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Abstract

Sus strozzii is the only species of Suinae occurring in the first part of Early Pleistocene in Europe and western Asia. It is characterized by a large body size and several morphological similarities with extinct and extant pigs from Island South East Asia (ISEA), such as the Javan Warty Pig S. verrucosus. In this study, a new mandible of S. strozzii from the Early Pleistocene of Pantalla (central Italy) is described and the diagnosis of the species is emended. Based on 52 craniomandibular and dental morphological characters, the first phylogenetic analysis of both living and fossil Eurasian and African Suinae is carried out to reconstruct their relationships. Our results are in agreement with the literature based on molecular and/or morphological analyses. The late Miocene Microstonyx is the first taxon to branch off the monophyletic Suinae clade. The separation between the African (Kolpochoerus/Hylochoerus and Metridiochoerus/Phacochoerus) and the Eurasian (Sus) clades occurred early, probably even in the late Miocene. The inclusion of Potamochoerus in the latter group is questionable, being probably due to the retaining of similar plesiomorphic characters in this African pig and in Sus. The Wild Boar S. scrofa and the Early–Middle Pleistocene S. lydekkeri are the species of Sus that display the most numerous plesiomorphic character states. They are followed by the monophyletic group of suines that show verrucosic lower canines, which includes the Pliocene S. arvernensis, S. strozzii, and the extinct and extant verrucosic pigs from ISEA.

Corresponding Author	Marco Cherin
Corresponding Author's Institution	Dipartimento di Fisica e Geologia, Università degli Studi di Perugia
Order of Authors	Marco Cherin, Leonardo Sorbelli, Marco Crotti, Dawid Iurino, Raffaele Sardella, Antoine Souron

Suggested reviewers	Dimitris Kostopoulos, Jan Van der Made, Raymond Bernor, Salvador Moya-Sola, Maëva Orliac

1 New material of *Sus strozzii* (Suidae, Mammalia) from the Early Pleistocene of Italy

2 and a phylogenetic analysis of suines

3

4 Marco Cherin[a,b,*], Leonardo Sorbelli[c], Marco Crotti[d], Dawid A. Iurino[b,e], Raffaele Sardella[b,e],

5 Antoine Souron[f]

6

7 [a] Dipartimento di Fisica e Geologia, Università degli Studi di Perugia, Via A. Pascoli, I-06123 Perugia, Italy

8 [b] PaleoFactory, Sapienza Università di Roma, Piazzale A. Moro 5, I-00185 Roma, Italy

9 [c] Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy

10 [d] Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow, UK

11 [e] Dipartimento di Scienze della Terra, Sapienza Università di Roma, Piazzale A. Moro 5, I-00185 Roma, Italy

12 [f] De la Préhistoire à l'Actuel: Culture, Environnement et Anthropologie (PACEA), UMR 5199 CNRS, Université de

13   Bordeaux, Bâtiment B18, Allée Geoffroy Saint Hilaire, CS 50023, 33615 Pessac, France

14 * Corresponding author. Tel.: +39 075 5852626. *E-mail address:* marco.cherin@unipg.it (M. Cherin)

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17 **ABSTRACT**

18

19 *Sus strozzii* is the only species of Suinae occurring in the first part of Early Pleistocene in Europe

20 and western Asia. It is characterized by a large body size and several morphological similarities

21 with extinct and extant pigs from Island South East Asia (ISEA), such as the Javan Warty Pig *S.*

22 *verrucosus*. In this study, a new mandible of *S. strozzii* from the Early Pleistocene of Pantalla

23 (central Italy) is described and the diagnosis of the species is emended. Based on 52

24 craniomandibular and dental morphological characters, the first phylogenetic analysis of both living

25 and fossil Eurasian and African Suinae is carried out to reconstruct their relationships. Our results

26 are in agreement with the literature based on molecular and/or morphological analyses. The late

27 Miocene *Microstonyx* is the first taxon to branch off the monophyletic Suinae clade. The separation

between the African (*Kolpochoerus*/*Hylochoerus* and *Metridiochoerus*/*Phacochoerus*) and the

Eurasian (*Sus*) clades occurred early, probably even in the late Miocene. The inclusion of

Potamochoerus in the latter group is questionable, being probably due to the retaining of similar

plesiomorphic characters in this African pig and in *Sus*. The Wild Boar *S. scrofa* and the Early–

Middle Pleistocene *S. lydekkeri* are the species of *Sus* that display the most numerous plesiomorphic

character states. They are followed by the monophyletic group of suines that show verrucosic lower

canines, which includes the Pliocene *S. arvernensis*, *S. strozzii*, and the extinct and extant

verrucosic pigs from ISEA.

1. Introduction

The family Suidae includes the pigs and their relatives, that is, artiodactylan ungulates

characterized by a robust and squat body, relatively short legs, large heads, and at least in extant

forms, short neurocranium and elongated splanchnocranium forming a tubular snout (Groves and

Grubb, 1993). Suids are part of the superfamily Suoidea together with the New World peccaries

Tayassuidae. The close relationship between Suidae and Tayassuidae is well documented on both

molecular (Irwin and Arnason, 1994; Randi et al., 1996) and morphological grounds (Gentry and

Hooker, 1988; Boisserie et al., 2005; Orliac et al., 2010a).

The phylogenetic status of the Suoidea has changed during the last decades. Classically, they

were considered as sister group of the Hippopotamidae, forming with them the suborder Suiformes.

However, molecular data questioned the monophyly of this group, considering the Hippopotamidae

as closer to the Cetacea and the Suoidea at the root of the whole clade Cetartiodactyla (Irwin et al.,

1991; Randi et al., 1996; Gatesy, 1997; Montgelard et al., 1997; Nikaido et al., 1999; Matthee et al.,

2001; Marcot, 2007; Agnarson and May-Collado, 2008). Conversely, alternative phylogenetic

reconstructions based on morphological data consistently place the Suoidea as the sister group of hippopotamids (Theodor and Foss, 2005; Thewissen et al., 2007). Even the origin of the Suoidea is the subject of controversy (Ducrocq, 1994; Ducrocq et al., 1998; Liu, 2001, 2003; Harris and Liu, 2007; Orliac et al., 2010a; Gongora et al., 2011; Frantz et al., 2016). Molecular evidence suggests that the first common ancestor of Suidae and Tayassuidae lived in a timespan close to the Oligocene-Eocene boundary (39.69–34.50 Ma) (Gongora et al., 2011).

Although wild and domestic pigs were introduced in the Americas and Oceania by humans, the original distribution of extant Suidae is restricted to the Old World (Eurasia and Africa), and the same goes for their extinct relatives. Thanks to its richness, the suid fossil record has been used in these areas as biostratigraphic tools for decades (e.g. Pliocene–Pleistocene African suids; White and Harris, 1977; Cooke, 1978a). At the origin of the ecological success of this family is the capability to adapt to different kind of environments. Today it is possible to find pigs in a wide range of habitats, from the tropical forests of Southeast Asia and Africa to the cold steppes of northern Europe and the open grasslands of Africa. Currently, the family is composed by a minimum of five genera and 17 species (Frantz et al., 2016). These were traditionally divided into three subfamilies Babyrousinae, Phacochoerinae, and Suinae (Groves and Grubb, 1993), but are today grouped in a single, widely-accepted living subfamily, the Suinae (Grubb, 2005; Harris and Liu, 2007; see Frantz et al., 2016 for the enigmatic phylogenetic position of *Babyrousa*). However, the modern diversity of Suidae is much lower than in the past. During the Neogene and Quaternary, the Suidae diversified into over 30 genera, representing several subfamilies (Pickford, 1993; Harris and Liu, 2007). Even if the earliest sporadic records of Suoidea in the Old World – with the radiation of at least three different lineages, Sanitheriidae, Palaeochoeridae, and hyotheriine Suidae (Orliac et al., 2010b) – are from the middle Oligocene, the first diversification and dispersal of these animals in Eurasia and Africa start only in the first stages of the Miocene (Frantz et al., 2016). About 15 Ma, the suids had spread in the whole Old World with at least four subfamilies, Listriodontinae, Cainochoerinae, Hyotheriinae, and Tetraconodontinae (Orliac et al., 2010a; Frantz et al., 2016),

80   showing a large spectrum of adaptive features. The most successful suid group, the Suinae, appears

81   in the fossil record around 10 Ma and expands rapidly in the Old World to the detriment of the

82   above subfamilies, which gradually disappeared from the Planet (Van der Made et al., 2006;

83   Geraads et al., 2008; Orliac et al., 2010a; Frantz et al., 2016). Shortly after the Miocene–Pliocene

84   boundary, almost all the non-Suinae subfamilies went extinct in Eurasia and Africa, while the

85   Suinae differentiated and spread out (Gongora et al., 2011; Pickford, 2012; Haile-Selassie and

86   Simpson, 2013; Frantz et al., 2016). Besides the Suinae, only the Tetraconodontinae occurred in

87   Africa and Eurasia during the Pliocene and the beginning of Pleistocene (Van der Made, 1998;

88   White and Suwa, 2004).

89   The evolutionary history of African suids has been strongly debated for decades. The centre

90   of origin of the African lineages is commonly placed in Eurasia (Pickford, 2012), but recent

91   molecular analysis by Gongora et al. (2011) suggests that the African suids form a monophyletic

92   group to the exclusion of Eurasian suids.

93   The African Miocene suid record is rich and diverse, including more than 20 species

94   belonging to six subfamilies (Kubanochoerinae, Listriodontinae, Tetraconodontinae,

95   Namachoerinae, Cainochoerinae, and Schizochoerinae) (Bishop, 2010), but the detailed description

96   of these forms is out of the scope of this article. On the other hand, three major groups of Suinae are

97   recognized in Africa from the Pliocene to Present (White and Harris, 1977; Harris and White,

98   1979). The genera *Kolpochoerus* and *Hylochoerus* form the first group. *Kolpochoerus* is a well-

99   documented genus, but still subject of taxinomic (see Section 2 for the use of this term) and

100   phylogenetic debates. Currently, at least ten species are recognized: *K. afarensis, K. cookei, K.*

101   *deheinzelini, K. limnetes* (*K. heseloni sensu* Cooke, 1997), *K. majus, K. olduvaiensis, K. paiceae, K.*

102   *phacochoeroides, K. millensis,* and *K. phillipi* (Souron et al., 2015 and references therein).

103   However, *K. phacochoeroides* from Maghreb as well as the disputed *"S." falconeri* from the

104   Siwalik Hills (India-Pakistan) referred to *K. falconeri* by Chavasseau (2008), Pickford (2012,

105   2013a), and Pickford and Obada (2016), likely belong to *Metridiochoerus* (Souron, 2012, 2015).

The origin of the living *Hylochoerus meinertzhageni* is still poorly known, but it likely originated from a derived species of *Kolpochoerus* (Harris and White, 1979; Geraads, 2004; Souron et al., 2015), which would render the latter genus paraphyletic. The second group includes the extant genus *Phacochoerus* (with the two species *Ph. aethiopicus* and *Ph. africanus*) and the paraphyletic genus *Metridiochoerus*, from which probably *Phachochoerus* descended (Cooke, 1978b; Harris and White, 1979). *Metridiochoerus* includes the species *Me. compactus*, *Me. andrewsi*, *Me. hopwoodi*, *Me. shawi*, and *Me. modestus* (Cooke, 2005; Bishop, 2010). The only member of the third group is *Potamochoerus*, with the existing species *Po. porcus* and *Po. larvatus*. The evolutionary history of this genus is poorly known due to the very scanty fossil record. According to Souron et al. (2015), *Potamochoerus* was used in the past as a "wastebasket taxon" to allocate many archaic remains characterized by simple-shaped, brachyodont, and bunodont teeth, thus confusing the identification of its origin. For example, *K. afarensis* is frequently placed into the genus *Potamochoerus* based on similarities of dental morphology (Harris and White, 1979; Bishop, 2010) that are likely symplesiomorphies shared by *Potamochoerus* and early members of *Kolpochoerus*. When considering overall craniomandibular morphology, *K. afarensis* is extremely different from *Potamochoerus* and clearly aligns with other species of *Kolpochoerus* (Souron, 2012; Souron et al., 2015).

In Eurasia, two distinct groups are recognized during the late Miocene, including *Microstonyx*/*Hippopotamodon* and *Korynochoerus*/*Propotamochoerus*, respectively (Pickford, 1988, 1993; Van der Made and Hussain, 1989; de Bonis and Bouvrain, 1996; Fortelius et al., 1996; Liu et al., 2005). The two genera of the first group share similar craniomandibular and dental features (Liu et al., 2005). *Microstonyx* is a polymorphic large-sized suine found in several Eurasian sites (Kostopoulos et al., 2001; Liu et al., 2005). Two chronologically-distinct species are currently documented: the poorly-known *Mi. antiquus* (Vallesian Land Mammal Age; LMA) and the more common *Mi. major* (late Vallesian–Turolian LMAs). However, the validity of the first species is doubtful, due to the poor fossil record (Liu et al., 2004). Some authors (Fortelius et al., 1996;

Geraads et al., 2005; Liu et al., 2005) consider *Mi. antiquus* as belonging to the genus

Hippopotamodon. A third species, *Mi. erymanthius*, is described based on a skull from Pikermi

(Greece) (Roth and Wagner, 1854), but this species is probably a synonym of *Mi. major* (Liu et al.,

2004, 2005). The genus *Hippopotamodon* – also including tentatively *Hi. antiquus* from Europe

(see above) – is mainly based on material from the Siwaliks (India), referred to the species *Hi.*

sivalense (Pickford, 1988; Liu et al., 2004). The relationships between *Hippopotamodon* and

Microstonyx are not clear and some authors even consider the former genus as a junior synonym of

Microstonyx (Van der Made and Hussain, 1989; Van der Made, 1997; Van der Made et al., 1999).

The relationships between *Korynochoerus* and *Propotamochoerus* are also uncertain.

Actually, *Korynochoerus* is frequently considered as a junior synonym of *Propotamochoerus* (Van

der Made, 1997). The latter genus was erected by Pilgrim (1926) and is probably another example

of "wastebasket taxon" for a large number of Miocene isolated suid remains. According to the most

recent literature, *Propotamochoerus* includes five species (most of them previously referred

generically to *Sus*): *Pr. hysudricus* (type species), *Pr. wui*, *Pr. hyotheroides*, *Pr. palaeochoerus*, and

Pr. provincialis, with the latter being the only species to survive beyond the Miocene–Pliocene

boundary, until the middle Pliocene (MN13–MN15) (Van der Made et al., 1999; Gallai, 2006;

Geraads et al., 2008). Unfortunately, most of the above species are described on the basis of scarce

material and it is likely that in the past, some species of *Propotamochoerus* (notably *Pr. hysudricus*

and *Pr. provincialis*) were confused with other suine species (Van der Made et al., 1999). Pickford

(2013a) reviewed the complex taxinomic history of the latter species (alternately referred to the

genera *Sus*, *Korynochoerus*, *?Potamochoerus*, and *Propotamochoerus*) and noticed that the

available diagnosis – probably based on specimens belonging to different taxa – is not useful to

support *Pr. provincialis* as a valid species.

The first representatives of the successful genus *Sus* appeared in Eurasia in the Pliocene and

spread in the Pleistocene. *Sus arvernensis* is the earliest recognized species of *Sus* (Gallai, 2006). It

is a small-sized suine that occurs in the Eurasian Pliocene (MN14–MN16; Ruscinian and Early

6

158   Villafranchian LMAs), from Spain to China (Van der Made and Moyà-Solà, 1989; Berdondini,

159   1992), although the latter record probably needs to be revised. This species overall shows a very

160   convoluted taxinomic history (Pickford and Obada, 2016). In this work, we consider *S. minor* as a

161   junior synonym of *S. arvernensis* following Guérin and Faure (1985).

