



A reappraisal of the lost suids from the Late Miocene of Gravitelli (Sicily, Italy) and paleobiogeographical implications

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Abstract

The long-lost mammal fauna from Gravitelli (Messina, Sicily, Italy) represents one of the most important records for investigating faunal dynamics during the Late Miocene of the Mediterranean, although it is unfortunately only known from descriptions carried out in the early 1900s, as the original collection was lost during the Messina Earthquake of 1908. Gravitelli suids have been referred to *Propotamochoerus* sp. after the redescription of the casts of two specimens that survived to the present day. However, there is further material that has not been considered, which makes that of Gravitelli one of the most abundant samples of Late Miocene suids from Italy, with a minimum number of four individuals represented. A reappraisal of all Gravitelli suids allows to ascribe them to *Propotamochoerus provincialis* (Suinae, Dicoryphochoerini), following a comparison with related Late Miocene to Pliocene species from Eurasia. Moreover, the re-examination of the geological setting of the locality reveals that the mammal fauna of Gravitelli occurred well below the pre-evaporitic deposits of the Tripoli Formation, whose base is dated in Sicily at ~7 Ma. Therefore, Gravitelli fauna either dates to the late Tortonian or, at most, to the earliest pre-evaporitic Messinian, corresponding to MN 11 or MN 12 in terms of mammal biochronology. This implies that the occurrence of *P. provincialis* at Gravitelli is the earliest in Italy and that emerged land masses connected Sicily with the European mainland earlier than 7 Ma. Available dates support a diachronous dispersal of *Propotamochoerus* in western Europe during the Turolian, being first known from the Balkans ~8.3 Ma, then from Gravitelli prior to 7 Ma, and then from the Iberian Peninsula since ~6.2 Ma. A similar pattern is known for *Mesopithecus* (Cercopithecidae). Although often discussed in light of its potential significance for Afro-Eurasian dispersals, only a fraction of the mammal fauna of Gravitelli has been reconsidered systematically. Notwithstanding the necessity of such dedicated studies, the faunal elements identified so far have an almost entirely European character and no species is shared with Cessaniti (Calabria), despite the two faunas have often been considered part of a paleobioprovince documenting a connection between southern Italy and northern Africa. At Gravitelli, the only species of African origin is the endemic hippo *Hexaprotodon? siculus*, but the extensive fossil record of insular hippopotamids testifies to their ability to colonize islands even in the absence of land bridges. Gravitelli hippos are nonetheless noteworthy, as the revised age of the site implies that they represent the earliest hippopotamids known outside Africa.

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1. Introduction

On December 28, 1908, early in the morning, a catastrophic earthquake shook the cities of Messina and Reggio Calabria, located on the facing shores of the Strait of Mes-

sina, which separates Sicily from the Italian mainland. The earthquake, with its epicenter in the Strait, was one of the most destructive and deadly ever (Mercalli, 1909; Platania, 1909; Pino et al., 2009). Alongside the immeasurable human tragedy, the event also caused a substantial loss of cultural heritage, including the paleontological collections recovered from the Late Miocene of Gravitelli, at

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the time stored in the “Museo Geologico Provinciale di Messina”. In the following decades, the city of Messina was rebuilt, and the urbanization reached the area of Gravitelli, around 2–3 km west of the modern city center, precluding direct investigations on the original outcrops (Marra, 2019).

Luckily, most of the mammal remains of Gravitelli were at least described and figured by Seguenza (1902, 1907), allowing some considerations on this important record in subsequent studies (e.g., Hooijer, 1946; Thomas et al., 1982; Marra, 2019). Gallai and Rook (2006) restudied two specimens of the material originally considered by Seguenza (1902), thanks to the rediscovery of their casts in the collections of the Natural History Museum of the University of Florence (Italy). These casts belong to a suid, which Gallai and Rook (2006) assigned to *Propotamochoerus* sp., further suggesting similarities with *P. provincialis* (Blainville, 1847) and *P. hysudricus* (Stehlin, 1899).

Propotamochoerus Pilgrim, 1925 is a genus of suine that was widespread during the Late Miocene, recorded from several localities across Eurasia, from the Iberian Peninsula to China (Pilgrim, 1926; Hünemann, 1968; Schmidt-Kittler, 1971; 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; Iannucci et al., 2021a; Iannucci and Begun, 2022).

Despite this extensive geographic range, the Italian occurrences of the taxon are limited to few localities, which apart from Gravitelli, include Baccinello V3, Brisighella (Monticino Quarry), Casino, Gretoni (Velona Basin), and Verduno. Of this list, only the remains recovered from the Casino Basin and Brisighella have been the subject of dedicated studies focused on suids (Gallai and Rook, 2011; Iannucci et al., 2021a). A portion of the material from the Velona Basin has been briefly described by Rook and Ghetti (1997) within an overview of the mammal fossils recovered from the area. The suid sample from Baccinello V3 was partly considered in a PhD thesis (Gallai, 2006) and often taken into account in comparative studies and discussions (Van der Made and Moyà-Solà, 1989; Fortelius et al., 1996; Van der Made, 1999; Iannucci et al., 2021a), although never properly published. As for Verduno, it is only known in the literature from a communication at a conference (Sorbelli et al., 2019).

Although *Propotamochoerus* is present in Europe since at least the early Vallesian (MN 9) — few putative earlier records are listed in previous studies (Iannucci and Begun, 2022), but they deserve revision, as it has been argued that pre-Vallesian material (e.g., Alba et al., 2006) pertains to a large tetraconodont (Pickford, 2016) — all localities of the previous list are considered Messinian in age and referred to MN 13. Indeed, Italian faunas correlative of the Vallesian and early Turolian of mainland Europe were characterized by a high degree of endemism documenting the existence of separated paleobioprovinces, as the emergent land masses that would eventually

constitute Italy were still far from taking the shape of the modern Peninsula (Rögl, 2001; Rook et al., 2006; Carminati et al., 2010). The suid *Propotamochoerus* was apparently not amongst the taxa that colonized this patchy landscape, but part of the non-endemic contingent that dispersed in Italy once the connection to the rest of Europe was established.

Like the other Late Miocene Italian faunas with *Propotamochoerus*, Gravitelli has usually been considered Messinian in age and referred to MN 13 (Rook et al., 2006; Van der Made et al., 2006), but older correlations have also been proposed (Ferretti, 2008; Masini et al., 2008). The latter are more in line with the geological setting of Gravitelli deposits (see Section 2), but in any case, few mammal remains have been revised systematically, limiting biochronological considerations.

Gallai and Rook (2006) offered an important contribution to the study of the fossil record of Gravitelli, providing direct evidence (even if from casts) of its lost mammalian fauna. However, they neither critically revised further material discussed by Seguenza (1902) that belong to a suid as well, nor mentioned the more abundant sample described in the following work of the same author (Seguenza, 1907). This precluded a more precise attribution of Gravitelli suids and led some authors to base their comparisons and considerations only on the two redescribed specimens (e.g., Pickford, 2013; Lazaridis et al., 2022).

The suid material from Gravitelli described by Seguenza (1902, 1907) is not extensive, but it nonetheless represents one of the most abundant Late Miocene samples from Italy, as well as the earliest occurrence of *Propotamochoerus* in the country. More importantly, Gravitelli, owing to its geographic position and chronology, offers a unique glimpse into the potential connections in the Mediterranean area before and during the Messinian Salinity Crisis. Here, Gravitelli suids are fully re-described, compared with related Late Miocene to Pliocene species from Eurasia, and discussed in light of their biochronological and paleobiogeographical significance.

2. Geological setting and historical background

Sicily is the southernmost region of Italy and the largest island of the Mediterranean Sea (Fig. 1). It is separated from the Italian Peninsula by the Strait of Messina, an extensional syn-tectonic basin that opened during the Pleistocene, around 0.8–0.6 Ma (Monaco et al., 1996; Di Stefano and Longhitano, 2009; Barreca et al., 2021). The city of Messina is located on the shore, facing the Strait from the Sicilian side. This area, unlike the rest of Sicily, is a part of the Apenninic-Maghrebian orogen known as the Calabrian-Peloritan Arc (also Siculo-Calabrian or simply Calabrian), a tectonically unstable area between the southern Apennines and the Sicilian Maghrebides (Carbone et al., 2007).

The geological setting of the fossil locality is unusually clear for an historical sample whose original outcrops were

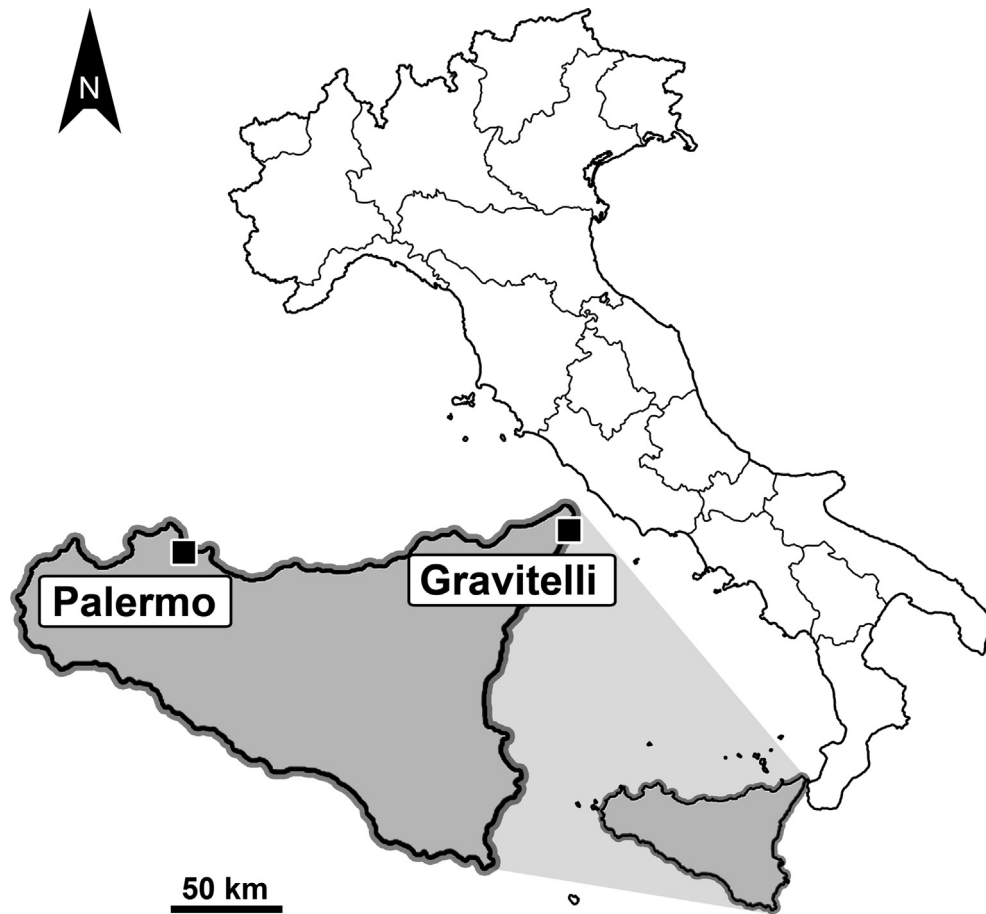


Fig. 1. Outline of Italy with emphasis on Sicily and geographic location of the Late Miocene vertebrate locality of Gravitelli (Messina).

obliterated. Indeed, the area of Gravitelli has been extensively investigated during the nineteenth and early twentieth centuries, having played a crucial role for the development of research on the Miocene and especially Pliocene succession and correlations in the Mediterranean area (Vai, 1997; Van Couvering et al., 2000). It is mainly on the base of considerations on the strata exposed at Gravitelli that G. Seguenza (1868) introduced the Zanclean Stage for the lower part of the Pliocene (Zanclea being the Greek name of Messina).

The first mention of suid remains recovered from Gravitelli is in G. Seguenza (1862), where the author reported a succinct faunal list, including *Sus choeroides* Pomel [= *Eumaiiochoerus etruscus* (Michelotti, 1861)], as recovered from clays close to a lignite formation generically referred to the Miocene. Subsequently, G. Seguenza (1868), while establishing the Zanclean, described this Stage as overlain the clays with a typical Late Miocene fauna, listing again the occurrence of suids. Moreover, in the same work the author also specified the presence of marine clays between the lacustrine layers with mammals and the overlain Zanclean deposits. Further detailed considerations are provided by G. Seguenza (1873a, 1873b), who thoroughly described the outcrops then exposed at Gravitelli. Several other sporadic mentions of Gravitelli suids appeared in

those years, mainly relying on these previous reports (see L. Seguenza, 1902, and references therein). The mammalian fauna was eventually described by L. Seguenza (1902, 1907), who continued his father's work on Sicilian geology and expanded the paleontological collections.

Gravitelli suids, alongside the other mammal remains, traces of fishes and plants (referred to as *Acer trilobatum* and *Eucalyptus oceanica* by L. Seguenza, 1902), and potentially two species of chelonians — all undescribed except mammals — were recovered from lacustrine clays and sands placed well below the Messinian Gessoso-Solfifera Formation, quintessential manifestation of the Messinian Salinity Crisis (Hsü et al., 1973a, 1973b), and the preceding pre-evaporitic deposits known as “Tripoli”. The latter are constituted by cyclically bedded diatomites that occur across the Mediterranean (Blanc-Valleron et al., 2002). The deposition of the Tripoli Formation is diachronous throughout the Mediterranean, but in Sicily its base was dated by Hilgen and Krijgsman (1999) at 7.01 Ma, and by Blanc-Valleron et al. (2002) at 6.96 Ma, using the astronomical tuning of individual cycles and cyclostratigraphy (the slightly divergent results being due to a different interpretation of the lowermost layers of the formation). Therefore, the mammal fossils of Gravitelli are constrained to be at least older than 7 Ma.

Moreover, the terrestrial mammals did not occur immediately below the Tripoli Formation but further beneath alternating layers of clays, marls, and sands, and marine clays from which L. Seguenza (1902) reported the presence of shark teeth and the whale *Heterocetus*. Unfortunately, these specimens were never properly described. The occurrence of *Heterocetus* — which is also considered today a *nomen dubium* (Steeman, 2010) — was tentatively suggested by Capellini (1877) based on few vertebral fragments. As for the sharks, L. Seguenza (1900, pl. 6, fig. 29) figured only one tooth of *Oxyrhina spallanzani* (= *Isurus oxyrinchus*), which is a species that does not help in refining the chronology of the deposits.

More detailed biostratigraphic analyses were planned by L. Seguenza (1908) but sadly debarred by his premature death during the Messina Earthquake of 1908. Nonetheless, considering the stratigraphic position of the mammal fauna reported by L. Seguenza (1902, 1907) a late Tortonian age, rather than earliest Messinian, seems the most likely. In terms of mammal biochronology, faunas of this age correspond to MN 11 or MN 12.

3. Materials and methods

3.1. The material from Gravitelli

Gravitelli suids are long lost, but Seguenza (1902, 1907) provided measurements, figures, and descriptions that allow thorough morphological and morphometric comparisons. The material consists of twelve specimens, including upper and lower teeth as well as two postcranial bones. The complete list is provided in Table 1.

Seguenza (1902, 1907) did not provide catalogue or identification numbers for Gravitelli specimens, therefore, to assure unambiguous indication throughout the text and for future reference, I denote them with the suffix Grav- (for Gravitelli), followed by the year of Seguenza's publication in which each specimen is figured (1902 or 1907), the number of the plate in Roman numbers (as appears in the original publications), and finally the number of the first figure in which the specimen is depicted

for the first time. For instance, the M3 figured by Seguenza (1902, pl. 6, figs. 14–16) is labelled Grav-1902.VI.14, the right p4 figured by Seguenza (1907, pl. 5, figs. 47, 48) is labelled Grav-1907.V.47, and so on. A few specimens were not figured by Seguenza (1907), and it is necessary to consider them as well. In these cases, a similar approach is followed, but referring to the page of the main text where each specimen is first mentioned, in the sections dedicated to systematic paleontology, further adding a sequential number to deal with multiple citations from the same page. For instance, the left p4 first mentioned on page 102 by Seguenza (1907), which is the second non-figured specimen listed on that page, is named Grav-1907.102.2. This approach could be easily expanded to incorporate further remains described by Seguenza (1902, 1907).

