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The Late Villafranchian Absence of Pigs in Europe. Comment on Iannucci, A. The Occurrence of Suids in the Post-Olduvai to Pre-Jaramillo Pleistocene of Europe and Implications for Late Villafranchian Biochronology and Faunal Dynamics. *Quaternary* 2024, *7*, 11

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Abstract: On 2015, after the direct study of the most important Late Villafranchian fossil collections of Europe and Western Asia, including Orce (Spain), Pirro Nord and Upper Valdarno (Italy), Appollonia (Greece), Dmanisi (Georgia) and 'Ubeidiya (Israel), among others, our team proposed the hypothesis that suids disappeared from Europe during the time span between 1.8 and 1.2 Ma. The implications of our conclusions were significant, the arrival of Early *Homo* into Western Europe, dated to 1.4 Ma at the site of Barranco León in Orce (Spain), preceded the return of pigs into the continent at 1.2 Ma. This hypothesis has been recently challenged because of the finding of an incomplete metatarsal ascribed to *Sus* sp., with no clear stratigraphic origin, found in the XIX Century Croizet collection of Peyrolles (France), which is housed in the Natural History Museum, London, together with other weak arguments based on the absence of reliable dating for many Early Pleistocene European sites, and other hypothetical records of pigs, with no real fossil support. We answer all these questions and defend that our 2015 hypothesis is correct.

Keywords: Epivillafranchian; *Sus strozzii*; Peyrolles; Orce; Dmanisi; 'Ubeidiya

1. Introduction

In a recent paper, Ianucci [1] criticized our previous study (Martínez-Navarro et al. [2]), which was focused on the absence of suids in the fossil record of Europe during the Late Villafranchian (i.e., between 1.8 and 1.2 Ma). The main conclusive hypothesis of our study was based on the direct revision of the fossil collections of the most relevant Late Villafranchian and Epivillafranchian (ca. 2.0–0.8 Ma) sites of Europe and Western Asia, including Orce (Venta Micena, Barranco León and Fuente Nueva 3), Cueva Victoria, La Boella, Vallparadís Section, or Incarcal Complex in Spain; Sainzelles and Vallonnet in France; Upper Valdarno, Pirro Nord and Pietrafita in Italy; Apollonia in Greece; Dmanisi and Ahkalkalaki in Georgia; and 'Ubediya, Bizat Ruhama, Evron Quarry, and Gesher Benot

Ya'aqov in the Levant, Israel. Our study was also complemented with an extensive revision of the literature and chronological estimates available for all late Early Pleistocene sites of Western Eurasia.

Suids are commonly recorded in Europe during the Middle Villafranchian and the base of the Late Villafranchian (ca. 2.4–1.8 Ma; [3] and references therein). This is evidenced at a number of sites, including Saint Vallier (ca. 2.4–2.3 Ma) [4] and Senèze (2.1–2.2 Ma) [5–7] in France; Pantalla (ca. 2.1–1.9 Ma) [8] and Poggio Rosso in the Upper Valdarno, Italy (ca. 1.8 Ma) [9], where they have been ascribed to the species *Sus strozzii;* or at Fonelas P1 (ca. 2.0 Ma) in the Guadix-Baza Basin, Spain, where the suid species was originally described as *Potamochoerus magnus* [10]. *Sus strozzii* is also recorded at the gates of Europe, in the Caucasus, during the Middle-Late Villafranchian transition at the site of Palantokan (ca. 2.1–1.9 Ma) [11] in Azerbaijan. Finally, the latest record of suids during the Late Villafranchian is also represented in the same region, at the site of Dmanisi, Georgia (ca. 1.8 Ma). In this locality, *Sus* sp. (most probably *Sus strozzii*) is recorded by only two fossil remains found during the latest excavation seasons. One of them is a right lower fourth premolar ([12,13] and pers. obs. BMN). Vekua [14] also described and figured an upper incisor, I2, ascribed to *Sus* sp. in Dmanisi, but the occurrence of this species disappeared from the faunal lists published later for the site [15]. Then, suids vanished from the European continent, but still continued living in Western Asia at the Levantine Corridor, in southern latitudes around the 32° parallel, at the site of 'Ubeidiya, where *Sus strozzii* and the African species *Kolpochoerus olduvaiensis* (together with other African immigrants) are reported in a chronology between 1.6 and 1.2 Ma [16–19]. *Kolpochoerus* (*K. evronensis*) is also mentioned as occurring in another Israeli site, Evron Quarry (ca. 0.8 Ma) [20–22].

A form of *Sus* reappeared in Europe at around 1.2 Ma, as recorded at level TE9 from Sima del Elefante in Atapuerca, Spain [23] and later, during the Epivillafranchian and more recent periods, suids become common elements in the European fossil assemblages of large mammals (see ref. [24] for a review).