162   *Sus arvernensis* is closely related and probably ancestral to the larger *S. strozzii* (Azzaroli,

163   1954, 1975; Berdondini, 1992; Pickford, 2012, 2013a; Pickford and Obada, 2016). The latter is a

164   common element of Eurasian mammal assemblages referred to the first half of the Early Pleistocene

165   (MN17–MNQ19; Middle to early Late Villafranchian LMA) (Rook and Martínez-Navarro, 2010)

166   and occurred in the whole southern part of Europe and western Asia, from Spain to the north-

167   eastern Azov Sea area in Russia (Titov, 2000; Kostopoulos and Athanassiou, 2003). However, the

168   recent paper by Bona and Sala (2016) describes a mandible clearly belonging to *S. strozzii* from the

169   Arda River (Italy) dated to about 0.99 Ma, which might represent the last occurrence of the species.

170   According to many scholars (Azzaroli, 1954, 1975; Berdondini, 1992; Pickford, 2012;

171   Pickford and Obada, 2016), *S. arvernensis* would be ancestral not only to *S. strozzii*, but also to a

172   wide group of Asian suids characterized by "verrucosic" lower canines (see Section 4). This group

173   includes some of the living Island South East Asia (ISEA) pigs (*S. verrucosus* and *S. celebensis*)

174   and some related fossil forms (*S. brachygnathus* and *S. macrognathus*) (Pickford, 2012). All the

175   above species (i.e. all the extinct and extant alleged relatives of *S. arvernensis* showing a verrucosic

176   lower canine) were referred to the genus *Dasychoerus* by Pickford (2012).

177   Numerous fossil species of Suinae are described in the Pleistocene of China. *Sus lydekkeri* is

178   restricted to the northern part of the Country, while *S. xiaozhu*, *S. bijiashanensis*, *S. peii* (including

179   *S. australis*), and *S. liuchengensis* are found in southern China (Han et al., 1975; Han, 1987; Liu et

180   al., 2017). Among them, only the closely related Early–Middle Pleistocene *S. lydekkeri* and *S. peii*

181   are represented by significantly rich fossil samples. These two species are approximately as large as

182   the European *S. strozzii*, but they show several morphological affinities with the extant *S. scrofa*

183   and might even be its ancestors (Dong et al., 2006, 2013; Liu et al., 2017). According to Fujita et al.

184   (2010), the similarities between *S. lydekkeri* and *S. scrofa* are so strong that the former should be

185   considered as a chronosubspecies of *S. scrofa*, namely *S. scrofa lydekkeri*.

186   After its appearance in Asia, *S. scrofa* spread in Europe at the end of the Early Pleistocene,

187   apparently finding empty ecological niches to fill. As a matter of fact, Martínez-Navarro et al.

188   (2015) showed that no suid remains are found in Europe during the last part of Villafranchian

189   (approximately from 1.8 to 1.2 Ma), in contrast to what is observed before and after this interval,

190   when these animals represent almost ubiquitous elements in the mammal faunas. After this hiatus,

191   "modern" suines re-appeared in the European Epivillafranchian record with fossils attributed to *Sus*

192   sp. (Sima del Elefante and Vallparadís Estacio in Spain; Vallonnet in France) or to the ancestor of

193   the living wild boar, *S. scrofa priscus* (Untermassfeld in Germany) (Bellucci et al., 2015; Martínez-

194   Navarro et al., 2015). The aforementioned late finding of *S. strozzii* from the Arda River (Bona and

195   Sala, 2016) should now be included in this Epivillafranchian suine contingent. In addition,

196   Freudenthal (1971) and De Giuli et al. (1986) include *Sus* sp. in the faunal list of Pirro Nord (latest

197   Villafranchian of southern Italy). Therefore, the "gap" in suid fossil record might be interpreted as a

198   mere lack of documentation.

199   Despite the rich fossil record of suines in Europe, with different species and several

200   specimens described, very little has been done so far to try reconstructing their phylogenetic

201   relationships, as well as those with Miocene to Pleistocene taxa from Africa and Asia, and with

202   living pigs. This paper tries to partially fill this gap by offering the first phylogenetic analysis based

203   on craniomandibular and dental characters of suines. The work is focused on *S. strozzii*, the best

204   represented fossil species from the Villafranchian LMA in Europe. Its record is here enriched with a

205   very well-preserved mandible from the Early Pleistocene site of Pantalla, central Italy. The main

206   research questions that we want to address are: *What are the relationships between* S. strozzii *and*

207   *its putative ancestor,* S. arvernensis*? How are these extinct pigs related to the living species of* Sus*?*

208   *In general, what phylogenetic relationships can be reconstructed between European, African, and*

209   *Asian taxa?*

210

2. Materials and methods

2.1. Materials

The new specimen of *S. strozzii* (SBAU 337647) from Pantalla (central Italy) is compared to the mandibles and lower teeth of the same species from the Upper Valdarno (IGF 414, 416, 418, 422, 424, 4006, 5979, 8968, 8970, 8975), Olivola (IGF 4007, 4008, 4606) and Senèze (NHMB Se-1775) (Azzaroli, 1954), from locality "Frantoio", Arda River (MCCA Vt-090) (Bona and Sala, 2016), and from the Sables marins de Montpellier (MNHN F.MON-13) (Pickford, 2013a). Additional comparisons are made with *S. arvernensis*, i.e. the Eurasian species preceding stratigraphically *S. strozzii*. The following lower jaw and teeth of *S. arvernensis* are considered: MNHN F.PET-2005 from Les Étouaires and IZASM no num. from Dermenji (Pickford and Obada, 2016); NHMB VI-144 and VI-145 from Villafranca d'Asti (Berdondini, 1992); CCECL Pp-195 and FSL Rss-70 from Perpignan (Azzaroli, 1954); FSL 40.061 and 40.154 from the Sables marins de Montpellier (Pickford, 2013a); MNHN ACA-311 from Çalta (Guérin et al., 1998). Using descriptions and illustrations available in the literature, the new material is compared to *S. lydekkeri* from China (Dong, 2008; Liu et al., 2017) and to *S. brachygnathus* and *S. macrognathus* from Indonesia (Hardjasasmita, 1987). The list of fossil Suinae considered in this paper (including those included in the phylogenetic analysis; see below) is in Table 1. The mandibles of the following living Suinae are also used for comparison: *Hy. meinertzhageni* (MZUF 1233, NHMUK 63.617, NHMUK 63.623); *Ph. aethiopicus* (MZUF 13305); *Ph. africanus* (MZUF 763, NHMUK 66.516, NHMUK 66.521); *Po. larvatus* (MZUF 2728, NHMUK 66.514); *Potamochoerus* sp. (MZUF 1977, NHMUK 6.12.4.71); *S. barbatus* (NHMUK 0.3.30.13, NHMUK 90.6.25.10); *S. celebensis* (NHMUK 61.12.11.26); *S. scrofa* (MZUF 754, MZUF 8516, MZUF 11917, NHMUK 1989.407,

235 NHMUK 76.410); and *S. verrucosus* (NHMUK 67.4.12.211, NHMUK 67.4.12.216). The dental

236 nomenclature (Fig. 1) follows Fujita et al. (2000).

237   Morphometric measurements (Fig. 1) of the Pantalla specimen were recorded to the nearest

238 0.1 mm with a digital calliper mainly following Von der Driesch (1976). Morphometric data for

239 comparison are from Hardjasasmita (1987) and Pickford (2012, 2013a, 2013b).

240   Following the proper Greek etymology (Pasteur, 1976), in this paper we prefer using the

241 spelling "taxinomy" (and "taxinomic") instead of the commonly used "taxonomy" (and

242 "taxonomic").

243

244 *2.2.   Tomography*

245

246   The analysed specimen was scanned through a Philips Brilliance CT 64-channel scanner at

247 the 'M.G. Vannini' Hospital of Rome (Italy) in order to study the internal anatomy and to

248 reconstruct a virtual 3D model. The specimen was scanned in the coronal (i.e. transverse) plane

249 from rostral to caudal. The scanning resulted in 476 slices (i.e. images) of 768x768 pixels each. The

250 slices were 0.8 mm thick with an interslice space of 0.4 mm. Segmentation and 3D rendering of the

251 fossil were computed using Osirix 3.9.4 32-bits for Mac, an open-source image processing software

252 dedicated to DICOM files, and the 3D open-source software Blender 2.63a Intel 32 bits for Mac. A

253 short video showing the 3D reconstruction of the specimen is available in Appendix 1.

254

255 *2.3.   Phylogenetic analysis*

256

257   In association with detailed observations of extant and fossil specimens and bibliographical

258 data, 52 morphological characters (23 cranial, 9 mandibular, and 20 dental) were coded for 19 taxa

259 (character list in Appendix 2; data matrix in Appendix 3). Of these characters, 32 were selected

260 from the literature (Azzaroli, 1954; Hardjasasmita, 1987; Geraads, 2004; Orliac et al., 2010a;

1

261 Souron, 2012; Souron et al., 2015) and either used directly or modified for coding, as specified in

262 Appendix 2. All characters were treated as unordered and unweighted. The phylogenetic

263 reconstruction was carried out in PAUP*4.0 (Swofford, 2002), under parsimony using heuristic

264 searches with tree bisection reconnection branch-swapping algorithm and ACCTRAN optimisation.

265 Branch support was calculated with 100000 bootstrap replicates with random stepwise addition, and

266 with Bremer index using the bremer.run script in TNT 1.5 (Goloboff and Catalano, 2016).

267 　　　As outgroup, we selected the tetraconodontine suid *Nyanzachoerus khinzir*, represented by

268 well-preserved craniomandibular material described and figured by Boisserie et al. (2014). The

269 ingroup consists of 18 extinct and extant Suinae. It includes all the aforementioned taxa used for the

270 comparative analysis of the new specimen from Pantalla, i.e. the extinct *S. strozzii*, *S. arvernensis*,

271 *S. lydekkeri*, and *S. brachygnathus* (we excluded only *S. macrognathus* given the absence of

272 sufficiently complete craniomandibular material) and the extant *S. barbatus*, *S. celebensis*, *S. scrofa*,

273 *S. verrucosus*, *H. meinertzhageni*, *Phacochoerus* spp. and *Potamochoerus* spp. Among the living

274 species, *S. scrofa* is characterized by a strongly marked polymorphism, which reflects in the

275 differentiation in a large number of geographical subspecies (Albarella et al., 2009 and references

276 therein). In order to minimize the influence of intraspecific variability, we analysed several

277 craniomandibular specimens of *S. scrofa* collected in different geographical areas, considering both

278 direct observation of museum samples (see above) and data gained from the literature

279 (Hardjasasmita, 1987).

280 　　　The taxinomic sample for the phylogenetic analysis was expanded with the Miocene Eurasian

281 species *Mi. major* (data from Van der Made and Hussain, 1989; Van der Made et al., 1992;

282 Kostopoulos et al., 2001; Liu et al., 2004, 2005; Sylvestrou and Kostopoulos, 2009) and with

283 representatives of the two most characteristic suine groups of the African Plio–Pleistocene record:

284 *Kolpochoerus* and *Metridiochoerus*. Taking into account the availability of well-preserved skulls

285 and based on previously published phylogenetic information, for each genus we selected two

286 species for each genus: *K. afarensis* (data from Cooke, 1978b; Harris and White, 1979; Geraads,

2004; Souron, 2012; Souron et al., 2015) and *K. phillipi* (data from Souron et al., 2015), *M. shawi*

(data from Bender, 1992; Cooke, 2005) and *M. andrewsi* (data from Harris and White, 1979;

Pickford, 2013c, 2013d), respectively. Finally, we also included in the ingroup also the disputed

species "*K.*" *phacochoeroides* from Maghreb (data from Geraads, 2004; Souron, 2012) and "*S.*"

falconeri from the Indian-Pakistan Siwalik Hills (Lydekker, 1884; Pickford, 2012; personal

observations of NMI F.18583 and NHMUK M2012).

Institutional abbreviations – CCECL: Centre de Conservation et d'Étude des Collections,

Lyon (France); FSL: Faculty of Science, Lyon (France); IGF: Museo di Storia Naturale, Sezione di

Geologia e Paleontologia, Università di Firenze (Italy); IZASM: Institute of Zoology, Academy of

Sciences of Moldova; MCCA: Museo "G. Cortesi" of Castell'Arquato, Piacenza (Italy); MNHN:

Muséum National d'Histoire Naturelle, Paris (France); MZUF: Museo di Storia Naturale, Sezione

di Zoologia "La Specola", Università di Firenze (Italy); NHMB: Natural History Museum of Basel

(Switzerland); NHMUK: Natural History Museum, London (UK); NMI: National Museum of

Ireland, Dublin (Ireland); NNMO: Nihewan National Nature Reserve Management Office, Hebei

Province (China); SBAU: Soprintendenza per i Beni Archeologici dell'Umbria, Perugia (Italy). ⊠

3. Systematic palaeontology

Order: Artiodactyla Owen, 1848

Family: Suidae Gray, 1821

Subfamily Suinae Zittel, 1893

Genus *Sus* Linnaeus, 1758

Sus strozzii Forsyth Major, 1881

1

312   (Fig. 1, Table 2)

313

314   Type material: Lectotype IGF 424, partial skeleton of an adult male including the cranium

315   with associated mandible, 4 cervical, 14 thoracic, and 2 lumbar vertebrae, some fragmented ribs,

316   both scapulae, and the proximal part of the left humerus. The lectotype was selected by Azzaroli

317   (1954) since no type material was reported by Forsyth Major (1881).

318

319   Emended diagnosis: Large-sized suine with relatively narrow parietal region of the cranium;

320   gently undulating dorsal cranial profile in lateral view, with slight ventral concavity in the middle

321   part; widely diverging and pneumatized zygomatic arches tending to be broader in the middle than

322   at the rear (more gracile in females); laterally expanded nasals separated by a bony prominence;

323   rostrocaudally elongated and rugose supracanine flange in males (more gracile in females); labial

324   longitudinal thickening of the mandibular corpus (more gracile in females), with major lateral

325   convexity in the middle; absence of I3; thick enamel in cheek teeth; verrucosic lower canines;

326   absent or very small talonid in p3 and p4; elongated m3 with single cuspid (hypopreconulid)

327   between the mesial and distal lobe and well-developed talonid composed by four main cuspids

328   arranged in a cross (modified and extended from Azzaroli, 1954, Koufos, 1986, Berdondini, 1992,

329   and Pickford and Obada, 2016).

330

331   Type locality: Upper Valdarno Basin, Tuscany (Italy).

332

333   Chronological occurrences: Early Pleistocene: Middle–early Late Villafranchian (about 2.5–

334   1.8 Ma) plus Epivillafranchian (about 1.2–1.0 Ma); no confirmed records from the late Late

335   Villafranchian (about 1.8–1.2) are known to date.

336

337   Geographical occurrences: Europe and western Asia, from Spain to Azerbaijan.

1

338

New material: SBAU 337647 (Fig. 2; 3D model in Appendix 1), left hemimandible still articulated with a small and damaged portion of the right corpus. Incisors' roots, lower canine, and p2–m3 are preserved. Specimen is referred to an adult male.

Geographical and geological framework: The site of Pantalla is located about 30 km south of Perugia (Italy; 42°52′46.79″N, 12°24′23.26″E; Fig. 3). The mammal assemblage was recovered from two different levels of a 15 m-thick stratigraphic succession referred to the Early Pleistocene Santa Maria di Ciciliano Unit (Gentili et al., 1997). SBAU 337647 come from the lowermost fossiliferous level. In addition to the suid described herein, the Pantalla mammal assemblage includes *Apodemus* cf. *A. dominans*, *Canis etruscus*, *Vulpes* sp., *Lynx issiodorensis valdarnensis*, *Acinonyx pardinensis*, *Lutraeximia umbra*, *Leptobos merlai*, *Pseudodama nestii*, *Equus* sp., and *Mammuthus* cf. *M. meridionalis* (Cherin et al., 2013a, 2013b, 2014a, 2014b, 2016, 2017). The assemblage is referred to the early Late Villafranchian LMA (Olivola/(Tasso?) Faunal Units) (Gentili et al., 1997; Cherin et al., 2017), in a time interval ranging approximately between 2.1 and 1.9 Ma (Nomade et al., 2014).

