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ORIGINAL PAPER

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

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).

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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.

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*,

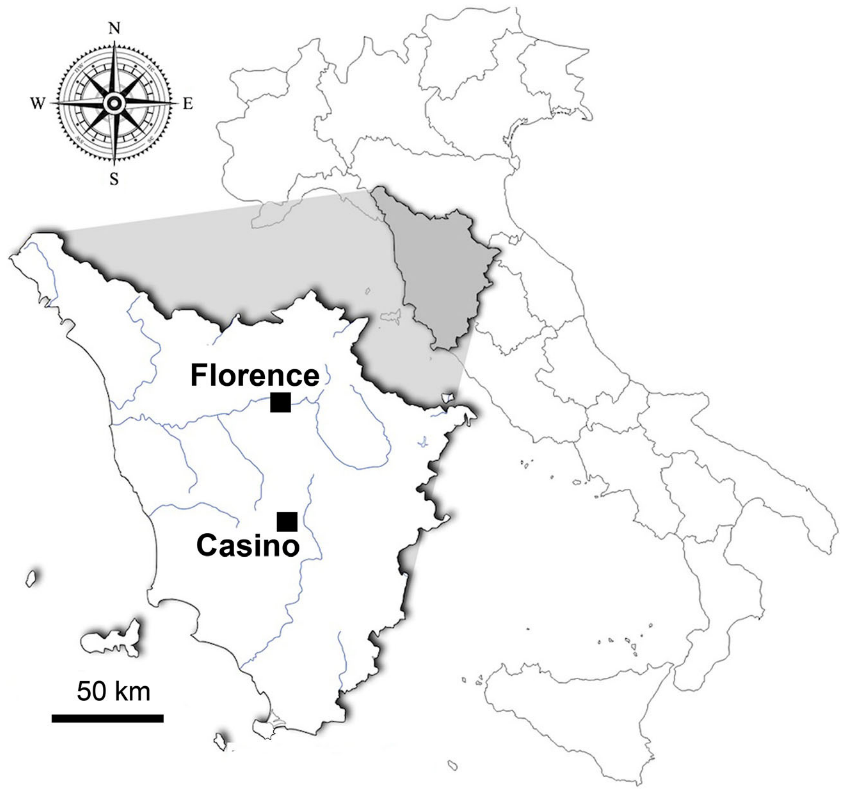


Fig. 1 Location of the Casino Basin fossil locality

H. erymanthius, *Propotamochoerus palaeochoerus*, *Propotamochoerus wui*, *P. provincialis*, *S. arvernensis*, *S. 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.

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

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	*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 40073	*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

