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Original article

Sus strozzii (Suidae, Mammalia) from the historical locality of Quercia (Early Pleistocene, Italy) ☆

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A B S T R A C T

Some remains of suids were recovered during the second half of the 1800s from Quercia (Tuscany, Italy), at a close distance to, but from a lower stratigraphic position than the better-known mammal fauna of Olivola. Although they were collected a long time ago, Quercia suids are described for the first time in this work. This sample represents one of the earliest occurrences (middle Villafranchian) of *Sus strozzii*, a large-sized suid present in Europe during the Early Pleistocene, but only abundant ~2.0–1.8 Ma. A biometric comparison with selected samples of Pliocene to early Middle Pleistocene European suids is carried out, showing some dimensional changes in *S. strozzii* as well as differences between *S. strozzii* and other species. Quercia has been somehow eclipsed by other historical samples from Tuscany, namely the extensive collection of the Upper Valdarno and the diverse fauna of Olivola, but it is a different and important palaeontological locality. Apart from *S. strozzii*, the local fauna of Quercia-Vaccareccia includes *Anancus arvernensis*, *Canis* sp., *Stephanorhinus etruscus*, *Leptobos etruscus*, '*Pseudodama*' sp., and *Castor* sp., representing one of the few mammal assemblages referable to the Faunal Unit of Coste San Giacomo (late middle Villafranchian, MNQ 17b), corresponding to ~2.2–2.1 Ma.

1. Introduction

The family Suidae includes around 20 extant species of even-toed ungulates commonly known as pigs, comprising babirusas, bushpigs, wild boars, and warthogs, among others (Melletti and Meijaard, 2017). Even though wild boars and domestic pigs were introduced by humans in many regions of Americas and Oceania (e.g., Bengsen et al., 2017; Majer, 2017; Salvador and Fernandez, 2017), extant and extinct Suidae are native to the Old World (Africa and Eurasia). Today the Eurasian wild boar, *Sus scrofa* Linnaeus, 1758 is the only wild species inhabiting Europe and by far the most widespread representative of the whole family, but the region was once home of many other pigs (Van der Made and Moyà-Solà, 1989; Pickford, 1993; Fortelius et al., 1996; Van der Made, 1996; Harris and Liu, 2007; Pickford and Obada, 2016; Iannucci et al., 2021a; Iannucci and Begun, 2022; McKenzie et al., 2022; Van der Made et al., 2022; Iannucci, 2023).

Before the wild boar appeared in the European fossil record close to the Early-Middle Pleistocene boundary (Van der Made et al., 2017; Cherin et al., 2020; Iannucci, 2022), *S. strozzii* Forsyth Major, 1881 occupied the territory for most of the Early Pleistocene, being recorded from several localities from Spain to western Asia (Mein et al., 1978; Van der Made and Moyà-Solà, 1989; Kostopoulos and Athanassiou, 2005; Cherin et al., 2018; Iannucci et al., 2020a; Iltsevich and Sablin, 2022). *Sus strozzii* was a large-sized suid closely related to the so-called warty pigs of Island Southeast Asia (Azzaroli, 1952, 1975; Cherin et al., 2018; Iannucci et al., 2020a), which constitute a diverse and yet relatively poorly known contingent of species (Hardjasasmita, 1987). *Sus strozzii* was mainly abundant in early late Villafranchian faunas, especially from sites of the Italian Peninsula referable to the Olivola and Tasso Faunal Units (FUs), i.e., ~2.0–1.8 Ma (Azzaroli, 1977; Gliozzi et al., 1997), but remains assigned to this species have been recovered from middle Villafranchian and Epivillafranchian localities as well (Van der Made and Moyà-Solà, 1989; Cherin et al., 2018, 2020; Iannucci et al., 2020a; Iannucci, 2022).

The taxonomic assignment of latest Early Pleistocene (Epivillafranchian) suids has been the subject of much controversy over the last years (Martínez-Navarro et al., 2015; Van der Made et al., 2017; Iannucci et al., 2020a), partly due to the paucity of specimens recovered from most Epivillafranchian localities and objective difficulties in the distinction between isolated remains of *S. strozzii* and *S. scrofa*. An attribution of the Epivillafranchian suids to *S. strozzii* represents the best fit for the available evidence

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(Cherin et al., 2020), although they show some differences from typical representatives of the species (Iannucci, 2022).

If the Epivillafranchian record is fundamental for investigating the relationship between the extinction of *S. strozzii* and the dispersal of *S. scrofa*, and the potential link between these bioevents and other environmental and faunal changes occurred during the Early–Middle Pleistocene Transition (Kahlke et al., 2011; Head and Gibbard, 2015; Iannucci et al., 2021b), the middle Villafranchian is similarly crucial for gaining knowledge on the origin of *S. strozzii* itself, in the framework of the faunal turnover that occurred in this biochron (Iannucci and Sardella, 2023; Iannucci et al., 2023). Even in this case, however, there are not but a few localities that have yielded remains of the appropriate age. Among these, those confidently dated more than 2.0 Ma include: two lower molars from Valdeganga II likely belonging to the same individual (Mein et al., 1978; van Dam et al., 2023); a fragmentary deciduous premolar from Saint-Vallier (Faure, 2004; Guérin et al., 2004); some fragmentary and/or isolated teeth from Coste San Giacomo (Bellucci et al., 2014); two maxillary fragments from Vigna Nuova likely belonging to the same individual (Azzarà et al., 2022); and finally, an almost complete subadult skeleton from Senèze (Schaub, 1943; Azzaroli, 1952). An even older record of *S.* cf. *strozzii* is cited from Bethlehem (Hooijer, 1958), which is tentatively placed in the late Pliocene (Rabinovich and Lister, 2017), but the fragmentary mandible and isolated incisor described by Hooijer (1958) should be restudied to validate this attribution. To this succinct record might be added other findings of less certain age (e.g., Cherin et al., 2018), but in any case, this list highlights the scanty and poorly informative nature of middle Villafranchian suid remains, apart from the Senèze skeleton, and the salient need for discovery and description of further material.

