The Fossil Record of Suoids (Mammalia: Artiodactyla: Suoidae) in Greece

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1 Introduction

Suoids (Superfamily Suoidea) include today 7 genera and 16 (or 19) species distributed in 2 families of distinct geographic ranges, the Old World suids or pigs (Family Suidae; 5 genera and 13–16 species) and the New World tayssuids or peccaries (Family Tayssuidae; 2–3 genera and 3 species) (McDonald 2009; Groves and Grubb 2011). Members of both families represent primarily omnivorous artiodactyls with a simple nonruminating stomach, a fairly characteristic cuneate-shaped cranium, absence of frontal appendages, complete tooth formula with low (apart from warthogs) crowned bunodont (or neobunodont sensu Stehlin 1899/1900) to bunolophodont molars, and as a rule, short tetradactyle acropodials (Hünnermann 1999; Harris and Liu 2007). Apomorphic features uniting Suoidea are the presence of ossified tympanic bullae, the dorsally open external auditory meatus, the elongated tympanic process of the squamosal, the rootless lower canine of males, the paraconid-metaconid fusion (or paraconid reduction), the lack of cingulum on the lingual wall of upper molars and the similarly shaped first and second lower incisors (Liu 2003).

Earliest known members of suoids are known from the Eocene of China and Thailand (Liu 2001), which makes Asia the most likely center of their origin. The early history of the group is still little understood and opinions among authors differ substantially. Primitive, Oligocene suoids, commonly referred to as "Old World peccaries" or Palaeochoeridae Matthew, 1924, are strongly debatable (e.g., McKenna and Bell 1998); some of them are currently seen as members of Suidae family while others as stem Suidae (Liu 2003; but see also van der Made 2010, 2020).

The first unequivocal occurrences of the Old World family Suidae are dated at the early Miocene of Eurasia and Africa, suggesting that suids already radiated

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during the Oligocene (Pickford 1993). During the Miocene Suidae show a remarkable morphological diversity. More than 20 suid genera are recorded, distributed in 6–9 subfamilies. Listriodontin, cainochoerin, and hyotheriin suids went extinct before the Pliocene and tetraconodontins during the Early Pleistocene, while at the same time suins diversified strongly (Franz et al. 2016; Harris and Liu 2007). Today suids may be found along a strickingly broad environmental spectrum, from tropical islands and rainforests to semi-desert grasslands and the high Himalayan plateaus (Meijaard et al. 2015).

As for other members of Artiodactyla, suids have been a basic source of food and other raw materials for prehistoric men. Cave paintings in Leang Bulu' Sipong 4 Cave in Sulawesi, Indonesia, dated at about 44,000 years nicely portray such relationship (Aubert et al. 2019). Zooarchaeological records from China, Near East, and Greece suggest that pigs were already domesticated by 8500–8000 years ago (Payne 1985; Franz et al. 2016).

Extant suoids are represented in Greece exclusively by the wild boar, *Sus scrofa* L., naturally recorded in Central and Northern Greece, as well as in Samos Island. Suoids were never exceptionally abundant or diversified according to the available Greek fossil record; still they are represented by 10 species at least during the last 17 Myr. The aim of this work is to present the Greek fossil Suoidea through time, providing taxonomical, phylogenetic, biogeographic, and chronological information. The bibliography on the topic has been condensed to the minimum possible and in cases of debatable taxonomic issues we follow the most recent reviews or author's point of view.

2 Historical Overview

Professors J. Roth and J.A. Wagner of the University of Munich were likely the first who reported on fossil suids from Greece. They described and illustrated (Roth and Wagner 1854: Pl. 11, fig. 4) a partial mandible from Pikermi, near Athens, introducing a new species, *Sus erymanthius*, inspired by the legend of the Erymanthian boar, from the feats of Hercules. In the following years more material of this taxon became known through the classic works of Gaudry (1862–1865), Forsyth-Major (1888, 1894), and Arambourg and Piveteau (1929). At the dawn of World War II, Professor I. Paraskevaidis of the Agricultural University of Athens extended the Greek suoid record to early Miocene by describing sanithere remains from "Michalos clay-pit" in Chios Island. During the 1950s Professor E. Thenius from the University of Vienna (Thenius 1950, 1955) reported two more taxa from Greece, *Sus antiquus* Kaup, 1833, and *Potamochoerus (Postpropotamochoerus) hyotheriodes* (Schlosser, 1903) from Sophades, Thessaly and Samos Island respectively. All of the aforementioned taxa participated in a series of taxonomic revisions in the coming years, while new paleontological excavations constantly enriched the Greek suid record by means of both specimens and species. Over the next decades new material from several sites partially completed the Greek suid record up to the Pleistocene (Steffens et al. 1979; Koufos 1986, 2007; Tsoukala

1989; de Bonis et al. 1997; Sylvestrou and Kostopoulos 2006, 2009). At the same time Bonis and Bouvrain (1996) provided the first revision of Greek Late Miocene suids.

