distal ridge. Being unworn, the tooth appears very elongated. A small opening in the premaxilla of IQW 1985/20 509 (Mei. 20 028), distal to DI^3, reveals the presence of a unerupted I^3, but its morphology is not observable (Figure 1a–c). I^3 is present in *S. scrofa*, while in *S. strozzii* it has only been observed in a subadult from Senèze (NMB Se. 1775) but not in several adults of the species (Azzaroli 1952; Iannucci et al. 2020a).

P^1 is preserved on both sides of the cranium IQW 1985/20 509 (Mei. 20 028) and also represented by an isolated specimen in a slightly more advanced stage of wear, IQW 1984/19 978 (Mei. 19 498) (Figure 3b–b''). P^1 has a main prominent central cusp, the paracone, and two lower areas hosting a paraprecrista (mesially) and a metacone (distally). Two well-separated roots develop below these areas. A small structure is present on the disto-lingual side (a potential protocone), more evident in IQW 1984/19 978 (Mei. 19 498) than in IQW 1985/20 509 (Mei. 20 028). In IQW 1985/20 509 (Mei. 20 028) there is no diastema between P^1 and DP^2. IQW 1985/20 709 (Mei. 20 228) comprises left and right germs of P^3 and P^4 of the same individual (Figure 3c–f). P^3 are apparently not fully formed and not very informative. P^4 has a trapezoidal occlusal outline, with the mesial side oblique to the mesio-distal axis of the tooth. There are three prominent cusps, protocone (lingually), paracone (mesio-labially), and metacone (disto-labially). A protofossa separates the protocone from the metacone, but mesially the profossa is filled by accessory developments of protocone and paracone.

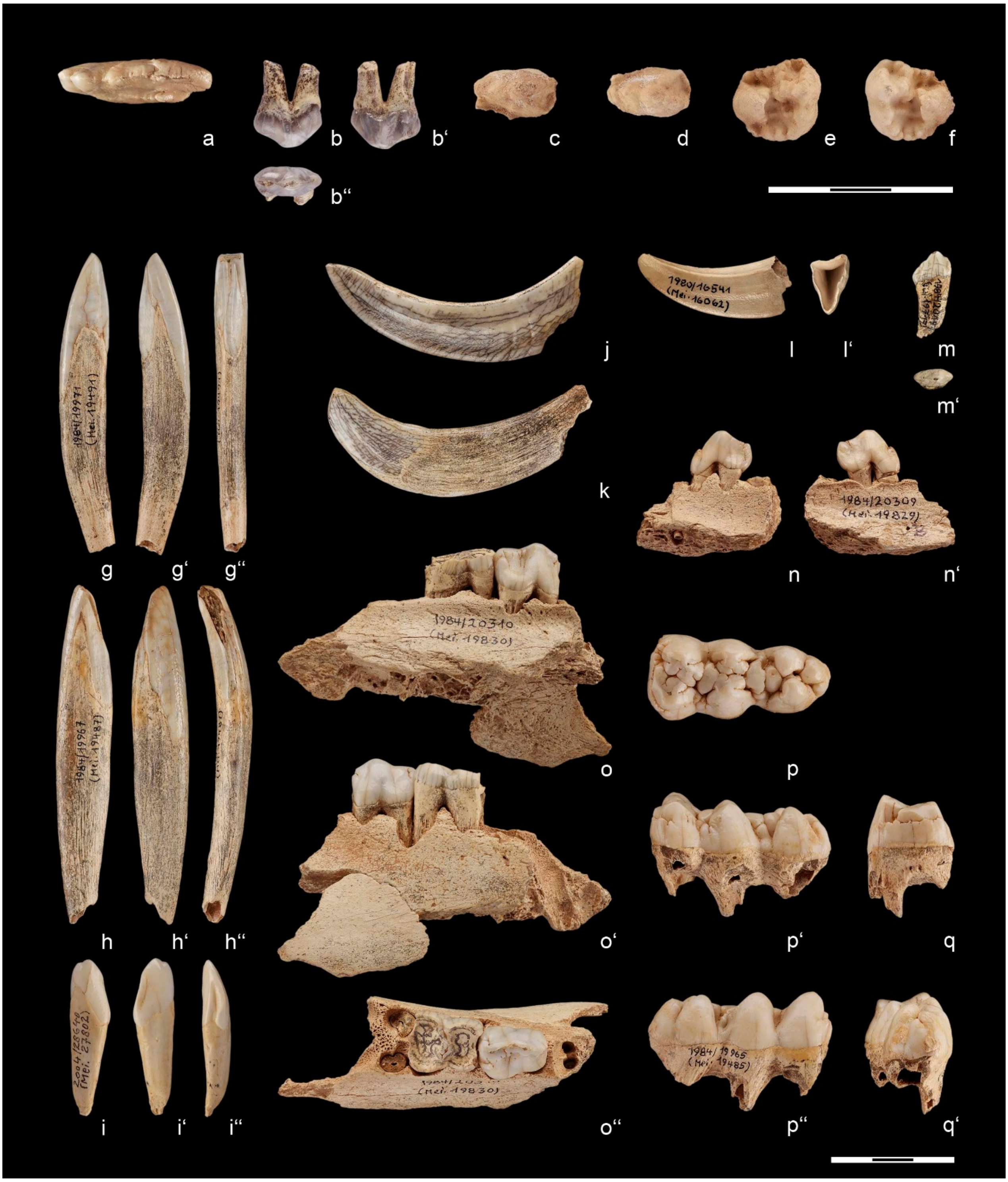

Figure 3 - *Sus strozzii* Forsyth Major, Untermassfeld. – **a** Left I^2 IQW 1984/20 307 (Mei. 19 827). – **b–b’’** Right P^1 IQW 1984/19 978 (Mei. 19 498). – **c** Germ of left P^3 IQW 1985/20 709 (Mei. 20 228). – **d** Germ of right P^3 IQW 1985/20 709 (Mei. 20 228). – **e** Germ of left P^4 IQW 1985/20 709 (Mei. 20 228). – **f** Germ of right P^4 IQW 1985/20 709 (Mei. 20 228). – **g–g’’** Left I_1 IQW 1984/19 971 (Mei. 19 491). – **h–h’’** Right I_2 IQW 1984/19 967 (Mei. 19 487). – **i–i’’** Right I_3 IQW 2004/28 640 (Mei. 27 802). – **j** Right C_m IQW 1984/20 299 (Mei. 19 819). – **k** Right C_f IQW 1984/19 966 (Mei. 19 486). – **l–l’** Left C_m IQW 1980/16 541 (Mei. 16 062). – **m–m’** Left P_1 IQW 1984/20 197 (Mei. 19 717). – **n–n’** Right P_2 IQW 1984/20 309 (Mei. 19 829). –

o–o'' Right hemimandible fragment with P_4-M_1 IQW 1984/20 310 (Mei. 19 830). – **p–q'** Left M_3 IQW 1984/19 965 (Mei. 19 485). – **a**, **b''**, **c**, **d**, **e**, **f**, **m'**, **o''**, **p** occlusal views; **b**, **l**, **n'**, **o**, **p'** labial views; **b'**, **g''**, **h''**, **i''**, **j**, **k**, **m**, **n**, **o'**, **p''** lingual views; **g**, **h'**, **i'**, **q'** distal views, **g'**, **h**, **i**, **q** mesial views; **l'** cross-section view. – Scale: 30 mm.

M^1 is preserved on both sides of the cranium IQW 1985/20 509 (Mei. 20 028). It is a bilobed tooth with four principal cusps and several crests that depart from them, resulting in a folded enamel pattern (Figure 1a–b). Both germs of M^2 are also present in IQW 1985/20 509 (Mei. 20 028). Apart from their wrinkled (unworn) enamel and minor differences in the development of the cingula, they only differ in size from M^1.

	Tooth	MDD	LLD
IQW 1986/21 130 (Mei. 20 749)	I^1		c. 8.0
IQW 1984/20 307 (Mei. 19 827)	I^2	24.7	7.2
IQW 1984/19 964 (Mei. 19 484)	I_1	6.4	9.7
IQW 1984/19 971 (Mei. 19 491)	I_1	6.9	11.8
IQW 1984/19 972 (Mei. 19 492)	I_1	6.5	11.1
IQW 1984/19 974 (Mei. 19 494)	I_1	6.3	11.0
IQW 1984/19 976 (Mei. 19 496)	I_1	6.0	10.4
IQW 1984/19 967 (Mei. 19 487)	I_2	7.3	13.1
IQW 1984/19 968 (Mei. 19 488)	I_2	7.5	12.9
IQW 1984/19 973 (Mei. 19 493)	I_2	8.2	14.2
IQW 1984/19 975 (Mei. 19 495)	I_2	8.9	13.9
IQW 1984/20 194 (Mei. 19 714)	I_3	17.2	6.0
IQW 1984/20 308 (Mei. 19 828)	I_3	17.4	6.2
IQW 2004/28 640 (Mei. 27 802)	I_3	17.2	6.5

Table 3 - *Sus strozzii* Forsyth Major, measurements (mm) of incisors, Untermassfeld. For abbreviations see section 2.

6.3.2.3. Lower permanent dentition

Lower incisors are relatively abundant (Figure 3g–i'', Table 3). In lingual view I_1 is an elongated tooth with a central ridge (endocristid) separating two lower areas (Figure 3g–g''). The cementoenamel junction is closer to the tip of the crown on the mesial side than on the distal side. I_2 has a similar basic structure, but it is markedly asymmetric in lingual view, with an internal (mesial) concavity (Figure 3h–h''). I_3 is a much smaller tooth with a low and asymmetric crown (Figure 3i–i''). The endocristid is relatively prominent and shifted distally, but clearly separated from the distal side by a groove. In *S. scrofa* the tooth is even more asymmetric and usually lacks prominent ridges. In typical *S. strozzii* I_3 is a stouter tooth with marked ridges, and other lower incisors are larger.

In addition to IQW 1984/19 622 (Mei. 19 492) + IQW 1984/19 970 (Mei. 19 490), already described by Guérin and Faure (1997, figs. 1–2, pl. 66) and rediscussed by Cherin et al. (2020, fig. 11), there are several C_m (Figure 3j, l–l', Table 4). Some specimens are small because they belong to subadults or juveniles, but even in the latter case the section is clearly verrucosic, excluding an attribution to *S. scrofa* (Figure 3l'). There is also a C_f, IQW 1984/19 966 (Mei. 19 486), in which the lateral facets are almost equal in length while the distal side is substantially smaller (Figure 3k). Unlike C_m, C_f has a properly developed root, and the distal side of the canine is covered by enamel and engraved by a groove.

	Tooth	cLi	cLa	cD
IQW 1980/16 541 (Mei. 16 062)	C_m	14.8	13.1	8.3
IQW 1984/19 622 (Mei. 19 492) + IQW 1984/19 970 (Mei. 19 490)	C_m	21.6	19.8	13.9
IQW 1984/20 192 (Mei. 19 712)	C_m	23.9	22.2	15.7
IQW 1984/20 193 (Mei. 19 713)	C_m	16.4	14.3	11.6
IQW 1984/20 299 (Mei. 19 819)	C_m	16.6	15.4	12.2
IQW 1984/19 966 (Mei. 19 486)	C_f	15.1	15.1	6.4

Table 4 - *Sus strozzii* Forsyth Major, measurements (mm) of lower canines, Untermassfeld. For abbreviations see section 2.

In the preserved P_1 IQW 1984/20 197 (Mei. 19 717) the main cuspid is shifted mesially, giving an asymmetric appearance to the tooth (Figure 3m–m'). In this specimen there is only one root, while the P_1 alveolus present in IQW 1980/16 539 (Mei. 16 060) has a small occlusal notch and below it only one opening in the bone, suggesting that two partly fused roots were present (Figure 2a–b). The absence of partly separated roots in IQW 1984/20 197 (Mei. 19 717) seems related to a reduction in size in comparison to P_1 of typical *S. strozzii*, observable in other Epivillafranchian samples as well (Bona and Sala 2016; Cherin et al. 2020). The remaining permanent premolars are observable in IQW 1984/20 309 (Mei. 19 829) and IQW 1984/20 310 (Mei. 19 830), which are part of an adult mandible preserved in several detached fragments that were recovered in close proximity from each other (from grid square Q 337, 1.07 m below site 0-level; Kahlke 2020; Kahlke et al. 2020). In lateral views P_2 is a triangular tooth with a high central cuspid and a mesial side lower than the distal side (Figure 3n–n'). This tooth appears more elongated and slenderer than that of typical *S. strozzii*, although not at the level observed in extant *S. scrofa*. An elongated P_2 is also present in other Epivillafranchian samples (Bona and Sala 2016; Cherin et al. 2020). Only a not very informative distal fragment of P_3 is present. P_4 is preserved on both sides. Its crown has a trenchant morphology, with the main cuspids approximately aligned along the same mesio-distal axis, and high mesial and distal sides (Figure 3o–o''). The tooth is wide, especially the distal lobe.

M_1 has a squared occlusal outline but it is severely worn, to the extent that its mesial side is concave (Figure 3o''). In the mandible IQW 1980/16 539 (Mei. 16 060) M_1 is well preserved (Figure 2a–b). Its structure is similar to M^1 but differs in several details. M_1 is more elongated and symmetric along the mesio-distal axis, the notch between the two lobes is more pronounced on the labial side, the distal lobe is clearly wider than the mesial, and in each lobe the lingual cuspid is the highest above the occlusal level. M_3 is represented by a fragment of the distal lobe, IQW 1984/19 793 (Mei. 19 313), and a complete specimen, IQW 1984/19 965 (Mei. 19 485) (Figure 3p–q'). M_3 is a trilobate tooth in which the mesial lobe is the widest. Cuspids that develop distally to the second lobe are rounded, as the enamel is not folded. The third lobe, separated from the second by a pronounced constriction, hosts five cuspids of relatively large size and two smaller cusplets. The first two large cuspids (mesially) are aligned along the same sagittal axis. This couple is pragmatically considered here a subdivided pentapreconulid because it would have been likely impossible to recognise two separate forms, had the tooth been in a more advanced stage of wear. The other cuspids are named topographically according to van der Made (1996), although the homology of these structures is not clear. There is a small pentaectoconulid on the labial side of the pentapreconulid, pentaconid and hexaconid are oriented transversally to the main axis of the tooth, and heptaconid and octaconid are also present. The pronounced notch of the third lobe is also present on M_3 from Frantoio (Bona and Sala 2016) and Le Vallonnet (Cherin et al. 2020), but not in typical *S. strozzii* (housed in IGF, MANA, MPM, NMB; pers. obs., N = 28). In general, Epivillafranchian samples have relatively slenderer M_3 than that of typical *S. strozzii*. In *S. scrofa* M_3 is extremely variable in size and morphology of the distal complex (e.g., Iannucci et al. 2020b; Cherin et al. 2020), and hence resemblances or differences should be considered with caution.

	Tooth	L	Wm	Wd	Wt
IQW 1984/19 978 (Mei. 19 498)	P^1	10.9	5.1		
IQW 1984/20 197 (Mei. 19 717)	P_1	9.8	4.3		
IQW 1980/16 527 (Mei. 16 048)	P_4		11.1		
IQW 1984/19 793 (Mei. 19 313)	M_3				> 12.3
IQW 1984/19 965 (Mei. 19 485)	M_3	44.8	20.9	19.4	16.4

Table 5 - *Sus strozzii* Forsyth Major, measurements (mm) of premolars and molars, Untermassfeld. For abbreviations see section 2.

6.3.3. Postcranial material

IQW 1984/20 212 (Mei. 19 732) is an almost complete atlas, only the right wing is slightly damaged (Figure 4). A narrowing partly divides the vertebral foramen into two halves. The ventral half is approximately circular, while the dorsal half is elongated laterally. In dorsal view, the tuberculum is placed in the middle of the bone and the alar foramina are elliptic and diagonally elongated. In ventral view, the atlantal fossae are deep and their medial margins develop slightly beyond the lateral edges of the cranial and caudal articulations. In general, the morphology is similar to that of *S. scrofa* apart from the alar foramina, which in the wild boar tend to be more circular and are often partly subdivided by a small notch. In the latter feature IQW 1984/20 212 (Mei. 19 732) more closely resembles *S. strozzii*, but other traits differ, including the position of the dorsal tuberculum and the shape of the vertebral foramen (Azzaroli 1952). The atlas of *S. scrofa* is polymorphic in its proportions, in the relative positioning of the dorsal tuberculum, and in the depth of the atlantal fossae (Azzaroli 1952; pers. obs.).

IQW 1984/19 927 (Mei. 19 447) is a right fragmentary tibia lacking the proximal epiphysis (Figure 5). The stoutness and curvature of the diaphysis, as well as the outline of the distal epiphysis are characteristic of a suid.

Figure 4 - *Sus strozzii* Forsyth Major, Untermassfeld. – **a–d** Atlas IQW 1984/20 212 (Mei. 19 732), cranial, dorsal, caudal, ventral views. – Scale: 30 mm.

Figure 5 - *Sus strozzii* Forsyth Major, Untermassfeld. – **a–e** Right tibia, distal fragment IQW 1984/19 927 (Mei. 19 447), anterior, external, posterior, internal, distal views. – Scale: 30 mm.

6.4. Discussion and conclusions

Untermassfeld suids have long been regarded as the earliest fossil evidence of the wild boar (Guérin and Faure 1997), but the presence of several verrucosic C_m excludes an attribution to *S. scrofa* and best fits with an assignment to *S. strozzii* (Cherin et al. 2020). In general, suid teeth from Untermassfeld, especially premolars, appear proportionally wider than those of *S. scrofa*, also differing in related morphological features (e.g., greater development of the hypoconid in lower premolars). The presence of relatively wide teeth is characteristic of *S. strozzii* (van der Made and Moyà-Solà 1989; Iannucci et al. 2021a), often useful for discriminating it from *S. scrofa* (van der Made 1998; Iannucci et al. 2020a). On the other hand, Untermassfeld suids deviate from typical *S.*

strozzii in some respects, with differences in the morphology of P_1, P_2, and M_3 which are consistently observed in other Epivillafranchian samples. Further research, discovery, and description of new material will likely identify other diverging features and provide more robust support for those recognised herein.

It is tempting to envision biochronological and palaeoecological implications for the observed morphological differences, but at the moment it is not possible to evaluate whether these traits emerged abruptly in Epivillafranchian populations or were the result of gradual changes not documented in the scanty post-Olduvai to pre-Jaramillo (~1.8–1.2 Ma) European suid record. In any case, while it is undeniable that suid fossils have not been recovered from several European localities dated between ~1.8 and 1.2 Ma (Martínez-Navarro et al. 2015), there are some remains that could fill this apparent gap (van der Made et al. 2017). Moreover, the unequal geographical distribution of Late Villafranchian palaeontological sites dated ~1.8–1.2 Ma does not allow to rule out the possibility that suid populations survived in scarcely sampled areas (e.g., France and Germany).

It also remains to be answered what role played the dispersal of new suid populations from Asia, whose systematic placement is controverse. In fact, despite expressing divergent taxonomic opinions, several authors agreed in interpreting Epivillafranchian suids as the likely arrival of new populations (Martínez-Navarro et al. 2015; van der Made et al. 2017; Cherin et al. 2020). A direct link was proposed by Moullé et al. (2006), who regarded Le Vallonnet suids as closely related to *Sus lydekkeri* Zdansky, 1928, defined from the Peking Man Site at Zhoukoudian. *Sus lydekkeri* has been considered a chronosubspecies of the extant wild boar, i.e., *S. scrofa lydekkeri* (Fujita et al. 2000), a geographical variant of *S. strozzii* (Dong 2008; Dong et al. 2013), or a valid and distinct suid species (Liu et al. 2017). These divergent opinions probably reflect the heterogeneous nature of the hypodigm of *S. lydekkeri* (Cherin et al. 2020). To clarify this issue an in-depth revision of *S. lydekkeri* and other Early Pleistocene Asian *Sus* species of comparable size (see e.g., Fujita et al. 2000; Liu et al. 2017) would be needed, but it is conceivable that some remains ascribed to *S. lydekkeri* are indeed related to *S.*

strozzii (see e.g., Dong et al. 2013, fig. 4D), and hence the dispersal of Asian populations does not necessarily imply a species replacement.

In referring Untermassfeld suids to *S. scrofa priscus* Guérin and Faure (1997) crowned an evolutionary hypothesis according to which earlier representatives of the extant wild boar would have been characterised by low molar complexity (mainly in third molars) and large size (Hünermann 1965, 1969, 1975; Faure and Guérin 1983; Guérin and Faure 1997), but the existence of progressive trends in the evolution of these features is now challenged by several studies (Lister et al. 2010; Iannucci et al. 2020b). For instance, *S. scrofa* remains from the early Middle Pleistocene of Mosbach 2 are on average smaller than those recovered from the Late Pleistocene of Taubach (Küthe 1933; Hünermann 1977; pers. obs.). These considerations do not argue against the potential importance of biometric or morphological changes in Quaternary suids but should push to analyse large samples and adopt quantitative approaches to evaluate the biological significance of the observed differences. Untermassfeld suids do not belong to *S. scrofa*, and the arrival of the wild boar into Europe does not characterise Epivillafranchian faunas since ~1.2 Ma. The wild boar dispersal into Europe probably occurred close to the Early-Middle Pleistocene boundary (van der Made et al. 2017; Cherin et al. 2020), in a period of marked environmental and faunal changes (Kahlke et al. 2011; Head and Gibbard 2015; Iannucci et al. 2021b). As for example evidenced by the impressive increase of wild boar populations in Europe over the last decades, *S. scrofa* is an extremely adaptable species, capable of coping with and taking advantage of environmental disturbances (Massei et al. 2015; Vetter et al. 2015). From this perspective, the *S. strozzii*-*S. scrofa* replacement was an important bioevent, representative of the faunal turnover occurred in Europe between the latest Early and early Middle Pleistocene.

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7. Paper 6

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

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Abstract

The Ponte Galeria area within the city of Rome has yielded numerous fossiliferous localities that represent a reference point for the study of the European Middle Pleistocene ecosystems. Within Ponte Galeria a rich collection of fossil mammals has been unearthed from Cava di Breccia – Casal Selce 2 (MIS 15) thus the site represents an optimal laboratory to investigate the palaeoenvironments of a defined territory during the Middle Pleistocene. We investigate the feeding behaviours of the ungulate community of Cava di Breccia – Casal Selce 2 to reconstruct the MIS 15 habitats and also compare the data with those of the nearby site of Fontana Ranuccio (MIS 11) which shares similar faunal composition with Cava di Breccia – Casal Selce 2 to test if ungulates occupied the same niches during two different interglacials. Open habitats with scattered woodlands characterised the Ponte Galeria area during MIS 15, whereas woodlands were more widespread during MIS 11 at Fontana Ranuccio. Ungulates display similar diets in both localities, suggesting that cervids, large bovids and equids adopted the same niche partitioning strategies during both interglacials.

Keywords: palaeoecology, Artiodactyla, Perissodactyla, mesowear, hypsodonty, early Middle Pleistocene transition

7.1. Introduction

The last major phase in the trend towards more intensive global glaciations, known as 'Early-Middle Pleistocene Transition' (EMPT), began about 1.2 Ma and persisted for more than 600 ka (Head and Gibbard 2015). The EMPT was marked by a prolongation and intensification of glacial–interglacial climate cycles from 41 ka to approximately 85–125 ka (Lisiecki and Raymo 2005, 2007) and the consequent sharpening of the contrast between warm and cold periods. Vegetation and terrestrial mammal communities of Europe experienced significant changes during the EMPT due to the increase of both seasonality and aridity in the Northern Hemisphere, though the effects were probably milder in the Mediterranean area (Suc and Popescu 2005; Kahlke et al. 2011; Magri and Palombo 2013). MIS 16 and MIS 12 were particularly severe glacials and, together with MIS 22, among the most extreme of the Pleistocene (Head and Gibbard 2015). The following interglacial periods were also characterised by some remarkable conditions (e.g., Strani et al. 2019a) with MIS 11 being the longest and warmest interglacial recorded in the last 0.4 Ma (Head and Gibbard 2015).

The fossiliferous deposits discovered during the second half of the 20th century in the surroundings of the city of Rome and the nearby Anagni Basin (Lazio, central Italian Peninsula) have been considered as a reference point for the biochronological and ecological study of the European Middle Pleistocene palaeocommunities. The Mammal Ages Galerian (Middle Pleistocene, ~800-400 Ka) and Aurelian (late Middle Pleistocene – Late Pleistocene, ~350-10 Ka) take their names from different fossil mammal assemblages discovered in the Ponte Galeria area and along 'Via Aurelia' state road, respectively (Gliozzi et al. 1997, Bellucci et al. 2015 and references therein). Cava di Breccia – Casal Selce 2 (CS2) (MIS 15, referred as Casal Selce Upper Level in Marra et al. 2014) (Figure 1) is one of the richest assemblages of the Ponte Galeria area, having yielded more than 300 mammal remains. The last Faunal Unit of the Galerian (Fontana Ranuccio FU) has been defined by Gliozzi et al. (1997) from the fossil mammal assemblage of Fontana Ranuccio (Anagni Basin). This site, located around 65 km east of CS2, is dated at 0.4 Ma (MIS 11) and while sharing a similar faunal composition with

CS2 yielded numerous bone and stone artefacts associated with human remains (Rubini et al. 2014; Pereira et al. 2018).

The reconstruction of the feeding behaviours of primary consumers is a common and well-tested method to investigate palaeoenvironmental conditions in those localities where vegetational information (e.g., palynological data) are not available (e.g., Kaiser and Rössner 2007: DeMiguel et al. 2011; Strani et al. 2015; Yamada et al. 2016). In particular, herbivorous ungulate taxa, being generally widespread and well-represented in fossil mammal assemblages can provide crucial data on type of vegetation and habitat, plant resource availability, niche occupation and other ecological parameters (DeMiguel et al. 2010). Here we examined the dietary behaviours of the herbivorous ungulates from CS2 in the Ponte Galeria area (MIS 15). Comparing the obtained results with those of the archaeo-palaeontological site of Fontana Ranuccio (Anagni Basin) (MIS 11), we investigate the evolution of palaeoenvironmental settings of central Italian Peninsula following two of the most intense glacials (MIS 16 and MIS 12) of the EMPT. We also test if different samples of related fossil ungulate taxa displayed the same ecological adaptations during these interglacials.

7.1.1. Ponte Galeria area

The Ponte Galeria area is set along the Latium Tyrrhenian margin and experienced extensional tectonic processes since the Late Miocene due to the opening of the Tyrrhenian basin that triggered intense volcanic activity culminating during the Middle-Late Pleistocene. This area hosted the inner delta of the Tiber River since the beginning of the Middle Pleistocene, allowing the deposition of a series of fluvial–lacustrine sedimentary successions controlled by the strong interconnection among the glacioeustatic sea-level fluctuations related to Quaternary climatic changes, volcanic activity and tectonic uplift of the Latium Tyrrhenian margin (Palombo and Milli 2011). Conato et al. (1980) carried out a pioneering work, subdividing the Pleistocene succession cropping out in this area into informal lithostratigraphic units ranging in age from the latest Early Pleistocene to the late Middle

Pleistocene, which were named, from the oldest to the youngest, Monte Mario Formation (Early Pleistocene, 'Calabrian'), and Ponte Galeria, S. Cosimato, Aurelia and Vitinia Formations (Middle Pleistocene) (Palombo and Milli 2011).

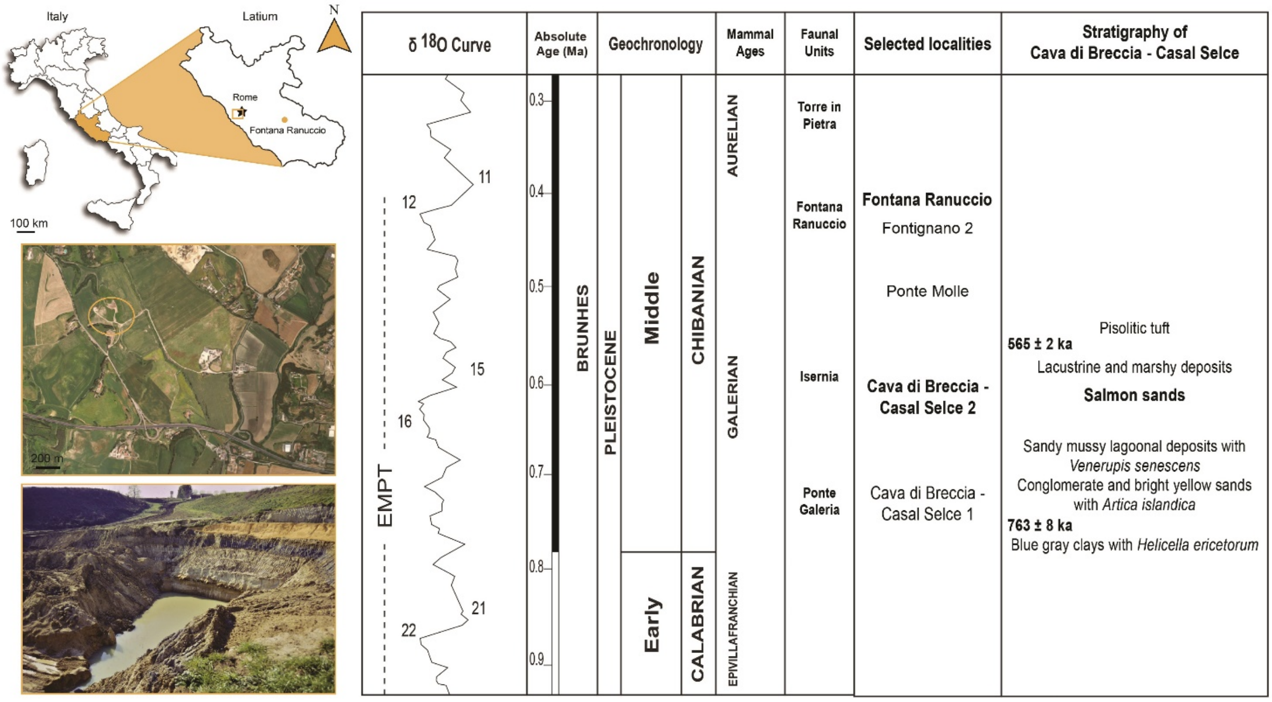

Figure 1 - Location and geochronological setting of Cava di Breccia – Casal Selce 2 (with focus on its position) and Fontana Ranuccio. Data from: Gliozzi et al. (1997); Milli and Palombo (2005); Palombo and Milli (2010); Sardella and Petrucci (2012); Marra et al. (2014); Sardella et al. (2015); Pereira et al. (2018); Iannucci et al. (2021).

Additional works (Milli and Palombo 2005; Marra et al. 2014; Sardella et al. 2015 and references therein) focused on calibrating the different mammal assemblages collected in this area and several authors (e.g., Blanc et al. 1951; Ambrosetti 1965, 1967; Caloi and Palombo 1978; Caloi et al. 1980a, 1980b, 1980c; Capasso Barbato et al. 1983; Petronio and Sardella 1998, 1999) refined the biochronological and Middle Pleistocene paleobiogeographic framework for the Italian Peninsula.