4. Description

4.1. *Mandible*

The specimen SBAU 337647 (Figs 2, 4A; 3D model in Appendix 1) is a left hemimandible with a small portion of the right corpus still preserved in the symphysis area. The fossil is overall undeformed and exquisitely preserved, although the fragmentation of the ramus prevents the description of the mandibular condyle.

In occlusal view, the mandibular corpus appears rather massive, in particular in the molar portion. The labial surface of the corpus is characterized by a longitudinal swelling (pachygnathy in Arambourg, 1947) running from the canine to the ramus base. This swelling is almost subparallel to the tooth row, but shows a greater lateral convexity in the middle part. The high density of this portion is evidenced by tomographic images (Fig. 4B). Distolabially to m3, the corpus enlarges in a triangular and very concave area. The preserved portion of the right corpus is extremely small, being represented only by the incisor area and a narrow strip of the rostromedial wall. Thanks to these preserved fragments, it is possible to estimate an angle of divergence between the corpi of about 30 degrees. The symphysis is relatively long and extends caudally up to half length of p2.

In labial view, the dorsal and ventral margins of the corpus are parallel each other. The rostroventral margin forms a wide obtuse angle with the ventral one (mental prominence in Von der Driesch, 1976), in correspondence of the diastema between p1 and p2. Two mental foramina are recognisable. The first, narrow and elongated, is in the rostrolabial part, just below the i3 alveolus. The second, smaller and rounded, is about 2 cm below the mesial margin of p2. The labial surface of the canine alveolus is characterized by a bulging rim. Similarly, a thin longitudinal swelling (extramolar ridge in Fujita et al., 2000) develops ventrally to the cheek teeth, from p3 to m3. In lingual view, the mandibular fossa extends rostrally up to the contact between m2 and m3.

The basal portion of the ramus is relatively flat laterally and markedly concave medially. The rostral margin of the ramus begins to rise vertically in a relatively backward position, so it does not cover the m3 nor in a labial or lingual view. The lateral surface of the gonial angle shows roughness and small undulations (lateral masseter tubercles), which correspond to the insertion area of the masseter muscle. The latter are much more marked on the medial surface, where they become at least four deep furrows (medial pterygoid tubercles) and correspond to the insertion area of the medial pterygoid muscle.

4.2.   *Lower dentition*

389

390   The hemimandible retains the canine, three of the four premolars (p2, p3, and p4), and the

391   three molars, while the crowns of the incisors and the p1 are not preserved. In occlusal view, the

392   teeth from the canine to m1 are aligned along an axis inclined caudomedially with respect to the

393   long axis of the corpus. The cheek teeth are low crowned and show a medium to high degree of

394   wear, with m1 being the most worn tooth. There is a short diastema between the canine and the p1

395   alveolus and a second, longer diastema between the latter and p2.

396

397   *4.2.1. Lower incisors*

398   The incisor crowns are not preserved. However, the analysis of tomographic images allows to

399   identify the roots of all the incisors (Fig. 4C). The roots of i1s and i2s are particularly well visible.

400   They are fusiform and elongated, extending up to the level of the p1 alveolus. The roots of i3s are

401   small and poorly preserved and the left one is positioned close to the canine.

402

403   *4.2.2. Lower canine*

404   The left canine is massive and well preserved. It projects dorsally and laterally, forming

405   angles of about 90 and 60 degrees with the main axis of the corpus in labial and occlusal views,

406   respectively. The apex of the canine is oriented slightly caudally. The canine can be defined as

407   "verrucosic", i.e. in a cross section of the crown, the labial and lingual sides are similar in size, and

408   are larger than the distal one. On the contrary, in the "scrofic" lower canines the distal side is larger

409   than the labial (Stehlin, 1899–1900; Hardjasasmita, 1987). A thin layer of enamel only covers the

410   labial and lingual surfaces of the tooth, although it is almost completely eroded from the latter

411   surface. Though oblique light it is possible to observe that the enamel surface is furrowed both by

412   parallel longitudinal lines and by curved enamel growth lines perpendicular to the long axis of the

413   tooth. CT images allow to appreciate the remarkable development of the canine root, whose open

414 inner extremity extends inside the dentary up to the mesial edge of m2, that is, up to half length of

415 the corpus (Fig. 4D).

416

417 *4.2.3. Lower premolars*

418   The p1 alveolus is small and sub-circular and located very close to the canine, after a 4-mm-

419 long diastema. The CT scans reveal that the alveolus is fully filled by sediment, thus suggesting that

420 the tooth has fallen before the burial. CT images, although not sufficiently clear due to the sediment

421 filling, suggest that p1 had single root. The p2, p3, and p4 have two roots. The p2 is almost

422 completely destroyed, with the exception of a thin enamel layer on the labial side.

423   The p3 is better preserved that p3, but lacks most of the lingual portion of the crown. In labial

424 view, the crown is trapezoidal in shape, with the dorsal angle formed by the high protoconid. The

425 latter forms a sharp cutting edge with the worn and steep paraconid (mesially) and metaconid

426 (distally), which are similar in height. Two small stylids are visible respectively on the mesiolabial

427 and distolabial extremities of the crown. The cervix is lowered below the paraconid and metaconid

428 to form the presynclinid and postsynclinid, respectively, while it is raised below the protoconid to

429 form a pointed anticlinid.

430   The p4 is the best-preserved premolar. It has a squared occlusal outline, which is broader than

431 that of p3. In occlusal view, the paraconid, metaconid, and hypoconid are aligned forming the main

432 cutting edge, although the metaconid is slightly shifted lingually. Conversely, the protoconid

433 occupies a labial position between the paraconid and metaconid. The protoconid is the highest cusp

434 in labial view. As in p3, the labial side of the tooth exhibits a mesial and a distal stylid, the latter

435 being preceded by a deep vertical furrow. The labial cervix undulates as in p3, but the anticlinid is

436 less marked.

437

438 *4.2.4. Lower molars*

1

439   The molars are robust, bunodont, and brachyodont. The tomographic images show that m1

440 and m2 have four slender roots in correspondence of the four main cuspids, while m3 has a fifth

441 accessory root below the talonid. The advanced state of wear makes the m1 difficult to describe. Its

442 occlusal outline is 8-shaped, with a medial constriction separating the mesial cuspids (protoconid

443 and metaconid) from the distal ones (hypoconid and entoconid). A small enamel island interpretable

444 as the hypoectoconulid, is visible on the labial side of the medial constriction. Distally, the crown

445 seems to show a small additional median cusp (pentaconid?).

446   The m2 is sub-rectangular in occlusal shape, with the distal portion slightly broader than the

447 mesial. The entoconid is the best preserved cuspid, while the hypoconid and especially the

448 protoconid and metaconid are heavily worn and fragmented. Between the distal and mesial main

449 cuspids, a distinct hypopreconulid is present and a small pentaconid is barely distinguishable at the

450 distal end of the crown. A swelling on the labial surface of the hypoconid can be interpreted as a

451 cingulum.

452   The m3 is very well preserved. It has an elongated and mesiodistally tapered occlusal

453 appearance, with relatively squared mesial outline and rounded distal outline. The occlusal

454 constrictions separating the three lobes of the tooth are not deep. The enamel is very thick and in the

455 four main cuspids, it is characterized by well-marked invaginations (furchen of Hünermann, 1968).

456 The metaconid is larger than the protoconid and in turn, the two are larger than the hypoconid and

457 entoconid. No mesial cingulum is present. In both the metaconid and protoconid, the distal furchen

458 (number 6 and 3, respectively; Fig. 1) is very deep. The hypopreconulid is large approximately half

459 of the main cuspids and is triangular in occlusal shape. The third lobe of the m3 is long and massive

460 and is composed by four main cuspids arranged in a cross. The pentapreconulid is slightly smaller

461 than the hypopreconulid and a pentaectoconulid is well visible on its labial side. The pentaconid,

462 hexaconid, and heptaconid are approximately the same size. A small tubercle is visible on the labial

463 corner of the heptaconid. Another, smaller tubercle develops lingually, between the entoconid and

464 hexaconid. In labial view, two vertical grooves cross the wall of the protoconid and two others that

1

465 of the hypoconid. Similarly, the walls of the talonid show some shallow vertical grooves or

466 undulations. The cervix is more undulated on the lingual side than on the labial.

467

468 **5. Comparisons and discussion**

469

470   Measurements of the hemimandible SBAU 337647 are given in Table 2 and a length-width

471 diagram of m3 of selected extant and extinct *Sus* species is available in Figure 5.

472   The studied specimen belongs to an adult individual, as evidenced by the complete eruption of

473 the permanent teeth and their state of wear. The massive and elongated lower canine and the labial

474 thickening of the corpus allow referring the hemimandible to a male.

475

476 *5.1. Comparisons with previously described specimens of* Sus strozzii

477

478   Most characters of SBAU 337647 clearly fit the general mandibular and lower tooth

479 morphology of *S. strozzii* described in the literature. Similarities with the lectotype IGF 424

480 (Azzaroli, 1954) are remarkable (Fig. 6A–B). In occlusal view, the symphysis area is equally

481 developed in the two specimens, extending distally up to the contact between p2 and p3. The labial

482 longitudinal swelling follows the same outline. In labial view, the two mandibles appear similarly

483 slender and elongated and the ventral outlines are almost identical. In both specimens, the labial

484 cervix of the lower canine and cheek teeth is ventrally bounded by a longitudinal ridge. Similar

485 features are recognisable in the other male mandibles from the Upper Valdarno (IGF 414, 8970) and

486 Olivola (IGF 4006), as well as in the complete mandible from Senèze NHMB Se-1775 (Azzaroli,

487 1954) (Fig. 6C), although the overall shape of this specimen is more gracile due to the subadult age

488 of the individual. The partial mandible from the Arda River MCCA Vt-090 (Bona and Sala, 2016)

489 differs from SBAU 337647 in the shorter symphysis, which does not exceed distally the mesial

490 margin of p2.

491   The lower teeth also exhibit the typical *S. strozzii* morphology. The shape, size, and

492   orientation of the impressive lower canine fit those of IGF 4006 from Olivola and MCCA Vt-090

493   from the Arda River. As in all the analysed *S. strozzii* specimens, p1 is very small and located few

494   millimetres behind the canine. Again, the lower cheek teeth of SBAU 337647 closely look alike

495   those of the lectotype IGF 424, also in the wear stage, suggesting a similar age for the two

496   individuals. In both specimens – as well as in IGF 416 and 8970 from the Upper Valdarno, IGF

497   4006 and 4007 from Olivola, and NHMB Se-1775 from Senèze – p2 and p3 are relatively narrow,

498   while p4 is wider, especially in the distal part. The m1 and m2 are poorly preserved in the Pantalla

499   hemimandible, but their general shape recalls that of the corresponding teeth of the lectotype. The

500   m2 of MCCA Vt-090 from the Arda River is peculiar in having a more-developed pentaconid. The

501   elongated m3 of SBAU 337647 displaying a long and robust talonid with distal lobe composed by

502   four main cuspids, is very similar to that of IGF 424, IGF 4006, NHMB Se-1775, and MCCA Vt-

503   090. Conversely, some other male specimens of *S. strozzii* such us IGF 414, 4007, and 8970, show

504   relatively shorter and stouter m3 talonids. The same condition is observed in the m3 MNHN

505   F.MON-13 from Montpellier (Pickford, 2013a), which also differs from the Pantalla m3 in the

506   presence of a well-developed mesial cingulum and in the different size and arrangement of the

507   talonid cuspids, dominated by the very large heptaconid located in distolabial position.

508   In light of the morphological comparisons, attribution of the new material to *S. strozzii* is well

509   supported. As for the size of m3 (Fig. 5), SBAU 337647 falls in the upper dimensional range of *S.*

510   *strozzii* and represents one of the larger *Sus* individuals among those analysed.

511

512   *5.2. Comparisons with* Sus arvernensis

513

514   According to many scholars, the Ruscinian to Early Villafranchian small-sized Eurasian pig *S.*

515   *arvernensis* is the putative ancestor of *S. strozzii*, from which it differs essentially in its smaller

516   dimensions (Azzaroli, 1954, 1975; Berdondini, 1992; Pickford, 2012, 2013a; Pickford and Obada,

517   2016). This is confirmed in our comparative morphometric analysis (Fig. 5), in which the

518   dimensional ranges of the length and width of m3 for the two species are completely separated, with

519   the values of *S. strozzii* larger than those of *S. arvernensis* by just over 30% on average.

520   When compared morphologically to the holotype of *S. arvernensis* MNHN F.PET-2005 from

521   Les Étouaires (Pickford and Obada, 2016: figs 3–6), SBAU 337647 is different in its significantly

522   longer symphysis in occlusal view. Conversely, the symphysis length and general shape of SBAU

523   337647 is similar to what observed in the exquisitely preserved mandible of *S. arvernensis* NHMB

524   VI-144 from Villafranca d'Asti (Berdondini, 1992, Pickford and Obada, 2016) (Fig. 6D). However,

525   the latter specimen differs from SBAU 337647 in the ventral outline of the corpus, which tapers

526   rostrally without the typical mental prominence below the p1–p2 diastema observed in *S. strozzii*

527   and in SBAU 337647.

528   The lower teeth of *S. arvernensis* from Les Étouaires (Pickford and Obada, 2016), Perpignan

529   (Azzaroli, 1954), Montpellier (Pickford, 2013a), Villafranca d'Asti (Berdondini, 1992, Pickford and

530   Obada, 2016), Dermenji (Pickford and Obada, 2016), and Çalta (Guérin et al., 1998) are smaller in

531   size but similar in shape to those of the mandible from Pantalla, but the enamel occlusal patterns

532   observed in the latter – and in *S. strozzii*, in general – are more complex that in *S. arvernensis*.

533

534   *5.3. Comparisons with* Sus lydekkeri

535

536   Among the numerous fossil species of *Sus* described in the Quaternary of China (see Section

537   1), we consider here only *S. lydekkeri* from the Early–Middle Pleistocene of the northern part of the

538   country, as it is the only species for which significantly preserved mandibular material is known.

539   The knowledge of this taxon is significantly increased thanks to the recent discovery of a complete

540   cranium (NNMO HY13-58.1) with mandible (NNMO HY13-58.2) from Yangshuizhan in Nihewan

541   Basin (Liu et al., 2017). However, contrary to what the authors wrote, we believe that the

2

Yangshuizhan skull belongs to a male, mainly on the basis of the very long lower canines and the well-developed supracanine flanges.

The mandible and lower teeth of *S. lydekkeri* (NNMO HY13-58.2) are overall similar to those from Pantalla in the following characters: development of the symphysis; obtuse angle between the corpus and ramus; shape of the labial longitudinal swelling of the corpus in occlusal view; occurrence of distinct stylids in p3 and p4; relative length of the m3 talonid.

On the other hand, the following are the main differences between the two specimens: in labial view, the gonial angle extends below the ventral margin of the corpus in *S. lydekkeri*; the lower canine is verrucosic in the Yangshuizhan fossil (Liu et al., 2017), but is generally defined as intermediate between scrofic and verrucosic in *S. lydekkeri* (Fujita et al., 2000; Chen, 2004; Dong, 2008), while it is always verrucosic in *S. strozzii* (including SBAU 337647); the p1 is absent in NNMO HY13-58.2; in the latter specimen, the p4 exhibits distinct separation between the metaconid and hypoconid; the pentaconid of m1 and m2 are much more developed; in the m3, the mesial cingulum, protopreconulid, and protoendoconulid (all absent in SBAU 337647) are well developed, while the heptaconid in much smaller than in SBAU 337647; overall, the lower molar enamel occlusal pattern of *S. lydekkeri* is less complex. Most of the above dental features fit the conditions observed in *S. scrofa*, confirming the putative relationships between these taxa (Fujita et al., 2000; Dong et al., 2006, 2013; Liu et al., 2017).