Martínez-Navarro et al. [2] were aimed to highlighting the chronological significance of the absence of suids from the European Late Villafranchian. They were also aware of the hotly debate around the adscription of the Epivillafranchian newcomer form, and decided to cite it as *Sus* gr. *scrofa* (e.g., the suid from Untermassfeld in Germany, dated to ca. 1.1 Ma, which is identified as *Sus scrofa priscus* [25]). Moroever, other authors classified this Epivillafranchian form as *Sus* sp. (e.g., Sima del Elefante [23]), or as *Sus strozzii* in Vallonnet, France (dated to ca. 1.2 Ma [26,27]), although in later studies the suid remains from this French site were reassigned to *Sus* sp. [28]. In more recent papers, this Epivillafranchian form has been reported as *Sus strozzii* ([24,29] and references therein), being recorded in Europe at the 1.2 to 0.9 Ma interval.

The implications of our conclusions are significant. The arrival of Early *Homo* into Western Europe, which has been dated to 1.4 Ma by the combination of ESR, paleomagnetism and biochronology at the site of Barranco León in Orce, Southern Spain [30], preceded the Epivillafranchian and the new arrival of pigs into the continent, which was dated to 1.2 Ma in Atapuerca TE9 level [23].

2. Discussion of Iannucci's Arguments Against Martínez-Navarro et al. Hypothesis

2.1. The Fossil Specimen NHMUK PV OR 27621 from Peyrolles

In his paper, Iannucci [1] suggests that the hypothesis proposed by Martínez-Navarro et al. [2] on the Late Villafranchian absence of suids is most probably incorrect. His main argument against our proposal is the presence of an incomplete distal fragment of a left fourth suid metatarsal from Peyrolles, in the French Central Massif. This specimen is part of the XIXth Century fossil collection of Jean Baptiste Croizet [31], which was purchased by the Natural History Museum, London, in January 1848 (specimen labelled NHMUK PV OR 27621) (N. F. Adams, per. inf.). The fossil collection of Auguste Bravard, the person who discovered the site of Peyrolles, was also purchased by the same Institution in 1852 [32]. It is worth noting that, at least to our knowledge, no information is available on the stratigraphic

layer from which the fossil was unearthed. It is also important to highlight that the exact geographical position of the paleontological site of Peyrolles was unknown for decades: Bravard, and the other researchers who followed him, like Croizet, never revealed the exact position of the site [32]. Also significant is the absence of any reference on the occurrence of suids (including the above-mentioned metatarsal) in any of the publications of Bravard or Croizet [31,33–37].

Iannucci [1] ascribed the Peyrolles specimen to *Sus* sp., arguing that it is similar in morphology to *Sus scrofa*, but there is not available material of *Sus strozzii* for a direct comparison. The only possibility would be the mounted skeleton of the species from Senèze (Central Massif, France), which is housed at the Naturhistorisches Museum Basel [5], but he could not perform a good comparison. For this reason, Iannucci [1] left the Peyrolles metatarsal undetermined at the specific level (*Sus* sp.). Although the short faunal list of the assemblage from Peyrolles is mainly composed of cervids, Valli et al. [32] suggested that this site is biochronologically close to 1.4–1.5 Ma. However, the presence of *Leptobos* cf. *etruscus* is suggestive of an earlier age, close to 1.8 Ma [8], because *Leptobos* disappeared in Europe in chronologies posterior to this age, and the continent was then populated by a more advanced buffalo form of the genus *Bison* [38].

The primary argument by Iannucci [1] is that the fossiliferous beds from Peyrolles have been dated by the $^{40}Ar/^{39}Ar$ method to 1.42 ± 0.20 Ma [39] and to 1.449 ± 0.024 Ma [6], based on indirect evidence from neighboring pyroclastic deposits. If correct, such chronologies would imply that the hypothesis of Martínez-Navarro et al. [2] is wrong. However, other numerical chronologies for Peyrolles were not mentioned or discussed by Iannuci [1], such as the K-Ar estimate of Poidevin et al. [40], with a result of 1.20 Ma, or the 1.54 Ma estimate derived by Couthures and Pastre [41].

In summary, the criticism of Iannucci [1] is based on a suid specimen that comes from a XIX Century collection, which was later transferred to London without any reference to the stratigraphic provenance of the fossil specimens apart from the name of the town, Peyrolles. The fossil record of Peyrolles (or Creux de Peyrolles) can proceed from different stratigraphic horizons: the layers cited by Bravard and Croizet, and those most recently suggested by Valli and colleagues. Additionally, the low diversity of mammals recorded in this/these site/sites does not allow to derive further biochronological considerations apart from a late Middle or early Late Villafranchian age.