Here, a small collection of suid remains recovered from Quercia (Tuscany, Italy) in the second half of the nineteenth century, is described. The existence of suid specimens from this locality, which constitutes one of the few middle Villafranchian occurrences of *S. strozzii*, has been occasionally reported for a long time (Forsyth Major, 1890; Azzaroli, 1950, 1952; Faure and Guérin, 1984; Azzaroli et al., 1988; Masini et al., 1994; Kahlke, 2009), but Quercia was not mentioned in recent works with dedicated discussions on suids in which one would have expected to find it (Van der Made et al., 2017; Cherin et al., 2018) and the material has never been described so far.

2. Geological setting, palaeontological framework, and historical background

The Aulla-Olivola Basin, in north-western Tuscany, Italy, is one of the northernmost intermontane basins of the northern Apennines (Fig. 1(A)). The area is part of a ~40 km long graben that stretches north also including the Pontremoli Basin, which is alternatively considered the result of an independent evolution (Bertoldi, 1988; Bernini and Papani, 2002), or once part, jointly with Aulla-Olivola, of a single larger basin, subsequently fragmented during the Pleistocene (Raggi, 1985). Both basins document a similar transition from fluvio-lacustrine to fluvial environments, but the base of the Aulla-Olivola deposits is considered older that of the Pontremoli Basin (Raggi, 1985; Bertoldi, 1988; Bernini and Papani, 2002). Federici et al. (1982) recognised three units within the Aulla-Olivola Basin, representing different stages of the sedimentary evolution of the basin. These are, from bottom to top: (*i*) lacustrine silts and clays; (*ii*) alternating clays, sands, and gravels; and (*iii*) prevalently fluvial conglomerates ("Olivola Conglomerates").

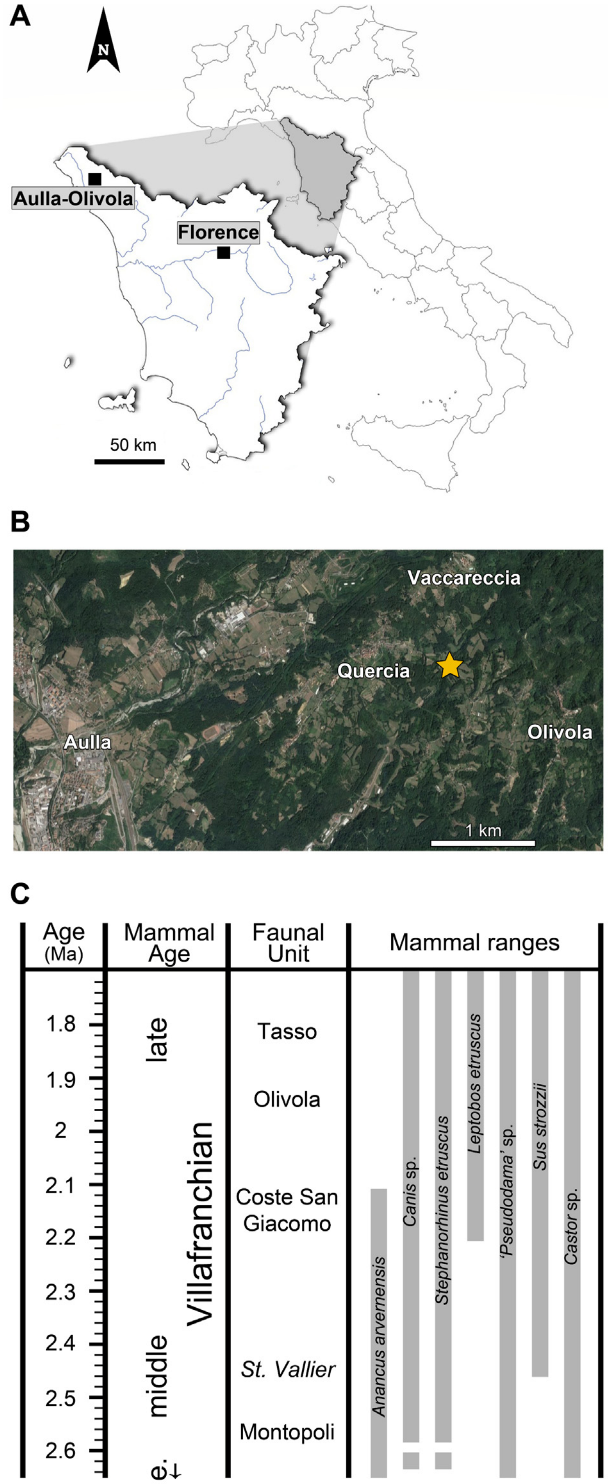

Fig. 1. **A**. Location of the Aulla-Olivola Basin in Italy. **B**. Magnified view of the area. **C**. Biochronological scheme. The star indicates the reconstructed position of the fossil site of Quercia.

The oldest mammal findings recorded from the Aulla-Olivola Basin are those recovered from a quarry north of Aulla, where the first unit is best exposed. The fossils collected therein consist of deer remains assigned to *Procapreolus cusanus* and *Pseudodama* ex gr. *pardinensis-lyra* by Abbazzi et al. (1995). These species tie the beginning of the continental succession in the basin at least to the middle Villafranchian, with an even older age suggested by palynological analyses (Bertoldi, 1988). Proceeding east, sediments of the second unit are well represented along the road between Quercia and Olivola, and those of the first at Olivola (Federici et al., 1982). The Olivola Conglomerates yielded an important large mammal fauna (Forsyth Major, 1890; Azzaroli, 1950). The occurrence of some fossil mammals from Olivola has already been reported in the second half the 1700s (Targioni Tozzetti, 1777). After almost a century, Cocchi (1856) provided detailed geological information on the area, and subsequently mentioned the presence of bones of large ruminants, pachyderms, and some carnivores (Cocchi, 1866). Apart from early findings and investigations (see also Forsyth Major, 1879, 1890; Capellini, 1889), the first proper study of Olivola was conducted by Forsyth Major (1890), who excavated the site in 1889. In his work, Forsyth Major also briefly mentioned some stratigraphically lower finds deriving from nearby outcrops, including few mammal remains from Quercia deposited in the Museum of Florence. According to Forsyth Major (1890), these fossils were recovered from clays outcropping at 120 m a.s.l., which allows to approximately locate the area from where these specimens were collected (Fig. 1(B)). In terms of mammal biochronology, the local fauna of Olivola has been taken as the reference of the homonymous FU, the first of the late Villafranchian (Azzaroli, 1970, 1977; Azzaroli et al., 1982, 1988; Gliozzi et al., 1997). The toponym Quercia (literally, Italian for "oak") stands for a small hamlet, only ca. 2 km west of Olivola, but far lesser known in the palaeontological community. Indeed, Quercia fossils are almost undescribed, but Masini et al. (1994) reported a faunal list including, apart from suids, *Anancus arvernensis*, *Stephanorhinus etruscus*, "a deer similar in size to *Pseudodama nestii*" (which should be conservatively referred to as '*Pseudodama*' sp.; see Cherin et al., 2022 for a recent discussion on the taxonomy of *Dama*-like deer), *Leptobos etruscus*, *Canis* sp., and *Castor plicidens* (alternatively considered a valid species or a subspecies of *Castor fiber*, hence *Castor* sp. is used herein; e.g., Barisone et al., 2006; Cuenca-Bescós et al., 2017). This list is actually composed of remains recovered from Quercia and outcrops of the same clay formation near to Vaccareccia – not to be confused with Vacchereccia, which is instead one of the localities from which part of the historical collections of the Upper Valdarno come from – ca. 1 km further north (Fig. 1(B)).