5.4. Comparisons with extinct and extant pigs from Island South East Asia (ISEA)

ISEA is today characterized by the occurrence of numerous *Sus* species, often endemic to one or more islands of variable size, suggesting multiple events of allopatric speciation. These species are sometimes grouped as the "warty pigs" (Groves and Grubb, 1993), being characterized by the presence of facial warts of different kind, particularly developed in males. However, warts occur also in the African *Phacochoerus*, *Potamochoerus*, and *Hylochoerus*, which are not

phylogenetically related to the ISEA pigs (Gongora et al., 2011, Frantz et al., 2013). For this, here we avoid using the term "warty pigs".

Among living ISEA species, we focused our comparative analysis on the three best known taxa, i.e. the Javan Warty Pig *S. verrucosus*, the Bearded Pig *S. barbatus*, and the Sulawesi Warty Pig *S. celebensis*. In addition, we considered the closely related extinct *S. brachygnathus* (Indonesia) and *S. macrognathus* (Indonesia and other Asian localities; see Table 1) (Hardjasasmita, 1987). We did not include in the comparison the Philippines species *S. philippensis*, *S. cebifrons*, *S. oliveri*, and *S. ahoenobarbus* (taxinomy from Frantz et al., 2016) due the small number of available samples in museums and the scarcity of the literature data available about their craniomandibular and dental anatomy.

The mandible and lower teeth of the Pantalla suid share several characters with living and fossil ISEA species: the ventral margin of the mandible is identical to that observed in *S. verrucosus*, *S. barbatus*, and *S. celebensis* (in *S. brachygnathus* the gonial angle is shifted ventrally; no mandibles of *S. macrognathus* are known to date); the symphysis is approximately as long as in the ISEA pigs (although in *S. barbatus*, the whole mandible including the symphysis area, appears more slender and elongated); the strong longitudinal swelling of the corpus with a major convexity in the median part is common to all species; in all taxa, the lower canine is verrucosic, p2 and p3 show distinct stylids, the p4 has aligned paraconid, metaconid, and hypoconid forming a continuous cutting edge, the enamel of the molars exhibits complex occlusal patterns. Although fragmented, the ascending ramus of SBAU 337647 seems to form a wide angle with the corpus, as observed in *S. barbatus*. The p1 is present in all species (not known in *S. macrognathus*), but is positioned very close to the canine only in SBAU 337647, *S. verrucosus*, and *S. brachygnathus*. The m3 of the Pantalla hemimandible is longer and wider than that of the considered ISEA pigs (Fig. 5). In general, the lower part of the dimensional range of *S. strozzii* partially overlaps the upper ranges of *S. verrucosus* and *S. barbatus*, while *S. brachygnathus* and especially *S. celebensis* are characterized by smaller dimensions (Fig. 5). The general morphology of m3 and cuspid size and topology are

594 similar in all taxa. In particular, they all share a strong talonid with distal lobe composed of four

595 main cuspid of similar size arranged in a cross. The relative length of the m3 talonid of SBAU

596 337647 fits that of *S. brachygnathus*, *S. macrognathus*, and *S. celebensis*, while the talonid is

597 slightly longer in *S. verrucosus* and *S. barbatus*.

598

599 *5.5. Comparisons with* Sus scrofa

600

601 The Wild Boar *S. scrofa* has one of the widest geographic distributions of all terrestrial

602 mammals, spanning the whole Eurasia and Maghreb. This is reflected in a wide range of

603 morphological and metrical variation (Groves and Grubb, 1993). Despite this strong polymorphism,

604 we recognized in the analysed mandibles the following morphological characters that differentiate

605 *S. scrofa* from SBAU 337647: the labial longitudinal swelling of the corpus is straight in occlusal

606 view, without the convexity in the middle part observed in the Pantalla specimen; the angle between

607 the corpus and the ramus is almost right; the lower canine is scrofic; p1 is small; p2 and p3 do not

608 show clear stylids; in the majority of the specimens, the cuspids of the p4 are clearly separated; the

609 occlusal enamel pattern of the molars is simpler than in SBAU 337647; m1 and m2 show a well-

610 developed pentaconid, mesially in contact with a smaller pentapreconulid; m3 has an evident mesial

611 cingulum; between the main mesial and distal cuspids of m3, the protoendoconulid and

612 hypopreconulid are equally developed and often associated to a hypoectoconulid in labial position.

613 From the morphometric point of view (Fig. 5), the considered Wild Boar's third lower molars

614 are smaller than those of *S. strozzii*, including SBAU 337647. The range of *S. scrofa* is intermediate

615 between those of *S. arvernensis* and *S. strozzii*, and partially overlaps those of *S. lydekkeri*, *S.*

616 *verrucosus*, and *S. barbatus*.

617

618 *5.6. Comparisons with* Potamochoerus

619

The mandible from Pantalla and that of the African *Potamochoerus* share some general features (e.g. the overall elongated shape in labial view, with abrupt angle between the ventral and the rostroventral margins and obtuse ramus with respect to the corpus), but a detailed analysis highlights the following significant differences: the symphysis is equally elongated, but *Potamochoerus* is distinguished in having a bony shelf at the caudoventral extremity of the symphysis, well visible in occlusal view (Souron, 2012); in *Potamochoerus*, the longitudinal swelling along the corpus is straight; the lower canine is scrofic; the cheek teeth are covered by thicker enamel and are relatively poorly folded; p1 is almost always absent; p2 is markedly smaller than p3 (this condition was also observed in *S. arvernensis* by Pickford and Obada, 2016); there are no stylids in p2 and p3; p4 is the most distinctive tooth, characterized by a massive and conical protoconid (Azzaroli, 1975); the pentaconid of m1 and especially m2 is well developed; the m3 talonid is proportionally shorter and has pentaconid and hexaconid smaller than pentapreconulid and heptaconid. Notwithstanding the above characters, it is worth noting that *Potamochoerus* is characterized by significant intraspecific variation in tooth number and morphology. For instance, Boisserie et al. (2014) observed absence of p2 in 2% of *Po. larvatus* and 16% of *Po. porcus* out of 132 specimens analysed, as well as a high degree of variation in the morphological complexity of the m3 talonid.

5.7. Comparisons with Kolpochoerus *and* Hylochoerus

The extinct African genus *Kolpochoerus* is closely related to the living *Hy. meinertzhageni* (White and Harris, 1977; Harris and White, 1979). As a matter of fact, the Giant Forest Hog should be considered as a member of *Kolpochoerus*, which is thus paraphyletic (Souron et al., 2015; see Section 6). The mandibles of these taxa share a number of morphological characters, which differentiate them from the Pantalla specimen: the symphysis area is relatively shorter and wider; the lower canine is verrucosic, but proportionally much more elongated, especially in

2

Kolpochoerus; p1 is usually absent and p2 is very reduced in *Kolpochoerus* and absent in

Hylochoerus; the postcanine diastema is much longer; p2 and p3 do not have visible stylids; the

main cuspids of p4 are clearly separated; the enamel folding pattern is less complex; in some

species of *Kolpochoerus* (i.e. *K. phillipi* and *K. majus*) and in *Hylochoerus*, the main cuspids of m3

are mesiodistally compressed (Souron et al., 2015); the m3 talonid is approximately as developed as

in SBAU 337647, but is characterized by an additional mesial cuspid adjacent and sometimes

partially fused to the pentapreconulid; *K. olduvaiensis*, *K. paiceae*, and *Hylochoerus* shows a longer

talonid with additional cuspids (Souron et al., 2015).

5.8. Comparisons with Metridiochoerus *and* Phacochoerus

The African Wart Hog *Phacochoerus* probably originated from the Plio–Pleistocene

Metridiochoerus clade (Cooke, 1978b, 1982; Harris and White, 1979). The mandible and lower

dentition of these taxa are considerably different from the Pantalla specimen in several aspects,

among which noteworthy are the relatively short and wide symphysis area in occlusal view

especially in males, the rostrocaudally enlarging labial longitudinal swelling of the corpus, the

elongated blade-like lower canines in males. In addition, late species of *Metridiochoerus* and the

living *Phacochoerus* are characterized by the absence of p1 and p2, the high-crowned molars, and

the extremely elongated m3 talonid with multiple tightly packed additional cuspids.

Most of the above characters are also observed is *"Kolpochoerus" phacochoeroides* from

Maghreb (Geraads 2004), which aligns better with *Metridiochoerus* as suggested by Souron (2012,

2015).

5.9. Comparisons with "Sus" falconeri

671   The only male mandible of *"S." falconeri* (NHMUK M2012) found to date in the Siwalik

672   Hills (Lydekker, 1884) shares some similarities with the hemimandible from Pantalla, that is, the

673   mesial position of p1, the blade-like occlusal pattern of p4, and the complexity of enamel folding in

674   molars. However, NHMUK M2012 differs from SBAU 337647 in the wide and short symphysis

675   area, in the longer m3 talonid with an additional distolingual cuspid, and especially in the high-

676   crowned cheek teeth (*"S." falconeri* is defined as hypsodont by Pickford, 2013a), characterized by

677   the presence of vertical grooves on the side cusps (Souron, 2012, 2015). All these characters

678   support the suggestion by Souron (2012, 2015) that *"S." falconeri* belongs to *Metridiochoerus*,

679   rather than to *Kolpochoerus* (Chavasseau, 2008; Pickford, 2012, 2013a; Pickford and Obada, 2016).

680   Already Colbert (1935) and Azzaroli (1954) had noticed the affinities between *"S." falconeri* and

681   *Phacochoerus* (i.e. an advanced relative of *Metridiochoerus*). Gaur (1987) had also detected the

682   similarity in third molar morphology between *Metridiochoerus* from eastern Africa and *S. choprai*,

683   a new species he described from the Siwaliks, now considered as a junior synonym of *"S."*

684   *falconeri.* Azzaroli (1954) and Gaur (1987) interpreted these similarities as a result of convergent

685   evolution.

686

687   **6.   Phylogenetic relationships**

688

689   The phylogenetic analysis produced two equally parsimonious phylogenetic trees of 143

690   steps, consistency index of 0.427 and retention index of 0.619. Figure 7 shows the strict consensus

691   tree, with node support indicated by Bremer and bootstrap values. The distribution of character

692   states in the most parsimonious trees is reported in Table 3.

693   *Microstonyx major* is the first taxon to branch off the Suinae clade (Node 1). This result

694   agrees with the early stratigraphic occurrence (i.e. late Miocene) of this Eurasian taxon displaying

695   numerous plesiomorphic character states. The basal position of *Microstonyx* is here supported for

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696 the first time by cladistic analysis, after being previously hypothesized in the phylogenetic tree of

697 Frantz et al. (2016), which however is a qualitative consensus based on the literature.

698 *Microstonyx major* is the sister taxon of a large clade (Node 23) including two branches. The

699 first (Node 29) includes the *Kolpochoerus* and *Metridiochoerus* lineages, the second (Node 22)

700 includes the genus *Potamochoerus* and the *Sus* lineage. Both the *Kolpochoerus* (Node 30) and

701 *Metridiochoerus* (Node 28) genera are paraphyletic, as they include the living *Hylochoerus* and

702 *Phacochoerus*, respectively. Within the first clade, the early branching of *K. afarensis* (Geraads,

703 2004; Haile-Selassie and Simpson, 2013; Souron et al., 2015) is confirmed, as well as the sister-

704 group relationship (Node 31) between *K. phillipi* and *H. meinertzhageni* (Souron et al., 2015). The

705 position of *"S." falconeri* at the base of the *Metridiochoerus* group allows us to confidently confirm

706 its attribution to the latter genus (Souron, 2012, 2015). The same goes for *"K." phacochoeroides*,

707 which occupies in the tree an intermediate position within the *Metridiochoerus* clade. A formal

708 reassignment of those two species to the genus *Metridiochoerus* is under preparation (Souron and

709 Chavasseau, in prep.). The fact that those two taxa branch early in the *Metridiochoerus* group could

710 explain why they were previously misidentified as *Kolpochoerus*. They do resemble species of

711 *Kolpochoerus* due to the retention of plesiomorphic character states and do not display all the more

712 derived character states found in "classic" *Metridiochoerus* species like *M. andrewsi*. Similarly, *M.*

713 *shawi* was also placed into a separate genus named *Potamochoeroides* based on its peculiar

714 morphology (Bender, 1992) that mostly reflect retention of plesiomorphic character states. The

715 close phylogenetic relationship between *Phacochoerus* and *Metridiochoerus* (Node 34) is largely

716 accepted in the literature (e.g. Cooke, 1978b; Harris and White, 1979; Bishop, 2010; Pickford,

717 2013c), and is here evidenced for the first time by means of cladistic analysis.

718 The African *Potamochoerus* is regarded as a morphologically primitive suine, retaining

719 several conservative anatomical characters that make it superficially similar to *Sus* in many features

720 (Groves and Grubb, 1993). This might explain the basal position of *Potamochoerus* with respect to

721 *Sus* in our tree (Node 11), which is not in accordance with previous studies either based on

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morphological (Geraads, 2004; Souron et al., 2015) or molecular (Wu et al., 2006; Gongora et al., 2011) data.

6.1. Phylogenetic relationships of Sus

The phylogenetic relationships between extinct and extant *Sus* species are still not fully understood. As for living taxa, some authors (Groves, 1981; Groves and Grubb, 1993; Pickford, 2012) separate the genus *Sus* in two groups on the basis of the lower canine morphology: the "scrofic group" includes only *S. scrofa* [the Pigmy Hog *"Sus" salvanius* of Groves and Grubb (1993) is today referred to the distinct genus *Porcula* (Funk et al., 2007)]; the "verrucosic group" is formed by all other living species of *Sus*, geographically restricted to ISEA. However, this separation is questioned by some evidence. Among them, Groves (1997) represents the first attempt to resolve the phylogenetic relationships of living *Sus* species. He coded 30 morphological characters for *S. scrofa* and several ISEA species and recovered two groups: one was formed by *S. barbatus* and *S. verrucosus*; in the other, *S. scrofa* is clustered with the "verrucosic" species *S. celebensis*, *S. philippensis*, *S. cebifrons*, and *S. oliveri*. Lucchini et al. (2005) intertwined molecular (two mtDNA cyt *b* fragments) and morphometric (cranial measurements) data, and identified three groups, one with *S. celebensis* and *S. cebifrons*, one with *S. barbatus*, and one with *S. scrofa*, *S. ahoenobarbus*, and *S. verrucosus* (although the latter was not analysed genetically). Wu et al. (2006) analysed the complete mtDNA cyt *b* sequences and obtained a similar grouping: *S. celebensis*, *S. cebifrons*, and *S. philippensis* are at the base of the *Sus* clade, followed by *S. scrofa* as sister taxon of the pair formed by *S. verrucosus* and *S. barbatus* (with the latter being paraphyletic with respect to the former). Although working again on mtDNA cyt *b* data, Mona et al. (2007) obtained rather different results, as they recognized two main clades including respectively *S. scrofa* plus *S. philippensis* and *S. verrucosus* plus the paraphyletic *S. barbatus* (haplotypes of *S. celebensis* were found in both groups, so the species was considered as polyphyletic). The phylogenetic

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affinity between *S. scrofa* and the Philippines suines was confirmed by Funk et al. (2007), who also focused on mitochondrial loci. On the contrary, the phylogenetic tree of Gongora et al. (2011) grounded on both nuclear and mitochondrial DNA sequences, found *S. scrofa* as the basal taxon of the *Sus* radiation, followed by the clade of ISEA pigs. Similar conclusions are reached by other molecular studies based on whole-genome data (Frantz et al., 2013; Ai et al., 2015), and are confirmed in the synthetic tree of Frantz et al. (2016: fig. 1), which accounts for both molecular and morphological data.

