Suidae Transition at the Miocene-Pliocene Boundary: a Reassessment of the Taxonomy and Chronology of *Propotamochoerus provincialis*

Alessio Iannucci¹ · Marco Cherin² · Leonardo Sorbelli³ · Raffaele Sardella¹

Accepted: 20 September 2020 / Published online: 6 October 2020
© The Author(s) 2020

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 strozzi*, 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

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).

✉ Alessio Iannucci
alessio.iannucci@uniroma1.it

¹ Dipartimento di Scienze della Terra, Sapienza Università di Roma, PaleoFactory, P.le Aldo Moro 5, 00185 Rome, Italy
² Dipartimento di Fisica e Geologia, Università degli Studi di Perugia, Via A. Pascoli, 06123 Perugia, Italy
³ Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c/ Columnes s/n, Campus de la UAB, 08193, Cerdanyola del Vallès, Barcelona, Spain

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 strozzi* 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.

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; Fig. 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).

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).

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*,

Fig. 1 Location of the Casino Basin fossil locality

H. erymanthius, *Propotamochoerus palaeochoerus*, *Propotamochoerus wui*, *P. provincialis*, *S. arvernensis*, *S. strozzi*) in order to undertake a thorough comparison of

Table 1 *Propotamochoerus provincialis* from Casino Basin, measurements of the teeth (mm)

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	

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

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.

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* (Fig. 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 (Fig. 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

Table 2 Measurements (mm) of the specimens of *Hippopotamodon*, *Propotamochoerus*, and *Sus* included in the statistical analysis