The presence of *A. arvernensis*, represented by a fragment of a molar described by Weithofer (1891), allows a reference to the middle Villafranchian, as accepted in subsequent studies in which Quercia is mentioned in passing (Abbazzi et al., 1995; Palombo et al., 2002; Bona and Sala, 2016). Indeed, the last firmly dated appearance of *A. arvernensis* in Italy is from the type fauna of the Coste San Giacomo FU, at ~2.2 Ma (Bellucci et al., 2014; Florindo et al., 2021). The last occurrence of the species in western Europe was often considered that from the French locality of Chilhac (Heintz et al., 1974; Boeuf, 1992), for which radiometric estimates obtained in the 1980s pointed to ~1.8 Ma (Azzaroli, 1983). Remains of *A. arvernensis* are also known from the historical collections of the Upper Valdarno, once generally altogether referred to the late Villafranchian (Zanchetta and Mazza, 1996). These are the main reasons why *A. arvernensis* was regarded as present until the Olivola FU in several biochronological schemes (e.g., Azzaroli, 1983). However, the fauna of Chilhac has been aligned to that of Coste San Giacomo (Palombo and Valli, 2004), which is consistent with current radiometric estimates for Chilhac, ~2.3–2.2 Ma (Paquette et al., 2021). Moreover, the historical findings of *A. arvernensis* from the Upper Valdarno are either referable to the middle Villafranchian or of uncertain provenance (Rook et al., 2013). Another putative late occurrence of *A. arvernensis* was reported by Zanchetta and Mazza (1996) from Monte Castello, in the Lower Valdarno. The authors interpreted the deposits yielding *A. arvernensis* as the basal portion of a formation with *Arctica islandica*, implying a last appearance of *A. arvernensis* in the Olivola or Tasso FUs (Zanchetta and Mazza, 1996; Palombo and Ferretti, 2005). However, subsequent studies clarified that the sediments bearing the remains of *A. arvernensis* are part of a different formation, underlying the *Arctica islandica*-bearing sands (Sarti et al., 2008). In sum, current evidence suggests that *A. arvernensis* was not documented in Europe after the middle Villafranchian (Coste San Giacomo FU, MNQ 17b).

The rest of the fauna listed by Masini et al. (1994) as from Quercia does not help in refining the chronology of the site, apart from *L. etruscus*, whose earliest occurrence is possibly from Senèze (Masini, 1989; Cherin et al., 2019), dated at ~2.2–2.1 Ma (Pastre et al., 2015; Paquette et al., 2021). Considering the co-occurrence of *A. arvernensis* and *L. etruscus*, is it possible to refer this local fauna to the Coste San Giacomo FU (Fig. 1(C)), as previously proposed (Masini et al., 1994; Palombo et al., 2002; Bona and Sala, 2016).

3. Material and methods

The Suidae material described herein consists of six isolated molars collected during the second half of the nineteenth century and housed in the Natural History Museum of the University of Florence, section Geology and Paleontology (formerly Istituto Geologico di Firenze, from which the acronym IGF on the specimens' labels derives). For the ease of reference, a sequential letter in alphabetical order (a, b, c) is added to refer unambiguously to those specimens catalogued with the same identification number.

Morphological and biometric comparisons were carried out by directly examining and measuring specimens stored in several institutions (see institutional abbreviations below). Measurements of length (L) and width (W; -m: mesial; -d: distal/second lobe in a molar; -t: third lobe in a molar) of each tooth were taken to the nearest 0.1 mm with a digital calliper, following Van der Made (1996). Dental nomenclature also follows the latter study.

For the biometric comparison, I considered:

- the most abundant sample of the Pliocene *Sus arvernensis* (Croizet and Jobert, 1828), from Villafranca d'Asti (housed in NMB);
- two samples of "typical *S. strozzii*" (*sensu* Iannucci, 2022), from Olivola (housed in IGF) and historical collections from the Upper Valdarno (housed in IGF, MPM, and NMB);
- a composite sample of Epivillafranchian *S. strozzii*, including specimens from Frantoio, Le Vallonnet, the Vallparadís Section, and Untermassfeld (Bona and Sala, 2016; Cherin et al., 2020; Iannucci, 2022);
- a large sample of early Middle Pleistocene *S. scrofa* from Mosbach (housed in NHMMZ).

Aside from part of the Epivillafranchian group, all measurements considered in the analyses are my own, and the selected samples have been chosen from representative localities that yielded abundant remains and are as geographically close as possible (Iannucci et al., 2020b). This approach should minimize potential confounding factors when evaluating biometric differences. I had, nonetheless, to consider a non-Italian sample for the early Middle Pleistocene *S. scrofa*, due to the paucity of remains of the species in the country (Strani et al., 2022). *Sus arvernensis* is included for comparative purposes as the species is regarded as ancestral to or closely related to *S. strozzii* (Azzaroli, 1952, 1975; Cherin et al., 2018; Iannucci et al., 2022a), although considering its substantially smaller size, there would have been clearly no risk of taxonomic misidentification with Quercia suids. Measurements of Quercia suids are provided in Table 1 and those of comparative samples in Table 2. Teeth are abbreviated to "m", standing for "molar", and a number indicates their meristic position, using uppercase for upper molars and lowercase for lower molars (i.e., m3 = lower third molar).