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

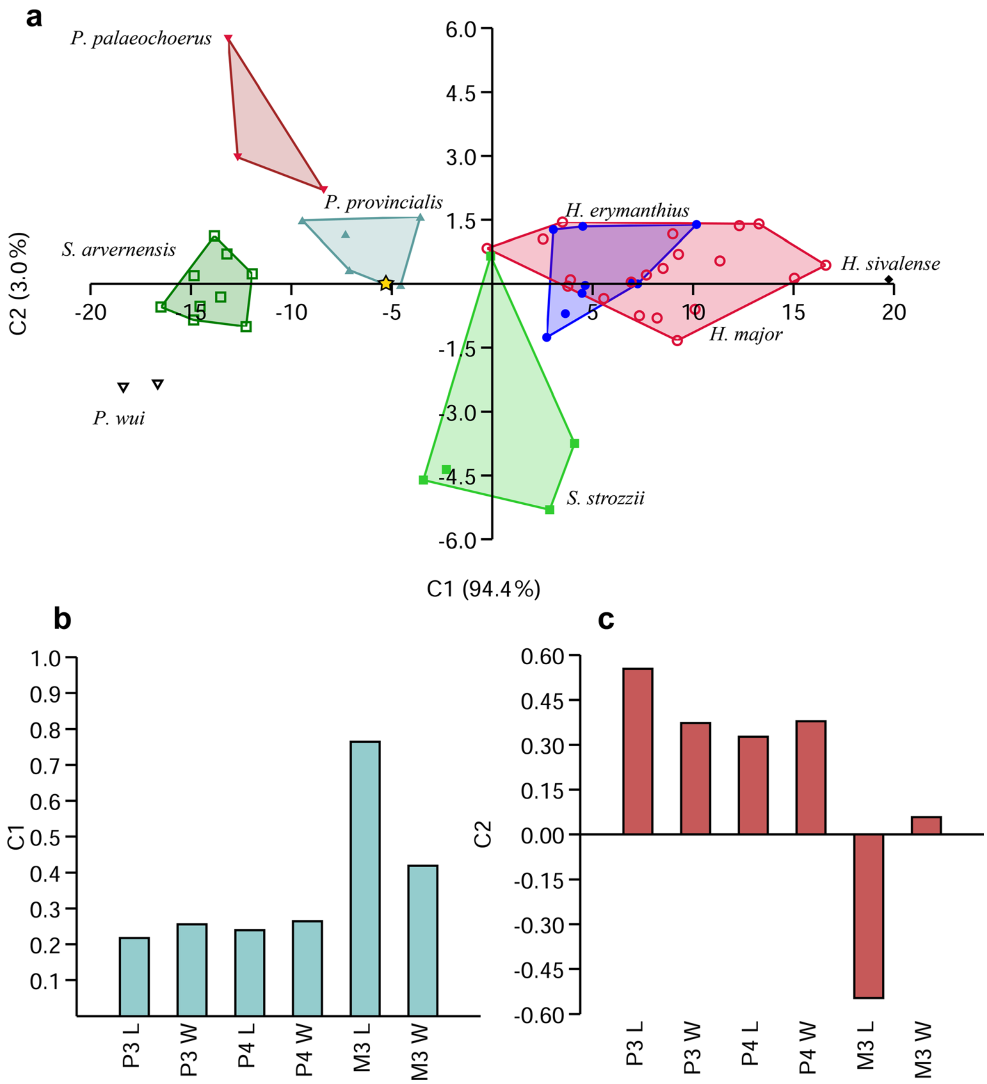


Fig. 2 PCA (unstandardized) of the compared Suinae species (*H. sivalense*, *H. major*, *H. erymanthius*, *P. palaeochoerus*, *P. provincialis*, *P. wui*, *S. arvernensis*, *S. strozzii*); scatter diagram (**a**) and loadings of the first (**b**) and second (**c**) components. The star indicates AFS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