Specimen Id.	Species	Locality	Reference	P3L	P3W	P4L	P4W	M3L	M3W
GSP 3789	<i>H. sivalense</i>	Loc. 106 (India)	Pickford (1988)	21	20.3	19.4	23.6	53.2	31.8
IPUW 4059	<i>H. erymanthius</i>	Pikermi (Greece)	Pickford (2015)	17.3	14.9	15.8	17.8	40.6	27.3
IPUW 5310	<i>H. erymanthius</i>	Pikermi (Greece)	Pickford (2015)	17.7	15.7	16.3	19.3	39.2	26.5
MNHN PIK 763	<i>H. erymanthius</i>	Pikermi (Greece)	Pickford (2015)	17.1	15.7	16.3	18.9	41.1	27
MNHN PIK 764	<i>H. erymanthius</i>	Pikermi (Greece)	Pickford (2015)	18	15.8	17.1	19.9	42.9	28.1
MNHN PIK 780	<i>H. erymanthius</i>	Pikermi (Greece)	Pickford (2015)	19	16.5	16.2	19.4	43.5	27.5
NHML M 9053	<i>H. erymanthius</i>	Pikermi (Greece)	Pickford (2015)	17.6	13.5	15.3	17.9	40.6	26
PIMUZ A/V 2371	<i>H. erymanthius</i>	Gulpinar (Turkey)	Pickford (2015)	18.4	15	17	19.2	42	24.9
PIMUZ A/V 2355	<i>H. erymanthius</i>	Karakai (Turkey)	Pickford (2015)	19.7	18.5	18.6	20.6	45.3	27.5
IPUW (Krahuletz Museum)	<i>H. major</i>	Sträzing bei Krems (Austria)	Pickford (2015)	18.4	16.9	16	21.6	44	28.4
Pk-5265	<i>H. major</i>	Petreluk (Bulgaria)	Kostopoulos et al. (2001)	17.8	17.2	15.8	19.3	44.1	29.2
FM-2801	<i>H. major</i>	Strumyani-2 (Bulgaria)	Geraads et al. (2011)	19.9	15.9	15.9	19.6	45.4	30.8
MNHN LUB 660	<i>H. major</i>	Luberon, Cucuron (France)	Pickford (2015)	18.5	17.2	18.2	21.3	45.4	31.3
MR 303442	<i>H. major</i>	Luberon, Cucuron (France)	Pickford (2015)	18	18.5	19	22.3	45.5	31.8
CCECL AA 114	<i>H. major</i>	Soblay (France)	Pickford (2015)	17	16.7	15	19.3	38.8	26.5
Tbilisi	<i>H. major</i>	Bazaleti (Georgia)	Pickford (2015)	18.5	17	18.1	20.2	44	29.8
NMT 343–13	<i>H. major</i>	Udabno (Georgia)	Pickford (2015)	20.7	20.4	17.6	22.6	50.5	31
NKT-68	<i>H. major</i>	Nikiti (Greece)	Kostopoulos (1994)	18	17.3	17.1	19.8	43.5	27.8
MNHN SLQ 1075	<i>H. major</i>	Salonique (Greece)	Pickford (2015)	18.4	15	16.3	18	40.9	26
MNHN SLQ 913	<i>H. major</i>	Salonique (Greece)	Pickford (2015)	16.2	16.8	17	18.8	40.6	26
AMNH 20653-Q5	<i>H. major</i>	Samos (Greece)	Sylvestrou and Kostopoulos (2009)	16.9	13.9	15.7	18.1	36.7	25.8
AMNH 20795-Q5	<i>H. major</i>	Samos (Greece)	Sylvestrou and Kostopoulos (2009)	18.6	15.5	15.3	19.5	39.3	27.5
MTLA-537	<i>H. major</i>	Samos (Greece)	Sylvestrou and Kostopoulos (2009)	19.8	14.9	16.8	19.3	43.4	27.2
MAFI Ob. 2784	<i>H. major</i>	Polgárdi (Hungary)	This work	18.4	16.1	16.7	19.1	45.3	29.4
MNCN BAT 1014 E346	<i>H. major</i>	Batallones (Spain)	Pickford (2015)	19.6	17.9	17.2	20.1	44.1	28.4
DT Ro 2992	<i>H. major</i>	La Roma 2 (Spain)	Pickford (2015)	17.2	16.1	16.6	19.4	42.2	26.8
IPS 2002	<i>H. major</i>	Piera (Spain)	van der Made et al. (1992)	17.9	19.5	18.5	23.3	48.7	31.6
IPS 9761	<i>H. major</i>	Terrasa (Spain)	Pickford (2015)	19.2	18	19.2	22.8	46.7	31.2
