Porcine Research

Sus strozzii Gray, 1821, and the early evolution of Eurasian pigs: zoological insights from a key fossil porcine

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Abstract. *Sus strozzii* Gray, 1821 is a large-bodied suine species that occupies a pivotal position in the early evolution of Eurasian pigs during the Early Pleistocene. As the only representative of the genus *Sus* documented in Europe and western Asia during the initial phase of this epoch, *S. strozzii* provides crucial insights into the transition from archaic suids to more derived wild boar lineages. This paper synthesizes current zoological, morphological, phylogenetic, ecological, and biostratigraphic evidence regarding *S. strozzii*, drawing on recent fossil discoveries and comparative analyses. The species is characterized by its large body size, robust mandible, massive cheek teeth, and a distinctive combination of plesiomorphic and derived dental traits, including verrucosic-type lower canines that link it to both Pliocene Eurasian taxa and Island Southeast Asian pigs. Its restricted temporal range, spanning the late Villafranchian to the onset of the Epivillafranchian, confers high biochronological value and makes it a key taxon for dating Early Pleistocene European faunas. Ecologically, *S. strozzii* is interpreted as a flexible omnivore adapted to mosaic environments, playing an important role in Early Pleistocene ecosystems as both a major consumer and a potential prey species. The disappearance of *S. strozzii* before the widespread establishment of *Sus scrofa*–like pigs has been central to debates on faunal turnover and early human dispersal into Europe, highlighting the close interweaving of suid evolution with paleoenvironmental and paleoanthropological reconstructions. Overall, *S. strozzii* emerges as a cornerstone species for understanding the early diversification, dispersal, and ecological significance of the genus *Sus* in western Eurasia.
Key Words: *Sus strozzii*, Suidae, Early Pleistocene, pig evolution, Eurasia, biostratigraphy, dental morphology, paleoecology, faunal turnover, Quaternary mammals.

Introduction. Among fossil pigs, the Early Pleistocene species *Sus strozzii* Gray, 1821 stands out for its zoological relevance (Gallai 2007). It is the only suine in Europe and western Asia during the first part of the Early Pleistocene and occupies a pivotal position in the evolution of the genus *Sus* and the transition from archaic suids to modern wild boar lineages (Cherin et al 2018). Its morphology, ecology, and biostratigraphic position make it a reference taxon for understanding pig evolution, faunal turnover, and environmental change in the Quaternary of Europe (Martínez-Navarro et al 2015; Cherin et al 2018; Iannucci et al 2021; Van Der Made 2025).

This study aims to provide a comprehensive zoological synthesis of *S. strozzii*, emphasizing its morphological distinctiveness, phylogenetic position, ecological role, and biostratigraphic significance, to clarify its contribution to the early evolutionary history of Eurasian pigs and to broader patterns of faunal turnover and environmental change during the Early Pleistocene.

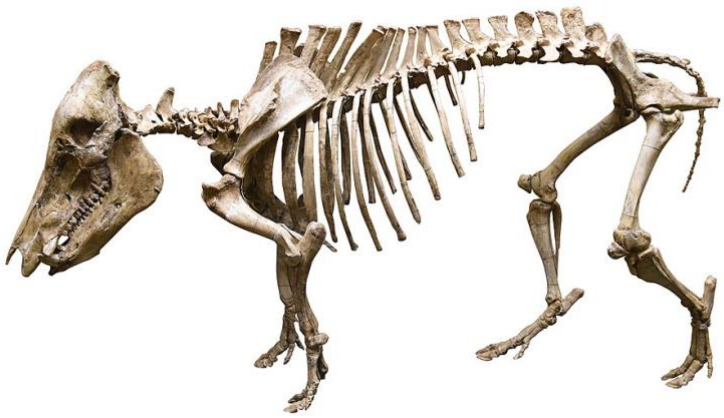

Figure 1. *Sus strozzii* skeleton. Source: Amada44 (CC BY-SA 3.0, Wikipedia.org).

Systematic position, age, and geographic distribution. *S. strozzii* is known from Early Pleistocene deposits (roughly between the late Villafranchian and the onset of the Epivillafranchian) across western and central Europe, including Italy and possibly parts of western Asia (Martínez-Navarro et al 2015; Cherin et al 2018; Iannucci et al 2021; Van Der Made 2025). It disappears before the widespread establishment of suids related to the modern wild boar *Sus scrofa* in Europe, which marks the beginning of the Epivillafranchian around 1.2 Ma (Martínez-Navarro et al 2015). This temporal restriction gives *S. strozzii* high biochronological value for dating Early Pleistocene sites (Turner 1992; Cherin et al 2018; Iannucci et al 2021; Van Der Made 2025).

Phylogenetic analyses that combine living and fossil Eurasian and African suines place *S. strozzii* within the Eurasian *Sus* clade, close to other "verrucosic" pigs such as the Pliocene *S. arvernensis* and various Island Southeast Asian species (e.g. *S. verrucosus*). In these analyses, the late Miocene *Microstonyx* is the first branch within the Suinae, and an early split separates the African lineages (*Kolpochoerus/Hylochoerus* and *Metridiochoerus/Phacochoerus*) from the Eurasian *Sus* lineage. Within *Sus*, *S. scrofa* and the Early-Middle Pleistocene *S. lydekkeri* retain many plesiomorphic traits, whereas *S. arvernensis, S. strozzii* and verrucosic pigs of Island Southeast Asia form a derived group characterized by particular lower canine morphology (Cherin et al 2018). This position makes *S. strozzii* crucial for reconstructing the early diversification of *Sus* and for linking Pliocene taxa (such as *S. arvernensis*) to later Quaternary species.