Bivariate diagrams and boxplots were produced with the software PAST v. 4.04 (Hammer et al., 2001). In boxplots, quartiles

Table 1
Sus strozzii Forsyth Major, 1881 from Quercia (Italy). Measurements are in mm. "-": measurements not taken due to imperfect preservation status; NA: not applicable. For other abbreviations, see Section 3.

Specimen Id.	Side	Tooth	L	Wm	Wd	Wt
IGF 4693a	Right	M3	-	-	-	-
IGF 4693b	Left	m2	27.6	17.3	19.8	NA
IGF 4694a	Left	m1	ca. 19.4	-	14.1	NA
IGF 4694b	Left	m2	26.3	16.4	17.3	NA
IGF 4694c	Left	m3	-	-	20.8	17.3
IGF 4695	Left	m3	-	22.7	22.0	18.3

Table 2
Comparative measurements (in mm) of the groups included in the biometric comparison. Mean values and number of specimens available for each group (in brackets) are provided.

Group	m1 Wd	m2 L	m2 Wd	m3 Wm	m3 Wd
Sus arvernensis, Villafranca d'Asti	11.2 (3)	19.2 (4)	14.7 (4)	16.6 (4)	14.7 (3)
Sus strozzii, Olivola	14.4 (2)	27.1 (3)	18.5 (3)	21.6 (2)	20.6 (2)
Sus strozzii, Upper Valdarno	14.2 (19)	26.4 (22)	18.4 (22)	21.4 (23)	20.7 (21)
Sus strozzii, Epivillafranchian	14.0 (7)	24.9 (6)	18.5 (6)	20.2 (10)	19.2 (10)
Sus scrofa, Mosbach	11.8 (8)	23.4 (11)	15.8 (11)	18.3 (13)	17.4 (15)

are constructed using the "interpolation" method provided by the software, following which non-integer ranks are treated using a linear interpolation between the two nearest ranks. Whiskers are drawn above and below the box, up to 1.5 times the box height, while observations outside this range are considered "outliers" and depicted with open dots.

Institutional abbreviations: CMNH: Civic Museum of Natural History, Trieste (Italy); **HNHM**: Hungarian Natural History Museum, Budapest (Hungary); **IGF**: Natural History Museum of the University of Florence, section of Geology and Paleontology (Italy); **IQW**: Senckenberg Research Station of Quaternary Palaeontology, Weimar (Germany); **IsIPU**: Italian Institute of Human Paleontology, Anagni (Italy); **MACUS**: Comparative Anatomy Museum 'Battista Grassi', Sapienza University of Rome (Italy); **MANA**: Civic Archaeological-Naturalistic Museum "Adolfo Klitsche de la Grange", Allumiere (Italy); **MNCN**: National Museum of Natural Sciences, Madrid (Spain); **MPM**: Paleontological Museum, Accademia Valdarnese del Poggio, Montevarchi (Italy); **MUST**: University Museum of Earth Sciences (including the former **MPUR**: Museum of Paleontology), Department of Earth Sciences, Sapienza University of Rome (Italy); **NMB**: Natural History Museum, Basel (Switzerland); **NHMMZ**: Mainz Natural History Museum/State Collection of Natural History of Rhineland-Palatinate (Germany); **NWHCM**: Norwich Castle Museum (UK); **PF**: PaleoFactory Laboratory, Department of Earth Sciences, Sapienza University of Rome (Italy).

4. Systematic palaeontology

Class Mammalia Linnaeus, 1758
Order Artiodactyla Owen, 1848
Family Suidae Gray, 1821
Subfamily Suinae Gray, 1821
Genus ***Sus*** Linnaeus, 1758
Sus strozzii Forsyth Major, 1881.
Fig. 2

Type material: IGF 424, a male adult specimen consisting of associated cranium, mandible, and part of the postcranial skeleton including part of the vertebral column and ribs, both scapulae, and fragmented left humerus lacking the distal epiphysis. Figured and selected as the lectotype of the species by Azzaroli (1952), since Forsyth Major (1881) did not establish a holotype.

Type locality: Upper Valdarno (Tuscany, Italy).

Stratigraphic range: Early Pleistocene (middle Villafranchian to Epivillafranchian).

Referred material from Quercia: Fragmented right M3 (IGF 4693a); left m2 (IGF 4693b); fragmented left m1 (IGF 4694a); left m2 (IGF 4694b); fragmented left m3 (IGF 4694c); fragmented left m3 (IGF 4695).

According to the information reported on the historical labels accompanying the specimens, IGF 4693 and IGF 4695 were a gift of U. Botti and were catalogued in the museum in 1863, while specimens labelled IGF 4694 derive from Forsyth Major's collections and entered the museum in 1889. This latter date coincides with the only proper excavation of the nearby site Olivola, carried out in 1889 by Forsyth Major himself (Forsyth Major, 1890).

Diagnosis (after Cherin et al., 2020): Large-sized suine with relatively narrow parietal region; gently undulating dorsal cranial profile in lateral view, with slight ventral concavity in the middle part; widely diverging and pneumatised zygomatic arches tending to be broader in the middle than at the rear (more gracile in females); laterally expanded nasals separated by a bony prominence; anteroposteriorly elongated and rugose supracanine flange in males (shaped as gracile and low crests in females); labial longitudinal thickening of the mandibular corpus (more gracile in females), with major lateral convexity in the middle; thick enamel in cheek teeth; verrucosic lower canines; elongated m3 with single cuspid (hypopreconulid) between the first and second lobes and well-developed talonid composed by four main distal cuspids arranged in a cross.

Description: Quercia suids are represented by isolated molars whose enamel is of a very dark colour. This is in sharp contrast with the appearance of remains of the Olivola fauna, which are almost white, with porous and friable bones, testifying a different taphonomic context (Azzaroli, 1950).

IGF 4693a is the only upper tooth of the sample, namely a fragment of a right M3 (Fig. 2(A)). The tooth preserves only the mesiolingual portion, hosting a protocone in moderate wear and about half of the mesial cingulum including the preconule, and part of the mesiobuccal side with the paracone. The preserved portion of the latter cusp is higher and less worn than the protocone.

