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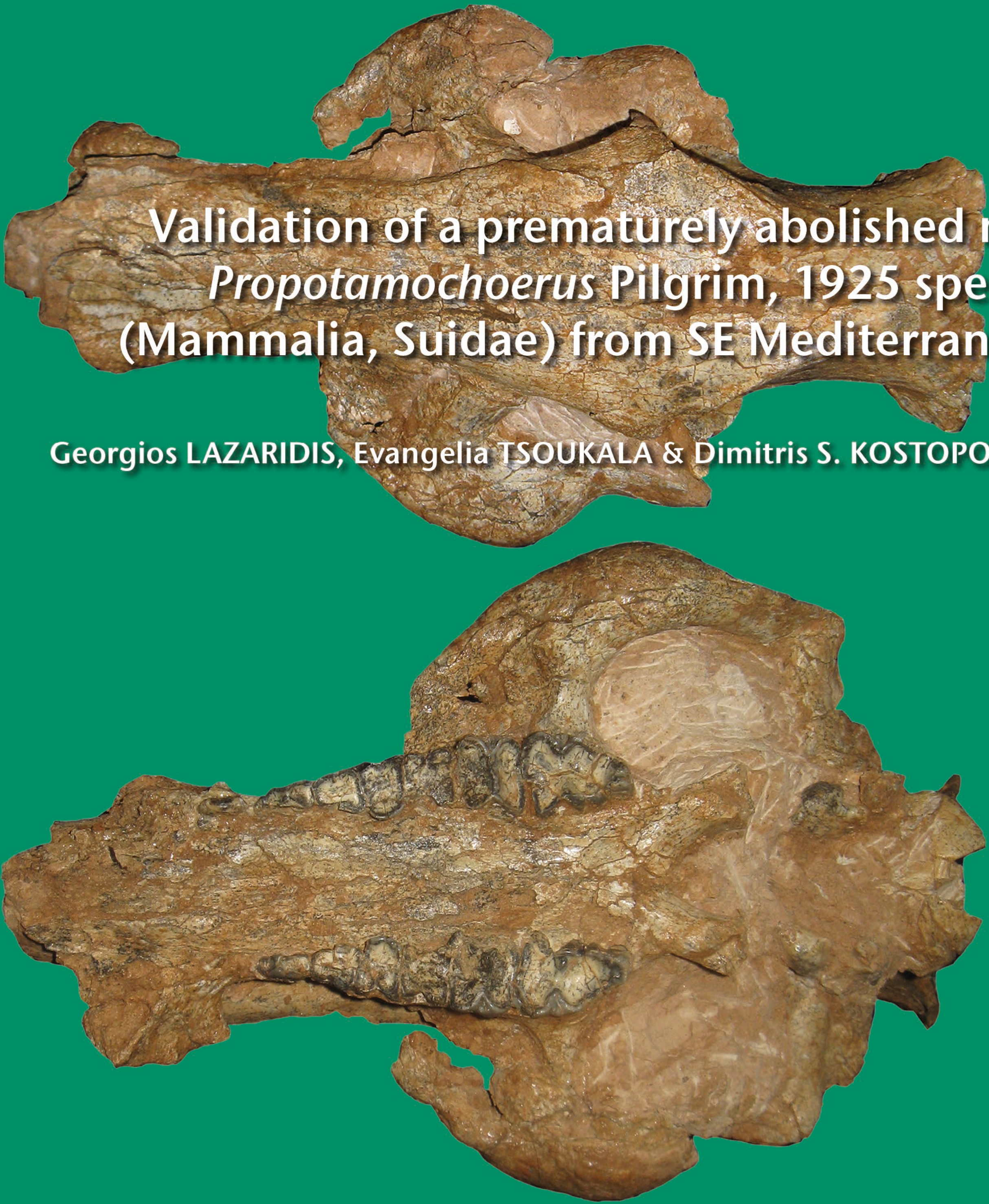

Validation of a prematurely abolished new *Propotamochoerus* Pilgrim, 1925 species (Mammalia, Suidae) from SE Mediterranean

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Validation of a prematurely abolished new *Propotamochoerus* Pilgrim, 1925 species (Mammalia, Suidae) from SE Mediterranean

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ABSTRACT

Fossil remains of late Miocene *Propotamochoerus* Pilgrim, 1925 from several sites of SE Europe are part of a long-lasting discussion. The sparsely known material, usually toothrows, does not fit well with any known *Propotamochoerus* species and therefore local peri-Balkan samples have been referred to different species. Based on a fairly complete cranium and a mandible from the Turolian fauna of Kryopigi (Northern Greece), and combined with other Balkan evidence, we propose that this Eastern Mediterranean taxon represents a new species. *Propotamochoerus aegaeus* n. sp. is characterized by moderate cranial and dental size, widely separated temporal lines, long zygomatic arches, elongated upper incisors and diastemata in each side of the first upper premolar; relatively small male lower canines, broad upper and lower third premolars and short lower fourth premolar, and a small hexaconid on the talonid of the lower third molar. A thorough morphological and metric analysis contradicts recent views of the taxon as invalid and provides new evidence on the late Miocene diversity and distribution of the genus.

KEY WORDS
Turolian,
Greece,
Suidae,
Propotamochoerus,
Mediterranean,
late Miocene,
new species.

RÉSUMÉ

Validation d'une nouvelle espèce de Propotamochoerus *Pilgrim, 1925 (Mammalia, Suidae) du sud-est de la Méditerranée abolie prématurément.*

Les restes fossiles de *Propotamochoerus* Pilgrim, 1925 du Miocène supérieur de plusieurs localités du sud-est de l'Europe sont au cœur d'une longue discussion. Le matériel peu connu, généralement composé de dentitions, ne semble correspondre à aucune espèce connue de *Propotamochoerus* ; par conséquent, les échantillons locaux péri-balkaniques ont été référés à différentes espèces. Sur la base d'un nouveau matériel crânien complet provenant de la faune du Turolien de Kryopigi (dans le nord de la Grèce), et en combinaison avec d'autres données des Balkans, nous proposons que ce taxon de la Méditerranée orientale représente une nouvelle espèce. *Propotamochoerus aegaeus* n. sp., se caractérise par une taille crânienne et dentaire modérée, des lignes temporales largement écartées, de longues arcades zygomatiques, des incisives supérieures allongées et des diastèmes de chaque côté de la première prémolaire supérieure ; des canines inférieures mâles relativement petites ; les troisièmes prémolaires supérieures et inférieures larges et la quatrième prémolaire inférieure courte ; ainsi qu'un petit hexaconid sur la talonid de la troisième molaire inférieure. Une analyse morphologique et métrique approfondie contredit les positions récentes sur l'invalidité du taxon et fournit de nouvelles données sur la diversité et la distribution du genre dans le Miocène supérieur.

MOTS CLÉS
Turolien,
Grèce,
Suidae,
Propotamochoerus,
mer Méditerranée,
Miocène supérieur,
espèce nouvelle.

INTRODUCTION

In the late Miocene of the Eastern Mediterranean suids are represented by two lineages: the very common *Hippopotamodon-Microstonyx*, known from several hundreds of specimens from more than 40 fossil sites (NOW database 2020), and the rarely recorded *Propotamochoerus* Pilgrim, 1925 (synonym of *Korynochoerus*; but see Geraads *et al.* 2008), often known from limited material that, in several cases, impedes confident species determination.

Propotamochoerus is a widely distributed small Dicoryphochoerini Schmidt-Kittler, 1971 suid (Pickford 1988; van der Made *et al.* 1999; for a brief taxonomic history see also de Bonis & Bouvrain 1996) recorded across Eurasia (from China to Spain) from the late Middle Miocene to the late Pliocene and in Africa during the late Miocene (Pilgrim 1926; Pearson 1928; van der Made *et al.* 1999; Nawaz *et al.* 2019; NOW database 2020). The origin of the genus is still under discussion; Pickford (1988) placed it in Asia, possibly from a hyotherin ancestor but Fortelius *et al.* (1996: 360) suggested that the origin of the genus cannot be settled until a critical re-examination of both *Hyotherium* von Meyer, 1834 and *Propotamochoerus* is made. In spite of its great geographic distribution and the rather high number of fossil sites (> 50 according to the NOW database 2020) where it occurs, the infrageneric taxonomy of *Propotamochoerus* is still not completely understood. This is mainly due to the usually fragmentary nature of the recovered material, which consists mostly of teeth. *Propotamochoerus hysudricus* (Stehlin, 1899-1900), the type species of the genus, is originally known from the late Miocene of Middle Siwaliks, Pakistan (see Pickford 1988); van der Made *et al.* (1999), Geraads *et al.* (2008) and Chit Sein *et al.* (2009) suggested, however, that it is a wastebasket species and a revision is needed. More species of *Propotamochoerus* have been named from the same area (Pilgrim 1926; Pickford 1988; Ahmed 2003, 2008; van der Made 2010; Nawaz *et al.* 2019) and it seems likely that at least one of them is valid (as for example the *Propotamochoerus* from the Chinji Fm). Nevertheless, their taxonomy is unclear and the synonymy issues are puzzling and beyond the scope of the present work. In China, *P. hyotherioides* (Schlosser, 1903), *P. parvulus* (Chang, 1974) and *P. wui* van der Made & Han, 1994 are reported from the late Miocene (Pilgrim 1926; Pickford 1988; van der Made & Han 1994). *Propotamochoerus wui* and *P. parvulus* have been regarded as synonyms by Pickford & Liu (2001) whereas Chit Sein *et al.* (2009) consider *P. parvulus* from Xiaolongtan, China as a member of *Parachleuastochoerus* Golpe-Posse, 1972.

Propotamochoerus palaeochoerus (Kaup, 1833) is the oldest known member of the genus recorded in several European faunas ranging from at least the late Astaracian (MN8 faunas) to Vallesian (van der Made & Moyà-Solà 1989; van der Made 1990; Fortelius *et al.* 1996). Although Pickford (1993) suggested a possible synonymy between *P. palaeochoerus* and *P. hysudricus*, the European species is currently accepted as distinct, distributed from Spain to the Ukraine (e.g. Hellmund 1995; de Bonis & Bouvrain 1996; Fortelius *et al.* 1996; van der Made *et al.* 1999). It was more abundant during the early Vallesian but less common during the late Vallesian, when it was likely replaced by younger members of the genus (van der Made *et al.* 1999). In the light of new evidence, the late Miocene/early Pliocene *Propotamochoerus* records previously attributed to *P. palaeochoerus* (e.g. Alcoy, Spain; Maramena, Greece) turned out to be doubtful and they were later revised (Fortelius *et al.* 1996; van der Made *et al.* 1999; Montoya *et al.* 2006; Geraads *et al.* 2008; Chit Sein *et al.* 2009).

Propotamochoerus provincialis (Blainville, 1847) is recorded in several European faunas ranging from the latest Miocene to the early Pliocene (MN13-MN15) (e.g. Morales 1984;

TABLE 1. — Skull measurements of the holotype of *Propotamochoerus aegaeus* n. sp. and data for *P. hysudricus* (Stehlin, 1899-1900) (according to Pickford 1988) and *P. palaeochoerus* (Kaup, 1833) (according to Mottl 1966).