The latter results are in agreement with those obtained in our phylogenetic analysis (Fig. 7), in which the Wild Boar is the first species to branch off the *Sus* lineage (Node 2). *Sus scrofa* is followed by *S. lydekkeri* (Node 4) from the Early–Middle Pleistocene of China. The morphological affinities between *S. scrofa* and *S. lydekkeri* are largely accepted (Fujita et al., 2000, Dong et al., 2006, 2013; Liu et al., 2017). However, our results question the alleged ancestor-descendant relationship between *S. lydekkeri* and *S. scrofa* (Dong, 2008; Liu et al., 2017) and even the fact that *S. lydekkeri* can be a chronological subspecies of *S. scrofa* (Fujita et al., 2000). Further insights on the phylogenetic and taxinomic status of *S. lydekkeri* could derive from future studies on the Chinese fossil record, including other Pleistocene species such as *S. peii*, which unfortunately are so far represented only by fragmentary remains. The lower canine of *S. lydekkeri* is morphologically intermediate between the scrofic and verrucosic conditions (Fujita et al., 2000; Chen, 2004; Dong, 2008). The remaining clade (Node 24) is composed by living and fossil species all characterized by verrucosic lower canine, among which *S. arvernensis* is the first branching (Node 3). This result is widely supported by previous works (Azzaroli, 1954, 1975; Berdondini, 1992; Pickford, 2012; Pickford and Obada, 2016), according to which *S. arvernensis* would be ancestral to *S. strozzii* and ISEA pigs. Unfortunately, the relationships between the latter taxa are not resolved in our tree (Node 26): *S. strozzii* is part of a polytomy that also includes *S. verrucosus*, *S. barbatus*, and the clade formed by *S. celebensis* and *S. brachygnathus*, whose affinity was already pointed out by Von Koenigswald (1933). In the two most parsimonious trees, the following topologies are recognized:

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774 ((*S. barbatus*, *S. verrucosus*), (*S. strozzii*, (*S. celebensis*, *S. brachygnathus*))) and (*S. barbatus*, ((*S.*

775 *strozzii*, *S. verrucosus*), (*S. celebensis*, *S. brachygnathus*))). The presence of this unresolved node is

776 indicative of the difficulty of finding diagnostic morphological characters useful to differentiate

777 these species, which all share similar conservative craniomandibular anatomy. Moreover, as also

778 hinted by the contrasting results obtained by the different molecular studies carried out on these

779 taxa (see above), there is the possibility that this polytomy may be due to rapid radiation of species

780 with strong hybridisation between the different taxa in the early stage of divergence.

781 　　Nevertheless, the position of *S. strozzii* in our tree is the first cladistic evidence of the affinity

782 between this species and verrucosic ISEA pigs, previously hypothesized by several authors

783 (Azzaroli, 1954; Berdondini, 1992; Faure, 2004; Pickford, 2013b) on the basis of morphological

784 observations but not supplemented by phylogenetic analyses.

785 　　Our results also have interesting taxinomic implications. Pickford (2012) resurrected the

786 genus name *Dasychoerus*, established by Gray (1873) for the "Warty Pigs" *D. verrucosus* and *D.*

787 *celebensis*. According to Pickford (2012), these species would be the present-day survivors of a

788 Plio–Pleistocene lineage started from *D. arvernensis* (and from the newly erected species *D.*

789 *natrunensis* from Egypt), and continued with *D. strozzii*, *D. brachygnathus*, and *D. macrognathus*.

790 *Sus barbatus* – for which Gray (1868) erected the separate genus *Euhys* – is not included into

791 *Dasychoerus* by Pickford (2012), due to its uncertain molecular phylogenetic affinities (Funk et al.,

792 2007; Gongora et al., 2011; see above). In this framework, our phylogenetic results do not support

793 the validity of *Dasychoerus sensu* Pickford (2012) (i.e. living and fossil verrucosic relatives of *D.*

794 *arvernensis*) because the corresponding clade in our tree (Node 24) also includes *S. barbatus*.

795 　　We also reject Pickford's (2012) phylogenetic hypothesis, according to which *"Dasychoerus"*

796 *arvernensis* would have given rise in Eurasia to the aforementioned lineage and in Africa to the

797 genus *Kolpochoerus*. Similarly, we do not support the hypothesis of a derivation of *Kolpochoerus*

798 from *S. arvernensis* through *S. strozzii* (Gallai, 2007). On the contrary, our phylogenetic

799 reconstruction is in agreement with an early separation between *Sus* and the "African" lineage

(including *Kolpochoerus*/*Hylochoerus* and *Metridiochoerus*/*Phacochoerus*), which is estimated at about 10 Ma (Frantz et al., 2016). The only anomaly in our results is the clustering of *Potamochoerus* with *Sus*, but it can be related to the fact that both these genera retain plesiomorphic craniomandibular and dental character states.

7. Conclusions

Sus strozzii is commonly found in Early Pleistocene European and western Asian land mammal assemblages. The new mandibular material from central Italy described herein expands our knowledge on this species' anatomy. Our phylogenetic analysis of extinct and extant Old World suines clarifies the relationships between *S. strozzii* and its putative relatives. Suinae probably originated in the late Miocene (Gongora et al., 2011). After the early separation of the *Microstonyx* lineage, Suinae branched into two main clades. The first comprises the African genera *Kolpochoerus* and *Metridiochoerus* and their respective modern relatives *Hylochoerus* and *Phacochoerus*. We also recovered as belonging to this group *"S." falconeri* from the Siwalik Hills and *"K." phacochoeroides* from Maghreb and refer them to *Metridiochoerus*. The second clade includes *Sus* and *Potamochoerus*. However, the position of the latter genus in our tree is likely due to its overall craniomandibular and dental similarity with *Sus*, and is questioned by molecular phylogenetic analysis (Gongora et al., 2011) that put *Potamochoerus* at the base of the African clade as a sister taxon to the clade (*Phacochoerus, Hylochoerus*). The Wild Boar *S. scrofa* is the first offshoot within its genus, followed by *S. lydekkeri* from the Pleistocene of northern China and by the group of verrucosic *Sus* species. This topology is in agreement with those obtained by previous phylogenetic analyses based on molecular data (Gongora et al., 2011) and on the overlapping between morphological and molecular data (Frantz et al., 2016). Our results support the primitive status of the *S. arvernensis* (Pliocene) with respect to *S. strozzii* (Early Pleistocene) (Fig. 8). Unfortunately, the phylogenetic relationships between the latter and verrucosic ISEA species are

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not totally resolved. This new evidence strongly suggests that the centre of origin of verrucosic

species of *Sus* is located in southeastern Asia and encourage new prospections especially in that

area to clarify the phylogenetic affinities between Asian and European pigs.

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FIGURE AND TABLE CAPTIONS

Fig. 1. Above: morphometric measurements taken on the analysed specimens. Measurement n. 10 (length of the symphysis) is not figured. Er, extramolar ridge; Goc, Gonion caudale; Id, Infradentale; Mp, mental prominence. Below: dental terminology used in this study after Fujita et al. (2010). Numbers in the four main cuspids of m3 refer to the furchen of Hünermann (1968). End, entoconid; Hepd, heptaconid; Hexd, hexaconid; Hyd, hypoconid; Med, metaconid; Pad, paraconid; Ped, pentaconid; Prd, protoconid. Colour online.

Fig. 2. *Sus strozzii* Forsyth Major, 1881 (SBAU 337647) from Pantalla (Italy) in labial (A), lingual (B), and occlusal (C) views. D, detail of p2–m3 in occlusal view. Scale bars represent 5 cm.

Fig. 3. Location of the palaeontological site of Pantalla (Italy). The intermontane Tiber Basin is highlighted along the middle part of the region Umbria. Colour online.

Fig. 4. Images resulting from the analysis of CT-scans of the specimen SBAU 337647. A, 3D model of the hemimandible in labial and occlusal views; B, same model with density filter applied; C, tomographic images showing the incisor roots (L, left; R, right); D, 3D model of the hemimandible in labial and occlusal views with transparent dentary bone; E, virtual reconstruction of the whole mandible of *S. strozzii* from Pantalla in occlusal view, obtained by cloning and mirroring the left hemimandible on the right side. Scale bars represent 5 cm. Colour online.

Fig. 5. Plot of length vs. width of the m3 in SBAU 337647 from Pantalla and other extinct and extant species of *Sus* (data from Hardjasasmita, 1987 and Pickford, 2012, 2013a, 2013b). Colour online.

Fig. 6. Morphological comparison between the mandibles of *Sus strozzii* SBAU 337647 from Pantalla (A), *S. strozzii* IGF 424 from the Upper Valdarno (lectotype) (B), *S. strozzii* NHMB Se-1775 from Senèze (subadult) (C), and *S. arvernensis* NHMB VI-144 from Villafranca d'Asti (D). B and C are redrawn from Azzaroli (1954); D is redrawn from Pickford and Obada (2016). Scale bar represents 3 cm.

Fig. 7. Strict consensus tree showing the phylogenetic relationships between selected extant and extinct (†) Suinae. Node numbers in white circles, Bremer support in black circles above node numbers, bootstrap values below node numbers. Skulls are not drawn to scale.

Fig. 8. Reconstructed life appearance of the Early Pleistocene *Sus strozzii* (left) and the Pliocene *S. arvernensis* (right), in which we emphasized some hypothetical morphological similarities with extant verrucosic ISEA pigs as supported by our phylogenetic results. Artwork by L.S. Colour online.

Table 1. List of fossil Suinae considered in this paper in stratigraphical order with corresponding age, localities, and references.

Table 2. Mandibular measurements (in mm) of *Sus strozzii* SBAU 337647 from Pantalla (Italy).

Table 3. Distribution of character states for nodes in the most parsimonious trees.

A

B

C

D

Tiber River

PERUGIA

Trasimeno
Lake

Pantalla

TODI

SPOLETO

TERNI

N

20 Km

Density

min ■■■■■■ max

Section plane

Ri3

Ri2

Ri1

Li1

Li2

Li3

C
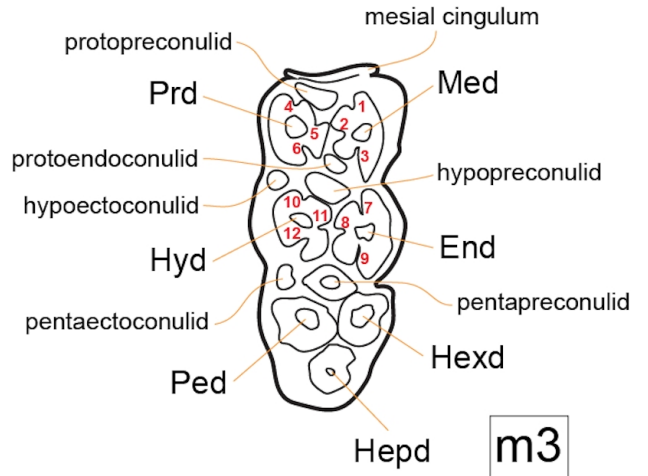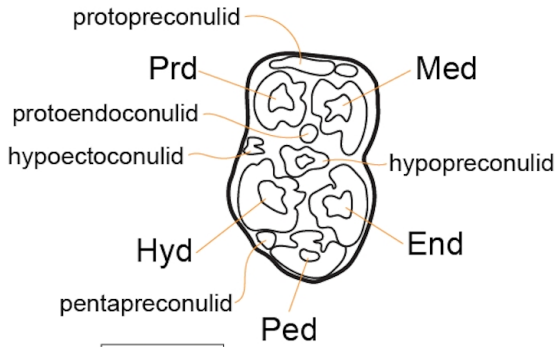
Legend:
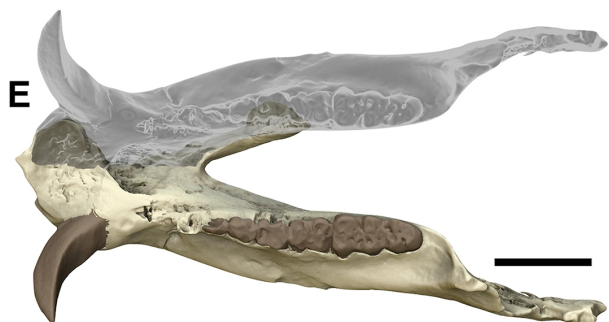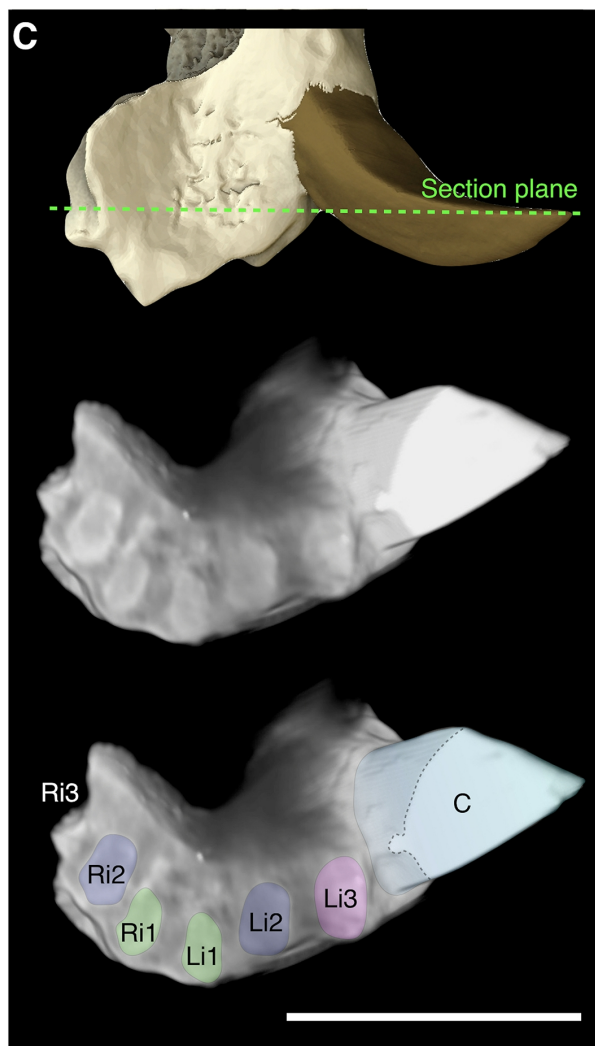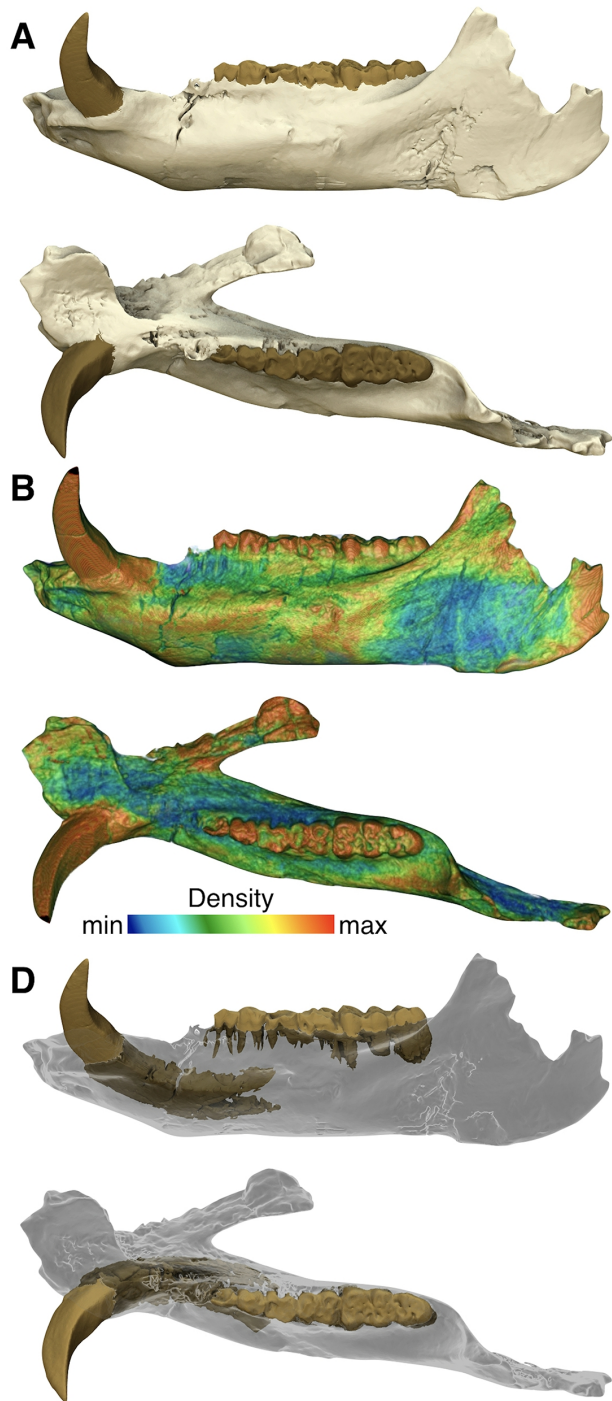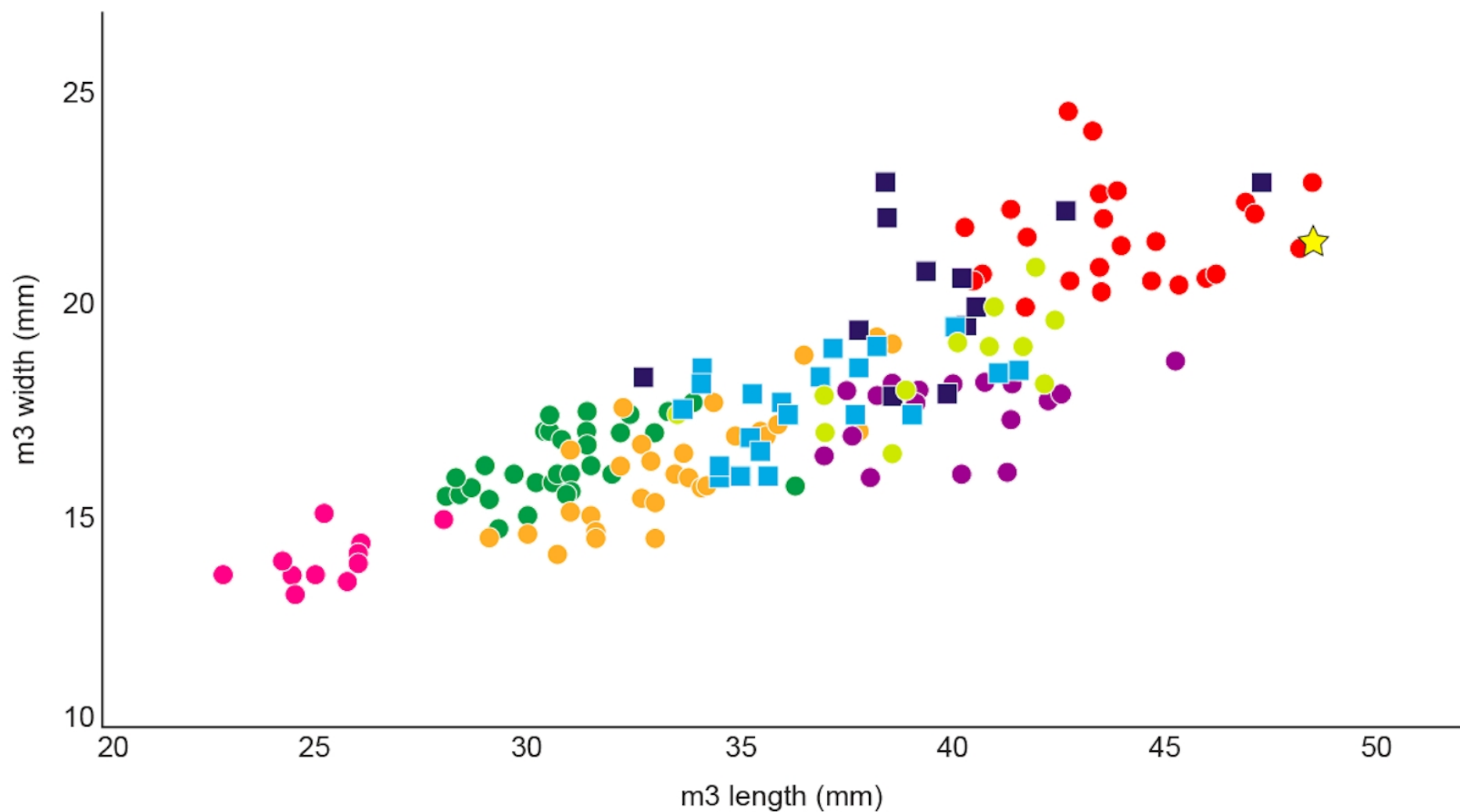
★ SBAU 337647