58-HAY-2/45	<i>H. major</i>	Sivas (Turkey)	van der Made et al. (2013)	17.7	15.9	16.7	19.9	43.8	27.6
LJG 60.258	<i>P. palaeochoerus</i>	Johnsdorf, Ost-Steiermark (Austria)	Hellmund (1995)	14.8	12.8	13.3	15.3	26	20.6
1956/520 (b-f)	<i>P. palaeochoerus</i>	Gauweinheim, Wissberg (Germany)	Hellmund (1995)	16.3	14.1	13.3	16.2	30.5	20.4
BSP AS 103	<i>P. palaeochoerus</i>	Münchener Flinz (Germany)	Hellmund (1995)	16.9	12.4	13.5	17	24.1	20.9
Vozarci-271	<i>P. provincialis</i>	Vozarci (Bulgaria)	Geraads et al. (2008)	14.5	13.1	13.2	16.6	29.5	21.1
KRY3820	<i>P. provincialis</i>	Kryopigi (Greece)	Lazaridis (2015)	14.5	13.8	13.1	17.2	33.5	24.8
AMGP-MA 501	<i>P. provincialis</i>	Maramena (Greece)	Hellmund (1995)	16.8	13	14	15.4	32	20.8
AMGP-MA 502	<i>P. provincialis</i>	Maramena (Greece)	Hellmund (1995)	15.4	12.3	14.8	15.7	32.4	21
AFS 2865	<i>P. provincialis</i>	Bacino del Casino (Italy)	This work	15	13.2	13.4	17	33.5	23.1
VM 628	<i>P. provincialis</i>	Venta del Moro (Spain)	Morales (1984)	17	14.1	15.1	16.8	34.1	23.6
No id.	<i>P. wui</i>	Lufeng (China)	van der Made and Han (1994)	11	9.7	10.1	11.9	25.2	16.3
No id.	<i>P. wui</i>	Lufeng (China)	van der Made and Han (1994)	10.8	10.3	9.6	12.9	25.9	18.5
FSL 40073	<i>S. strozzii</i>	Montpellier (France)	Pickford (2013)	17.5	14	14.6	18	37	26
GER-51	<i>S. strozzii</i>	Gerakarou (Greece)	Koufos (1986)	12.7	11.5	13.2	15.2	37.1	24.4
IGF 424	<i>S. strozzii</i>	Upper Valdarno (Italy)	This work	13.2	14.2	13.6	17	42.5	26.2
FPI–2001-0251	<i>S. strozzii</i>	Fonelas P-1 (Spain)	Arribas and Garrido (2008)	15	13.9	15	18.1	42.8	26.5
IPS 107041a	<i>S. strozzii</i>	Vallparadis Estació EVT7 (Spain)	Cherin et al. (2020)	13.1	12	12.9	15.7	38.2	24.1
NHMB Perp	<i>S. arvernensis</i>	Perpignan (France)	Pickford and Obada (2016)	13.3	10.8	12	14.6	26.6	17.5
CCECL Pp 198	<i>S. arvernensis</i>	Perpignan, Citadelle (France)	Pickford and Obada (2016)	13.4	10	11	12.7	25.6	17.6
NHMB Rss 70	<i>S. arvernensis</i>	Perpignan, Roussillon (France)	Pickford and Obada (2016)	14	11	12	14	28	18
CCECL Br 87	<i>S. arvernensis</i>	Trévoux, Reyrieux (France)	Pickford and Obada (2016)	13.3	10.7	11.6	14.5	28.7	20.2
NHMB VI 1	<i>S. arvernensis</i>	Villafranca D'Asti (Italy)	Pickford and Obada (2016)	12.2	13.3	11	16.3	28	20.4
NHMB VI 144	<i>S. arvernensis</i>	Villafranca D'Asti (Italy)	Pickford and Obada (2016)	13	10.4	11	13.9	26.5	19.8
NHMB VI 146	<i>S. arvernensis</i>	Villafranca D'Asti (Italy)	Pickford and Obada (2016)	12.6	12.6	11.6	15.4	26	20
NMENHM	<i>S. arvernensis</i>	Musaitu (Moldova)	Pickford and Obada (2016)	14	11.5	11.8	14.6	27	20
Piedrabuena	<i>S. arvernensis</i>	Piedrabuena (Spain)	Pickford and Obada (2016)	14	9.5	10.3	14	27	18.5