	Measurements (in mm)	***P. hysudricus* (Stehlin, 1899-1900) AM101203**	***P. palaeochoerus* (Kaup, 1833)**	***P. aegaeus* n. sp. KRY 3820**
1	Incisive notch-tip of nuchals	330	390	> 370
2	Length of canine alveolar crest	43	67	45.6
3	Palatal length (I1 to posterior choanae)	180	222	> 196
4	Length of zygomatic arch	135	138	162
5	P2-M3 length	103	103	110.5
6	Height of occipitals (nuchal to foramen magnum)	111	126	112.5
7	Height of zygomatic arches	32	50	46.6
8	Zygomatic width	178	205	212
9	Orbital width	71	87	87.5
10	Muzzle breadth at M1	70	78	64.9
11	Muzzle breadth at P3	54	62.5	66.7
12	Cranial width at canine alveolar crests	85	119	103.4
13	Palatal breadth at M1	29	36	36.8
14	Orbit to hindmost part of skull	155	–	172
15	Orbit to foremost tip of skull	175	–	> 200
16	Premolar series length	50	–	58.3
17	Molar series length	65	–	67.9
18	Snout height (palate to dorsal surface) at M1	48 (crushed)	70	55
19	Snout height at P3	38 (crushed)	60	51

van der Made & Moyà-Solà 1989; Radulescu *et al.* 2003; Gallai & Rook 2011) but its taxonomic definition and relationships remained questionable (see discussions in van der Made & Moyà-Solà 1989). In a recent review of the suid material from the 'sables marins de Montpellier', the type locality of *P. provincialis*, Pickford (2013) suggested that part of the original hypodigm ascribed to this species belongs to *Sus strozzii* Forsyth Major, 1881, and he accordingly modified it. Pickford (2013) also challenged the generic attribution of *Propotamochoerus* by proposing that it should be referred instead to *Sus*.

A Turolian (MN11-MN13) representative of *Propotamochoerus* from SE Europe, tentatively ascribed to either the Indian *P. hysudricus* (e.g. de Bonis & Bouvrain, 1996) or the Chinese *P. hyotherioides* (e.g. Thenius 1950), is part of a long-lasting discussion (e.g. van der Made & Moyà-Solà 1989; de Bonis & Bouvrain 1996; Fortelius *et al.* 1996; van der Made *et al.* 1999; Geraads *et al.* 2008; Lazaridis & Tsoukala 2014). Despite similarities with these two taxa, most scholars consider the SE European sample as possibly representing a new, unnamed taxon waiting for more and better-preserved material to be confirmed (see van der Made *et al.* 1999; Geraads *et al.* 2008; Chit Sein *et al.* 2009; Pickford 2013). Based on a fairly well-preserved cranium from the upper Miocene site of Kryopigi (Chalkidiki peninsula, Greece), Lazaridis in his PhD thesis (Lazaridis 2015) established a new species, "*Propotamochoerus aegaeus*", in which he included several of the aforementioned Turolian records from SE Europe. However, Lararidis' PhD thesis is unpublished under the criteria set by the ICZN and therefore the new species name was till now pending formal publication. Meanwhile, Iannucci *et al.* (2020) directly referred to the Kryropigi taxon and challenged its validity. According to these authors: 1) all Turolian European *Propotamochoerus* belong to *P. provincialis*; and 2) there is no compelling evidence of Ruscinian records of this species.

Here we describe in detail the Kryopigi *Propotamochoerus* material and comment on a set of late Miocene SE Mediterranean records that altogether provide sufficient evidence for the denomination of a new species, namely *P. aegaeus* n. sp.

The Kryopigi locality (KRY) is found in red beds of the Triglia Formation (see Syrides 1990 for local lithostratigraphy). The collection includes more than 7000 identifiable specimens and the material comes from a fossiliferous lens of about two meters in thickness. It comprises a diverse fauna with 32 species of mammals, reptiles and birds. The mammal association is indicative of a late middle to early late Turolian fauna, inferring an age between 7.3 and 6.4 Ma (Lazaridis 2015; Lazaridis *et al.* 2018).

MATERIAL AND METHODS

Linear cranial and dental measurements (Tables 1; 2) were taken with a digital caliper with 0.01 mm accuracy and they are given in mm. Cranial measurements follow Mottl (1966) and Pickford (1988). Dental measurements and nomenclature follow van der Made (1996). Upper teeth are in uppercase and lower teeth in lowercase letters.

Metric comparison of the crania was performed by a diagram of % size differences, with the cranium AM101203 of *P. hysudricus* (Pickford 1988) served as a standard.

Principal Component Analyses (PCA) based on the variance-covariance matrices of both original and log-shape ratio transformed (Mosimann 1970) upper and lower dental measurements (length and width of P3, P4, M3 and p3, p4, m2, m3) were applied to examine dental metrical differences between the studied and comparative material. For the upper teeth PCA listwise deletion was followed for the comparative data matrix in order to exclude incomplete specimens. This was not possible in the case of *P. provincialis*, resulting in 2% of missing data. For the lower teeth all specimens with at least half of the measurements were kept in the analysis in order to maximize sample per species. About 70% of the included specimens are incomplete resulting in about 23% of missing data. Nevertheless, results did not change significantly when incomplete specimens were restricted to those of a single tooth (data not shown). In both PCA analyses of upper and lower dental raw data, missing values were treated by the iterative imputation method (Ilin & Raiko 2010). Mean value imputation was instead applied for missing values prior to the log-shaped data transformation. Scatter diagrams per teeth show metrical differences and variance of the various species.

One way Multivariate ANOVA (MANOVA) or (in case multivariate normality was violated) non-parametric MANOVA (PERMANOVA with Euclidean distance) were used to test the probability of same multivariate means or variance, respectively per teeth of different species.

The software package PAST (Hammer *et al.* 2001) was used for quantitative analyses. The level of significance was set at $\alpha = 0.05$. Results not shown within the main text are provided as supplementary information.

Abbreviations

Institution

ICZN	International Commission on Zoological Nomenclature;
LGPUT	Museum of Geology-Palaeontology-Palaeoanthropology of the Aristotle University of Thessaloniki.

Technical abbreviations

DAP	anteroposterior diameter;
DT	transverse diameter;
L	length;
max	maximum;
W	width.

Other abbreviation

ANOVA	analysis of variance;
M	upper molar;
m	lower molar;
MANOVA	multivariate analysis of variance;
PERMANOVA	permutational multivariate analysis of variance;
P	upper premolar;
p	lower premolar;
PCA	principal component analyses.

SYSTEMATIC PALAEONTOLOGY

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

Propotamochoerus aegaeus n. sp.

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"*Postpotamochoerus*" subgen. nov. *hyotherioides* – Thenius 1950: 25; figs 1; 2.
Hyotherium palaeochoerus – Hürzeler & Engesser 1976: 335.
Korynochoerus palaeochoerus – Hellmund 1995: 143-144, pls 1; 2.
Propotamochoerus cf. *hysudricus* – de Bonis & Bouvrain 1996: 122; figs 9; 10.
« the MN11-13 » *Propotamochoerus* – van der Made *et al.* 1999: 285.
Propotamochoerus – Gallai 2007: 19; fig. 2. — Lazaridis *et al.* 2018: 131.
Propotamochoerus sp. – Fortelius *et al.* 1996: 357. — Montoya *et al.* 2006: 144. — Geraads *et al.* 2008: 104; fig 2. — Chit Sein *et al.* 2009: 26. — van der Made 2010: 79, 81, 83. — Pickford 2013: 682. — Lazaridis & Tsoukala 2014: 164.
Propotamochoerus aegaeus – Lazaridis 2015: 138; figs 26-28 (*nomen nudum*): PhD thesis.
Propotamochoerus provincialis – Iannucci *et al.* 2020: 330. — Gallai & Rook 2011: 33.

Holotype. — Cranium LGPUT KRY3820 preserving the right P1-M3 and the left P2-M3.

Paratypes. — Mandible LGPUT KRY1094 (fragment LGPUT KRY3490 is part of this mandible) with right p2-m3, c and right and left i1-i2; upper canines, C: LGPUT KRY1092, LGPUT KRY1193; p2: LGPUT KRY1096.

Repository. — Museum of Geology-Palaeontology-Palaeoanthropology, Aristotle University of Thessaloniki (LGPUT).

Etymology. — The species is named after its area of distribution around the Aegean Sea.

Type locality. — Kryopigi, Chalkidiki Peninsula, Greece.

Geographic distribution. — Greece: Kryopigi and Polychrono (Kassandra, Chalkidiki Peninsula), Ravin des Zouaves-5 (Axios Valley), Samos, Thermopigi (Serres); North Macedonia: Vozarci, Kalnitsa; Bulgaria: Kalimantsi; Possible occurrences: Achladi, Maramena (Greece); Gravitelli, Casino, Baccinello V3 (Italy); Salihpasalar, (Turkey).

Age. — Late Miocene (Turolian, MN11-MN13).

Diagnosis (after Fortelius *et al.* 1996; van der Made *et al.* 1999; Montoya *et al.* 2006; Geraads *et al.* 2008; Chit Sein *et al.* 2009; van der Made 2010; and present study). — A species of *Propotamochoerus* with widely separated temporal lines running parallel to each other in their caudal part; zygomatic arches originated above the M1; small I1 lacking a distal cusp; elongated and narrow I2 and I3; presence of a long diastema between C-P1 and a shorter between P1-P2; moderately large M3; relatively small male lower canines with the posterior face narrower than both the labial and the even wider and more convex lingual one; broad p3/P3; short p4 with small to absent metaconid and reduced precristid; presence of a small hexaconid on the third lobe of m3.

Differential diagnosis. — *Propotamochoerus aegaeus* n. sp. differs from *P. palaeochoerus* in having wider parietals; temporal lines that do not merge; longer anteroposteriorly zygomatic; slender muzzle above the M1; shorter diastema between P2 and P1; longer I2 and I3; longer P2 compared to P3 but equally broad in its anterior and posterior part; shorter p4; broader p3; and a distinct hexaconid in the talonid of the m3.

It differs from *P. hysudricus* in the slightly larger size (6% on average in linear cranial and dental measurements); the more separated caudal parts of the temporal lines; the longer and slender muzzle above the M1; the presence of diastemata between C-P1 and P1-P2; the longer P2 than P3; the larger M3/m3; the smaller lower male canine; the presence of diastema between p1-p2; the broader p3/P3 and the presence of a hexaconid in the talonid of m3.

It differs from *P. hyotherioides* in the longer I2, shorter and broader P3 and P4, and the broader p3.

FIG. 1. — *Propotamochoerus aegaeus* sp. nov: **A**, dorsal and; **B**, ventral view of the holotype cranium KRY3820. Scale bars: 50 mm.

TABLE 2. — Dental measurements of *Propotamochoerus aegaeus* n. sp. from Kryopigi. Abbreviations: **C**, canine; **L**, length; **M**, molar; **P**, premolar; **W**, width; **Wp**, posterior width; **Wpp**, third molar posterior width; measurements in mm.