IGF 4694a is an almost complete left m1 (Fig. 2(B)). The specimen is fragmented at its mesiobuccal extremity, preserving only two distal enamel folds of the protoconid. The tooth is bunodont and brachydont, bilobed along the mesiodistal axis, with the notch separating the two lobes being more pronounced on the buccal side. Apart from the protoconid, the other main cuspids are all preserved. The hypoconid is merging with the hypopreconulid due to

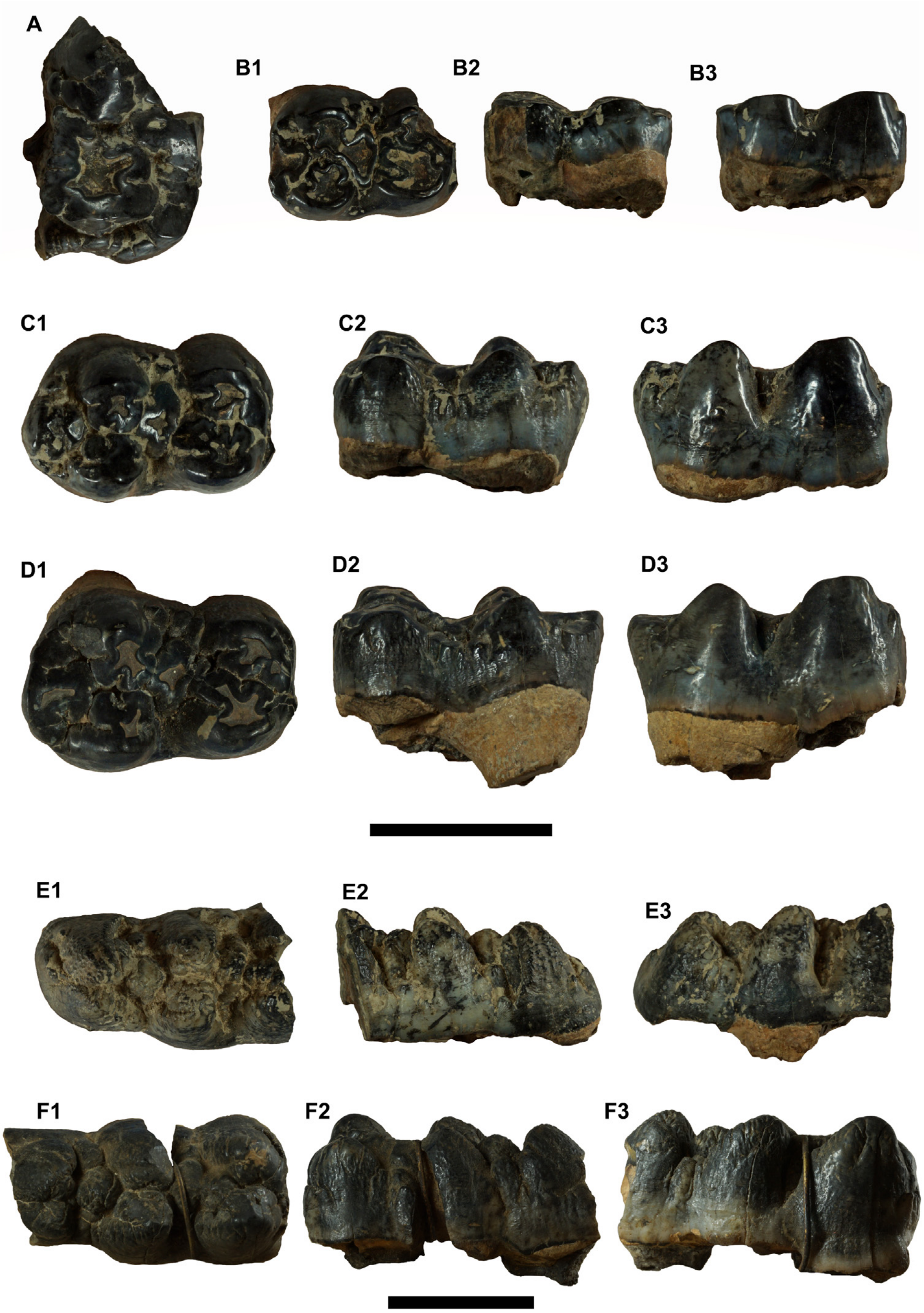

Fig. 2. *Sus strozzii* Forsyth Major, 1881 from Quercia (Italy). **A**. Right M3 IGF 4693a in occlusal view. **B**. Left m1 IGF 4694a. **C**. Left m2 IGF 4694b. **D**. Left m2 IGF 4693b. **E**. Left m3 IGF 4694c. **F**. Left m3 IGF 4695. Specimens shown in occlusal (1), buccal (2), and lingual (3) views. Scale bars: 20 mm (refer to specimens above them).

the advancement of wear, while metaconid and entoconid are still well separated. Each main cuspid has four enamel crests that develop – approximately – mesiomedially, distomedially, mesially, and distally from the centre of the cuspid. It is at the level of the former of these crests that the exposed dentine is merging with the hypopreconulid. Lingual cuspids are slightly higher above the occlusal level than the buccal ones. A small portion of four roots is also preserved, each of which is placed below one of the main cuspid.

The two preserved m2, IGF 4693b and IGF 4694b, are basically only distinct in size from m1, apart from superficial differences due to the different degree of wear (Fig. 2(C, D)). In the previously described m1, IGF 4694a, the wear is more advanced, and consequently the distal side of the tooth is almost straight and the pentaconid is only partly preserved. Conversely, in both m2, which are less worn, the occlusal outline appears more elongated, even pointed distally. Cuspid areas are also more clearly separated and obviously the percentage of dentine exposed is lower.

The m3 is represented by two specimens, IGF 4694c and IGF 4695, neither of which is complete (Fig. 2 (E, F)). Nonetheless, both teeth are unworn and collectively allow to appreciate the full outline of crown morphology. The tooth has a similar structure than other lower molars, but it has a third lobe, and the mesial lobe is the widest. The enamel is wrinkled, and folds that would be evident in a more advanced degree of wear are not always clearly detectable. The notch between the second and third lobe is not pronounced and hosts a pentapreconulid in the middle and smaller tubercles on both sides. The third lobe is slightly shifted buccally and hosts a buccolingual pair of large cuspids. A further distal faint tubercle is also present in IGF 4694c, while this portion is not preserved in IGF 4695.