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 (Fig. 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 (Fig. 3a). Along the PC1 axis, M3 L is the most influential variable, separating

Fig. 2 PCA (unstandardized) of the compared Suinae species (*H. sivalense*, *H. major*, *H. erymanthius*, *P. palaeochoerus*, *P. provincialis*, *P. wui*, *S. arvernensis*, *S. strozii*); 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

species with proportionally small (*P. palaeochoerus*) and proportionally large (*S. strozii*) 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 (Fig. 3b). Along the PC2 axis, none of the species considered is clearly separated and only *S. strozii* 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 (Fig. 3c), this indicates that only *S. strozii* possesses, on average, relatively wider teeth.

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)

Selected Synonymy List

- Sus* different from *Sus choeroides* and *Sus strozii* 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

Fig. 3 PCA (standardized) of the compared Suinae species (*H. sivalense*, *H. major*, *H. erymanthus*, *P. palaeochoerus*, *P. provincialis*, *P. wui*, *S. arvernensis*, *S. strozii*); 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

Emended Diagnosis

Propotamochoerus species larger than *S. arvernensis*, *P. wui*, and *P. palaeochoerus*; smaller than *S. strozii* 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).

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. strozii*).

Stratigraphic Range

Late Miocene (Turolian, MN11–MN13).

Referred Material from the Casino Basin

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

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 (Fig. 413). 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 $\sim 110^\circ$ (Fig. 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 (Fig. 4b). 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 (Fig. 4c), with a rounded development on the lingual side. Its reduced development allows us to hypothesize that it belonged to a female individual.

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

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

The P4 is a trapezoidal-shaped tooth, broader than it is long (Fig. 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; Fig. 4a). The tooth has an asymmetric talon with a slightly lingually placed pentacone.

In the preserved p3 (AFS 2869; Fig. 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 cuspid 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 (Fig. 4e). The development of the mesial cingulum is limited to the mesial part of the tooth. In the third lobe there are two prominent cuspid, pentaconid and pentapreconid, which are aligned mesiodistally. The tooth is curved along the mesiodistal axis.

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 *Eumaiiochoerus 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,”

Fig. 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); Hünemann (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)

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* (Figs. 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 (Figs. 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* (Fig. 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

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

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.

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. strozzi*) suid taxa.

The other Pliocene remains tentatively ascribed to *P. provincialis* do not provide convincing evidence for this attribution. Suidae from the Ruscinian of Mălușteni (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 (Fig. 6). In turn, this strengthens the biochronological value of the *Sus* dispersal bioevent at the Miocene-Pliocene boundary.

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).

Acknowledgements We are grateful to all the people that helped and supported us in the study of museum collections: A. Benocci (AFS), M. Gasparik (HNHM), E. Cioppi (IGF), W. Wessels (IVAU), L. Makadi (MAFI), M. Aiglstorfer, and T. Engel (NMM). We sincerely thank J. van der Made and A. van de Weerd for discussion and feedback. L. Rook kindly provided insightful suggestions on an earlier version of this paper. We thankfully acknowledge two anonymous reviewers for their comments and suggestions. This research was supported by Sapienza University of Rome “fondi di dotazione del Dottorato di Ricerca in Scienze della Terra” to AI.