3 Phylogenetic Relationships

Both morphological and molecular evidence suggest that the sister extant Families Suidae Gray, 1821, and Tayssuidae Palmer, 1897, included into the suborder Suina Gray, 1868 (or Suiformes Jaeckel, 1911), represent together a distinct monophyletic clade of the even-toed hoofed mammals—Mammalia: Artiodactyla Owen, 1848 (e.g., Boiserie et al. 2005; Marcot 2007). Relationships of Suina with other groups of artiodactyls are however less clear. Boiserie et al. (2005) and Boisserie and Lihoreau (2006) recognized Suina as the sister group of a clade uniting Hippopotamidae, Anthracotheriidae, and Ceracea, whereas Spaulding et al. (2009) based on morphological data suggest sister group relationships between Hippopotamidae and Suidae. Pickford (1993) also proposed the ancestry of hippos among "Palaeochoerinae."

Most authors agree that Suidae, Tayssuidae, and the extinct Sanitheriidae Simpson, 1945 (or Saniitheriinae according to other scholars), constitute a taxon of superfamily level, Suoidea. Suidae appears to be the most diversified among suoid families; Harris and Liu (2007) recognize seven subfamilies: Listriodontinae Lydekker, 1884, Kubanochoerinae Gabunia, 1958, Tetraconodontinae Lydekker, 1876, Namachoerinae Pickford, 1995, Cainochoerinae Pickford, 1988, Taucanaminae van der Made, 1997 (= Schizochoerinae Golpe-Posse, 1972), and Suinae Gray, 1821 but opinions among scholars vary considerably (e.g., Orliac et al. 2010: tab. 1; van der Made 2010).

4 Distribution

The Greek fossil record of Suoidea ranges from the middle Miocene to the Late Pleistocene. Earliest known occurrences are from the middle Aragonian (MN5–6; Orleanian/Astaracian) faunas of Antonios, and Thymiana (Chios Island) representing mostly sanithere and listriodontine taxa (Appendix). During the Late Miocene the Greek record is monopolized by the genus *Hippopotamodon* (=*Microstonyx*) though sparse evidences of *Propotamochoerus* are also present. From the early Ruscinian onwards, suids are represented in Greece exclusively by the genus *Sus*. Suid diversity remains always low in the Greek fossil record reaching a maximum of only two species per site (Fig. 1 and Appendix). As a whole, 5 suoid genera and 10 species at least are known from Greece during the last 17 Myr. Geographic affinities of Greek suoids are exclusively Eurasian and most recorded taxa show a wide pan-Eurasian distribution. A list of localities with the most important suoid occurrences is given in the Appendix.