Remarks:

Morphology. The overall molar morphology of the compared species is highly conservative, if not for differences in dental proportions that are detailed below, and the intraspecific variability quite important (Fig. 3). In general, the third lobe of m3 is the most variable anatomical region between and among species. For instance, Cherin et al. (2018) considered a disposition of four cuspids arranged in a cross typical for the m3 talonid of *S. strozzii*, but the configuration of three cuspids observed in IGF 4694c from Quercia is also frequent in the species (Fig. 3(H)). In *S. arvernensis*, the third lobe of m3 is mainly composed of a pentepreconulid and a pentaconid placed along the same mesiodistal axis, with smaller cuspids at their sides. In Epivillafranchian *S. strozzii*, the third lobe is often separated from the rest of the tooth by a more pronounced notch than in earlier representatives of the species (Iannucci, 2022). In *S. scrofa*, the number and disposition of cuspids is more variable.

Biometric comparisons. Quercia suids are compared with the geographically close and slightly younger samples from Olivola and the Upper Valdarno, which are typical representatives of *S. strozzii*; Epivillafranchian suids assigned to the same species; and material of the Pliocene *S. arvernensis* and early Middle Pleistocene of *S. scrofa*, selecting localities with abundant samples (Fig. 4). In most measurements, Quercia suids rank among the largest specimens of *S. strozzii*. The m2 is the best-preserved tooth within the sample of Quercia, and allows to observe some differences between IGF 4694b, which falls in the lower part of the range of *S. strozzii*, and IGF 4693b, which is instead among the largest specimens (Fig. 4(A)). The observed value of m1 Wd for Quercia is close to the averages for other *S. strozzii* groups (Fig. 4(B)). Other measurements are again quite large in the specimens from Quercia (Fig. 4(C, D)). In general, *S. arvernensis* is markedly smaller than the other species, with minimal overlap with the smallest speci-

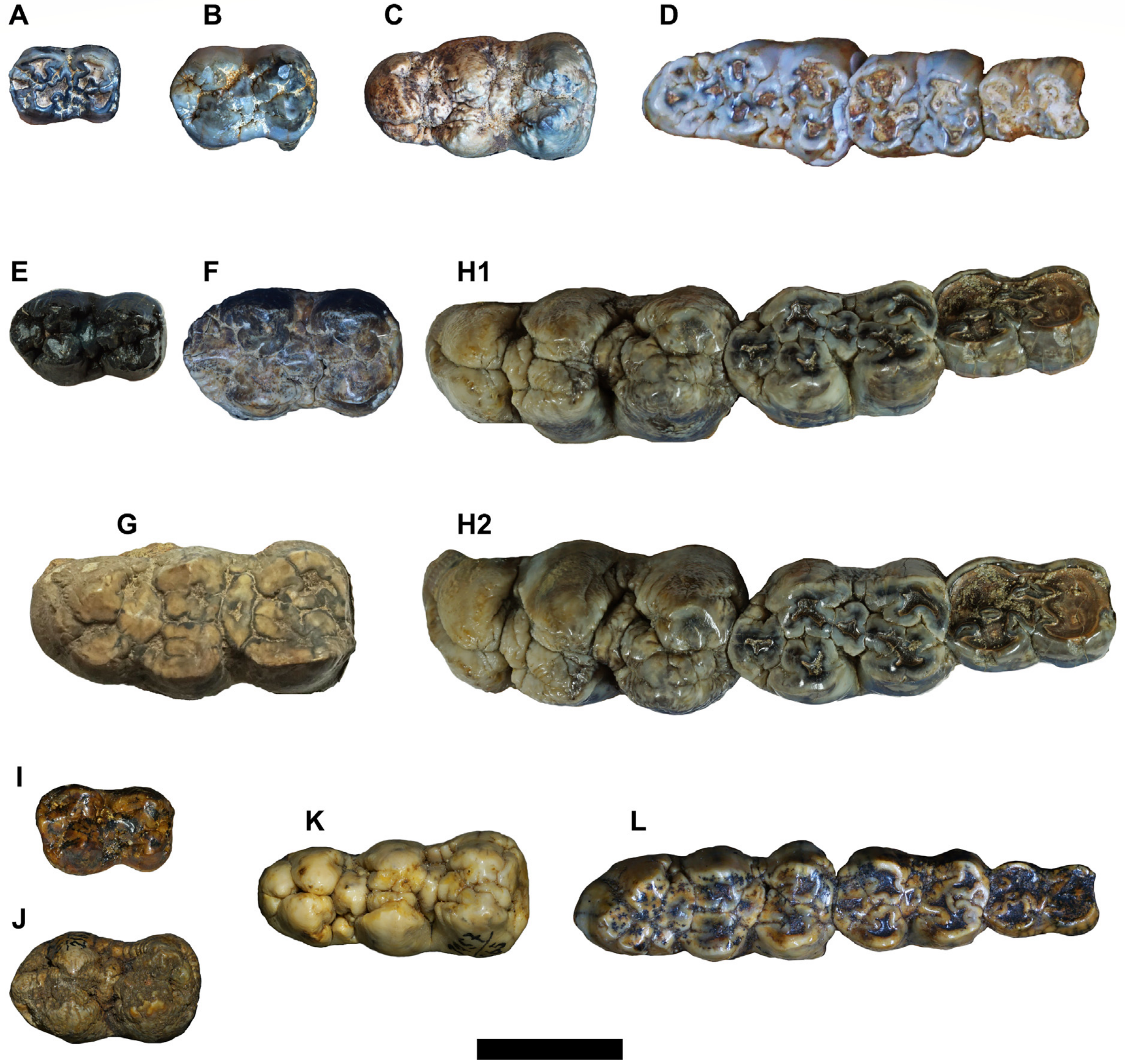

Fig. 3. Comparison of lower molars morphology between selected suid samples. **A-D**. *Sus arvernensis* from Villafranca d'Asti (Italy). A: right m1 NMB V.J. 170; B: right m2 NMB V.J. 169; C: left m3 NMB V.J. 168; D: right m1-m3 part of NMB V.J. 145. **E-H**. *S. strozzii* from the Upper Valdarno (Italy). E: right m1 IGF 4692; F: right m2 NMB V.A. 1577; G: left m3 MPM 964; H: left m1-m3 part of IGF 6281 V. **I-L**. *S. scrofa* from Mosbach (Germany). I: right m1 NHMMZ 1955/187; J: left m2 NHMMZ 1952/624; K: left m3 NHMMZ 1957/665; L: left m1-m3 part of NHMMZ 1960/5. All specimens shown in occlusal view; H1 and H2 are stereo-occlusal views. Scale bar: 20 mm.