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 (Fig. 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 (Fig. 3c), this indicates that only *S. strozzii* possesses, on average, relatively wider teeth.

Systematic Paleontology

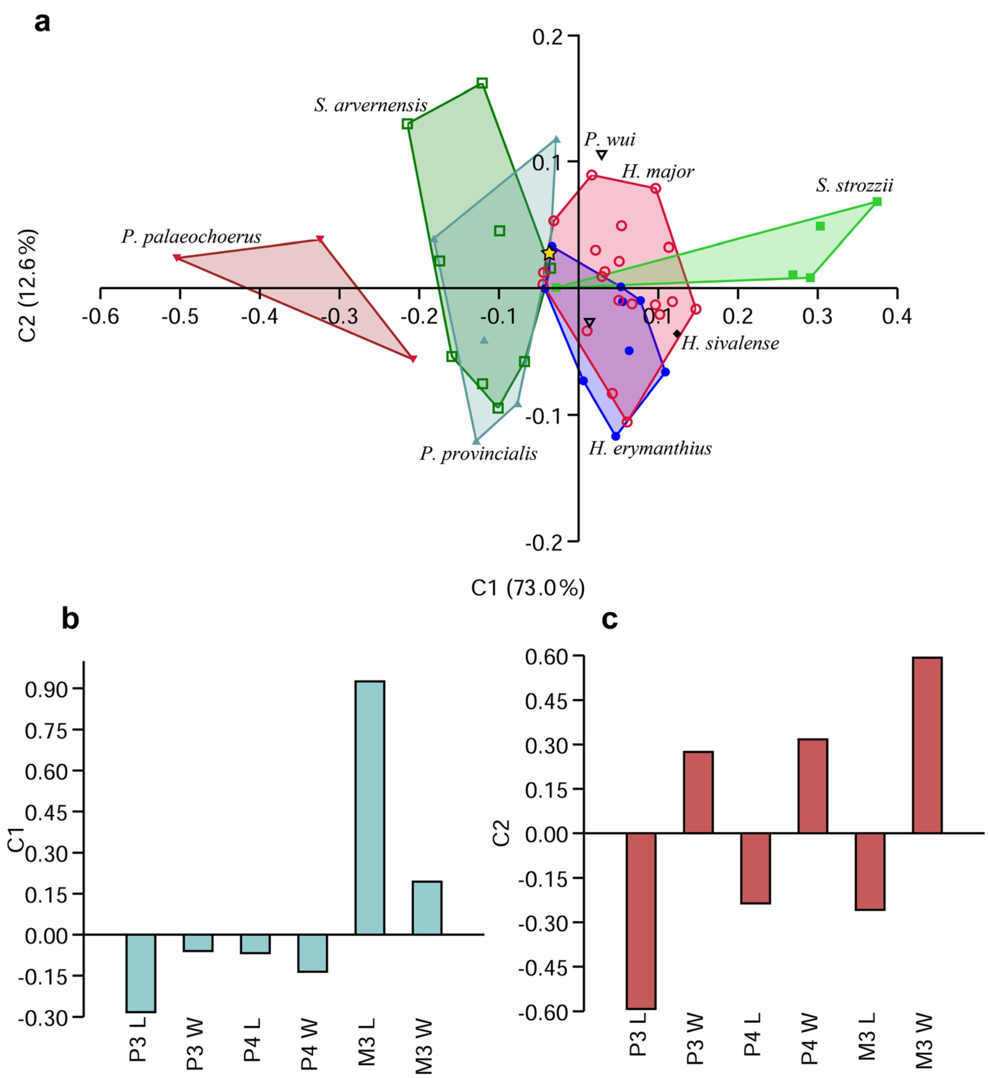
Order Artiodactyla Owen, 1848
Family Suidae Gray, 1821
Subfamily Suinae Gray, 1821
Tribe Dicoryphochoerini Schmidt-Kittler, 1971
Genus *Propotamochoerus* Pilgrim, 1925