The fossil sample found at Casal Selce, along the via Aurelia (Rome), was recovered in a quarry called Cava di Breccia (Petronio and Sardella 1999; Sardella and Petrucci 2012). The 40 m thick sedimentary sequence exposed in the quarry consists, from bottom to top, of: (a) fluvial conglomerates, (b) blue-grey clays with *Helicella ericetorum*, (c) beach conglomerates with sandy lens and levels with fragmented remains of *Arctica islandica* (d) pebble gravels and sands with cross laminations, (e) sandy-muddy lagoonal deposits with *Venerupis senescens*; (f) salmon sands, (g) lacustrine and marshy deposits (h) volcanoclastic materials. These levels were studied by Milli et al. (2004) and Milli and Palombo (2005), which referred them to the Ponte Galeria Sequence (PGS): a + b + c = PG1; d + e = PG2; f + g = PG3; h = PG3 and PG4.

Mammal fossils were found in two different levels, d and f. The lower faunal assemblage, which also includes one of the first occurrences of *Crocuta crocuta* in Europe (Sardella and Petrucci 2012), has been chronologically referred to the early Middle Pleistocene (between 763 ± 8 ka and ca. 700 ka). Based on this mammal assemblage, together with other fossils recovered from the deposits outcropping in the Ponte Galeria area, Petronio and Sardella (1998) defined a new biochronologic unit, the Ponte Galeria Faunal Unit.

Mammal remains collected from level f were referred to the Isernia FU due to the occurrence of *Arvicola mosbachensis* (= *Arvicola cantianus*) (Petronio and Sardella 2001) and correlated with the Santa Cecilia formation dated between 615 ± 3 ka and 565 ± 2 ka (Karner and Marra 1998) with pumice falls intercalated within the sand deposits from which the faunal assemblage was recovered yielding an age of 611 ± 6 ka (Marra et al. 2014).

7.1.2. Anagni Basin

The intermontane Anagni Basin developed between the Late Pliocene and the early Middle Pleistocene (Galadini and Messina 2004). Many rich vertebrate fossil sites are located in this area, spanning from the Early Pleistocene (Coste San Giacomo) to the Middle Pleistocene (Colle Marino, Fontana Ranuccio) (Segre Naldini et al. 2009; Bellucci et al. 2012; Strani et al. 2015; Strani 2020; Strani et al. 2018a and Florindo et al. 2021). The site of Fontana Ranuccio was discovered in the 1970s, following different surveys carried out by the Italian Institute of Human Palaeontology (IsIPU) and a large number of archaeological artefacts (>100) and fossil remains (>25,000) were unearthed alongside four human teeth (Cassoli and Naldini 1984; Segre and Ascenzi 1984; Rubini et al. 2014; Strani et al. 2018b; Grimaldi et al. 2020; Bona and Strani 2021). The archaeo-palaeontological layer that yielded *Homo* teeth has been recently dated by ^{40}Ar/^{39}Ar to around 0.4 Ma (Pereira et al. 2018). This site thus records the climatic transition of the 'Mid-Brunhes Event' (MIS 12–11) with the consolidation of the EMPT (Head and Gibbard 2015).

7.2. Materials and methods

The fossil materials from CS2 (catalogue number CS-, 380 remains) are housed at the PaleoFactory laboratory of the Department of Earth Sciences of Sapienza University of Rome (Table 1) (Figure 2). The CS2 mammal assemblage consists of 16 taxa (Table 1), although some taxonomical attributions are still uncertain due to the lack of a formal description of the material (Marra et al. 2014, 2015; Sardella et al. 2015): *Cervus elaphus* (referred as *C. e. acoronatus* in Marra et al. 2014), *Dama* sp. (referred as *Axis eurygonos* in Marra et al. 2014), *Praemegaceros* sp., *Capreolus* sp., a large Bovidae indet. (referred as *Bison* cf. *B. schoetensacki* in Marra et al. 2014), *Equus* cf. *E. altidens* (referred as *E. altidens* Marra et al. 2014), *Equus* cf. *E. mosbachensis* (referred as *E. sussembornensis* Marra et al. 2014), *Stephanorhinus* sp., *Hippopotamus antiquus, Sus scrofa* (referred as *S. s. priscus* in Marra et al. 2014), Elephantidae indet., *Macaca sylvanus, Canis* sp., *Meles meles, Vulpes* sp., *Lynx pardinus* (referred as *Lynx pardina spelaea* in Marra et al. 2014). The sole exception is represented by the badger remains recently studied and attributed to *Meles meles* (Mecozzi 2021). Cervids are the best represented group (52% of total specimens) (Table 1) followed by equids (11.6%) and the wild boar *S. scrofa* (11%) (Table 1). Elephants (3.8%), rhinos (2.1%) and hippos (3.5%) as well as carnivorans (3.2%) are poorly documented (Table 1). Dental and postcranial remains of *Macaca sylvanus* (3.7%) represent one of the few Pleistocene record of the Barbary macaque in the Italian Peninsula (Table 1).

	***Stephanorhinus* sp.**	**Elephantidae**	***Sus scrofa***	***Hippopotamus antiquus***	**Bovidae indet.**	***Praemagaceros* sp.**	***Cervus elaphus***	***Dama* sp.**	***Capreoulus* sp.**	***Equus* cf. *altidens***	***Equus* cf. *mosbachensis***	***Macaca sylvanus***	***Canis* sp.**	***Vulpes* sp.**	***Lynx pardinus***	***Meles meles***	**Total**
Antler							3	1									
Corn					1												
Tusk		13															
Cranium			1	1	1		1				1		1			3	
Upper tooth			4	1	6	2	30	4		1	11	5		1		1	
Mandible			2				5					1				4	
Lower tooth			19	2	3		20	7	2	2	6	7					
Tooth fragment	3			8													
Scapula							5	6		1	1						
Humerus			1		3		8								1		
Radius	1		2				7	6		2	2						
Ulna			1		6		3	1				1					
Metacarpal	1		3				5	2									
Carpal			1		2		12				1						
Vertebra		1	1		3					1							
Femur			1	1	2		2	2									
Patella										1							
Tibia			1				8	3							1		
Malleolar bone							1										
Metatarsal	1				1		5	2		1	2						
Metapodial					1		5	2		1							
Talus							3	2		1							
Calcaneous	1						7	1		1	1						
Tarsal	1				1		3				2						
I Phalange			3		2		10	4			1						
II Phalange					3		7	2			2						
III Phalange			1								2						
Total	**8**	**14**	**41**	**13**	**35**	**2**	**150**	**45**	**2**	**12**	**32**	**14**	**1**	**1**	**2**	**8**	**380**
%	**2.1**	**3.8**	**11**	**3.5**	**9.2**	**0.5**	**39**	**12**	**0.5**	**3.1**	**8.5**	**3.8**	**0.2**	**0.2**	**0.5**	**2.1**	**100**

Table 1 - List of the mammal taxa remains from CS2.

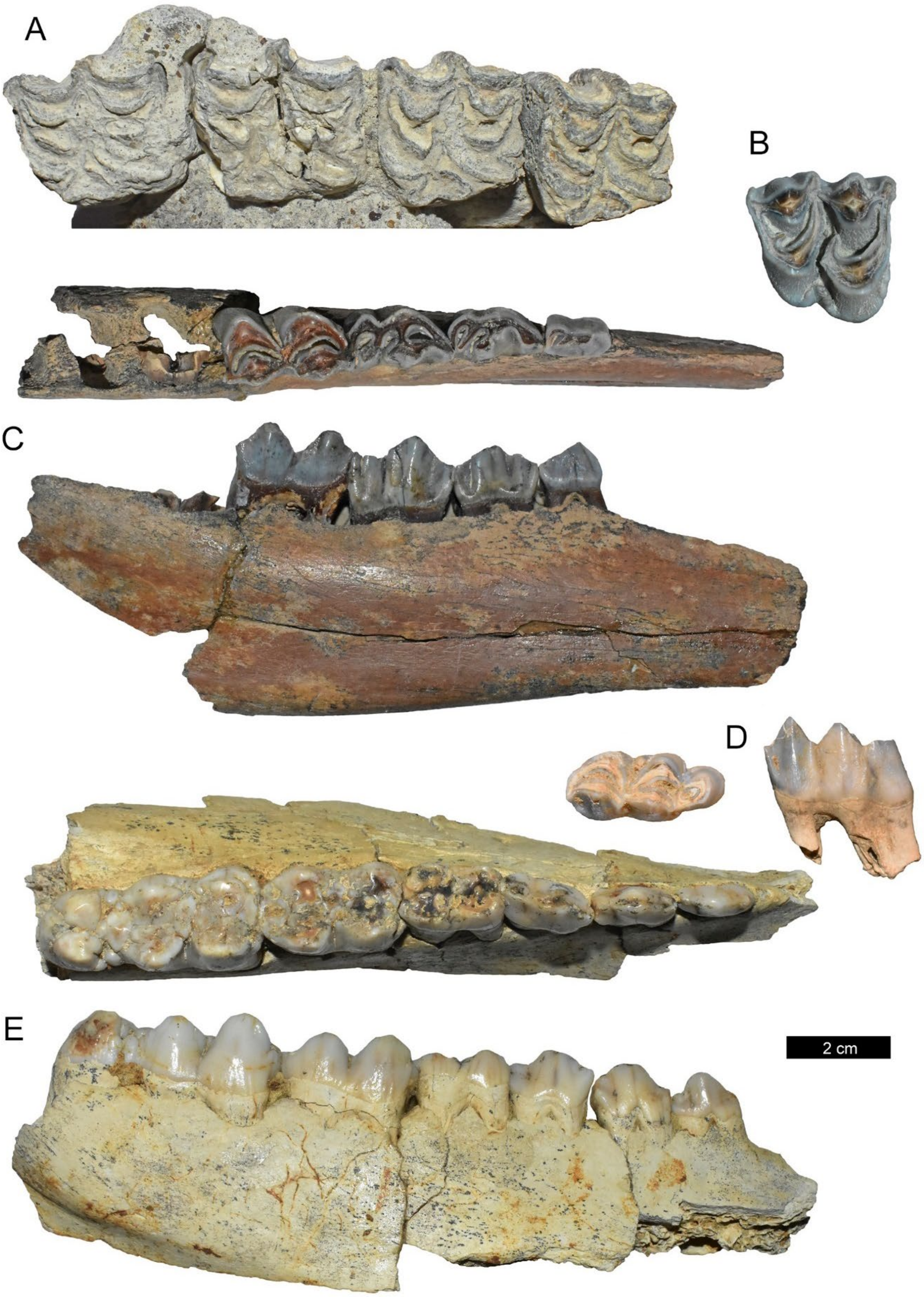

Figure 2 - Selected fossil material from Cava di Breccia – Casal Selce 2. *Equus* cf. *E. mosbachensis* left upper tooth row with P3 – M2 (CS279) (occlusal view) (A); *Praemegaceros* sp. right M1 (CS533) (occlusal view) (B); *C. elaphus* left hemimandible with p2 – m1 (CS531) (occlusal and lingual view) (C); *Dama* sp. right m3 (CSSD10) (occlusal and lingual view) (D); *S. scrofa* left hemimandible with p2 – m3 (CS2073) (occlusal and lingual view) (E).

Among fossil mammal remains recovered from Fontana Ranuccio, herbivorous ungulates are represented by: *Stephanorhinus* sp., *Equus* cf. *E. mosbachensis, Hippopotamus amphibius, Dama clactoniana, Cervus elaphus eostephanoceros, Praemegaceros* sp., *Bos primigenius* (Segre and Ascenzi 1984; Strani et al. 2018b). Other taxa include: *Sus scrofa, Ursus deningeri, Ursus* sp., *Panthera* sp., *Crocuta crocuta, Canis mosbachensis, Macaca sylvanus* and *Homo* sp. (Segre and Ascenzi 1984; Rubini et al. 2014; Strani et al. 2018b; Conti et al. 2021). Small mammals are represented by few remains belonging to *Microtus* (*Terricola*) sp., *Eliomys* sp., cf. *Glis* sp., *Lepus* sp., *Talpa* sp. and *Erinaceus* sp. (Bona and Strani 2021). Cervids are the most abundant group in this locality (68.7% of all remains) (Strani et al. 2018b). Fontana Ranuccio fossil material is currently stored at the Italian Institute of Human Paleontology (Anagni, Italy).

7.2.1. Hypsodonty

Molar crown height (or hypsodonty) is considered a good proxy of environmental conditions (especially habitat openness aridity degree) and feeding ecology (Janis 1988). Traditionally, high-crowned teeth in herbivorous ungulates are believed to be an adaptative response to high rates of tooth wear due to the mastication of highly abrasive items (Janis 1988). Given that grasses tend to be tough and rich in abrasive phytoliths and that feeding in dry landscapes usually leads to the ingestion of grit or dust, it is hypothesised that high molar crown evolved for grazing in open dry habitats (Janis 1988; MacFadden 1997; Strömberg 2006; Eronen et al. 2010). However recent studies suggest additional explanations for the evolution of high-crowned dentition such as a biomechanical adaptation to improve feeding efficiency (DeMiguel et al. 2015) or to function as an auxiliary root to endure strong stress during mastication (observed in Equus; Solounias et al. 2019).

Crown height in the fossil specimens has been measured according to the index defined by Fortelius et al. (2002): a hypsodonty index has been determined as height-to-length ratio for unworn or minimally worn upper and lower molars (HIMm2). Teeth were then classified as either brachydont

(HIMm2 < 0.8), mesodont (0.8 ≤ HIMm2 ≤ 1.2) or hypsodont (HIMm2 > 1.2). A total of 13 specimens belonging to 5 taxa have been measured and classified with this method (Table 2). Hypsodonty data have been compared with those from the Fontana Ranuccio mammal assemblage published in Strani et al. (2018b), which have been collected following the protocol of Fortelius et al. (2002).

	Taxon	**N**	**HIMm2**	**Classification**
CS2	*Cervus elaphus*	4	0.8	Mesodont
	Dama sp.	2	1.0	Mesodont
	Praemegaceros sp.	2	1.0	Mesodont
	Capreolus sp.	/	/	/
	Bovidae indet.	2	1.7	Hypsodont
	Equus cf. *E. mosbachensis*	2	2.9	Hypsodont
FR	*Cervus elaphus eostephanoceros*	7	0.9	Mesodont
	Dama clactoniana	4	0.8	Mesodont
	Praemegaceros sp.	1	0.8	Mesodont
	Bos primigenius	4	1.5	Hypsodont
	Equus cf. *E. mosbachensis*	3	2.4	Hypsodont
	Stephanorhinus sp.	/	/	/

Table 2 - Summary of hypsodonty results. Abbreviations: number of specimens measured (N); hypsodonty index (HIMm2) as in Fortelius et al. (2002). FR data from Strani et al. (2018b).

7.2.2. Dental mesowear

Dental mesowear analysis provides information on long-term feeding behaviours of extinct species and has been developed to investigate ungulate diets (though the analysis has been recently expanded to other groups e.g., Saarinen et al. 2015) and examine the effects produced by items ingested (e.g., foods and exogenous particles such as dust and grit) on tooth morphology over the span of months or years (Fortelius and Solounias 2000; Ackermans et al. 2018). This method is based on the relief of the worn occlusal surface and on the shape of the cusps, which are heavily influenced by tooth-to-tooth (attrition) and tooth-to-food (abrasion) contact. High levels of attrition are generally linked to a browse-rich diet which produces sharper cusps and higher tooth relief, while high levels of abrasion are usually associated to grazing and produce blunter cusps and lower tooth relief (Fortelius and

Solounias 2000). The original mesowear analysis limited to the second upper molars (M2) was here extended to upper (M1–M3; following Kaiser and Solounias 2003) and lower molars (m1–m3; following DeMiguel et al. 2010, 2012) in cervids and bovids, and to upper molars (M1– M3) and fourth premolars (P4) (following Kaiser and Solounias 2003) in *E.* cf. *E. mosbachensis*. Regardless, to stay true to the original method, second upper molars were preferably selected if available. The apex of the paracone and metacone (for upper cheek teeth) and the metaconid and entoconid (for lower cheek teeth) have been examined with the naked eye or at low magnification and when cusps of the same tooth displayed different cusp shapes, the sharpest one was selected. A total of 43 dental specimens were examined with this method and compared with data of 54 modern ungulate taxa with well-defined diets (from Fortelius and Solounias 2000). Teeth that were heavily worn, damaged or belonging to juveniles were excluded from this analysis. Mesowear relief and cusps variables were also converted to a single score (MWS) following Mihlbachler et al. (2011). The method is based on seven cusp types (numbered from 0 to 6), ranging in shape from high and sharp (stage 0) to completely blunt with no relief (stage 6). Additionally, a 'stage 7' is given to teeth with a convex cusp apex. Obtained data have been compared with those from the Fontana Ranuccio mammal assemblage published in Strani et al. (2018b, 2019a), which have been collected following the same protocol.

7.2.3. Statistical analysis

Discriminant analysis was performed to examine the resolution of mesowear variables applied to the fossil taxa. The percentages of high relief, rounded and blunt cusps were used as independent variables and two dietary (conservative and radical) classifications were used as grouping variables (data of modern taxa from Fortelius and Solounias 2000). Non-parametric Mann–Whitney U test (two independent samples) was run to examine similarity between the MWS of taxa that occurs both at CS2 and FR (*Cervus, Dama*, Bovidae indet./*Bos* and *Equus*). No test was run for *Praemegaceros* as in FR since it is represented by a single individual. All analyses were performed using the software IBM SPSS Statistics 24.

7.3. Results

7.3.1. Hypsodonty

All examined taxa display generally high-crowned molars (Table 2), with a hypsodonty index ranging from 0.8 to 2.9. Cervids show a mesodont dentition with hypsodonty indices ranging from 0.8 (*C. elaphus*) to 1.0 (*Dama* sp. and *Praemegaceros* sp.), with the exception of *Capreolus* sp. for which no data are available due to the lack of unworn molars, while Bovidae indet. and *E.*cf. *E. mosbachensis* display a hypsodont dentition with hypsodonty indices of 1.7 and 2.9 respectively. No brachydont taxa are observed though *C. elaphus* hypsodonty index of 0.8 is at the threshold between brachydont and mesodont dentition. These values are comparable with those observed at FR (Table 2), where all cervids display a mesodont dentition (*C. e. eostephanoceros* hypsodonty index = 0.9; *Dama clactoniana* and *Praemegaceros* sp. hypsodonty index = 0.8) and both *B. primigenius* (hypsodonty index = 1.5) and *E.*cf. *E. mosbachensis* (hypsodonty index = 2.4) show a hypsodont condition. This is not unexpected because hypsodonty also carries phylogenetic information by summarising the evolutionary adaptation of a group (Janis 1988). It is thus not unusual for closely related taxa (or for the same species) to display similar molar crown height.

7.3.2. Dental mesowear

All cervids from the Casal Selce faunal assemblage display mesowear patterns characterised by high occlusal relief (100%) and either sharp or rounded cusps (Table 3). *Cervus elaphus* mesowear pattern is characterised by a slight predominance of rounded cusps (55.6%) over sharp ones (44.4%) with an MWS of 1.4, pointing to a relative predominance of attrition over abrasion in the wear process (Table 3). A similar condition is observed in *Praemegaceros* sp. with an equal distribution of sharp and rounded cusps (50%) and an MWS of 1.8 (Table 3). Conversely, *Dama* sp. mesowear patterns show a predominance of sharp apices (66.7%) over rounded ones (33.3%) and an MWS of 1.0 suggesting an attrition-dominated diet. The two individuals of *Capreolus* sp. display rounded cusps and an MWS of 2 (Table 3), the highest recorded among the CS2 cervids, suggesting a more abrasive diet. Bovidae indet. mesowear pattern is characterised by a predominance of high (66.6%) over low (33.3%) occlusal relief with a predominance of round apices (83.3%) and there is no incidence of sharp cusps (Table 3) which results in an MWS of 3.2. This indicates a feeding behaviour characterised by a relatively high abrasion level. *Equus* cf. *E. mosbachensis* is the only taxon where all specimens display a low occlusal relief and a predominance of blunt cusps (Table 3) with a rounded cusp being recorded only in one individual resulting in an MWS of 5.4, the highest recorded in this site. This pattern suggests a marked level of abrasion in the diet of this species.

	Taxon	**N**	**#High**	**#Low**	**%High**	**%Low**	**PerSharp**	**PerRound**	**PerBlunt**	**MWS**	**CONS**	**RAD**
CS2	*Cervus elaphus*	18	18	0	100.00	0.00	44.4	55.6	0.0	1.4	M	M
	Dama sp.	6	6	0	100.00	0.00	66.7	33.3	0.0	1.0	B	B
	Praemegaceros sp.	4	4	0	100.00	0.00	50.0	50.0	0.0	1.8	M	M
	Capreolus sp.	2	2	0	100.00	0.00	0.0	100.0	0.0	2	M	G
	Bovidae indet.	6	4	2	66.67	33.33	0.0	83.3	16.7	3.2	G	G
	Equus cf. E. mosbachensis	7	0	7	0.00	100.00	0.0	14.3	85.7	5.4	G	G
FR	*Cervus elaphus eostephanoceros*	31	31	0	100	0	45.2	54.8	0	1.3	M	M
	Dama clactoniana	40	39	1	97.5	2.5	57.5	42.5	0	1.0	B	B
	Praemegaceros sp.	1	1	0	100	0	100.0	0.0	0	1.0	B	B
	Bos primigenius	24	21	3	87.5	12.5	4.2	95.8	0	2.5	M	G
	Equus cf. E. mosbachensis	10	0	10	0.0	100.0	30.0	50.0	20.0	4.8	G	G
	Stephanorhinus sp.	1	0	1	0	100	0	0	100	6.0	G	G

Table 3 - Summary of dental mesowear analysis. Abbreviations: number of specimens measured (N); percentage of specimens with high (%High) and low (%Low) occlusal relief; percentage of specimens with sharp (PerSharp), rounded (PerRounded) and blunt (PerBlunt) cusps; mesowear score after Mihlbachler et al. (2011) (MWS); browser (B); mixed feeder (M); grazer (G) conservative classification (CONS); radical classification (RAD). FR data from Strani et al. (2018b) and Strani et al. (2019b) for *Equus* cf. *E. mosbachensis.*

Discriminant analysis performed with the mesowear variables provides a dietary discrimination with 74.1% of extant taxa correctly classified according to the conservative and radical classifications

(68.5% and 74.1%, respectively, in cross-validation). Bivariate diagrams (Figure 3A, B) show that *C. elaphus* and *Praemegaceros* sp. are classified as mixed feeders in both conservative (Figure 3A) and radical classifications (Figure 3B). *Dama* sp. is classified as a browser in both classifications (Figure 3A, B) while *Capreolus* sp. is classified as a mixed feeder according to the conservative classification (Figure 3A) but it's considered a grazer according to the radical one (Figure 3B). This discrepancy may suggest a mixed feeding behaviour with a tendency towards grazing, though these results should be tentatively interpreted due to the particularly small sample size (N = 2). Bovidae indet. and *E.*cf. *E. mosbachensis* are classified as grazers according to the conservative and radical classifications (Figure 3A, B).

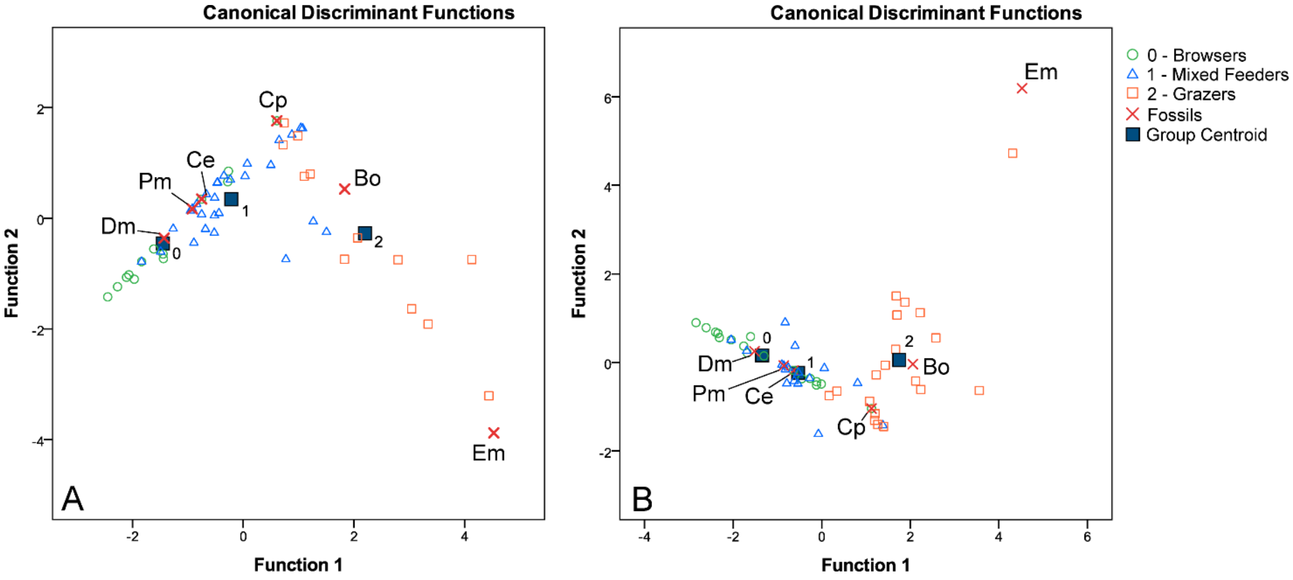

Figure 3 - Bivariate diagrams based on discriminant analysis: conservative classification (A) and radical classification (B). Minute abraded brachydont species have been excluded. Fossil taxa Ce, *Cervus elaphus*; Dm, *Dama* sp.; Pm, *Praemegaceros* sp.; Cp, *Capreolus* sp.; Bo, Bovidae indet.; Em, *Equus* cf. *E. mosbachensis*. Group centroids: browsers (0); mixed feeders (1); grazers (2).

The mesowear data of the CS2 ungulate community are similar to those collected at FR with groups showing patterns that reflect a wide range of dietary behaviours (Table 3). In both sites *Cervus* and *Dama* display comparable patterns comprising high occlusal relief and a slight predominance of rounded (*Cervus*) or sharp cusps (*Dama*). *Bos primigenius* at FR do not display blunt cusps pointing to a less abrasive diet while *Equus* shows a higher percentage of blunt cusps at CS2 (85.7%) than at FR (20.0%). Despite these, MWS of taxa which are recorded in both localities (*Cervus, Dama*, Bovidae indet./*Bos* and *Equus*) do not show a significant difference (Table 4. p-value > 0.05 in all instances), suggesting that they occupied similar niches in both areas. *Praemegaceros* sp., represented by single individual from FR, displays however a mesowear pattern that points to a browsing behaviour compared to the mixed one of the CS2 small population (Table 3).

	P values (MWS)
Cervus CS2 / *Cervus* FR	0.651
Dama CS2 / *Dama* FR	1-000
Bovidae CS2 / *Bos* FR	0.135
Equus CS2 / *Equus* FR	0.115

Table 4 - P values for non-parametric Mann–Whitney U test (exact corrected ties). Abbreviation: mesowear score after Mihlbachler et al. (2011) (MWS).

7.4. Discussion

The onset of the Pleistocene glacial/interglacial cycles led to global lower average temperatures and to the gradual disappearance of humid tropical and subtropical habitats in the Northern Hemisphere (Fortelius et al. 2006; Bertini 2010; Combourieu- Nebout et al. 2015; Head and Gibbard 2015). High dental crown height is generally correlated with an abrasive feeding behaviour in open and dry environments (Janis 1988). The relative abundance of ungulates displaying either a mesodont or hypsodont dentition and the lack of brachydont taxa at CS2 attest to the presence of grasslands which is in accordance with the trend towards cooler and less humid conditions following the initiation of the glacial cycles around 2.6 Ma and their increase in amplitude between 1.2 and 0.4 Ma. However, while hypsodonty may have evolved with the spread of grasslands during the Miocene (Cerling et al. 1997; Strömberg 2011; Chen et al. 2015) and thus represents a typical trait of grass-eating taxa, the occurrence of high-crowned teeth does not always reflect an obligate grazing behaviour as this trait does not preclude animals from feeding on other plant resources (Feranec 2003; DeMiguel et al. 2014;

Bellucci et al. 2021). These results are in line with what is usually observed in late-Early and Middle Pleistocene ungulates, with equids and bovids displaying a hypsodont dentition (a marked one in the case of equids), and cervids a mesodont one (Strani 2020).

Mesowear patterns of the fossil ungulates community indicate a medium-to-high abrasion degree in their feeding behaviours, with most taxa displaying features comparable to those of modern mixed feeders (*C. elaphus, Praemegaceros* sp. and *Capreolus* sp.) and grazers (Bovidae indet., *E*. cf. *E. mosbachensis*), with the fallow deer *Dama* sp. being the only species displaying mesowear patterns consistent with a browsing behaviour. These diversified dietary adaptations suggest that during MIS 15 the CS2 area was characterised by a heterogeneous landscape which allowed animals to exploit different types of plant resources.

The presence of a single browser, albeit abundant (Table 3), coupled with the presence of two obligate grazers (Bovidae indet. and *E. cf. E. mosbachensis*) and a grass-dominated mixed feeder (*Capreolus* sp.) implies that closed canopies rich in soft plant resources may have not been the dominant element of the CS2 palaeoenvironment. Furthermore, while no dental wear patterns data are available for the *E*. cf. *E. altidens* population of CS2, other studies from different European localities (e.g., Pakefield in Britain and Vallparadís Estació in the Iberian Peninsula) suggest that *E. altidens* also exhibited a mostly grazing behaviour in open habitats although with a certain degree of dietary plasticity as suggested by the mesowear data of the Cúllar de Baza 1 population (Bellucci et al. 2021) and to dental microwear patterns (Rivals and Lister 2016; Strani et al. 2019a). The abundant remains of the mixed feeder *C. elaphus*, the best represented taxon at CS2 (39% of specimens; Table 2), however suggest that wooded areas might have still be common in the form of thickets scattered through open landscapes or near water bodies. This is in accordance with paleoenvironmental data obtained from the study of the CS2 fossil bird assemblage which records the presence of open habitats with patchy wooded areas and extensive wetlands (Pavia et al. 2018).

Palynological data from several localities of the Italian Peninsula indicate that during the Middle Pleistocene *Quercus* was the dominant element of the deciduous forests that spread during interglacial phases, with *Tsuga* being the only subtropical element sporadically recorded (Combourieu-Nebout et al. 2015). Oaks might thus have represented the most abundant source of food for herbivorous mammals that fed in wooded areas.