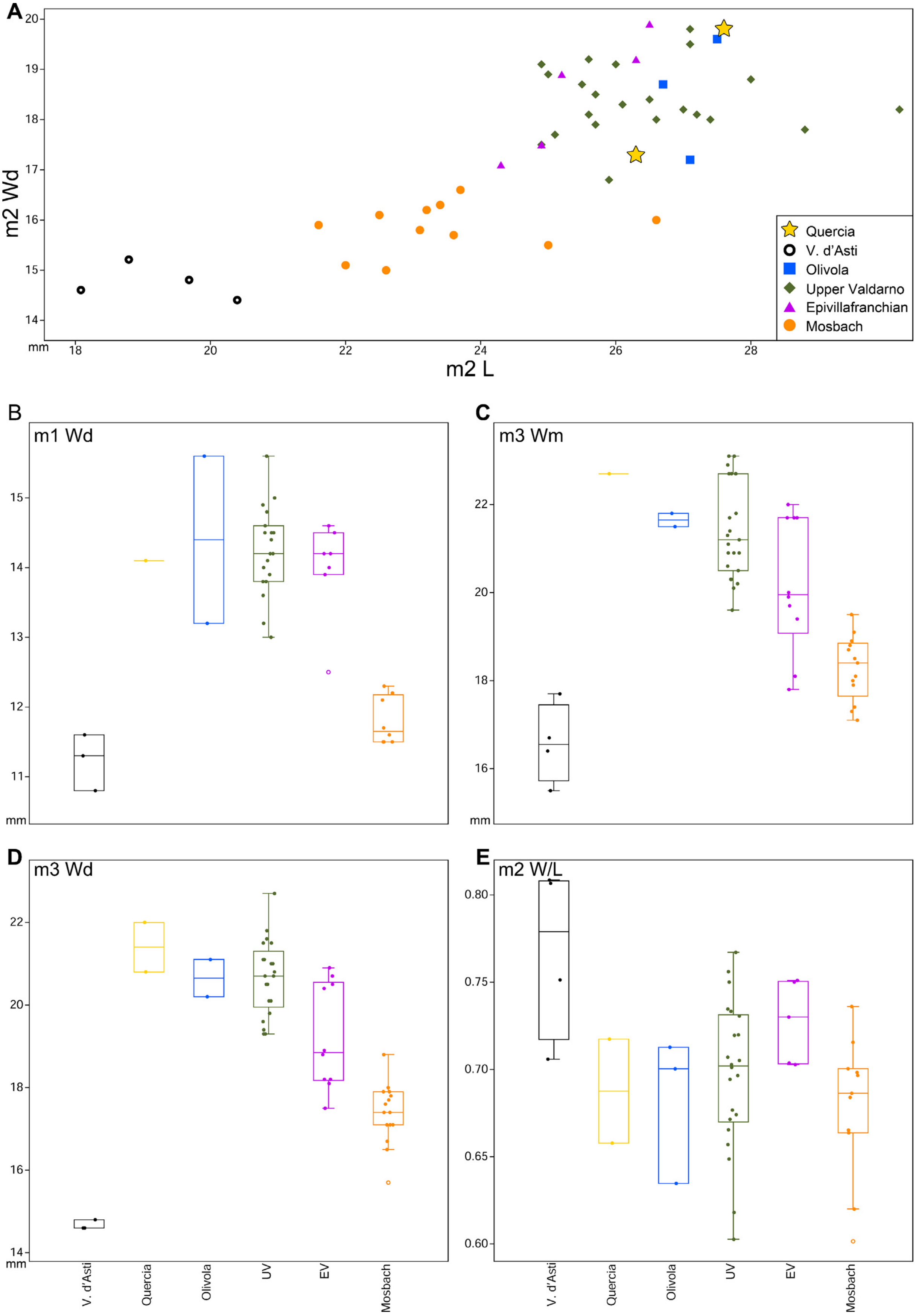

Fig. 4. Biometric comparisons between *Sus strozzii* Forsyth Major, 1881 from Quercia (Italy) and selected samples of *S. arvernensis*, *S. strozzii*, and *S. scrofa* from Europe. **A**. Bivariate diagram of m2 L *vs.* m2 Wd. **B-E**. Boxplots of m1 Wd (B), m3 Wm (C), m3 Wd (D), and m2 W/L (E). UV: Upper Valdarno, historical collections; EV: Epivillafranchian. For other abbreviations, see Section 3.

mens of *S. scrofa* in m1 Wd and m3 Wm. There is good dimensional separation between *S. strozzii* and *S. scrofa*, the latter species being smaller (Fig. 4). Nonetheless, in m3 Wm and m3 Wd there is overlap between Epivillafranchian and early Middle Pleistocene suids (Fig. 4(C, D)). The ratio between m2 W and m2 L reveals how *S. arvernensis* has proportionally wider teeth than the other species, although this might partly reflect an allometric consequence of its substantially smaller size (i.e., with m2 L decreasing relatively more than m2 W). Conversely, the ratio does not show a clear distinction between *S. strozzii* and *S. scrofa*, with only the Epivillafranchian group being characterised by proportionally wider molars, but still within the range of the more abundant Upper Valdarno sample (Fig. 4(E)).

<u>Notes on further material</u>. Forsyth Major (1890), apart from the fossils described herein, also reported a faunal list composed of specimens collected from a clay quarry exploited by the Fornace Cocchi at Quercia, belonging to a collection he examined in the house of Cocchi at Terrarossa. Although coming from a different site, it is likely that this fauna was recovered within the same unit than other Quercia fossils. Unfortunately, it is not clear what this material consisted of, and there is no mention of it in subsequent studies.