Propotamochoerus provincialis (Blainville, 1847)

Selected Synonymy List

Sus different from *Sus choeroides* and *Sus 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

Fig. 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



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).

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*).

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. 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° (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.

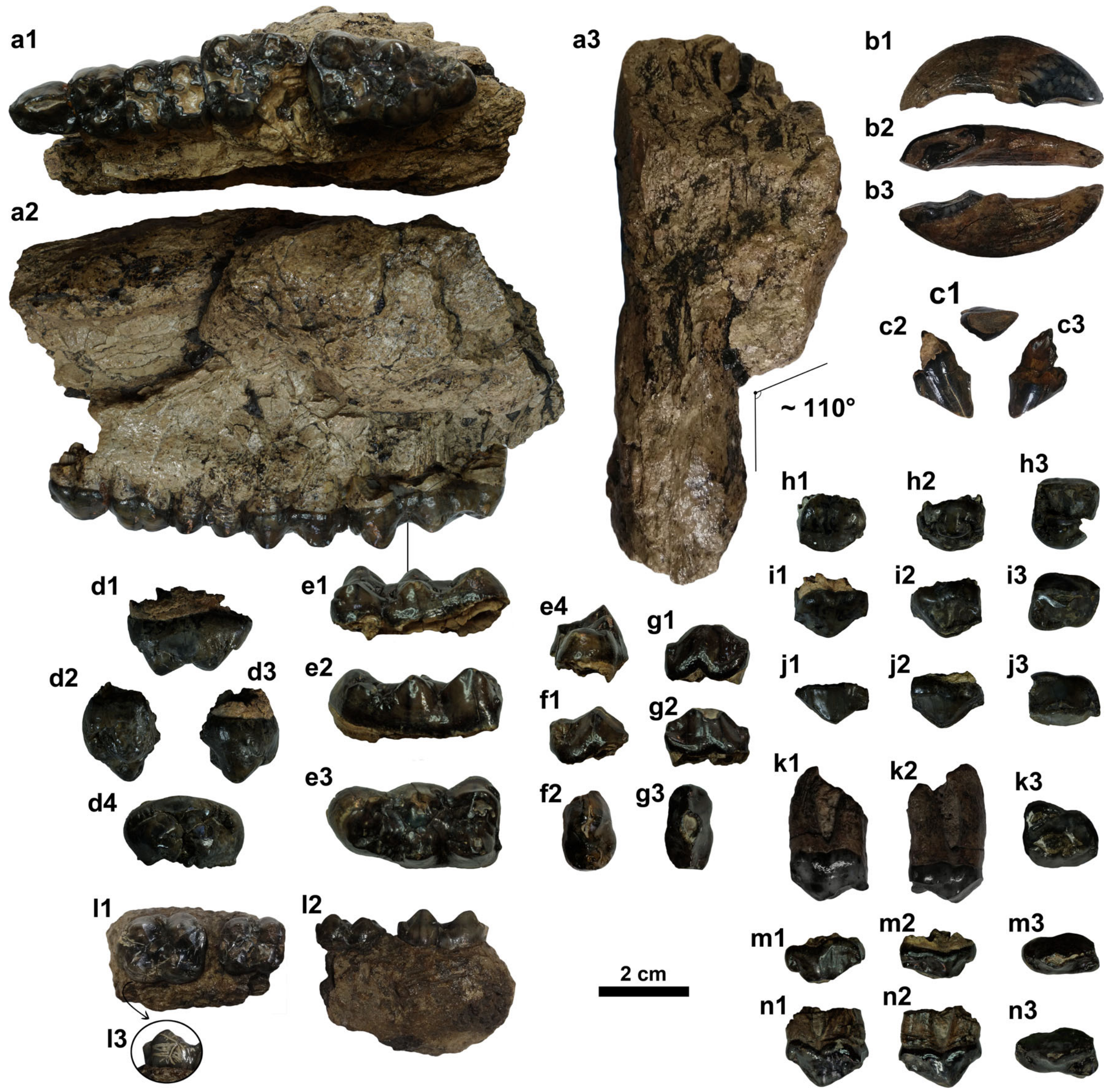


Fig. 4 *Propotamochoerus provincialis* from Casino: **a** - left maxillary with P3-M3 in occlusal (1), buccal (2), and dorsal (3) views (AFS 2865); **b** - left I1 in buccal (1), occlusal (2), and mesial (3) views (AFS 2840); **c** - right upper female canine in occlusal (1), lingual (2), and buccal (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 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 (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 cuspids, 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 *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,”