2.2. The Other Arguments

Together with the suid fossil record from Peyrolles, Iannucci [1] supports his thesis discussing the following questions: (a) chronology of the fossil assemblages; (b) the fossil record of pigs in several sites not considered by Martínez-Navarro et al. [2]; and (c) the irrelevance of the suid *r* reproductive strategy for the fossil record (i.e., the relationship between the rate of reproduction and population turnover, on the one hand, and the fossilization potential, on the other). These questions need to be discussed:

(a) Chronology of the fossil assemblages:

Iannucci [1] emphasizes the deficiency of numerical dating in most of the Early Pleistocene sites of Europe, where most localities are dated on the base of biochronology. This is true, but unfortunately it is not always possible to apply numerical methods. However, this deficiency is gradually being corrected, and new numerical dates are being published, for example for Orce, Pirro Nord and Vallonnet [27,30,42,43]. The problem is that Iannucci [1] does not discuss on the reliability of the chronologies derived by the $^{40}Ar/^{39}Ar$ method for Peyrolles or for other sites. He textually affirms that "the $^{40}Ar/^{39}Ar$ method, which can be considered the gold standard for dating Early (but also Middle) Pleistocene sites, has been successfully applied only on a fraction of them".

(b) The Late Villafranchian suid fossil record:

Iannucci argues that Martínez-Navarro et al. [2] did not consider the occurrence of suids in several European sites in the 1.8–1.2 Ma time span, such as those from the

Ellera Basin in Italy [44], or a list included by Van der Made et al. [45]. The latter are, in chronological order: Mugello [46], Selvella [47] and Pirro Nord [48] in Italy; and Peyrolles and Ceyssaguet in France (cited by Guérin and Faure in their study of the suids from Untermassfeld [25]). Van der Made et al. [45] also included 'Ubeidiya in Israel [16], but this is Southwestern Asia, not Europe, and it is in a very low latitude, as said before.

Concerning the suid record of Ellera Basin, it is worth reminding that two faunal assemblages are reported from this basin [44]. The first comes from the Early Pleistocene San Biagio Unit and is composed by latest Villafranchian/Galerian taxa. The second comes from the Late Pleistocene Santa Sabina Unit. The revision of historical collections [44] together with the preliminary results obtained in the last excavations [49] are suggestive of an early Galerian Colle Curti Faunal Unit attribution for the oldest assemblage from Ellera Basin (i.e., the assemblage including the *Sus* second upper molars mentioned in Pazzaglia et al. [44]).

Iannucci [1] cited the fauna from Mugello Basin as referred to the Tasso or Farneta Faunal Units [46]. The suid specimens from Mugello (two upper M2 permanent teeth, IGF4828V, and one juvenile upper M3, IGF988V) come from the surroundings of Ronta. These specimens, together with an upper molar fragment of *Hippopotamus,* were donated to the Florence Museum in 1895 by Mr. Ing. Guaterio. As for most of the Mugello fossiliferous sites, the faunal assemblage is actually so scanty that a firm biochronologic attribution is highly arbitrary.

The record of *Sus* in Selvella is described as follows: "The diaphysis of a humerus can be assigned to this genus because of its strong curvature" [47]. No measurements of the specimen were provided, but it was figured in Plate 1 of the cited paper. The specimen is not a humerus, as reported in the museum catalogue (under inventory number IGF1414) or in the Plate 1 caption by De Giuli [47], but a radius diaphysis that corresponds to a medium-sized indeterminate ungulate. Therefore, its adscription to *Sus* is really doubtful.

The record of *Sus* in Pirro Nord is cited as follows: "In these cave-fillings a rich mammalian fauna was found yielding: *Equus*, several species of Cervidae, Bovidae, *Sus*, *Elephas meridionalis*, *Hyaena*, *Machairodus*, *Ursus*, a Rhinocerotid, *Hystrix*, *Allophaiomys*, *Apodemus*, *Lepus*, and other vertebrates" [50], with no other description of this fauna. During a visit in the year 2000, two of the authors, (BMN and LR), personally revised this old collection from the Freudenthal excavations, which is housed in Bari. They didn't find any fossil that could be unequivocally ascribed to *Sus*. De Giuli et al. [47], referring the Freudenthal's work, cited the presence of *Sus* sp. in Pirro Nord, and also included the citation of *Sus* sp. in their Table 1 for PN5. However, in the description of the fauna, which includes rodents, lagomorphs, cervids, bovids, equids, and also carnivores (e.g., *Megantereon*), there is no reference to suids and no other explanation is included, nor the occurrence of a suid in the faunal assemblage from Pirro Nord has been mentioned in subsequent papers [51–54]). Moreover, Pirro Nord was dated by biochronology between 1.3–1.6 Ma [55], but recently, as it is pointed out by Iannucci, it has been dated by a combination of numerical methods to the latest Early Pleistocene, with an Epivillafranchian age [43,56].