	KRY3820			KRY 3490 + 1094	
	right	left		right	left
LP1	12.25	–	L i1	7.45	8.01
WP1	4.37	–	W i1	14.61	14.84
LP2	15.10	14.66	L i2	6.39	7.12
WP2	8.47	7.99	W i2	15.83	17.95
LP3	14.50	14.50	L c	11.37	–
WP3	13.76	13.95	W c	10.57	–
LP4	13.12	13.72	L p1	–	–
WP4	17.17	17.91	W p1	–	–
LM1	15.96	14.93	L p2	15.90	–
–	–	21.41	W p2	6.23	–
LM2	20.23	21.13	L p3	16.59	–
WM2	22.50	–	W p3	9.79	–
LM3	33.46	33.62	L p4	15.70	–
WM3	24.83	23.48	W p4	12.13	–
–	–	–	Wp p4	–	–
–	–	–	L m1	14.87	–
–	–	–	W m1	–	–
–	–	–	Wp m1	13.31	–
–	–	–	L m2	23.32	–
–	–	–	W m2	18.10	–
–	–	–	Wp m2	18.87	–
–	–	–	L m3	34.92	–
–	–	–	W m3	18.07	–
–	–	–	Wp m3	15.03	–
–	–	–	Wpp m3	13.75	–

It differs from *P. provincialis* in the smaller size; more elongated I2, I3; the presence of diastemata between C-P1 and P1-P2; the bi-rooted P1; the longer P2 than P3; and the shorter p4, m2 and both M3/m3.

Propotamochoerus aegaeus n. sp. is nearly 30% larger in linear dental measurements than *P. wui*, which also lacks a hexaconid on the third lobe of m3.

DESCRIPTION

The cranium KRY3820 is almost complete and belongs to an old individual based on its heavily worn molars (Figs 1; 2; Tables 1; 2). In most respects (measurements 1-3, 7, 12, 18, 19 in Table 1), its overall size appears intermediate between those of male crania of *P. hysudricus* and *P. palaeochoerus*. The snout is broken anterior to the canines, which are also missing. Nevertheless, the supra canine flange (also known as canine alveolar crest or canine boss) is preserved in the right side and bears a relatively large alveolus of triangular cross-section. Its posterior edge is placed above the posterior end of the first premolar. Although slightly deformed, the cross section of the snout is almost square. However, the cheek region is slightly concave. The supra canine flange is large, rather short with rough surface and curved anteroposteriorly. The zygomatic arches are wide, and deep at their central part. They flare outwards from the facial surface at a right angle. Anteriorly, they extend to the level above the anterior part of the M1. On both the dorsal and ventral surfaces of the prezygomatic shelf there are wide but shallow fossae. The orbits are small compared to the size of the cranium and associated with large and deep lachrymal notches. The dorsal surface of the skull is flat; slightly concave anteroposteriorly in the fronto-nasal region and weakly convex in the fronto-parietal one. The parietal lines run in parallel caudally, reaching a minimum distance of about 40 mm just in front of the nuchal crest. The supraorbital grooves are deep and extend anteriorly to a level above the P2. The infraorbital foramen is located above the contact of P3/P4. The posterior part of the skull is strongly elevated and the occiput is fan-shaped with strongly concave central part. The condyles are small compared to the size of the cranium. The U-shaped choanae open posterior to the M3s. The paroccipital processes are placed behind the auditory bullae and they do not fuse to them.

A diastema of 10 mm exists between C and P1, and a smaller diastema (*c.* 4 mm) between P1 and P2. The incisors are not preserved. The upper canine alveolus has a triangular shape (DAPmax = 24 mm; DTmax = 19 mm) with the posterior face longer than the lateral one; the canines themselves are not preserved but the isolated and extremely worn upper canines KRY1092, and KRY1193 likely belong to the cranium KRY3820. In their preserved proximal part, they show an oval cross section and remnants of a thick cement cover. P1 is relatively narrow, bi-rooted and slightly worn. P3 is wider at its posterior half. Although heavily worn, the M2 and M3 show a small, low cusp (ectostyle) on the buccal side and between the two lobes. The talon of the M3 is offline compared to the anteroposterior axis of the tooth and of the entire dentition, fully shifted towards the palatine and occupied by a large pentacone.

The mandible is robust and rather high but partially preserved (Fig. 2; Table 2), retaining the left and right i1 and i2, the right canine and the right p2-m3. The left mandibular corpus posterior to the symphysis is missing. The symphysis ends posteriorly at the level of p2. The ventral part of the right mandibular corpus posterior to the m1 is missing, as well as most of the vertical ramus and part of the mandibular condyle. The corpus is much wider (thicker) below the premolars and gradually thins towards the molars. The teeth are heavily worn, similarly to those of the cranium KRY3820 and the perfect teeth occlusion suggests they belong to the same individual. The alveolus of p1 is poorly preserved but it seems that p1 is closer to c than to p2, although accurate measurements cannot be taken. The preserved incisors are set horizontally. The lower canine strongly curves outwards in its preserved part, however keeping its dorsal surface roughly at the same level as that of the incisors. It has a sub-triangular cross-section with the posterior face slightly narrower than the labial or lingual ones (9.4 mm, 11.2 mm, and 12.7 mm respectively; measurement taken just above the alveolus). The premolars are less worn than the molars and they appear broader at their posterior half.

It is highly possible that all the specimens from Kryopigi belong to the same senile individual. The large supra canine flanges, the fairly large upper canines with traces of a thick cement cover, the strongly inflated and flaring zygomatic arches and the relatively large lower canines suggest a male individual.

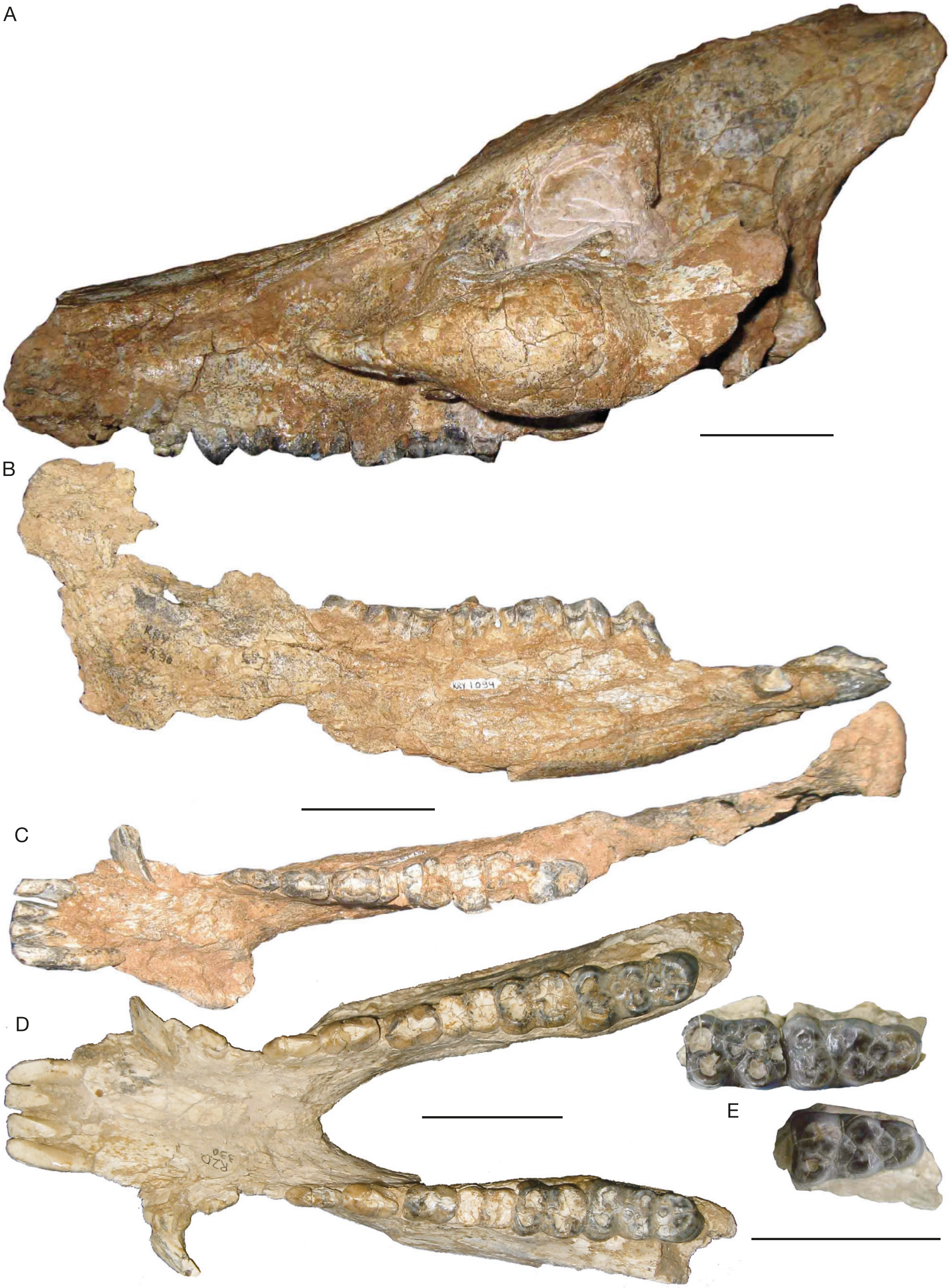
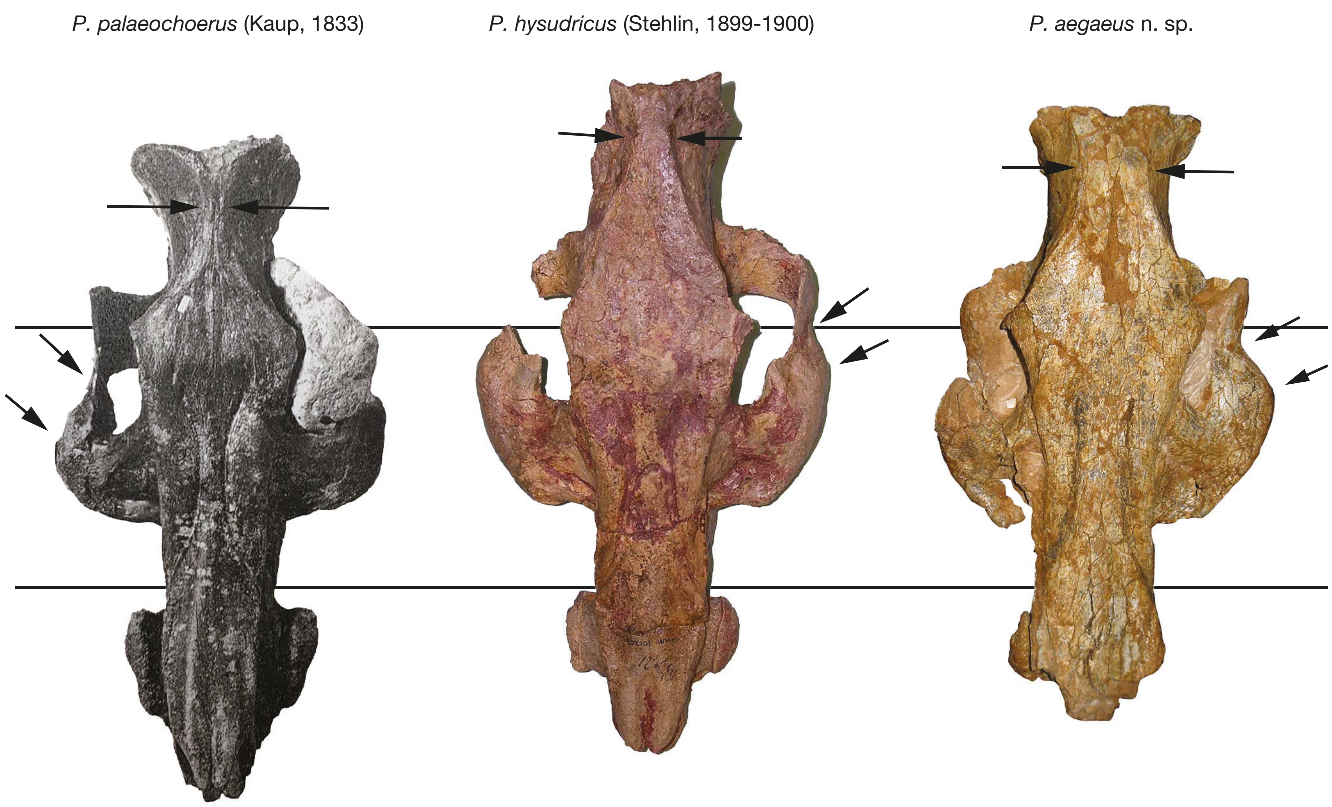