● *Sus strozzii*

● *Sus arvernensis*

● *Sus verrucosus*

● *Sus barbatus*

● *Sus celebensis*

● *Sus brachygnathus*

■ *Sus scrofa*

■ *Sus lydekkeri*
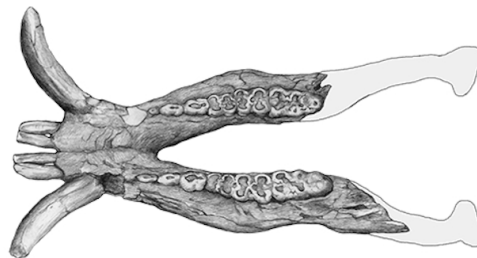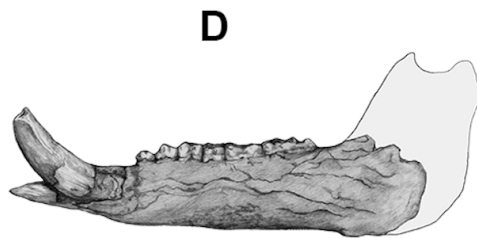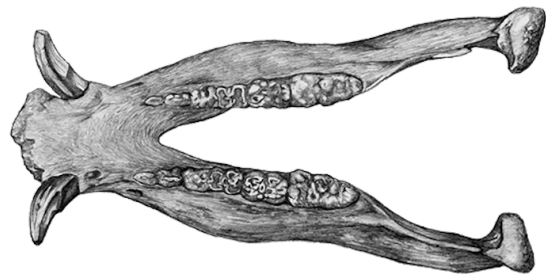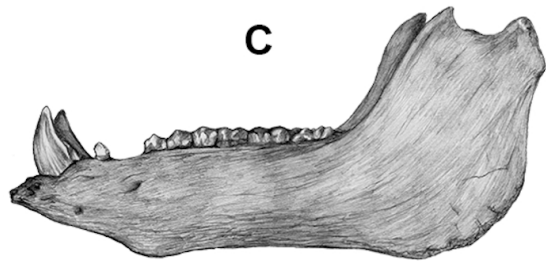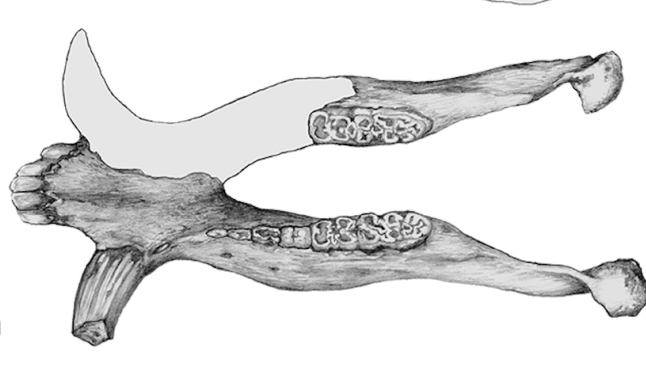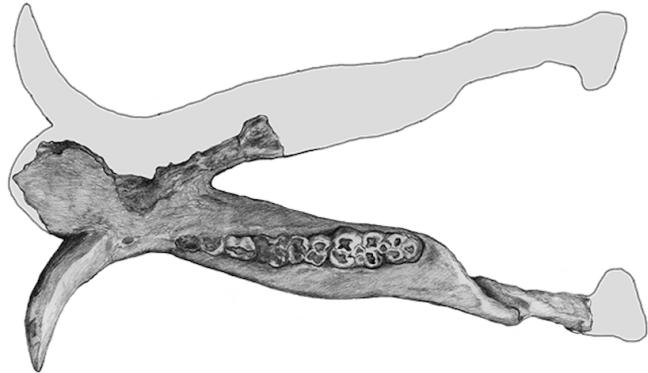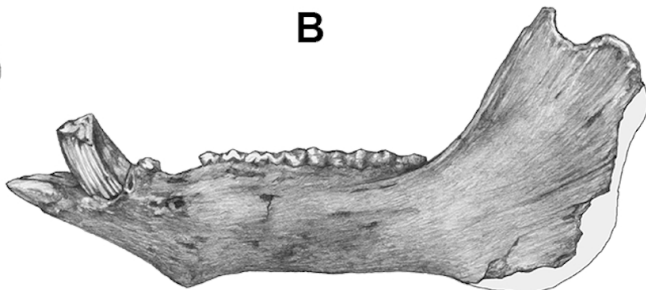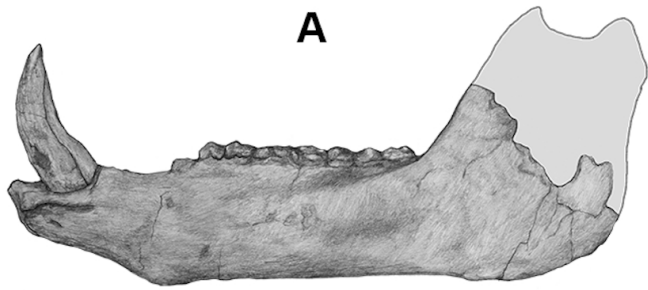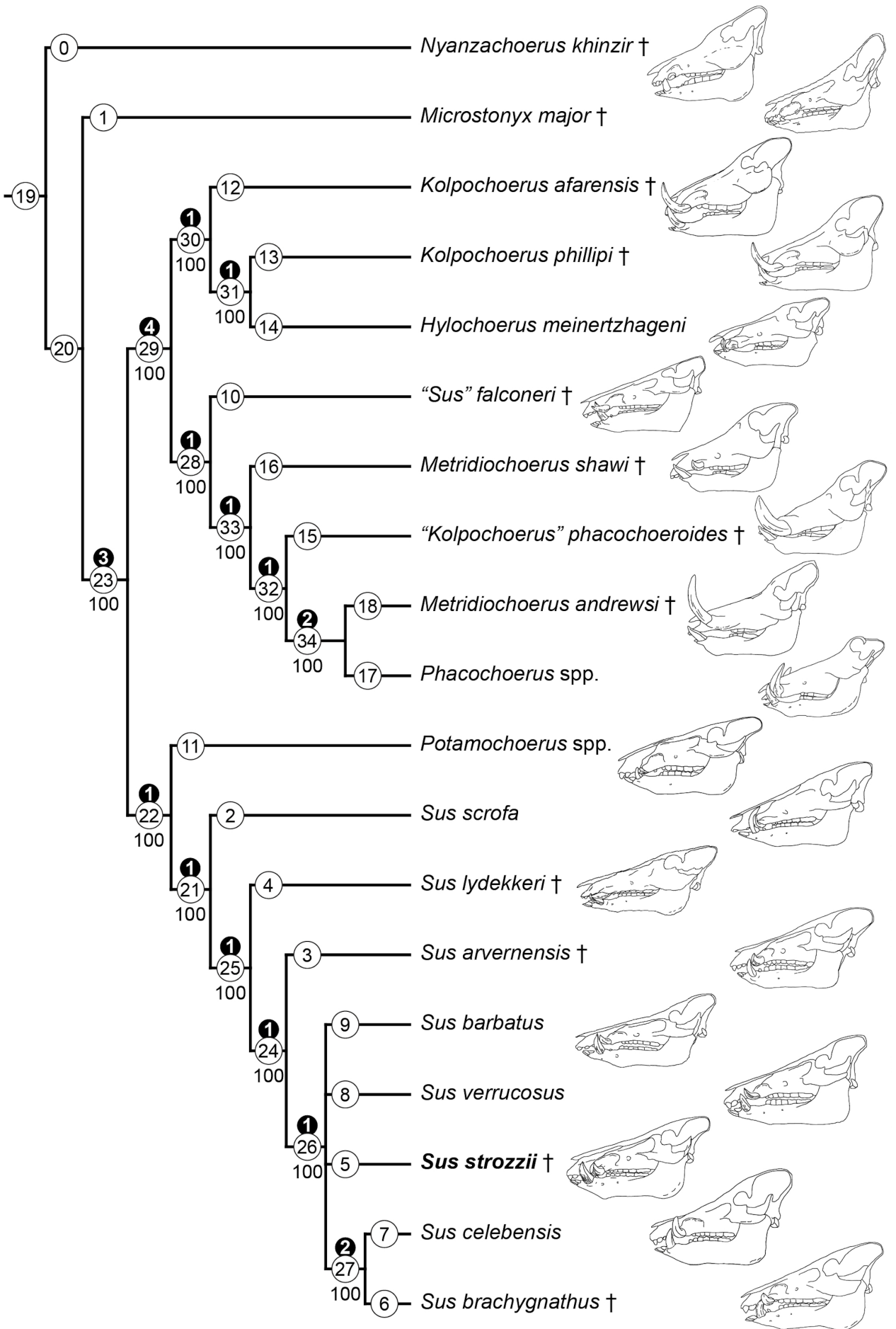
Nyanzachoerus khinzir †

Microstonyx major †

Kolpochoerus afarensis †

Kolpochoerus phillipi †

Hylochoerus meinertzhageni

"Sus" falconeri †

Metridiochoerus shawi †

"Kolpochoerus" phacochoeroides †

Metridiochoerus andrewsi †

Phacochoerus spp.

Potamochoerus spp.

Sus scrofa

Sus lydekkeri †

Sus arvernensis †

Sus barbatus

Sus verrucosus

Sus strozzii †

Sus celebensis

Sus brachygnathus †

TABLE 1. List of fossil Suinae considered in this paper in stratigraphical order with corresponding age, localities, and references.