Morphology and size. *S. strozzii* is characterized by large body size, exceeding that of most extant Eurasian wild pigs and even many contemporary fossil suids (Cherin et al 2018; Iannucci et al 2021; Van Der Made 2025). Newly described mandibular material from Pantalla (central Italy) confirms its robust jaws, large cheek teeth, and specific craniodental proportions that distinguish it from both *S. arvernensis* and *S. scrofa*. Its dentition shows a combination of primitive and derived features: bunodont molars with relatively complex cusp patterns, and lower canines of the "verrucosic" type, shared with

Island Southeast Asian verrucosic pigs and setting it apart from generalized wild boar morphology (Cherin et al 2018).

Comparisons of tooth dimensions and morphology indicate that *S. strozzii* is consistently larger than *S. arvernensis*, with more massive molars and premolars, a pattern corroborated across European localities. This large size has been used in biostratigraphy: assemblages dominated by very large *Sus* teeth in Early Pleistocene European sites are typically attributed to *S. strozzii* rather than to later *Sus* taxa (Martínez-Navarro et al 2015; Cherin et al 2018; Iannucci et al 2021; Van Der Made 2025).

Ecology, diet, and environmental context. Although direct isotopic data for *S. strozzii* are limited, its dental morphology suggests an omnivorous to herbivorous diet similar to that of modern wild boar and some insular pigs, rather than highly specialized grazing as in African warthogs. Comparative studies on Neogene African suids show that evolutionary shifts toward higher, more complex molars correlate with increased grazing on C4 grasses. In contrast, *Sus* lineages, including *S. strozzii*, retain lower-crowned, bunodont molars suited to mixed feeding on roots, fruits, invertebrates, and small vertebrates (Harris & Cerling 2006; Cherin et al 2018; Rannikko et al 2020). This is consistent with the ecological flexibility of *Sus*, which is often associated with mosaic environments and forest–open habitat ecotones.

The presence of *S. strozzii* in European faunas coincides with major climatic oscillations and faunal turnovers around the Plio-Pleistocene boundary and early Pleistocene, when suid assemblages elsewhere (e.g., in the Turkana Basin and the Siwaliks) show parallel trends in dental evolution linked to grass expansion and habitat change (Harris & Cerling 2006; Pickford & Gommery 2020; Rannikko et al 2020; Aslam et al 2021; Van Der Made et al 2022). As a large, omnivorous, r-selected mammal with high reproductive output, *S. strozzii* would have been an abundant and ecologically important member of Early Pleistocene mammal communities, potentially influencing vegetation through rooting and seed dispersal and serving as prey or competitor to large carnivores and early hominins (Harris & Cerling 2006; Martínez-Navarro et al 2015; Van Der Made 2025).

Biostratigraphic and paleoanthropological significance. *S. strozzii* plays a key role in debates about the "suid gap" and human dispersal into Europe. A hypothesis proposed that humans arriving around 1.8 Ma competitively displaced *S. strozzii*, creating a continent-wide absence of pigs until their reappearance around 1.2 Ma. A recent critical review of this hypothesis re-examined the evidence and concluded that the "suid gap" as originally formulated is not supported; instead, the record reflects incomplete sampling, taxonomic issues, and taphonomic biases (Van Der Made 2025). Nevertheless, the discussion underscores how tightly the temporal distribution of *S. strozzii* is interwoven with reconstructions of early human ecology and faunal turnover in Europe.

More broadly, the arrival and later replacement of *S. strozzii* by *Sus cf. scrofa*–like pigs in Europe is part of a major Suidae transition at the Miocene-Pliocene and Pliocene-Pleistocene boundaries, where Asian suines dispersed westward and replaced older suid lineages such as *Propotamochoerus* and *Listriodon* (Aslam et al 2021; Iannucci et al 2021; Van Der Made et al 2022). In this context, *S. strozzii* represents a key early representative of the *Sus* radiation in western Eurasia, linking Pliocene forms (*S. arvernensis*) to the later, more generalized wild boar complex (Cherin et al 2018; Iannucci et al 2021; Iannucci et al 2024).

Evolutionary connections and legacy. Phylogenetic analyses indicate that the divergence between African and Eurasian suines occurred early, probably already in the late Miocene, after which the *Sus* lineage diversified across Eurasia and later into Island Southeast Asia. *S. strozzii*, with its morphological affinities to present and extinct Island Southeast Asian pigs such as *S. verrucosus*, highlights historical connections between continental and insular suids, foreshadowing the complex patterns of dispersal and admixture later documented genetically in *Sus scrofa* and related species (Gongora et al 2011; Cherin et al 2018; Liu et al 2019). Its combination of large body size, distinctive

dentition, and restricted temporal range makes it a cornerstone taxon for reconstructing the early history of modern pigs and for calibrating faunal and environmental changes in the Early Pleistocene of Europe.

Conclusions. *Sus strozzii* is not merely a fossil wild boar; it is a morphologically distinctive, biostratigraphically important, and phylogenetically informative species that illuminates the evolution, ecology, and paleobiogeography of suids and their mammalian communities at a critical juncture in Eurasian Quaternary history. Its significance extends beyond morphology, encompassing its biochronological utility and its key role in reconstructing Early Pleistocene ecosystems

Conflict of interest. The authors declare that there is no conflict of interest.

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