Seguenza (1902, p. 161) concluded the discussion on suids mentioning that while that work was in press, he obtained further material from Gravitelli, namely a second and a third molar. I presumed this refers to the associated M3 and fragmented M2 Grav-1907.V.43, of which he later figured only the M3 (Seguenza, 1907), and not to further undescribed material.

There exist two casts of suid specimens from Gravitelli, curated in IGF (see below for abbreviations), which were the subject of a short note by Gallai and Rook (2006). Since measurements collected on casts might differ from those taken on the original material, they are compared in Table 2. There is good agreement between values reported in the two works (differences being less than 1 mm for all but one measurement), acknowledging potential variation due to slightly different measuring protocols followed, and the approximation used. This comparison indirectly supports the reliability of other measurements taken by Seguenza (1902, 1907). In the following, the original measurements are used for comparative purposes (Tables 2, 3).

Seguenza (1902, 1907) collected linear measurements for most, but not all specimens, namely, not for Grav-1907.V.37, which was a well-preserved mandible fragment with part of the deciduous dentition. To include this specimen

Table 1

List of the material of *Propotamochoerus provincialis* (Blainville, 1847) from the Late Miocene of Gravitelli (Sicily, Italy), with anatomical identification and reference to the original depiction in Seguenza (1902, 1907), when applicable.

Specimen	Anatomical element	Figure
Grav-1902.VI.12	Maxillary fragment with right P4-M1	12, 13
Grav-1902.VI.14	Right M3	14–16
Grav-1902.VI.17	Fragmentary left distal tibia	17–19
Grav-1902.VI.20	Left astragalus	20
Grav-1907.V.37	Mandible fragment with left dp3-dp4 and dp2 alveoli	37, 38
Grav-1907.V.39	Left i1 with fragmented root	39, 40
Grav-1907.V.41	Left? i2 with fragmented crown	41, 42
Grav-1907.V.43	Left M3 and associated distal fragment of M2	43, 44
Grav-1907.V.45	Mandible fragment with right m1-m2 and fragmented m3	45, 46
Grav-1907.V.47	Right p4	47, 48
Grav-1907.102.1.	Left m2	No
Grav-1907.102.2.	Left p4	No

Table 2

Propotamochoerus provincialis (Blainville, 1847) from the Late Miocene of Gravitelli (Sicily, Italy). Comparable measurements of the teeth (in mm) taken by Seguenza (1902) on the original material and Gallai and Rook (2006) on the respective casts. L = length, Wm = mesial/first lobe width, Wd = distal/second lobe width, Hmb = height of the crown at the first buccal cusp, Hdb = height of the crown at the second buccal cusp. Note: ¹ The authors reported to have taken these measurements transversally to cusps pairs, but there is only one main lingual cusp in P4 (protocone), and hence only one (largest) width measurement is customarily collected for this tooth. Seguenza (1902) also measured the largest width of P4 = 16.5 mm.

Reference	Specimen	Side	Tooth	L	Wm	Wd	Hmb	Hdb
Seguenza (1902)	Grav-1902.VI.12	Right	P4	14	16 ¹			
		Right	M1	19	15.5	15.5	6	6
Gallai and Rook (2006)	Grav-1902.VI.14	Right	M3	32	22	21	10	10
	IGF 9261V (cast)	Right	P4	13.88	16.02 ¹	15.12 ¹		
		Right	M1	18.18	15.93	15.45	6.2	6.3
	IGF 9262V (cast)	Right	M3	30.45	22.79	20	10.21	9.63

Table 3

Propotamochoerus provincialis (Blainville, 1847) from the Late Miocene of Gravitelli (Sicily, Italy). Measurements of the teeth (in mm) taken by Seguenza (1907). “-” denotes measurements not taken by the author, either due to imperfect preservation status or simply not taken. L = length, Wm = mesial/first lobe width, Wd = distal/second lobe width. Note: ¹ This value should be considered an approximation, as the tooth appears fragmented mesially.

Specimen	Side	Tooth	L	Wm	Wd
Grav-1907.V.43	Left	M3	35	24.5	20.5
	Left	M2	-	-	20.5
Grav-1907.V.45	Right	m1	16.5 ¹	-	13.5
	Right	m2	23	16.5	16.5
	Right	m3	-	19	-
Grav-1907.V.47	Right	p4	18	-	13

in the morphometric comparison, measurements are taken from the original plate with the software ImageJ, version 1.6 (Schneider et al., 2012). Seguenza (1907) reported to have figured most specimens at natural size and Grav-1907.V.37 at twice of natural size. However, as noted by Hooijer (1946), the scaling of Seguenza’s plates is not perfect. Therefore, I evaluated the extent of the differences between values reported in the text (Table 3) and as they appear in the plate, comparing the error range between couples of measurements. The largest difference obtained is between M3 L values estimated from the buccal and occlusal views of Grav-1907.V.43, corresponding to 2.8 mm. This value is considered the range within which true measurements would have fall. Resulting estimates for Grav-1907.V.37 are provided in Table 4. To validate the procedure, measurements collected by Seguenza (1907) on the original material were compared with their values estimated from the plate (Table S1).

3.2. Repositories and institutional abbreviations

Apart from data and considerations available from previous studies as detailed below, the suid sample from Gravitelli has been compared, by direct examination, with specimens stored in the following institutions:

AFS: Museum of Natural History, Accademia dei Fisiocritici, Siena (Italy)

HNHM: Hungarian Natural History Museum, Budapest (Hungary)

Table 4

Propotamochoerus provincialis (Blainville, 1847) from the Late Miocene of Gravitelli (Sicily, Italy). Estimated measurements of the teeth (in mm) of Grav-1907.V.37 based on Seguenza (1907, pl. 5). L = length, Wm = mesial/first lobe width, Wd = distal/second lobe width, Wt = third lobe width, HM = height of mandible mesial to tooth. Judging from the training set (Table S1), true values should have been between “mean” and “min” estimates. Note: ¹ This measurement is taken in front of where m1 would be present, if preserved in the mandible, i.e., distal to dp4.

Measurement	Estimates		
	mean	min	max
dp3 L	12.6	11.2	14
dp3 Wm	5.7	4.3	7.1
dp3 Wd	7.9	6.5	9.3
dp4 L	23.5	22.1	24.9
dp4 Wm	9.2	7.8	10.6
dp4 Wd	10	8.6	11.4
dp4 Wt	11.5	10.1	12.9
L dp2-dp4	41.9	40.5	43.3
L dp3-dp4	32.3	30.9	33.7
HMdp3	23.1	21.7	24.5
HMdp4	23.7	23.3	25.1
HMm1 ¹	22.2	20.8	23.6

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

IsIPU: Italian Institute of Human Paleontology, Anagni (Italy)

MBFSZ: Geological Museum of the Mining and Geological Survey of Hungary, Budapest

MNCN: National Museum of Natural Sciences, Madrid (Spain)

MUST: University Museum of Earth Sciences (including the former MPUR: Museum of Paleontology), Department of Earth Sciences, Sapienza University of Rome (Italy)

NMB: Natural History Museum, Basel (Switzerland)

NHMMZ: Mainz Natural History Museum/State Collection of Natural History of Rhineland-Palatinate (Germany)

3.3. Comparison

Gravitelli suids are compared with related Late Miocene to Pliocene species from Eurasia, including *Propotamochoerus wui* Van der Made and Han, 1994, *P. hyotherioides*

(Schlosser, 1903), *P. hysudricus* (Stehlin, 1899), *P. palaeochoerus* (Kaup, 1833), *P. provincialis* (Blainville, 1847), and *Sus arvernensis* (Croizet and Jobert, 1828). Univariate, bivariate, and multivariate comparisons of linear measurements are carried out. Measurements of the comparative material rely on published information or derive from direct examination in several institutions (see Section 3.2). For *P. wui*, measurements are from Van der Made and Han (1994). For *P. hyotherioides*, measurements are from Schlosser (1903), Pearson (1928), Van der Made and Han (1994), and Hou et al. (2019). For *P. hysudricus*, measurements are from Pickford (1988), Sein et al. (2009), Khan et al. (2010), Batool et al. (2015), Sarwar et al. (2016), Aslam et al. (2021), and direct examination in NMB. For *P. palaeochoerus*, measurements are from Mottl (1966), Hünemann (1968), Hellmund (1995), Van der Made et al. (1999), Fortelius et al. (2005), Iannucci and Begun (2022), and direct examination in MBFSZ, NHMMZ, and NMB. For *P. provincialis*, measurements are from Thenius (1950), Geraads et al. (2008), Gallai and Rook (2011), Pickford (2013), Lazaridis (2015), Iannucci et al. (2021a), and direct examination in AFS, IGF, MNCN, and NMB. For *S. arvernensis*, measurements are from Dal Piaz (1930), Hünemann (1971), Samson et al. (1971), Mazo and Torres (1990), Montoya et al. (2006), Guérin and Tsoukala (2013), Pickford and Obada (2016), Iannucci et al. (2022a), and direct examination in AFS and NMB.

The recently formally named *Propotamochoerus aegaeus* Lazaridis, Tsoukala, and Kostopoulos, 2022, previously introduced in a PhD thesis (but in this instance a *nomen nudum*) by Lazaridis (2015), is treated within *P. provincialis*, following Iannucci et al. (2021a). Notwithstanding the possibility that early Turolian remains of *Propotamochoerus* represent a different species than *P. provincialis*, the differential diagnosis proposed by Lazaridis et al. (2022) lists morphological traits that cannot be checked on the material apparently included within *P. provincialis* by the same authors, and morphometric differences that are too subtle to warrant species distinction. Adopting *P. aegaeus* and its differential diagnosis from *P. provincialis* as valid would result in leaving most Turolian samples as *Propotamochoerus* sp.

Propotamochoerus hysudricus, which is regarded as the type species of the genus (Pickford, 1988), also represents a problematic case. The most abundant material assigned to the species originates from the Siwaliks of northern Pakistan. Barry et al. (2002) inferred first and last appearance of *P. hysudricus* from some controlled occurrences, resulting in a chronological range of 10.2–6.5 Ma. Moreover, for most of the extensive historical material collected from the Siwaliks detailed information on the provenance is either not available or limited to toponyms or formation names that give only vague constraints. In particular, specimens simply labelled as from Dhok Pathan are potentially as younger as the upper boundary of the Dhok Pathan Formation (~3.5 Ma). Basically, remains assigned to *P.*

hysudricus spans a considerable amount of time, comparable to the combined chronological range of three-four European species, and very likely represents a heterogeneous sample that needs to be revised. Following common practice (e.g., Sein et al., 2009), *P. hysudricus* is nonetheless treated as a single distinct and valid species for the purposes of this paper.

Synonymy between genera follows Iannucci et al. (2021a).

In the morphological description, the dental nomenclature proposed by Van der Made (1996) is used, but some abbreviations differ as detailed below. Tooth type and position are abbreviated by combining their initial letter with a sequential number, using uppercase for upper teeth and lowercase for lower teeth. A lowercase “d” is added before deciduous teeth (i.e., M3 = upper third molar; dp4 = lower fourth deciduous premolar).

Measurements abbreviations: L: length; W: width (-m: mesial; -d: distal/second lobe; -t: third lobe); Hmb: height of the crown at the first buccal cusp; Hdb: height of the crown at the second buccal cusp; HM(x): height of mandibular corpus (measured on the buccal side in front of “x” tooth). Tooth rows lengths are measured at the alveoli on the buccal side, and they are inclusive of the indicated teeth (e.g., L dp2-dp4 = length of deciduous premolar row).

3.4. Statistical analysis

A principal component analysis (PCA) on the variance-covariance matrix of p4 L, p4 W, m1 W, m2 L, m2 W, and m3 W was carried out. Selected variables are those reliably taken on the p4-m3 series formed by Grav-1907.V.45 and Grav-1907.V.47, which according to Seguenza (1907) belonged to the same individual. Species incorporated in the PCA are the same considered in the rest of the comparison, but here only specimens for which the entire set of measurements is available are included. In other terms, missing data are not allowed, as their imputation for a relatively small dataset such as this might fabricate substantially biased observations. Two hemimandibles from Grytsiv (Van der Made, 1999, pl. 1) have very similar morphology and measurements, and hence they could have been part of the same individual. They are treated in the PCA as a single specimen, using the mean of the values provided by Van der Made et al. (1999). The mean values of the sample from Vozarci (“Vozarci-mean” in Geraads et al., 2008) are also considered a single entry. A total of 34 specimens was included in the PCA (*P. wui*, n = 3; *P. hyotherioides*, n = 1; *P. hysudricus*, n = 9; *P. palaeochoerus*, n = 9; *P. provincialis*, n = 8; *S. arvernensis*, n = 3; Gravitelli, n = 1). Raw measurements were log-transformed or divided by the geometric mean (gm-) of the measurements of each specimen. The two datasets obtained were used to compute two different PCAs, referred to as logPCA and gmPCA in the text. LogPCA was focused on dental measurements (hence reflecting both size and dental propor-

tions) and gmPCA on dental shape ratios (without correcting for allometry). The software PAST, version 4.04 (Hammer et al., 2001), was used for the analysis.

Log-transforming linear measurements before these kinds of analyses is a common practice that offers several advantages, although should not be used carelessly (Jungers et al., 1995; Feng et al., 2014). On the other hand, there are countless “size-adjusting” methods (Jungers et al., 1995). Dividing values of each specimen by the geometric mean of all measurements for that specimen, is the simplest (i.e., requiring less steps) correction among “Mosimann shape ratios”, and it effectively produces dimensionless variables (Mosimann, 1970; Mosimann and James, 1979; Jungers et al., 1995). This approach was first adopted for fossil suids by Iannucci et al. (2021a) and using Mosimann shape ratios is widespread in studies focused on other mammal groups in the fossil record (e.g., Alba et al., 2014; Ercoli et al., 2019; Iannucci et al., 2021b).

4. 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)
(Figs. 2, 3)

Referred material from Gravitelli: The complete list of the material is provided in Table 1. Most specimens were illustrated by Seguenza (1902, 1907) and are all refigured herein, presenting an extract of the original plates (Figs. 2, 3).