The diversified fauna of CS2 is also suggestive of a mixed environment and the common occurrence of *S. scrofa* is an important ecological indicator. The wild boar is an adaptable species nowadays widespread in a variety of environments, whose dispersal was likely favoured by the EMPT (Iannucci et al. 2020a). Nonetheless, during the Middle Pleistocene it is scarcely represented in Europe during the glacial phases, whereas it becomes abundant when more less harsh conditions occur (Collinge 2001). In particular, when energy-rich foods such as acorns are available, they may account for most of *S. scrofa* diet (Massei et al. 1996), and the mast yield of oak is also positively correlated with larger body mass and litter size in the species (Frauendorf et al. 2016). As such, a similar link between the abundance of *S. scrofa* and the spread of *Quercus*-dominated deciduous forest during Middle Pleistocene interglacial phases seems conceivable. Indeed, a relation between size and climate shifts has been documented for the Late Pleistocene of southern Italy and interpreted as an ecomorphological response of *S. scrofa* to the availability of trophic resources (Iannucci et al. 2020b). Remains of *H. antiquus* and *M. sylvanus* are rare but provide significant palaeoecological insights. The hippopotamus is a sensitive indicator of the presence of wetlands, and by extension of warm-temperate and humid climate (Eltringham 1999), even though the species also exhibited size changes during the Pleistocene that have been suggested to represent plastic responses to less optimal environmental conditions (Mazza and Bertini 2013). Throughout its extant geographic range, the Barbary macaque is associated with a Mediterranean climate (dry summers and wet winters), and the species also require presence of arboreal cover, with preference for evergreen forest of cedar and oak (Fooden, 2007; Masseti and Bruner 2009). There seems to be a marked relation between climate and range fluctuations in the species, with most findings concentrated in the Mediterranean area, some records at northern latitudes favoured by warmer conditions, and a few occurrences during glacial phases (Elton and O'Regan 2014; Mecozzi et al. 2021). At close geographic and temporal proximity with CS2, the cooccurrence of *H. antiquus* and *M. sylvanus* is documented at Isernia la Pineta (MIS 15) (Thun Hohenstein et al. 2015). At Notarchirico, *H. antiquus* and *M. sylvanus* are both present from levels correlated to MIS 17, whereas these species are absent from the rest of the sequence, which mainly spans the severe MIS 16 glacial period (Moncel et al. 2020).

7.4.1. Comparison with Fontana Ranuccio

The FR assemblage dated around MIS 11 displays a remarkable similarity with CS2 in terms of faunal composition and palaeoecological adaptations of the herbivorous ungulate community. Cervids, bovids and equids occupied similar niches in both localities and the occurrence of *H. amphibius* and *M. sylvanus* in both localities (Strani et al. 2018b) indicates similar warm climatic conditions. However, while most of the CS2 and FR ungulates exhibit comparable long-term dietary adaptations, *Praemegaceros* sp. displays a mesowear pattern comparable with a browsing behaviour at FR and remains of *Dama* (obligate browser in both sites) are more abundant in this locality than at CS2 (most common ungulate followed closely by *Cervus*; Table 3) suggesting that woodlands could have been better represented at this locality during MIS 11. A predominance of wooded areas in FR is supported also by the isotopic signal obtained from *Equus* material which indicates that horses exploited also less open habitats in this locality (Strani et al. 2019a). Furthermore, dental microwear patterns of the FR *B. primigenius* population indicate that this bovid showed a certain degree of dietary flexibility feeding at times also on soft plant resources possibly during adverse seasons (Strani et al. 2018b).

Another difference is observed in terms of abundance in *S. scrofa* whose remains are rare at FR representing only 0.6% of all the mammal remains (Strani et al. 2018b), but relatively abundant at CS2 (Table 1). It should be noted that many sites of this time interval record direct or indirect evidence of human presence and exploitation of the faunal remains (e.g., Thun Hohenstein et al. 2015; Moncel et al. 2020), and anthropogenic selection is thus an important factor to consider when inferring palaeoenvironmental reconstructions for the Middle Pleistocene. In this scenario, it is possible that the scarce representativeness of *S. scrofa* at FR where human presence is well-attested (Segre and Ascenzi 1984; Rubini et al. 2014) or in other *Homo*-bearing Middle Pleistocene localities of central Italy (Thun Hohenstein et al. 2015; Moncel et al. 2020), as well as the abundance of *Dama* at FR may be related to a different prey preference of human populations although more archeozoological data from FR are required to support this hypothesis. The possibility that this also affected the abundance of already rare elements, such as hippos and macaques, should be carefully considered, as it may hamper our understanding of the real complexity of past ecosystems.

It should also be noted that CS2 is part of a fluvial–lacustrine sedimentary succession (Marra et al. 2014) contrary to FR where the fossiliferous layer is located within a succession of pyroclastic deposits (Pereira et al. 2018), and that this depositional context may have a role in the bone accumulation process.

Overall, the discrepancies between the two localities seem to suggest that more arid climatic conditions characterised central Italian Peninsula during the MIS 15 than during the MIS 11 which is in accordance with the spread of open habitats around 0.6 Ma attested at Isernia La Pineta (Molise) where arboreal vegetation is infrequent and herbaceous plants are the most represented in the pollen record (Arobba et al. 2004). Palynological data obtained from Vallo di Diano (Campania) record suggest that mean summer precipitation and mean annual precipitation values during the MIS 15–13 interglacials were lower than those observed during the MIS 11 at Boiano (Molise) (Combourieu-Nebout et al. 2015), corroborating this scenario. However, it is also plausible that the observed differences do not reflect regional environmental changes through time but are driven by local-scale spatial variation, as the two sites are geographically close but in two different basins.

7.5. Conclusions

Fossil ungulates niche occupation from the CS2 (MIS 15) locality and its comparison with data from the *Homo*-bearing site of FR (MIS 11) provide information on Middle Pleistocene terrestrial ecosystems of central Italian Peninsula (Tyrrhenian side). While fossil ungulates occupy similar niches in both CS2 and FR, mesowear patterns point to the occurrence of mostly open habitats with scattered woodland at CS2, whereas the abundance of cervids displaying a mixed or browsing diet suggests that wooded habitats were more widespread at FR. Moreover, while wild boars are relatively common at CS2, they are extremely rare at FR. This discrepancy, however, may be linked to anthropogenic selection or to the type of bone accumulation and thus palaeoenvironmental conditions may had been more similar from what is inferred by dental wear patterns and taxa abundances alone. Medium-to-high hypsodonty indices of the CS2 ungulate community suggests that these groups evolved to feed in more arid environments in accordance with the trend towards less humid conditions in the Northern Hemisphere which led to the gradual decline of subtropical habitats from the Late Pliocene/Early Pleistocene onwards and to their definitive disappearance during the EMPT.

Author contributions

F.S. and L.B. conceived the idea. F.S. designed the analysis and collected the dental mesowear and hypsodonty data. D.A.I. collected preliminary data on the mammal fauna and B.M. and A.I. elaborated it. F.S. led the writing of the manuscript with the support of L.B., A.I. and B.M. R.S. provided inputs and comments for the manuscript and supervised the project.

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8. Paper 7

Redefining Ponte Molle (Rome, central Italy): an important locality for Middle Pleistocene mammal assemblages of Europe

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Abstract

In this work, the Middle Pleistocene mammal assemblage from Ponte Molle, a historical locality of the urban area of Rome, has been revised together with a review of the stratigraphical succession of the deposit. This allows us to reconstruct the provenance of the fossil material and to provide chronological constrains trough the correlation with the lithostatigraphic and syn-themic units of the national geological cartography and the geochronologically-constrained aggradational units of the Paleo-Tiber reported in literature. The paleontological study together with the geological and stratigraphical review allow us to redefine the Ponte Molle deposit and its Middle Pleistocene faunal assemblage. In its new look, the age of the faunal assemblage from Ponte Molle could be referred to a time span ranging from 550 ka to 450 ka.

Keywords: fossil vertebrates, biochronology, Galerian, paleoecology

8.1. The urban area of Rome

The city of Rome lays in one of the most important sedimentary basins of Italy for the paleontological research, considering the very high number of fossiliferous findings. The city is crossed by the Tiber River, whose evolution is the result of complex geological processes including tectonic, volcanism and glacio-eustatic fluctuations (Conato et al. 1980; Milli 1997; Karner et al. 2001; Giordano et al. 2003; Funiciello and Giordano 2008a, b). The Tiber River fluvio-deltaic evolution (the "Paleo-Tiber" system), which commenced during the latest Early-earliest Middle Pleistocene (1.1-0.7 Ma; Milli et al. 2016), mainly includes sedimentation linked to sea-level rises during the Pleistocene glacial terminations (Pandolfi and Marra 2015). What follows is a discontinuous stratigraphic record constituted by twelve low rank and high frequency (80-100 ka spaced) depositional sequences, complexly stacked within the basin and deposited by the start of MIS 32-31 (Marine Isotopic Stage) (late Early Pleistocene). In fact, forced by the eustatic and relative falls of the sea level, the Tiber River cyclically excavated the fluvial valleys and coastal plain incisions into the bedrock, later filled during the following transgressive and highstand phases with deposits often including pyroclastic products. These were sourced from the Alban Hills and Sabatini Mounts Volcanic Districts, with main activity spanning the 600-250 ka time interval (De Rita et al. 1993; Marra et al. 2009, 2014; Funiciello and Giordano 2010). The presence of volcanic material, among which pumice and tephra interbedded with alluvial-deltaic sediments, is of considerable interest to obtain $^{40}Ar/^{39}Ar$ radiometric age dates and therefore to provide reliable geochronological constraints for the sediments (Marra and Florindo 2014 and references therein). What makes this territory important for paleontological research is the exceptional number of remains recovered over the last 150 years from the alluvial deposits of the Paleo-Tiber River and its tributaries (e.g., Di Stefano et al. 1998; Petronio and Sardella 1998, 1999; Milli et al. 2004). The first findings took place in the 1800s, when the fluvial deposits were investigated by eminent scientists of the time, such as Giuseppe Ponzi and Alessandro Portis (Funiciello and Rosa 1995; Funicello and Giordano 2008b; Romano et al. 2021). The majority of the fossil remains was collected from deposits outcropping in the urban area of Rome and its periphery, due to the intense urbanization and quarry activities (e.g., Portis 1893, 1896, 1900). Many works focused on the description of these fossiliferous localities and their remains (e.g., Di Stefano et al. 1998; Petronio and Sardella 1999), even if often most of them lacks exact stratigraphic constrains and is not always associated to a precise sedimentary level (gravel, sand, clay) (Pandolfi and Marra 2015). Most of the historical collections from the area of Rome is stored at the "Museo Universitario di Scienze della Terra (MUST)" (Earth Science University Museum, Sapienza University of Rome) (including the former Museo di Paleontologia di Roma, MPUR). Unfortunately, the paleontological collections endured a series of misadventures, as for instance the overflow of the Tiber River in 1870 (Portis 1893) or the bombardment that struck the Department of Earth Sciences of Sapienza University (Rome) carried out by the American Army during World War II (Fabiani and Maxia 1953; Mecozzi et al. 2020). These episodes caused the loss and damage of many fossil specimens or of their associated labels. Nonetheless, the fossil remains recovered from the urban area of Rome and its surroundings, also known as Campagna Romana (Roman Campaign), represent the most abundant Middle Pleistocene fossil samples founded in Italy, and thus the area assumes a key-role in the study of vertebrate assemblage evolutionary trends and paleoenvironmental reconstructions. The importance of this territory is reflected in the Large Land Mammal Biochronological Scale, where two Roman localities are chosen as Faunal Units: Ponte Galeria and Torre in Pietra (Gliozzi et al. 1997).

In this work, we analyze the fossil sample from Ponte Molle (also known as Ponte Milvio) (PM), a historical locality of the urban area of Rome described by Portis (1893). The revision of the stratigraphical succession of the deposit allows us to reconstruct the provenance of the fossil material and to provide chronological constrains trough the correlation with the lithostatigraphic and synthemic units of the national geological cartography (CARG Project; Funiciello and Giordano 2008a, b) and the geochronologically-constrained aggradational units of the Paleo-Tiber reported in literature (Marra et al. 2014).

8.2. Ponte Molle and its troubled history

The presence of the fossil remains in the Tiber alluvial deposit in the Tor di Quinto area was already reported in the second half of the 19th century, when Ponzi (1867) recognized the occurrence of several species from the quarries opened at PM, from the same gravels quarried for building material (Table 1). The stratigraphical succession exposed in the quarry called Cava D'Alessandri was firstly described by Portis (1893). In this work, he illustrated several sedimentary deposits occurred in the city of Rome, with a special focus on the northern-western area, where in addition to Cava D'Alessandri, the successions exposed at Tor di Quinto (=Torretta di Quinto) and Acquatraversa (all located in the Tor di Quinto district) were also described (Figure 1). The author pointed out the presence of fossil remains referable to the "classical" fauna of PM (implying that findings of similar assemblages were already common) only from the lowermost level of the stratigraphic succession (Table 1). This level, consisting of tuffaceous gravels and sands (i.e., with tuffaceous clasts and minerals of volcanic origin), and including a diversified faunal assemblage, was the first properly described outcrop of the "cosiddette ghiaie diluviali di Ponte Molle" [so-called diluvial gravel of Ponte Molle]. Later, Portis (1902) described an isolated upper molar belonging to a juvenile specimen classified as *Elephas antiquus* (=*Palaeoloxodon antiquus*) (Table 1). Portis (1907) analyzed the sample of Bovidae from several deposits of the urban area of Rome and its surroundings, attributing several cranial remains from PM to *Bos primigenius* (Table 1). Portis (1909) studied the canid fossil remains from the urban area of Rome, among which two fragments of hemimandible and one isolated lower carnassial from the "cosiddette ghiaie di Ponte Molle presso Cava D'Alessandri" were referred to a small-sized form of *Canis lupus* (Table 1). In addition, he noticed that in the fossil collection of Ponzi two replica, a fragment of maxillary and a fragment of hemimandible, respectively, were present, but the original remains were missing. These two fossils were also referred to *C. lupus*. Portis (1909) also attributed a complete femur to *Meles meles* (=*Meles taxus*) and an upper canine to the genus *Lynx,* both collected from the basal level of Cava D'Alessandri (Table 1). Later, Portis (1920)

Taxa	Ponzi (1867)	Portis (1893)	Portis (1902)	Portis (1907)	Portis (1909)	Portis (1920)	Caloi and Palombo (1986)	Di Stefano and Petronio (1992)	Capasso Barbato et al. (1998)	Cassoli and Segre (2004)	Martínez-Navarro and Palombo (2007)	Billia and Petronio (2009)	Pandolfi and Marra (2015)
Elephantidae		X											
Palaeoloxodon (*Elephas*) *antiquus* (=*Palaeoloxodon antiquus*)			X					X	X				
Hippopotamidae	X	X											
Hippopotamus incognitus							X						
Hippopotamus cf. *amphibius*								X	X				
Hippopotamus sp.								X	X				
Hippopotamus cf. *antiquus*									X				
Rhinocerotidae	X	X											
Dicerorhinus sp. (=*Stephanorhinus* sp.)								X					X
Stephanorhinus hemitoechus									X				X
Stephanorhinus kirchbergensis									X			X	X
Stephanorhinus hundsheimensis													X
Bovidae	X	X											
Bos primigenius				X				X	X				
Bubalus murrensis										X			
Hemibos galerianus											X		
Sus scrofa								X	X				
Cervidae	X	X											
Cervus (*Praealces*) *latifrons*						X							
Megaceros cf. *solihacus* (=*Cervus* [*Praealces*] *latifrons*)							X						
Cervus (*Cervus*) *acoronatus* (*Cervus elpahus acoronatus*)							X	X	X				
Cervus elephus elaphus								X	X				
Cervus (*Dama*) *dama* ssp. (=*Cervus* [*Dama*] *quirinus*)							X						
Dama dama								X	X				
Dama dama clactoniana								X	X				
Euraxis eurygonos									X				
Capreolus capreolus								X	X				
Equus caballus (=*Equus ferus*)								X	X				

Equus (*Asinus*) *hydruntinus* (=*Equus hydruntinus*)				X	X
Ursus sp.				X	X
Canis lupus			X		X
Canis cf. *mosbachensis*					X
Crocuta crocuta					X
Lynx sp.	X		X		X
Meles meles	X		X		X
Carnivora		X			

Table 1 - Mammal taxa from Ponte Molle reported in previous works.

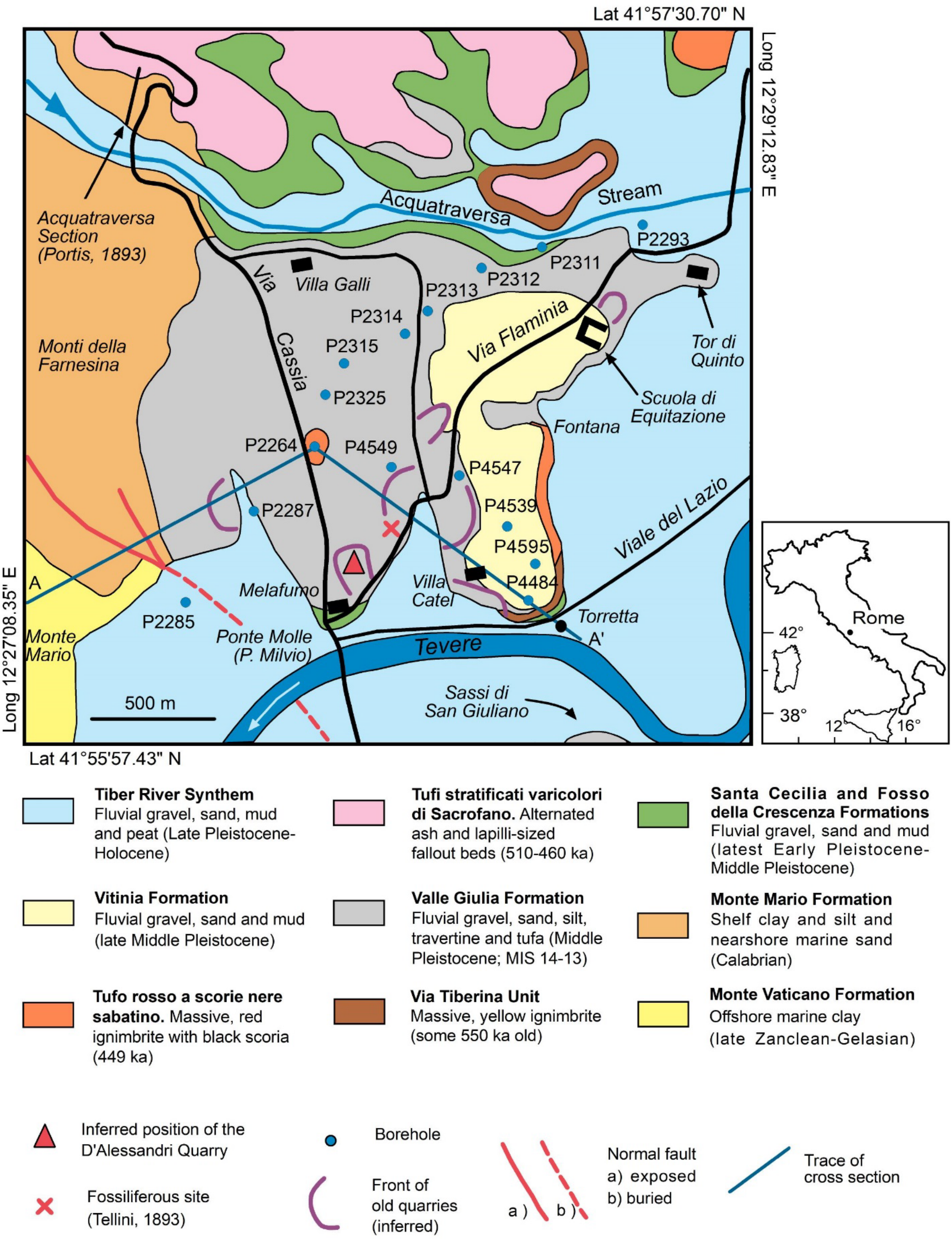

Figure 1 - Geological sketch map of the Ponte Molle-Tor di Quinto area (from Funiciello and Giordano 2008a; modified), with trace of the geological cross section (Figure 2), the location of the Cava D'Alessandri and boreholes used for stratigraphic analysis (Figures 4, 5). Toponyms refer to the historical geological maps by Tellini (1893) and Verri (1915); see also Figure 3.

listed the Cervidae taxa identified in the city of Rome and its surroundings, reporting the presence of *Cervus* (*Praealces*) *latifrons* from PM (Table 1). However, due to the intense urbanization of the area, the quarries and the other aforementioned outcrops were destroyed or buried below anthropogenic deposits. Following this, subsequent studies were conducted exclusively on the historical fossil collections recovered during the end of 1800s and the first decades of 1900. During the 1960s, Ambrosetti and Bonadonna (1967) resumed the paleontological research on this locality and correlated the PM fauna with the Ponte Galeria formation (*sensu* Conato et al. 1980) exclusively on the basis of the occurrence of some Galerian taxa, even if no description of the materials was performed. After decades, Caloi and Palombo (1986) carried out the revision of the fossiliferous localities of the area of Rome and listed the following species from the lower level of Ponte Milvio (=Ponte Molle): *Cervus* (*Cervus*) *acoronatus, Cervus* (*Dama*) sp. (=*Cervus* [*Dama*] *quirinus*), *Megaceros* cf. *solilhacus* (=*Cervus* [*Praealces*] *latifrons*) and *Hippopotamus incognitus* (Table 1). Even in this case, neither descriptions nor figures of the fossil sample were included. Di Stefano and Petronio (1992) firstly described the mammal assemblage from PM, identifying two distinct faunal assemblages, as they regarded some mammals as Galerian forms (e.g., *C. elaphus acoronatus*) and others as more typical elements of late Middle to Late Pleistocene assemblages (e.g., *Dama clactoniana*) (Table 1). Capasso Barbato et al. (1998) carried out a preliminary revision of the deposit, recognizing at least three different assemblages of Middle Pleistocene age and also referring a few specimens to the Holocene (Table 1). Shortly after, Di Stefano et al. (1998) further detailed the “two-assemblages” hypothesis, attributing the first to Isernia Faunal Unit (early Middle Pleistocene) and the second to Vitinia Faunal Unit (late Middle Pleistocene), mainly on the ground of the presence of different fallow deer subspecies, respectively *Dama clactoniana* and *Dama dama tiberina*.

More recently, an isolated horn-core stored at the Monastery of Santa Scolastica in Subiaco (Rome), previously referred to *Bubalus murrensis* by Cassoli and Segre (2004), was ascribed to *Hemibos galerianus* by Martínez-Navarro and Palombo (2007) (Table 1). Palombo (2004) figured a partial cranium with nearly complete antler classified as *C. elaphus acoronatus* and a partial cranium and complete antler ascribed to *D. dama tiberina* (=*Dama quirinus*).

Billia and Petronio (2009) revised the Rhinocerotidae sample, recognizing only the presence of *Stephanorhinus kirchbergensis*, whereas Pandolfi (2013) and Pandolfi and Marra (2015) identified three different taxa: *S. kirchbergensis, Stephanorhinus hemitoechus and Stephanorhinus hundsheimensis*, as well as several remains undeterminable at specific level (*Stephanorhinus* sp.) (Table 1). Pandolfi and Marra (2015) also proposed a reinterpretation of the age of the deposit. They noticed that part of the specimens labels report that fossils were collected from “gravels and sands” and others from “tuffaceous conglomerates”, and supposed this as indicative of the presence of two levels of different age: the lower one, a gravel and sand level where *S. hundsheimensis* occurred; and the upper one, a tuffaceous conglomerate level which included *S. kirchbergensis* and *S. hemitoechus*. This upper level was correlated with a tephra detected at 1.5 km along Via Flaminia Nuova, dated at 465±7 ka, whereas the lower level was correlated to the base of the Paleo-Tiber 2 cycle at 810-790 ka (Pandolfi and Marra 2015). However, from an historical perspective, this label-based repartition of the assemblage is not supported. In fact, even not accepting early researchers’ interpretations, they explicitly regarded the fauna of PM as coming from a single level (Ponzi 1867; Portis 1893). Consequently, they would not have reported on the labels a separation that they had not observed in the field. Moreover, even though some labels do report “gravels and sands” and others “tuffaceous conglomerates”, others again indicate “gravels, sands, and tuffaceous conglomerates”, or even “so-called gravels of Ponte Molle” or variable combinations of these forms, which clearly were all different ways to refer to the same thing: a fluvial formation with gravel and sand, rich in fossils and volcanic material.

The so-called fauna of PM was the typical assemblage recovered from the gravel quarries and other sporadic findings occurred during construction works in the district of Tor di Quinto, in the northern-western area of Rome (Ponzi 1867). Several specimens were recovered from Cava D’Alessandri, which was also the first properly described outcrop (Portis 1893). Despite several specimens from this site have been object of study (e.g., Capasso Barbato et al. 1998; Di Stefano et al. 1998), an in-depth analysis is still needed to redefine the faunal assemblage.

8.3. Geological setting

The study area of PM and Tor di Quinto is located on the right bank of the Tiber River and corresponds to a well preserved fluvial terrace, with 50-60 m a.s.l. mean elevation, laying eastward of the N-S directed Monte Mario-Monti della Farnesina ridge, up to 140 m high (Figure 1). The terrace is bounded to the east and south by the alluvial plain of the meandering Tiber River, at 16 m a.s.l., and to the north by the narrow valley of Fosso dell'Acquatraversa.

The original terrace relief, as deduced by the observation of historical geological and topographic maps (Tellini 1893; Verri 1915; IGM 1936), was characterized by a gentle undulating topography interrupted, internally, by small N-S oriented valleys and at the northern and eastern edges by steep scarps, where natural outcrops were exposed and examined by the authors (Portis 1893; De Stefani 1904). Nowadays the natural landform is strongly modified after a reshaping from the intense urban transformations of the last 120 years, and almost no exposures are preserved.

On the local stratigraphy, the bedrock corresponds to the marine clay, silt and sands of the Monte Vaticano and Monte Mario Formations, attributed respectively to the Zanclean-Gelasian and to the late Santernian (Calabrian) (Funiciello and Giordano 2008a, b). The bedrock crops out along the Monte Mario-Monti della Farnesina ridge, is found in the subsoil of the fluvial terrace (Figure 2), and is crossed by NW-SE trending normal faults down-throwing the north-eastern blocks (Funiciello and Giordano 2008a; Cosentino et al. 2009).

The terrace is composed of an approximately 50 m thick succession of fluvial deposits with interbedded pyroclastic units, which covers with angular unconformity the bedrock; it is interpreted as an alluvial fill terrace (Merrits 2007; Pazzaglia 2013). At the base are present alternated gravel, sand and silt of the Fosso della Crescenza and Santa Cecilia Formations of the latest Early

Pleistocene-early Middle Pleistocene. They record the oldest fluvial sedimentation in the area, up to the MIS 16-15, and are covered by the Via Tiberina Unit (Tufo Giallo della Via Tiberina Auct) an approximately 550 ka old and few meters thick ignimbrite (Karner et al. 2001), sourced by the Sabatini Mts District and cropping out close to the Torretta site.

Most of the fill terrace is represented by the fluvial Valle Giulia Formation (MIS 14-13), up to 30 m thick and composed of basal channel gravels grading upward into cross bedded sands, travertine, tufas and floodplain muds. This formation has a relatively high-relief basal unconformity carved into the bedrock and older fluvial deposits and defines an approximately N-S directed paleo-valley infill (Giordano et al. 2003; Funiciello and Giordano 2008a; Marra and Florindo 2014; Giustini et al. 2018). The formation is rich in volcanoclastic material, resedimented in the fluvial environment, and crystals of volcanic origin found in the sandy matrix of the gravels. North of the Acquatraversa Stream the “Tufi stratificati varicolori di Sacrofano” crop out, composed of alternated ash and lapilli sized fallout beds (510-460 ka old) that, along with the Valle Giulia Formation, define the Villa Glori Synthem.

On the top of the terrace there are locally present the “Tufo rosso a scorie nere sabatino”, a red massive ignimbrite with back scoria (about 449 ka old; Karner et al. 2001) and the overlaying Vitinia Formation (late Middle Pleistocene, approximately 285-270 ka old; Karner et al. 2001; Giordano et al. 2003) composed of few meters thick pebbly sand and mud, rich in volcanic minerals. The Vitinia Formation corresponds in this area to the “Formazione fluvio-lacustre” by Ventriglia (1971, 2002).

Finally, the Tiber River plain and Acquatraversa valley are composed of basal gravels and overlaying channel sands and floodplain mud with interbedded peat layers of the Tiber River Synthem (or Tiber Depositional Sequence, *sensu* Milli et al. 2016), which records the last cycle of fluvial incision and sedimentation of Late Pleistocene-Holocene (MIS 5d-1). Anthropogenic deposits, up to 15 m thick, cover the natural substratum in most of the study area.

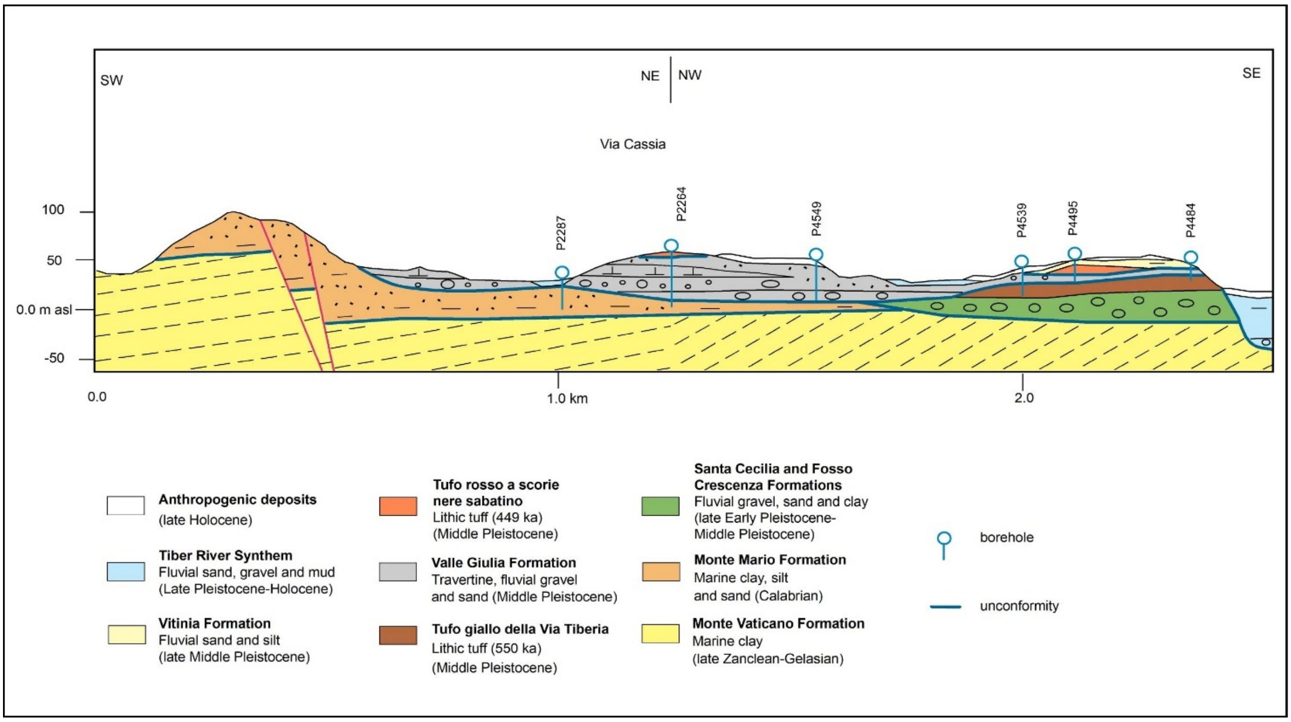

Figure 2 - Geological cross section of the Ponte Molle area. The trace of the section is represented on Figure 1.