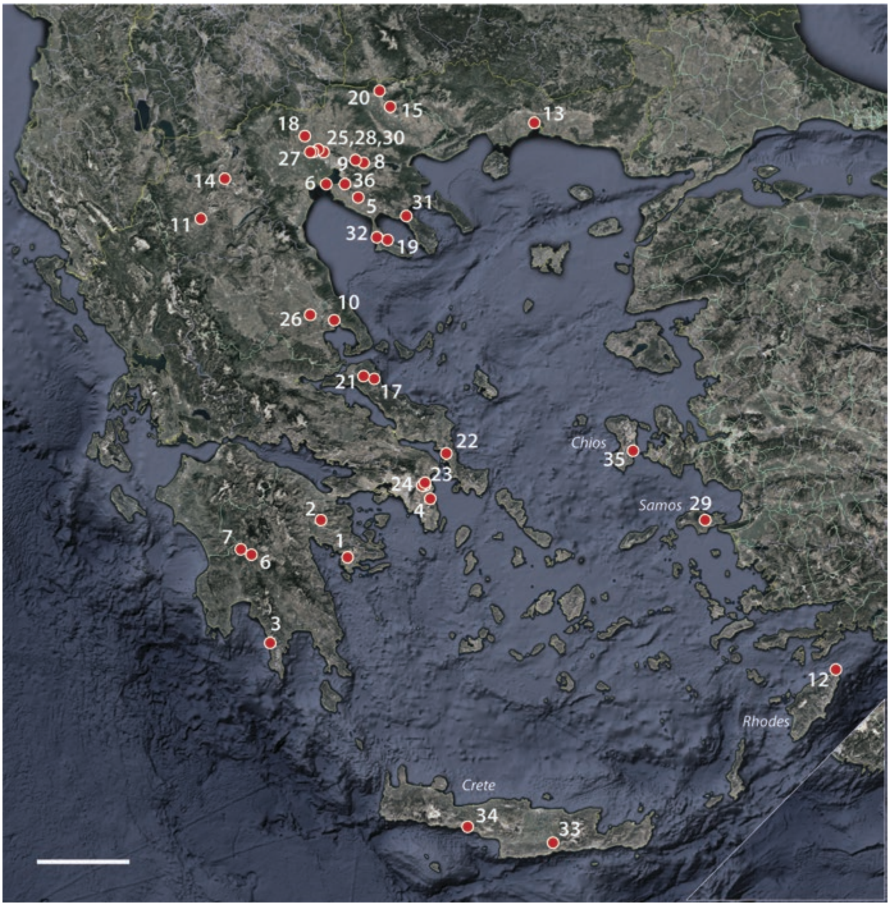

Fig. 1 Map of Greece showing the geographic distribution of the most important localities with suoid fossils. **1**, Franchthi Cave; **2**, Klisoura Cave; **3**, Kalamakia Cave; **4**, Vraona Cave; **5**, Petralona Cave; **6**, Megalopolis; **7**, Kyparíssia localities; **8**, Vassiloudi 1; **9**, Gerakarou 1; **10**, Sesklon lower level; **11**, Milia localities; **12**, Damatria; **13**, Kessani localities; **14**, Kardia; **15**, Maramena; **16**, Samos, various localities; **17**, Achladion; **18**, Dytiko 1; **19**, Kryopigi; **20**, Thermopigi; **21**, Kerassia localities; **22**, Halmyropotamos; **23**, Chomateri; **24**, Pikermi localities; **25**, Ravin X; **26**, Perivolaki; **27**, Prochoma-1; **28**, Vathylakkos localities; **29**, Samos localities; **30**, Ravin de Zouaves-5; **31**, Nikiti-1; **32**, Fourka; **33**, Kastellios K2; **34**, Plakias; **35**, Thymiana; **36**, Antonios. See Appendix for more information. Image exported from Google Earth Pro © 2019, map data from US Dept. of State Geographer, SIO, NOAA, U.S. Navy, NGA, GEBCO, image from Landsat/Copernicus. Scale bar equals 80 km, North faces upward

5 Systematic Paleontology

Suoidea Gray, 1821

Sanitheriidae Simpson, 1945
Sanitherium von Meyer, 1866
(=*Xenochoerus* Zdarsky, 1909)

Type Species *Sanitherium schlaginweiti* von Meyer, 1866, by original designation.

Distribution Early-middle Miocene of Africa, Europe, Turkey, Pakistan, and India. *Sanitherium* sp. is also mentioned from the Oligocene of Pakistan.

Other Taxa Included *S. leobense* (Zdarsky, 1909); *S. jeffreysi* (Forster-Cooper, 1913); *S. africanus* (Stromer, 1926); *S. nadirum* Wilkinson, 1976.

Remarks Pickford (1984) recognized within the family Sanitheriidae both *Diamantohyus* Stromer, 1926, and *Sanitherium* von Meyer, 1866, as distinct genera but van der Made and Hussain (1992) drastically revised the systematics of the group by recognizing a single genus *Sanitherium* with only three valid species (*S. schlaginweiti, S. africanus,* and *S. jeffreysi*). Harris and Liu (2007) follow Pickford in retaining *Diamantohyus* for *D. africanus* and *D. jeffreysi* and recognized *S. leobense* as a valid species. According to Pickford (1984) *Sanitherium* is characterized by a P4 with six subequally developed cusps and wider lower molars than in *Diamantohyus* but van der Made and Hussain (1992) doubt most morphometric differences between the two genera.

Sanitherium schlaginweiti von Meyer, 1866
(= ★*Sanitherium masticum* Paraskevaidis, 1940)

Nomenclatural and Taxonomic History See Pickford (1984), van der Made and Hussain (1992), van der Made (1998).

Type Material Left m2–3 (von Meyer 1866: Pl. 2, figs 9–12).

Type Locality Koshialgarh Punjab, India, middle Miocene.

Age Early-middle Miocene.

Distribution Early-middle Miocene of Austria, Greece, Indo-Pakistan, and possibly East Africa.

Fig. 2 Left lower toothrow AMPG(v)47 of *Sanitherium schlaginweiti* from Thymiana Chios (Orleanian) in lateral (buccal) view. The specimen is a syntype of *Sanitherium masticum*. Scale bar equals 1 cm. Photograph courtesy of S. Roussiakis

Remarks According to van der Made (1998) *S. leobense* from Seegraben, Austria cannot distinguish from *S. schlaginweiti* from Koshialgarh, India, although van der Made and Hussain (1992) stated that premolars of *S. leobense* may have a less complicated structure, which would re-validate the species. Paraskevaidis (1940) described from "Michalos clay-pit" in Chios Island, a site later known as Thymiana, rich sanithere material attributed to the new species *S. masticum* (Fig. 2). *S. masticum* is considered as a junior synonym of *S. leobense* by Pickford (1984), whereas van der Made (1998) suggested both taxa as synonymous of *S. schlaginweiti*. De Bonis et al. (1997) described more sanithere material from the MN5 Thymiana B fauna in Chios. They confirmed close similarity between Chios and the Leoben taxa, and they accepted both samples as better attributable to *S. schlaginweiti*. Koufos (2007) provided new material of *S. schlaginweiti* from the MN4/5 fauna of Antonios in Chalkidiki Peninsula.

Suidae Gray, 1821

Listriodontinae [Authorship debated; see van der Made 1996; Pickford and Morales 2003].

Listriodon von Meyer, 1846
(=*Bunolistriodon* Arambourg, 1963)

Type Species *Listriodon splendens* von Meyer, 1846, by original designation.

Distribution Early to late Miocene of Europe, Africa, and Asia.

Other Taxa Included *L. lockharti* (Pomel, 1848); *L. pentapotamiae* (Falconer, 1868); *L. latidens* (Biedermann, 1873); *L. affinis* (Pilgrim, 1908); *L. guptai* (Pilgrim, 1926); *L. jeanneli* (Arambourg, 1933); *L. intermedius* Liu and Li, 1963; *L. akatikubas* (Wilkinson, 1976); *L. anchidens* van der Made, 1996; *L. meidamon* Fortelius, van der Made and Bernor, 1996; *L. bartulensis* Pickford, 2001; *L. retamaensis* Pickford and Morales, 2003.

Remarks Pickford and Morales (2003) suggested *Bunolitriodon* Arambourg, 1963 (sensu van der Made 1996a), as a junior synonym of *Listriodon* von Meyer, 1846. Both taxa are thoroughly discussed in van der Made (1996a). They represent bunodont to sublophodont suids with strong, laterally expanded processes above the canines, decreasing bunodonty and increasing postcranial robusticity in later forms, some of them additionally characterized by high crowned canines curved outward and upward (van der Made 1996a; Harris and Liu 2007; Pickford and Morales 2003; Orliac 2009).