FIG. 2. — *Propotamochoerus aegaeus* n. sp.: **A**, lateral view of holotype cranium KRY3820; **B**, **C**, paratype mandible KRY1094 (+KRY3490) in lateral (**B**) and occusal (**C**) views; **D**, mandible RZO-330 from Ravin des Zouaves 5 (Axios Valley) in occlusal view; **E**, mandible fragments KPO2 and KPO3 with right m2 and m3 and left m3, respectively from Polychrono (Kassandra, Chalkidiki Peninsula). Scale bars: 50 mm.



P. palaeochoerus (Kaup, 1833)

P. hysudricus (Stehlin, 1899-1900)

P. aegaeus n. sp.

FIG. 3. — Cranium of *Propotamochoerus aegaeus* n. sp. from Kryopigi compared with *P. palaeochoerus* (Kaup, 1833) (photo taken from Mottl (1966) and *P. hysudricus* (Stehlin, 1899-1900) (AMNH101203) in dorsal view. Not to scale: **horizontal lines** indicate the same anatomical points. **Arrows** point to anatomical differences discussed in text.

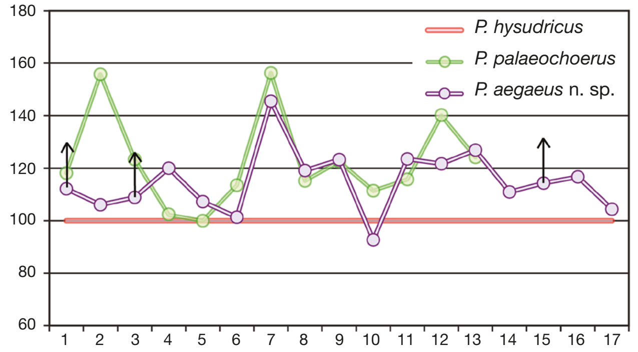


FIG. 4. — Diagram of % size differences of the cranium of *Propotamochoerus aegaeus* n. sp. from Kryopigi compared with *P. hysudricus* (Stehlin, 1899-1900) (AMNH 101203; standard) and *P. palaeochoerus* (Kaup, 1833) (LJG 60.258 [raw data from Pickford (1988) and Mottl (1966), respectively]). **Arrows** indicate minimum values (preserved parts) for the holotype of *P. aegaeus* n. sp. in cases of missing parts. Numbers correspond to measurements seen in Table 1.

COMPARISONS

The medium size, the morphological features of the facial cranium, the morphology and placement of the zygomatic arches, the development and convergence pattern of the parietal lines, the shape of the snout, the long symphysis and the canine placement are suitable for the genus *Propotamochoerus*, according to the diagnosis provided by Pickford (1988). Three Asian (*P. hysudricus*, *P. hyotherioides*, *and P. wui*) and two European (*P. palaeochoerus*, and *P. provincialis*) species of late Miocene *Propotamochoerus* are currently recognized by most scholars. Unfortunately, cranial anatomy is known only for *P. palaeochoerus*, and *P. hysudricus* (Pilgrim 1926; Mottl 1966; Schmidt-Kittler 1971; Pickford 1988).

The cranium of *P. palaeochoerus* from Johnsdorf, Austria, differs from that of the Kryropigi taxon in the larger (especially longer) supra canine flanges; the more posterior origin of the zygomatic arch (above M2 instead of M1 in Kryopigi); the converging temporal lines behind the postorbital processes of the frontals, tightly spaced along the parietal; the more constricted laterally parietals; the less compressed zygomatic-temporal join on the temporal fossa (dorsal view); the well concave nuchal crest (in dorsal view); the less widen rostral part of the nasals; and the more posteriorly extended and well curved supraorbital grooves (Fig. 3). *P. hysudricus* cranium from Siwaliks differs from the Kryopigi one in the more converging temporal lines towards the occipital; the more posterior origin of the zygomatic arch on the face (above M2); the less compressed zygomatic-temporal joint on the temporal fossa (dorsal view); the concave profile of the nuchal crest (in dorsal view); the narrower rostral part of the nasals; the shallower depressions on prezygomatic shelf; and, possibly, in the longer rostral part of the snout (in front of the supra canine flange) (Fig. 3).

Metrically, the cranium from Kryopigi appears longer than that of *P. hysudricus*. (measurement 1 in Fig. 4) and possibly closer to the cranial length of *P. palaeochoerus*. The length

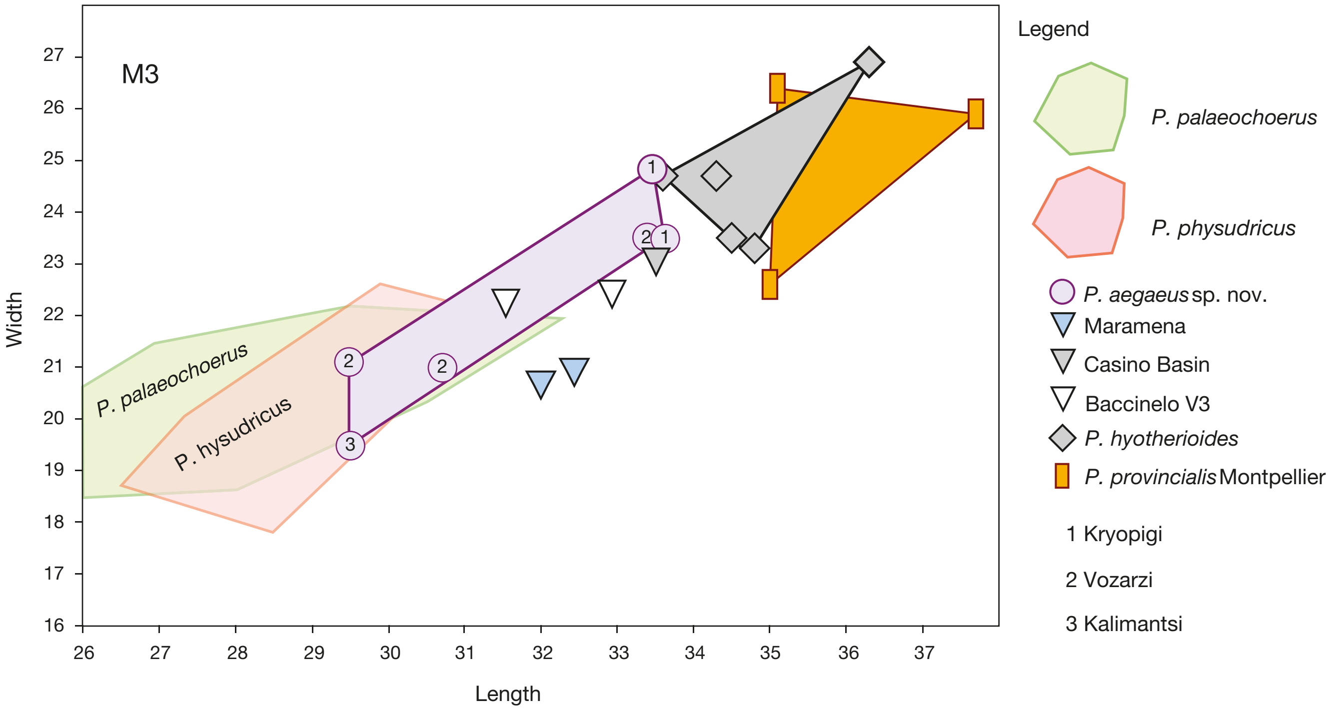


FIG. 5. — Scatter diagram of the upper third molar, M3 of various *Propotamochoerus* species compared with *P. aegaeus* n. sp. Raw data collected from Hünermann (1961), Pickford (1988, 2013), van der Made & Han (1994), van der Made *et al.* (1999), Geraads *et al.* (2008), Gallai & Rook (2011), Iannucci *et al.* (2020), and our data.

of the supra canine flange is larger than that of *P. hysudricus*, but significantly smaller in comparison with that of *P. palaeochoerus* (measurement 2 in Fig. 4). The partially preserved palatal length (measurement 3 in Fig. 4) is intermediately placed to the other two species, but it was probably closer to *P. palaeochoerus*. The length of the zygomatic arch (measurement 4 in Fig. 4), and the length of the cheek teeth (P2-M3; measurement 5 in Fig. 4) surpass both *P. hysudricus* and *P. palaeochoerus*. The height of the occipital (measurement 6 in Fig. 4) is similar to that of *P. hysudricus* and smaller than that of *P. palaeochoerus*. The height (measurement 7 in Fig. 4) and width (measurement 8 in Fig. 4) of the zygomatic arches, and the orbital width (measurement 9 in Fig. 4) are close to those of *P. palaeochoerus*. Furthermore, the Kryopigi taxon displays a narrower snout above the M2 and likely larger at P3 (measurement 10 and 11 in Fig. 4, respectively); although this may be exaggerated due to distortion. The breadth between the supra canine flanges is intermediate to the compared species. The palatal breadth (measurement 13 in Fig. 4) is about 27% larger than in *P. hysudricus* and similar to that of *P. palaeochoerus*. The length from the orbit to the hindmost part of the skull (measurement 14 in Fig. 4) and to the foremost part of the skull (measurement 15 in Fig. 4; partially preserved) exceeds the dimensions of *P. hysudricus*. Although the foremost part of the skull in the studied cranium is missing, it can be estimated to be 3% to 15% longer than that of the standard. Premolar and molar series length (measurement 16 and 17 in Fig. 4) are 17% and 4% larger than in *P. hysudricus*, respectively.