8.4. Materials and methods

The osteological analyses of the large mammal fauna from the Middle Pleistocene site of PM were carried out, considering remains collected from the end of 1800 to early decades of 1900. The fossil remains are stored at MUST. Taxonomic and skeletal element identifications made in this study are based on the reference collection of the PaleoFactory Laboratory, Department of Earth Sciences, Sapienza University of Rome (PF). In order to evaluate species abundance, the count of the number of remains (NISP) (Grayson 1984) and the estimate of the minimum number of individuals (MNI) (Bökönyi 1970) have been performed (Table 2). In addition, the age at death was also determined.

We carried out biometric comparisons for a selection of taxa relevant for their biochronological and paleoenvironmental significance: *Bos primigenius*, medium-sized deer (*Dama* spp. and *Dama*-like), *Sus scrofa*, and *Hippopotamus*. For *B. primigenius* and medium-sized deer, we measured the maximum meso-distal length above the root-crown junction of the lower third molar (M_3L). For *S. scrofa,* measurements of the lower third molar were taken following von den Driesch (1976). For

Hippopotamus ssp. measurements of the lower third molar were taken following Mazza (1995): OL: outer length; AB: anterior breadth. Measurements were taken with a digital caliper to the nearest 0.1 mm.

For *Bos primigenius* we considered specimens stored in the following institutions: Contrada Cozze, Casa Minniti (National Archeological Museum of Melfi); as well as literature data: Punta Lucero (Gomez-Oliveira et al. 2015); Malagrotta (Caloi and Palombo 1979); Igue des Rameaux, Lunel-Viel, Pech de l'Azé II (Uzunidis-Boutillier 2017); Fara Sabina (Angelelli 1981); Ilford (Wright 2013). Subfossil samples of *Bos taurus* from Elvas-Kreuzwiese (Boschin 2018) and Silves-lix (Davis et al. 2008) were also included. We selected the M_3 since it is the best documented tooth in the studied sample. In addition, this tooth is easily distinguishable from the other lower molars, which makes more reliable the literature data used for comparison.

Morphometric data of medium-sized deer from Pirro Nord and extant Italian specimens of *Dama dama dama* stored at PF have been considered. Literature data of several medium-sized deer taxa have been included: *Pseudodama* group: Kalamotó (*Dama* sp., Tsoukala and Chatzopoulou 2005); Saint-Prest (*Dama* sp., Guérin et al. 2003), Erpfinger Höhle (*Dama nestii*, Lehmann 1957), Le Vallonnet (*Dama vallonnetensis,* de Lumley et al. 1988), Cueva Victoria (*Pseudodama vallonnetensis*, van der Made 2012), Atapuerca TD8 (*Dama vallonnetensis*, van der Made et al. 2017a); *Dama roberti*: Pakefield, Westbury, West Runton (Breda and Lister 2013), Contrada Monticelli (*Dama* cf. *roberti*; Stefanelli et al. 2021), Valdemino (Breda 2015); *Dama clactoniana*: Fontana Ranuccio, Grays Thurrock, Jarwick, Visogliano (Di Stefano 1994), Notarchirico (Cassoli et al. 1999), Atapuerca TD11 (Azanza and Sanchez 1990), Caune de l'Arago (*Dama* cf. *clactoniana*, Magniez et al. 2013). We selected the lower third molar (M_3) since it is the best documented tooth in our *Dama* sample. In addition, this tooth can be easily recognized from the other lower molars, and therefore a misleading interpretation can be excluded from the data taken from the paleontological literature.

For *Sus scrofa* we considered specimens studied in the following institutions: Bristie 1 (Civic Museum of Natural History, Trieste), Melpignano (PF), and literature data for West Runton, Trimingham, Grays Thurrock, Oreston, Hutton (Lister et al. 2010); Petralona (Tsoukala and Guérin 2016); Kyparíssia (Atanassiou et al. 2018); Gajtan, Lunel-Viel (Fistani 1996); Cerè (Fabiani 1919); Torre del Pagliaccetto (Caloi and Palombo 1978), and extant Italian wild boar (Iannucci et al. 2020b); considering that a relationship between size shifts in *S. scrofa* and environmental fluctuations has been recently recognized in late Middle Pleistocene-Early Holocene Apulia (southern Italy), we also included several Late Pleistocene Apulian localities in the comparison, grouped in "Glacial" (MIS 4 and 2) and "Interglacial" (MIS 5 and 3) samples (Iannucci et al. 2020b). We selected M_3 as it is widely available in our sample and in the literature, as well as being easily identifiable and common focus of studies on wild boar morphometry.

We also considered morphometric literature data of genus *Hippopotamus* from Plio-Pleistocene sites of Europe as well as extant *Hippopotamus amphibius* (Mazza 1995). We selected M_3 because it is the most numerous tooth in our sample.

For investigating chronological and/or geographical biometric variability and possible size variations in the selected taxa we used boxplots of M_3 length, for *B. primigenius*, medium-sized deer, and *S. scrofa*; and plot of length vs breadth of M_3 for *Hippopotamus*.

Species	*Palaeoloxodon antiquus*		*Hippopotamus* ex gr. *antiquus*		*Stephanorhinus kirchbergensis*		*Stephanorhinus hemitoechus*		*Stephanorhinus* sp.		*Bos primigenius*	
Anatomical portion	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Horn core/Antler/Tusk	2	1									1	
Cranium											2	1
Maxillary	1	1										
Hemimandible	4	2	2	1							11	9
Upper Teeth	9	1	9	3	6	2	4	1	23	1	142	17
Lower Teeth	9	1	29	4	3	1			16	1	145	23
Teeth	10		1						4			
Scapula	1	1									1	1
Humerus											2	2
Radius											1	1
Ulna												
Metacarpal			1	1							3	3
Carpal												
Vertebra	11		2								42	
Rib	3		3									
Pelvi											1	
Femur									1	1	3	2
Tibia			1	1							3	3
Fibula												
Astragalus	1	1	1	1							10	5
Calcaneous											1	1
Tarsal												
Metatarsal	1	1	1	1							1	1
Metapodial												
I Phalange											3	
II Phalange											2	
III Phalange												
Total	52	2	50	4	9	2	4	1	44	1	374	23

Table 2 - Mammal fossil remains from Ponte Molle stored at MUST (continues on next page).

Sus scrofa		*C. elpahus acoronatus*		*C. elpahus eostephanoceros*		*Dama clactoniana*		*Capreolus capreolus*		*Equus mosbachensis*		*Equus hydruntinus*		*Lepus sp.*	
NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
				2	1	13	2								
		1	1	3	3										
				1	1										
				8	6	7	5	1	1						
3	1			7	2	6	2			28	3	6	1		
4	1			38	11	11	3			27	3	5	1		
														1	1
						7								1	
														1	
										1	1				
				1	1					1	1				
				1	1										
						1				1					
										2					
7	1	1	1	61	11	45	5	1	1	60	3	11	1	3	1

Table 2 - Mammal fossil remains from Ponte Molle stored at MUST (continues on next page).

Castor fiber		*Canis mosbachensis*		*Crocuta crocuta*		*Lynx pardinus*		*Meles meles*	
NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
		1	1						
1	1	1	1						
				1	1				
						1	1	1	1
						1	1		
						2	1		
						1			
						2	1		
						2	1		
						2	1		
						2	1		
						1	1		
1	1	2	1	1	1	14	1	1	1

Table 2 - Mammal fossil remains from Ponte Molle stored at MUST.

8.4.1. Cartography and stratigraphic analysis

Historical and modern geological and topographic maps have been analyzed and compared among each other (Tellini 1893; Verri 1915; IGM 1936; Ventriglia 1971, 2002; Funiciello and Giordano 2008a), coupled with a bibliographic review of scientific articles and historical chronicles (Ponzi 1867; Portis 1893; De Stefani 1904; Ranzato 2019), in order: 1) to locate as precisely as possible the Cava D'Alessandri, other old toponyms and fossil sites of PM, and the described stratigraphic sections no longer observable; 2) to infer the position and areal extension of other old quarries active between the last decades of the 19th and first half of the 20th century (Figure 1).

In particular, the synoptic observation of old maps, from the oldest to the youngest, has allowed to identify changes in the shape of topographic contour lines (i.e., from a convex to a concave one) resulting in half-circular morphologies in plain view, here interpreted as ancient quarry fronts and floors (see also Ciotoli et al. 2015, for the method). *In situ* observations and 3D views from the software Google Earth Image©2019TerraMetrics has permitted, in some cases, to recognize steep scarps and differences in heights within the urbanized area, strengthening the hypothesis of old quarry fronts.

The stratigraphic section of Cava D'Alessandri has been drawn basing on the description by Portis (1893), who reported the precise position of the unique vertebrate-bearing level of the quarry.

To reconstruct the stratigraphic architecture of the PM-Tor di Quinto infill terrace, two correlation panels among the Cava D'Alessandri section and 15 borehole logs have been realized. The latter deriving from literature and unpublished data (Ventriglia 2002) and stored in the CNR IGAG database of subsoil data of Rome (Cavarretta et al. 2005). Correlation was based on the application of standard methods of physical stratigraphy on core data (Bridge 2003; Collinson et al. 2006) with particular emphasis on the identification of key bounding surfaces and architectural elements: main unconformities, channel bodies, floodplain deposits. This has allowed to put the vertebrate-bearing level of Cava D'Alessandri into the correct physical and chronostratigraphic frame.

8.5. Results

8.5.1. Geography and stratigraphy

From the compared analysis of cartographic and literature data (Portis 1893; Tellini 1893; De Stefani 1904; Verri 1915) it appears that Cava D'Alessandri was likely sited on the northern flank of via Flaminia about 150 m north of the Osteria di Melafumo (Tavern), with this tavern located just after PM (Figure 1). Figure 1 shows the localities mentioned by the authors and ancient toponyms, in some cases no longer in use, plotted on a sketch of the modern geological map of Rome (Funiciello and Giordano 2008a).

On the Tellini's (1893) geological map a small N-S trending topographic depression can be noticed, which cuts transversally the southern slope of the PM-Tor di Quinto terraced relief. This place roughly corresponds to the C. d'Alessandri toponym, as reported on the later Verri's (1915) geological map (Figure 3). The topographic depression of the Tellini's (1893) map is interpreted as the ancient Cava D'Alessandri (Figure 1), being it substituted by a re-covered area with small buildings above it in the Verri's (1915) map. This testifies the very rapid changes of the growing city in the PM area. Another fossiliferous site was shown by Tellini (1893) further north along the Via Flaminia, and is reported on Figure 1, as other old quarries and the outcrops described by Portis (1893): Torretta and Acquatraversa.

The stratigraphy of Cava D'Alessandri described by Portis (1893) is represented on Figure 4. The vertebrate-bearing level was located in the lower cross bedded fluvial gravels, 8.5 m thick, that are replaced above by calcareous sand and silt (1.5 m thick) and by a fining-upward succession (16 m thick) of sandy pebbles, grey sand and silt with concretions, plant fragments and freshwater and terrestrial mollusks (*Corbicula fluminalis*, Helicidae). From the modern geological map, Cava D'Alessandri belongs to the Valle Giulia Formation (Figure 1), ascribed to the intermediate portion of Middle Pleistocene and correlated with MIS 14-13 (Funiciello and Giordano 2008b).

The stratigraphic-sedimentological log of Cava D'Alessandri is correlated with nearby borehole logs (see also Figures 1 and 2 for their location), which allows to define the stratigraphic architecture of the PM-Tor di Quinto infill terrace. The two produced correlation panels are presented on Figure 5. The first panel (Figure 5a), in which the Cava D'Alessandri log is plotted, is NW-SE oriented with an across-valley direction; the other (Figure 5b) is almost perpendicular in the along-valley direction (NE-SW).

The panels detail the stratigraphic setting already shown in the cross section of Figure 2, with the marine bedrock of the Monte Vaticano and Monte Mario Formations, the overlaying Middle Pleistocene formations composing the aggradational terrace (Fosso della Crescenza and Santa Cecilia Formations, Via Tiberina Unit, Valle Giulia Formation, "Tufo rosso a scorie nere sabatino", Vitinia Formation), the late Pleistocene-Holocene Tiber River Synthem in the plain, the anthropogenic deposits. The main unconformity separating the bedrock from the overlaying infill terrace of PM-Tor di Quinto results from the enveloping of the singular basal unconformities of the fluvial Fosso della Crescenza, Santa Cecilia and Valle Giulia Formations, all incised by the ancient Tiber into the bedrock in response of recurrent sea level falls and lowstands. The infill terrace is thus the result of the complex vertical and lateral stack of several Middle Pleistocene units, with a discontinuous stratigraphic-sedimentologic record occurred throughout the approximate 0.80-0.27 Ma time interval. The oldest fluvial and pyroclastic units (Fosso della Crescenza, Santa Cecilia Formations and Via Tiberina Unit) are rarely crossed by the well cores in the eastern portion of the terrace. The fluvial sediments are represented by prevailing beige sand and silt, with intercalated pebbles and with a reddish-brown paleosol on the top (P2313 borehole; Figure 5b).

Conversely, the panels show for the Valle Giulia Formation the classical pattern of infill of the Quaternary fluvial incised valleys in the Rome area, i.e., that related both to the Tiber River and tributaries (Milli 1997; Milli et al. 2008, 2016; Mancini et al. 2018), with a high relief unconformity, basal gravels and overlaying alternated sand and fine deposits.

The basal unconformity of Valle Giulia Formation is well incised into the marine bedrock and the older Fosso della Crescenza-Santa Cecilia Formations and Via Tiberina Unit (550 ka old); it records the sea level fall occurred between the MIS 15 and MIS 14, and the MIS 14 lowstand of sea level (glacial phase).

The lower portion of the incised-valley fill corresponds to amalgamated sandy gravels, 10-15 m thick, with cross bedded bars and bedforms of the braided river environment. The fossiliferous gravels correspond to the *"cosiddette ghiaie diluviali di Ponte Molle"* by Portis (1893) and form a laterally and downstream continuous body with tabular shape. They are related to the onset of the sea level rise occurred between MIS 14 and MIS 13 (latest lowstand and early transgressive phases of filling), at the end of the glacial phase.

Above the gravels, fluvial pebbly-silty sands alternate with floodplain fine deposits and with travertines and freshwater tufas. All these deposits recorded the fluvial sedimentation in response to the late rise and highstand of sea level during the MIS 13 (transgressive and highstand phases) and under interglacial climate conditions.

The sands define at least three vertically stacked channel bodies (*sensu* Gibling 2006), each 10 m thick, lens shaped and with fining upward arrangement of facies, from pebbly to silty sand (Figure 5a). The channel sands, likely attributed to a meandering-style fluvial system (as compared to other analogues in the Rome area; Milli et al. 2016), are laterally confined by planar bedded floodplain silt and muds, and by travertines and tufas of fluvial and spring environments. Travertines and tufas, cropping out at Tor di Quinto, define a down-stream almost continuous tabular body in the intermediate portion of the incised valley fill, at 20-30 m a.s.l. elevations (Figure 5b). These continental carbonates record a well-known phase of increasing $CaCO_3$ deposition by spring waters, related to a renewal of the local tectonic activity during the MIS 13 (Funiciello and Giordano 2008b).

On the top, the Valle Giulia Formation is constrained by the 449 ka old "Tufo rosso a scorie nero sabatino", which deposited on a morphologically very articulated surface recording the main fluvial incision at the MIS 13-12 transition. A following phase of fluvial sedimentation is represented by the Via Tiberina Unit, which deposited at the end of MIS 9 and MIS 8.5 (Giordano et al. 2003).

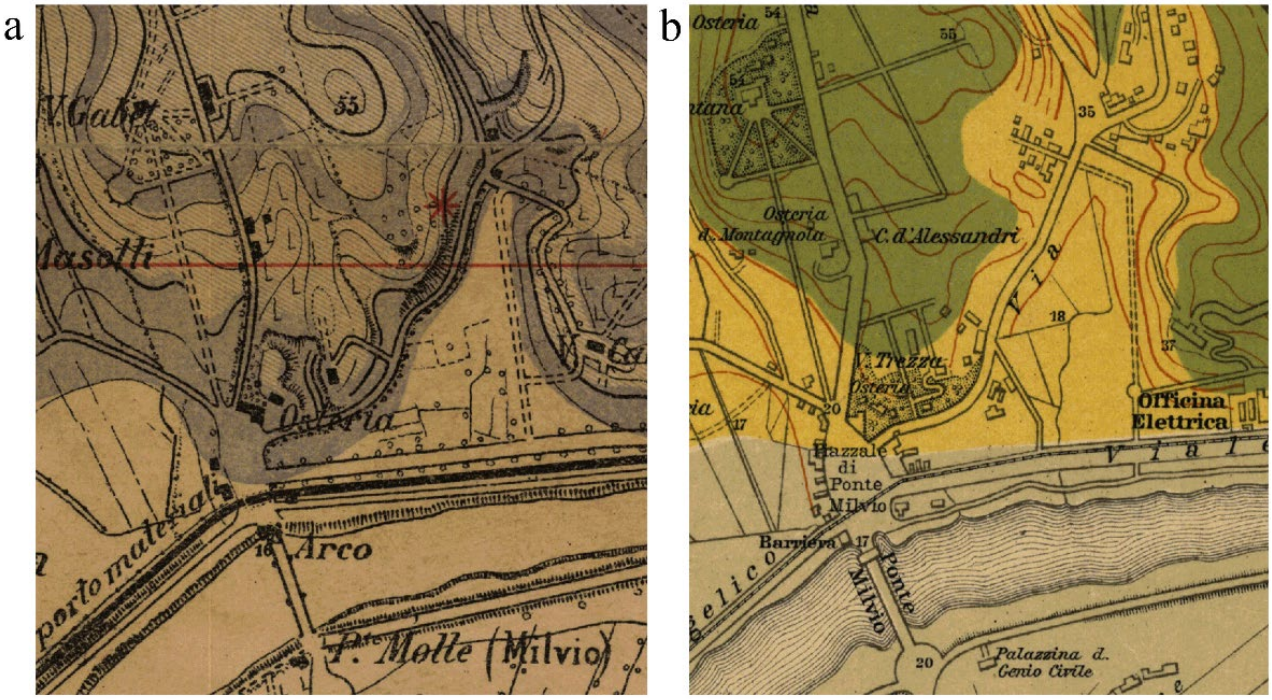

Figure 3 - Sketches of the historical geological maps by Tellini (1893) on the left, and Verri (1915) on the right, showing the area of Ponte Molle and its transformations between the late 19th and the early 20th century. In the Tellini's (1893) map there are featured a small N-S oriented topographic depression, just north-east of the Osteria (di Melafumo) toponym, in the same area described by Portis (1893), and a fossil site (red asterisk; see also Figure 1). In the Verri's (1915) map it is reported the C. d'Alessandri toponym just north of the Osteria, and the topographic depression (the former quarry) is replaced by a newly built area (V. Trezza toponym).

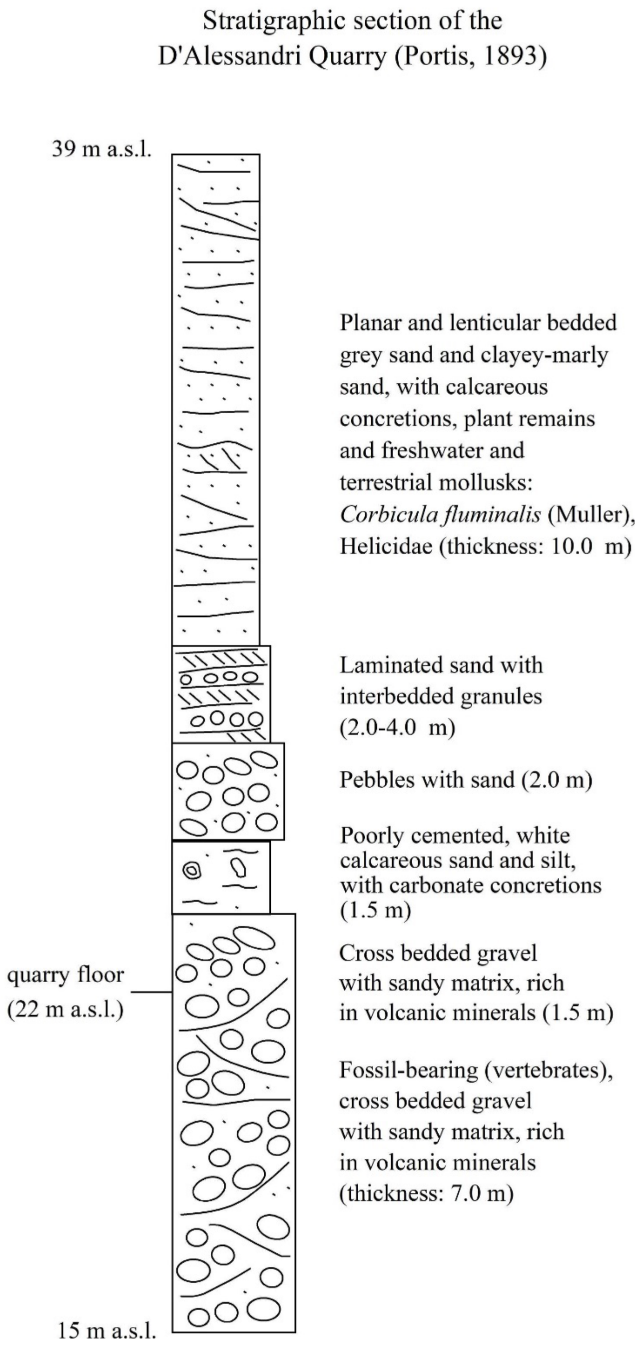

Figure 4 - Stratigraphic-sedimentologic log of the Cava D’Alessandri; see Figure 1 for the location of the log (red triangle).

8.5.2. Faunal assemblage from Ponte Molle

The fossil sample from PM includes 741 taxonomically identified elements recovered from the lower part of the deposit, chronologically referred to the Middle Pleistocene (Table 2) (Figure 6). The faunal assemblage is largely dominated by *Bos primigenius* (50.5%), which is mainly represented by isolated upper and lower teeth (Table 2). The cervids (*Cervus elaphus eostephanoceros* and *Dama* *clactoniana*) (14.5%), a large equid (*Equus mosbachensis*) (8.1%), the straight tusked elephant (*Palaeoloxodon antiquus*) (7%), rhinos (*Stephanorhinus hemitoechus, Stephanorhinus kirchbergensis, Stephanorhinus* sp.) (7.6%) and *Hippopotamus* ex gr. *antiquus* (*=Hippopotamus tiberinus*) (6.7%) are well represented, whereas *Sus scrofa*, *Equus hydruntinus* and *Capreolus capreolus* are quite scarce (Table 2). A single antler testifies the presence of *Cervus elaphus acoronatus* (Figure 7). The middle- to small-sized mammals are represented by a lower number of fossils (2.7%), Among these, there are 14 remains ascribed to a single *Lynx* individual.

A restricted part of the sample is referred to juvenile individuals (9.8%), nearly exclusively represented by isolated teeth: *H.* ex gr. *antiquus* (2 specimens), *S. hemitoechus* (2 specimens), *Stephanorhinus* sp. (3 specimens), *B. primigenius* (37 specimens), *C. elaphus eostephanoceros* (1 specimen), *E. mosbachensis* (13 specimens) and *E. hydruntinus* (1 specimen). An exception is represented by the remains of *Lynx sp.,* where 14 juvenile postcranial specimens belonging to the same skeleton. The fossils are in a good state of preservation, although often enwrapped by a thin crust of sand with abundant volcanic material that range from reddish to greyish. A few specimens, especially the remains referable to large herbivores, are partially embedded in pebbles whose dimension vary from a few millimeters to more than ten centimeters. In the fossil material there is no sign of bite marks or rodent gnaw marks, or human butchering and exploiting activity. Therefore, it is possible to suggest that carnivorans or humans did not play any key role in the accumulation of the fossil remains. Unfortunately, the stratigraphic information written on specimen's labels is quite limited, preventing further taphonomic analyses.

Finally, likely deriving from the upper part of the deposit, clearly chronologically referable to the Holocene due to their preservation, several species were identified: *B. primigenius* (11 specimens), *Bubalus* sp. (1 specimen), *C. elaphus* (1 specimen), *Equus ferus* (6 specimens), *E. hydruntinus* (5 specimens) and *M. meles* (14 specimens; Mecozzi 2021).

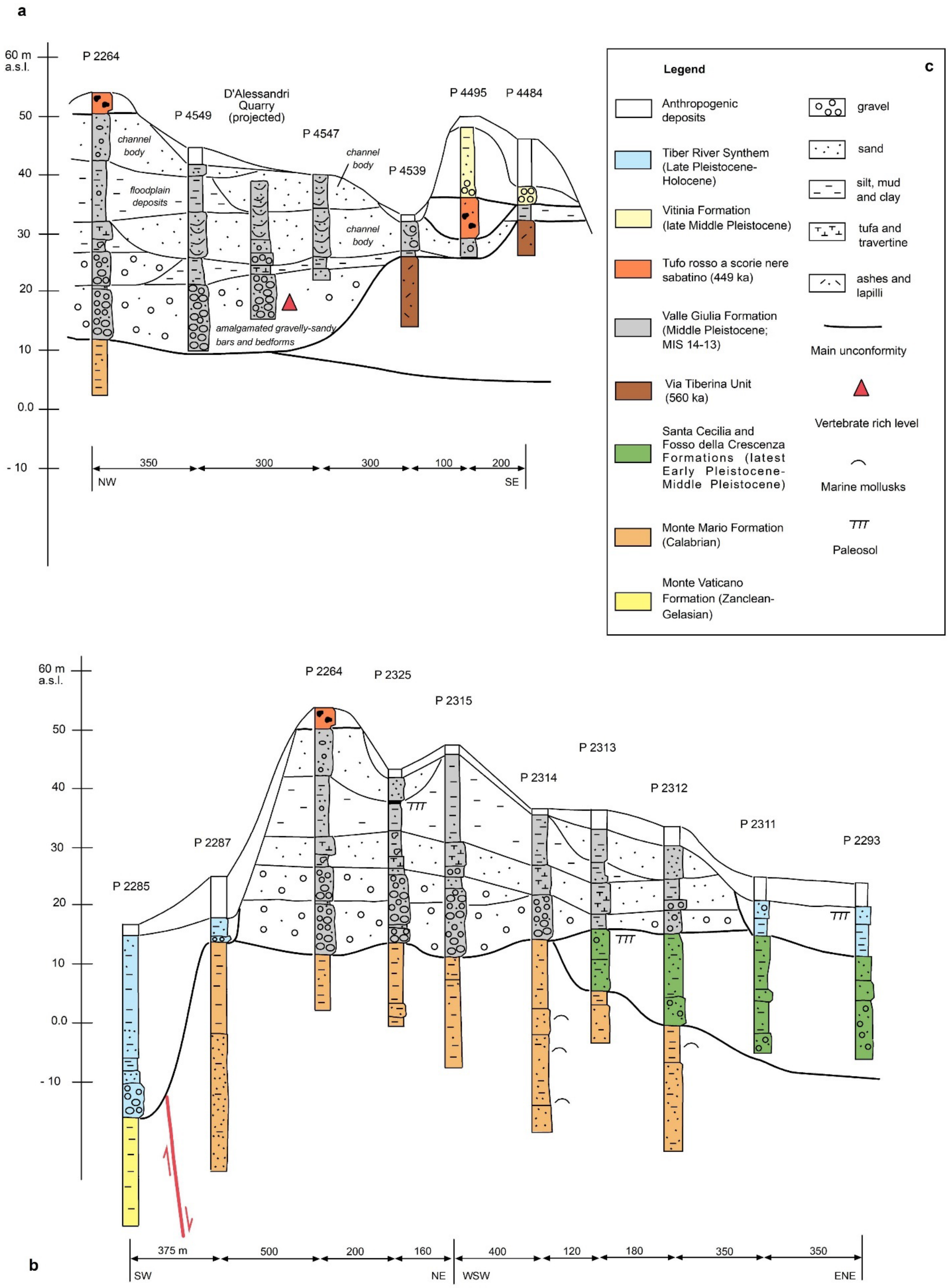

Figure 5 - Correlation panels among borehole logs and the Cava D'Alessandri log detailing the stratigraphic architecture of the Ponte Molle-Tor di Quinto terrace: a) across-valley panel; b) down valley panel; c) legend. The location of boreholes is on Figure 1.

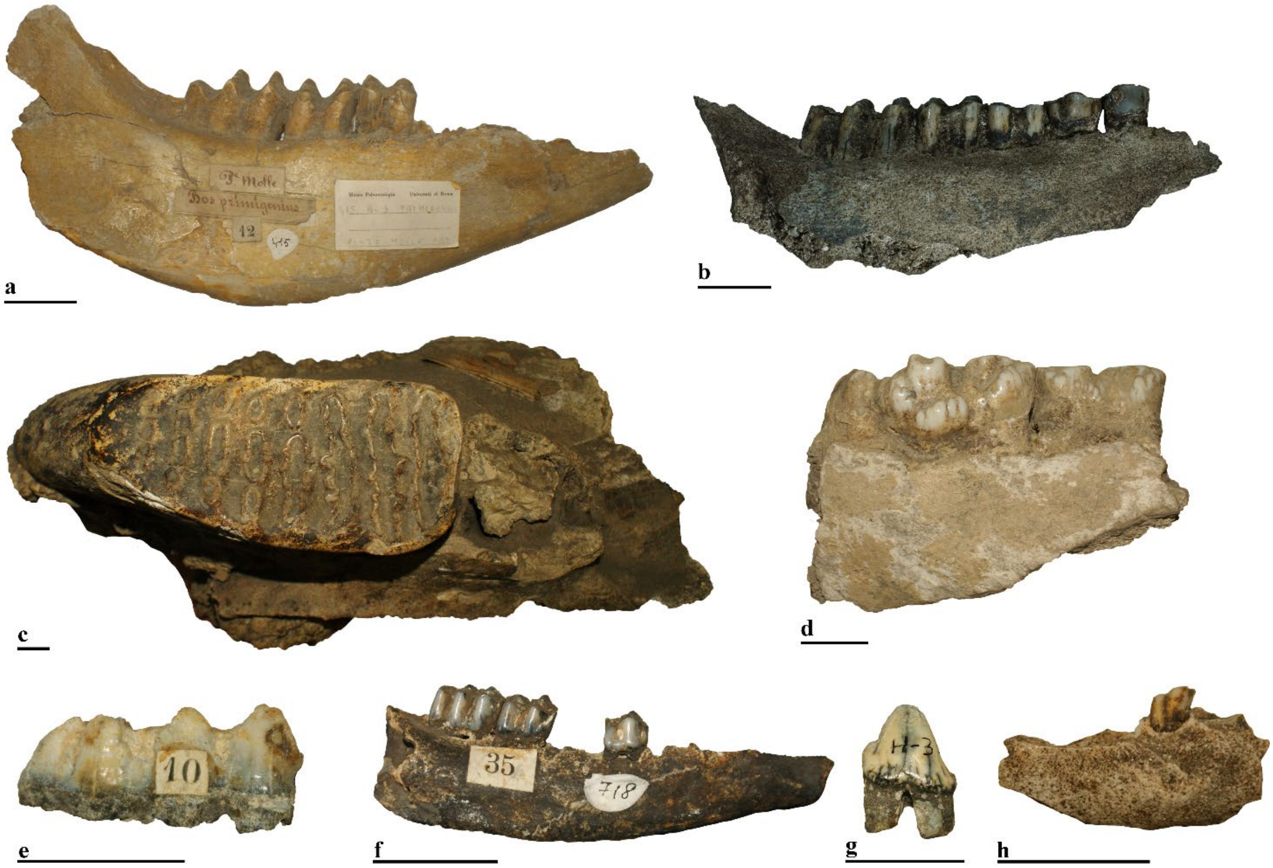

Figure 6 - Mammal fossils from Ponte Molle: a - 415, right hemimandible of *Bos primigenius* in labial view; b - 426, right hemimandible of *Bos primigenius* in labial view; c -1857, right maxillary of *Palaeoloxodon antiquus* in occlusal view; d - 46, left hemimandible of *Hippopotamus* ex gr. *antiquus* in lingual view; e - 166, left lower third molar of *Sus scrofa* in lingual view; f - 718, right hemimandible of *Capreolus capreolus* in labial view; g - 1175, right lower third premolar of *Crocuta crocuta* in labial view; h - 128, right hemimandible of *Castor fiber* in lingual view. Scale bar 3 cm.