Funding Open access funding provided by Università degli Studi di Roma La Sapienza within the CRUI-CARE Agreement.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Abbazzi L, Benvenuti M, Ceci ME, Esu D, Faranda C, Rook L, Tangocci F (2008) The end of the Lago-Mare time in the SE Val d'Elza Basin (central Italy): interference between local tectonism and regional sea-level rise. *Geodiversitas* 30:611–639
- Agusti J, Cabrera L, Garcés M, Krijgsman W, Oms O, Parés JM (2001) A calibrated mammal scale for the Neogene of Western Europe. *State of the art. Earth-Sci Rev* 52:247–260. doi: [https://doi.org/10.1016/S0012-8252\(00\)00025-8](https://doi.org/10.1016/S0012-8252(00)00025-8)
- Albarella U, Dobney K, Rowley-Conwy P (2009) Size and shape of the Eurasian wild boar (*Sus scrofa*), with a view to the reconstruction of its Holocene history. *Environ Archaeol* 14:103–136. doi: <https://doi.org/10.1179/146141009X12481709928283>
- Arribas A, Garrido G (2008) Un nuevo jabalí del género *Potamochoerus* (Suidae, Artiodactyla, Mammalia) en el Plioceno superior terminal euroasiático (Fonelas P-1, Cuenca de Guadix, Granada). In: Arribas A (ed) *Vertebrados del Plioceno superior terminal en el suroeste de Europa: Fonelas P-1 y el Proyecto Fonelas*. Instituto Geológico y Minero de España, serie Cuadernos del Museo Geominero 10, Madrid, pp 337–364
- Azzaroli A (1952) Filogenesi e biologia di *Sus strozzi* e *Sus minor*. *Palaeontogr Ital* 48:41–76
- Azzaroli A (1975) Remarks on the Pliocene Suidae of Europe. *Z Säugetierkd* 40:355–367
- Berdondini E (1992) Suids of the Early Villafranchian of Villafranca d'Asti and China. *Rend Lincei* 3:109–124. doi: <https://doi.org/10.1007/BF03002969>
- Bernor RL, Andrew PJ, Solounias N, Van Couvering JAH (1979) The evolution of “Pontian” mammal faunas: some zoogeographic, palaeoecologic and chronostratigraphic considerations. *Ann Géologiques Pays Hell Tome Hors Série* 1:81–89
- Bernor RL, Fessaha N (2000) Evolution of late Miocene Hungarian Suinae (Artiodactyla, Suidae). *Carolinea* 58:83–92
- Blainville HMD de (1847) *Ostéographie ou description iconographique comparée du squelette et du système dentaire des cinq classes d'animaux vertébrés récents et fossiles, pour servir de base à la Zoologie et à la Géologie*. Vol. 4, AA, Sur les Hippopotames et les Cochons. Atlas 4. Bertrand, Paris
- Boisserie J-R, Souron A, Mackaye HT, Likius A, Vignaud P, Brunet M (2014) A new species of *Nyanzachoerus* (Cetartiodactyla: Suidae) from the late Miocene Toros-Ménalla, Chad, Central Africa. *PLoS ONE* 9: e103221. <https://doi.org/10.1371/journal.pone.0103221>
- Bossio A, Mazzei R, Salvatorini G, Sandrelli F (2002) Geologia dell'area compresa tra Siena e Poggibonsi (“Bacino del Casino”). *Atti Soc Toscana Sci Nat Mem A* 107:69–85
- Broggi A (2011) Bowl-shaped basin related to low-angle detachment during continental extension: the case of the controversial Neogene Siena Basin (central Italy, Northern Apennines). *Tectonophysics* 499:54–76. doi: <https://doi.org/10.1016/j.tecto.2010.12.005>
- Carnegie G, Gennari R, Lozar F, Natalicchio M, Pellegrino L, Dela Pierre F (2019) Living in a deep desiccated Mediterranean Sea: an overview of the Italian fossil record of the Messinian salinity crisis. *Boll Soc Paleontol Ital* 58:109–140. <https://doi.org/10.4435/BSPI.2019.04>
- Cerling TE, Harris JM, MacFadden BJ, Leakey MG, Quade J, Eisenmann V, Ehleringer JR (1997) Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389:153–158. doi: <https://doi.org/10.1038/38229>
- Cherin M, Alba DM, Crotti M, Menconero S, Moullé PÉ, Sorbelli L, Madurell-Malapeira J (2020) The post-Jaramillo persistence of *Sus strozzi* (Suidae, Mammalia) in Europe: new evidence from the Vallparadis Section (NE Iberian Peninsula) and other coeval sites. *Quat Sci Rev* 233:106234. doi: <https://doi.org/10.1016/j.quascirev.2020.106234>
- Cherin M, Sorbelli L, Crotti M, Iurino DA, Sardella R, Souron A (2018) New material of *Sus strozzi* (Suidae, Mammalia) from the early Pleistocene of Italy and a phylogenetic analysis of suines. *Quat Sci Rev* 194:94–115. doi: <https://doi.org/10.1016/j.quascirev.2018.06.029>
- Croizet J-B, Jobert A-C-G (1828) *Recherches sur les ossements fossiles du département du Puy-de-Dôme*. Clermont-Ferrand, Paris
- de Bonis L, Bouvrain G (1996) Suidae du Miocène supérieur de Grèce. *Bull Mus Natl Hist Nat C Sci Terre Paleontol Geol Mineral* 18:107–132