Azzaroli (1975) listed "La Quercia (lacustrine basin of Barga, Tuscany)" among the Italian localities with *Sus minor* (=*Sus arvernensis*), mentioning the existence of an unpublished first lower molar, but without specifying its whereabouts. However, this is either a mistake or represents a different site, considering that the Barga Basin is a different, although not far, Tuscan locality (Coltorti et al., 2008). Moreover, *S. arvernensis* is a small-sized Ruscinian to Early Villafranchian suid whose teeth are well outside the dimensional range of Quercia suids described herein (Pickford and Obada, 2016; Iannucci et al., 2022a; Fig. 4).

5. Discussion

Quercia suids comfortably adhere in size and dental proportions to *S. strozzii*, supporting previous attributions (Forsyth Major, 1890; Azzaroli, 1950). Molar morphology is highly conservative in the compared suid species, but the preserved third lobe of m3 of IGF 4694c (Fig. 2(E)) closely matches that of some typical (*sensu* Iannucci, 2022) representatives of the species (Fig. 3(H)). The examination of historical literature and museum information also allow to confirm the stratigraphic provenance of the remains, which were recovered from clays underlying the Olivola Conglomerates, and to confidently reconstruct the place of the original findings, with a notable accuracy for such an old collection. Quercia suids represent one of the few middle Villafranchian occurrences of *S. strozzii*.

The biometric comparisons between different samples of *S. strozzii* and early Middle Pleistocene *S. scrofa* support a good dimensional separation between the two species, with *S. strozzii* being usually larger than *S. scrofa*. Notwithstanding these results, *S. scrofa* is an extremely variable species in size and morphology, hence attributions should not be solely based on size (Cherin et al., 2020; Iannucci et al., 2020b).

An often useful feature for discriminating isolated teeth of the two species are their proportions, with *S. strozzii* usually possessing relatively wider teeth (Van der Made and Moyà-Solà, 1989; Iannucci et al., 2021a). Quercia suids allow to test these differences only in m2. In this case, although the m2 W/L ratio is indeed on average larger in *S. strozzii*, there is no absolute separation between *S. strozzii* and *S. scrofa*, (Fig. 4(A, E)). This indicates that premolars are more suitable for differentiating the two species, but these results might also be partly due to the sample choice, considering that the presence of relatively wider teeth at Mosbach has been already noted by Küthe (1933). More precisely, the author identified two groups within Mosbach suids, possessing wide ("breite Typ") or slender ("schlanken Typ") m3, considering the former exclusively present in fossil forms of *S. scrofa*. In any case, Mosbach wild boars were selected for the comparison because they constitute the most abundant early Middle Pleistocene sample of *S. scrofa*, which is not represented by extensive remains during this period (Strani et al., 2022).

The comparison also supports the existence of some differences between typical late Villafranchian *S. strozzii* and Epivillafranchian samples (Iannucci, 2022), which are characterised by values of m3 Wm and m3 Wd intermediate between typical *S. strozzii* and early *S. scrofa* (Fig. 4(C, D)). It cannot be ruled out that differences will emerge from middle Villafranchian and late Villafranchian samples as well, when further data on the scanty former contingent will become available. Indeed, while Quercia suids are not represented by many remains, they constitute the most abundant middle Villafranchian sample of *S. strozzii* described so far.

The evolution of a large-sized suid like *S. strozzii*, presumably deriving from the small *S. arvernensis* or a closely related form (Azzaroli, 1952, 1975; Cherin et al., 2018; Iannucci et al., 2022a), was evidently an important bioevent, which judging from the available data should have happened shortly after the Pliocene-Pleistocene transition. This period, coinciding with the beginning of the Quaternary, witnessed substantial changes in climate and environment, which promoted a remarkable faunal turnover (the "Elephant-*Equus* event"; Azzaroli, 1977, 1983; Lindsay et al., 1980; now more appropriately referred to simply as the "*Equus* event", Iannucci and Sardella, 2023). Unfortunately, there are not but a few mammal localities of this age in Europe, and as previously remarked even less document the occurrence of suid for the whole middle Villafranchian. *Sus strozzii* and *S. arvernensis* are usually regarded as species adapted to tropical to subtropical or even swampy environments (e.g., Pickford and Obada, 2016; Iltsevich and Sablin, 2022), a consideration that rests mainly on their phylogenetic proximity to warty pigs from Island Southeast Asia and on the presence, at least in *S. strozzii*, of some anatomical similarities with *Potamochoerus* (Azzaroli, 1952, 1975; Faure and Guérin, 1984; Iannucci et al., 2020a). If this palaeoecological interpretation is correct, the onset of the Quaternary glaciations and the consequent spread of open environments at ~2.6 Ma may have forced suid populations to cope with stressful conditions, eventually promoting the evolution of *S. strozzii*, a new species able to survive during the Early Pleistocene. Even so, our comprehension of this event is still rather vague, and the discovery and description of further material will be key to clarifying.

Revisions of historical collections are often prompted by renewed research in old localities and/or when specimens of stand-alone importance are rediscovered (e.g., Bona, 2021; Fabbi et al., 2021; Mecozzi et al., 2022), but old collections often lack adequate constraints and are not perceived "original" as those gathered from new excavations (Iannucci et al., 2022b). Consequently, many historical samples are deemed not important and remain undescribed, especially if constituted by few specimens. The case of Quercia is emblematic in this regard. Even if their existence has been known for a long time (Forsyth Major, 1890), Quercia suids were at most reported in faunal lists (e.g., Masini et al., 1994; Palombo et al., 2002), but they have never been described. As a result, the locality was not mentioned in recent works with dedicated discussions on suids (Van der Made et al., 2017; Cherin et al., 2018). Yet, among the historical collections of *S. strozzii* it is nonetheless one of the few with reliable geographical and stratigraphical data, allowing a confident reference to the middle Villafranchian (Coste San Giacomo FU) and thus representing one of the oldest occurrences of the species. Moreover, as much as it might sound surprising, the six teeth from Quercia represent the most abundant sample of middle Villafranchian *S. strozzii* described to date. This emphasises the crucial need for appropriate description and contextualisation of historical material (Iannucci et al., 2022b).

Data availability

Data will be made available on request.

Declaration of Competing Interest

The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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