8.5.3. Taxonomic revision

The fossil sample from PM was never systematically studied, with only a preliminary faunal list reported by Di Stefano and Petronio (1992) and Capasso Barbato et al. (1998) (Table 1). Here, we revised the fossil material stored at MUST.

The cervid sample is referred to four taxa: *C. elaphus acoronatus*, *C. elaphus eostephanoceros*, *D. clactoniana* and *C. capreolus*. The subspecies *C. elaphus acoronatus* is represented by a partial cranium and a nearly complete antler (Figure 7), whereas the rest of the red deer sample is classified as *C. elaphus eostephanoceros* (Figure 7). These two red deer subspecies differ in the terminal part

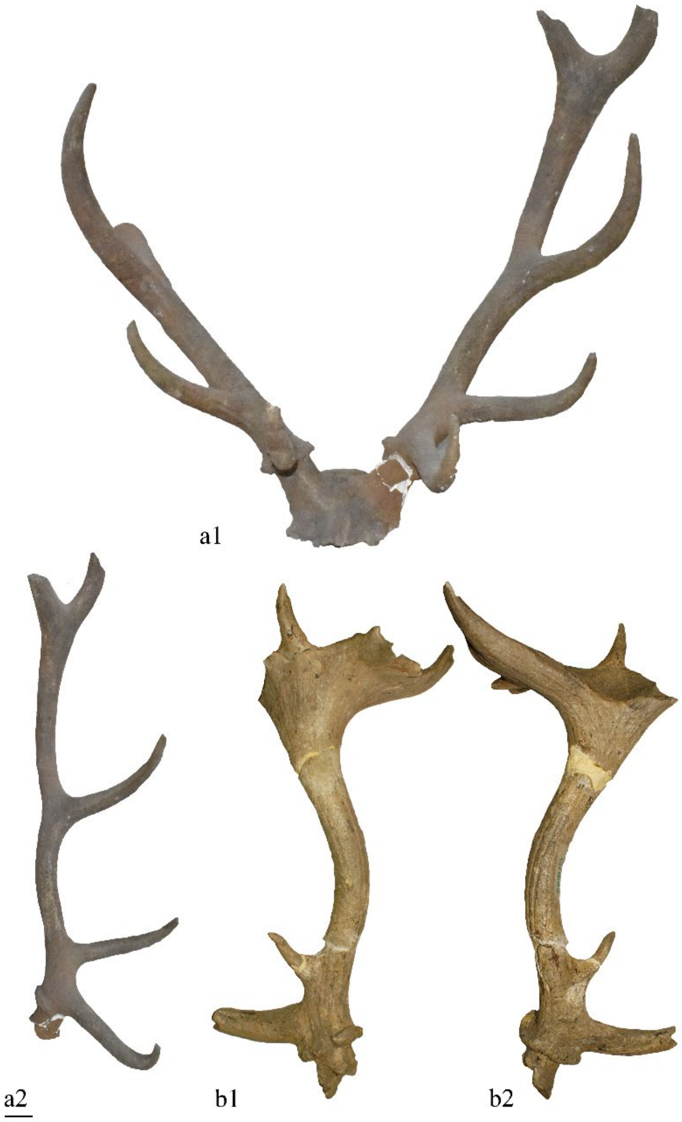

Figure 7 - Antlers of *Cervus elaphus* from Ponte Molle: a, CE 4 *Cervus elaphus acoronatus* in frontal (1) and medial (2) views; b, SN151/FS, *Cervus elaphus eostephanoceros* in lateral (1) and medial (2) views. Scale bar 3 cm.

of the antler: a simple bifurcation in *C. elaphus acoronatus* and a real crown with at least 5 tines in *C. elaphus eostephanoceros*. These two taxa were reported by Di Stefano and Petronio (1992, 1993) and their presence in the faunal assemblage from PM is confirmed.

Considering the medium-sized deer, no remain can be attributed to *Euraxis eurygonos* (=*Axis eurygonos*). The only fallow deer recognized from PM is *D. clactoniana* (Figure 8). Di Stefano and Petronio (1997) proposed a new fallow deer subspecies based on the sample of PM, *D. dama tiberina*. The main diagnostic features of this taxon are related to the morphology of the antlers, which should

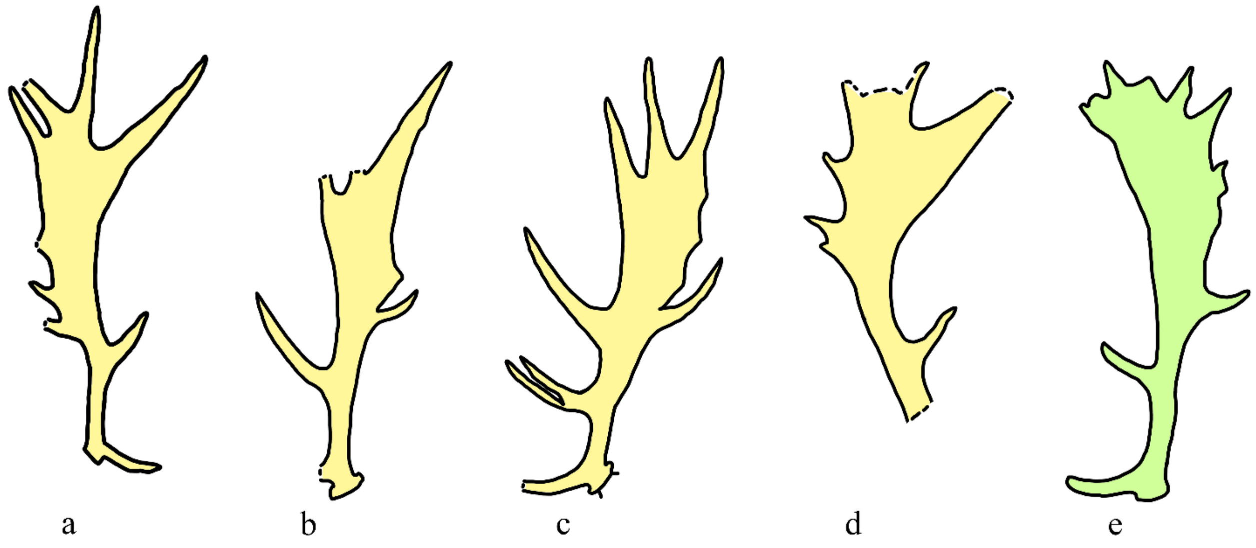

Figure 8 - Antlers of fallow deer: a, MPUR 605 from Ponte Molle; b, Riano 6 from Riano (Leonardi and Petronio 1976); c, 16349 from Swanscombe (Leonardi and Petronio 1976); d, FR56539 from Fontana Ranuccio (Cassoli and Segre Naldini 1993); e, no catalogue number of extant Italian specimen of *D. dama dama* (Di Stefano and Petronio 1993). Colours: yellow - *Dama* clactoniana; green - extant *Dama dama dama.* The images are not in scale.

be different from *D. clactoniana* in: a posterior direction of the spellers on the palm; a more basally located brow tine; brow tine and the trez tine less developed; flatter palm and terminal tines. Nevertheless, the morphology of the antler from PM is extremely close to that of *D. clactoniana* from Fontana Ranuccio, Riano and Swanscombe (Figure 8). Considering that the taxonomy of the Plio-Pleistocene cervid is mainly based on antler (e.g., Di Stefano and Petronio 1993; Breda and Lister 2013), the morphological affinity of the antler from PM to that of *D. clactoniana* suggests it belongs to the same species, thus invalidating the subspecies *D. dama tiberina*. The differences proposed by Di Stefano and Petronio (1997) are not enough to separate *D. clactoniana* and *D. dama tiberina*, but rather fall within the intraspecific morphological variability of the former. By contrast, the overall antler morphology of *D. clactoniana* largely differs from that of *D. dama* (see Leonardi and Petronio 1976 for discussion).

A small-sized deer is also documented at PM, attested by a nearly complete hemimandible. Its morphology cannot be distinct from that of the extant specimens of *Capreolus capreolus.* Another cervid taxon was reported at PM, classified as *Megaceros* cf. *solilhacus* (=*Cervus* [*Praealces*] *latifrons*) (Table 1). Despite this, no remains of the MUST collection can be referred to a megacerine deer, but we cannot exclude that specimens of this taxon are stored in other repositories, as in the case of the horn core of *Hemibos galerianus*.

The taxonomical identification of Middle Pleistocene bovids faced considerable difficulties, especially for isolated and/or fragmented fossils. Nevertheless, the sample from PM includes 374 remains, including diagnostic elements (Table 2). Portis (1907) also described several cranial fragments. We were able to recognize only a few of these specimens in MUST. There are, however, a few crania and cranial fragments in the old collection of MUST without information on their provenance and in need of restoration, some of which could have been recovered from PM. Several features can be detected in the PM sample: horn cores inserted in the cranium in a more latero-posterior position, with an outward and backward direction in the proximal part, and upward and slightly forward in the terminal part (e.g., Portis 1907, plate XIII, fig. 3); well-developed entostyle and a more columnar and hypsodont appearance (swelling absent) of the upper molars; V-shaped enamel around the central cavity of both the upper and lower molars; the two main lobes more mesiodistally developed in the lower molars; presence of a small accessory stylid between hypoconid and hypoconulid in the lower third molar (see Sala 1986 for discussion). In postcranial elements, clear diagnostic features are less numerous but however significative, as the distally divergence of the medial and lateral intercondylar crests in metapodials (see Sala 1986, for the description of other diagnostic features). The overall morphology of the sample from PM is close to that of *B. primigenius*.

Equids are the other well represented group in the faunal assemblage from PM, with two forms well-different in size. The taxonomic status of the Middle Pleistocene *Equus* is still a controversial topic, and no consensus is reached (van Asperen 2012; Boulbes and van Asperen 2019). The open issues concern how to interpret the biometric variations, if related to intraspecific variability or ecomorphotypes (e.g., van Asperen 2012; Boulbes and van Asperen 2019). As such, several authors referred the Middle Pleistocene fossils to *E. mosbachensis,* taxon only characterized for its large size and a few features of the postcranial elements (e.g., presence of the tendon insertion of the anterior brachialis muscle on the inner edge of the diaphysis of the radius, strong supra-articular tuberosities on metapodials) (e.g., Uzunidis-Boutillier 2017; Boulbes and van Asperen 2019). Conversely, van Asperen (2013) considered the European Middle Pleistocene sample as a single species, *E. ferus* ssp. The dental remains from PM are large-sized, whereas the postcranial elements provided no element for a taxonomical allocation. Considering the dimensions, the specimens are referred to the European Middle Pleistocene *E. mosbachensis.*

A few teeth of equid from PM can be instead referred to a small-sized form. Dental diagnostic features of *E. hydruntinus* have been summarized by Boulbes (2009): angular parastyle, rounded and narrow normally mesostyle, a deep postprotoconal valley, pli caballin simplified and short protocone in the upper teeth; metastylid longer than metaconid, with a less deep lingual groove, a deep ectoflexid (on molars) and a few marked or absent pli caballin in the lower teeth. These features have been observed in the sample from PM, and therefore the presence of *E. hydruntinus* can be confirmed.

The hippo remains are very common in the European Plio-Pleistocene record, but even in this case there are conflicting opinions on their systematics and evolution (see van der Made et al. 2017b for discussion). Three forms are generally recognized: *Hippopotamus antiquus*, *Hippopotamus* ex gr. *antiquus* (= *H. tiberinus*) and *Hippopotamus amphibius*. Whereas the last shows clearly diagnostic morphological characters, well different than the other two taxa, *H. antiquus* and *H.* ex gr. *antiquus* differ mainly for their size (Mazza 1995; Mazza and Bertini 2013). Following the taxonomical diagnosis proposed by Mazza (1995), the morphology of the specimens from PM falls in the variability of *H. antiquus*. Based on the medium size of the remains, the sample from PM is ascribed to *H.* ex gr. *antiquus.*

The elephant sample from PM includes fragmentary tusks, partial maxillaries and hemimandibles, isolated upper and lower teeth and several postcranial elements (Table 2). Tusks are incomplete and no useful taxonomical characters can be observed. Dental remains are hypsodont and generally possess a high number of laminae, a high lamellar frequency, reduced enamel thickness and less developed cementum. These features are considered typical of *P. antiquus* (Palombo 1986, 1995; Palombo et al. 2003).

One of the groups better investigated from PM is the Rhinocerotidae. The sample was taxonomically identified for the first time by Capasso Barbato et al. (1998), who recognized the presence of *S. kirchbergensis* and *S. hemitoechus*. Six isolated teeth of *S. kirchbergensis* were carefully described by Billia and Petronio (2009) (Table 3). Pandolfi (2013) revised these specimens and studied other rhino remains from PM (Table 3). The author classified as *S. hundsheimensis* four teeth previously attributed by Billia and Petronio (2009) to *S. kirchbergensis*, and referred other three teeth to *S. kirchbergensis* and four to *S. hemitoechus.* We need to take into account that Pandolfi (2013) recognized two distinct faunal assemblages, referred to Ponte Galeria and Vitinia FUs respectively. Following this chronological repartition, the author attributed a few fossils from this hypothetical "lower level" to *S. hundsheimensis.* The revision of the material from PM supports the classification of Billia and Petronio (2009) for MPUR 1412/8, MPUR 1417/115, MPUR 1421/107, MPUR 1445/27, MPUR 1454/117 and MPUR 1454/118 as *S. kirchbergensis.* The revision of MPUR 1420/97 led doubt on the presence of *S. hundsheimensis*. In fact, its morphology differs from the P4 of *S. hundsheimensis* from Isernia La Pineta (Ballatore and Breda 2013) in the profile of the postfossette and the medisinus. In this scenario, we confirm the presence of *S. kirchbergensis* and *S. hemitoechus*, whereas that of *S. hundsheimensis* cannot be supported.

Sus scrofa is the only suid species documented in the European Middle Pleistocene, it differs from the Early Pleistocene *Sus strozzii* in several anatomical features, the most notable on wild boar remains from PM are the presence of a "scrofic" cross-section of male lower canines and the proportionally narrower teeth (Iannucci et al., 2020a). The chronosubspecific repartition in a large-sized *Sus scrofa priscus* eventually giving rise to a small-sized *S. scrofa scrofa* (e.g., Fistani, 1996) seems a too simple interpretation of a more complex pattern, with several dimensional shifts occurred during the Pleistocene (Lister et al., 2010; Iannucci et al., 2020b).

Catalogue number	Bilia and Petronio (2009)		Pandolfi (2013)	
	Anatomical identification	Specific attribution	Anatomical identification	Specific attribution
MPUR 1412/8	M_1 or M_2	*S. kirchbergensis*	M_1	*S. hundsheimensis*
MPUR 1417/115	M^2	*S. kirchbergensis*	M^2	*S. kirchbergensis*
MPUR 1421/107	P^4	*S. kirchbergensis*	P^4	*S. kirchbergensis*
MPUR 1445/27	M^1	*S. kirchbergensis*	DP^4	*S.* aff. *S. hundsheimensis*
MPUR 1454/117	M^3	*S. kirchbergensis*	M^3	*S. hundsheimensis*
MPUR 1454/118	M^3	*S. kirchbergensis*	M^3	*S. hundsheimensis*
MPUR 1420/97			P^4	*S. hundsheimensis*
MPUR 1438/18			DP^4	*S. hemitoechus*
MPUR 1439-134			P^3	*S. hemitoechus*
MPUR 1451/26			M^1	*S. hemitoechus*
MPUR 1448/51			DP_4	*S. hemitoechus*
MPUR 1456/126			P^4	*S. kirchbergensis*
MPUR 1446/49			M_1	*S. kirchbergensis*
MPUR1415/63			M_3	*S. kirchbergensis*
MPUR 1523/2			Femur	*S.* aff. *S. hundsheimensis*
MPUR 1465-114			DP^1	*Stephanorhinus* sp.
MPUR 1444-95			upper tooth	*Stephanorhinus* sp.
MPUR 1452-112			upper tooth	*Stephanorhinus* sp.
MPUR 1452-113			upper tooth	*Stephanorhinus* sp.
MPUR 1492			P^4	*Stephanorhinus* sp.
MPUR 1414-94			M^2	*Stephanorhinus* sp.
MPUR 1419-39			lower molar	*Stephanorhinus* sp.
MPUR 1416-43			M_2	*Stephanorhinus* sp.
MPUR 1416-42			M_3	*Stephanorhinus* sp.
MPUR 1456-127			upper tooth	*Stephanorhinus* sp.
MPUR 1440-119			upper molar	*Stephanorhinus* sp.
MPUR 1418-23			M^1	*Stephanorhinus* sp.
MPUR 1460-55			P_4	*Stephanorhinus* sp.
MPUR 1442-65			M_3	*Stephanorhinus* sp.
MPUR 1441-70			M_1 or M_2	*Stephanorhinus* sp.
MPUR 1450-64			M_2 or M_3	*Stephanorhinus* sp.

Table 1 - *Stephanorhinus* remains identified in previous works

Two taxa are here identified for the first time: *Castor fiber* and *Lepus* sp. The European beaver is documented only by a partial hemimandible, which possesses features falling in the variability of the extant specimens of *C. fiber* (Komosa et al. 2007; Nowicki et al. 2019). In addition, the specimen is similar to those reported from Cuenca-Bescos et al. (2017) from several Spain Pleistocene deposits, with a lower first molar squared in shape in occlusal view, both mesial and posterior sides planar, less brachyodont chewing teeth and lacking fossettids (isolated enamel islands on the occlusal surface). Few fragmentary postcranial elements can be attributed to hare. Lack of clear diagnostic features prevents a specific attribution.

Carnivorans at PM are quite scarce. Portis (1909) reported the presence of *Lynx*, *Canis lupus* and *Meles meles* (Table 1). According to the author, the lynx sample included a partial hemimandible, currently lost. Other fossils belong to the same skeleton probably found in anatomic connection. A recent study focuses on evolutionary history of European fossil lynxes, which reveals as *L. pardinus* (=*Lynx spelaeus/Lynx pardinus spelaeus*) is the only lynx recognized during the Middle Pleistocene (Mecozzi et al., 2021a). In the PM sample, only skeletal remains are documented, which have small dimensions. Nevertheless, postcranial diagnostic characters in fossil lynxes are quite unmapped. Considering this, we attributed these specimens to *Lynx* sp., avoiding the taxonomical attribution based on chronological grounds.

The canid sample consists of a lower canine and two replica of left maxillary and right hemimandible respectively. Portis (1909, p. 220) noted the lack of the original specimens, writing: "*Dove si trovano conservati gli originali di questi due modelli?*" (Where are the original specimens of these two replica stored?). In addition, three specimens, two partial hemimandibles and a lower first molar described by Portis (1909), are not present in the MUST sample. The available material shows a reduced size and the protocone of the upper fourth premolar is aligned with the mesial margin of the teeth. A small-sized *Canis,* currently lost, was also reported by Portis (1909). Thus, we suggest a possible attribution to *Canis* cf. *mosbachensis*.

Portis (1909) also described the right complete humerus of the European badger. The revision of this fossil confirms its attribution to *M. meles.*

The last carnivoran species, reported only by Capasso Barbato et al. (1998) (Table 1), is *Crocuta crocuta*. An upper third premolar and a replica of coprolite can be assigned to the spotted hyaena. The P3 is squared in shape in occlusal view, its labial margin is quite straight and the lingual cingulum is absent; distal accessory cusp is connected to the paracone with a weak crest. These features resemble those of *C. crocuta,* and differ from those of *Hyaena prisca* (*=Pliocrocuta perrieri*).

Two additional carnivorans, an ursid and a large felid, were reported by previous works (Table 1). Nevertheless, no fossils of the MUST sample can be attributed to these taxa, thus their presence at PM cannot be confirmed. Similarly, to large-sized deer, we cannot exclude that additional fossils could be stored in other repository, as the Scientific Cabinet of high schools of Rome or the Monastery of Santa Scolastica in Subiaco (Rome). Finally, considering the misadventures suffered by the paleontological collection of MUST during the 1900 century, we cannot exclude that part of the sample from PM has been destroyed.

8.5.4. Biometry of selected taxa

The biometric comparison of the M_3 of *B. primigenius* from Middle Pleistocene European sites highlights no chronological or geographical trend (Figure 9). In particular, the rich sample from PM (21 specimens) shows a large variability, which encompasses that of the fossil specimens from Middle Pleistocene sites of Europe. Subfossil samples of *B. taurus* include specimens with shorter M_3.

The length of M_3 of the fossil samples belonging to the fallow deer lineage shows a large variability (Figure 10). The sample from Pirro Nord displays the smallest size among the considered samples, well different from the other contemporaneous materials (late Early Pleistocene). No great difference can be detected among the fossil taxa, which generally possess a longer M_3 than the extant Italian specimens of *D. dama dama.* It is noteworthy that the two smallest samples in Figure 10 are from

Pirro Nord and Contrada Monticelli sites, both geographically located in the Apulian Peninsula (southern Italy), which represent the southern margin of their geographical range.

The biometric comparison of *S. scrofa* M3 length also shows a large variability, with no clear chronological or geographical trend identifiable (Figure 11). Middle Pleistocene specimens are on average larger than the extant Italian populations, and the sample of Late Pleistocene MIS 4 and MIS 2 Apulian sites is the only one markedly smaller. Remains from PM are among the largest of the European Middle Pleistocene.

The plot of the M3 of fossil and extant hippos reveals differences between the groups: *H. antiquus* which generally has longer teeth. *H.* ex gr. *antiquus*, fossil and extant *H. amphibius* are characterized by reduced dimensions (Figure 12).

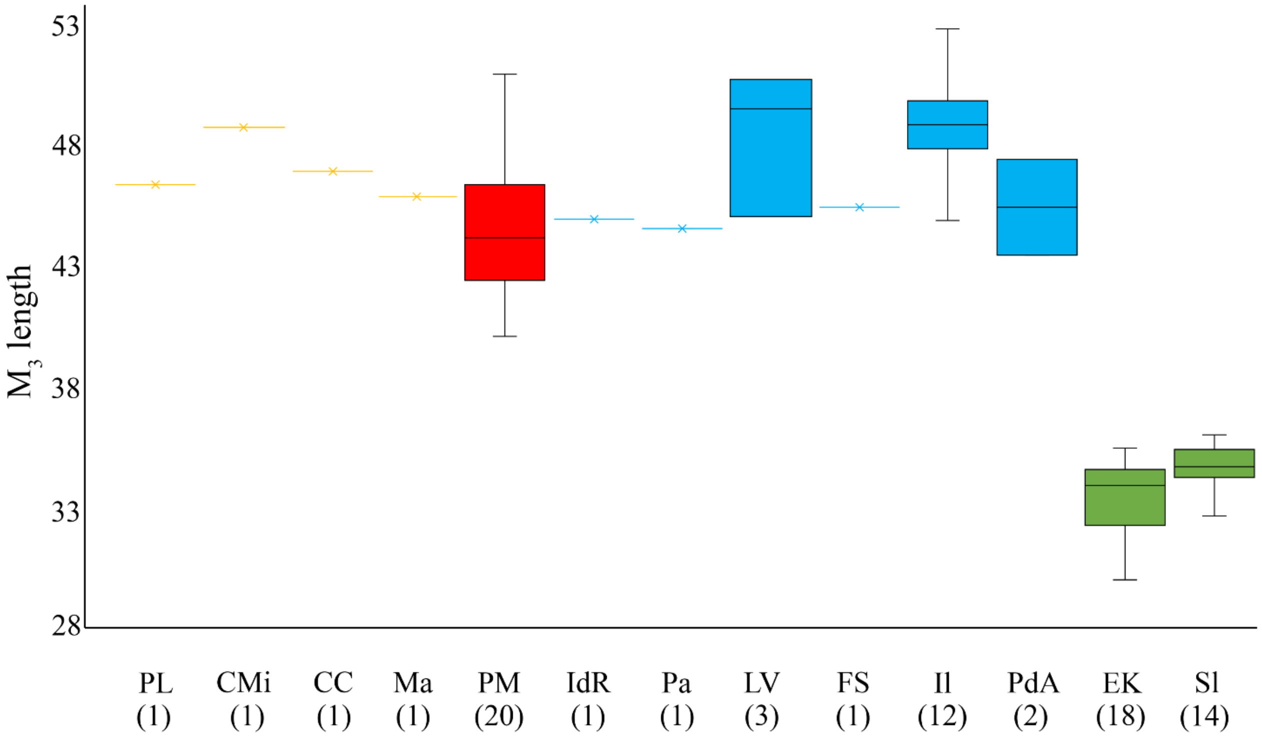

Figure 9 - M3 length (mm) of *Bos primigenius* from Middle Pleistocene sites of Europe and subfossil specimens of *Bos taurus*. Colors: Orange - early Middle Pleistocene: PL, Punta Lucero; CMi, Casa Minniti; CC, Contrada Cozze; Ma, Malagrotta; Red - PM, Ponte Molle; Light blue - late Middle Pleistocene: IdR, Igue des Rameaux-amont; Pa, Payre; LV, Lunel-Viel; FS, Fara Sabina; Il, Ilford; PdA, Pech de l'Azé II; Green - subfossil specimens of *Bos taurus;* EK, Elvas-Kreuzwiese; Sl, Silves-lix. Number of specimens indicated in the brackets.

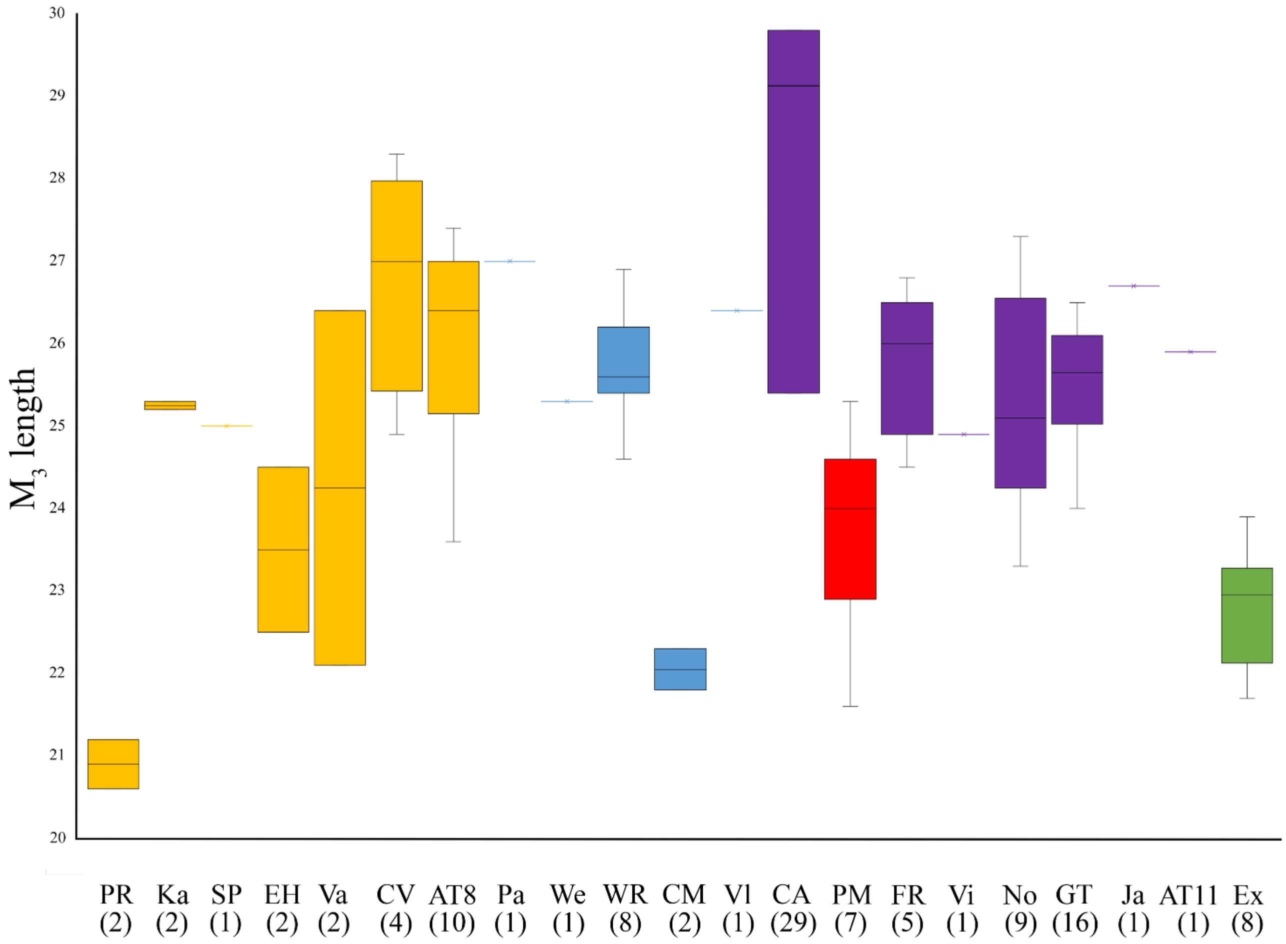

Figure 10 - M_3 length (mm) of medium-sized deer from late Early Pleistocene to late Middle Pleistocene sites of Europe and extant specimens. Colors: Orange - *Pseudodama* group: PR, Pirro Nord; Ka, Kalamotó; SP, Saint-Prest; EH, Erpfinger Höhle; Va, Le Vallonnet; CV, Cueva Victoria; AT8, Atapuerca TD8; Light blue - *Dama roberti*: Pa, Pakefield; We, Westbury; WR, West Runton; CM, Contrada Monticelli (*Dama* cf. *roberti*); Vl, Valdemino; red - PM, Ponte Molle; Purple: *Dama clactoniana*; CA, Caune de l'Arago (*Dama* cf. *clactoniana*); FR, Fontana Ranuccio; Vi, Visogliano; No, Notarchirico; GT, Grays Thurrock; Ja, Jarwick; AT11, Atapuerca TD11; Green - Ex, extant specimens of *Dama dama dama*. Number of specimens indicated in the brackets.

