



Domestication and management of suids (Suidae): an archaeozoological mini-review

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Abstract. This archaeozoological mini-review synthesizes current evidence on the domestication and management of suids (Suidae), with a primary focus on *Sus scrofa*, the only species within the family that underwent full domestication. Drawing on archaeological, morphometric, isotopic, and genomic data, the study highlights multiple independent domestication events in northern Mesopotamia and East Asia, followed by complex processes of dispersal, hybridization, and regional adaptation. The domestication trajectory of *S. scrofa* is shown to be non-linear, characterized by continuous gene flow with wild populations, extensive introgression, and varying management strategies ranging from free-range husbandry to intensive penning systems. The review emphasizes the role of ecological plasticity, omnivory, and behavioral adaptability in facilitating the integration of pigs into diverse human socio-economic systems. It also explores the variability of human-pig relationships across regions, including cases of limited or failed domestication. In contrast, other suid taxa remained largely undomesticated, being subject instead to hunting or low-level management. Additionally, the study addresses the importance of taxonomy and phylogeny in reconstructing domestication pathways, as well as the phenomenon of feralization, whereby domestic pigs revert to free-living conditions and form genetically admixed, highly invasive populations. Overall, the evidence supports a model of pig domestication as a dynamic, reticulate, and regionally contingent process rather than a single evolutionary event.

Key Words: ancient DNA, animal management, archaeozoology, feralization, hybridization, introgression, morphometrics, Neolithic, phylogeny, pig domestication, suids, *Sus scrofa*.

Introduction. The archaeological and genetic record shows that true domestication within Suidae is overwhelmingly focused on *Sus scrofa*, whereas other suids have remained hunted, managed, or locally exploited without reaching a fully domestic state. The Eurasian pig provides an exceptionally well-documented model for understanding how behavioral flexibility, ecology, and culture interact in domestication processes.

The aim of this study is to provide a comprehensive and integrative synthesis of archaeozoological, genetic, and morphometric evidence concerning the domestication and management of suids, with a particular focus on *S. scrofa* as the only fully domesticated representative of the family. The paper seeks to clarify the main centers and pathways of pig domestication, to examine the diversity of human-pig interactions across different ecological and cultural settings, and to assess the role of hybridization and introgression in shaping domestic populations. It also aims to contextualize *S. scrofa* within the broader framework of Suidae by evaluating why other suid species did not undergo comparable domestication processes. Furthermore, the study integrates taxonomic and phylogenetic perspectives to refine interpretations of domestication histories and incorporates the phenomenon of feralization in order to frame domestication as a dynamic, ongoing, and partially reversible evolutionary process.

Major domestication events in *Sus scrofa*. Zooarchaeological syntheses identify independent domestication of wild boar in northern Mesopotamia by c. 7500 cal BC and China by c. 6000-8000 BP (Kusatman 1991; Price & Hongo 2020; Hongo et al 2021). In the Near East, pigs followed a mixed "commensal and prey" pathway: wild boar initially exploited anthropogenic niches, then became targets of game management, finally

entering loose, extensive husbandry systems where animals ranged freely and interbred with wild populations (Price & Evin 2017; Price & Hongo 2020; de Groene et al 2021).

In China, early sedentary communities in both Yellow and Yangtze river basins provided the ecological context for pig domestication, with evidence for more intensive management (pens, fodder) that generated relatively rapid phenotypic divergence from wild morphotypes (Price & Hongo 2020; Cucchi et al 2021; Dai & Zhang 2021; Hongo et al 2021). Ancient genomic work confirms northern China as the primary center of origin for modern East Asian domestic pigs and documents subsequent dispersal along with millet farmers into southern and southwestern China, with admixture from local wild boar and signatures of inbreeding under intensified management (Larson et al 2010; Han et al 2025).

Molecular analyses further show independent domestication from distinct wild boar lineages in Europe and Asia, with divergence of ancestral wild populations ~0.5-1 million years ago and later introgression of Asian domestic lineages into European breeds (Giuffra et al 2000; Groenen et al 2012). Ancient DNA and morphometrics trace a complex history of Near Eastern domestic pigs moving into Europe, replacement by European wild boar matriline, and later “backflow” of European domestic lineages into Anatolia and parts of the Middle East (Ottoni et al 2012; Caliebe et al 2017; Stanc et al 2022; Demirbaş et al 2025).

Human-pig relations, hybridization, and management diversity. Long-term morphometric studies in the northern Fertile Crescent (11,000-2000 cal BC) show a gradual size reduction and attainment of a morphological plateau in the 4th millennium cal BC, with sustained presence of large, wild-like individuals and extensive hybridization between domestic pigs and wild boar (Price & Evin 2017). Similar wild-domestic blending is documented in Neolithic Romania and other European regions, where free-range husbandry and recurrent introgression from local wild boar shaped domestic populations (Price & Evin 2017; Stanc et al 2022).

Stable isotope and biometric analyses repeatedly reveal mixed assemblages in which wild boar and domestic pigs cannot be sharply separated by diet or size, particularly under extensive or free-range systems (Price & Evin 2017; de Groene et al 2019; Price & Hongo 2020; Dai & Zhang 2021; Brusgaard et al 2022). In early Dawenkou China, suids show diverse C₃ and C₃/C₄ diets, with free-range domestic pigs supplemented by small amounts of cultivated by-products, highlighting low-intensity control and regionally variable husbandry strategies (Dai & Zhang 2021). In Mesolithic–Neolithic northern Europe, sequences from the Netherlands and southeastern Europe show transitions from exclusive hunting of wild boar to the sporadic presence of small, possibly domestic or hybrid suids well before full local pig husbandry is established (de Groene et al 2019; Brusgaard et al 2022).