Taking into account the restricted evidence available (e.g. Pearson 1928; Mottl 1966; Schmidt-Kittler 1971; Pickford 1988, 2013; van der Made & Han 1994; van der Made *et al.* 1999), it appears that the Kryopigi taxon also differs from *P. hysudricus* in the presence of diastemata between C-P1 and between P1-P2. In the *P. palaeochoerus* upper dentition, the C-P1 diastema is slightly shorter or equal to that between P1-P2, which is different from the Kryopigi, Samos (Thenius 1950), Maramena (Hellmund 1995) and Vozarci (Geraads *et al.* 2008) *Propotamochoerus*, all exhibiting a very short to absent P1-P2 diastema but a significant C-P1 one. As in *P. provincialis* from its type locality (Pickford 2013: fig. 8), *Propotamochoerus* lower dentition from Samos (Thenius 1950), Ravin de Zouaves 5 (de Bonis & Bouvrain 1996), Vozarci (Geraads *et al.* 2008), and likely Kryopigi show a long p1-p2 diastema, compared to the c-p1 one. No data are known to us for *P. hyotherioides* or *P. palaeochoerus*, whereas limited data for *P. hysudricus* and *P. wui* (Pickford 1988; van der Made & Han 1994) rather indicate a shorter c-p1 diastema. In any case, diastema length appears to be highly variable in recent Suidae, depending on both ontogenetic age and sex (e.g. van der Made 1991) and hence, the discriminant value of the observed features may be limited.

Van der Made *et al.* (1999: fig. 4; see also Montoya *et al.* 2006: fig. 6; van der Made 2010: figs 16; 18) have already shown that the Samos, and Maramena *Propotamochoerus* are characterized by a small I1 without distal cusp and elongated and narrow I2 and I3, features that altogether differentiate the Balkan taxon form other species, apart the significantly smaller *P. wui*. According to data provided by van der Made *et al.* (1999: fig. 1) the lower male canine of the Kryopigi taxon, as well as that from Ravin de Zouaves 5, are significantly smaller than the canine of *P. hyotherioides*,

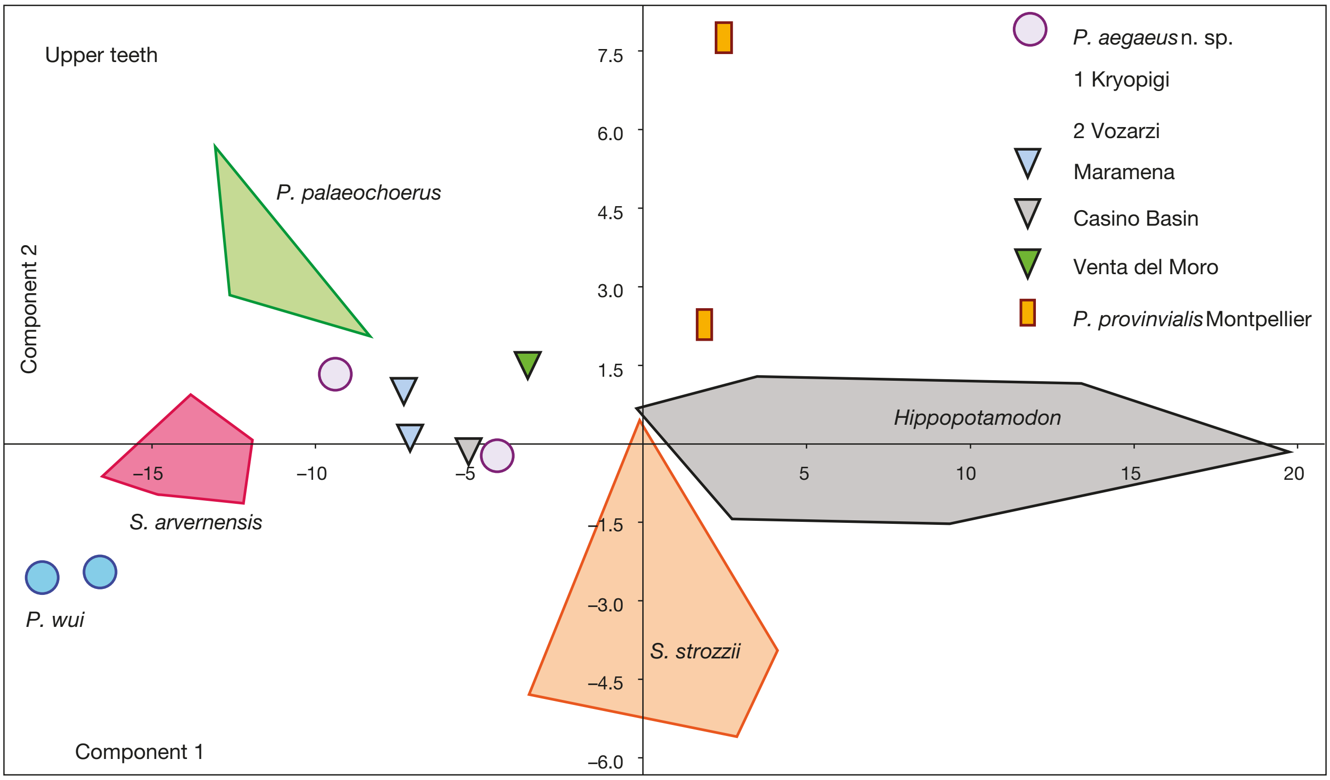


FIG. 6. — Morphospace occupation of upper teeth (P3, Pr, M3) of Miocene suids as shown by a principal component analysis. The observed range (**polygons**) of each taxon is displayed. Comparative data come from Iannucci *et al.* (2020) and Pickford (2013).

TABLE 3. — Pairwise comparison (p values/uncorrected significance) for M3 multivariate MANOVA (length and width) among several *Propotamochoerus* species.

M3	***P. hysudricus***	***P. aegaeus* n. sp.**	***P. provincialis***	***P. hyotherioides***	**Maramena suid**
P. hysudricus	0	0.014	3E-04	1E-04	0.002
P. aegaeus n. sp.	–	0	0.029	0.047	0.060
P. provincialis	–	–	0	0.525	0.330
P. hyotherioides	–	–	–	0	0.133
Maramena suid	–	–	–	–	0

smaller on the average than the single known specimen of *P. hysudricus* and close to the minimum values obtained for *P. palaeochoerus*. In both the Kyropigi and Ravin des Zouaves 5 *Propotamochoerus* (Fig. 2C-D), the lingual side of the lower male canine is slightly wider and more convex than the labial one and both are slightly wider than the posterior side.

A metrical comparison of the upper third molar (Fig. 5) shows that the Kryopigi taxon, along with those from Vozarci (Northern Macedonia) and Kalimantsi (Bulgaria) form a rather distinct cluster between the relatively smaller *P. hysudricus* and *P. palaeochoerus* and the larger *P. hyotherioides* and *P. provincialis* from Montpellier. A M3 from Casino Basin, and two M3 from Baccinello V3 (Italy) are plotted with the larger specimens of *Propotamochoerus* from the Balkans and well below the range of *P. provincialis*. Two M3 from Maramena locality are plotted close to the largest specimens of *P. aegaeus* n. sp. but they appear relatively narrower. The hypothesis of same multivariate mean (based on the length and maximum width) of the M3 of *Propotamochoerus* from the Balkans and the rest of the other species in comparison (with more than two observations) is rejected in all cases apart from the Maramena suid and marginally from *P. hyotherioides* (Table 3). No significant morphological differences in M3 have been observed among different species and samples.

A PCA by Iannucci *et al.* (2020: figs 2; 3) based on the length and width of P3, P4 and M3 is interpreted as indicating close proximity between the Balkan group and *P. provincialis*. Nevertheless, data on *P. provincialis* from its type locality are missing from their analysis (partly because P3 and P4 are not recorded there; see Pickford 2013). A repetition of the PCA (Fig. 6) using the same matrix but with the inclusion of the two M3 attributed to this species by Pickford (2013) from the “sables marins de Montpellier” provides exactly the same results as in Iannucci *et al.* (2020: fig. 2). The first component explains more than 90% of the variance, affected positively mostly by the M3 dimensions (Appendices 1; 2). *P. provincialis* from Montpellier is well distinct from the SE Mediterranean cluster, just because of its significantly larger M3 (compare also with Fig. 5). The Casino specimen groups with the Balkan taxon whereas the Venta del Moro, Spain specimen keeps an intermediate position between the Balkan taxon and *P. provincialis* from Montpellier

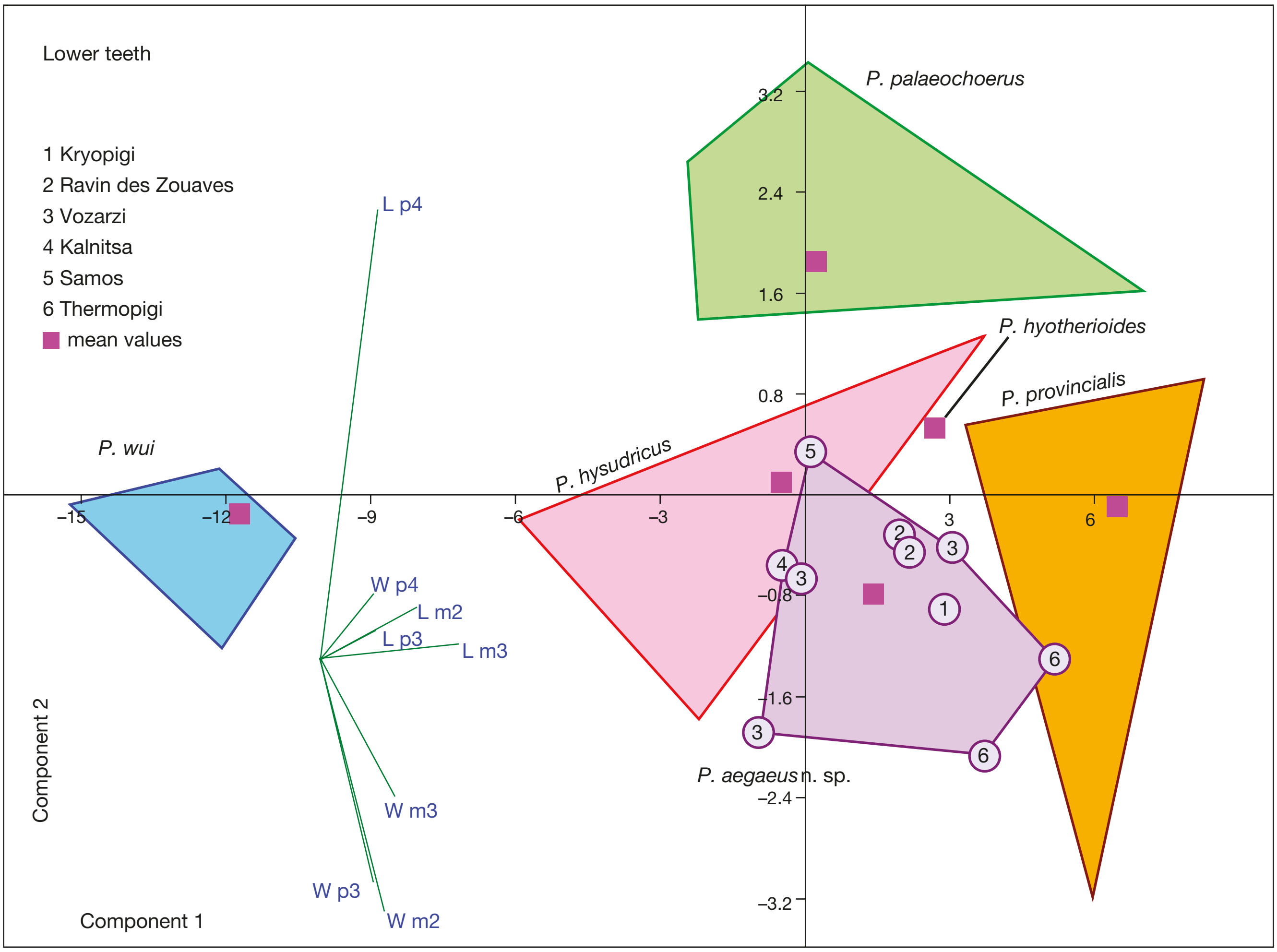


FIG. 7. — Morphospace occupation of lower teeth (p3, p4, m2, m3) of Miocene suids as shown by a principal component analysis. The observed range (**polygons**) of each species and mean values (**solid square**) are displayed.