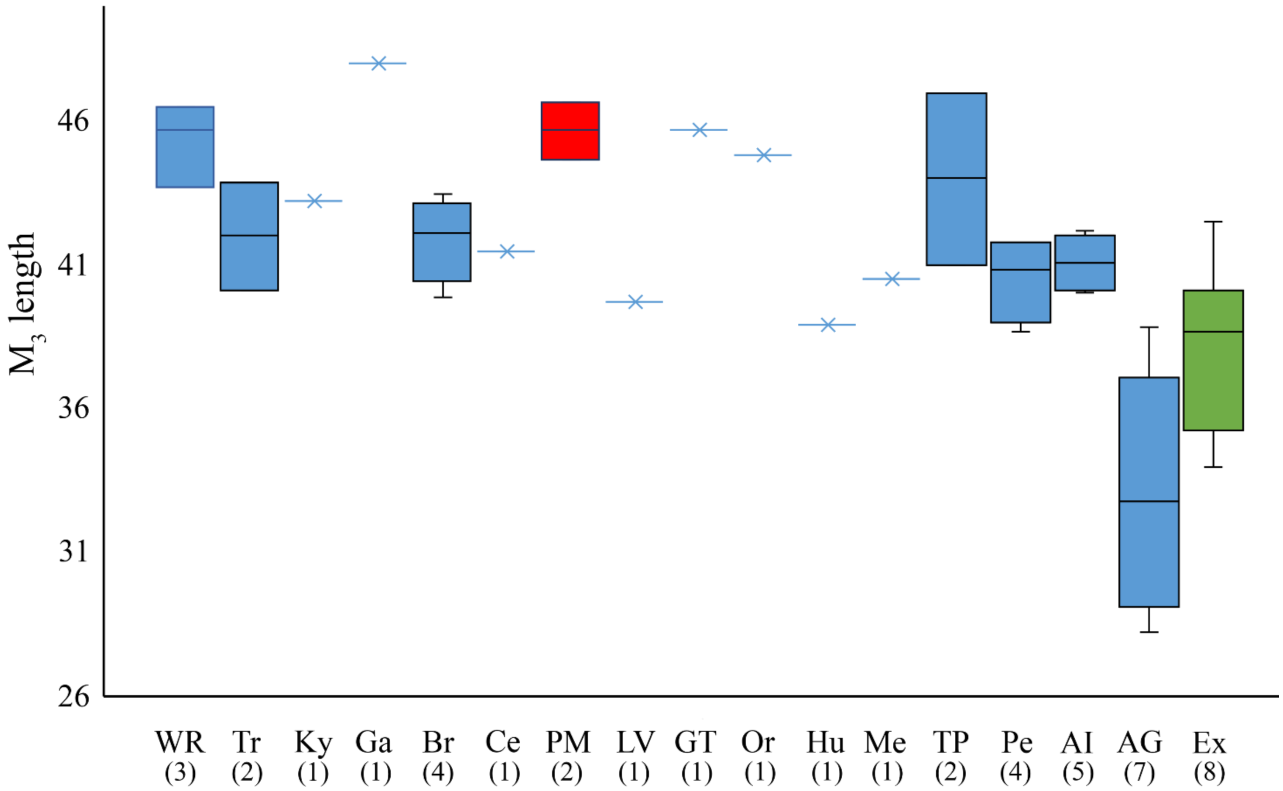

Figure 11 - M_3 length (mm) of *Sus scrofa* from Middle Pleistocene sites of Europe and extant specimens. Colors: Light blue - *Sus scrofa*: WR, West Runton; Tr, Trimingham; Ky, Kyparissia; Ga, Gajtan; Br, Bristie 1; Ce, Cerè; LV, Lunel-Viel; GT, Grays Thurrock; Or, Oreston; Hu, Hutton; Me, Melpignano; TP, Torre del Pagliaccetto; Pe, Petralona; AI, Apulia Interglacial (MIS 5 and MIS 3 Apulian sites); AG, Apulia Glacial (MIS 4 and MIS 2 Apulian sites); Red - PM, Ponte Molle; Green - Ex, extant specimens of *Sus scrofa*. Number of specimens indicated in brackets.

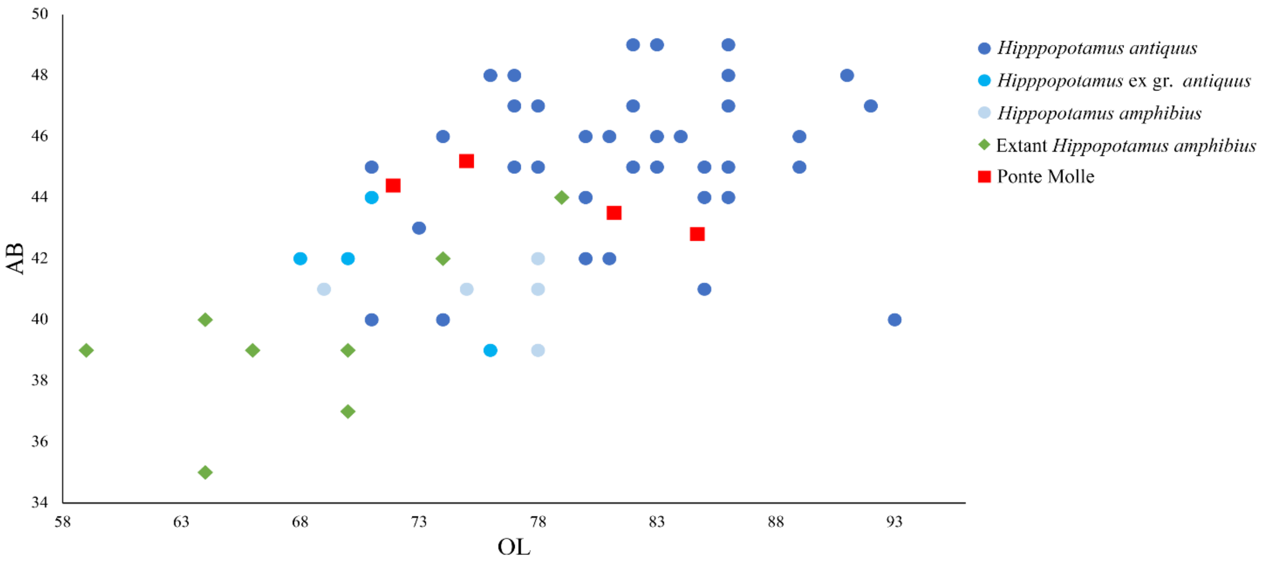

Figure 12 - Plot of outer length (OL) vs. anterior breadth (AB) of M_3 of fossil and extant hippos.

8.6. Discussion

8.6.1. The age of the deposit

From the stratigraphic analysis, the fauna from Cava D'Alessandri can be attributed to the lower gravelly level of the Valle Giulia Formation. This formation is chronologically constrained by two radiometrically well dated ignimbrites, i.e., at the base by the 550 ka old Via Tiberina Unit and on the top by the 449 ka "Tufo rosso a scorie nere sabatino". On the basis of the detailed sedimentological reconstruction of the internal architecture of the PM-Tor di Quinto fill terrace (*sensu* Pazzaglia 2013), it is excluded that the basal gravels of PM (*"cosiddette ghiaie diluviali di Ponte Molle"*) could be attributed to other fluvial formations older than the Valle Giulia Formation. In fact, the Fosso della Crescenza and Santa Cecilia Formations in the study area are very different from the basal gravels, being represented by prevailing sand and silt.

This suggests, for this restricted area, the occurrence of different facies for the different formations (or portions of them) to be correlated to diverse depositional environments: gravelly-dominated braided river environment for the basal Valle Giulia Formation; sand-dominated meandering-style river environment for the Fosso della Crescenza-Santa Cecilia Formations (Figure 5).

8.6.2. Biochronological implications

The revision of the geological and stratigraphic data indicates a time deposition between 540 and 460 ka for the mammal faunal assemblage from PM, which confirms a Middle Pleistocene age for the deposit. Among mammals identified in the MUST sample, several species provide further biochronological insights.

The first group considered is Rhinocerotidae, with two species recorded: *Stephanorhinus kirchbergensis* and *S. hemitoechus*. *Stephanorhinus kirchbergensis* is poorly documented in Italy, but in addition to PM this species was recorded from the Middle Pleistocene sites of Visogliano (MIS 13-10) (Pandolfi 2013) and Tor di Quinto (MIS 13) (Pandolfi and Marra 2015). *Stephanorhinus* *hemitoechus* can be considered an important marker as its earliest occurrence in Europe is from an undefined site of Campagna Romana, approximately dated at about 0.5 Ma (age estimated from the correlation of the encrusted pumice after texture and the geochemical analyses; Pandolfi et al. 2013), and from the Caune de l'Arago, from levels chronologically referred to MIS 14 (Moigne et al. 2006). The second group with strong chronological implications is Cervidae. The presence of *D. clactoniana* and *C. elaphus eostephanoceros* clearly indicates a Middle Pleistocene age. The Clacton fallow deer (*D. clactoniana*) appears in several European localities during MIS 11 (Breda et al. 2013) but it is possible that its dispersal predates this age. Indeed, in central Italy an earlier occurrence may be that from the levels alfa and a of Notarchirico (Cassoli et al. 1999), whose interbedded reworked volcanic minerals have been recently dated between 658±9 Ka and 612±5 Ka (Moncel et al. 2020; Mecozzi et al. 2021b). The other cervid group, the red deer, is represented by two different subspecies: *C. elaphus acoronatus* and *C. elaphus eostephanoceros*. The first subspecies is represented by an isolated partial cranium and complete antler (Figure 7). In Italy, the crownless red deer (*C. elaphus acoronatus*) is recorded from Slivia to Isernia FUs (ca 850-550 ka) (e.g., Palombo et al. 2001; Petronio et al. 2011). Its presence at PM is quite surprising, since it is the only taxon that would suggest an early Middle Pleistocene age. Despite this, we need to consider that these fossils were collected during the end of 1800s and early decades of 1900s, during quarrying activity. Moreover, this is one of those remains that are not accompanied by a historical label, and the possibility that it may have been recovered from an older deposit outcropping in the surrounding area should be taken into account. The other red deer, most common in the studied sample, is the eostephanoceros red deer (*C. elaphus eostephanoceros*) (Figure 7). This taxon was instituted by Di Stefano and Petronio (1993) mainly considering the antler discovered at Cava Nera Molinario (Rome, central Italy) and Fontana Ranuccio, localities chronologically ranging between about 500 - 400 Ka (Marra et al. 2018; Strani et al. 2018). However, considering the chronostratigraphic revision carried out by Marra et al. (2014, 2018), it seems that both subspecies are documented from deposits of the area of Rome referred to

MIS 13, namely *C. elaphus acoronatus* from Via Flaminia Km 8.2, and *C. elaphus eostephanoceros* from Cava Nera Molinario) (see Iannucci et al. 2021 for discussion).

Among the equids, of considerable interest is the presence of *E. hydruntinus*, whose evolutionary history was recently redefined by Boulbes and van Asperen (2019). The authors suggested a clear presence of this taxon in the European record since the late Middle Pleistocene (MIS 11), with a possible first dispersal during MIS 15. In Italy, this taxon was considered as a marker of the Aurelian large mammal faunal assemblage (late Middle Pleistocene, Gliozzi et al. 1997). However, new findings from Vallparadís Section (level 11, EVT3, dated later than 600 ka) (Aurell-Garrido et al. 2010; Martínez et al. 2014) and quarry Carpentier d'Abbeville (dated and correlated with MIS 15) (Antoine et al. 2016) suggest an earlier dispersal of the Regalìa Ass (*E. hydruntinus*) in Europe.

The wild boar, *S. scrofa*, is scarcely represented during early Middle Pleistocene glacial stages, and the relatively large size of the remains recovered from PM is close to that of other findings referred to MIS 13, MIS 11 or MIS 9 interglacials (Figure 11; Iannucci et al. 2020b).

Other mammal taxa identified in the PM faunal assemblage indicate a Middle Pleistocene age, but with no clear chronological definition, among which *H.* ex gr. *antiquus, E. mosbachensis*, and *C.* cf. *mosbachensis*. Finally, several species from PM provide no constraints, since they are characterized by a long chronological distribution (Middle to Late Pleistocene or Holocene), as *P. antiquus, B. primigenius, S. scrofa, C. capreolus, C. fiber, C. crocuta*, *Lynx* sp. and *M. meles*. In this scenario, the faunal assemblage of PM could be referred to MIS 13.

8.6.3. Paleoenvironmental implications

Redefining the PM faunal assemblage provides important paleoenvironmental and paleoecological clues. Indeed, the species represented constitute a faunal assemblage typical of Middle Pleistocene interglacials of Italy (Strani et al. 2018). The presence and relative abundance of *P. antiquus, H.* ex gr. *antiquus, C. elaphus eostephanoceros, D. clactoniana, S. scrofa* and *B. primigenius* indicate warm and humid climatic conditions. This could be also true for *Hemibos galerianus,* ancestral to the *Bubalus* lineage (Petronio and Sardella 1998; Martínez-Navarro et al. 2011), considering the occurrences and plausible ecological preferences of the extinct buffalo (Koenigswald et al. 2019). Nonetheless, the mix of taxa adapted to different environments suggests the presence of a mosaic of open spaces (e.g., rhinos and equids) and woodlands (e.g., cervids and *S. scrofa*).

Other ecological and paleoenvironmental information can be inferred from the biometric comparisons of *S. scrofa* and *D. clactoniana*. In fact, even though these species are greatly chronologically and geographically variable (Lister et al. 2010; van der Made et al. 2014; Di Stefano et al. 2015; Iannucci et al. 2020a; Stefanelli and Mecozzi 2020), shifts in size can be influenced by ecological factors (Geist 1971, 1987; Lindstedt and Boyce 1985; Weinstock 1997).

Focusing on a temporal and chronologically well-constrained sample, Iannucci et al. (2020b) recognized several size shifts experienced by *S. scrofa* during the late Middle Pleistocene to Early Holocene of Apulia in southern Italy, with smaller population occurring during glacial stages. They suggest an indirect triggering role of climate, in reducing the availability of trophic resources. Even though more data are needed to substantiate this hypothesis and elucidate its geographical constraints, *S. scrofa* remains from the Middle Pleistocene of the area of Rome are scanty but usually large-sized (Figure 11), and thus fit well with what expected for interglacial stages in the Mediterranean area.

The very small size of the fallow deer of PM is also interesting though puzzling to interpret. Indeed, according to Weinstock (1997) the more severe winters of glacial stages should cause a strong decrease of the food supply and lead to a higher mortality rate. This leads to a decrease of the intraspecific competition during the following growth season (Guthrie 1984), which implies a higher quality and quantity of food resources (Weinstock 1997). Therefore, glacial and interglacial size fluctuations in cervids should be observed. Nevertheless, the dimensions of the late Early to Middle Pleistocene European samples do not support this separation (Figure 10). It is possible that this reflects a different ecological adaptation in the species, which would be worth to be investigated in future research.

8.7. Conclusions

The large mammal faunal assemblage from Ponte Molle is dominated by *Bos primigenius*, with *Palaeoloxodon antiquus*, *Hippopotamus* ex gr. *antiquus, Cervus elaphus eostephanoceros* and *Equus mosbachensis* well represented (Table 1). Carnivorans are documented by a few taxa, all represented by a limited sample.

Aside from a few spurious Holocene specimens, most of the faunal elements are consistent with an attribution to a single assemblage, which best fits within the Fontana Ranuccio FU. The historical background and geological constraints also support the view that the recovery of fossil remains from the area of PM was concentrated in the Valle Giulia Formation, which is dated between 540 ka and 460 ka. Even though we cannot exclude that a few specimens may have been misreported or mixed from different layers, an age older than 550 Ky seems highly unlikely, as no formation of such an old age is documented in the area.

Moreover, the presence or relative abundance of species usually widespread during warm periods, such as *B. primigenius, P. antiquus, H.* ex gr. *antiquus, C. elaphus eostephanoceros* and *D. clactoniana,* is also suggestive of an interglacial environment.

The reassessment of the classical fauna from PM, and the redescription of the sections of Cava D’Alessandri, Torretta di Quinto, and Acquatraversa will serve as a basis for reinterpreting other historical and recent collections of the area of Rome, as well as providing new data for our understanding of Middle Pleistocene mammal assemblages of Europe.

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9. Paper 8

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

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Abstract

The extant wild boar *Sus scrofa* has one of the largest geographical ranges 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.

Keywords: Quaternary; large mammals; Aurelian; body mass; Euro-Mediterranean; Bergmann's rule

9.1. Introduction

The extant wild boar (*Sus scrofa*) is one of the widest-ranging mammals in the world, occurring natively throughout the Palaearctic, 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 (Groves 2007; Albarella et al. 2009). The species originated in Asia during the Early Pleistocene and spread in Europe during the late Early Pleistocene (Epivillafranchian) (Bellucci et al. 2015; Martínez-Navarro et al. 2015; Frantz et al. 2016; Cherin et al. 2018; Iannucci et al. 2020). 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 (Ambrosetti et al. 1979; Petronio et al. 2011). 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 (Hünermann 1969, 1975; Faure and Guérin 1983; Guérin and Faure 1997; Petronio et al. 2011; Tsoukala and Guérin 2016). The validity of this taxon is often questioned, but there is a general consensus in recognizing the large dimensions of early wild boars (Lister et al. 2010; Made et al. 2017). 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 (Hünermann 1969), eventually leading to the modern *S. s. scrofa* since the Late Pleistocene (Faure and Guérin 1983). However, this scenario is in a contradiction with the high adaptive plasticity exhibited by the species (Ballari and Barrios-Garcia 2014), which displays substantial variation in size and morphology throughout its geographic range (Genov 1999; Albarella et al. 2009).

In Italy —an especially suitable territory for biochronological and paleoenvironmental studies of the Mediterranean area (Azzaroli 1977; Sardella et al. 2018a)— 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., Del Campana 1909; Mirigliano 1942; Minieri et al. 1995), and more generally in Europe (e.g., Faure and Guérin 1983; Moigne et al. 2006; Lister et al. 2010), thus challenging the hypothesis of a gradual size reduction.

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

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

9.1.1. 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, Gaillard et al. 1989; Martínez-Navarro et al. 2015).

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 (Okarma et al. 1995; Nores et al. 2008; Frauendorf et al. 2016).

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.

9.2. 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 (Masini et al. 1990; Sala et al. 1992; Gliozzi et al.

1997; Bedetti et al. 2001; Sala and Masini 2007; Petronio et al. 2007). 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 Southwest-Northeast axis, represents a noteworthy case, a peninsula in the peninsula (Figure 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 in 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., Botti 1874a, 1874b, 1890; Blanc 1920). 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 (Sala et al. 1992; Bedetti et al. 2001; Petronio et al. 2007; 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 (Sala et al. 1992; Bologna et al. 1994; Sardella et al. 2005), 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) (Petronio et al. 2008; Pandolfi et al. 2011, 2013). Later, the revision of the material from the uppermost fossiliferous layer of the succession (bed 8) led to refer this level to MIS 3 (Mecozzi and Bartolini Lucenti 2018; Salari et al. 2019). 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 (Braun and Palombo 2012; Pandolfi and Petronio 2015; Mecozzi et al. 2018; Sardella et al. 2018b; among others).

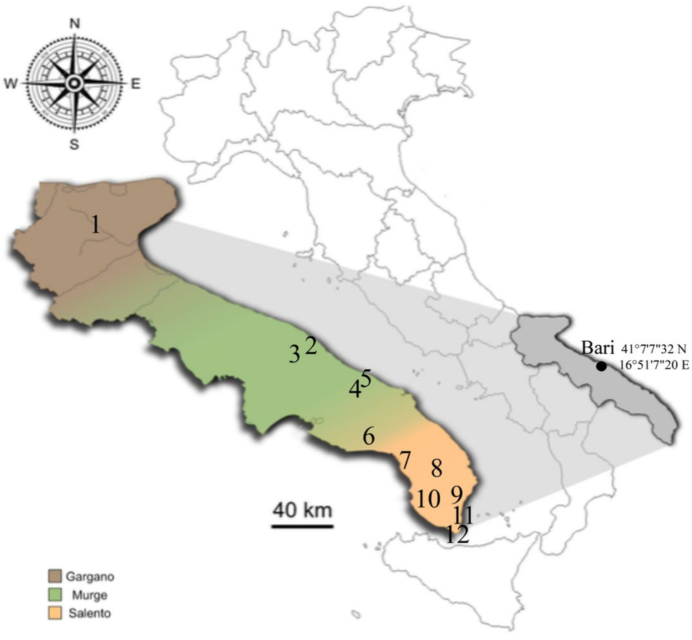


Figure 1 - Location of Apulia (grey area) along the Italian Peninsula. The Gargano, Murge and Salento areas are indicated. 1 – Grotta Paglicci; Murge: 2 – Grotta delle Mura; 3 – Grotta della Jena; 4 – Grotta Laceduzza; 5 – SMA-esterno; 6 – Avetrana; 7 –Grotta Mario Bernardini; Grotta Uluzzo C; 8 – Melpignano; 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 (References in Table 1).

9.3. Materials and methods

The sample of Suidae analysed herein is housed in several Italian institutions and museums (Table 1 and Supplementary Material). We built our dataset by considering the available studies on specimens from the late Middle Pleistocene to the Early Holocene of the Apulian region (Table 2 and Supplementary Material). 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 Table 3 (upper teeth), Table 4 (lower teeth), and Table 5 (postcranial). Craniodental and postcranial measurements were taken to the nearest 0.1 mm with a digital caliper, as reported by von den Driesch (1976).

We also performed body mass estimates (Tables 5-6) 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 (GLl) of the talus (Tsubamoto 2014). Slope and intercept values are given in Table 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., Asperen 2010; Mazza and Bertini 2013; Marciszak et al. 2019). Moreover, this resolution is at a finer scale than what adopted in previous works on *S. scrofa* (Faure and Guérin

1983; Guérin and Faure 1997; Tsoukala and Guérin 2016). 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 (Sadori and Narcisi 2001; Martrat et al. 2014; Giustini et al. 2018). 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 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-value > 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).

9.3.1. 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”.

Site Anatomical portion	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										1					
Femur			1						2													1		
Tibia			3	1					1										1					
Fibula																						2		
Metatarsal			2									1	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

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 1); 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.

Site	Reference	MIS	Date
San Sidero	Sala et al. (1992); Mecozzi et al. (2019a); This work	?9-8	Biochronology
Melpignano	Sala et al. (1992); Mecozzi et al. (2019a); This work	?9-8	Biochronology
Grotta delle Striare	Cigna and Orlandi (1954); Maviglia (1955); This work	?7-5	Biochronology
Grotta delle Tre Porte	Blanc (1958); This work	?7-5	Biochronology
Avetrana beds 2-7	Sardella et al. (2005); Petronio et al. (2008)	5	Biochronology
Grotta dei Giganti	Blanc (1958); Aureli and Ronchitelli (2018)	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	Mecozzi and Bartolini Lucenti (2018); Salari et al. (2019)	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	Baills (2015); Coppola et al. (2017)	2	Radiometric data
Grotta Romanelli	Sardella et al. (2018b); Calcagnile et al. (2019)	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 (1966, 1969)	1	Stratigraphy and Chrono-cultural

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

Site	Reference	MIS	P^3L	P^3W	P^4L	P^4W	M^1L	M^1W	M^2L	M^2W	M^3L	M^3W
Melpignano	Bologna (1992)	?9-8									38.5	19.0
Grotta delle Tre Porte	This work	?7-5									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 *Sus scrofa*	Kuşatman (1991); This work	14.5	10.9	14.2		14.6		16.4 (min=15.0-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=19.0-max=21.8)

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_2L	P_2W	P_3L	P_3W	P_4L	P_4W	M_1L	M_1W	M_2L	M_2W	M_3L	M_3W
Melpignano	This work	?9-8					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	?7-5							16.2	11.8				
Avetrana 2-7	This work	5									25.9	17.5	41.1 (min=40.3-max=41.9)	17.7 (min=17.5-max=17.9)
Grotta dei Giganti	This work	4									22.8	15.1	37.1	16.7
Grotta Zinzulusa - B6	This work	4	13.2	7.6			15.3	9.0	15.6	10.6	22.1	14.5	33.0 (min=32.8-max=33.1)	15.9 (min=15.2-max=16.6)
Grotta Mario Bernardini	This work	4					13.8	9.7	16.6	12.6				
Grotta Uluzzo C	This work	4											29.1	15.4
Grotta Laceduzza	This work	4									21.2	12.7	30.5	14.6
Avetrana 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)	23.8 (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										
Grotta Zinzulusa - B5-3	This work	2							16.7 (min=16.2-max=17.1)	11.3 (min=11.1-max=11.4)				
Grotta Paglicci	Boscato (1994)	2											38.8	17.8
SMA-esterno - Epigravettian	This work	2											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	15.0 (min=14.6-max=15.3)	34.2 (min=32.0-max=36.4)	15.9 (min=14.7-max=17.1)
Grotta della Jena	This work	1											29.0	14.6
Grotta delle Mura	Bon and Boscato (1993)	1									23.7	14.0	34.0	16.7

Grotta delle Prazziche	This work	1			12.1	7.0			17.8	13.2	22.9	15.7	35.9 (min=35.7-max=36.2)	16.0 (min=15.6-max=16.4)
Extant *Sus scrofa*	Kuşatman (1991); This work		11.5	5.3	14.2	7.4	14.7 (min=14.2-max=15.6)	9.3 (min=8.9-max=9.8)	15.5 (min=13.5-max=18.0)	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 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	Humerus Bd	Humerus estimate	Radius Bd	Radius estimate	Talus GLl	Talus estimate
Melpignano	This work	?9-8			37.4	111.4		
Grotta Mario Bernardini	This work	4	47.7	159.1				
Avetrana 8	This work	3	51.2 (min=50.4-max=52)	198.2 (min=188.7-max=207.7)			58.9 (min=57.1-max=60.8)	289.6 (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 (min=46-max=52.4)	166.3 (min=132.9-max=199.8)
Grotta Romanelli	This work	1	45.3	137.1				

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	M^1L	M^2L	M^3L	M_1L	M_2L	M_3L
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	Boscato (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 Boscato (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 *Sus scrofa*	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)

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.

Equation	Reference	Measure (a)	Slope (b)	Intercept (c)
Body mass = a x b + c	Damuth (1990)	M^1L	3.09	1.21
Body mass = a x b + c	Damuth (1990)	M^2L	3.03	1.06
Body mass = a x b + c	Damuth (1990)	M^3L	2.81	1.29
Body mass = a x b + c	Damuth (1990)	M_1L	3.11	1.24
Body mass = a x b + c	Damuth (1990)	M_2L	3.07	1.07
Body mass = a x b + c	Damuth (1990)	M_3L	2.99	0.80
Log_{10}(Body mass) = Log_{10}(a) x b + c	Scott (1990)	Humerus Bd	3.09	0.02
Log_{10}(Body mass) = Log_{10}(a) x b + c	Scott (1990)	Radius Bd	2.48	1.14
[Ln(Body mass) = Ln(a) x b + c] x 1.345	Tsubamoto (2014)	Talus GLl	3.12	-0.46

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.

9.4. Results and discussion

9.4.1. Morphometry

Suidae from the late Middle-Late Pleistocene of Apulia display a huge dental variability (Figures 2, 3, and 4). Nevertheless, the statistical analysis of M_3L 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) (Figure 5).

Lower third molars are larger in Melpignano (M_3L 40.5 mm) and interglacial specimens (Avetrana 2-7: M_3L mean 41.1 mm, min 40.3 mm, max 41.9 mm; Avetrana 8: M_3L mean 41.1 mm, min 40.0 mm, max 42.2 mm) than in the glacial ones (the longest specimen is from Grotta Paglicci: M_3L 38.8 mm) and extant wild boar (M_3L mean 38.2 mm, min 34.0 mm, max 42.5 mm) (Table 4, Figure 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) M_3L of 41.1 mm is 20.2% larger than the average glacial length of 32.8 mm, with no overlap in measurement (Table 4, Figure 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, M_3L from Avetrana are comparable to Bristie 1 (Trieste) (M_3L mean 42.3 mm, min 39.6 mm, max 44.1 mm; M_3W mean 18.9 mm, min 18.0 mm, max 19.7 mm), Cerè (M_3L 41.5.0 mm, M_3W 17.5 mm;) and the upper levels of Torre del Pagliaccetto (Rome) (Id. n.399: M_3L 47.0 mm, M_3W 20.0 mm; Id. n.624: M_3L 41.0 mm M_3W 19.0 mm) chronologically referred to the Middle Pleistocene (Fabiani 1919; Caloi and Palombo 1978; Lugli and Sala 2000; Ghezzo et al. 2013). Conversely, small-sized *S. scrofa* is reported from Grotta della Cala (Salerno) levels dated to 26.380 ± 260 ^{14}C yr BP and 26.680 ± 320 ^{14}C yr BP (MIS 2) (M^3L 30.1 mm, M^3W 17.6 mm; M_2L 25.2 mm, M_2W 17.0 mm; M_3L 27.5 mm, M_3W 15.6 mm) (Boscato et al. 1997). Second molar measurements are consistent with these results (interglacial-glacial divergence: M^2L 3.2%, M_2L 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 (Tables 3-4, Figures 3-4).

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; 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: 51 mm; 54 mm; 57.5 mm) (Table 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 (Guérin and Faure 1997; Lister et al. 2010), 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., Hünermann 1969, 1975; Faure and Guérin 1983; Guérin and Faure 1997). Conersely, 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 (Sadori and Narcisi 2001; Martrat et al. 2014; Giustini et al. 2018), 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 M_3L (min 28.2 mm; max 38.8 mm). The variability of this group, unfortunately represented by only two specimens (Table 4), exceeds that of the extant sample, even if it does not overlap with MIS 3 and MIS 5 specimens.