- de Bruijn H, Daams R, Daxner-Höck G, Ginsburg L, Mein P, Morales J (1992) Report of the RCMNS working group on fossil mammals, Reisensburg 1990. *Newsl Stratigr* 26:65–118
- De Giuli C, Ficarelli G, Mazza P, Torre D (1983) Confronto tra successioni marine e continentali del Pliocene e Pleistocene inferiore in Italia e nell'area mediterranea. *Boll Soc Paleontol Ital* 22:323–328
- Eronen JT, Ataabadi MM, Micheels A, Karne A, Bernor RL, Fortelius M (2009) Distribution history and climatic controls of the late Miocene Pikermian chronofauna. *Proc Natl Acad Sci USA* 106:11867–11871. doi: <https://doi.org/10.1073/pnas.0902598106>
- Faure M, Guérin C (1982) Les Suidae (Mammalia, Artiodactyla) du Pliocène d'Europe occidentale. Problèmes et intérêt stratigraphique. In: 9th RAST (réunion annuelle des sciences de la Terre) Société géologique de France, Paris
- Forsyth Major CI (1875) Considerazioni sulla Fauna dei Mammiferi pliocenici e post-pliocenici della Toscana. *Atti Soc Toscana Sci Nat* 1:223–245
- Forsyth Major CI (1881) Studi sugli avanzi pliocenici del genere *Sus*. *Atti Soc Toscana Sci Nat*, P V 2:227
- Fortelius M, Eronen J, Liu L, Pushkina D, Tesakov A, Vislobokova I, Zhang Z (2006) Late Miocene and Pliocene large land mammals and climatic changes in Eurasia. *Palaeogeogr Palaeoclimatol Palaeoecol* 238:219–227. doi: <https://doi.org/10.1016/j.palaeo.2006.03.042>
- Fortelius M, van der Made J, Bernor RL (1996) Middle and late Miocene Suoidea of Central Europe and the Eastern Mediterranean: evolution, biogeography, and paleoecology. In: Bernor RL, Fahlbusch V, Mittmann H-W (eds) *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York, pp 348–377
- Frantz L, Meijaard E, Gongora J, Haile J, Groenen MAM, Larson G (2016) The evolution of Suidae. *Annu Rev Animal Biosci* 4:61–85. doi: <https://doi.org/10.1146/annurev-animal-021815-111155>
- Gallai G (2005) Tafonomia e paleobiologia della fauna mammaliana turoliana (Miocene superiore) del Bacino del Casio (Siena): risultati preliminari. *Rend Soc Paleontol Ital* 2:119–125
- Gallai G (2006) Sistematica, Paleoeologia, Paleogeografia dei Suidae fossili italiani. PhD Thesis, Università degli Studi di Firenze, Firenze
- Gallai G, Rook L (2011) *Propotamochoerus provincialis* (Gervais, 1859) (Suidae, Mammalia) from the latest Miocene (late Messinian; MN13) of Monticino Quarry (Brisighella, Emilia-Romagna, Italy). *Boll Soc Paleontol Ital* 50:29–34
- García-Castellanos D, Estrada F, Jiménez-Munt I, Gorini C, Fernández M, Vergés J, De Vicente R (2009) Catastrophic flood of the Mediterranean after the Messinian salinity crisis. *Nature* 462:778–781. doi: <https://doi.org/10.1038/nature08555>
- Geraads D, Spassov N, Garevski R (2008) New specimens of *Propotamochoerus* (Suidae, Mammalia) from the late Miocene of the Balkans. *Neues Jahrb Geol Paläontol - Abh* 248:103–113. doi: <https://doi.org/10.1127/0077-7749/2008/0248-0103>
- Geraads D, Spassov N, Hristova L, Markov GN, Tzankov T (2011) Upper Miocene mammals from Strumyani, south-western Bulgaria. *Geodiversitas* 33:451–484. doi: <https://doi.org/10.5252/g2011n3a3>
- Gervais P (1850) Zoologie et Paléontologie française (animaux vertébrés) ou nouvelles recherches sur les animaux vivants et fossiles de la France. Arthus-Bertrand, Paris
- Gray JE (1821) On the natural arrangement of vertebrate animals. *Lond Med Repository Monthly J Rev* 15:296–310
- Gray JE (1854) On the painted pig of the Cameroons (*Potamochoerus penicillatus*). *Proc Zool Soc Lond* 20:129–132
- Gray JE (1873) L.—Observations on pigs (*Sus*, Linnæus; Setifera, Illiger) and their skulls, with the description of a new species. *Ann Mag Nat Hist* 11:431–439. doi: <https://doi.org/10.1080/00222937308696847>
- Guérin C, Faure M (1985) Les Suidae (Mammalia, Artiodactyla) du Pliocène de la Formation de Perpignan (Roussillon). In: Colloque Hommage à Charles Depéret: Paléontologie et Géologie néogènes en Roussillon, p 22