Description: Grav-1902.VI.12 is a maxillary fragment with right P4-M1 that preserves a small portion of the bone

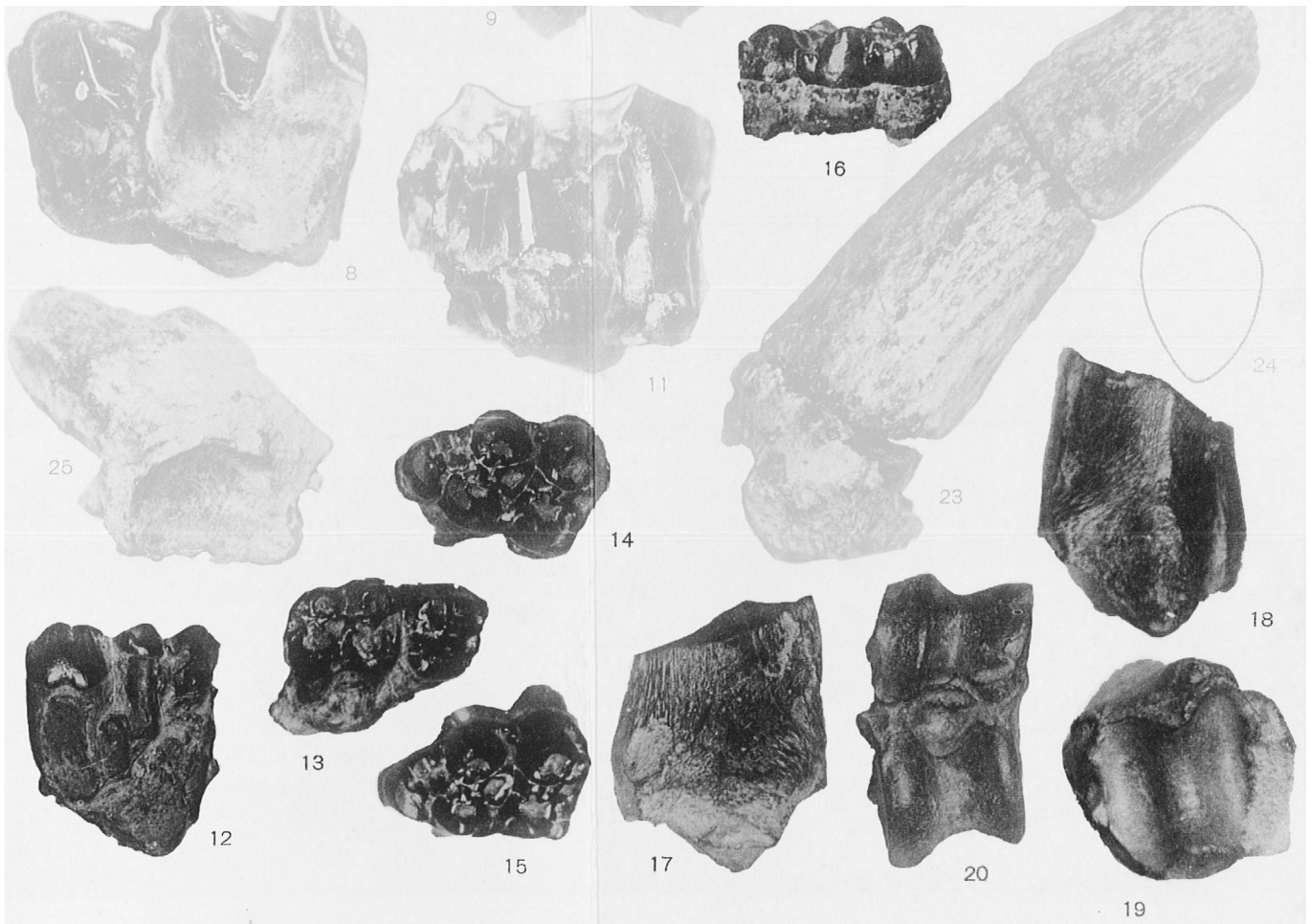


Fig. 2. Extract of Seguenza (1902, pl. 6), modified to emphasize suid remains, which are assigned herein to *Propotamochoerus provincialis* (Blainville, 1847). Grav-1902.VI.12: maxillary fragment with right P4-M1 in buccal (12) and occlusal (13) views; Grav-1902.VI.14: right M3 in stereo occlusal (14, 15) and buccal (16) views; Grav-1902.VI.17: fragmentary left distal tibia in anterior (17), posterior (18), and distal (19) views; Grav-1902.VI.20: left astragalus in anterior view (20). According to Seguenza (1902), the latter two specimens were found articulated and hence belonged to the same individual.

hosting the roots of the teeth, three beneath P4 and four below M1. In Seguenza (1902, pl. 5, fig. 13) the anatomical orientation of the fragment is not perfect, but this is one of the specimens of which a cast is still curated in IGF (Gallai and Rook, 2006, fig. 1). P4 has a trapezoidal shape in occlusal view. The tooth is wider than longer, shorter (mesiodistally) on the lingual side than on the buccal. It hosts three main cusps of comparable size, two buccal (paracone and metacone) and one lingual (protocone), the paracone perhaps being slightly larger. The buccal cusps are higher than the protocone. The deepest point of the tooth is close to its middle point. Apart from this, there does not seem to be a pronounced valley between the main cusps, or in other terms the profossa appears filled and the main cusps connected, without sharp interruptions. The lingual side of the tooth, hosting the protocone, is somewhat tilted mesially, and as a result the mesial cingulum is slightly concave.

M1 has a rectangular outline in occlusal view, being longer than wider. The molar has two lobes with two cusps each. In each pair, the buccal cusp is more mesially located, and it is higher on the occlusal plane. The mesial and distal cingula approximately develop in parallel. The notch between the lobes is similarly pronounced on both sides, hosting a faint tubercle on the buccal side. Slightly on the rear relative to the axis connecting the notches, close to the middle of the tooth in occlusal view, there is a large tetrapreconule.

According to Seguenza (1907), a distal fragment of M2 was associated with Grav-1907.V.43. Unfortunately, he chose not to figure it. He described it as preserving part of the two distal cusps and a marked distal cingulum but lacking the roots and being too much worn for allowing detailed morphological considerations.

The only upper tooth position that remains to describe is M3, which is represented at Gravitelli by two specimens, one right (Grav-1902.VI.14) and one left (Grav-1907.V.43). The tooth replicates the basic pattern of M1, but it has a third distal lobe, it is more asymmetric relative to the mesiodistal axis, the mesial lobe is clearly the largest, and cingula and accessory cusplets are more pronounced. The occlusal outline of the tooth is roughly triangular, with the buccal side longer than the lingual. In detail, however, only part of the mesial side is straight to slightly concave, at the point of contact with M2, while the rest of the contour is interrupted by a series of marked notches between the lobes on the lateral sides, and it is rounded at the mesial and distal ends. The mesial cingula are pronounced and host a protopreconule. A distinct tetrapreconule is present between the two first lobes. The third lobe is constituted by a single prominent cusp, a pentacone, and a series of small tubercles (two-three detectable) on the buccal side. Grav-1902.VI.14 is more worn than Grav-1907.V.43 and its mesial end is placed more buccally. In Grav-1907.V.43, there is a particularly marked accessory cusplet on the lingual side of the tetracone, which is apparently separated from it.

Grav-1907.V.37 is a mandible fragment bearing left dp3-dp4 and the alveoli of dp2. A small diastema separates dp2

and dp3. All teeth are implanted close to lingual side of the corpus, which maintains an approximately constant height in the preserved portion. No foramina are present in the preserved portion of the mandibular corpus.

Of the two preserved deciduous teeth, dp3 is markedly the smallest. The tooth has a piriform shape in occlusal view, the distal lobe being larger than the mesial, especially on the buccal side. A slight concavity is present distally at the point of contact with dp4. One main cuspid (protoconid) develops roughly in the middle of the tooth. The mesiodistal ridge hosting the protoconid virtually divides the tooth into two halves, whose morphology differ. The lingual side has a roughly plain appearance, while a cingulum-like development is present on the buccal side.

The other preserved deciduous premolar, dp4, is a trilobed tooth. Among these lobes, unlike those of M3/m3, the widest is the distal and the narrowest is the mesial. The notches between the lobes are more pronounced on the buccal side. Each lobe hosts a pair of main cusps, like in the permanent molars, but seemingly with a different enamel pattern. Basically, the cusps are closer to each other, and hence they mainly develop mesiodistally. This is especially true in the mesial lobe, where an accessory mesial cuspid seems also present medially, but not at the notch between the first and second lobes. The latter has apparently four cusps arranged in a cross. In the distal lobe, the cusps replicate the arrangement seen in the second lobe, but here they are larger and more clearly separated. The distal accessory cuspid projects distally. A series of five-six tubercles is observable on its distobuccal side. Seguenza (1907) also described the roots of dp4, which were presumably exposed on the ventral side of the mandible (which he did not figure), as being five, three of which developing below the buccal cusps, and two beneath the second and third lobes of the tooth on the lingual side, the former subdivided into two parts projecting mesially and distally.

According to Seguenza (1907), the remains of the lower permanent dentition were recovered in close proximity to each other and belonged to a single individual. The most complete fragment is Grav-1907.V.45, bearing a small portion of the corpus with right m1-m3. However, both m1 and m3 are fragmented. In m1, only a portion of the mesiobuccal side is missing, while m3 preserves only the mesial lobe. The molar row is also extremely worn and thus poorly informative of the original morphology. All preserved mesial and distal sides of the teeth are practically straight, which gives to m2 a rectangular shape in occlusal view. The preserved portion of the first lobes of m2 and m3 is seemingly more developed on the lingual side. Seguenza (1907) did not figure the left m2 (Grav-1907.102.1.) but described it as perfectly equivalent in size and morphology to the right m2.

Similarly pronounced wear is observable on the right p4 Grav-1907.V.47, not allowing to discriminate how many cusps were originally present on the crown. The tooth appears as a conical structure dominated by a massive

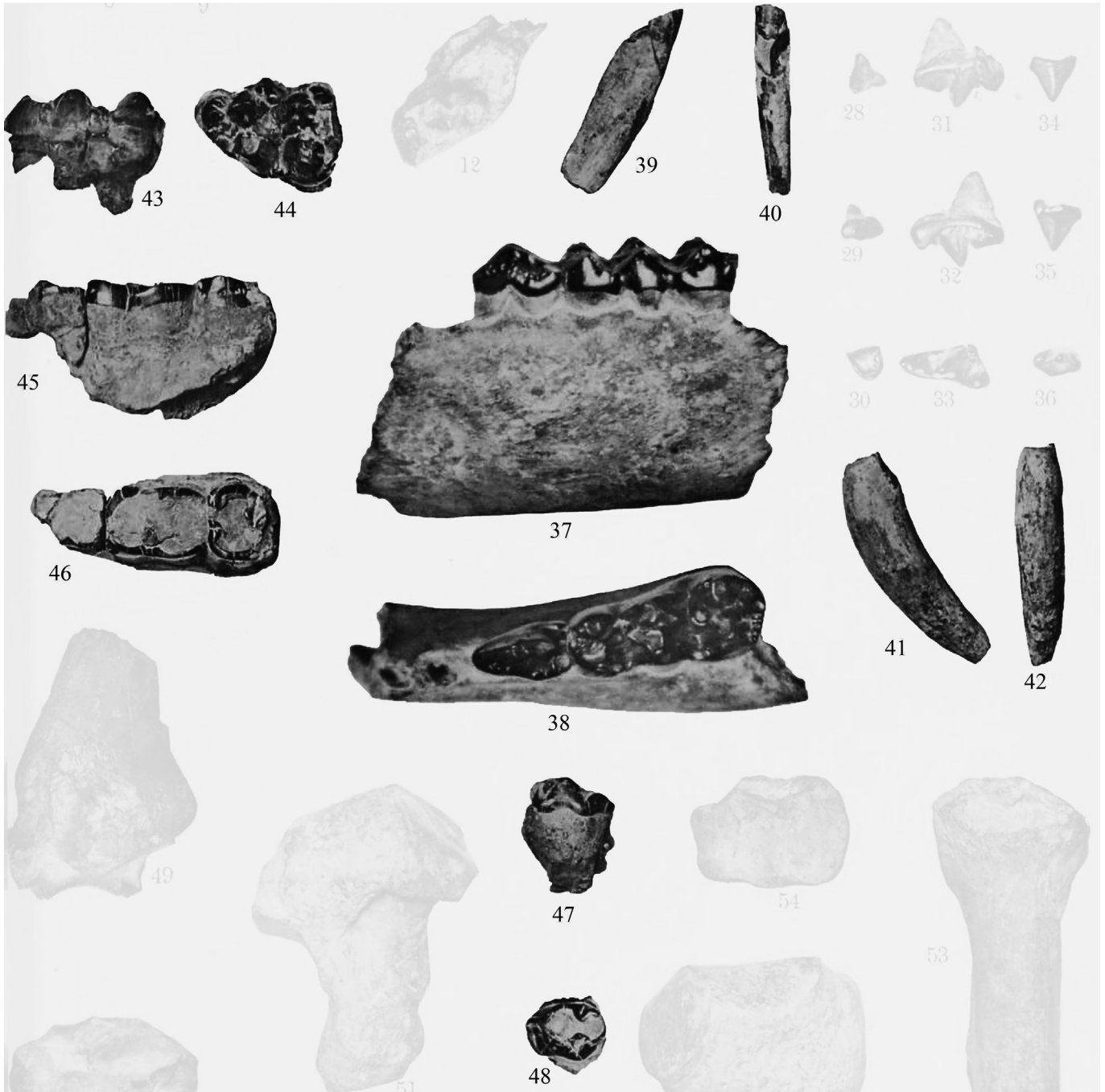


Fig. 3. Extract of Seguenza (1907, pl. 5), modified to emphasize suid remains, which are assigned herein to *Propotamochoerus provincialis* (Blainville, 1847). Grav-1907.V.37: mandible fragment with left dp3-dp4 in buccal (37) and occlusal (38) views; Grav-1907.V.39: left i1 in mesial (39) and buccal (40) views; Grav-1907.V.41: left? i2 in mesial or distal (41) and buccal (42) views; Grav-1907.V.43: left M3 in buccal (43) and occlusal (44) views; Grav-1907.V.45: mandible fragment with right m1-m3 in lingual (45) and occlusal (46) views; Grav-1907.V.47: right p4 in lingual (47) and occlusal (48) views. Grav-1907.V.37 is figured at twice the size of the other specimens.

central “cuspid” (actually resulting from the merging of metaconid and protoconid), which due to the wear is connected to the distal portion of the crown. The latter area is lower on the occlusal plane and inclined distally. A ridge is present on the mesial side of the tooth, connecting the main cone with a cingulum. The left antimer of p4 (Grav-1907.102.2.) was not figured by Seguenza (1907) but

described as perfectly equivalent in size and morphology to the right p4.

Lower incisors are represented by two specimens, documenting i1 and i2 tooth loci. Grav-1907.V.39 is a left i1. The root is fragmented, and the crown is preserved but unfortunately only figured in mesial and buccal views. The specimen displays a pronounced wear, having almost

reached the cemento-enamel junction (cervix) on the mesial side. A faint longitudinal groove is discernible on the same side.

Seguenza (1907) assigned Grav-1907.V.41 to a left i2. The attribution to i2 is substantiated by the curvature of the root, more pronounced than that of i1. The side of the tooth is less certain judging from the original plate, also considering that the tip of the tooth is missing. Nonetheless, in buccal view the cemento-enamel junction is apparently detectable and placed markedly mesially, which would confirm Seguenza's interpretation.

Apart from the dentognathic specimens, two postcranial bones also belong to a suid, and actually to the same individual, since according to Seguenza (1902) they were recovered in anatomical connection. These are a left fragmentary distal tibia (Grav-1902.VI.17) and an astragalus (Grav-1902.VI.20) that were originally assigned to *Tragocerus* sp. by Seguenza (1902). The tibia is apparently fragmented along the anterior margin of the articular surface and at the level of the medial malleolus, but the outline of the distal articulation has a clearly squared to broad-rectangular shape. The astragalus seems complete on the only side figured (the anterior). It has an asymmetric appearance, with the two trochleae inclined relative to each other.

Minimum number of individuals: Grav-1907.V.37 has a deciduous dentition and hence belonged to a young individual. The mandible fragment with the partly preserved molar row (Grav-1907.V.45), and the isolated but associated right and left p4 (Grav-1907.V.47 and Grav-1907.102.2.), left m2 (Grav-1907.102.1.), and very likely the two incisors (Grav-1907.V.39 and Grav-1907.V.41), as indicated by Seguenza (1907), are the remains of a senile individual with teeth in an advanced wear stage. The wear observable on the upper teeth is less pronounced, and thus they could not have belonged to the same individual. The two M3 (Grav-1902.VI.14 and Grav-1907.V.43), despite being from opposite sides, differ in the wear pattern (more advanced in Grav-1902.VI.14) and in M3 L values (3 mm). Such differences appear too marked to be encountered between the left and right side of a single individual.

Collectively, these observations allow to infer the presence at Gravitelli of a minimum number of four individuals, one young individual and three adults, one of which senile.