In the reference used by Iannucci [1] to cite the presence of suids in Ceyssaguet [45], these authors referenced it to Guérin and Faure [25], who described in their work the suid fossil remains from Untermassfeld in Germany (1.1 Ma) and ascribed them to *Sus scrofa priscus*. In the same paper, Guérin and Faure said that they compared the sample with the post-Villafranchian Lower Pleistocene of *Sus scrofa priscus* material from other European sites included in the MNQ20, such as Ceyssaguet, Vallonnet, Châlon-Saint-Cosme, and Mosbach, as well as many other more recent sites. Although Van der Made et al. [45] suggested that the suids from Ceyssaguet should be ascribed to *Sus strozzii*, no description/figuration of the material or any other information on the suids from Ceyssaguet has been published. We have to add here that the chronology of Ceyssaguet, which was biochronologically dated to the end of the Late Villafranchian [57], is probably younger, Epivillafranchian and close to 1.2 Ma, as discussed by Iannucci [1].

(c) Reproduction rate/fossilization potential:

In his argumentation, Iannucci [1] made suggested the obvious claim that the absence of a particular taxon in the fossil record of a site does not imply that this taxon did not inhabit the ancient ecosystem populated by the taxa represented in the site assemblage (he said "suids might easily be apparently absent in a time span during which few fossil sites and/or suboptimal environmental conditions occurred"). In their reasoning of the biochronological implications of the absence of suids in the Late Villafranchian European continent, Martínez-Navarro et al. [2] argued that Suidae is the only family of the Old World ungulates that has developed a truly *r* reproductive strategy (which is also similar to its New World sister family Tayassuidae), in contrast to all other ungulate groups with a mostly *K* reproductive strategy. Probably inspired in Martínez-Navarro et al. [2], Iannucci [1] offered an interesting comparison of the reproductive strategies of different artiodactyl families (Suidae, Tayassuidae, Antilocapridae, Bovidae, Camelidae, Cervidae, Giraffidae, Hippopotamidae, Moschidae, and Tragulidae), including ten variables (body mass, longevity, age at female sexual maturity, age at first reproduction, gestation length, litter size, litters per year, interbirth interval, weaning age, and generation length). Following this comparison, Iannucci insisted in his proposal that although pigs have a high reproductive rate, this does not imply that their fossilization potential is higher than in other ungulates. He also added literally the sentence: "Since suids are intelligent, robust, and more aggressive than many other artiodactyls, it is likely that predators usually preferred preys other than suids". This is a contradiction, however, because the high reproduction rate of pigs is an adaptation to the high mortality rate of their juveniles, which are easily hunted by many predators. The combination in suids of a high reproductive rate with a high mortality rate translates in an elevated population turnover, which in turn means that their fossilization potential is higher than in other ungulates with a *K* reproductive strategy. More specifically, Damuth [58] proposed that in a fossil assemblage taphonomically unbiased, the abundance of skeletal remains for a given mammalian species would exclusively depend on the number of individuals that died while the assemblage was being formed. In this way, the relative abundance of each species can be estimated as a function of its mean population density in the paleocommunity (which scales to the -0.75 power of the species body mass [59,60]) and its population turnover rate (which scales to the -0.3 power of the species body mass and depends on a number of parameters, including birth rate, duration of postnatal growth or the reciprocal of life expectancy at birth, which all take elevated values in pigs). For this reason, the remains of juvenile pigs, especially teeth, use to be relatively abundant in the fossil collections. Among others, this is the case of the Epivillafranchian suid from the site of Dunaalmás, Hungary [29]. Not in vain, as happens in the case of rodents (which also have a very developed *r* reproductive strategy), suids are an important tool for biochronology, as happens in Africa, where biochronology has been traditionally based on pig records. Of course, this does not imply that suids are dominant in the fossil assemblages but, if present in the fossil ecosystems as other large mammals, they are normally represented or even well represented in the fossil assemblages. In any case, suids are well recorded in Europe during the Middle Villafranchian and the base of the Late Villafranchian (i.e., before 1.8 Ma), but also in the Epivillafranchian and later, after 1.2 Ma, but not in between these chronologies.

3. Conclusions

Anatomically, the identification of fossil specimen NHMUK PV OR 27621 as a suid is correct. However, the specimen belongs to a very old collection without documentation of its exact site of provenance, which casts serious doubts on its age. A "new finding" that is too weak to reject the hypothesis of Martínez-Navarro et al. [2].

By the moment, it is known that the most important European Early Pleistocene fossil sites dated between 1.8 and 1.2 Ma do not include suids in their faunal lists. No evidence conclusively supports the occurrence of pigs in Europe during this time span, while in the same chronology they are well represented in both Asia and Africa. The reason why pigs

disappeared from Europe at 1.8 Ma and reappeared again at 1.2 Ma is still open and needs to be solved.

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