- Guérin C, Tsoukala E (2013) The Tapiridae, Rhinocerotidae and Suidae (Mammalia) of the Early Villafranchian site of Milia (Grevena, Macedonia, Greece). *Geodiversitas* 35:447–489. doi: <https://doi.org/10.5252/g2013n2a7>
- Hammer Ø, Harper DAT, Ryan PD (2001) Past: paleontological statistics software package for education and data analysis. *Palaeontol Electron* 4:4
- Hellmund M (1995) The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian boundary (Neogene). 13. Suidae (Artiodactyla, Mammalia). *Münchner Geowiss Abh A Geol Paläontol* 143:1–156
- Herbert TD, Lawrence KT, Tzanova A, Peterson LC, Caballero-Gill R, Kelly CS (2016) Late Miocene global cooling and the rise of modern ecosystems. *Nat Geosci* 9:843–847. doi: <https://doi.org/10.1038/ngeo2813>
- Hilgen FJ, Lourens LJ, Van Dam JA (2012) The Neogene Period. In: Gradstein FM, Ogg JG, Schmitz MD, Ogg G (eds) *The Geologic Time Scale 2012*. Elsevier, Amsterdam, Boston, Heidelberg, London, New York, Oxford, Paris, San Diego, San Francisco, Singapore, Sydney, Tokyo, pp 923–978
- Hordijk K, de Bruijn H (2009) The succession of rodent faunas from the Mio/Pliocene lacustrine deposits of the Florina-Ptolemais-Servia Basin (Greece). *Hell J Geosci* 44:21–103
- Hou S, Su DF, Kelley J, Deng T, Jablonski NG, Flynn LJ, Ji X, Cao J, Yang X (2019) New fossil suid specimens from the terminal Miocene hominoid locality of Shuitangba, Zhaotong, Yunnan Province, China. *J Mammal Evol* 26:557–571. doi: <https://doi.org/10.1007/s10914-018-9431-3>
- Hsü KJ, Montadert L, Bernoulli D, Cita MB, Erickson A, Garrison RE, Kidd RB, Mélières F, Müller C, Wright R (1977) History of the Mediterranean salinity crisis. *Nature* 267:399–403. doi: <https://doi.org/10.1038/267399a0>
- Hünemann KA (1968) Die Suidae (Mammalia, Artiodactyla) aus den Dinotheriensanden (Untherpliozän=Pont) Rheinheßens (Südwestdeutschland). *Schweiz Paläontol Abh* 86:1–96
- Hürzeler J (1982) Sur le suidé du lignite de Montebamboli (prov. Grosseto, Italie). *C R Acad Sci* 2 295:697–701
- Iannucci A, Gasparik M, Sardella R (2020a) First report of *Sus stozzii* (Suidae, Mammalia) from the early Pleistocene of Hungary (Dunaalmás) and species distinction based on deciduous teeth. *Sci Nat* 107:5. doi: <https://doi.org/10.1007/s00114-019-1661-6>
- Iannucci A, Sardella R, Strani F, Mecozzi B (2020b) Size shifts in late middle Pleistocene to early Holocene *Sus scrofa* (Suidae, Mammalia) from Apulia (southern Italy): ecomorphological adaptations? *Hystrix* 31:10–20. doi: <https://doi.org/10.4404/hystrix-00258-2019>
- Kaup JJ (1833) Descriptions d'ossements fossiles de mammifères inconnus jusqu'à présent qui se trouvent au Muséum grand-ducal de Darmstadt. Second cahier. Heyer, Darmstadt, pp 1–31
- Kaya F, Bibi F, Žliobaitė I, Eronen JT, Hui T, Fortelius M (2018) The rise and fall of the Old World savannah fauna and the origins of the African savannah biome. *Nat Ecol Evol* 2:241–246. doi: <https://doi.org/10.1038/s41559-017-0414-1>
- Kostopoulos DS (1994) *Microstonyx major* (Suidae, Artiodactyla) from the late Miocene locality of “Nikiti-1”, Macedonia, Greece; some remarks about the species. *Bull Geol Soc Greece* 30:341–355
- Kostopoulos DS, Spassov N, Kovachev D (2001) Contribution to the study of *Microstonyx*: evidence from Bulgaria and the SE European populations. *Geodiversitas* 23: 411–437
- Koufos GD (1986) The presence of *Sus stozzii* in the Villafranchian (Villanyian) of Macedonia (Greece). *Paläontol Z* 60:341–351. doi: <https://doi.org/10.1007/BF02985678>
- Koufos GD (2003) Late Miocene mammal events and biostratigraphy in the Eastern Mediterranean. *Deinsea* 10:343–371
- Koufos GD, Vasileiadou K (2015) Miocene/Pliocene mammal faunas of southern Balkans: implications for biostratigraphy and palaeoecology. *Palaeobio Palaeoenv* 95:285–303. doi: <https://doi.org/10.1007/s12549-015-0201-4>