(Fig. 6). By removing the absolute size effect (Appendix 16), it appears that only *P. palaeochoerus* is clearly separated from other *Propotamochoerus* species due to its proportionally longer upper premolars, whereas both the Balkan taxon and *P. provincialis* overlap significantly in the morphospace with the smaller *Sus arvernensis* Croizet & Jobert, 1828.

A PCA with the length and width of p3, p4, m2, and m3 in a number of *Propotamochoerus* species (Fig. 7) shows that the new material from Kryopigi is plotted together with that from other Greek, Bulgarian and North Macedonian localities in a distinct space between *P. hysudricus* and *P. provincialis*. On this diagram, the first principal component displays a great variance (Appendix 3) and is positively affected by all the variables, especially the length and width of m2, and m3 (Appendix 4). Thus, species with larger molars are plotted to the right side of the diagram. The PC2 axis is positively affected mostly by the length of p4 and negatively by the width of p3, m2, and m3 (Appendix 4). The Balkan taxon is overall larger than *P. wui* (see also Fig. 8) and well distinguished from *P. palaeochoerus* by its shorter p4 and slightly wider p3, m2, and m3 (see also Fig. 8). The mean of *P. hyotherioides* indicates a rather similar size to the Balkan taxon, both distinguished from *P. provincialis* by their shorter molars (see also Fig. 8). As for the upper toothrow, transformed data show (Appendix 17) that only *P. palaeochoerus* can be clearly distinguished in the dental morphospace mostly by its p4 proportions; the Balkan taxon greatly overlaps with both *P. provincialis*, and *P. hysudricus*.

Scatter plots (Fig. 8) of individual teeth proportions (length against width) provide some additional information. The Balkan group of samples forms a cluster that overlaps partially with *P. hysudricus* and less with *P. palaeochoerus* (especially in p4 and m1). *Propotamochoerus hyotherioides* is not so well represented in these diagrams. However, it displays some differences such as narrower premolars plotted outside of the 95% confidence interval of the Balkan taxon; in molars the difference is not so sharp. *Propotamochoerus provincialis* from Montpellier forms a well-defined cluster that occupies mainly the area of the largest dimensions in the diagrams (especially for m2), overlapping significantly with *P. palaeochoerus* in the p4 and m1 size. Apart from the p3, the Balkan taxon discriminates in all other examined teeth from *P. provincialis*. In the p4 and especially the m2, the separation of the two groups is clear as most *P. provincialis* teeth are plotted outside the 95% ellipses of the Balkan taxon. Specimens from

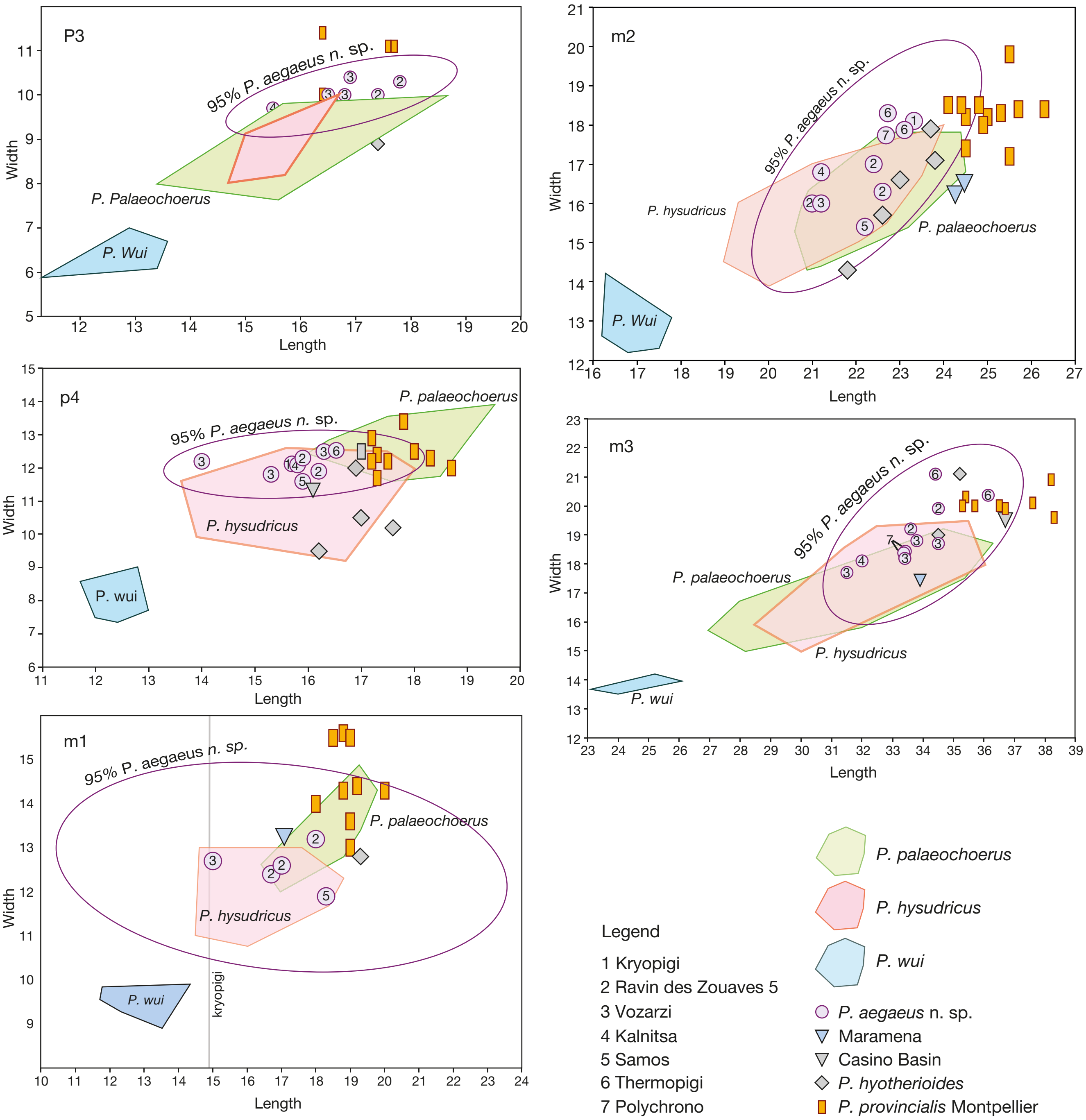


FIG. 8. — Scatter diagrams of the lower teeth of *Propotamochoerus aegaeus* n. sp. compared with other *Propotamochoerus* species. Data come from Hünermann (1961), Pickford (1988; 2013), van der Made & Han (1994), Iannucci *et al.* (2020), Geraads *et al.* (2008), and our data.

the Casino Basin are plotted close to both the Balkan taxon and *P. provincialis*, except for the p4 which is grouped with the former species. Specimens from Maramena are plotted inside the confidence interval of the rest Balkan samples for m1 and m3 but outside for the p3 and m2.

The probability of same multivariate variance in the lower teeth (p4, m1, m2, m3) between the Balkan taxon and all the compared *Propotamochoerus* species is summarized in Table 4 (pairwise comparisons per tooth among all species are provided as supplementary information, Appendices 9-12 . A statistically significant difference for all compared teeth is found between the Balkan taxon and *Propotamochoerus provincialis*, as well as between the Balkan taxon and *P. wui*. With the rest of the species, the null hypothesis for same multivariate variance is rejected in at least one tooth (Table 4). Even by using a single Balkan sample (in this case Vozarci, which has the most specimens), the results (Appendices 13-15) hold well, with one exception in the p3 of *P. provincialis* (the null hypothesis cannot be rejected; see supplementary information, Appendix 13).

According to the PCA loadings and original metrical data, two of the main metrical differences of the Balkan species from the rest of the compared *Propotamochoerus* taxa concern the width of the p3 and the length of the p4; this is summarized in the scatter diagram of Figure 9. In this plot, the Balkan taxon, *P. wui*, *P. provincialis*, *P. hysudricus* and *P. palaeochoerus* are well separated, whereas the mean of *P. hyotherioides* is plotted between the last two taxa indicating some overlap among those species. *P. provincialis* from the type locality shows a longer p4 compared to the Balkan taxon. Iannucci *et al.* (2020) also recognize a size difference in the p4 length between the Balkan taxon and the west European *P. provincialis* but they interpret it as trivial and possibly related to ecological adaptations. In fact, the average length difference of 1.5 mm represents about 11% of size difference between the two samples.

Although intraspecific dental morphological variability cannot be controlled by the available data (Pickford 1988; van der Made & Han 1994; van der Made *et al.* 1999), the Balkan taxon seems to differ from *P. palaeochoerus*, *P. hysudricus* and *P. wui* in the presence of a distinct hexaconid in the third lobe of m3. Hexaconids occur in the m3s of *P. hyotherioides* and *P. provincialis* (van der Made & Han 1994; Pickford 2013); compared to the latter taxon, the hexaconid of m3 in the Ravin des Zouaves 5, Polychrono (Fig. 2D-E), Maramena, and Vozarci lower dentitions is less developed and lingually restricted. The p4 of *P. hysudricus*, *P. palaeochoerus*, *P. hyotherioides*, *P. wui*, and to a lesser degree that of *P. provincialis*, show a distinct metaconid (synonym of Innenhügel; Pickford 1988, 2013; see van der Made & Han 1994; van der Made *et al.* 1999), which is smaller to absent in the studied taxon (see also Thenius 1950; de Bonis & Bouvrain 1996; Geraads *et al.* 2008; and pers. obs. on the Maramena suid). Additionally, the precristid of the p4 is reduced in the Balkan taxon as well as in *P. provincialis* (Pickford 2013).