Listriodon lockharti (Pomel, 1848)

Nomenclatural and Taxonomic History *Sus lockharti* in Pomel 1848 (new species); *Bunolistriodon lockharti* in Arambourg 1963 (new combination); *Listriodon lockhardi* in Stehlin 1899/1900 (new combination); see also Pickford and Morales (2003).

Type Material Museum National d'Histoire Naturelle, Paris MNHN CHE 30, mandible (lectotype selected by van der Made 1996a).

Type Locality Chevilly, France, lower Miocene MN4.

Age Early Miocene, MN4.

Distribution Early-middle Miocene of Europe and Saudi Arabia.

Remarks According to van der Made (1996a) and Pickford and Morales (2003) the species is characterized by large size, increased bunodonty, mesiodistally long incisors with the first one having one or three lobes, and strongly curved upper canines. The species has a rather good record in Western Europe (especially in France) but in Greece is so far known with certainty only from the Orleanian (MN4/5) fauna of Antonios, Chalkidiki peninsula (Koufos 2007). An upper third molar from Thymiana in Chios Island is also referred to as *Listriodon* (n. sp.?) *lockharti* var. *michali* by Paraskevaidis (1940). Van der Made (1996a) suggested however that the molar size is too small for this species and, although the absence of incisors and canines makes any assignment difficult, van der Made (2020) implies that the Chios species may turn out to be a senior synonym of *Eurolistriodon adelli* Pickford and Moyà Solà, 1995.

Suinae Gray, 1821

Propotamochoerus Pilgrim, 1925 (= *Korynochoerus* Schmidt-Kittler, 1971)

Type Species *Sus hysudricus* Stehlin, 1899/1900, by original designation.

Distribution Late middle Miocene to late Pliocene of Europe, Turkey, India, Myanmar China; Late Miocene of Africa.

Other Included Taxa *P. palaeochoerus* (Kaup, 1833); *P. provincialis* (Gervais, 1859); *P. hyotheroides* (Schlosser, 1903); *P. wui* van der Made and Han, 1994; *Propotamochoerus* sp. nov.

Remarks According to van der Made et al. (1999) *Propotamochoerus* represents small dicoryphochoerin suids with relatively large canines. Their cranium shows a relatively long face with square snout in cross section, strongly expanded laterally zygomatic arches and large supra-canine flanges (Pickford 1988; Harris and Liu 2007). The dentition is characterized by a lower third molar with simple talonid and a predominantly tall protoconid on p4. *Propotamochoerus* possibly arose from an Asian hyotherin suid at about 11 Ma ago and dispersed toward SW Asia and Europe during the Late Miocene (Pickford 1988; Fortelius et al. 1996).

Propotamochoerus palaeochoerus (Kaup, 1833)

Nomenclatural and Taxonomic History *Sus palaeochoerus* in Kaup 1833 (new species); *Korynochoerus palaeochoerus* in Schmidt-Kittler (1971) (new combination); *Propotamochoerus palaeochoerus* in Pickford (1988) and van der Made et al. (1992) (new combination).

Type Material Hessisches Landesmuseum, Darmstadt, HLD Din 3, right mandible with p3–m3 (lectotype selected by Hünermann 1968: Pl. 1, fig. 1).

Type Locality Eppelsheim, Germany, Upper Miocene.

Age Early late Miocene, early Vallesian (MN9).

Distribution Late middle-late Miocene (latest Aragonian–Vallesian) of Europe.

Remarks *P. palaeochoerus* is the oldest representative of its genus known from several west European faunas ranging from the latest Aragonian (MN8; late Astaracian) to the late Vallesian (MN10). The species is extensively discussed in Schmidt-Kittler (1971) and later commented by Pickford (1988), van der Made and Moyà-Solà (1989), and Fortelius et al. (1996). Its eastern most known record comes from Ukraine (van der Made et al. 1999). It is about the size of a wild boar, characterized by a concave cranial profile and elevated occiput, inflated zugomatic arches, large upper third incisor, proportionally small third molar, and strong metaconid on the lower fourth premolar (Schmidt-Kittler 1971; van der Made and Moyà-Solà 1989; van der Made et al. 1999). van der Made (1996b) refers a lower second milk molar from the likely early Vallesian (MN9) fauna of Plakias, Crete (de Bruijn et al. 2012), to as cf. *Propotamochoerus palaeochoerus*, whereas Lazaridis (2015) reports a lower m2–m3 and an astragalus from the late Vallesian mammal assemblage of Fourka sand-pits (Chalkidiki Peninsula) to *P.* cf. *palaeochoerus*. Hellmund (1995) also refers a partial cranium and some isolated teeth and toothrows from the latest Miocene (end of MN13) fauna of Maramena, Serres basin, to *P. palaeochoerus* but Geraads et al. (2008) doubt this attribution and van der Made et al. (1999) suggest it represents a different SE European taxon.

★*Propotamochoerus* sp. nov.

Nomenclatural and Taxonomic History The new species has been originally described by Lazaridis in his PhD thesis (2015) but is still pending for a formal publication (under ICZN rules) and, therefore, it is referred here to as *Propotamochoerus* sp. nov. (Lazaridis et al. 2021 under review)

Age Late Miocene, Turolian (MN11–13).