- Krijgsman W, Hilgen FJ, Raffi I, Sierro FJ, Wilson DS (1999) Chronology, causes and progression of the Messinian salinity crisis. *Nature* 400:652–655. doi: <https://doi.org/10.1038/23231>
- Lazaridis G (2015) Study of the late Miocene vertebrate locality of Krypigi and other localities of Kassandra Peninsula, Chalkidiki (Greece). Systematics, taphonomy, paleoecology, biochronology. PhD Thesis, Aristotle University, Thessaloniki
- Lazarotto A, Sandrelli F (1977) Stratigrafia e Assetto Tettonico delle Formazioni Neogeniche nel Bacino del Casino (Siena). *Boll Soc Geol Ital* 96:747–762
- Lister AM, Parfitt SA, Owen FJ, Collinge SE, Breda M (2010) Metric analysis of ungulate mammals in the early middle Pleistocene of Britain, in relation to taxonomy and biostratigraphy: II: Cervidae, Equidae and Suidae. *Quat Int* 228:157–179
- Lydekker R (1877) Notices of new or rare mammals from the Siwaliks. *Rec Geol Surv India* 10:76–83
- Mazza P, Rustioni M (1997) Neotype and phylogeny of the suid *Eumaiocoerus etruscus* (Michelotti) from Montebamboli (Grosseto, southern Tuscany). *Paleontol Evol* 5–17
- Meijer P, Krijgsman W (2005) A quantitative analysis of the desiccation and re-filling of the Mediterranean during the Messinian Salinity Crisis. *Earth Planet Sci Lett* 240:510–520. doi: <https://doi.org/10.1016/j.epsl.2005.09.029>
- Mein P (1975) Résultats du groupe de travail des vertébrés. Report on activity of the RCMNS working groups (1971–1975): 78–81
- Michelotti G (1861) Études sur le Miocène inférieur de l'Italie septentrionale. *Natuurkundige Verhandelingen van de Hollandsche Maatschappij der Wetenschappen te Haarlem* 15:1–184
- Montoya P, Ginsburg L, Alberdi MT, van der Made J, Morales J, Soria MD (2006) Fossil large mammals from the early Pliocene locality of Alcoy (Spain) and their importance in biostratigraphy. *Geodiversitas* 28:137–173
- Morales J (1984) Venta del Moro: Su macrofauna de mamíferos y biostratigrafía continental del Mioceno terminal Mediterráneo. PhD Thesis, Universidad Complutense de Madrid, Madrid
- Mosimann JE (1970) Size allometry: size and shape variables with characterizations of the lognormal and gamma distributions. *J Am Stat Assoc* 930–945
- Owen R (1848) Description of teeth and portions of jaws of two extinct anthracotheriid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the N.W. coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the classification of pachyderms by the number of their toes. *Q J Geol Soc Lond* 4:103–141
- Pantaneli D (1879) Sugli strati miocenici del Casino (siena) e considerazioni sul miocene superiore. *Atti Regia Accad Lincei Mem Cl Sci Fis Mat Nat* 3 3:309–327
- Pickford M (1988) Revision of the Miocene Suidae of the Indian subcontinent. *Münchner Geowiss Abh A Geol Paläontol* 12:1–92
- Pickford M (2012) Ancestors of Broom's pigs. *Trans R Soc South Afr* 67:17–35
- Pickford M (2013) Re-assessment of the suids from the Sables marins de Montpellier and selection of a lectotype for *Sus provincialis* Blainville, 1847. *Geodiversitas* 35:655–689
- Pickford M (2015) Late Miocene Suidae from Eurasia: the *Hippopotamodon* and *Microstonyx* problem revisited. *Münchner Geowiss Abh A Geol Paläontol* 42:1–126
- Pickford M, Obada T (2016) Pliocene suids from Musaitu and Dermenji, Moldova: implications for understanding the origin of African *Kolpochoerus* Van Hoepen & Van Hoepen, 1932. *Geodiversitas* 38:99–134
- Pilgrim GE (1925) Presidential address to the Geological Section of the 12th Indian Science Congress. In: *Proceedings of the 12th Indian Scientific Congress*, pp 200–218
- Radulescu C, Samson P-M, Petculescu A, Stiuca E (2003) Pliocene large mammals of Romania. *Coloq Paleontol Ext* 1:549–558
- Rook L (1992) Italian Messinian localities with vertebrate faunas. *Paleontol Evol* 24/25:141–147
- Rook L (2016) Geopalaeontological setting, chronology and palaeoenvironmental evolution of the Baccinello-Cinigiano Basin continental successions (late Miocene, Italy). *C R Palevol* 15:825–836. doi: <https://doi.org/10.1016/j.crpv.2015.07.002>
- Rook L, Abbazzi L, Engesser B (1999) An overview on the Italian Miocene land mammal faunas. In: Agustí J, Rook L, Andrews P (eds) *The Evolution of Neogene Terrestrial Ecosystems in Europe*. Cambridge, pp 191–204
- Rook L, Bernor RL (2013) *Hippotherium malpassii* (Equidae, Mammalia) from the latest Miocene (late Messinian; MN13) of Monticino gypsum quarry (Brisighella, Emilia-Romagna, Italy). *Bolle Soc Paleontol Ital* 52:95–102. doi: <https://doi.org/10.4435/BSPI.2013.12>
- Roth J, Wagner A (1854) Die fossilen knochenüberreste von Pikermi in Griechenland. *Abh Bayer Akad Wiss* 7:371–464
- Schmidt-Kittler N (1971) Die obermiozäne Fossilgerstätte Sandelzhausen - 3. Suidae (Artiodactyla, Mammalia). *Mitt Bayer Staatssammlung Paläontol Histor Geol* 11:129–170
- Sein C, van der Made J, Rössner GE (2009) New material of *Propotamochoerus* (Suidae, Mammalia) from the Irrawaddy Formation, Myanmar. *Neues Jahrb Geol Paläontol - Abh* 251:17–31
- Simionescu I (1930) Vertebratele Pliocene dela Mălușteni (Covurlui). *Publicațiunile Fondului Vasilie Adamachi Acad Română* 9:83–148
- Soldani A (1789) *Testaceographiae ac Zoophytographiae parvae et microscopicae tomus primus*. Typographia Francisci Rossi, Siena
- Stehlin HG (1900) Über die Geschichte des Suiden-Gebisses. *Abh schweiz paläontol Ges* 26–27:1–527
- Sylvestrou IA, Kostopoulos DS (2009) The late Miocene mammal faunas of the Mytilinii Basin, Samos Island, Greece: new collection. 12. Suidae. *Beitr Paläontol* 31:283–297
- Thenius E (1950) *Postpotamochoerus* nov. subgen. *hyotherioides* aus dem Unterpliozän von Samos (Griechenland) und die Herkunft der Potamochoeren. *Sitzungsberichten Österr Akad Wiss Math-Naturwissenschaftliche Kl* 159:25–36
- van Asperen EN (2010) Ecomorphological adaptations to climate and substrate in late middle Pleistocene caballoid horses. *Palaeogeogr Palaeoclimatol Palaeoecol* 297:584–596. doi: <https://doi.org/10.1016/j.palaeo.2010.09.007>
- van de Weerd A (1979) Early Ruscinian rodents and lagomorphs (Mammalia) from the lignites near Ptolemais (Macedonia, Greece). *Proc Kon Ned Akad Wetensch* 82:127–170
- van der Made J (1990) A range chart for European Suidae and Tayassuidae. *Paleontol Evol* 23:99–104
- van der Made J (1996) Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. *Meded Werkgr Tert Kwart Geol* 33:3–254
- van der Made J, Belinchón M (1991) *Korynochoerus palaeochoerus* from the uppermost Miocene of Alcoy. *Revista Española de Paleontología n.º Extraordinario*:173–180
- van der Made J, Güleç E, Erkman AC (2013) *Microstonyx* (Suidae, Artiodactyla) from the upper Miocene of Hayranlı-Haliminhani, Turkey. *Türk J Zool* 37:106–122
- van der Made J, Han D (1994) Suidae from the upper Miocene hominoid locality of Lufeng, Yunnan province, China. *Proc Kon Ned Akad Wetensch* 97:27–82
- van der Made J, Krakhmalnaya T, Kubiak H (1999) The pig *Propotamochoerus palaeochoerus* from the upper Miocene of Grytsiv, Ukraine. *Estud Geol* 55:283–292
- van der Made J, Montoya P, Alcalá L (1992) *Microstonyx* (Suidae, Mammalia) from the upper Miocene of Spain. *Geobios* 25:395–413
- van der Made J, Moyà-Solà S (1989) European Suidae (Artiodactyla) from the late Miocene onwards. *Boll Soc Paleontol Ital* 28:329–339
- Vekua A (1972) Kvabetskaia fauna Akhagylskih Pozvonochnyh. Nauka, Moskva