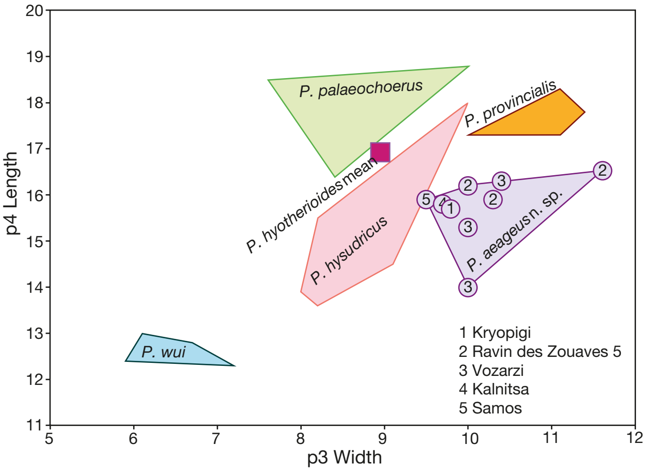


Fig. 9. — Scatter diagram of p3 breadth against p4 length of *Propotamochoerus aegaeus* n. sp. from Kryopigi (**circle**) Samos, Ravin des Zouaves 5 and Bulgaria (**circle**). Observed range (**convex hulls**) and mean values (**squares**) of *P. wui* van der Made & Han, 1994, *P. provincialis* (Blainville, 1847), *P. hysudricus* (Stehlin, 1899-1900), *P. palaeochoerus* (Kaup, 1833) and *P. hyotherioides* (Schlosser, 1903)? are also plotted. Comparative data from Thenius (1950), van der Made & Han (1994), de Bonis & Bouvrain (1996), Geraads *et al.* (2008), and Pickford (2013).

Table 4. — Lower teeth: p values from one way non-parametric multivariate ANOVA (PERMANOVA with Euclidean distance) for species compared with *Propotamochoerus aegaeus* n. sp. **Bold** data represent p values higher than the level of significance.

	p4	m1	m2	m3	data from
P. hysudricus	0.0491	**0.3687**	**0.1189**	0.0427	Pickford 1988
P. wui	0.0001	0.0004	0.0001	0.0002	van der Made & Han 1994
P. palaeochoerus	0.0006	**0.0918**	**0.0721**	0.0001	Hünermann 1961
P. provincialis	0.0001	0.0006	0.0001	0.0003	Pickford 2013
P. hyotherioides	0.0015	no data	**0.209**	**0.2064**	van der Made & Han 1994

DISCUSSION AND CONCLUSIONS

As mentioned by previous authors (e.g. van der Made & Moyà-Solà 1989; van der Made *et al.* 1999; Geraads *et al.* 2008; Chit Sein *et al.* 2009; Pickford 2013) and the present comparison clearly demonstrates, Turolian *Propotamochoerus* from the Balkans sufficiently distinguishes itself from already known species of this genus by several morphological and metrical features that (*contra* Iannucci *et al.* 2020) do merit a distinction at the species level. Based on the well-preserved Kryopigi skull, the name *Propotamocoerus aegaeus* n. sp., already proposed by Lazaridis (2015), is applied to this taxon. The Greek *Propotamochoerus* samples from Samos (Thenius 1950; Sylvestrou & Kostopoulos 2009), Ravin de Zouaves 5 (de Bonis & Bouvrain 1996), Thermopigi (Geraads *et al.* 2007, 2008), and Polychrono (Lazaridis 2015), as well as the material from Vozarci, Kalnitsa (North Macedonia), and Kalimantsi (Bulgaria) described by Geraads *et al.* (2008) are directly referred here to *P. aegeaus* n. sp. *Propotamochoerus* from Achladi (Euboia, Greece), and Salihpasalar (Turkey) may also ascribe to the same species (i.e., Geraads *et al.* 2008) but we did not have access to these samples in order to confirm it. The end-Miocene Maramena *Propotamochoerus*, previously referred to *Korynochoerus palaeochoerus* by Hellmund (1995), is tentatively ascribed here to *P. aegeaus* n. sp., due to minor size differences.

Based on metric evidence, we follow Gallai & Rook (2011) in ascribing the latest Miocene Monticino Gypsum Quarry (Brisighella) suid to *P. provincialis* (but see comments in Pickford 2013). The same is likely to be true for the end-Miocene Verduno *Propotamochoerus* briefly communicated by Sorbelli *et al.* (2019). The species attribution of the end-Miocene Gravitelli, Baccinello V3, and Casino Basin *Propotamochoerus* (e.g. Gallai & Rook 2006; Montoya *et al.* 2006; Gallai 2007; Iannucci *et al.* 2020), is more intriguing. Judging by the small M3 from Gravitelli and Baccinello V3, the elongated I2 and I3 from Baccinello V3 (i.e., van der Made *et al.* 1999; Gallai 2007; van der Made 2010), and the small p3 and p4 from Casino, an attribution of these samples to *P. aegeaus* n. sp. seems more likely (as already proposed by van der Made *et al.* 1999 and Montoya *et al.* 2006 for Baccinello V3).

Despite the relatively low number of specimens, *P. aegaeus* n. sp. occurs in a significant number of SE Mediterranean localities. According to the available data (see also Geraads *et al.* 2008), the species appears in the Balkans shortly before 8 Ma (first local occurrence in the Ravin des Zouaves 5 fauna, Axios Valley), and seems to survive here till the Miocene/Pliocene boundary at about 5.3 Ma (i.e., the Maramena record). Italian *Propotamochoerus* records dated around the Miocene Salinity Crisis imply an end-Miocene westward expansion of the taxon in agreement with other mammal evidence (Rook *et al.* 2006; Marra 2019; Pandolfi *et al.* 2021). *Propotamochoerus provincialis* emerged in or entered western Europe roughly at the same time (e.g. van der Made & Moyà-Solà 1989; van der Made *et al.* 1999; Gallai & Rook 2011) and it seems that the end Miocene Italian territories represent the overlapping area of the two taxa, which shared common morphofunctional characteristics.

Ginsburg (1980) and Geraads *et al.* (2008) recognized significant morphometric similarities between *P. provincialis* and the Vallesian *P. palaeochoerus*, suggesting the former as a possible direct offshoot of the latter (though the revision of *P. provincialis* by Pickford 2013 may call for a reconsideration). On the other hand, *P. aegaeus* n. sp. approaches in several cranial and dental aspects the Indian *P. hysudricus* and a direct relationship (or with one of the *Propotamochoerus* taxa from Siwaliks mixed under this name; see discussions in van der Made *et al.* 1999; Geraads *et al.* 2008) does not seem unlikely. Besides India, *P. hysudricus* has been described from the Late Miocene fauna of Baynunah Formation, Abu Dhabi (Bishop & Hill 1999). The dimensions of the Baynunah M3 (*c.* 30 mm × 20 mm) and m3 (32 mm × 16 mm) are well within the range of *P. hysudricus* but also towards the minimum values of *P. aegaeus* n. sp. Interestingly, according to the description of m3 by Bishop & Hill (1999), the talonid bears a well-developed hexaconid ("*The talonid is strong, with two very well-developed cusps...*" in their own words), a feature that is reported to be absent in the Indian taxon (Pickford 1988; van der Made *et al.* 1999) but present in the Balkan one (but see also Geraads *et al.* 2008: 109-110).

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APPENDICES — SUPPLEMENTARY MATERIAL

Appendix 1. — Eigenvalues and variance per principal component of PCA for upper teeth comparison.

PC	Eigenvalue	% variance
1	98.4463	93.276
2	4.42199	4.1898
3	1.31194	1.243
4	0.724283	0.68624
5	0.421928	0.39977
6	0.216525	0.20515

Appendix 2. — Loadings for PCA of upper teeth comparison.

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
P3L	0.22037	0.5677	-0.64409	-0.28728	-0.36015	0.045434
P3W	0.25802	0.37072	0.31822	0.61669	-0.25585	0.49896
P4L	0.24173	0.32421	-0.14562	0.05186	0.89327	0.12093
P4W	0.26611	0.3675	0.3224	0.14154	-0.050445	-0.81707
M3L	0.76324	-0.54579	-0.27728	0.18625	-0.054901	-0.070661
M3W	0.41603	0.047218	0.53089	-0.69264	-0.036605	0.24849

Appendix 3. — Eigenvalues and variance per principal component of PCA for lower teeth comparison.

PC	Eigenvalue	% variance
1	41.5031	92.275
2	1.48039	3.2914
3	0.617696	1.3733
4	0.453765	1.0089
5	0.354834	0.78892
6	0.26444	0.58794
7	0.199574	0.44372
8	0.103671	0.23049

Appendix 4. — Loadings for PCA of lower teeth comparison.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
L p3	0.2496	0.0494	0.1040	0.0272	0.7680	-0.2773	-0.1089	0.4952
W p3	0.2346	-0.3806	0.0808	0.0132	0.2640	-0.1655	0.7059	-0.4450
L p4	0.2551	0.7687	0.0266	-0.0902	-0.0966	0.1911	0.5124	0.1636
W p4	0.2379	0.1126	0.8890	0.0730	-0.1374	-0.1088	-0.2353	-0.2215
L m3	0.6192	0.0262	-0.3266	-0.4091	-0.2544	-0.4488	-0.2407	-0.1333
W m3	0.3323	-0.2343	0.0574	-0.4302	0.1865	0.7695	-0.1378	-0.0210
L m2	0.4312	0.0892	-0.2617	0.7656	0.0680	0.2300	-0.1984	-0.2337
W m2	0.2850	-0.4308	0.1151	0.2171	-0.4563	0.02883	0.2359	0.6389

Appendix 5. — Eigenvalues and variance per principal component of PCA for upper teeth comparison with normalized data.

PC	Eigenvalue	% variance
1	0.001865	46.446
2	0.000929	23.141
3	0.00071	17.688
4	0.000377	9.3911
5	0.000134	3.3335
6	1.02E-19	2.54E-15

Appendix 6. — Loadings for PCA of upper teeth comparison with normalized data.

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
P3L	-0.63058	-0.15369	0.55783	0.30707	0.08132	0.40825
P3W	0.003405	0.53455	-0.46803	0.51582	0.24993	0.40825
P4L	-0.21414	-0.60959	-0.57796	-0.26573	0.10596	0.40825
P4W	-0.126	0.37755	-0.02162	-0.38052	-0.72777	0.40825
M3L	0.67442	-0.36201	0.20327	0.36369	-0.27175	0.40825
M3W	0.29289	0.2132	0.30651	-0.54033	0.56231	0.40825

Appendix 7. — Eigenvalues and variance per principal component of PCA for lower teeth comparison with normalized data.