Distribution Late Miocene (Vallesian–Turolian) of Greece, Northern Macedonia, Bulgaria, Turkey.

Remarks Turolian propotamochoerid samples recorded in SE Europe, especially around the Aegean Sea, and attributed to several species (e.g., *P. hysudricus* in Bonis and Bouvrain 1996; *P. palaeochoerus* in Hellmund 1995; *P. hyotherioides* in Thenius 1955, and Fortelius et al. 1996) are part of a long lasting discussion (e.g., van der Made and Moyà-Solà 1989; Fortelius et al. 1996; van der Made et al. 1999; Geraads et al. 2008). Geraads et al. (2008) suggested that all these records likely represent a new *Propotamochoerus* species which has to be formally established on the basis of adequate cranial material. Lazaridis (2015) based on a fairly complete skull from Kryopigi, Chalkidiki Peninsula, revised previous data and proposed a new, though still unpublished, species, characterized by medium size, converging but not merging temporal lines, presence of diastemata between the first two premolars and the canine, wide third premolars, and comparatively large lower third molars with a hexaconid. The earliest occurrence of *Propotamochoerus* sp. nov. in Greece is in Ravin des Zouaves 5 (MN11; Fig. 3) and the latest likely in Maramena (MN13/14) (van der Made et al. 1999; Pickford 2013; Lazaridis 2015; Lazaridis et al. 2021 under review).

Hippopotamodon Lydekker, 1877
(= *Microstonyx* Pilgrim, 1926 = *Dicoryphochoerus* Pilgrim, 1926 = *Eumaiochoerus* Hürzeler, 1982)

Fig. 3 Lower mandible LGPUT RZO-330 of *Propotamochoerus* sp. nov. from Ravin des Zouaves 5, Axios valley (early Turolian) in occlusal view. The specimen has been illustrated as *Propotamochoerus* cf. *hysudricus* in Bonis and Bouvrain (1996: fig. 9). Scale bar equals 5 cm

Type Species *Hippopotamodon sivalense* Lydekker, 1877, by original designation.

Distribution Late Miocene of Europe; late Miocene to Early Pleistocene of Asia.

Other Included Taxa *H. antiquus* (Kaup, 1833); *H. major* (Gervais, 1850); *H. ultimus* (Han, 1987); *H. pilgrimi* (Pickford, 1988); *H. etruscus* (Michelotti, 1861).

Remarks Giant European Late Miocene dicoryphochoerin suins referred to the genus *Microstonyx* Pilgrim, 1926, and their Asian counterparts, referred to the genus *Hippopotamodon* Lydekker, 1877, build a still unresolved taxonomic group extensively discussed over the years (e.g., Pickford 1988, 2015; van der Made et al. 1992, 2013; van der Made and Hussain 1989; Fortelius et al. 1996; Liu et al. 2004). Here we follow the most recent review by Pickford (2015) in recognizing synonymy between these two genera. *Hippopotamodon* is characterized by large to very large size, the male canines vary from relatively large and flaring (in *H. sivalense*) to reduced, usually associated by prominent supra-canine flanges, the snout is elongated, the braincase is broad and flat with elevated occiput, and the zygomatic arches are strongly inflated.

Hippopotamodon major (Gervais, 1848–1852)
(= ★*Sus erymanthius* Roth and Wagner, 1854)

Nomenclatural and Taxonomic History See Trofimov (1954). There is no current consensus among scholars about the species context. Here we follow Liu et al. (2004) in recognizing *Sus erymanthius* Roth and Wagner, 1854 (type locality

Fig. 4 Male cranium of *Hippopotamodon major* AMNH. Samos MTLA-537 from Mytilinii 1A, Samos (middle Turolian) in dorsal view. The specimen is illustrated as *Microstonyx major* in Sylvestrou and Kostopoulos (2009: Pl. 1). Scale bar equals 5 cm

Pikermi, Greece), as a junior synonym of *Sus major* Gervais, 1848 (but see also van der Made et al. 2013; Pickford 2015).

Type Material Upper left third molar from Cucuron, France, illustrated by Gervais (1850: Pl. 12, fig. 2; *fide* Pickford 2015).

Type Locality Cucuron, France, upper Miocene.

Age Late Miocene, Turolian.

Distribution Late Miocene (latest Vallesian to latest Turolian; end MN10–endMN13) of Eurasia.

Remarks Liu et al. (2004) analysis of several *Microstonyx* samples across Eurasia revealed no temporal or spatial pattern on observed morphometrical variability, and thus the species *M. major* is proposed as polymorphic, absorbing past distinctions at species or subspecies level. *M. major* is characterized by smaller size, longer snout, deep infraorbital incisure, weaker canines, tendency of losing the first premolars, and longer diastemata, compared to the isochronous Indian taxon (Fig. 4). *M. major* is by far the most common among Neogene suins in Greece, recorded in almost every Turolian mammal assemblage. Greek material is discussed in detail by Bonis and Bouvrain (1996), Liu et al. (2004), and Sylvestrou and Kostopoulos (2006, 2009). Its earliest known local record comes from the latest Vallesian fauna of Nikiti-1, Chalkidiki Peninsula, and the latest from Dytiko-1, Axios Valley. According to Fortelius et al. (1996) and Kostopoulos et al. (2001), *H. antiquus* record from Sophades (Thenius 1950) needs further documentation.