5. Comparison

5.1. Upper dentition

Measurements of P4 reveal a large overlap between most of the considered species, with Gravitelli close to mean values of *P. provincialis* but also falling within the variability of *P. hysudricus* and *P. palaeochoerus* (Fig. 4A). Gravitelli M1 is somewhat more elongated than in the other species, but it is close to the ranges of *P. palaeochoerus* and *P. provincialis* (Fig. 4B). M2 is represented at Gravitelli exclusively by a distal fragment part

of Grav-1907.V.43, only M2 Wd is therefore considered in the comparison. The specimen from Gravitelli is above the mean but within the ranges of *P. provincialis*, *P. palaeochoerus*, and *P. hysudricus*, and below the mean but between the range of *P. hyotherioides* (Fig. 4C). In the latter graph and due to the otherwise paucity of comparative material of the taxon, values of *P. hysudricus* include the maximum width (M2 W), when measurement of M2 Wd were not provided in previous studies. The two M3 from Gravitelli appear in general large among those of the considered species but also reveal important variability within the sample (Fig. 4D). Grav-1902.VI.14 is smaller and falls within the largest values of *P. palaeochoerus* and below the mean of *P. provincialis*, but it is also close to the largest specimens of *P. hysudricus* and the smallest of *P. hyotherioides*. Grav-1907.V.43 is instead larger and only comparable to remains of *P. hyotherioides* and *P. provincialis*. The P4 L/M3 L ratio, based on the mean values of the considered species, reveals sharp differences between *P. wui* (0.38), which has a relatively elongated M3, and *P. palaeochoerus* (0.50), which has a proportionally enlarged P4 (Fig. 5). The value of Gravitelli is equivalent to that of *P. provincialis* (0.42), possessing a comparatively more elongated M3 than *P. hyotherioides* (0.43), *S. arvernensis* (0.44), and *P. hysudricus* (0.45).

5.2. Lower deciduous dentition

Comparative data for the deciduous dentition are somewhat limited but informative as well. Cross-checking values estimated with ImageJ with those provided by Seguenza (1907), it appears that original measurements are mainly comprised between the minimum and the mean of the estimates (Table S1). Therefore, such error range is displayed in Fig. 6A. In absolute values, Gravitelli has a large dp4 L and a small dp4 W. The dp4 W/dp4 L ratio is outside the range observed for all other specimens, and especially far from *P. hysudricus* and *S. arvernensis* (Fig. 6B). Basically, the dp4 appears distinctly elongated at Gravitelli. This feature is not an artifact of the measuring estimates, as the occlusal proportions of the tooth would be the same, whatever the bias associated with the single measurements truly is. Indeed, that this feature is genuine is corroborated by Seguenza (1907, p. 102) who described the tooth, exaggerating, as almost three times longer than wider. A detailed biometric investigation for dp3 is not attempted, due to the paucity of available comparative material, but the observed enlargement of the distal lobe appears remarkable, as it is the presence of a buccal cingulum.

5.3. Lower permanent dentition

The lower permanent dentition has been compared through PCAs. The first two components of logPCA jointly account for 89.6% of explained variance, but the proportion explained by PC1 (81.9%) is predominant (Fig. 7, Table 5). This axis is mostly influenced by size,

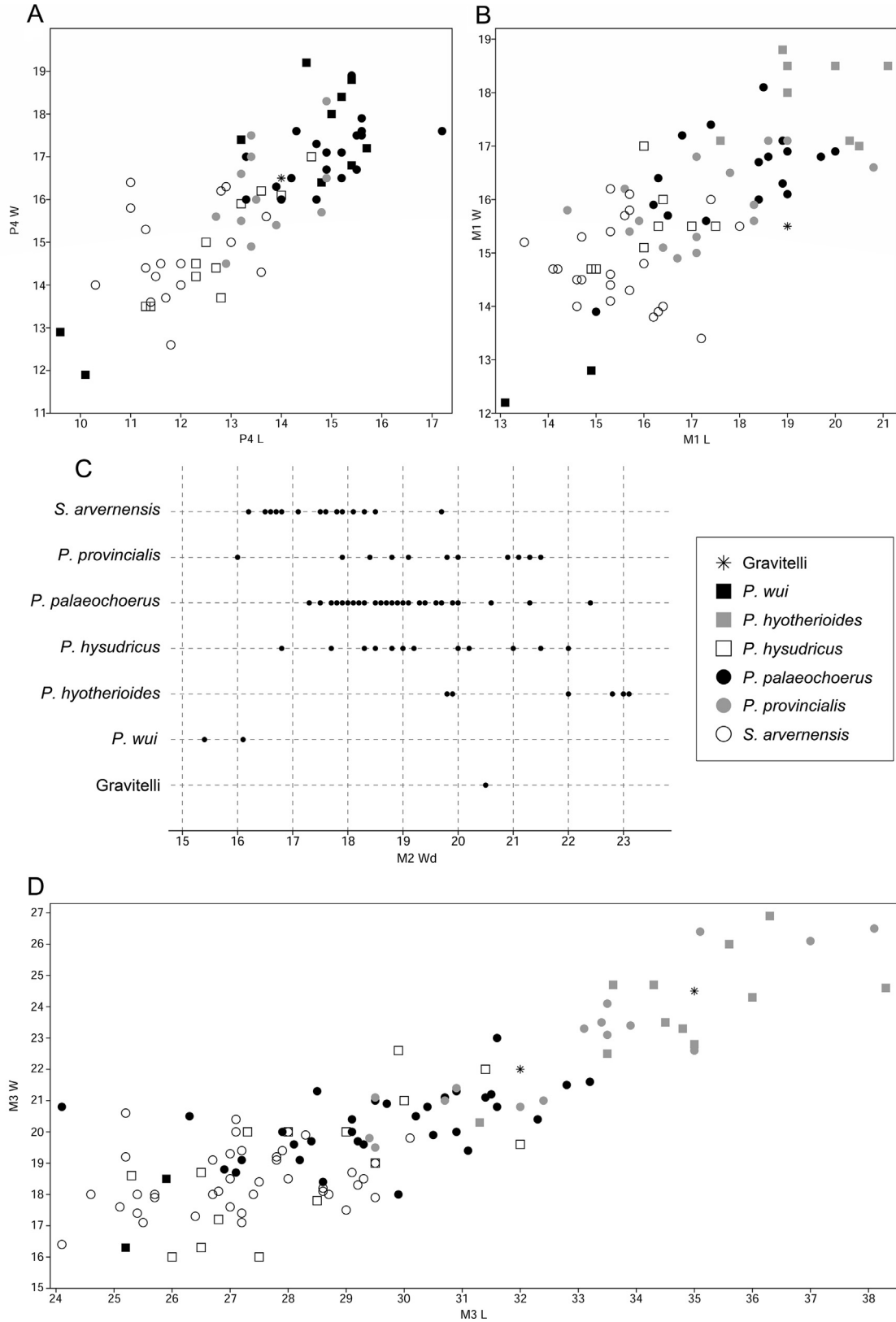


Fig. 4. Bivariate and univariate comparisons of dental measurements (in mm) of *Propotamochoerus provincialis* (Blainville, 1847) from the Late Miocene of Gravitelli (Sicily, Italy) with different species of *Propotamochoerus* and *Sus arvernensis*. (A) P4 L x W, (B) M1 L x W, (C) M2 Wd, (D) M3 L x W. For details and abbreviations, see Section 3.

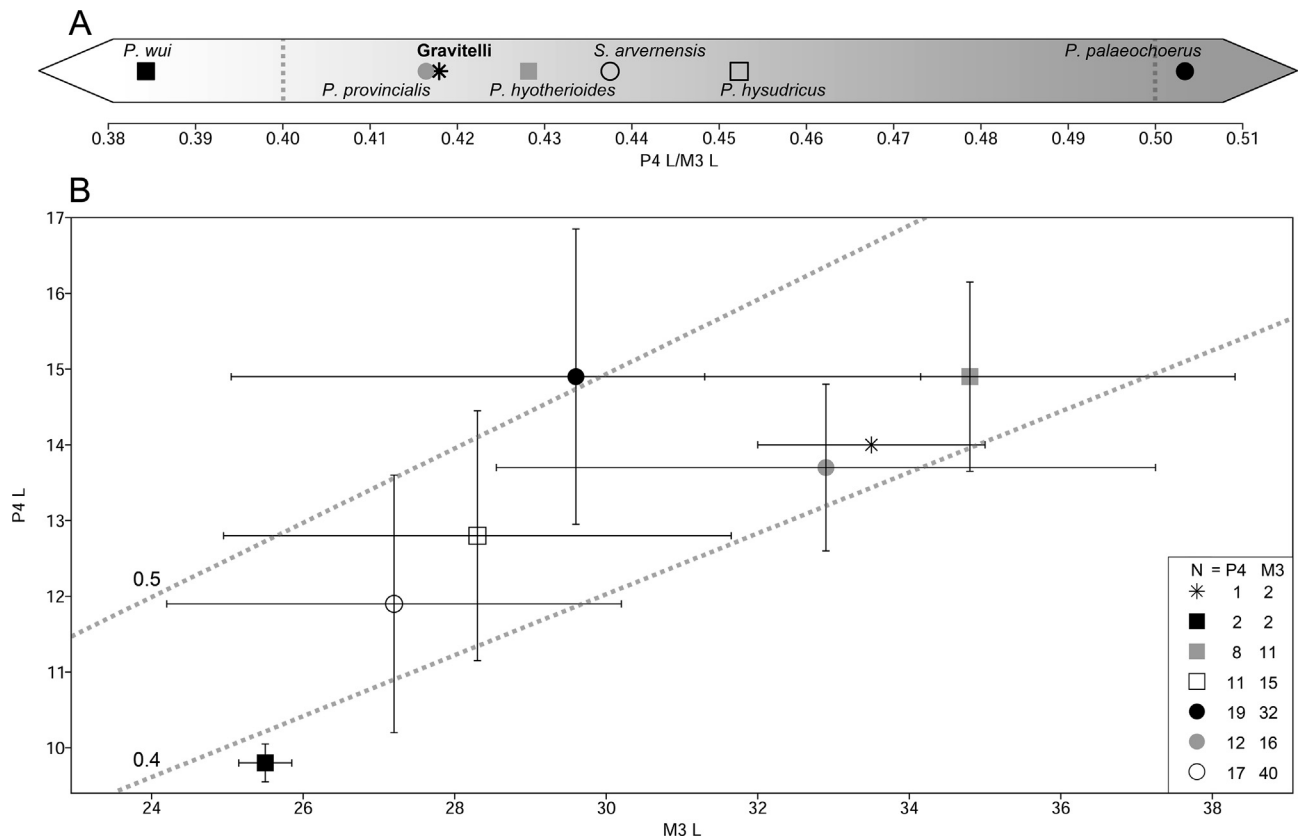


Fig. 5. Relative elongation of M3 (on the left) and P4 (on the right) in *Propotamochoerus provincialis* (Blainville, 1847) from the Late Miocene of Gravitelli (Sicily, Italy) and in different species of *Propotamochoerus* and *Sus arvernensis*, as expressed by the P4 L/M3 L ratio (A). Bivariate comparison (in mm) of M3 L x P4 L, the same samples are considered (B). Each point is the species mean value; bars represent the species ranges; dotted lines are drawn at P4 L/M3 L = 0.4 and 0.5; N = sample size.

showing a positive contribution of all considered variables, with no sharp differences between them. PC2 (7.7% of explained variance) is mainly influenced by the opposite contribution of p4 L and especially p4 W on one side, and m2 L, m2 W, and m3 W on the other, with m1 W having a marginal impact. The resulting projected morphospace allows a good discrimination between species. *Propotamochoerus wui* is substantially smaller, *S. arvernensis* is also small but close to the range of *P. hysudricus*. Along PC1, there is overlap between *P. hysudricus*, *P. palaeochoerus*, and *P. provincialis*. The overlap is small between *P. hysudricus* and *P. provincialis*, and more important between both of them and *P. palaeochoerus*. The latter species is, however, almost completely separated along PC2, which indicates that *P. palaeochoerus* has relatively larger p4. The single specimen of *P. hyotherioides* plots in the upper right corner of the graph, being larger and with relatively larger molars. The Gravitelli specimen is also large but falls between the areas occupied by *P. palaeochoerus* and *P. provincialis*.

Size-adjusting between specimens measurements reveals more dimensions of variability that are important for the considered sample (Fig. 8, Table 6). In gmPCA, PC1 accounts for 39% of explained variance, but up to PC4 all components explain more than 5% of the total variance. The scree plot in Fig. S1 also does not show a clear

“elbow”, hence the first four components (jointly 95.3% of variance) are all interpreted herein. PC1 is similar to PC2 of logPCA, although variables have slightly different loadings, separating specimens with proportionally larger p4 (on the left) from those with larger molars (on the right). This results in a good but not complete separation of *P. palaeochoerus* from the other species, and large overlap between all the other groups. PC2 (24.6% of variance) mainly represents length to width proportions, which apparently do not discriminate effectively between species, although the single specimen of *P. hyotherioides* has relatively elongated teeth. PC3 and PC4 are difficult to interpret and seem to document mainly intraspecific variability. PC3 (18.5% of variance) is mainly influenced by the opposite contributions of p4 measurements (mainly p4 L) and m3 W on one side, and all other variables (especially m2 W) on the other. Along PC4 (13.2% of variance) the sample is distributed according to p4 L and m2 W on one side, and p4 W and m2 L on the other. On this axis, it is perhaps important the good separation of *P. wui*, with relatively elongated p4 and wide m2.

5.4. Postcranial material

The associated fragmentary left distal tibia (Grav-1902.VI.17) and astragalus (Grav-1902.VI.20), originally

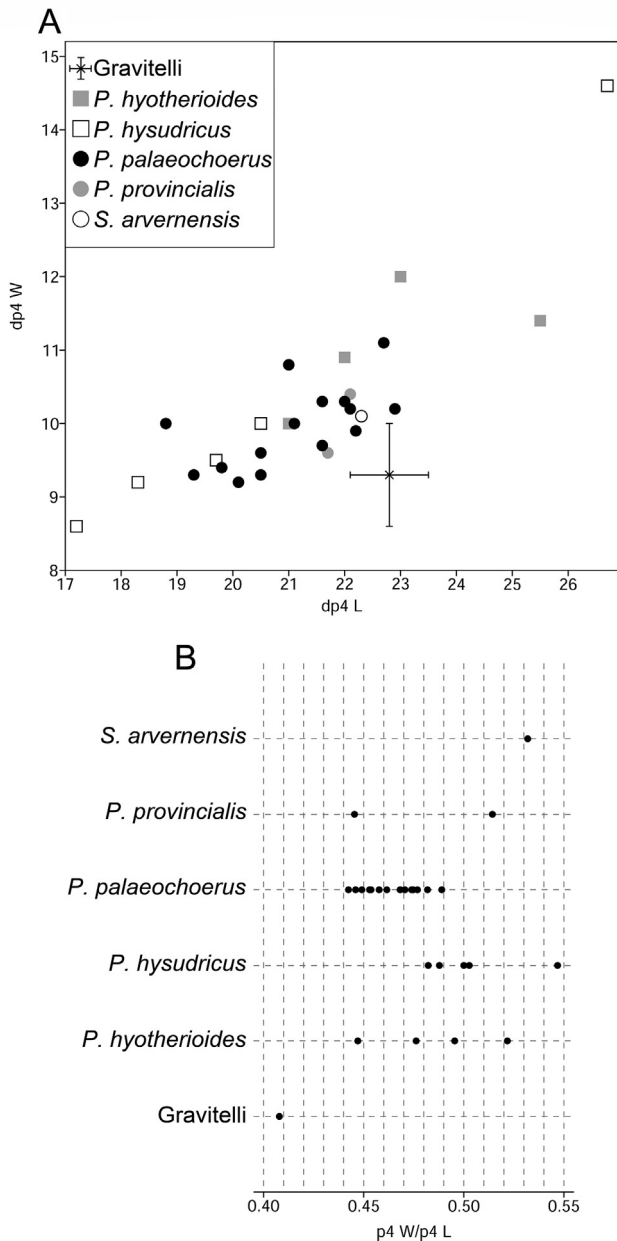


Fig. 6. Bivariate and univariate comparisons of dp4 measurements (in mm) of *Propotamochoerus provincialis* (Blainville, 1847) from the Late Miocene of Gravitelli (Sicily, Italy) with different species of *Propotamochoerus* and *Sus arvernensis*. (A) L x W, (B) W/L. The error range of estimated measurements is shown. For details and abbreviations, see Section 3.

assigned to *Tragocerus* sp. by Seguenza (1902), belong to a suid. Seguenza (1902) measured the astragalus “length” (49.5 mm), “width” (26.5 mm), and “depth” (26.5 mm), but he did not specify how these measurements were taken. There can be little doubt that the “length” corresponds to the largest anatomical dimension measurable on an astragalus, i.e., the greatest proximodistal diameter of the lateral side. The other two measurements are more difficult to interpret, but presumably were taken perpendicular to each

other and, in any case, Seguenza (1902) reported the same value for both. Even acknowledging a bit of uncertainty on how measurements were taken, their values are close to those reported for *P. palaeochoerus*, *P. provincialis*, and small specimens of *Hippopotamodon major* (Van der Made, 2005, fig. 30; formerly included in *Microstonyx*). The distal epiphysis of the tibia is partly fragmented, but Seguenza (1902) reported 36×36 mm for its “greatest diameters”, measurements which are in line with the size of the astragalus.