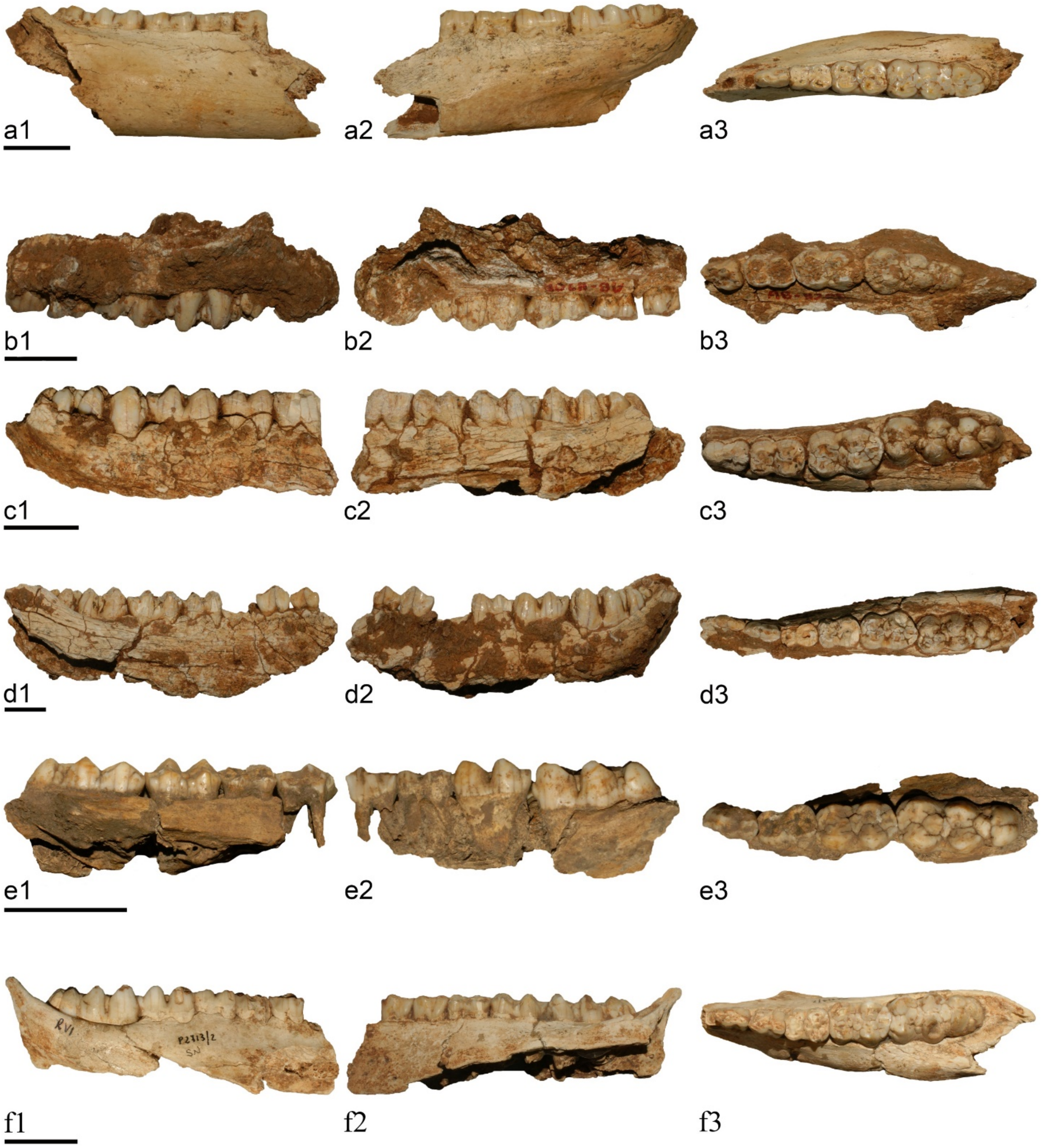


Figure 2 - Fossil specimens from Apulian sites: a – MPND683, right hemimandible from Melpignano; b – A8-11-205, left maxillary from Avetrana; c – AND1694, left hemimandible from Avetrana; d – AND1695, right hemimandible from Avetrana; e – ISIPU-GZ482, right hemimandible from Grotta Zinzulusa; f – MUCIV-GR3499, left hemimandible from Grotta Romanelli. Fossils are figured in labial (1), lingual (2), and occlusal (3) views. Scale bars 3 cm.

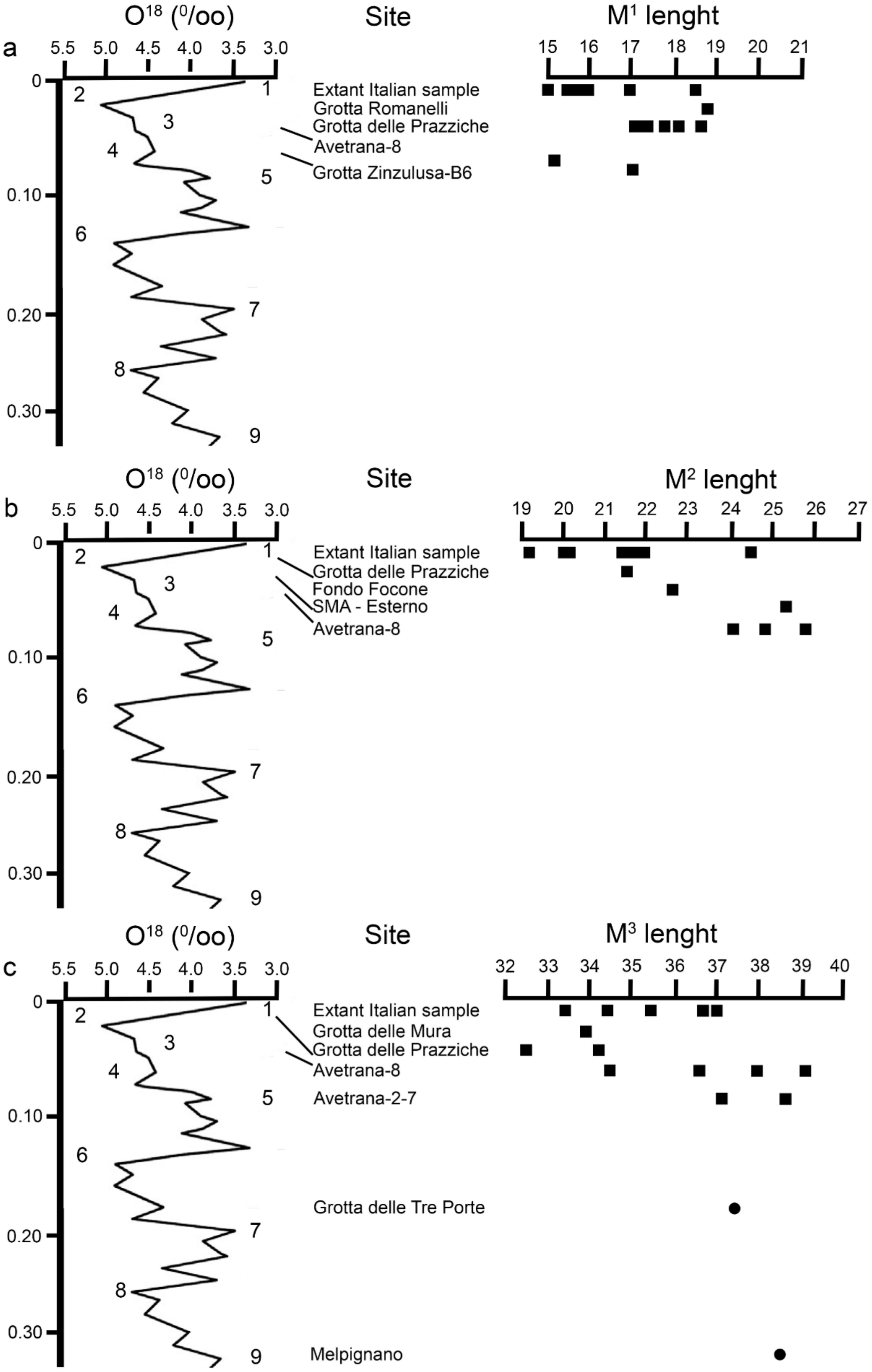


Figure 3 - The variation in size in *Sus scrofa*, as indicated by the length of the upper first (a), second (b), and third (c) molar. Age in millions of years (vertical axis) and oxygen isotope curves (horizontal axis; after Shackleton, 1995) on the left, followed by the fossiliferous sites and their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

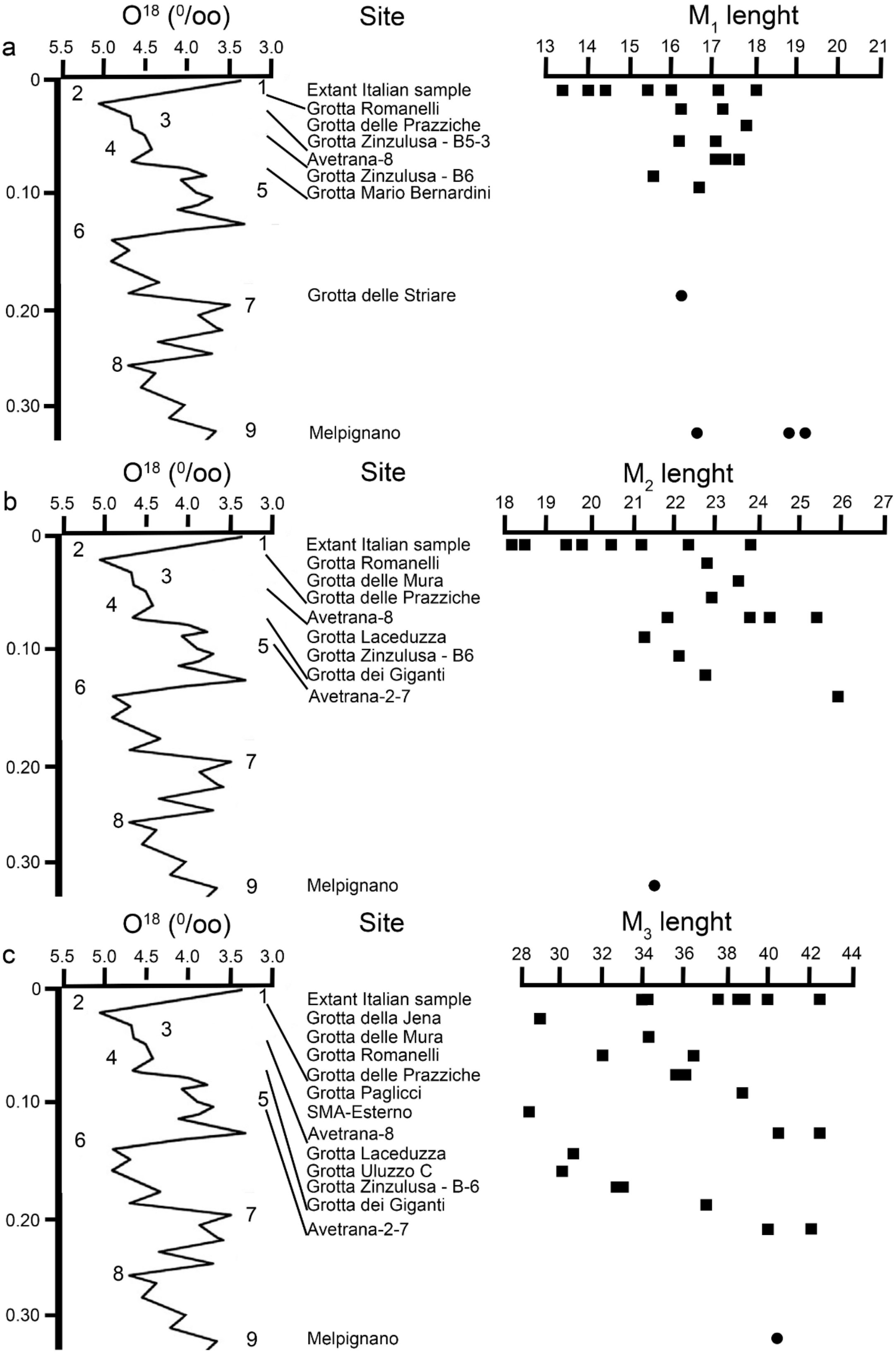
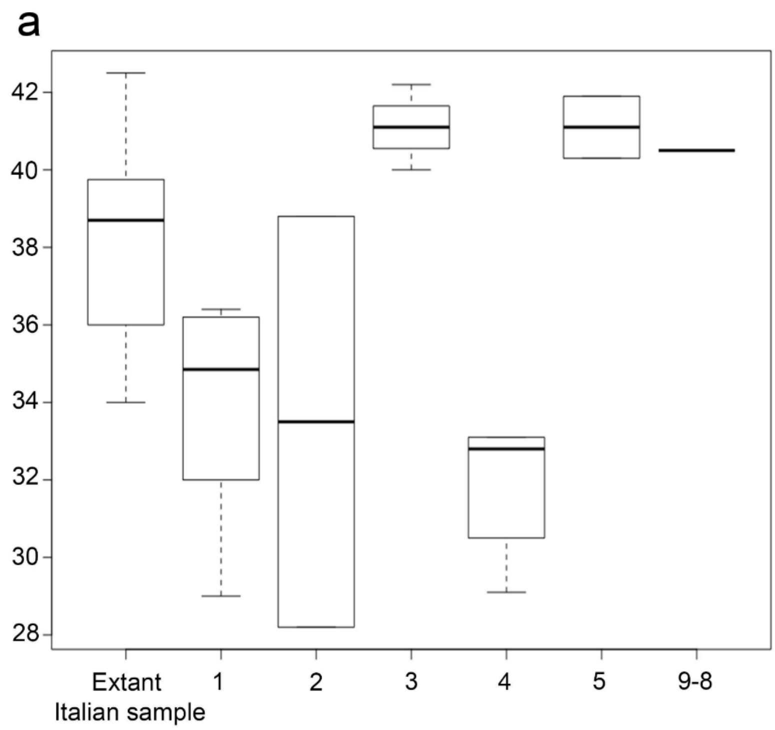


Figure 4 - The variation in size in *Sus scrofa*, as indicated by the length of the lower first (a), second (b), and third (c) molar. Age in millions of years (vertical axis) and oxygen isotope curves (horizontal axis; after Shackleton, 1995) on the left, followed by the fossiliferous sites and their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



b

Groups	p-value
Extant Italian sample	**0.00**
MIS 2	0.88
MIS 3	**0.00**
MIS 4	0.48
MIS 5	**0.00**
MIS 9-8	**0.04**

Figure 5 - (a) Boxplot of M_3 length from the late Middle Pleistocene-Early Holocene sites grouped for chronology (MIS) (see Table 1); (b) Table of p-values for the linear model.

9.4.2. Body mass

Predicted values vary greatly between different measured elements (teeth: M^1L min estimate: 49.4 kg; M_3L max estimate: 127 kg; Humerus Bd min estimate: 137.1 kg; max estimate: 207.7 kg; Tables 5-6). 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 (Janis 1990; Scott 1990; Fortelius et al. 1996). 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 (Janis 1990; Fortelius et al. 1996). 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 (Table 6). In fact, M^2L 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. M_2L 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. M_1L, M^3L, and M_3L estimates are consistent with these results, even though they provide less reliable absolute values. The only exception are M^1L 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.

9.4.3. 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 (Faure and Guérin 1997; Albarella et al. 2009). This pattern has been suggested to be valid even through time for other species, with large-sized *Crocuta crocuta* (Klein and Scott 1989), *Bos primigenius* (Cerilli and Petronio 1992; Wright 2013) and *Canis lupus* (Sansalone et al. 2015; Mecozzi and Bartolini Lucenti 2018) 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., Demment and Van Soest 1985; Dayan et al. 1991; Ashton et al. 2000; Yom-Tov and Geffen 2006; Meiri et al. 2007; McNab 2010; Huston and Wolverton 2011). Indeed, contrary to the rule predictions, several fossil mammals underwent drops in size in colder climatic conditions (Kurtén 1968; Collinge 2001; Lister et al. 2010) or exhibited a series of size fluctuations for which climate is hardly the solely responsible (Made et al. 2014; Marciszak et al. 2019). 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.

During glacial periods, in the Mediterranean area the reduced availability of trophic resources was pronounced, with generally open palaeoenvironments dominant (steppe and/or grasslands) (Allen and Huntley 2009; Renault-Miskovsky et al. 2011, 2015; 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; McNabb 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 (Ashton et al. 2000; Freckleton et al. 2003; Meiri and Dayan 2003), 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 (Steudel et al. 1994; Ashton et al. 2000). The paradox is solved if another underlying principle is proposed to describe the observed pattern: the availability of trophic resources (McNab 2010; Huston and Wolverton 2011). 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 (Pianka 1970; Tuomi 1980). Palaeontologists are well aware of the dissimilar rate of change in small and large mammals, which enhance the importance of integrated biochronological scales (Gliozzi et al. 1997; Masini and Sala 2007).

Of course, the dichotomy between r and K strategy is an empirical generalization and species are distributed along an ecological continuum (Pianka 1970; Tuomi 1980). 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).

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 Supplementary Material).

9.5. 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 M_3L 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%). M^2L, M_2L, and M^3L are consistent with these results, even though differences are less pronounced for second molars and we lack M^3 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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9.S1. Late Middle Pleistocene-Early Holocene Apulian fossil Suidae

9.S1.1. Melpignano

The site of Melpignano, near the homonymous town, is a quarry area where several karst fissures — locally known as "ventarole"— are exposed (Figure 1). The deposits are filled with reddish sediments (called *terre rosse*) in the lower part and brownish sediments (called *terre brune*) in the upper, both particularly rich in vertebrate fossil remains (Bologna et al. 1994). After the first description provided by Mirigliano (1941), several Institutions, as the IsIPU and the IIPP, with the support of the local Salentine Speleological group, finely investigated the fossiliferous area of Melpignano (De Lorentiis 1958; Cardini 1962a). Recently, the age of the lower deposit has been extended to the late Middle Pleistocene (Mecozzi et al. 2019a). The Suidae sample was recovered from the *terre rosse* of different karst cavities (Tables 1-2, Figure 2). Furthermore, an isolated upper tooth reported by Bologna (1992) from "Cava Nuzzo" of Melpignano was included.

Repository: MPUN: Mirigliano collection - PF: Cava Nuzzo and Cava Bianco.

9.S1.2. San Sidero

The "ventarole" of San Sidero are located along the state road (SS16) between the towns of Corigliano d'Otranto and Maglie (Figure 1). The first description of the deposit and its faunal assemblage was reported by Cardini (1962b). The mammal fauna from San Sidero was also studied by other authors (De Giuli 1980, 1983; Bedetti et al. 2004; Petrucci et al. 2012; Iurino et al. 2013, 2015). Similarly to the Melpignano sediments, these "ventarole" include *terre rosse* layers in the lower part and *terre brune* layers in the upper part. The Suidae sample has been collected from the *terre rosse* of Cava L (Tables 1-2).

Repository: PF; MGP.

9.S1.3. Avetrana

The site, located in an abandoned quarry near the town of Avetrana, was described in 2005 by a team of palaeontologists of Sapienza University of Rome. It consists of a fossiliferous karst filling deposit within the Early Pleistocene limestone known as "Calcareniti di Gravina" (Figure 1). The rich faunal assemblage recovered from the deposit has been studied in a number of works (Sardella et al. 2005; Petronio et al. 2008; Mecozzi and Bartolini Lucenti 2018; Salari et al. 2019; among others). The studied sample has been collected from beds 2-8 and is here subdivided according to the chronology of the layers (beds 2-7, MIS 5; bed 8, MIS 3; Tables 1-2, Figure 2).

Repository: MUST.

9.S1.4. Grotta delle Striare

This site includes several caves, North-South exposed, located along the road connecting Castro to Santa Cesarea Terme (Figure 1). This cave complex was discovered by Paolo Emilio Stasi in 1879, but geo-palaeontological surveys were carried out only in the 1950s (Cigna and Orlandi 1954; Maviglia 1955; Orlandi and Cigna 1955). Some vertebrate remains were described by Di Stefano et al. (1992). Only an isolated lower tooth has been attributed to *Sus scrofa* (Tables 1-2).

Repository: IsIPU.

9.S1.5. Grotta delle Tre Porte

The coastal cave, located at Punta Ristola, was discovered in 1936 during a field survey of the IsIPU conducted by Gian Alberto Blanc (Blanc 1958) (Figure 1). The cave includes three different rooms, with two of these, Antro del Bambino and Grotta Titti, containing Pleistocene deposits. The Suidae material was recovered from level F of Antro del Bambino, associated with Mousterian (Middle Palaeolithic) lithic industry (Tables 1-2).

Repository: IsIPU.

9.S1.6. Grotta Mario Bernardini

Discovered in 1961, Grotta Mario Bernardini (also known as Grotta di Santa Margherita) is located along the Ionian coast of Apulia near the village of Santa Caterina (Borzatti von Löwenstern 1970, 1971) (Figure 1). The vertebrate fauna has never been studied in detail, although a preliminary mammal list was provided by Borzatti von Löwenstern (1970, 1971). The Suidae material has been recovered from levels B4-3 and A8, associated with Mousterian (Middle Palaeolithic) lithic industry (Tables 1-2).

Repository: IGF.

9.S1.7. Grotta Uluzzo C

The cave opens into the Cretaceous limestone of the Calcari di Melissano Formation at 15 m a.s.l., located in the Uluzzo Bay near the town of Nardò. (Figure 1). The deposit and its stratigraphic sequence were described by Borzatti von Löwenstern (1965, 1966a) and Borzatti von Löwenstern and Magaldi (1969). Borzatti von Löwestern (1965, 1966a) reported a preliminary list of the fossil mammals recovered from this locality. The studied fossils have been recovered from levels G-E (Tables 1-2). In these levels, the human presence is documented by lithic industry attributed to the Mousterian (Middle Palaeolithic).

Repository: IGF.

9.S1.8. Grotta dei Giganti

The site is a coastal cave located between Punta Ristola and Punta Marchiello (Blanc 1958) (Figure 1). In the 1930s, the cave was discovered by the IsIPU during a field survey conducted by G.A. Blanc. A list of the faunal remains was reported by Blanc (1958). The radiocarbon dating attempt performed by Alessio et al. (1978) yielded no results. The material was found in levels 3f-3c (Tables 1-2), where artefacts referred to as Mousterian (Middle Palaeolithic) were also recovered.

Repository: ITCGC.

9.S1.9. Grotta Laceduzza

The fossiliferous site is located on the Adriatic coast of the Apulian Peninsula, about 154 m a.s.l., near the town of San Michele Salentino (Figure 1). The cave was discovered by the "Gruppo Speleologico Salentino Pasquale de Lorentiis" in 1970 (Coppola 2012). A preliminary description of the mammal assemblage from the lower part of the deposit, including a rich sample of *Meles meles*, was recently carried out and few remains of *Sus scrofa* were found (Tables 1-2) (Mecozzi et al. 2019b). In the lower part of the deposit, lithic industry referred to Mousterian (Middle Palaeolithic) was also collected (Spera 2012).

Repository: MPCCSM.

9.S1.10. Grotta Zinzulusa

Grotta Zinzulusa is located along the Adriatic coast of the Salentine Peninsula, near the town of Castro (Figure 1). Francesco Antonio Del Duca, bishop of the diocese of Castro, described for the first time the cave in 1793 in a letter to Ferdinando IV, king of the Kingdom of the Two Sicilies. A century after the discovery, the Pleistocene sedimentary succession and its archaeological and palaeontological content were described by Botti (1874a). In the cave, there are several infilling successions, called Vestibolo, Antro B, Antro C, Antro D, Antro E, and Duomo (Blanc 1962). The Suidae material was found in the Antro B, from levels B6 and B5-3 (Blanc 1962; Cardini 1962b) (Tables 1-2, Figure 2). The artefacts from level B6 were attributed to Mousterian (Middle Palaeolithic), instead those from levels B5-3 were referred to Gravettian (Upper Palaeolithic). Nowadays, the cave is a well-known geoheritage resource and it is visited annually by approximately 70,000 people (Sardella et al. 2019).

Repository: IsIPU.

9.S1.11. Fondo Focone

The site, located near the town of Ugento (Figure 1), was discovered in the early 1960s during a survey conducted by Decio de Lorentiis, but the first excavations in the sinkhole were performed by Luigi Cardini (Cardini 1965). During the 1970s, the fieldwork stretched on under the direction of Eugenia Segre Naldini, who opened a trench, 3 x 3 m, called “Trincea B” (Cancellieri 2017). Cardini (1965) reported a list of both vertebrate and archaeological content. Associated to fossil remains (Tables 1-2), artefacts attributed to Early Epigravettian (Upper Palaeolithic) were found (Cancellieri 2017).

Repository: IsIPU.

9.S1.12. Santa Maria d’Agnano – esterno (SMA-esterno)

The Grotta di Santa Maria di Agnano is located near the town of Ostuni, on the north-western margin of Risieddi promontory, at about 175 m a.s.l. (Coppola 2012) (Figure 1). The site was discovered during the 1960s by the “Associazione Studi e Ricerche” (Studies and Research Association) (Coppola 2012). The systematic excavation of the deposit started in 1991 and continues still today (Coppola 1992, 2012; Vacca et al. 1992; Vacca and Coppola 1993). The area of SMA-esterno is outside the cave, close to the present entrance (Coppola and Baills 2008; Baills 2015; Renault-Miskovsky et al. 2015; Coppola et al. 2017; Chakroun et al. 2018). The fossil remains come from level 8, dated 26339-25779 ^{14}C cal yr BP and from levels 6A-4C, dated 16745-16401 ^{14}C cal yr BP and 18013-17587 ^{14}C cal yr BP respectively (Tables 1-2) (Renault-Miskovsky et al. 2011; Baills 2015). Instead, the artefacts collected from the level 8 were attributed to Gravettian and those from level 6A-4C to Early Epigravettian (Renault-Miskovsky et al. 2011; Baills 2015).

Repository: MPCCSM.

9.S1.13. Grotta Romanelli

The site, located along the Adriatic coast near the town of Castro (Figure 1), was discovered in 1874 by Ulderigo Botti (Botti 1874b) and in 1900 Paolo Emilio Stasi realized its remarkable importance as the first evidence of the Upper Palaeolithic in Italy. In 1914, Gian Alberto Blanc began a pioneering excavation campaign, during which the first systematic archaeological/palaeontological and stratigraphic study using scientific methods was carried out. Nowadays, Grotta Romanelli is recognized as a key site for the Mediterranean Pleistocene for its archaeological and palaeontological content and the relative stratigraphical, geomorphological and radiometric data (Sardella et al. 2014, 2018, 2019). The upper complex (level E-A) was referred to the end of Late Pleistocene and Early Holocene on the basis of radiocarbon-dated during the 1960s (Bella et al. 1958; Vogel and Waterbolk 1963; Alessio et al. 1964, 1965; Sardella et al. 2018). In 2015, a new excavation campaign began, led by a team from Sapienza University of Rome, with the aim to provide an updated stratigraphic and chronological scheme as well as to describe the fossil remains and artefacts (Giustini et al. 2018; Sardella et al. 2018, 2019). Recently, new fossil remains were submitted for ^{14}C dating in order to confirm the chronology of the cave (Calcagnile et al. 2019). The results expand and refine the previous chronology, with a time span for the level D and B respectively from 11858 ± 85 ^{14}C yr BP to 8397 ± 45 ^{14}C yr BP (Calcagnile et al. 2019). The sample considered in this study has been found in the upper part of the deposit (level E-A) (Tables 1-2, Figure 2). The lithic industry found in the upper complex (level E-A) has been attributed to final Epigravettian (Upper Palaeolithic).

Repository: MUCIV; PF.

9.S1.14. Grotta della Jena

The cave, located 2 km from the town of Castellana, was discovered in 1872 (Figure 1). The site belongs to the well-known karst system of Pozzo Cucù, one of the greatest of the Italian Peninsula. Grotta della Jena has an historical importance, since it represents the first show cave in Apulia, and more general in Italy. The site and the faunal assemblage from the lower part of the deposit (*terre rosse*) was studied by Giuscardi (1873) and Anelli (1956, 1959). Instead, the fossil sample from the upper part of the sedimentary succession, including specimens attributed to *S. scrofa* (Tables 1-2), was never described.

Repository: SMCC.

9.S1.15. Grotta della Prazziche

The cave, discovered by Edoardo Borzatti von Löwenstern in 1964, is located near the town of Novaglie (Figure 1). The succession consists of five archaeological levels: F-D, Middle Pleistocene - Mousterian; C-B, Early Holocene - final Epigravettian; A, Middle Holocene - Neolithic (Borzatti von Löwenstern 1966b, 1969). The mammal assemblages from levels F-D and C-B were presented by Borzatti von Löwenstern (1966b, 1969). The studied sample, associated to artefacts attributed to final Epigravettian (Upper Palaeolithic), was collected from level B (Tables 1-2).

Repository: IGF.

9.S2. Biochronology

The Pliocene-Quaternary Italian large mammal biochronological scale is subdivided in mammal ages (Villafranchian, Epivillafranchian, Galerian, Aurelian), which constitute a reliable tool for correlating the geological time scale to biological events in the continental realm (Azzaroli 1977; Gliozzi et al. 1997; Petronio et al. 2011; Bellucci et al. 2015). Transitions between mammal ages are denoted by marked faunal renewals, related to the evolution, extinction, and dispersal of different species. During the late Middle-Late Pleistocene (Aurelian) of Italy, mammal assemblages progressively acquired modern features, associations became poor with the extinctions generally prevailed on the appearance of new taxa (Gliozzi et al. 1997; Petronio et al. 2007; Masini and Sala 2007) (Figure S1). Indeed, throughout the Last Interglacial (MIS 5) took place the last appearance of two of the most common and widely diffused species in the Italian Peninsula during the Middle Pleistocene: the straight-tusked elephant *Palaeoloxodon antiquus* (Falconer and Cautley, 1847), and the hippo (*Hippopotamus* ex. gr. *antiquus* Desmarest, 1822 (=*Hippopotamus tiberinus* Mazza, 1991) - *Hippopotamus amphibius* Linnaeus, 1758) (Caloi and Palombo 1995; Mazza 1995; Caloi et al. 1998; Braun and Palombo 2012; Mazza and Bertini 2013; Pandolfi and Petronio 2015). The occurrences chronologically referred to the early Late Pleistocene (MIS 4) (Caloi and Palombo 1995; Petronio and Sardella 1998; Pandolfi and Petronio 2015) are actually questionable due to their uncertain stratigraphic and geological framework, with no compelling evidence of such attributions (Mazza 1995; Bedetti et al. 2001; Braun and Palombo 2012). During the MIS 3 the narrow-nosed rhinoceros *Stephanorhinus hemitoechus* (Falconer, 1868) (Pandolfi et al. 2017) and the fallow deer *Dama dama* (Linnaeus, 1758) (Boscato et al. 1997) disappeared, whereas the large-sized form of *Canis lupus* spread in the Italian Peninsula (Mecozzi and Bartolini Lucenti 2018).

The faunal impoverishment occurred during the late Middle-Late Pleistocene of Europe is the result of a strong climatic recrudescence, which caused the disappearance of species adapted to warm climatic condition and the establishment of the core of modern mammalian assemblages (Gliozzi et al. 1997; Masini and Sala 2007). Due to the monotonous taxonomical composition and marked regionalization of these associations, biochronological scales of this time-span became difficult to define, eventually leading to no consensus for the Late Pleistocene (Masini and Sala 2011). Body size changes in large mammals can provide new palaeobiological and palaeoecological insights and constitute a reliable biochronological tool, since they can be observed through time on the basis of a continuous fossil documentation. The wild boar is particularly promising from this perspective, being a species prone to adapt to environmental changes with shifts in size (Genov 1999; Albarella et al. 2009). In fact, according to our results, the size reduction of *S. scrofa* sounds likely occurred during glacial stages, MIS 4 and MIS 2, and MIS 1 (Early Holocene).