Sus Linnaeus, 1758

Type Species *Sus scrofa* Linnaeus, 1758, by original designation.

Distribution Pliocene to Pleistocene of Eurasia.

Other Included Taxa *S. arvernensis* Croizet and Jobert, 1828; *S. strozzii* Forsyth-Major, 1881*; S. falconeri* Lydekker, 1884; *S. macrognathus* Dubois, 1908; *S. brachygnathus* Dubois, 1908 (=? *S. sangirensis* von Koenigswald, 1963); *S. lydekkeri* Zdansky, 1928; *S. bijiashanensis* Han et al., 1975 (=? *S. liuchengensis* Han, 1987); *S. australis* Han, 1987 (=?*S. peii* Han, 1987); *S. xiaozhu* Han, 1987, *Sus sondaari* van der Made, 1999; for extant taxa see Groves and Grubb (2011).

Remarks *Sus* likely emerged at the end of Miocene in Asia and by the Late Pliocene, had colonized most of Eurasia (see Franz et al. 2016 for a brief evolutionary history). Depending mostly on the type of male lower canine, *Sus* species are divided into two groups: the "verrucosic" and the "scrofic" one, already separated each other during the Pliocene. Pickford (2012) ascribes Eurasian taxa of the "verrucosic" group to the genus *Dasychoerus* Gray, 1873, but this taxonomic opinion has been challenged by Cherin et al. (2018) and it is not widely adopted (e.g., Liu et al. 2017; Iannucci et al. 2020a). During the Middle Pleistocene *S. scrofa* replaced most other Eurasian *Sus* species, becoming the only suin of European Mid-Late Pleistocene continental faunas (Franz et al. 2016).

Sus arvernensis Croizet and Jobert, 1828
(= *Sus minor* Gervais, 1848)

Nomenclatural and Taxonomic History *Aper arvernensis* in Croizet and Jobert 1828 (new species); *Sus provincialis* var. *minor* in Depéret 1890 (new subspecies); *Sus minor* in Azzaroli 1954 (new combination); *Sus arvernensis* in Gervais, 1859 (new combination).

Type Material MNHN-no cat. No, juvenile mandible and maxilla (holotype) illustrated by Croizet and Jobert (1828: Pl. 13, figs. 3–5).

Type Locality Les Étouaires, Perrier, France, Pliocene.

Age Early Villafranchian (MN16).

Distribution Ruscinian to middle Villafranchian (MN14–MN17) of Europe.

Remarks The smaller among Plio-Pleistocene suins of continental Europe characterized by proportionally long premolar row, simple third molars, and low anterior and posterior ends on the lower third premolar. The Greek record of the species is rather poor restricted in a few isolated teeth and partial toothrows from the Ruscinian faunas of Kessani 1,2, and Megalo Emvolo, as well as from the early Villafranchian faunas of Milia and the lower levels of Sesklo (Koufos et al. 1991; Syrides et al. 1997; Guérin and Tsoukala 2013; Athanassiou 2018).

Sus strozzii Forsyth-Major, 1881

Nomenclatural and Taxonomic History See Azzaroli (1954).

Type Material Museum of Geology and Paleontology of Florence, IGF 424, adult male skull, mandible, and partial skeleton (lectotype selected by Azzaroli, 1954).

Type Locality Upper Val d'Arno, Italy (unknown fossil horizon), Plio-Pleistocene.

Age Late Pliocene–Early Pleistocene (MNQ17–19).

Distribution Late Pliocene (late early Villafranchian, MN16b) to Middle Pleistocene of Southern Europe, Azov Sea region, Azerbaijan, and Israel.

Remarks Cherin et al. (2018) recently rediscussed the diagnostic features of this large sized suin, characterized basically by a narrow cranium on the parietal region, and smoothly undulating dorsally, inflated and broad in the middle zygomatic arches, long and rugose male supra-canine flanges, verrucosic lower canines, and elongated lower third molars with a single cuspid between the first and second lobe. *Sus strozzii* may appear at the SE of Greece (Damatria, Rhodes Island) as early as late early Villafranchian (van der Made 1988). It possibly occurs at Sesklo during MN17, though it is characteristically missing from other contemporaneous Greek assemblages, and it certainly occurs during the late Villafranchian in Mygdonia Basin (sites Gerakarou, Fig. 5a and Vassiloudi) (Koufos 1986; Kostopoulos and Athanassiou 2005). The taxon seems to disappear temporarily from Europe during late Villafranchian and re-dispersed at the beginning of Epivillafranchian, ca. 1.2 Ma ago (Cherin et al. 2020).

Sus scrofa Linnaeus, 1758

Nomenclatural and Taxonomic History Extant; see Groves and Grubb (2011).

Distribution Middle Pleistocene to Recent; originally Eurasian and North African.