6. Discussion

6.1. Comparative discussion

Gravitelli suids have been initially referred to *S. choeroides* — a name of doubtful application that has long been used for material currently placed in *Eumaiiochoerus etruscus* — (G. Seguenza, 1862, 1868), then described as *Sus* (= *Hippopotamodon*) *major* (L. Seguenza, 1902, 1907), subsequently suggested to represent the African *Nyanzachoerus* (Rook et al., 2000), and finally recognized as belonging to *Propotamochoerus* (Gallai and Rook, 2006; Van der Made et al., 2006). However, Gallai and Rook (2006) only considered two casts and assigned them to *Propotamochoerus* sp., while Van der Made et al. (2006, p. 235) argued in passing for a conceivable reference of Gravitelli suids to *P. provincialis* based on “figures and description by Seguenza (1902)”, but without further details. The latter attribution is substantiated herein by redescribing and comparing all suids specimens discussed by Seguenza (1902, 1907), including those that were originally misidentified.

An assignment of Gravitelli suids to *E. etruscus*, an endemic suid of the Tusco-Sardinian paleobioprovince (Hürzeler, 1982) or to the African *Nyanzachoerus* (Boisserie et al., 2014) is discouraged by clear morphological differences. For instance, M3 in *E. etruscus* has a simpler (less folded) enamel pattern (e.g., Mazza and Rustioni, 1997, pl. 2), while p4 in *Nyanzachoerus* is markedly enlarged (Boisserie et al., 2014). *Hippopotamodon* Lydekker, 1877, like *Propotamochoerus*, is another widespread dicoryphochoerine (Liu et al., 2004; Van der Made et al., 2013; Pickford, 2015). *Hippopotamodon* mainly differs from *Propotamochoerus* — considering traits observable in the suid sample from Gravitelli — in its larger dimensions and proportionally elongated M3 (Iannucci et al., 2021a).

Detailed comparisons of Gravitelli suids have been therefore focused on the different species of *Propotamochoerus*, including *P. wui*, *P. hyotherioides*, *P. hysudricus*, *P. palaeochoerus*, and *P. provincialis*, and on *Sus arvernensis*. Apart from *P. wui*, which is a substantially smaller species, these small and medium-sized Suinae from the Late Miocene to Pliocene of Eurasia constitute a group whose isolated remains are often difficult to identify, sharing an

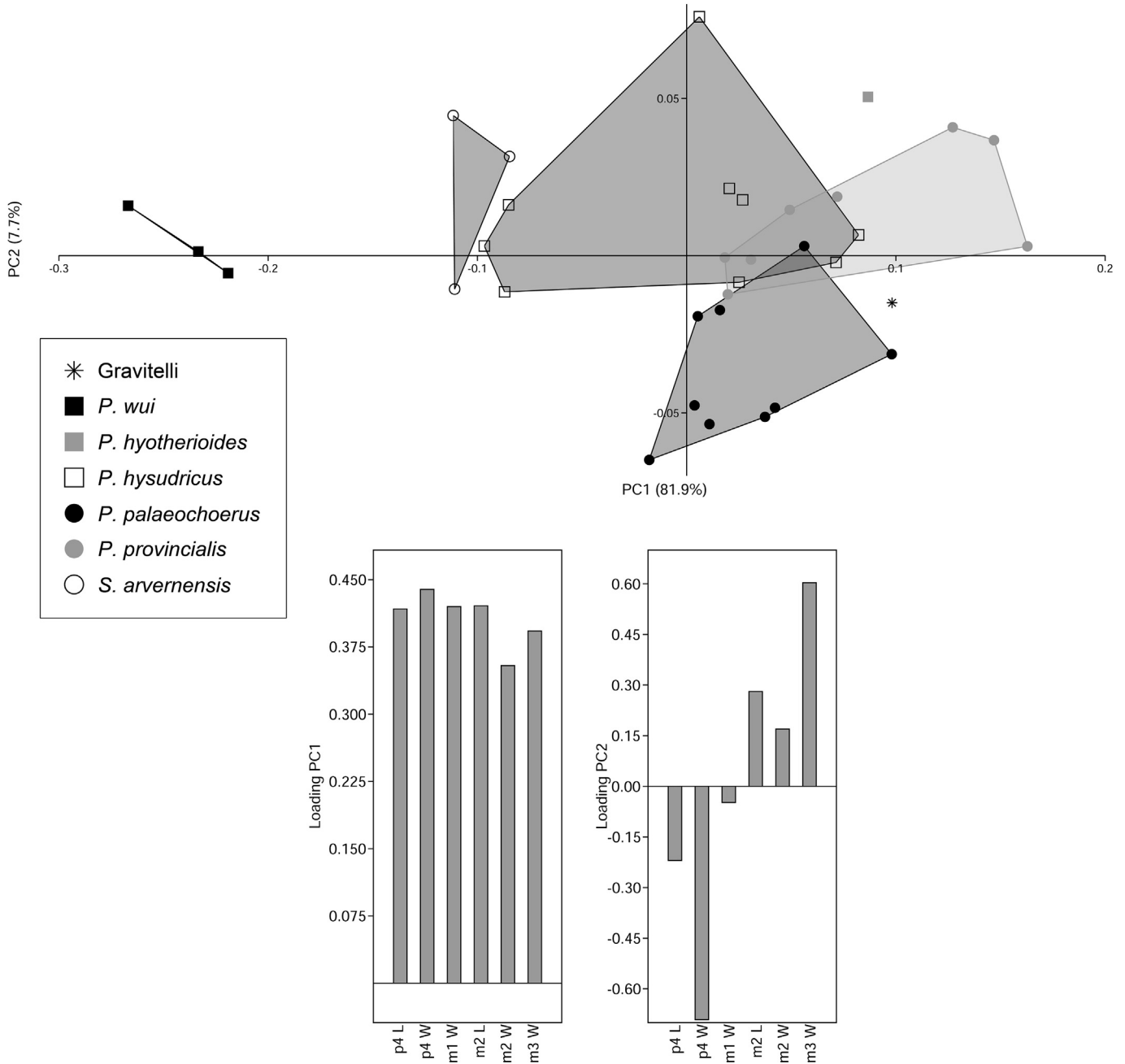


Fig. 7. Morphospace projection of logPCA onto the plane described by the first two components, and their respective loadings.

Table 5

Eigenvalues, percentage of explained variance, and loadings of logPCA. The first two components (jointly 89.6% of explained variance) are interpreted herein.

logPCA	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
Eigenvalue	0.01063	0.00100	0.00052	0.00040	0.00027	0.00016
% variance	81.867	7.6924	4.0121	3.104	2.068	1.2567
p4 L	0.41728	-0.21953	-0.77628	0.00945	0.41831	-0.00029
p4 W	0.43911	-0.69138	0.34273	-0.36031	-0.15653	0.23956
m1 W	0.41985	-0.04768	0.23629	0.28281	-0.01230	-0.82794
m2 L	0.42082	0.2807	-0.26822	0.18549	-0.77429	0.19555
m2 W	0.35417	0.16989	0.35892	0.58898	0.38895	0.46765
m3 W	0.39276	0.60322	0.15271	-0.63938	0.22261	-0.01369

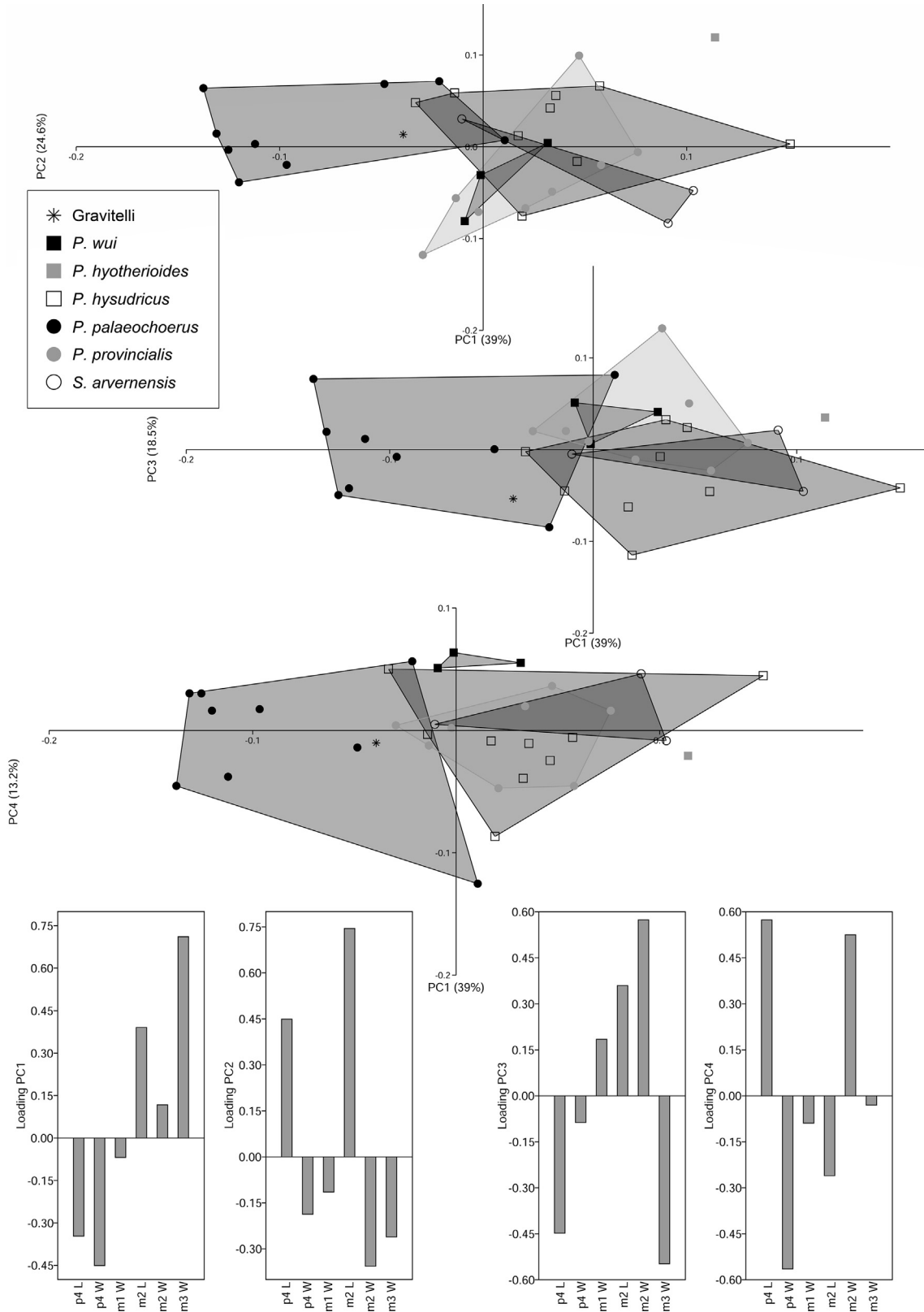


Fig. 8. Morphospace projections of gmPCA onto the planes described by the first and second, third, and fourth components, and their respective loadings.

overall conservative similar morphology and partly overlapping in several dental measurements (Iannucci and Begun, 2022).

Concerning the specific attribution of Gravitelli suids, Pickford (2013, p. 682) commented that: “The lack of third molars in the material makes it difficult to decide on the

Table 6

Eigenvalues, percentage of explained variance, and loadings of gmPCA. The first four components (jointly 95.3% of explained variance) are interpreted herein.

gmPCA	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
Eigenvalue	0.00522	0.00329	0.00248	0.00176	0.00063	2.36E-06
% variance	38.992	24.583	18.516	13.188	4.7031	0.01763
p4 L	-0.34676	0.44913	-0.44785	0.57342	0.025579	0.38471
p4 W	-0.45079	-0.18721	-0.08694	-0.56467	0.398	0.52624
m1 W	-0.06852	-0.11443	0.18433	-0.08885	-0.84537	0.47507
m2 L	0.39056	0.74484	0.35926	-0.26056	0.1308	0.28037
m2 W	0.11715	-0.35667	0.57356	0.525	0.32532	0.38553
m3 W	0.71105	-0.26103	-0.54759	-0.03029	0.05788	0.34949

status of this material”, while Lazaridis et al. (2022, p. 543) listed Gravitelli among the possible occurrences of *P. aegaeus*, “Judging by the small M3”. However, these authors did not consider all the sample described by Seguenza (1902, 1907) but likely relied only on the casts discussed by Gallai and Rook (2006). In the latter work, only one M3 replica was considered, and the measurements provided are also slightly smaller than those taken by Seguenza (1902) on the original material. Unfortunately, at Gravitelli, m3 is indeed represented only by a mesial fragment that does not allow considerations on its proportions, which would have been diagnostic (Iannucci and Begun, 2022). On the other hand, there are two complete M3 amongst Gravitelli specimens, whose measurements are in-between those of samples sometimes referred to *Propotamochoerus* sp. and those of remains from the type locality of *P. provincialis*, Montpellier (Iannucci et al., 2021a; Fig. 4A, Tables 2, 3).

More broadly, the implication of the comparison (see Section 5.1) is that size alone cannot be used for an effective specific discrimination, unless “extreme” specimens or mean values of abundant samples—which are very few—are considered. The two M3 from Gravitelli differ of 3 mm in length, or even 4.5 mm, if measurements collected by Gallai and Rook (2006) on the cast are considered. Such variability might seem important and indeed places the two specimens within the ranges of different species (Fig. 4D). Nevertheless, there are several confounding factors that should be taken into account. For a start, the comparative measurements considered here and in many previous studies (e.g., Geraads et al., 2008; Iannucci et al., 2021a; Lazaridis et al., 2022) have been collected over many years by different researchers who have adopted, implicitly or explicitly, divergent measuring protocols. For instance, Van der Made (1996) collected the length of upper molars perpendicular to the mesial side of the tooth, while Hellmund (1995) used basically the greatest mesiodistal diameter, and others considered different lengths measurements (Fortelius et al., 2005). Then, one should consider differences due to dental wear and sexual dimorphism, which are significant sources of variation (e.g., Zeder and Lemoine, 2020). Moreover, even assuming to eliminate all operational, age- and sex-related variability, size differences might also represent further intraspecific variation.

The relationship between size and environment is indeed well documented in extant populations of the wild boar, *Sus scrofa* Linnaeus, 1758, from different geographic areas and through time (e.g., Albarella et al., 2009; Iannucci et al., 2020a, 2020b). It is worth expressing differences as percentages, to put them into perspective. Differences between M3 L values measured at Gravitelli are 9% (or 13%, considering the difference of 4.5 mm), those documented in the Late Pleistocene to Holocene record of *S. scrofa* from a well-constrained geographical region in southern Italy already surpass this percentage, reaching 17% (Iannucci et al., 2020b); in a more abundant recent sample from Hakel (Germany), representing a good approximation of a natural population, differences between extreme observations are 33% (Kuşatman, 1991); and largest extant individuals of *S. scrofa* can be more than twice as larger (in M3 L) than the smallest (Albarella et al., 2009). Few other extant suids have wide geographic distributions, but important morphometric variation is also documented in the African *Potamochoerus* Gray, 1854 (Boisserie et al., 2014). Considering the extensive geographic range of *Propotamochoerus* (but also of *Hippopotamodon* and other fossil suids) throughout Eurasia, it is well possible that fossil species displayed ecomorphological differences similar to those observables within the extant wild boar, especially for those taxa that maintained an overall generalized morphology and, presumably, ecology.