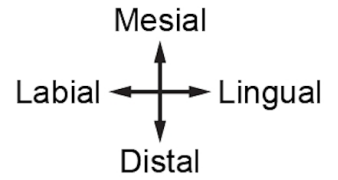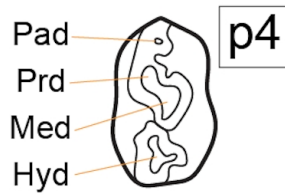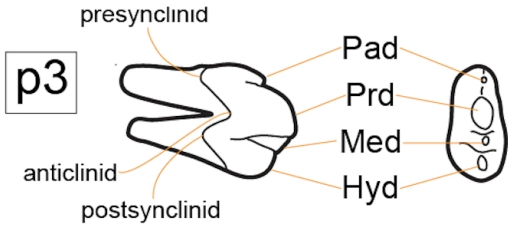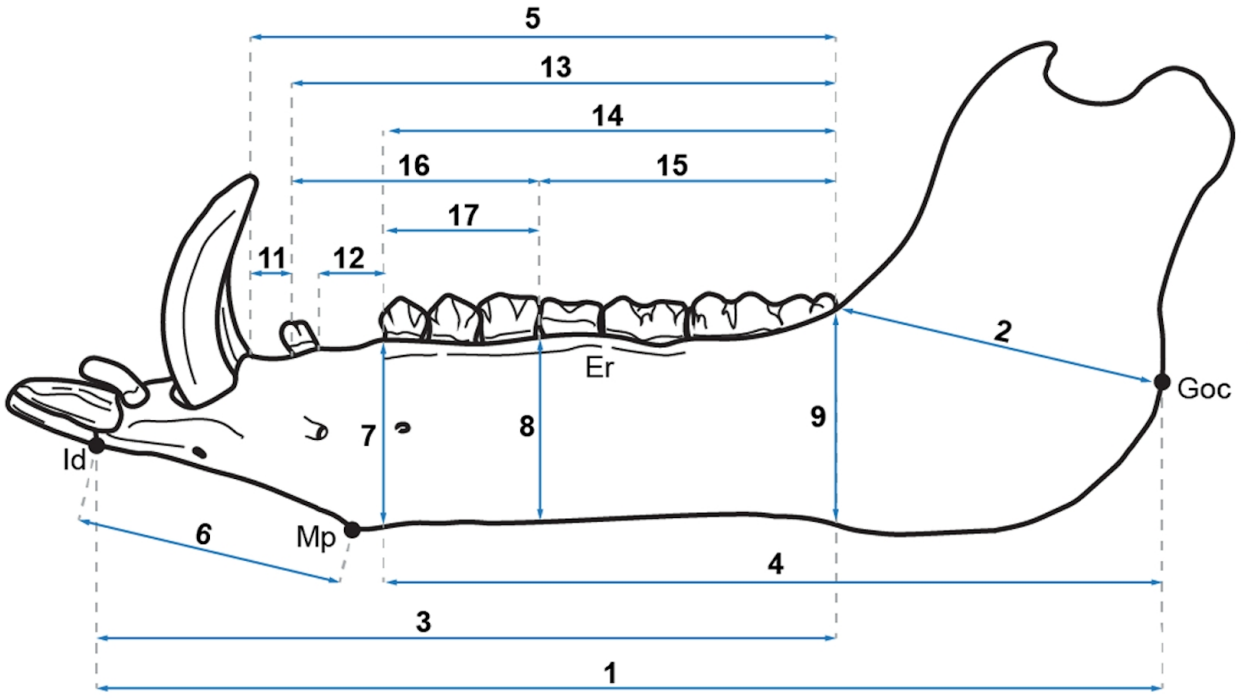| Species	Age	Localities	References
Microstonyx major	Late Miocene	**Bulgaria** Kalimanci, Ezerovo, Hadjidimovo, Petrelik	Kostopoulos et al. (2001)
		China Hezheng, Lantian, Binxian	Liu et al. (2004)
		France Luberon	Gervais (1848-1952)
		Germany Dorn-Dürkheim	Van der Made (1997)
		Greece Vathylakkos-2, Ravin de Zouaves-5, Dytiko-1, Nikiti-1, Sophades, Perivolaki, Kerassia, Pikermi, Samos, Vathylakkos 2, Proxoma, Axios Valley	Gaudry (1862-1867); Bonis and Bouvrain (1996); Kostopoulos et al. (2001)
		Iran Maragheh	De Bonis and Bouvrain (1996)
		Macedonia Titov Veles	Kostopoulos et al. (2001)
		Russia Eldar, Berislave, Grossulovo, Grebeniki, Taraklia	Trofimov (1954); Van der Made and Moyà-Solà (1989)
		Spain Crevillente 2-15-16 (Segura-Vinalopó Basin); La Roma 2, Masía del Barbo 2B, Peralejos, La Cantera, Puente Minero, Barranco de las Calaveras, Cerro de la Garita, Las Pedrizas (Teruel Basin); Terrassa, Terral d'en Maties, Piera (Vallès-Penedès Basin); La Cerdaña Basin	Van der Made (1992)
		Turkey Akkaş Dağı	Liu et al. (2005)
		Ukraine Grebeniki	Kostopoulos et al. (2001)
Sus arvernensis	Pliocene	**Bulgaria** Mussielevo	Spassov (2005)
		China ?Nanzhuanggou (Shanxi Basin)	Berdondini (1992)
		England Red Crag	Lydekker (1885, 1886); Newton (1891); Guérin et al. (1998)
		France Les Étouaires, Perpignan, Mas Bruno near St. Estève, Autrey near Gray (Haute Saône), Vialette, Trévoux-Reyrieux, Sables marins de Montpellier (composite unit)	Croizet and Jobert (1828); Depéret (1890); Azzaroli (1954); Bout (1960); Guérin et al. (1998); Pickford (2012, 2013a)
		Germany Herbolzheim, Wölfersheim-Wetterau	Tobien (1951, 1952); Guérin et al. (1998)
		Greece Milia, ?Damatria Formation (Rhodes), ?Ptolemaida/Servia, Megalo Emvolon, ?Sesklo[1]	Tobien (1981); Koufos (1986); Kostopoulos and Athanassiou (2003); Radulescu et al. (2003), Guérin and Tsoukala (2013)
		Hungary Süttö, ?Gödöllő	Mottl (1939); Guérin and Tsoukala (2013); Pickford and Obada (2016)
		India-Pakistan Siwalik Hills[2]	Pickford and Obada (2016)
		Italy Val di Pugna, ?Casino Basin, Villafranca d'Asti area, ?Collepardo (Anagni Basin)	Azzaroli (1954, 1975); Berdondini (1992); Guérin et al. (2004); Gallai (2006); Guérin and Tsoukala (2013)
		Moldova Musaitu, Dermenji (Moldovian Faunal Complex)	Pickford and Obada (2016)
		Romania Capeni-Virghis, Baraolt Basin	Radulescu et al. (2003); Radulescu (2005)
		Slovakia Hajnacka, Ivanovce	Fejfar (1961, 1964); Hünermann (1971)
		Spain Gorafe IV, Piedrabuena, Alcoy	Van der Made and Moyà-Solà (1989); Mazo and Torres (1990); Montoya et al. (2006)
		Taiwan Qiding[3]	Pickford and Obada (2016)
		Turkey Afyon Dinar Akçakoy, Çalta, Afyon Karahisar (Sandiki-Garkin area)	Hünermann (1975); Guérin et al. (1998); Guérin and Tsoukala (2013); Pickford and Obada (2016)
Kolpochoerus afarensis	Pliocene	**Ethiopia** Hadar (Sidi Hakoma, Denen Dora and Kada Hadar members), Shungura Formation (Member B), Dikika, Maka sands (Middle Awash research area)	Cooke (1978b); Souron (2012)

		Tanzania Laetoli (Upper Laetolil Beds)	Harris (1987); Bishop (2010); Souron (2012)
		Chad Koro Toro	Brunet et al. (1995)
Metridiochoerus shawi	Late Pliocene	**South Africa** Makapansgat Member 3	Bender (1992); Cooke (2005)
Metridiochoerus andrewsi	Late Pliocene-Early Pleistocene	**Ethiopia** Shungura Formation, Konso Formation, Ledi-Geraru research area, Middle Awash research area	Harris and White (1979); de Heinzelin et al. (1999); Suwa et al. (2014); DiMaggio et al. (2015)
		Kenya Koobi Fora Formation, Nachukui Formation, Kanjera Formation, Homa Mountain, Marsabit Road.	Harris and White (1979) ; Medin et al. (2015)
		Malawi Chiwondo Beds	Kullmer (2008)
		South Africa Swartkrans (Member 2), Bolt's Farm, Gondolin, Kromdraai A	Cooke (1993); Pickford (2013d); Pickford and Gommery (2016)
		Tanzania Olduvai Beds I and II	Harris and White (1979)
		Uganda Kaiso Formation	Cooke and Coryndon (1970)
"Kolpochoerus" phacochoeroides	Early Pleistocene	**Algeria** Aïn el Bey[4]	Thomas (1884)
		Morocco Ahl al Oughlam	Geraads (2004)
"Sus" falconeri	Early Pleistocene	**India-Pakistan** Siwalik Hills[5]	Lydekker (1884)
Kolpochoerus phillipi	Early Pleistocene	**Ethiopia** Matabaietu (Middle Awash research area), Ledi-Geraru research area	DiMaggio et al. (2015); Souron et al. (2015)
Sus brachygnathus	Early-Late Pleistocene	**Indonesia** Trinil, Kebonduren, Bangle, Kaligede, Teguan, Watualang[6]	Hardjasasmita (1987)
Sus strozzii	Early Pleistocene	**Azerbaijan** Palan-Tyukan	Titov (2000); Kostopoulos and Athanassiou (2003)
		England Red Crag	Owen (1856); Lydekker (1885, 1886); Stuart (1982); Van der Made and Moyà-Solà (1989)
		France Sables marins de Montpellier (composite unit), Senèze, ?Le Coupet, Saint-Vallier	Schaub (1943); Azzaroli (1954, 1975); Fejfar (1964); Geraads et al. (1986); Faure (2004); Pickford (2013a)
		Greece Gerakarou, Vassiloudi	Koufos (1986); Kostopoulos and Athanassiou (2003)
		Holland Tegelen	Richarz (1921); Bernsen (1931); Schreuder (1945); Hooijer (1947); Van der Made and Moyà-Solà (1989)
		Israel Oubeidiyeh	Geraads et al. (1986); Kostopoulos and Athanassiou (2003)
		Italy Upper Valdarno, Olivola, ?Casino Basin, Coste San Giacomo, Monte Riccio, Mugello, Torre Picchio, Villa San Faustino, Santa Sabina, Frantoio (Arda River)	Forsyth-Major (1881); Stehlin (1899-1900); Azzaroli (1954, 1975); Faure and Guérin (1984); Ambrosetti et al. (1995); Girotti et al. (2003); Mazzini et al. (2000); Pazzaglia et al. (2013); Bellucci et al. (2014); Bona and Sala (2016); Pickford and Obada (2016)
		Moldova ?Khaprovian and Odessian Faunal Complexes	David et al. (1997)
		Romania Valea Graunceanului (Dacian Basin)	Bolomey (1965); Faure (2004)
		Russia Khapry, ?Taman Peninsula[7]	Alekseeva (1977); Titov (2000)
		Spain Fonelas[8], Valdeganga	Van der Made and Moyà-Solà (1989); Opdyke et al. (1997); Pickford and Obada (2016)

Sus lydekkeri	Early-Middle Pleistocene	**China** Lantian Man Site of Gongwangling, Hexian Man Site, Nanjing Man Site, Yunxian Man Site, Tuozi Cave, Yangshuizhan, Nihewan Basin, Peking Man Site (Locality 1) of Zhoukoudian, Xinyaozi	Teilhard de Chardin and Piveteau (1930); Hu and Qi (1978); Huang et al. (1982); Liu (1991); Huang (1996); Dong (1999); Dong et al. (2007); Dong and Fang (2008); Echassoux et al. (2008); Liu et al. (2017)
Sus macrognathus	Middle-Late Pleistocene	**China** Liucheng *Gigantopithecus* Cave[9], Bijiashan Cave	Han et al. (1975); Pickford and Obada (2016)
		Indonesia Kedungbrubus, Kebonduren, Bangle, Ngandong, Sumberkepuh, Teguan, Watualang, Sangiran	Hardjasasmita (1987); Pickford (2013b)
		Myanmar Naungkwe Taung	Pickford (2013b)
		Taiwan Qiding	Qi et al. (1999); Pickford and Obada (2016)

[1]*Sus* cf. *strozzii* in Symeonidis (1992).
[2]*Sus hysudricus* in Falconer and Cautley (1846) and Pilgrim (1925, 1926).
[3]*Sus houi* in Qi et al. (1999).
[4]*Sus phacochoeroides* in Thomas (1884).
[5]*Kolpochoerus falconeri* in Chavasseau (2008), Pickford (2012, 2013a), and Pickford and Obada (2016).
[6]*Sus vatualangensis* in Von Koenigswald (1933).
[7]*Sus tamanensis* in Vereshchagin (1957).
[8]*Potamochoerus magnus* in Arribas and Garrido (2008).
[9]*Sus australis* in Han (1987).

TABLE 2. Mandibular measurements (in mm) of *Sus strozzii* SBAU 337647 from Pantalla (Italy).

1	Length from the gonial angle (Infradentale - Gonion caudale)	*329.0*
2	Distance between distal border of m3 and Gonion caudale	*110.5*
3	Distance between Infradentale and distal border of m3	225.2
4	Distance between mesial border of p2 and Gonion caudale	*237.0*
5	Distance between distal border of c1 and distal border of m3	170.2
6	Rostroventral length of the mandibular corpus (Infradentale-mental prominence)	101.7
7	Height of the mandibular corpus at the mesial border of p2	57.2
8	Height of the mandibular corpus at the mesial border of m1	66.3
9	Height of the mandibular corpus at the distal border of m3	66.9
10	Length of the symphysis	105.4
11	Length of the c1-p1 diastema	6.7
12	Length of the p1-p2 diastema	23.6
13	Length of the cheektooth row (p1 included)	163.3
14	Length of the cheektooth row (p1 excluded)	133.3
15	Length of the molar row	90.3
16	Length of the premolar row (p1 included)	73.1
17	Length of the premolar row (p1 excluded)	43.5
	c1 labial length	23.2
	c1 lingual length	26.7
	c1 distal width	19.6
	p1 alveolus length	7.4
	p1 alveolus width	5.1
	p2 length	14.0
	p2 width	*9.4*
	p3 length	13.2
	p3 width	10.3
	p4 length	14.8
	p4 width	13.1
	m1 length	17.6
	m1 mesial width	13.8
	m1 distal width	14.5
	m2 length	22.8
	m2 mesial width	16.8
	m2 distal width	18.0
	m3 length	49.8
	m3 maximum width	22.0
	m3 talonid length	34.9
	m3 talonid mesial width	19.8
	m3 talonid distal width	17.4

Numbers in the first column correspond to those in Fig. 1 (measurement 10 not figured). Values in italics are estimated. All dental measurements are taken at the cervix, except when stated otherwise.

TABLE 3. Distribution of character states for nodes in the most parsimonious trees.

Node	**Character**(state transformations)
<u>1</u>	**7(0>1), 9(0>1)**
<u>2</u>	**6(1>0), 7(1>0), 27(1>0), 32(1>0), 46(1>0)**
<u>3</u>	**23(0>1)**
<u>4</u>	**21(1>0), 25(1>0)**
<u>5</u>	**28(0>1), 36(0>1),** *8(1>0)*
<u>6</u>	**20(1>0), 25(1>0), 50(1>0)**
<u>7</u>	**19(0>1), 46(0>1),** *3(0>1)*
<u>8</u>	**7(0>1),** *8(1>0)*, **27(1>0),** *51(1>2)*
<u>9</u>	**6(1>0), 13(1>0), 33(0>1), 46(0>1),** *51(1>2)*
<u>10</u>	**11(0>1), 12(0>1), 13(2>1), 14(1>0), 45(1>0)**
<u>11</u>	**5(0>2), 11(0>1), 24(0>1)**
<u>13</u>	**15(1>2), 27(1>0)**
<u>14</u>	**2(0>1), 3(1>0), 4(2>1), 8(1>0), 9(0>1), 11(0>1), 14(1>0), 29(0>1), 30 (1>0), 34(0>1), 35(0>1), 36(0>1), 37(0>1), 44(0>1), 47(0>1), 48(0>1)**
<u>15</u>	**2(0>1), 3(1>0), 48(0>1)**
<u>17</u>	**1(1>0), 13(2>0)**
<u>18</u>	**7(0>1)**
21	**13(2>1), 14(1>0)**
22	**3(1>0), 4(2>1), 12(0>1)**
23	**33(1>02), 39(1>0), 47(1>0), 51(0>1)**
24	**5(0>1)**
25	**22(1>0), 26(0>1), 39(0>1)**
26	**41(0>2), 50(0>1)**
27	**17(1>0), 23(0>1),** *27(1>0)*
28	**8(1>2), 21(1>2), 38(0>1), 50(0>1)**
29	**0(1>0), 23(0>1), 28(0>1), 41(0>1)**
30	**5(0>1), 10(0>1), 16(0>1), 20(1>0)**
31	**7(0>1), 40(0>1), 43(0>1)**
32	**29(0>1), 44(0>1), 51(1>2)**
33	**30(1>0), 37(0>1)**
34	**11(0>1), 12(0>1), 18(1>0), 35(0>1)**

Node numbers refer to nodes in the strict consensus tree (Fig. 7). Terminal nodes are underlined. Italics indicate ambiguous apomorphies inferred here using the ACCTRAN optimization.