Remarks *S. scrofa* distinguishes by a fairly long snout, rather shallow preorbital fossa, discontinuous postorbital bar, short premolar row, relatively long third upper molars, elevated mesial and distal end of the second and third upper premolars, and lower male canines of "scrofic" type (van der Made and Moyà-Solà 1989; Groves and Grubb 2011). Already present in Atapuerca TD6, Spain (~0.9 Ma; van der Made 1988), early members of *Sus scrofa,* commonly referred to as *S. s. priscus*, expanded across Europe at the first part of Middle Pleistocene, as evidenced by data from Gombaszög (Slovakia), Dorn Dürkheim 2, Voigtstedt and Mosbach (Germany), Pakefield and West Runton (Britain), and likely Kyparissia 1, 4 in Megalopolis

Fig. 5 Selected specimens of *Sus* from Greece. (**a**) Partial cranium LGPUT GER-51 of *Sus strozzii* from Gerakarou, Mygdonia Basin (late Villafranchian) in lateral view, originally described by Koufos (1986). (**b**) Left mandible LGPUT PEC of *Sus scrofa* from Petralona Cave, Chalkidiki Peninsula (Middle Pleistocene) in occlusal view, originally described by Tsoukala (1989). Scale bars equal 5 cm

Basin, Greece (Athanassiou et al. 2018; Cherin et al. 2020). Based on some teeth and postcranials, again from the Middle Pleistocene of Megalopolis Basin, Melentis (1965) was likely the first to report the species in Greece. Tsoukala and Guérin (2016) also described primitive *Sus scrofa* from the Middle Pleistocene of Petralona Cave (Fig. 5b), whereas the species appears to be quite common in Late Pleistocene faunal assemblages discovered in several cave deposits (Tsoukala 1992 and Appendix).

Suinae Insertae Sedis

“*Sus*” *provincialis* (de Blainville, 1847)

Nomenclatural and Taxonomic History *Sus provincialis* de Blainville, 1847 (new species); for a full history of the species see Pickford (2013).

Type Material University of Montpellier II UM SM 460, right M3 (lectotype selected by Pickford 2013: fig.1).

Type Locality Montpellier France, Lower Pliocene.

Age Early Pliocene, Ruscinian.

Distribution Latest Miocene to early Pliocene of Europe.

Remarks Pickford (2013) recently revised the suin species originally known from the Pliocene marine sands at Montpellier, suggesting that authorship has also to be transferred from Gervais (1859) to Blainville (1847), who first illustrated and named the taxon. The species is commonly referred to as *Propotamochoerus* or to as "*Propotamochoerus,"* is part of a long discussion (e.g., Fortelius et al. 1996; van der Made et al. 1999; Geraads et al. 2008) but Pickford (2013) avoids a direct reference to a particular genus as he considers that the type material does not have enough diagnostic characters. Dental size places "*Sus" provincialis* between *S. arvernensis* and *S. strozzii*. A female cranium from the Lower Pliocene coal deposits of Kardia, Ptolemais, is so far the only evidence of this species in Greece (van der Made and Moyà-Solà 1989), although Iannucci et al. (2020b) recently questioned this affiliation.

6 Conclusions

Two suoid families, 5 genera and 10 species have been so far reported from the Greek fossil record, suggesting a diachronously much lower diversity than other artiodactyls or ungulates, and a rather even temporal distribution of one to two species per time interval. Among the recorded taxa, two species have been originally named based on Greek material (*Sanitherium masticum* Paraskevaidis, 1940 and *Sus erymanthius* Roth and Wagner, 1854); both however have been later proved or suggested as junior synonyms of other taxa. The longer lasting taxon appears to be *Hippopotamodon major*, known from the latest Vallesian to the latest Turolian, hence for about 3.5 Myr.

Known major faunal turnovers are fairly well evidenced on the Greek suoid record in accordance with other European data (e.g., Fortelius et al. 1996; Cherin et al. 2020), though the Greek Astaracian-early Vallesian data are extremely poor prohibiting certain conclusions about the middle-late Miocene transition. Listriodontines and sanitheres predominate during the early Aragonian (Orleanian). They will be replaced toward the Vallesian by dicoryphochoerin suids of the genus *Propotamochoerus*. *Hippopotamodon antiquus* is so far unknown from Greece but it is present nearby (e.g., Geraads et al. 2005; Kostopoulos and Sen 2016) suggesting its absence from Greece as rather accidental. *Hippopotamodon major* (= *Microstonyx major*) enters in the local record at the end of Vallesian, at about 8.7–9.0 ma ago, followed by a new SE European species of *Propotamochoerus*, and marking quite sharply the rise of the Pikermian faunas in the area. They both went extinct during or soon after the Messinian Salinity Crisis, replaced by early members of the genus *Sus*. The Mid-Pleistocene transition will finally allow *Sus scrofa* entering the local record, leading to the extinction of verrucosic taxa such as *Sus strozzii*.

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Appendix

List of fossil localities with occurrences of suoids in Greece. Locality numbers refer to the collection numbers of the PaleoBiology Database (PBDB)