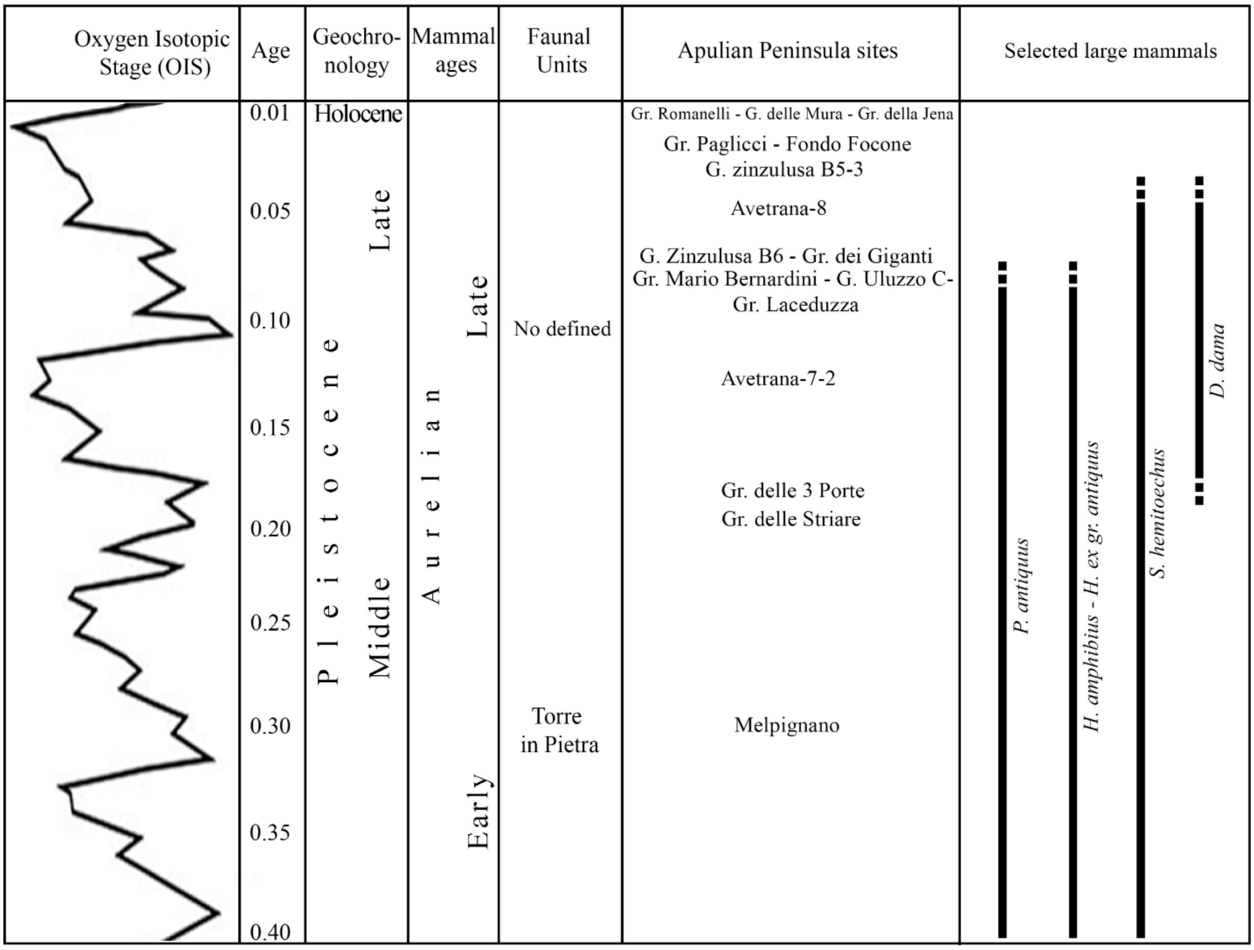

Figure S1 - Biochronological scheme of the Apulian region during the Middle Pleistocene to Early Holocene.

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10. Paper 9

On the authorship, availability, and improper use of *Sus scrofa ferus* for referring to wild pigs

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Abstract

The wild boar, *Sus scrofa*, is one of the most successful large mammals in terms of geographic distribution. Along with its domestic descendant, the pig, they are extremely important animals for conservation, economy, human sustenance, and well-being. Naming wild and domestic pigs in a way that allows them to be distinguished effectively and unambiguously is crucial for a number of studies in archaeozoology, biomedicine, genetics, epidemiology, paleontology, and wildlife management. *Sus scrofa ferus*, or less commonly, *Sus ferus*, is often used to refer to wild populations, frequently in opposition to *S. scrofa domesticus*, or *S. domesticus* in reference to domestic pigs. Here, it is argued that *S. scrofa ferus* is available for nomenclatural purposes but should not be regarded as valid from a taxonomic perspective. Authors should refer wild populations to valid subspecies, e.g., *S. scrofa scrofa*, or to *S. scrofa* ssp., when information on the subspecific status is not available or relevant for the research questions under consideration. This remark is not a mere nomenclatural clarification, because the potential identification of differences between wild boar taxa is often hidden behind a simplistic dichotomy between wild and domestic forms. requirements.

Keywords: nomenclature; taxonomy; Suidae; Artiodactyla; Mammalia; domestication; wild boar; *nomen protectum*; *nomen oblitum*; reversal of precedence

10.1. Introduction

Suids (Suidae, Artiodactyla, Mammalia), or simply pigs, comprise about twenty extant species (Groves and Grubb 2011; Melletti and Meijaard 2017). The wild boar, *Sus scrofa* Linnaeus, 1758, stands out as the most widely distributed wild pig, natively present in most of Eurasia and North Africa and introduced in all continents apart from Antarctica (Keuling et al. 2017). Wild boars are characterized by an extremely high reproductive rate in comparison to other artiodactyls of similar body mass, which exacerbates their impact on conservation and the economy, as well as explaining their evolutionary success (Bieber and Ruf 2005; Barrios-Garcia and Ballari 2012; Iannucci et al. 2020b).

The domestic pig, derived from the wild boar, is also an enormously important animal for human subsistence and welfare, being the only domesticated omnivore among major livestock species (Clutton-Brock 1999). This relationship goes back several millennia, meaning that the correct identification of pig remains (wild or domestic) is a crucial archeozoological question (Albarella et al. 2007; Rowley-Conwy et al. 2012).

Naming wild and domestic pigs in a way that allows them to be distinguished effectively and unambiguously is crucial for addressing several research questions. There is a widespread approach in referring to wild boar populations as *Sus scrofa ferus* or less frequently as *Sus ferus*, as opposed to domestic pigs, named *S. scrofa domesticus* or *S. domesticus*. Here, it is argued that *S. scrofa ferus* is available for nomenclatural purposes but should not be regarded as valid from a taxonomic perspective, also clarifying the authorship of the taxon and providing a concise review of the development of this concept.

10.2. The problem of naming domestic species

Scientific names based on domestic animals fall within the scope of the International Code of Zoological Nomenclature (hereafter, the Code; ICZN 1999), but they are not accompanied by particular recommendations. Many wild ancestral species and their domestic relatives share the same Latin name, but in some cases, wild and domestic forms are denoted by traditionally separated epithets (Gentry et al. 2004). Basically, some domestic animals differ substantially from their wild progenitors to the extent that is often desirable and hence common practice to refer to them with distinct names, but in the absence of specific guidelines in the Code, a variety of approaches have been proposed.

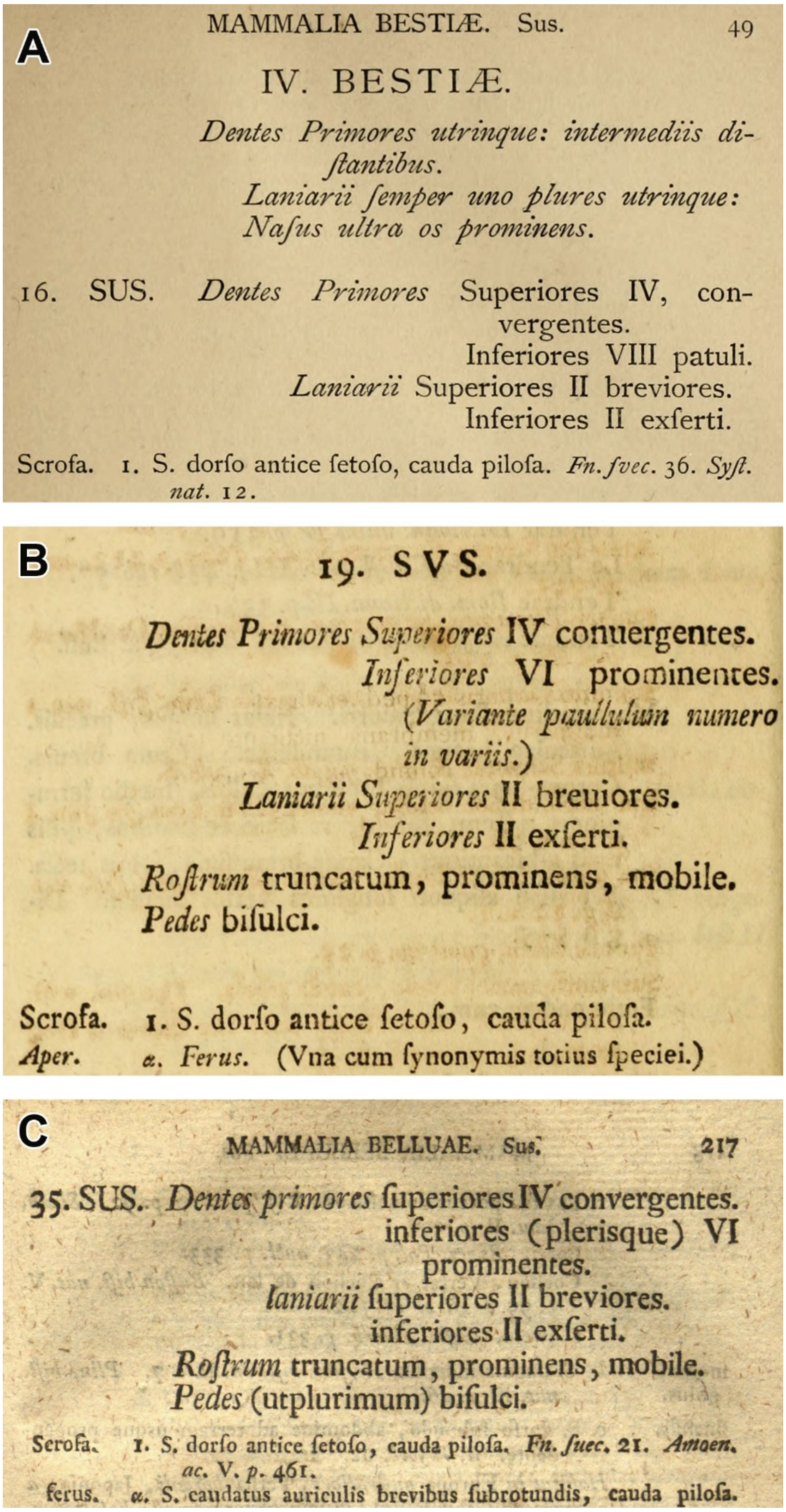
This has long engendered nomenclatural instability (Groves 1971, 1995; Gentry et al. 2004). Different proposals for naming domestic animals included, among others, referring to them solely by using vernacular names, as a consequence of the application for excluding names based on domestic animals from zoological nomenclature (Groves 1971); the adoption of an infrasubspecific distinction of domestic species, mediated by the word "forma" (f.), e.g., *Canis lupus* f. *familiaris* for referring to the dog (Bohlken 1958, 1961); the apposition of "familiaris" after the species name, e.g., *C. lupus* "familiaris" (Dennler de La Tour 1960, 1968); using a single Latin word in capitals and italics, such as *CANIS* or *SUS* (Uerpmann 1993). Eventually, a relatively recent ruling of the International Commission on Zoological Nomenclature (ICZN) conserved the widespread usage of 17 specific names based on wild species, which were coined at the same time or later than those available for their domestic counterparts (ICZN 2003). This ruling does not regulate whether to include a wild ancestor and its domestic descendant in the same species or to separate them into different species and/or subspecies—nor should it, in compliance with the principle of taxonomic freedom endorsed by the Code—but it is indeed advisable to adopt separate names for domestic animals (Gentry et al. 2004).

10.3. The case of *Sus scrofa ferus*

Whilst in most cases names available for domestic animals predate or are a contemporary of those used for their wild relatives, *S. scrofa* was considered an exception, with *S. domesticus* Erxleben, 1777, only named later (Gentry et al. 2004). The epithet *ferus* means "wild", and it has been often employed for designating wild forms of domestic animals, for instance, *Equus ferus* Boddaert, 1785, in place of *Equus caballus* Linnaeus, 1758. Referring to the wild boar as "*ferus*" has a long history, as it is, for instance, present in Pliny the Elder's *Naturalis Historia* (available online: https://la.wikisource.org/wiki/Naturalis_Historia, accessed on 20 December 2021). However, discussing the nomenclatural availability and taxonomic validity of *S. scrofa ferus* is not a straightforward task. *Sus scrofa ferus* was first used as a valid taxon (as requested in Art. 11.5 of the Code for being considered available) in the first part of the thirteenth edition of the *Systema Naturae*, curated by Gmelin and published in 1788, ten years after Linnaeus' death. (Figure 1). In those few cases where the authorship of *S. scrofa ferus* is credited, it is indeed attributed to Gmelin, 1788 (Wilson and Reader 2005; Mayer and Brisbin 2008).

However, according to Art. 11.6.1, if a name published as a junior synonym had been treated before 1961 as an available name and either adopted as the name of a taxon or treated as a senior homonym, it is thus made available but dates from its first publication as a synonym (ICZN 1999). This case applies here, because Erxleben (1777) had already published *S. scrofa ferus* within the synonymy of its newly named *S. scrofa aper*. Therefore, Gmelin's validation of the taxon satisfies the provisions of Art. 11.6.1 for making *S. scrofa ferus* Erxleben, 1777, available (see also Art. 50.7 for remarks on the authorship).

In any case, it could be argued that *S. scrofa aper* has priority over *S. scrofa ferus*. Even though this is undeniable, it is also true that *S. aper* or *S. scrofa aper* never gained widespread usage. This is perhaps because "*aper*"—which in Latin basically means "wild boar"—was also applied to many different suid taxa (especially but not only in pre-Linnean taxonomy, see, e.g., the synonymy lists in Gmelin 1788). For example, as a genus in *Aper aethiopicus* Pallas, 1766, in which instance the name was suppressed under the plenary powers by the ICZN, for the purposes of the principle of priority but not for those of the principle of homonymy (Melville and Smith 1987). The same epithet can of



MAMMALIA BESTIÆ. Sus. 49

IV. BESTIÆ.

Dentes Primores utrinque: intermediis diſtantibus.
Laniarii ſemper uno plures utrinque:
Naſus ultra os prominens.

16. SUS. *Dentes Primores* Superiores IV, convergentes.
Inferiores VIII patuli.
Laniarii Superiores II breviores.
Inferiores II exſerti.

Scrofa. 1. S. dorſo antice ſetoſo, cauda piloſa. *Fn. ſvec.* 36. *Syſt. nat.* 12.

19. SVS.

Dentes Primores Superiores IV conuergentes.
Inferiores VI prominentes.
(*Variante paullulum numero in variis.*)
Laniarii Superiores II breuiores.
Inferiores II exſerti.
Roſtrum truncatum, prominens, mobile.
Pedes biſulci.

Scrofa. 1. S. dorſo antice ſetoſo, cauda piloſa.
Aper. α. *Ferus.* (Vna cum ſynonymis totius ſpeciei.)

MAMMALIA BELLUAE. Sus. 217

35. SUS. *Dentes primores* ſuperiores IV convergentes.
inferiores (plerisque) VI prominentes.
laniarii ſuperiores II breviores.
inferiores II exſerti.
Roſtrum truncatum, prominens, mobile.
Pedes (utplurimum) biſulci.

Scrofa. 1. S. dorſo antice ſetoſo, cauda piloſa. *Fn. ſuec.* 21. *Amoen. ac.* V. *p.* 461.
ferus. α. S. caudatus auriculis brevibus ſubrotundis, cauda piloſa.

Figure 1 - Extract of Linnaeus' description of *Sus* in the tenth edition of the *Systema Naturae* (**A**), extract of Erxleben's description of *Sus* in the *Systema Regni Animalis* (**B**), and extract of Gmelin's description of *Sus* in the thirteenth edition of the *Systema Naturae* (**C**).

course be used at different taxonomic ranks without this being in violation of the principle of homonymy, but the case of the desert warthog testifies to another example of a seldom used "*aper*", which was eventually replaced by another name (i.e., *Phacochoerus*). It is possible that Gmelin's choice of replacing *S. scrofa aper* with *S. scrofa ferus* was partly due to the intention to provide a name of a less equivocal application, despite being in violation of the principle of priority as currently recognized.

Nevertheless, the provisions of the principle of priority are moderated in cases where a strict adherence to it would be detrimental for stability. A quick search on Google Scholar for "*Sus scrofa ferus*" yielded more than 1180 results (on January 22, 2022), but no recent mention for "*Sus scrofa aper*", providing an indication of the widespread usage of *S. scrofa ferus* as a valid taxon. In a more formal way and with specific reference to Art. 23.9 of the Code, which regulates the admissible cases for reversal of priority, I observe that: 1) to the best of my knowledge, *S. aper* or *S. scrofa aper* have seldom been used and never after 1899 (Art. 23.9.1.1), if not merely under the conditions of Art. 23.9.6; 2) *S. scrofa ferus* has been widely adopted, including its usage as a presumed valid name in at least 25 works, published by at least 10 authors in the last 50 years and encompassing a span of not less than 10 years (e.g., Figure 2; Fischer 1800; Rütimeyer 1861; Gray 1862; Rolleston 1877, Popescu et al. 1980; Bonfiglio 1983; Zapfe 1983; Sysa et al. 1984; Hartl and Csaikl 1987; Hraste et al. 1995; Perez et al. 1999; Rowley-Conwy 1997; Vieites et al. 2001, 2003; Harapin et al. 2003; Genov 2004; Jovanović et al. 2005; Bejenaru et al. 2009; Matiuti et al. 2010; Oroian I.G. et al., 2010; Postolache et al. 2011, 2015; Sant'Ana et al. 2011; Manning et al. 2013; Lazar et al. 2014; Oroian T.E. et al. 2014; Botha et al. 2016; Strani et al. 2018; Dashti et al. 2020; Gaudreault et al. 2020; Rivero-Juarez et al. 2020; Genualdo et al. 2021; Petroman et al. 2021) (Art. 23.9.1.2). Therefore, the necessary conditions listed under Art. 23.9 for maintaining prevailing usage of *S. scrofa ferus* instead of *S. scrofa aper* by reversal of precedence without a formal ruling of the ICZN are met (ICZN 1999). Following this nomenclatural act, *S. scrofa ferus* becomes a *nomen protectum*, while *S. scrofa aper* is now a *nomen oblitum*.

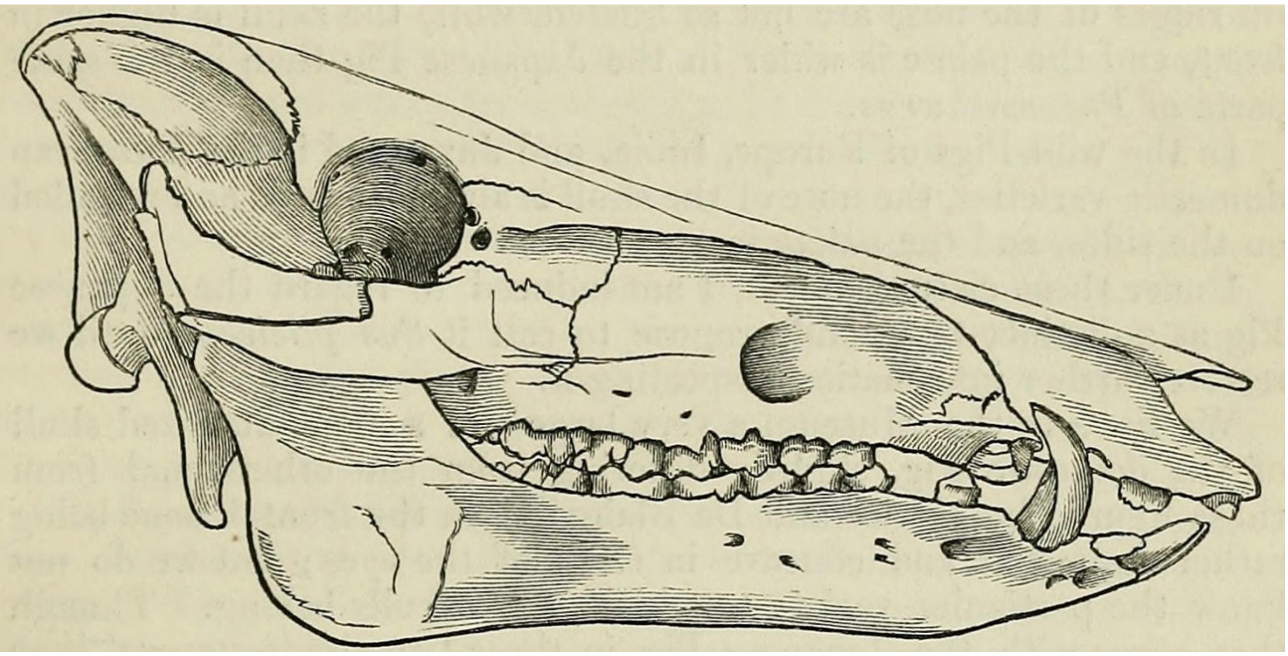


Figure 2 - Depiction of a wild boar skull labelled *Sus scrofa ferus*. Modified from Gray (1862).

10.4. Discussion

After Gmelin’s adoption of *S. scrofa ferus* for denoting the wild boar in the thirteenth edition of the *Systema Naturae* (Gmelin 1788), the usage of the name became widespread (Fischer 1800; Rütimeyer 1861; Gray 1862; Rolleston 1877). However, although *S. scrofa ferus* Erxleben, 1777, is available for nomenclatural purposes, it should not be regarded as valid from a taxonomic perspective, as treating the wild boar as a single entity is a reductive and arguably undesirable approach in many fields of research (Groves and Grubb 2011; Keuling et al. 2017). *Sus scrofa* is a widely distributed species with several recognized subspecies, and there are proposals to raise many of them to full species (Groves and Grubb 2011; Keuling et al. 2017). While the validation of these proposals needs further efforts, and the delimitation of boundaries between recognized taxa is challenging, avoiding referring to wild boars simply as *S. scrofa ferus* would likely facilitate gathering further data and knowledge on the differences within the species.

Indeed, changing the scale of analysis often provides new insights into long-standing issues. For instance, it has long been hypothesized that the wild boar underwent a dimensional change from large- to small-sized forms during the Pleistocene, eventually reaching the size of extant populations (Hünermann 1965, 1969; Faure and Guérin 1983; Guérin and Faure 1997). Testing this observation necessitates geographically constrained settings, because the extant populations vary markedly in size, encompassing the entire fossil record of the taxon (Albarella et al. 2009; Iannucci et al. 2020a). When this has been properly taken into account, resulting analyses have revealed more complex evolutionary scenarios than the simple dimensional trend suggested by previous research conducted at a coarser geographic scale (Lister et al. 2010; Iannucci et al. 2020b).

Sus scrofa was not included in the previously mentioned application to the ICZN for preserving the usage of several names adopted for wild progenitors whose establishment postdate or is a contemporary of that of their domestic derivatives (ICZN 2003), as it was considered that *S. scrofa* Linnaeus, 1758, for the wild boar predates *S. domesticus* Erxleben, 1777 (Gentry et al. 2004). However, Linnaeus' concept of *S. scrofa* encompassed both wild and domestic pigs, and separate names that are available according to the Code were both established by Erxleben (1777). For maintaining prevailing usage and ensuring consistency and stability, it is argued here to continue referring to the wild boar as *S. scrofa* and the domestic pig as *S. domesticus*. Authors should maintain the taxonomic freedom to decide whether to include the domestic pig in the wild species concept (e.g., *S. scrofa domesticus*), while using *S. scrofa ferus* should be avoided. Following this approach, *S. scrofa ferus* falls in synonymy with the nominotypical *S. scrofa scrofa* (Wilson and Reader 2005). Authors should refer wild populations to valid subspecies—e.g., *S. scrofa scrofa*—or to *S. scrofa* ssp., when information on the subspecific status is not available or relevant for the research questions under consideration.

Nevertheless, it could be argued that referring to the domestic pig as a single taxonomic entity is inconsistent as well. In fact, the domestication of the pig occurred independently at least twice, in the Near East and East Asia (Giuffra et al. 2000; Jing and Flad 2002; Larson et al. 2005; Cucchi et al. 2011; Larson and Burger 2013; Price and Hongo 2020). As a result, *S. domesticus* as commonly conceived is polyphyletic, implying that the descendants of the two domestication processes should be placed in different taxa. On the other hand, an effective allocation to one group or the other would often be difficult, generating confusion instead of promoting clarity and stability. Therefore, at least for the moment it is advisable to continue pragmatically to refer the domestic pig to a single taxon. Moreover, although the case for an independent domestication of the pig is the most supported by zooarchaeological and genetic evidence (Larson et al. 2005; Price and Hongo 2020), it is likely that other domestic mammals have multiple origins as well (Frantz et al. 2020).

Finally, even the use of vernacular names is a source of great ambiguity. For instance, “wild pigs” is often used in a systematic sense to refer to all wild species of Suidae, but also to domestic pigs returned to a wild state (Melletti and Meijaard 2017). Pigs are extremely important animals to humans, which partly explains why there are many ways to refer to them [e.g., (wild) boar, hog, and swine]. These terms are today used sometimes interchangeably or in other cases with a particular meaning, partly but not only depending on the common practice of different research fields. A cohesive nomenclatural solution would thus require a collective effort. For the time being, in studies, documents, and reports in which confusion may arise, it would be appropriate to include a concise explanation of the nomenclature adopted.

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11. Conclusions

This thesis, dealing with the late Miocene to Quaternary European fossil record of suids, contributes to gain knowledge and perspective on several entwined aspects of their evolution, biochronology, and paleobiology. Two events that were of special relevance for the evolution of the group, i.e., the appearance and spread of *Sus* at the Miocene-Pliocene transition, and that of *Sus scrofa* during the Pleistocene, have been discussed in several chapters. In general, main bioevents in the evolution of European suids seem linked to the concomitant changing environmental conditions, which likely favored the establishment of more adaptable species.

Propotamochoerus palaeochoerus was a common element of early Vallesian (~11.2–9.7 Ma) faunas of Europe. This period represented an optimum of diversity for suids and more generally for mammalian paleocommunities of Europe, with a high number of species adapted to forested environments. *Propotamochoerus palaeochoerus*, as well as tetraconodonts and the folivore listriodonts, apparently could not cope with the environmental changes that led to the so-called (mid)Vallesian Crisis, within a major decline of woodland-adapted faunas. (**Chapter 2**).

Turolian assemblages (~8.9–5.3 Ma) were characterized by the presence of *P. provincialis*, which, although not represented by abundant remains, survived during the dramatic period of the latest Miocene, when more open and drier conditions arose, culminating in the Messinian salinity crisis. However, it was the return to more humid conditions after the long-lasting previous trend of increasing aridity that likely triggered the spread of *Sus arvernensis*, and hence the rise of *Sus* during the Pliocene of Eurasia (**Chapter 3**).

Sus arvernensis is often considered ancestral or close to the ancestor of several suid lineages, with putatively related remains reported from Africa and Asia. Despite its presumed wide geographical distribution and key phylogenetic position, several aspects of the paleobiology of *S. arvernensis* still remain obscure. For instance, investigating the inner cranial anatomy of the species revealed unexpected similarities in the general morphological architecture of the brain with the Asian

Babyrousa and the African *Hylochoerus* (**Chapter 4**). These species substantially differ in size and are representatives of two widely diverging phylogenetic clades (**Chapter 1**), excluding relatively simple evolutionary or allometric explanations for brain morphology in Suidae.

Of the many potential descendants of *S. arvernensis*, *S. strozzii* was likely the only that inhabited continental Europe during most of the Early Pleistocene. The species was a typical element of ~2.0–1.8 Ma faunas, especially common in the Italian Peninsula. After this acme of abundance, there is a period of poor suid documentation in Europe, which engendered debate and speculation on the phylogenetic affinities of Epivillafranchian (~1.2–0.8 Ma) suids (**Chapter 5**).

In the last couple of years, it has become evident that Epivillafranchian suids do not belong to *S. scrofa* and best fit with an attribution to *S. strozzii*. Epivillafranchian samples do differ from typical representatives of *S. strozzii* in some morphological features, as evidenced by the description of the suid material from Untermassfeld, which can be considered a reference fauna for the Epivillafranchian (**Chapter 6**). It remains to be answered whether the observed morphological differences were the result of gradual changes or emerged abruptly in Epivillafranchian samples, and eventually what role played the dispersal of new suid populations from Asia, whose taxonomic attribution is controverse. Part of the problem rests on the scantiness of suid remains in Europe between ~1.8 and 1.2 Ma. The extent of this implied demographic reduction is exacerbated by the unequal geographical distribution of fossil localities of appropriate age, which does not allow to rule out that suid populations survived in scarcely sampled areas (e.g., France and Germany).

The extant wild boar, *S. scrofa*, likely dispersed into Europe close to the Early-Middle Pleistocene transition, in a period of major environmental and faunal changes. *Sus scrofa* is one of the widest-ranging and most adaptable extant large mammals, natively widespread throughout most of Eurasia and basically capable of establishing viable populations in every region of the world where it has been introduced. It is thus surprising that wild boar remains are seldom abundant during the Middle Pleistocene. *Sus scrofa* is locally well-represented in the fossil record only during some interglacial periods, when favorable environmental (and likely taphonomic) conditions occurred (**Chapter 7**).

Investigating size changes in *S. scrofa* over time has revealed no clear trend, although Middle Pleistocene samples are usually larger than extant populations, at least when considering similar geographical regions (**Chapter 8**). In any case, the chronosubspecific repartition in a large-sized *Sus scrofa priscus* eventually giving rise to a small-sized *S. scrofa scrofa*, sometimes reported in previous studies, seems a too simple interpretation of a more complex pattern. This picture may also be partially biased by the fact that most Middle Pleistocene sites are referred to interglacial periods. The extant wild boar is indeed a species that shows a huge morphological and biometric variability in response to the environmental variations encountered throughout its wide geographical range. The biometric study of Quaternary Apulian wild boar carried out in **Chapter 9**, focusing on a well-constrained chronological record in a specific geographical region, documented several size oscillations between glacial and interglacial periods. These results suggest that *S. scrofa* was capable to cope with environmental changes through a plastic ecomorphological response, whereas other large mammals reacted by modifying their range or went extinct. Moreover, the occurrence of several size shifts is in sharp contrast with the supposed existence of a progressive dimensional trend from large to small-sized forms during the evolution of the species.

Chapter 10 presents some remarks on the nomenclature of *S. scrofa*, focusing in particular on the status of *S. scrofa ferus*, a name often improperly used to refer to wild populations as a whole, frequently in opposition to *S. scrofa domesticus* in reference to domestic pigs. This final paper reconnects with the domestication of the pig from the wild boar, an ongoing evolutionary process that recalls the extreme importance of suids to humans, as well as the significance of investigating the evolution of the group.