Further univariate and bivariate comparisons consistently recover Gravitelli as “large-sized” among the samples considered herein, close to values of *P. hyotherioides*, *P. palaeochoerus*, and *P. provincialis*. More in-depth analyses have been possible considering the measurements of a partly preserved p4-m3 series. Results of the PCA point out similarities between Gravitelli, *P. provincialis*, and *P. palaeochoerus*. In particular, the Gravitelli sample falls within the range of *P. palaeochoerus* in the projected morphospaces of gmPCA, although never too far from values of some specimens of *P. provincialis* and *P. hysudricus*. These results are potentially very interesting but must be critically evaluated considering the status of the observation from Gravitelli, which is made up by an isolated p4 and its associated molar row (m1-m3), which belong to a senile individual with very worn teeth. This introduces a two-fold bias in the measurements. First, since the greatest

length (mesiodistal diameter) of these teeth is not at the occlusal level, the value measured for the isolated p4 by Seguenza (1907) is probably more precise than those taken on the molars. Second, and especially relevant if Seguenza (1907) collected molar lengths on the occlusal surface, the advancing of wear affects molar lengths more severely than that of p4 (Van der Made, 1996). A precise correction for this bias is not attempted here, as it would require dedicated empirical tests on an abundant sample. Nonetheless, as a thumb rule, adjusted measurements would be somewhat larger (correcting for wear) and result in proportionally larger molars, whose lengths are more affected by wear than that of p4 and more difficult to take on teeth that are not isolated. Basically, the resulting adjusted proportions of the individual from Gravitelli would be closer to *P. provincialis* than to *P. palaeochoerus*.

Previous studies have shown that *P. provincialis* and *P. palaeochoerus* differ substantially in the relative elongation of third molars and fourth premolars (Iannucci et al., 2021a; Iannucci and Begun, 2022). Basically, *P. palaeochoerus* has relatively enlarged P4/p4 and *P. provincialis* has proportionally elongated M3/m3, to some extent approaching the condition observed in *Hippopotamodon*. The P4 L/M3 L ratio of Gravitelli is almost equivalent to the mean value of *P. provincialis* (0.42) and very far from the proportions shown by *P. palaeochoerus* (0.50).

Collectively, these results allow to ascribe Gravitelli suids to *P. provincialis*, representing the earliest occurrence of the species in Italy. It should be pointed out that here, as in most previous studies (Pickford, 1988; Van der Made et al., 1999; Fortelius et al., 2005; Iannucci et al., 2021a), the specific attribution of Gravitelli suids is based on a joint consideration of all available specimens, assuming that they represent only one species. It is indeed unlikely that two species of a generalist suid like *Propotamochoerus* are represented in the same fauna, and there is no indication of a substantially time-averaged deposition of the fossiliferous layer that would allow to hypothesize a replacement between two forms. Nonetheless, if taken alone most isolated remains could not have been identified beyond the genus level.

6.2. Mammal biochronology and paleobiogeography

The re-examination of the geological setting described by Seguenza (1902, 1907, and references therein) revealed that the mammal fauna of Gravitelli is at least older than 7 Ma and likely dates to the late Tortonian rather than the earliest Messinian (see Section 2). This is in contrast with a reference to MN 13 (late Turolian) in terms of mammal biochronology, often supposed in previous studies (Rook et al., 2006; Van der Made et al., 2006; Sardella, 2008). Notwithstanding problems in the divergent adoptions of the MN system, typical localities with MN 13 faunas are indeed usually considered younger than 7 Ma (Hilgen et al., 2012). However, different, and older correlations for the fauna of Gravitelli, either to MN 12–MN 13

(Masini et al., 2008), or even to MN 11 (Ferretti, 2008), have also been proposed. In general, all these references should be considered with caution, due to the uncertain attributions of several taxa, as they more likely reflect assumptions based on the supposed age of the fossil horizon, rather than being the result of correlations based on large mammals. In the following, the most significant available studies on the mammal fauna of Gravitelli are briefly reviewed.

The faunal list originally reported by Seguenza (1902) comprised *Semnopithecus monspessulanum*, *Machairodus ogygia*, *Ictitherium hipparionum*, *Gazella deperdita*, *Antilope* sp., *Tragocerus* sp., *Sus erymanthius*, *Hippopotamus (Hexaprotodon) sivalensis*, *Rhinoceros (Dihoplus) schleiermacheri*, *Mastodon borsoni*, and *Mastodon turicensis*. Later, Seguenza (1907), while describing further material recovered in the following years, removed the subgeneric distinction for the hippo (i.e., assigning it simply to *Hippopotamus sivalensis*) and identified another hyaenid species, *Ictitherium orbigny*.

Although several authors mentioned Gravitelli in the following decades (e.g., Parona, 1924; Pilgrim, 1931), Hooijer (1946) was the first to critically revise part of Gravitelli mammals on the base of Seguenza's description and figures. In doing so, he recognized the hippo as a new species, *Hippopotamus siculus*, reassigned to *Parabos* (?) spec. and *Diceros* aff. *pachygnathus* some of the specimens previously attributed to the hippo, and to *Dicerorhinus* (?) spec. the remaining rhinocerotids. Boisserie (2005) performed an important cladistic analysis of hippopotamids, demonstrating the paraphyly of *Hexaprotodon* as traditionally conceived and referring several taxa of uncertain status to *Hexaprotodon?*, including *Hexaprotodon? siculus*. Martino et al. (2021) accepted the validity of the hippo as a distinct species, tentatively allocated to *Hexaprotodon*, and reassigned to the hippo the fragmentary radius previously regarded by Hooijer (1946) as *Parabos* (?) spec., i.e., as the potential presence of a large bovid.

Delson (1975) tentatively referred Gravitelli cercopithecids to *Mesopithecus monspessulanus* and suggested they could have represented a transitional population from *M. pentelici*, but Rook (1999) favored an open attribution, as *Mesopithecus* sp., in general adhering to Delson's opinion but doubting of the reliability of Seguenza (1902, 1907) measurements. Alba et al. (2015) also listed the cercopithecoid of Gravitelli as *Mesopithecus* sp. indet.

Thomas et al. (1982) argued that remains of Gravitelli bovids are not identifiable with certainty, suggesting a reference to Reduncini for the fragmentary cranium attributed to *G. deperdita* by Seguenza (1902) and reassigning an astragalus of "*Tragocerus*" to a suid — to which an associated tibia similarly referred to *Tragocerus* sp. belong as well (see Section 4). This leaves only a fragmentary tooth within the remains assigned to the genus by Seguenza (1902). It cannot be ruled out that the latter specimen belongs to Seguenza's "*Antilope*", which according to the author was instead only represented by part of the deciduous

dentition. Bibi et al. (2009) also mentioned the potential occurrence of reduncines at Gravitelli, but Vrba et al. (2015) regarded it as doubtful.

Rook et al. (1991) briefly commented on Gravitelli carnivorans while discussing of the record of the group from Italian Messinian localities. In so doing, they suggested a reassignment of the saber-toothed cat to *Metailurus parvulus* [instead of *Machairodus* (= *Paramachairodus*) *ogygia*] and of the hyena *I. hipparionum* to *Thalassictis hyaenoides*. As for Seguenza's "*Ictitherium orbigny*", they regarded it as a probable viverrid (Viverridae indet. in Rook et al., 1999). Sardella (2008) also reconsidered the carnivorans, but reporting *Plioviverrops orbigny*, *Hyaenictitherium* (= *Thalassictis*) *hyaenoides*, and *M. parvulus*. The scanty sample from Gravitelli of the latter taxon should be likely reexamined in light of recent studies on metailurine felids, in which new species have been erected and their relationships discussed (e.g., Spassov and Geraads, 2015; Jiangzuo et al., 2022).

Guérin (2000, p. 121), discussing of African rhinocerotids, argued that: "Material from Gravitelli [...] clearly represents *Diceros* but is not sufficient for a determination at the specific level", while Pandolfi and Rook (2017) suggested an affinity with *Ceratotherium neumayri* for Gravitelli rhinos. No further justification is provided in both works, but considering that Guérin (2000) retained *C. neumayri* and *C. pachygnathus* within *Diceros*, these two opinions are compatible. The previous hypothesis of the presence of two rhinocerotids, suggested by Hooijer (1946), was apparently abandoned.

Van der Made et al. (2006) commented that figures and descriptions by Seguenza (1902) suggest a reference to *P. provincialis* for the suids, while Gallai and Rook (2006), considering two casts housed in IGF, favored an open attribution to *Propotamochoerus* sp., and eventually the assignment to *P. provincialis* is supported in this work.

Ferretti (2008) rejected the presence of two "*Mastodon*" reported by Seguenza (1902), recognizing only one mammutid species, *Zygodon turicensis*.

In brief, an updated faunal list of Gravitelli mammals is provided as follows: *Mesopithecus* sp., Metailurini indet., *Hyaenictitherium hyaenoides*, *Plioviverrops orbigny*, *Zygodon turicensis*, *Ceratotherium* sp., Bovidae indet., *Hexaprotodon?* *siculus*, and *Propotamochoerus provincialis*. This fauna does not help in refining the chronology of the site and none of the taxa identified is exclusively reported from MN 13. Moreover, most groups have been the subject of divergent or preliminary opinions published without dedicated studies, deserving reconsiderations.

Gravitelli has often been considered potentially part of a non-endemic paleobioprovince documenting a connection between southern Italy and northern Africa, together with the locality of Cessaniti, in Calabria (Ferretti et al., 2003; Rook et al., 2006; Marra, 2019; Georgalis et al., 2020). However, apart from their geographic proximity, the two localities do not share any common faunal element amongst those so far identified. Moreover, although

different opinions have been expressed on the potential African affinity of some Gravitelli mammals, like bovids and hyaenids (e.g., Howell, 1980; Thomas et al., 1982) — which is not surprising, bearing in mind the aforementioned uncertainty in the attribution of several taxa — up to now, the only species of clear African origin amongst those identified at Gravitelli is the hippo, *Hexaprotodon?* *siculus*. However, it is worth noting that the extensive fossil record of insular hippopotamids testifies to their ability to colonize islands even in the absence of land bridges, whose existence is therefore not needed to justify their dispersal during the pre-evaporitic Messinian (Boisserie, 2007; Masini et al., 2008; Gibert et al., 2013; Delfino et al., 2021). Aside from hippopotamids, the rest of Gravitelli fauna has a clear European character and none of the species so far identified precludes a reference to the late Tortonian (Turolian, MN 11–MN 12).

The revised age of Gravitelli also implies that the hippopotamid record of this site is the earliest in Europe and likely outside Africa. Not in Africa but still within the Saharo-Arabian region is the hippopotamid record of the Baynunah Formation, assigned to *Archaeopotamus qeshta*, which might also be older than 7 Ma (Boisserie and Bibi, 2022), and a similar age for the earliest record of *Hexaprotodon sivalensis* in the Pakistan Siwaliks is not likely but cannot be ruled out (Barry et al., 2002). In any case, Gravitelli *Hexaprotodon?* *siculus* predates the earliest occurrences of hippopotamids in the Iberian Peninsula (6.3–6.2 Ma; Gibert et al., 2013) by at least 0.7 Ma. *Hexaprotodon* is a genus of convoluted application, which has long been used as a wastebasket taxon and has been shown to be paraphyletic (Boisserie, 2005). Still, several circum-Mediterranean occurrences from the Late Miocene of Europe and North Africa are provisionally often referred to as *Hexaprotodon?* (Boisserie, 2005, 2007; Martino et al., 2021). Taxonomic opinions expressed on the European portion of this contingent range from recognizing only one to up to four different species, part of the debate resting on the scanty nature of several samples (Van der Made, 1999; Boisserie, 2005, 2007; Martino et al., 2021). The relationships between circum-Mediterranean Late Miocene hippopotamids are far from solved, but morphological evidence supports the presence in Europe of at least two lineages. Most notably, the Gravitelli hippopotamid is hexaprotodont (i.e., it has six incisors) (Seguenza, 1907, p. 119), while a tetraprotodont (i.e., with four incisor) condition is observable in a mandible from La Portera, in the province of Valencia (Lacomba et al., 1986). Perhaps the presence of these two lineages document different dispersal events from North Africa to Iberia and Sicily, the small expanse of salt water to cross not representing a substantial biogeographic barrier for hippopotamids.

7. Conclusions

Although *Propotamochoerus* was present in Europe at least since the early Vallesian (MN 9), with *P. palaeo-*

choerus, this species is not unambiguously recorded after the so-called (mid-)Vallesian Crisis ~ 9.7 Ma (Iannucci and Begun, 2022). Remains of *Propotamochoerus* are known again from Europe after a certain gap, likely documenting a new dispersal from Asia. The earliest calibrated Turolian occurrence of *Propotamochoerus* sp. is dated at ~ 8.3 Ma, based on undescribed material reported from Gorna Sushitsa (Bulgaria; Böhme et al., 2018). There are then several localities from the Balkans referred to the early Turolian (MN 11 or MN 12), although with less precise constraints (Geraads et al., 2008). Before *P. provincialis* became relatively widespread in MN 13 faunas (Van der Made and Moyà-Solà, 1989; Iannucci et al., 2021a), the species reached Sicily, as testified by the record of Gravitelli described herein. In sum, although this might be due to the paucity of the fossil record, available dates support a diachronous dispersal of *Propotamochoerus* in western Europe during the Turolian, being first known from the Balkans ~ 8.3 Ma, then from Gravitelli earlier than 7 Ma, and then from the Iberian Peninsula since ~ 6.2 Ma (the latter being the age of the earliest calibrated locality of the region with *P. provincialis*, Venta del Moro; Gibert et al., 2013). A similar pattern is observed for *Mesopithecus*, first documented in eastern Europe and the Balkans in the early Turolian (MN 11), then in Italy (Gravitelli being its earliest record), and finally in the Iberian Peninsula at Venta del Moro (Alba et al., 2015), supporting the view of a diachronic faunal dispersal of Asian elements during the Turolian.

Gravitelli suids are assigned to *Propotamochoerus provincialis*. They represent the earliest occurrence of the species (and genus) in Italy and indirectly document the existence of emerged land masses in the Italian Peninsula connecting mainland Europe to Sicily earlier than 7 Ma. The latter is the age of the base of the Tripoli Formation in Sicily (Hilgen and Krijgsman, 1999; Blanc-Valleron et al., 2002), which represents the maximum age for the fossil fauna of Gravitelli. However, the mammal fauna of Gravitelli have been recovered near the bottom a succession of clays, sands, and marls below the Tripoli Formation. Therefore, Gravitelli mammals are likely late Tortonian in age or, at most, earliest Messinian (MN 11 or MN 12). A thoughtful integration of data of borehole lithology, information derived from the historical literature concerning outcrops and sections no longer exposed, and renewed biostratigraphic investigations may be key to refine the age of the mammal bearing deposits.

Seguenza (1908, p. 385) just a few months before dying during the Messina Earthquake, which struck its city and destroyed the collections he and his father assembled over the years, wrote: “Esaminare minuziosamente le faune del nostro Miocene, la successione ed i rapporti reciproci di esse, studiare la tettonica dei diversi affioramenti per trarne possibili deduzioni, sarà quindi lo scopo di una mia monografia per la quale ho già raccolto larga messe di materiali ed osservazioni” (“Examining meticulously the faunas of our [i.e., of Messina] Miocene, the succession and the reciprocal relationships between them, studying the tectonics of

the different outcrops to draw reasonable inferences, it will be the aim of a monograph of mine for which I already collected a wealth of materials and observations”; own translation from the original Italian). That this monograph never came to light is a sad and unexpected epilogue of Seguenza’s studies on the Miocene of Sicily, but it does not have to be the definitive conclusions of the research on the Late Miocene mammal fauna of Gravitelli. Indeed, it was not, as several works relied on or reconsider Seguenza’s descriptions (e.g., Hooijer, 1946; Thomas et al., 1982; Marra, 2019; Martino et al., 2021). Yet, further research aimed at critically re-evaluate the fauna of Gravitelli and contextualize it within an updated systematic and methodological framework is still needed for most taxa, as shown by the case of the suid record discussed herein. The case of Gravitelli is emblematic of the importance of revising historical collections, even when the original material is lost (Iannucci et al., 2022b), and with this contribution I hope to renew the interest on the study of this extremely important fauna.