Appendix 1

LIST OF CRANIOMANDIBULAR AND DENTAL CHARACTERS USED IN THE CLADISTIC ANALYSIS

Unordered and unweighted states for all characters.

All characters were coded on male individuals unless otherwise stated.

0. Cranium, greatest frontal width relative to 1/3 of cranial length: similar or longer (0); shorter (1).

Remarks: This character describes the general shape of the cranium: species exhibiting character state 0 have relatively shorter and wider crania than those with character state 1. The greatest frontal width corresponds to the greatest width across the orbital processes of the frontal bone; the cranial length is measured as the distance between Akrokranion and Prosthion. Character modified from Souron et al. (2015: 3).

1. Cranium, angulation between splanchnocranium and neurocranium in lateral view: absent (0); present (1).

Remarks: This character describes the general dorsal profile of the cranium in lateral view and reflects the vertical development of the forehead. Character modified from Souron et al. (2015: 4).

2. Cranium, notch at level of frontoparietal suture in lateral view: absent (0); present (1).

3. Splanchnocranium, length relative to 60% of total cranial length: similar or shorter (0); longer (1).

Remarks: This character describes the relative elongation of the rostrum. The length of the splanchnocranium is measured as the distance between Supraorbitale and Prosthion. Cranial length is measured as in character n. 0.

4. Splanchnocranium, height relative to cranial height: high (0); very high (1).

Remarks: This character describes the relative dorsoventral development of the rostrum. Splanchnocranium height is measured at the mesial border of M1; cranial height is measured between the distal border of M3 and the dorsal margin of the orbit. The character is coded as follows: ratio >60% (0); ratio ≤60% (1). Character modified from Souron et al. (2015: 5).

5. Splanchnocranium, development of rhinarium muscle scars: absent or indistinct (0); present (1); very marked (2).

    Remarks: Character modified from Souron et al. (2015: 7).

6. Premaxillae, proportions: relatively narrow (0); relatively wide (1).

    Remarks: The relative width of the premaxillary area is measured as the ratio between the distance between the mesial border of canines and that between the latter point and the Prosthion. We assign character state 0 to taxa with average ratio <85% and character state 1 to taxa with average ratio ≥85%. Character modified from Souron et al. (2015: 8).

7. Neurocranium, relative width of postorbital constriction: relatively narrow (0); relatively wide (1).

    Remarks: In taxa with character state 0, the ratio between the least width of the postorbital constriction and the greatest frontal width (see character n. 0) is <45%, while in taxa exhibiting a relatively wider parietal area (character state 1), this ratio is ≥45%. Character modified from Souron et al. (2015: 6).

8. Neurocranium, nuchal crest, width relative to the greatest frontal width: very large (0); large (1); narrow (2).

    Remarks: The relative width of the nuchal crest is measured as the ratio between the width of the nuchal crest in dorsal view and the greatest width across the orbital processes of the frontals. The character is coded as follows: ratio ≤100% (0); ratio >100% and <140% (1); ratio ≥140% (2). Character modified from Souron (2012: 4).

9. Neurocranium, parietal dorsal surface: flat or convex (0); concave (1).

    Remarks: Character modified from Geraads (2004: 1).

10. Neurocranium, morphology of the parietal ventrally to the temporal line: inflated (0); flat or concave (1).

    Remarks: In taxa showing character state 0, there is not a distinct change of slope between the dorsal part of the temporal fossa and the parietal roof. Whereas, this change of slope is visible in taxa showing character state 1. Character from Souron (2012: 6).

11. Nasals, length relative to 1/2 of total cranial length: equal or lower (0); higher (1).

    Remarks: Cranial length is measured as in character n. 0.

12. Zygomatic arch, height relative to 1/2 of height of the occipital region: higher (0); lower (1).

  Remarks: The height of the zygomatic arch is measured at the medioventral border of the orbit. The height of the occipital region corresponds to the distance between Akrokranion and Basion.

13. Zygomatic arch, outline of the rostral border in dorsal view: straight (0); inclined (1); transverse (2).

  Remarks: In taxa showing character state 0, the rostral border of the zygomatic arch forms a flat outline in continuity with the lateral border of the maxilla; in those showing character state 1, the rostral border of the zygomatic arch forms an obtuse angle with the lateral border of the maxilla; in those showing character state 2, this angle is about 90°. Character modified from Souron et al. (2015: 1).

14. Zygomatic arch, ventral outline in lateral view: straight (0); drooping (1).

  Remarks: Character modified from Souron et al. (2015: 10).

15. Zygomatic arch, mediolateral thickness in dorsal view: thin (0); thickened (1); rounded knob-shaped (2).

  Remarks: Character modified from Souron et al. (2015: 2).

16. Zygomatic arch, lateral protuberance in females: absent (0); present (1).

  Remarks: Character modified from Souron (2012: 10).

17. Orbit, position of the rostral border in lateral view: above M3 (0); posterior to M3 (1).

  Remarks: Character from Geraads (2004: 4).

18. Preorbital fossa: indistinct (0); present (1).

  Remarks: The preorbital fossa is here interpreted as the "well marked fossa on the side of the face immediately in front of the eye, involving parts of the lachrymal, jugal and maxillary bones" (Ewer, 1958: 141), representing the posterior insertion area of the *levator rostri* muscle. Character from Orliac et al. (2010a: 9).

19. Preorbital fossa, depth: deep (0); shallow (1).

20. Tympanic bullae, development: relatively large (0); relatively small (1).

Remarks: Character modified from Geraads (2004: 14).

21. Occipital condyles, position relative to cheektooth row in lateral view: low (0); high (1); very high (2).

Remarks: Character modified from Geraads (2004: 17).

22. Occipital region, overall shape in caudal view: high and narrow (0); low and wide (1).

Remarks: This character is measured as the ratio between the greatest width of the nuchal crest and the height of the occipital region (i.e., distance between Akrokranion and Basion). We assign character state 0 to taxa with average ratio <75% and character state 1 to taxa with average ratio ≥75%.

23. Mandible, shape of the symphysis area in occlusal view: long and narrow (0); short and wide (1).

Remarks: In taxa exhibiting character state 0, the average ratio between the mandible width at the labial margin of canine alveoli and the symphysis length is <85%; in taxa exhibiting character state 1, this ratio is ≥85%. Character modified from Souron et al. (2015: 13).

24. Mandible, bony shelf at the caudoventral corner of the symphysis: absent (0); present (1).

25. Mandible, ventral extension of the angular process: present (0); absent (1).

Remarks: The ventral extension of the angular process is coded as present when the Gonion ventrale is more ventral than the ventral margin of the corpus in labial view. Character modified from Orliac et al. (2010a: 34).

26. Mandible, corpus, shape of the labial longitudinal swelling in males: sub-parallel to the tooth row (0); showing a convexity in the median part (1); enlarging rostrocaudally (2).

Remarks: For the evaluation of this character, mandibles are observed in occlusal view. *Sus scrofa* exhibits character state 0, although the forms from Flores (*S. scrofa vittatus* or *S. scrofa floresianus*; Hardjasasmita, 1987) shows a strong but relatively small bony protuberance on the labial side of each mandible corpus (see Hardjasasmita, 1987: 57). However, this protuberance is here interpreted as a derived sexual character of these subspecies and is different from the undulate labial margin of the corpus which characterise the taxa coded with character state 1. Character modified from Souron et al. (2015: 15).

27. Mandible, angle between corpus and ascending ramus: approximately right (0); obtuse (1).

28. Upper canines, length: long (0); very long (1).

Remarks: We consider the canine as long when it extends over the lateral margin of the maxilla, without reaching that of the zygomatic arch; very long when it exceeds the lateral margin of the zygomatic arch. Character modified from Geraads (2004: 29).

29. Upper canines, enamel: present (0); absent (1).

Remarks: Given the possible ontogenetic variation of this character (e.g., enamel present in juveniles and absent in adults), we coded it only for adult individuals. Character from Geraads (2004: 20).

30. Upper canines, supracanine flange: absent or weak (0); crest-like (1).

Remarks: Character modified from Souron et al. (2015: 10).

31. Upper canines, supracanine flange dorsoventral development: low (0); high (1).

Remarks: Character from Souron et al. (2015: 11).

32. Upper canines, supracanine flange rostrocaudal development: short (0); elongated (1).

Remarks: Character from Souron et al. (2015: 12).

33. Upper tooth row, relative length of the upper post-canine diastema: short (0); medium (1); long (2).

Remarks: The relative length of the diastema is calculated as the ratio between the actual length of the diastema and the palate width at the mesial border of M1. The character is coded as follows: ratio ≤25% (0); ratio >25% and <40% (1); ratio ≥40% (2).

34. Upper incisors, size of I1: large (0); small (1).

Remarks: Character from Geraads (2004: 21).

35. Upper incisors, I2: present (0); absent or very reduced (1).

36. Upper incisors, I3: present (0); absent or very reduced (1).

Remarks: Character from Geraads (2004: 23).

37. Upper premolars, P2: present (0); reduced or absent (1).

Remarks: Character modified from Souron et al. (2015: 18).

38. Upper premolars, molarization of P4: absent (0); present (1).

39. Upper and lower premolars, style/stylid in P3-P4/p3-p4: weak (0); well developed (1).

Remarks: Character discussed in Hardjasasmita (1987).

40. Upper and lower molars, mesiodistal compression of the main cusps/cuspids: absent (0); present (1).

Remarks: Character from Souron (2012: 24).

41. Upper and lower molars, complexity of enamel figures exposed at the occlusal surface: low (0); high (1); very high (2).

Remarks: In taxa showing character state 0, the enamel figures exposed at the occlusal surface of worn cusps/cuspids are sub-circular or with very few invaginations. The latter figures are instead well visible in taxa showing character state 1 and became even more complex and deep in taxa showing character state 2.

42. Lower canines, morphology: verrucosic (0); scrofic (1).

Remarks: See the manuscript for details on this character.

43. Lower incisors, development of i1-i2: i1-i2 very long and parallel, forming a comb (0); i2 smaller than and oblique to i1 (1).

Remarks: Character from Souron et al. (2015: 19).

44. Lower incisors, arcade angle: acute (0); right or obtuse (1).

Remarks: The angle is measured between two lines passing through the mesial margin of the canine alveolus and the Infradentale.

45. Lower premolars, p1: present (0); reduced or absent (1).

46. Lower premolars, p1 position: very close to the lower canine (0); about in the middle of the post-

canine diastema (1).

47. Lower premolars, p2: present (0); reduced or absent (1).

48. Lower premolars, p3: present (0); reduced or absent (1).

49. Lower premolars, occlusal shape of p4: sub-quadrangular (0); mesiodistally elongated (1).

50. Lower premolars, morphology of p4: one main cuspid clearly separated from a low talonid (0); high talonid, forming a blade with the main cuspid or a wide and flat occlusal surface (1).

Remarks: Character discussed in Azzaroli (1954).

51. Lower molars, relative size of the distal part of the m3 talonid: short (0); long (1); very long (2).

Remarks: The relative length of the distal part of the m3 talonid is measured as the ratio between the distal talonid length (i.e., length of the portion distal to the hypoconid and entoconid) and the total length of m3. The character is coded as follows: ratio ≤35% (0); ratio >35% and <45% (1); ratio ≥45% (2).

Additional reference

Ewer, R.F., 1958. Adaptive features in the skulls of African Suidae. Journal of Zoology 131, 135–155.

Appendix 3
CHARACTER-TAXON MATRIX

		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
1	*Nyanzachoerus khinzir*	?	0	0	?	1	0	0	0	?	0	0	?	0	2	1	1	0	1	1	1	0	1	?	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	-	1	0	0	0	0
2	*Microstonyx major*	1	1	0	1	1	0	1	1	1	1	0	0	0	2	1	1	?	1	1	0	1	1	1	0	0	?	0	?	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	1	1	-	1	0	1	0	0
3	*Sus scrofa*	1	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0/1	1
4	*Sus arvernensis*	1	0	0	0	0	1	1	0	?	0	0	0	1	1	0	0	0	1	1	0	?	1	?	1	0	?	1	?	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1
5	*Sus lydekkeri*	1	0	0	0	0	0	1	0	1	0	0	0	1	1	0	1	0	1	1	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0/1	0	0	0/1	0	0	0	1	0	1
6	*Sus strozzii*	1	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1	0	1	1	0	1	1	0	0	0	1	1	1	1	0	1	1	1	0	0	0	1	0	0	1	0	2	0	0	0	0	0	0	0	1	1	1
7	*Sus brachygnathus*	1	0	0	0	0	1	1	?	?	0	0	0	1	1	?	0	0	0	1	0	0	1	?	1	0	0	1	0	?	0	1	1	1	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	1	0	1
8	*Sus celebensis*	1	0	0	1	0	1	1	0	1	0	0	0	1	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	2	0	0	0	0	1	0	0	1	1	1
9	*Sus verrucosus*	1	0	0	1	0	1	1	0	0	0	0	0	1	1	1	1	0	1	1	0	1	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	1	1	2
10	*Sus barbatus*	1	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	2	0	0	0	0	1	0	0	1	1	2
11	*"Sus" falconeri*	0	0	0	1	1	?	1	0	2	0	0	1	1	1	0	1	0	1	1	1	2	1	1	0	1	?	1	?	?	1	1	1	0	0	0	0	0	0	1	0	0	1	0	?	0	0	0	0	0	1	1	1
12	*Potamochoerus* spp.	1	0	0	0	0	2	1	0	1	0	0	1	1	2	1	0	1	0	1	0	1	1	0	1	1	0	1	0	0	1	1	2	0	0	0	0	0	0	0	0	1	0	1	1	-	0	0	1	0	1	0	1
13	*Kolpochoerus afarensis*	?	1	0	?	1	1	?	0	1	?	1	?	?	2	1	1	1	1	1	0	?	?	1	0	1	?	?	?	0	1	?	?	?	0	0	0	0	0	0	0	0	0	1	0	0	1	-	0	1	0	0	1
14	*Kolpochoerus phillipi*	0	1	0	1	1	1	1	1	1	0	1	0	0	2	1	2	?	1	1	1	?	1	?	1	0	1	1	0	1	0	1	1	1	0	0	0	0	0	0	0	1	1	0	1	0	1	-	0	1	1	0	1
15	*Hylochoerus meinertzhageni*	0	1	1	0	0	1	1	1	0	1	1	1	0	2	0	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	0	-	-	2	1	1	1	1	0	0	1	1	0	1	1	-	1	1	1	1	1	1
16	*"Kolpochoerus" phacochoeroides*	0	1	1	0	1	0	1	0	2	1	0	0	0	2	1	2	?	1	1	1	1	2	1	1	0	?	2	?	1	1	0	-	-	2	0	0	0	1	1	0	0	1	0	0	1	1	-	1	1	1	1	2
17	*Metridiochoerus shawi*	0	1	0	1	1	0	1	0	2	0	0	0	0	2	1	?	?	1	1	1	1	2	?	?	?	?	?	?	?	?	0	0	-	-	1	1	0	1	1	1	0	0	1	0	?	0	1	-	?	0	1	1
18	*Phacochoerus* spp.	0	0	0	1	1	0	1	0	2	0	0	1	1	0	1	2	0	1	0	-	1	2	1	1	0	1	2	1	1	1	0	-	-	2	1	1	1	1	1	0	0	0	0	1	1	-	1	0	1	1	1	2
19	*Metridiochoerus andrewsi*	0	1	0	1	1	0	1	1	2	1	0	1	1	2	1	2	0	1	0	-	1	2	?	1	0	1	2	1	1	1	0	-	-	2	1	1	1	1	1	0	0	2	0	0	1	1	-	1	0	1	1	2