Localities$^{\text{PBDB No}}$	Age (MN, MNQ)	Taxa	Refs
Franchthi Cave^{182709}	latest Pleistocene	*Sus scrofa*	1
Klisoura Cave^{184243}	latest Pleistocene	*Sus scrofa*	2
Kalamakia Cave^{184245}	latest Pleistocene	*Sus scrofa*	3
Vraona Cave^{183130}	latest Pleistocene	*Sus scrofa*	4
Petralona Cave^{183123}	Middle Pleistocene	*Sus scrofa priscus*	5
Megalopolis	Middle Pleistocene	*Sus scrofa*	6
Kyparissia 1, 4$^{194472,\ 194,475}$	Middle Pleistocene	*Sus scrofa*	7
Vassiloudi 1^{34651}	Early Pleistocene (MNQ18)	*Sus strozzii*	8
Gerakarou 1^{34617}	Early Pleistocene (MNQ18)	*Sus strozzii*	9
Sesklon lower level^{205043}	Late Pliocene (MN16)	*Sus arvernensis*	10
Milia^{185859}	Late Pliocene (MN16)	*Sus arvernensis arvernensis*	11
Damatria^{34591}	Late Pliocene (MN16)	*Sus strozzii*	12
Megalo Emvolon^{36579}	Early Pliocene (MN15)	*Sus arvernensis*	13
Kessani 1^{205296}, 2^{205297}	Early Pliocene (MN14)	*Sus arvernensis*	14
Kardia^{204752}	Early Pliocene (MN14–15)	*"Sus" provincialis*	15
Maramena^{32189}	latest Miocene/earliest Pliocene (MN13/14)	*Propotamochoerus* sp. nov.	16, a
Samos, unknown level: NHMW collection^{182751} NHML collection^{202120} BSPM collection^{207137} IGPM collection^{207193}	Late Miocene (MN11–13)	*Hippopotamodon major* *Propotamochoerus* sp. nov.	17, a
Achladion^{207133}	Late Miocene (MN11–13)	*Propotamochoerus?* sp. nov.	18, a
Dytiko-1^{32374}	Late Miocene (MN13)	*Hippopotamodon major*	19
Kryopigi^{157582}	Late Miocene (MN12–13)	*Propotamochoerus* sp. nov. *Hippopotamodon major*	20, a
Samos Q5^{95690}	Late Miocene (MN12/13)	*Hippopotamodon major*	17
Thermopigi^{73553}	Late Miocene (MN12)	*Hippopotamodon major* *Propotamochoerus* sp. nov.	21, a
Kerassia-1^{195432}	Late Miocene (MN12)	*Hippopotamodon major*	22

(continued)

Localities$^{\text{PBDB No}}$	Age (MN, MNQ)	Taxa	Refs
Halmyropotamos^{202213}	Late Miocene (MN12)	*Hippopotamodon major*	23
Chomateri^{195562}	Late Miocene (MN12)	*Hippopotamodon major*	18
Pikermi Valley-3^{202631}	Late Miocene (MN12)	*Hippopotamodon major*	24
Pikermi Valley-1^{202630}	Late Miocene (MN12)	*Hippopotamodon major*	24
Pikermi^{182754}	Late Miocene (MN12)	*Hippopotamodon major*	25
Ravin X^{182745}	Late Miocene (MN12)	*Hippopotamodon major*	19, 26
Perivolaki^{194879}	Late Miocene (MN12)	*Hippopotamodon major*	27
Prochoma-1^{202222}	Late Miocene (MN12)	*Hippopotamodon major*	19
Vathylakkos-3^{182750}	Late Miocene (MN12)	*Hippopotamodon major*	19
Vathylakkos-2^{202703}	Late Miocene (MN12)	*Hippopotamodon major*	19
Samos Mytilinii 1A^{202215} (MTLA)	Late Miocene (MN12)	*Hippopotamodon major*	17
Samos Q1^{95691}	Late Miocene (MN12)	*Hippopotamodon major*	17
Samos Q4^{95689}	Late Miocene (MN12)	*Hippopotamodon major*	17
Mytilinii-4	Late Miocene (MN11/12)	*Hippopotamodon* sp.	17
Ravin de Zouaves-5^{195489}	Late Miocene (MN11)	*Hippopotamodon major* *Propotamochoerus* sp. nov.	19, 20, a
Nikiti-1^{202729}	Late Miocene (MN10)	*Hippopotamodon major*	28
Fourka sand pits	Late Miocene (?MN10)	*Propotamochoerus* cf. *palaeochoerus*	20
Kastellios K2	Late Miocene (MN10)	*Taucanamo?*	29
Plakias	Late Miocene (MN9)	*Propotamochoerus* cf. *palaeochoerus*	29
Thymiana^{182752}	early Middle miocene (MN5)	*Listriodon* sp. *Sanitherium schlaginweiti*	30 31
Antonios^{73861}	early Middle miocene (MN5)	*Listriodon lockharti* *Sanitherium schlaginweiti*	32

MN, Mammal Neogene

[1]Stiner and Munro (2011), [2]Starkovich (2012), [3]Harvati et al. (2013), [4]Symeonidis et al. (1980), [5]Tsoukala and Guérin (2016), [6]Melentis (1965), [7]Athanassiou et al. (2018), [8]Kostopoulos and Athanassiou (2005), [9]Koufos (1986), [10]Athanassiou (2018), [11]Guérin and Tsoukala (2013), [12]Van der Made (1988), [13]Steffens et al. (1979), [14]Syrides et al. (1997), [15]Van der Made and Moyà-Solà (1989), [16]Hellmund (1995), [17]Sylvestrou and Kostopoulos (2009), [18]Koufos (2006), [19]Bonis and Bouvrain (1996), [20]Lazaridis (2015), [21]Geraads et al. (2007), [22]Theodorou et al. (2003), [23]Melentis (1969), [24]Roussiakis et al. (2014), [25]Gaudry (1862-65), [26]Arambourg and Piveteau (1929), [27]Sylvestrou and Kostopoulos (2006), [28]Kostopoulos (1994), [29]Van der Made (1996b), [30]Paraskevaidis (1940), [31]de Bonis et al. (1997), [32]Koufos (2007)

[a]Lazaridis et al. (2021 under review)

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