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Supplementary data

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References

- Alba, D.M., Moyà-Solà, S., Casanovas-Vilar, I., Galindo, J., Robles, J. M., Rotgers, C., Furió, M., Angelone, C., Köhler, M., Garcés, M., Cabrera, L., Almécija, S., Obradó, P., 2006. Los vertebrados fósiles del Abocador de Can Mata (els Hostalets de Pierola, l’Anoia, Catalunya), una sucesión de localidades del Aragonense superior (MN6 y MN7 +8) de la cuenca del Vallès-Penedès. *Campañas 2002-2003, 2004 y 2005. Estudios Geológicos* 62 (1), 295–312.
- Alba, D.M., Delson, E., Carnevale, G., Colombero, S., Delfino, M., Giuntelli, P., Pavia, M., Pavia, G., 2014. First joint record of *Mesopithecus* and cf. *Macaca* in the Miocene of Europe. *Journal of Human Evolution* 67, 1–18.
- Alba, D.M., Montoya, P., Pina, M., Rook, L., Abella, J., Morales, J., Delson, E., 2015. First record of *Mesopithecus* (Cercopithecidae, Colobinae) from the Miocene of the Iberian Peninsula. *Journal of Human Evolution* 88, 1–14.

- Albarella, U., Dobney, K., Rowley-Conwy, P., 2009. Size and shape of the Eurasian wild boar (*Sus scrofa*), with a view to the reconstruction of its Holocene history. *Environmental Archaeology* 14 (2), 103–136.
- Aslam, S., Khan, A.M., Ahmad, R.M., Iqbal, A., Waseem, M.T., 2021. Systematic study of the new remains of *Propotamochoerus hysudricus* (Suidae, Mammalia) from the Late Miocene–Early Pliocene of Middle Siwaliks (Pakistan). *Arabian Journal of Geosciences* 14, Article number 73, doi: 10.1007/s12517-020-06300-y.
- Barreca, G., Gross, F., Scarfi, L., Aloisi, M., Monaco, C., Krastel, S., 2021. The Strait of Messina: Seismotectonics and the source of the 1908 earthquake. *Earth-Science Reviews* 218, 103685.
- Barry, J.C., Morgan, M.E., Flynn, L.J., Pilbeam, D., Behrensmeyer, A.K., Raza, S.M., Khan, I.A., Badgley, C., Hicks, J., Kelley, J., 2002. Faunal and environmental change in the late Miocene Siwaliks of northern Pakistan. *Paleobiology* 28 (S2), 1–71.
- Batool, A., Khan, M.A., Qureshi, N.A., 2015. New fossils of Suidae (Mammalia, Artiodactyla) from the Hasnot Late Miocene, northern Pakistan. *The Journal of Animal & Plant Sciences* 25 (2), 578–590.
- Bibi, F., Bukhsianidze, M., Gentry, A.W., Geraads, D., Kostopoulos, D. S., Vrba, E.S., 2009. The fossil record and evolution of Bovidae: state of the field. *Palaeontologia Electronica* 12 (3), 10A.
- Blainville, H.M.D. 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. Tome Quatrième Quaternatés — Maldentés.* A. Bertrand, Paris (in French).
- Blanc-Valleron, M.M., Pierre, C., Caulet, J.P., Caruso, A., Rouchy, J.M., Cespuglio, G., Sprovieri, R., Pestrea, S., Di Stefano, E., 2002. Sedimentary, stable isotope and micropaleontological records of paleoceanographic change in the Messinian Tripoli Formation (Sicily, Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology* 185 (3–4), 255–286.
- Böhme, M., Van Baak, C.G., Prieto, J., Winklhofer, M., Spassov, N., 2018. Late Miocene stratigraphy, palaeoclimate and evolution of the Sandanski Basin (Bulgaria) and the chronology of the Pikermian faunal changes. *Global and Planetary Change* 170, 1–19.
- Boisserie, J.-R., 2005. The phylogeny and taxonomy of Hippopotamidae (Mammalia: Artiodactyla): a review based on morphology and cladistic analysis. *Zoological Journal of the Linnean Society* 143 (1), 1–26.
- Boisserie, J.-R., 2007. Family Hippopotamidae. In: Prothero, D.R., Foss, S.E. (Eds.), *The Evolution of Artiodactyls*. The Johns Hopkins University Press, Baltimore, pp. 106–119.
- Boisserie, J.-R., Bibi, F., 2022. Hippopotamidae from the Baynunah Formation. In: Bibi, F., Kraatz, B., Beech, M.J., Hill, A. (Eds.), *Sands of Time. Ancient Life in the Late Miocene of Abu Dhabi, United Arab Emirates*. Springer, Cham, pp. 243–260.
- Boisserie, J.-R., Souron, A., Mackaye, H.T., 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 (8), e103221, doi: 10.1371/journal.pone.0103221.
- Capellini, G., 1877. Balenottere fossili e *Pachyacanthus* dell'Italia meridionale. *Atti della Reale Accademia dei Lincei. Memorie della Classe di Scienze Fisiche, Matematiche e Naturali, Serie 3* 1, 1–22 (in Italian).
- Carbone, S., Messina, A., Lentini, F., 2007. Note illustrative della carta geologica d'Italia alla scala 1:50.000. Foglio 601. Messina-Reggio di Calabria. ISPRA – Servizio Geologico d'Italia, S.E.L.C.A. s.r.l., Firenze, 179 pp. (in Italian).
- Carminati, E., Lustrino, M., Cuffaro, M., Doglioni, C., 2010. Tectonics, magmatism and geodynamics of Italy: what we know and what we imagine. *Journal of the Virtual Explorer* 36, 9, doi: 10.3809/jvirtex.2010.00226.
- Croizet, J.-B., Jobert, A.-C.-G., 1828. *Recherches sur les ossements fossiles du département du Puy-de-Dôme. Clermont-Ferrand, Paris, 224 pp.* (in French).
- Dal Piaz, G., 1930. Sopra gli avanzi di un Suide scoperti nel Pleiocene superiore di Bra in Piemonte. *Atti della Reale Accademia delle Scienze di Torino, Parte Fisica* 65, 299–303 (in Italian).
- Delfino, M., Luján, À.H., Abella, J., Alba, D.M., Böhme, M., Pérez-Ramos, A., Tschopp, E., Morales, J., Montoya, P., 2021. Late Miocene remains from Venta del Moro (Iberian Peninsula) provide further insights on the dispersal of crocodiles across the late Miocene Tethys. *Journal of Paleontology* 95 (1), 184–192.
- Delson, E., 1975. Evolutionary history of the Cercopithecidae. *Contributions to Primatology* 5, 167–217.
- Di Stefano, A., Longhitano, S.G., 2009. Tectonics and sedimentation of the lower and Middle Pleistocene mixed siliciclastic/bioclastic sedimentary successions of the Ionian Peloritani Mts (NE Sicily, Southern Italy): the onset of opening of the Messina Strait. *Central European Journal of Geosciences* 1 (1), 33–62.
- Ercoli, M.D., Ramírez, M.A., Morales, M.M., Álvarez, A., Candela, A. M., 2019. First record of Carnivora (Puma Lineage, Felidae) in the Uquía Formation (Late Pliocene–Early Pleistocene, NW Argentina) and its significance in the Great American Biotic Interchange. *Ameghiniana* 56 (3), 195–212.
- Feng, C., Wang, H., Lu, N., Chen, T., He, H., Lu, Y., Tu, X.M., 2014. Log-transformation and its implications for data analysis. *Shanghai Archives of Psychiatry* 26 (2), 105–109.
- Ferretti, M.P., 2008. Miocene proboscideans from Italy: African elements and palaeogeographic implications. *Geology of East Libya* 3, 325–334.
- Ferretti, M.P., Rook, L., Torre, D., 2003. *Stegotrabelodon* (Proboscidea, Elephantidae) from the late Miocene of southern Italy. *Journal of Vertebrate Paleontology* 23, 659–666.
- Fortelius, M., Van der Made, J., Bernor, R.L., 1996. Middle and late Miocene Suidae of Central Europe and the Eastern Mediterranean: evolution, biogeography, and paleoecology. In: Bernor, R.L., Fahlbusch, V., Mittmann, H.-W. (Eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York, pp. 348–377.
- Fortelius, M., Armour-Chelu, M., Bernor, R.L., Fessaha, N., 2005. Systematics and paleobiology of the Rudabánya Suidae. *Palaeontographia Italica* 90, 259–278.
- Gallai, G., 2006. *Sistematica, paleoecologia, paleogeografia dei Suidae fossili italiani*. PhD Thesis, Università degli Studi di Firenze, Firenze, 186 pp. (in Italian).
- Gallai, G., Rook, L., 2006. *Propotamochoerus* sp. (Suidae, Mammalia) from the late Miocene of Gravitelli (Messina, Sicily, Italy) rediscovered. *Rivista Italiana di Paleontologia e Stratigrafia* 112 (2), 317–321.
- 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). *Bollettino della Società Paleontologica Italiana* 50 (1), 29–34.
- Geraads, D., Spassov, N., Garevski, R., 2008. New specimens of *Propotamochoerus* (Suidae, Mammalia) from the late Miocene of the Balkans. *Neues Jahrbuch für Geologie und Paläontologie* 248, 103–113.
- Georgalis, G.L., Insacco, G., Rook, L., Spadola, F., Delfino, M., 2020. Turtle remains from the late Miocene of the Cessaniti area, southern Italy — insights for a probable Tortonian chelonian dispersal from Europe to Africa. *Swiss Journal of Paleontology* 139, Article number 1, doi: 10.1186/s13358-020-00202-y.
- Gibert, L., Scott, G.R., Montoya, P., Ruiz-Sánchez, F.J., Morales, J., Luque, L., Abella, J., Leriá, M., 2013. Evidence for an African-Iberian mammal dispersal during the pre-evaporitic Messinian. *Geology* 41 (6), 691–694.
- Gray, J.E., 1821. On the natural arrangement of vertebrate animals. *The London Medical Repository Monthly Journal and Review* 15, 296–310.
- Gray, J.E., 1854. On the painted pig of the Cameroons (*Potamochoerus penicillatus*). *Proceedings of the Zoological Society of London* 20, 129–132.
- Guérin, C., 2000. The Neogene rhinoceroses of Namibia. *Palaeontologia Africana* 36, 119–138.
- Guérin, C., Tsoukala, E., 2013. The Tapiridae, Rhinocerotidae and Suidae (Mammalia) of the Early Villafranchian site of Milia (Grevena, Macedonia, Greece). *Geodiversitas* 35 (2), 447–489.

- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4, 4.
- Hellmund, M., 1995. 13. Suidae (Artiodactyla, Mammalia). In: Schmidt-Kittler, N. (Ed.), *The Vertebrate Locality Maramena (Macedonia, Greece) at the Turolian–Ruscian Boundary (Neogene)*. Münchner Geowissenschaftliche Abhandlungen. Reihe A: Geologie und Paläontologie 28, 143–156.
- Hilgen, F.J., Krijgsman, W., 1999. Cyclostratigraphy and astrochronology of the Tripolo diatomite formation (pre-evaporite Messinian, Sicily, Italy). *Terra Nova* 11 (1), 16–22.
- Hilgen, F.J., Lourens, L.J., Van Dam, J.A., 2012. The Neogene Period. In: Gradstein, F.M., Ogg, J.G., Schmitz, M.D., 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.
- Hooijer, D.A., 1946. Notes on some Pontian mammals from Sicily, figured by Seguenza. *Archives Néerlandaises de Zoologie* 7, 301–333.
- Hou, S., Su, D.F., Kelley, J., Deng, T., Jablonski, N.G., Flynn, L.J., Ji, X., Cao, J., Yang, X., 2019. New fossil suid specimens from the terminal Miocene hominoid locality of Shuitangba, Zhaotong, Yunnan Province, China. *Journal of Mammalian Evolution* 26, 557–571.
- Howell, F.C., 1980. Zonation of late Miocene and early Pliocene circum-Mediterranean faunas. *Geobios* 13 (4), 653–657.
- Hsü, K.J., Cita, M.B., Ryan, W.B.F., 1973a. The origin of Mediterranean evaporites. *Initial Reports of the Deep Sea Drilling Project* 13 (2), 1203–1231.
- Hsü, K.J., Ryan, W.B.F., Cita, M.B., 1973b. Late Miocene desiccation of the Mediterranean. *Nature* 242, 240–244.
- Hünemann, K.A., 1968. Die Suidae (Mammalia, Artiodactyla) aus den Dinotheriensanden (Untherpliozän=Pont) Rhein Hessens (Südwestdeutschland). *Schweizerische Paläontologische Abhandlungen* 86, 1–96 (in German).
- Hünemann, K.A., 1971. Die Plio-Pleistozänen Wirbeltierfaunen von Hajnacka und Ivanovce (Slovakie) CSR. VII: *Sus minor* (Depéret, 1890). *Neues Jahrbuch für Geologie und Paläontologie – Monatshefte* 1971, 213–230 (in German).
- Hürzeler, J., 1982. Sur le suidé du lignite de Montebamboli (prov. Grosseto, Italie). *Comptes rendus de l'Académie des Sciences, Série 2* 295, 697–701 (in French).
- Iannucci, A., Begun, D.R., 2022. Suidae (Mammalia, Artiodactyla) from the late Miocene hominoid locality of Alsótelekes (Hungary). *Geobios* 71, 39–49.
- Iannucci, A., Gasparik, M., Sardella, R., 2020a. First report of *Sus strozzii* (Suidae, Mammalia) from the Early Pleistocene of Hungary (Dunaalmás) and species distinction based on deciduous teeth. *The Science of Nature* 107, Article number 5, doi: 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 (1), 10–20.
- Iannucci, A., Cherin, M., Sorbelli, L., Sardella, R., 2021a. Suidae transition at the Miocene–Pliocene boundary: a reassessment of the taxonomy and chronology of *Propotamochoerus provincialis*. *Journal of Mammalian Evolution* 28, 323–335.
- Iannucci, A., Mecozzi, B., Sardella, R., Iurino, D.A., 2021b. The extinction of the giant hyena *Pachycrocuta brevirostris* and a reappraisal of the Epivillafranchian and Galerian Hyaenidae in Europe: Faunal turnover during the Early–Middle Pleistocene Transition. *Quaternary Science Reviews* 272, 107240.
- Iannucci, A., Bellucci, L., Conti, J., Mazzini, I., Mecozzi, B., Sardella, R., Iurino, D.A., 2022a. Neurocranial anatomy of *Sus arvernensis* (Suidae, Mammalia) from Collepardo (Early Villafranchian; central Italy): taxonomic and biochronological implications. *Historical Biology* 34 (1), 108–120.
- Iannucci, A., Cherin, M., Sardella, R., 2022b. The lost hyena from Pacciano (Umbria, Italy) reconsidered. *Alpine and Mediterranean Quaternary* 35 (2), 105–117.
- Jiangzuo, Q., Niu, K., Li, S., Fu, J., Wang, S., 2022. A diverse metailurine guild from the latest Miocene Xingjiawan fauna, Yongdeng, north-western China, and generic differentiation of metailurine felids. *Journal of Mammalian Evolution* 29, 845–862.
- Jungers, W.L., Falsetti, A.B., Wall, C.E., 1995. Shape, relative size, and size-adjustments in morphometrics. *Yearbook of Physical Anthropology* 38, 137–161.
- Kaup, J.-J., 1833. Descriptions d'ossements fossiles de mammifères inconnus jusqu'à présent qui se trouvent au Muséum grand-ducal de Darmstadt. Second cahier. J.G. Heyer, Darmstadt, 31 pp. (in French).
- Khan, M.A., Akhtar, M., Iqbal, M., 2010. The late Miocene artiodactyls in the Dhok Pathan type locality of the Dhok Pathan formation, the Middle Siwaliks, Pakistan. *Pakistan Journal of Zoology Supplementary Series* 10, 1–88.
- Kuşatman, B., 1991. The origins of pig domestication with particular reference to the Near East. PhD Thesis, University College London, London, 454 pp.
- Lacomba, J.I., Morales, J., Robles, F., Santisteban, C., Alberdi, M.T., 1986. Sedimentología y paleontología del yacimiento finimioceno de La Portera (Valencia). *Estudios Geológicos* 42, 167–180.
- Lazaridis, G., 2015. Study of the Late Miocene vertebrate locality of Kryopigi and other localities of Kassandra Peninsula, Chalkidiki (Greece). Systematics, Taphonomy, Paleoecology, Biochronology. PhD Thesis, Scientific Annals of the School of Geology, Aristotle University of Thessaloniki 174, 350 pp. (in Greek).
- Lazaridis, G., Tsoukala, E., Kostopoulos, D.S., 2022. Validation of a prematurely abolished new *Propotamochoerus* Pilgrim, 1925 species (Mammalia, Suidae) from SE Mediterranean. *Comptes Rendus Palevol* 21 (26), 531–549.
- Linnaeus, C., 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. 10th ed. Laurentii Salvii, Stockholm, 824 pp. (in Latin).
- Liu, L., Kostopoulos, D.S., Fortelius, M., 2004. Late Miocene *Microstonyx* remains (Suidae, Mammalia) from northern China. *Geobios* 37, 49–64.
- Lydekker, R., 1877. Notices of new or rare mammals from the Siwaliks. *Records of the Geological Survey of India* 10, 76–83.
- Marra, A.C., 2019. Contribution of the late Miocene mammals from Calabria and Sicily to the palaeogeography of the central Mediterranean. *Atti della Accademia Peloritana dei Pericolanti-Classe di Scienze Fisiche, Matematiche e Naturali* 97 (S2), A29, doi: 10.1478/AAPP.97S2A29.
- Martino, R., Pignatti, J., Rook, L., Pandolfi, L., 2021. Hippopotamid dispersal across the Mediterranean in the latest Miocene: a re-evaluation of the Gravittelli record from Sicily, Italy. *Acta Palaeontologica Polonica* 66 (Supplement to 3), S67–S78.
- Masini, F., Petruso, D., Bonfiglio, L., Mangano, G., 2008. Origination and extinction patterns of mammals in three central Western Mediterranean islands from the Late Miocene to Quaternary. *Quaternary International* 182, 63–79.
- Mazo, A.V., Torres, T., 1990. El pozo de Piedrabuena, un nuevo yacimiento de vertebrados pliocenos en el Campo de Calatrava (Ciudad Real). *Paleontología i Evolució* 23, 213–222 (in Spanish).
- Mazza, P., Rustioni, M., 1997. Neotype and phylogeny of the suid *Eumaichoerus etruscus* (Michelotti) from Montebamboli (Grosseto, southern Tuscany). *Paleontologia i Evolució* 30–31, 5–18.
- Mercalli, G., 1909. Contributo allo studio del terremoto calabro-messinese del 28 dicembre 1908. *Atti del Reale Istituto d'Incoraggiamento alle Scienze Naturali di Napoli* 3, 1–46 (in Italian).
- 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 (in French).
- Monaco, C., Tortorici, L., Cernobori, L., Nicolich, R., Costa, M., 1996. From collisional to rifted basins: an example from the southern Calabria Arc (Italy). *Tectonophysics* 266, 233–249.
- Montoya, P., Ginsburg, L., Alberdi, M.T., Van der Made, J., Morales, J., Soria, M.D., 2006. Fossil large mammals from the early Pliocene