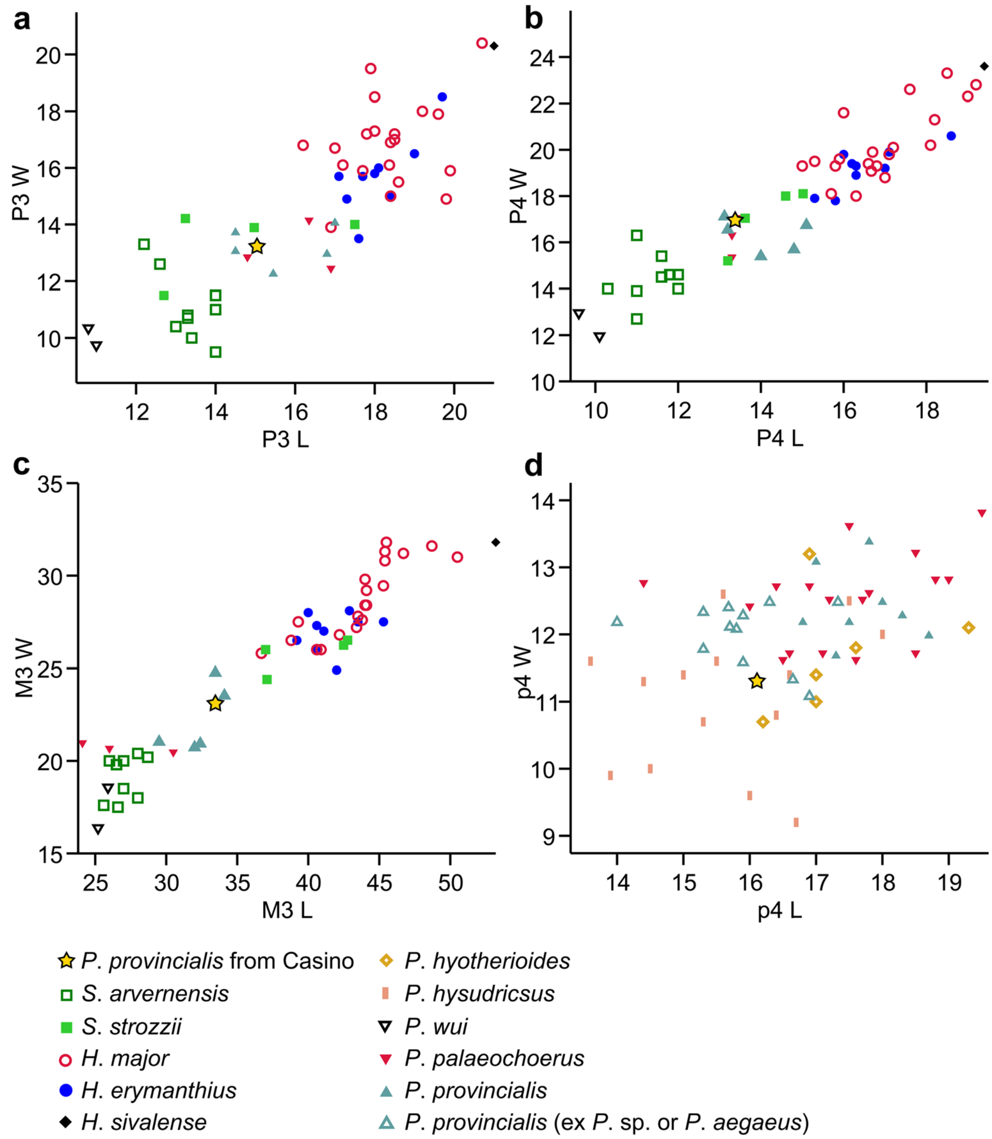


Fig. 5 Bivariate diagrams (L x W; in mm) of P3 (**a**), P4 (**b**), and M3 (**c**) of the specimens included in the statistical analysis; p4 (**d**) of *Propotamochoerus* species. Data from Thenius (1950); Hünermann (1968); van der Made and Han (1994); Hellmund (1995); de Bonis and Bouvrain (1996); Gallai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

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

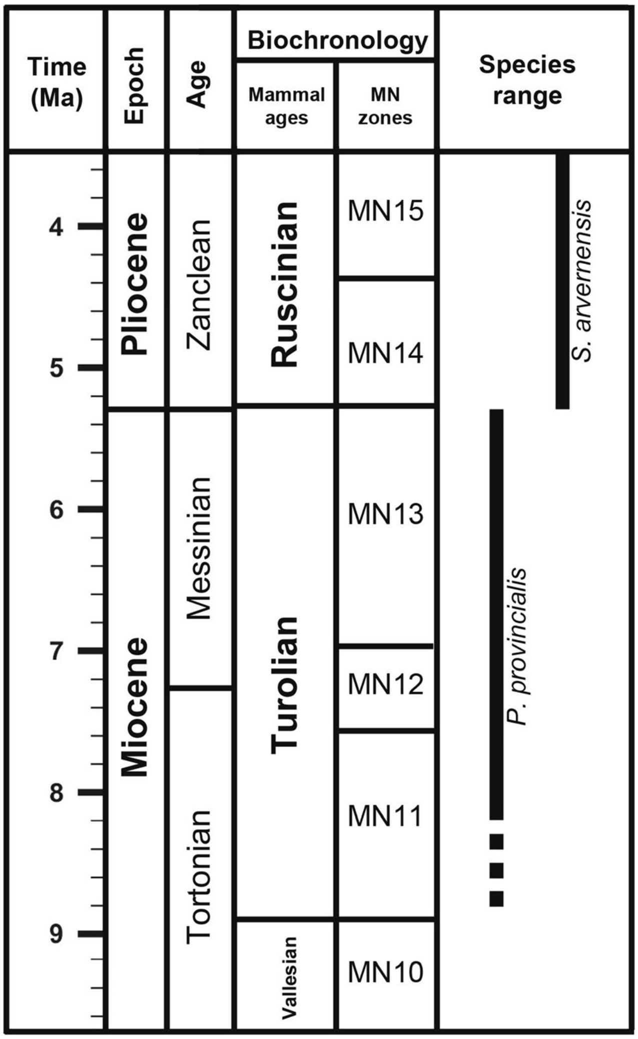


Fig. 6 European mammal biochronological scale, with the ranges of *Propotamochoerus provincialis* and *Sus arvernensis*. Subdivisions are after Hilgen et al. (2012)

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. 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 (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).

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