PC	Eigenvalue	% variance
1	0.002705	40.279
2	0.001408	20.976
3	0.001012	15.075
4	0.000808	12.035
5	0.000428	6.3771
6	0.000207	3.0896
7	0.000146	2.1693
8	7.30E-20	1.09E-15

Appendix 8. — Loadings for PCA of lower teeth comparison with normalized data.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
L p3	0.1848	-0.0859	-0.3431	-0.3847	-0.7515	0.0428	0.0343	0.3536
W p3	0.6098	0.4530	0.4199	-0.2701	0.2051	-0.0660	-0.0481	0.3536
L p4	0.1094	-0.5259	-0.3350	-0.3076	0.5759	0.2187	-0.0080	0.3536
W p4	0.3754	-0.3482	0.0843	0.7657	-0.1344	-0.0369	-0.0069	0.3536
L m3	-0.1949	0.3737	-0.3964	0.1629	0.1767	-0.3975	0.5696	0.3536
W m3	-0.2757	0.4200	-0.268	0.2102	0.0528	0.2987	-0.6439	0.3536
L m2	-0.4069	-0.2707	0.3629	-0.1653	-0.0331	-0.6197	-0.3034	0.3536
W m2	-0.4020	-0.0158	0.4754	-0.0111	-0.0915	0.5598	0.4065	0.3536

Appendix 9. — Pairwise comparison for p4 PERMANOVA of several *Propotamochoerus* species.

p values/uncorrected significance

p4	*P. hysudricus*	*P. wui*	*P. palaeochoerus*	*P. aegaeus n. sp.*	*P. provincialis*	*P. hyotherioides*
P. hysudricus	0	0.0001	0.0003	0.0491	0.0002	**0.1216**
P. wui	–	0	0.0001	0.0001	0.0001	0.001
P. palaeochoerus	–	–	0	0.0006	**0.9316**	0.0305
P. aegaeus n. sp.	–	–	–	0	0.0001	0.0015
P. provincialis	–	–	–	–	0	0.003
P. hyotherioides	–	–	–	–	–	0

Appendix 10. — Pairwise comparison for m1 PERMANOVA of several *Propotamochoerus* species

p values/uncorrected significance					
m1	***P. hysudricus***	***P. wui***	***P. palaeochoerus***	***P. aegaeus* n. sp.**	***P. provincialis***
P. hysudricus	0	0.0001	0.0001	**0.3687**	0.0001
P. wui	–	0	0.0001	0.0004	0.0001
P. palaeochoerus	–	–	0	**0.0918**	0.0005
P. aegaeus n. sp.	–	–	–	0	0.0006
P. provincialis	–	–	–	–	0

Appendix 11. — Pairwise comparison for m2 PERMANOVA of several *Propotamochoerus* species

p values/uncorrected significance							
m2	***P. hysudricus***	***P. wui***	***P. palaeochoerus***	***P. aegaeus* n. sp.**	***P. provincialis***	***Maramena***	***P. hyotherioides***
P. hysudricus	0	0.0001	**0.1131**	**0.1189**	0.0001	**0.0521**	0.1795
P. wui	–	0	0.0001	0.0001	0.0001	0.0199	0.0011
P. palaeochoerus	–	–	0	**0.0721**	0.0001	**0.0526**	**0.4933**
P. aegaeus n. sp.	–	–	–	0	0.0001	0.0167	**0.209**
P. provincialis	–	–	–	–	0	0.0115	0.0002
Maramena	–	–	–	–	–	0	**0.2808**
P. hyotherioides	–	–	–	–	–	–	0

Appendix 12. — Pairwise comparison for m3 PERMANOVA of several *Propotamochoerus* species.

p values/uncorrected significance						
m3	***P. hysudricus***	***P. wui***	***P. palaeochoerus***	***P. aegaeus* n. sp.**	***P. provincialis***	***P. hyotherioides***
P. hysudricus	0	0.0001	0.0356	0.0427	0.0001	**0.0664**
P. wui	–	0	0.0001	0.0002	0.0005	0.0376
P. palaeochoerus	–	–	0	0.0001	0.0001	0.0061
P. aegaeus n. sp.	–	–	–	0	0.0003	**0.2064**
P. provincialis	–	–	–	–	0	0.0401
P. hyotherioides	–	–	–	–	–	0

Appendix 13. — Pairwise comparison for p3 MANOVA of several *Propotamochoerus* species. *Propotamochoerus aegaeus* n. sp. from Vozarzi is kept separately from the rest *P. aegaeus* n. sp. sample in order to test consistency of results for a single locality sample.

p values/uncorrected significance							
p3	***P. hysudricus***	***P. wui***	***P. palaeochoerus***	***P. aegaeus* n. sp.**	***P. aegaeus* n. sp. Vozarzi**	***P. provincialis***	***P. hyotherioides***
P. hysudricus	0	0.0006	**0.2157**	0.0442	**0.0555**	0.0034	**0.1939**
P. wui	–	0	5.95E-07	7.59E-05	0.0006	5.03E-05	0.0086
P. palaeochoerus	–	–	0	0.0412	0.0256	0.0001	**0.4088**
P. aegaeus n. sp.	–	–	–	0	**0.7805**	**0.0964**	**0.1988**
P. aegaeus n. sp. Vozarzi	–	–	–	–	0	**0.3718**	**0.2610**
P. provincialis	–	–	–	–	–	0	**0.0639**
P. hyotherioides	–	–	–	–	–	–	0

Appendix 14. — Pairwise comparison for p4 PERMANOVA of several *Propotamochoerus* species. *Propotamochoerus aegaeus* n. sp. from Vozarzi is kept separately from the rest *P. aegaeus* n. sp. sample in order to test consistency of results for a single locality sample.

p values/uncorrected significance

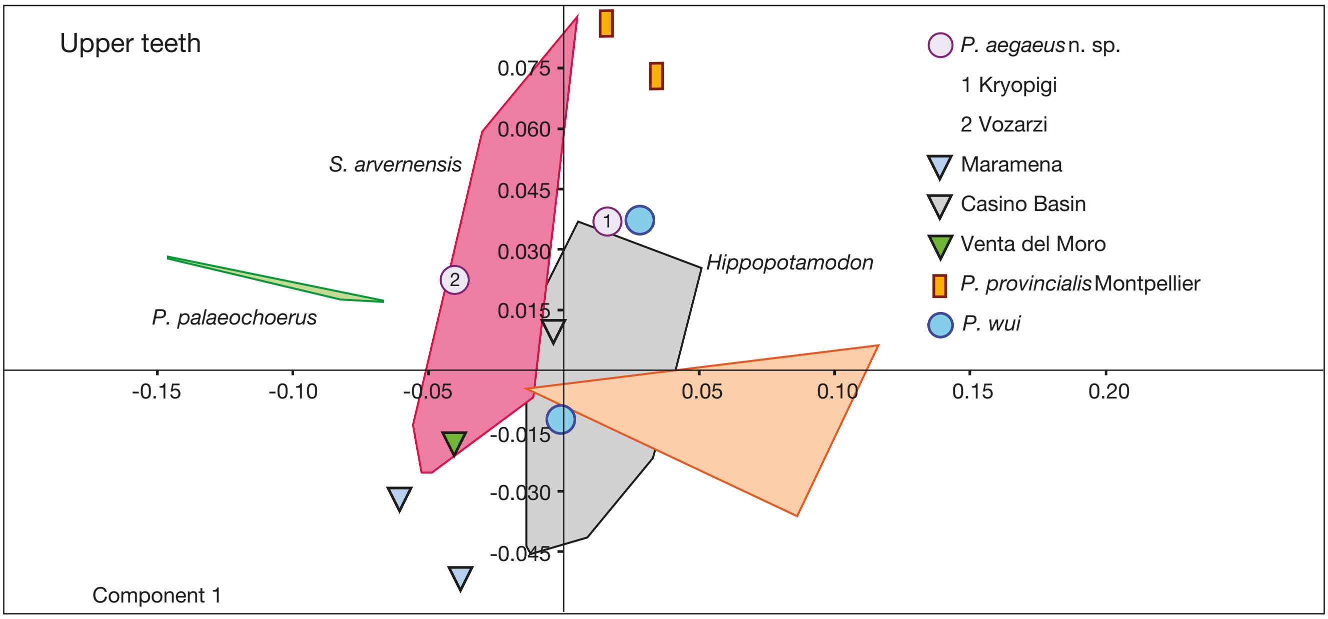
p4	***P. hysudricus***	***P. wui***	***P. palaeochoerus***	***P. aegaeus* n. sp.**	***P. aegaeus* n. sp. Vozarzi**	***P. provincialis***	***P. hyotherioides***
P. hysudricus	0	0.0001	0.0003	**0.096**	**0.283**	0.0001	**0.1227**
P. wui	–	0	0.0001	0.0002	0.0027	0.0001	0.0005
P. palaeochoerus	–	–	0	0.0077	0.0091	**0.9303**	0.0318
P. aegaeus n. sp.	–	–	–	0	**0.1346**	0.0003	0.0049
P. aegaeus n. sp. Vozarzi	–	–	–	–	0	0.0036	**0.0600**
P. provincialis	–	–	–	–	–	0	0.0022
P. hyotherioides	–	–	–	–	–	–	0

Appendix 15. — Pairwise comparison for m3 PERMANOVA of several *Propotamochoerus* species. *Propotamochoerus aegaeus* n. sp. from Vozarzi is kept separately from the rest *P. aegaeus* n. sp. sample in order to test consistency of results for a single locality sample.

p values/uncorrected significance

m3	***P. hysudricus***	***P. wui***	***P. palaeochoerus***	***P. aegaeus* n. sp.**	***P. aegaeus* n. sp. Vozarzi**	***P. provincialis***	***P. hyotherioides***
P. hysudricus	0	0.0001	0.0358	0.0315	**0.5711**	0.0001	**0.0683**
P. wui	–	0	0.0001	0.0006	0.0057	0.0008	0.0359
P. palaeochoerus	–	–	0	0.0001	**0.1056**	0.0001	0.0077
P. aegaeus n. sp.	–	–	–	0	**0.2700**	0.0018	**0.3987**
P. aegaeus n. sp. Vozarzi	–	–	–	–	0	0.0018	**0.1375**
P. provincialis	–	–	–	–	–	0	0.0451
P. hyotherioides	–	–	–	–	–	–	0

Appendix 16. — Scatter diagram of principal component analysis on log-shaped transformed upper teeth data of *Propotamochoerus aegaeus* n. sp. from the localities of Kryopigi and Vozarci (Geraads *et al.* 2008) compared with *P. wui* (van der Made & Han, 1994, Lufeng), *P. provincialis* (Blainville, 1847) from the type locality Montpellier (Pickford 2013) and the localities of Casino Basin and Venta del Moro. Comparative data come from Iannucci *et al.* (2020) and Pickford (2013).



Appendix 17. — Scatter diagram of principal component analysis on log-shaped transformed lower teeth data of *Propotamochoerus aegaeus* n. sp. from the Greek localities Kryopigi, Ravin des Zouaves 5, Samos, Thermopigi, and the Bulgarian localities Vozarci and Kalnitsa (Geraads *et al.* 2008), compared with *P. provincialis* (Blainville, 1847) (Montpellier, Pickford 2013), *P. hysudricus* (Stehlin, 1899-1900) (Pickford 1988), *P. palaeochoerus* (Hünermann 1961). The observed range (polygons) of each species is displayed.