- locality of Alcoy (Spain) and their importance in biostratigraphy. *Geodiversitas* 28, 137–173.
- Mosimann, J.E., 1970. Size allometry: size and shape variables with characterizations of the lognormal and gamma distributions. *Journal of the American Statistical Association* 65 (330), 930–945.
- Mosimann, J.E., James, F.C., 1979. New statistical methods for allometry with applications to Florida red-winged blackbirds. *Evolution* 23, 444–459.
- Mottl, M., 1966. Ein vollständiger *Hyotherium palaeochoerus*-Schädel aus dem Altpliozän (Pannon) Südost-Österreichs. *Mitteilungen des Museums für Bergbau, Geologie und Technik am Landesmuseum "Joanneum" Graz* 28, 73–103 (in German).
- 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. *Quarterly Journal of the Geological Society of London* 4, 103–141.
- Pandolfi, L., Rook, L., 2017. Rhinocerotidae (Mammalia, Perissodactyla) from the latest Turolian localities (MN 13; late Miocene) of central and northern Italy. *Bollettino della Società Paleontologica Italiana* 56 (1), 45–56.
- Parona, C.F., 1924. Trattato di geologia con speciale riguardo alla geologia d'Italia. Casa editrice Francesco Vallardi, Milano, 648 pp. (in Italian).
- Pearson, H.G., 1928. Chinese fossil Suidae. *Palaeontologia Sinica Series C* 5, 1–75.
- Pickford, M., 1988. Revision of the Miocene Suidae of the Indian subcontinent. *Münchener Geowissenschaftliche Abhandlungen. Reihe A: Geologie und Paläontologie* 12, 1–92.
- 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. *Münchener Geowissenschaftliche Abhandlungen. Reihe A: Geologie und Paläontologie* 42, 1–126.
- Pickford, M., 2016. Biochronology of European Miocene Tetraconodontinae (Suidae, Artiodactyla, Mammalia) flowing from recent revision of the subfamily. *Annalen des Naturhistorischen Museums in Wien, Serie A* 118, 175–244.
- Pickford, M., Obada, T., 2016. Pliocene suids from Musaitu and Dermeni, Moldova: implications for understanding the origin of African *Kolpochoerus* Van Hoepen & Van Hoepen, 1932. *Geodiversitas* 38, 99–134.
- Pino, N.A., Piatanesi, A., Valensise, G., Boschi, E., 2009. The 28 December 1908 Messina Straits earthquake (Mw 7.1): A great earthquake throughout a century of seismology. *Seismological Research Letters* 80 (2), 243–259.
- Pilgrim, G.E., 1925. Presidential address to the Geological Section of the 12th Indian Science Congress. In: *Proceedings of the 12th Indian Science Congress*, pp. 200–218.
- Pilgrim, G.E., 1926. The fossil Suidae of India. *Memoir of the Geological Survey of India, Palaeontologica Indica* 8 (4), 1–65.
- Parona, C.F., 1924. Trattato di geologia con speciale riguardo alla geologia d'Italia. Casa editrice Francesco Vallardi, Milano, 648 pp. (in Italian).
- Platania, G., 1909. Il maremoto dello Stretto di Messina del 28 dicembre 1908. *Bollettino della Società Sismologica Italiana* 13, 369–458 (in Italian).
- Rögl, F., 2001. Mid-Miocene Circum-Mediterranean paleogeography. *Berichte des Institute für Geologie und Paläontologie der Karl-Franzens-Universität Graz* 4, 49–59.
- Rook, L., 1999. Late Turolian *Mesopithecus* (Mammalia, Primates, Colobinae) from Italy. *Journal of Human Evolution* 36, 535–547.
- Rook, L., Ghatti, P., 1997. Il bacino neogenico della Velona (Toscana, Italia): stratigrafia e primi ritrovamenti di vertebrati fossili. *Bollettino della Società Geologica Italiana* 116, 335–346 (in Italian, with English abstract).
- Rook, L., Ficarelli, G., Torre, D., 1991. Messinian carnivores from Italy. *Bollettino della Società Paleontologica Italiana* 30 (1), 7–22.
- 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 University Press, Cambridge, pp. 191–204.
- Rook, L., Mazza, P., Rustioni, M., Torre, D., 2000. Lands and endemic mammals in the Late Miocene of Italy: paleogeographic outlines of Tyrrhenian and Adriatic areas between 11–9 and 7–4 Ma. ESF Scientific Programme on "Environments and Ecosystem Dynamics of the Eurasian Neogene" (EEDEN). Workshop on "State-of-the-art". University of Lyon, Lyon, pp. 56–58.
- Rook, L., Gallai, G., Torre, D., 2006. Lands and endemic mammals in the Late Miocene of Italy: constraints for paleogeographic outlines of Tyrrhenian area. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238 (1–4), 263–269.
- Samson, P., Radulesco, C., Kisgyörgy, Z., 1971. Nouvelles données sur la faune de Mammifères du Villafranchien inférieur de Capeni-Virghis. *E&G Quaternary Science Journal* 22 (1), 64–88 (in French, with English abstract).
- Sardella, R., 2008. Remarks on the Messinian carnivores (Mammalia) of Italy. *Bollettino della Società Paleontologica Italiana* 47 (2), 195–202.
- Sarwar, H.M.A., Waseem, M.T., Khan, A.M., Ahmad, R.M., 2016. *Propotamochoerus hysudricus* remains from late Miocene deposits of Hasnot, Pakistan. *Punjab University Journal of Zoology* 31 (2), 243–248.
- Schlosser, M., 1903. Die fossilen Säugethiere Chinas nebst einer Odonotographie de recenten Antilopen. *Abhandlungen der Mathematisch-Physikalischen Klasse der Königlich Bayerischen Akademie der Wissenschaften* 22 (1), 1–221 (in German).
- Schmidt-Kittler, N., 1971. Die obermiozäne Fossilagerstätte Sandelzhausen 3. Suidae (Artiodactyla, Mammalia). *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie* 11, 129–170 (in German, with English abstract).
- Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH image to ImageJ: 25 years of image analysis. *Nature Methods* 9, 671–675.
- Seguenza, G., 1862. Notizie succinte intorno alla costituzione geologica dei terreni terziarii del distretto di Messina. *Dissertazione pel concorso alla cattedra di storia naturale nell'Università di Messina*. Stamperia di Tommaso Capra, Messina, 34 pp. (in Italian).
- Seguenza, G., 1868. La Formation Zanciénne, ou recherches sur une nouvelle formation tertiaire. *Société Géologique de France, Bulletin, Série 2* 25, 465–485 (in French).
- Seguenza, G., 1873a. Studii stratigrafici sulla formazione pliocenica dell'Italia meridionale. *Bollettino del Regio Comitato Geologico d'Italia* 4 (1–2), 29–45; (3–4), 84–103; (5–6), 131–153; (7–8), 213–230; (9–10), 259–270 (in Italian).
- Seguenza, G., 1873b. Brevissimi cenni intorno la serie terziaria della Provincia di Messina. *Bollettino del Regio Comitato Geologico d'Italia* 4 (7–8), 231–238 (in Italian).
- Seguenza, L., 1900. I vertebrati fossili della Provincia di Messina. Parte I. Pesci. *Bollettino della Società Geologica Italiana* 19, 443–520 (in Italian).
- Seguenza, L., 1902. I vertebrati fossili della Provincia di Messina. Parte seconda. Mammiferi e geologia del Piano Pontico. *Bollettino della Società Geologica Italiana* 21, 115–175 (in Italian).
- Seguenza, L., 1907. Nuovi resti di mammiferi pontici di Gravittelli presso Messina. *Bollettino della Società Geologica Italiana* 26, 89–122 (in Italian).
- Seguenza, L., 1908. *Atti della Reale Accademia dei Lincei. Serie Quinta. Rendiconti Classe di Scienze Fisiche, Matematiche e Naturali* 17, 379–385 (in Italian).
- Sein, C., Van der Made, J., Rössner, G.E., 2009. New material of *Propotamochoerus* (Suidae, Mammalia) from the Irrawaddy Formation, Myanmar. *Neues Jahrbuch für Geologie und Paläontologie* 251, 17–31.

- Sorbelli, L., Cherin, M., Kostopoulos, D.S., Pavia, M., Carnevale, G., 2019. Partial cranium of *Propotamochoerus* (Cetartiodactyla, Suidae) from the late Miocene of Northern Italy. *Paleodays 2019 – XIX Giornate di Paleontologia. Parte 1: Volume dei riassunti. Ente GeoPaleontologico di Pietraraja, Benevento*, pp. 42–43.
- Spassov, N., Geraads, D., 2015. A new felid from the late Miocene of the Balkans and the contents of the genus *Metailurus* Zdansky, 1924 (Carnivora, Felidae). *Journal of Mammalian Evolution* 22, 45–56.
- Steeiman, M.E., 2010. The extinct baleen whale fauna from the Miocene–Pliocene of Belgium and the diagnostic cetacean ear bones. *Journal of Systematic Palaeontology* 8 (1), 63–80.
- Stehlin, H.G., 1899–1900. Ueber die Geschichte des Suiden-gebisses. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft* 26–27, 1–527 (in German).
- Thenius, E., 1950. *Postpotamochoerus* nov. subgen. *hyotherioides* aus dem Unterpliozän von Samos (Griechenland) und die Herkunft der Potamochoeren. *Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse* 159, 25–36 (in German).
- Thomas, H., Bernor, R., Jaeger, J.J., 1982. Origines du peuplement mammalien en Afrique du Nord durant le Miocène terminal. *Geobios* 15 (3), 283–297 (in French, with English abstract).
- Vai, G.B., 1997. Twisting or stable Quaternary boundary? A perspective on the glacial late Pliocene concept. *Quaternary International* 40, 11–22.
- Van Couvering, J.A., Castradori, D., Cita, M.B., Hilgen, F.J., Rio, D., 2000. The base of the Zanclean Stage and of the Pliocene Series. *Episodes* 23 (3), 179–187.
- Van der Made, J., 1996. Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie* 33, 3–254.
- Van der Made, J., 1999. Superfamily Hippopotamoidea. In: Rössner, G. E., Heissig, K. (Eds.), *The Miocene Land Mammals of Europe*. Verlag Dr Friedrich Pfeil, Munich, pp. 203–208.
- Van der Made, J., 2005. Le Pliocène Moyen, le Villafranchien inférieur. La faune du Velay vers 3 millions d’années. – cf. “*Microstonyx*” *major*. In: Lacombe, F. (Ed.), *Les grands Mammifères fossils du Velay. Les collections paléontologiques du Plio-Pléistocène du musée Crozatier, le Puy-en-Velay*. Annales des Amis du musée Crozatier 13/14. Phil’ Print, Yssingeaux, pp. 58–59 (in French).
- Van der Made, J., Han, D., 1994. Suidae from the upper Miocene hominoid locality of Lufeng, Yunnan province, China. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* 97, 27–82.
- Van der Made, J., Moyà-Solà, S., 1989. European Suinae (Artiodactyla) from the late Miocene onwards. *Bollettino della Società Paleontologica Italiana* 28, 329–339.
- Van der Made, J., Krakhmalnaya, T., Kubiak, H., 1999. The pig *Propotamochoerus palaeochoerus* from the upper Miocene of Grytsiv, Ukraine. *Estudios Geológicos* 55, 283–292.
- Van der Made, J., Morales, J., Montoya, P., 2006. Late Miocene turnover in the Spanish mammal record in relation to palaeoclimate and the Messinian Salinity Crisis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 228–246.
- Van der Made, J., Güleç, E., Erkman, A.C., 2013. *Microstonyx* (Suidae, Artiodactyla) from the Upper Miocene of Hayranlı-Haliminhani, Turkey. *Turkish Journal of Zoology* 37, 106–122.
- Vrba, E.S., Bibi, F., Costa, A.G., 2015. First Asian record of a late Pleistocene reduncine (Artiodactyla, Bovidae, Reduncini), *Sivacobus sankaliai*, sp. nov., from Gopnath (Miliolite Formation) Gujarat, India, and a revision of the Asian genus *Sivacobus* Pilgrim, 1939. *Journal of Vertebrate Paleontology* 35 (4), e943399.
- Zeder, M.A., Lemoine, X., 2020. Factors affecting molar size in *Sus scrofa*. *Journal of Archaeological Science* 124, 105266.