Conversely, some regions with suitable environments show limited or failed domestication trajectories. In Japan, pig domestication “failed to take off” despite commensal possibilities, probably due to the absence of domestic crops and cultural reluctance to conceptualize animals as property (Price & Hongo 2020). Early Neolithic sites in the northern Balkans exhibit extremely low frequencies of suids despite agricultural economies and favorable oak-riparian habitats, suggesting only peripheral engagement with pigs along certain Neolithic dispersal routes (de Groene et al 2019).

Biological and genetic features underpinning *Sus scrofa* domestication. Comparative genomics emphasizes that behavioral and ecological flexibility in *S. scrofa* - omnivorous diet, scavenging ability, and adaptability across Eurasian habitats - underpins its exceptional domestic success (Larson et al 2010; Groenen et al 2012; Price & Hongo 2020). The species harbors deep phylogeographic structure, with numerous wild populations that never contributed to modern domestic stocks, underscoring strong human-mediated selection and replacement (Larson et al 2010; Groenen et al 2012).

Genome-wide analyses of domestic pigs highlight rapid evolution in olfactory receptor and immune genes, consistent with selection in anthropogenic environments and reliance on smell in a scavenging, commensal lifestyle (Groenen et al 2012). Ancient DNA

and geometric morphometrics reveal that early domestication is expressed phenotypically through reduction in body size, changes in tooth shape, and island-specific dwarfing or sub-speciation (e.g., *S. scrofa circeus* on Cyprus), with subsequent local domestication of such insular lineages under reproductive isolation (Price & Hongo 2020; Cucchi et al 2021).

The repeated documentation of hybrid origins, introgression-driven domestication, and replacement of Near Eastern by European matriline in Europe and Anatolia illustrates that pig domestication is often a protracted, reticulate process rather than a single, linear transition from wild to domestic (Larson et al 2010; Ottoni et al 2012; Caliebe et al 2017; Price & Evin 2017; Stanc et al 2022) (Table 1).

Table 1
Geographic foci and pathways of *Sus scrofa* domestication (summarized by Consensus, 2026)

<i>Region / Context</i>	<i>Domestication / Management pattern</i>	<i>Citations</i>
Northern Mesopotamia (NFC)	Early domestication via commensal-prey pathway, extensive free-range husbandry with wild introgression	(Kusatman 1991; Price & Evin 2017; Price & Hongo 2020; de Groene et al 2021)
China (Yellow/Yangtze)	Independent domestication, more intensive pen- and fodder-based systems, later dispersal south with admixture	(Larson et al 2010; Price & Hongo 2020; Cucchi et al 2021; Dai & Zhang 2021; Hongo et al 2021; Han et al 2025)
Europe (Neolithic onward)	Near Eastern pigs introduced, then largely replaced by European wild boar lineages; local domestication via introgression	(Giuffra et al 2000; Larson et al 2010; Ottoni et al 2012; Caliebe et al 2017; Price & Evin 2017; de Groene et al 2019; Brusgaard et al 2022; Stanc et al 2022)
Cyprus and Eastern Mediterranean	Introduction of wild boar, insular evolution (<i>S. scrofa circeus</i>), local domestication of insular lineage	(Ottoni et al 2012; Price & Hongo 2020; Cucchi et al 2021)
Japan, Northern Balkans	Commensal opportunities but limited or failed domestication, low suid exploitation despite agriculture	(de Groene et al 2019; Price & Hongo 2020)

Other suids: managed, exploited, but rarely domesticated. The available archaeozoological and genetic literature focuses almost exclusively on *S. scrofa*; other suid species (e.g., *Sus celebensis*, *Babyrousa*, *Phacochoerus*, *Potamochoerus*, *Hylochoerus*) appear in this corpus only as comparative wild taxa or in methodological discussions of distinguishing endemic wild pigs from introduced *S. scrofa* (Albarella et al 2007; Ingicco et al 2017). Metric and morphometric methods can separate local wild suids from *S. scrofa* in regions such as the Philippines and Island Southeast Asia, allowing detection of the first introductions of domestic pigs into landscapes already occupied by endemic suids (Albarella 2007; Larson et al 2010; Ingicco et al 2017).

However, there is no robust zooarchaeological or genetic evidence in these studies for fully domestic lineages in non-*S. scrofa* suids. Instead, the pattern that emerges is one of hunting, occasional captivity, and localized management of wild suids, without the sustained, multi-millennial selection regimes, introgression cycles, and global dispersal that characterize *S. scrofa*.

Discussions on pig domestication. Taken together, the archaeological, morphometric, genomic, and isotopic data converge on a strongly asymmetric picture of suid domestication. *S. scrofa* is the only suid for which repeated, independent domestication events, long-term husbandry trajectories, and global dispersal are securely documented (Larson et al 2010; Groenen et al 2012; Ottoni et al 2012; Giuffra et al 2000; Price &

Hongo 2020). Its ecological plasticity, omnivorous diet, high reproductive potential, and social behavior made it particularly suited to commensal pathways and to integration into diverse agricultural systems.

Within *S. scrofa*, domestication is not a singular event but a mosaic of regional experiments: some succeed and are intensified (Northern Mesopotamia, northern China), some remain marginal or revert to hunting (Japan, parts of the Balkans), and others are reshaped by hybridization and introgression (Europe, Anatolia, Cyprus, Romania) (Ottoni et al 2012; Caliebe et al 2017; Price & Evin 2017; de Groene et al 2019; Price & Hongo 2020; Cucchi et al 2021; Stanc et al 2022). This confirms that “domestic pig” represents a dynamic continuum of wild, feral, hybrid, and managed forms rather than a fixed endpoint.

By contrast, the broader family Suidae, though behaviorally diverse and widely exploited, shows no comparable signature of sustained domestication beyond *S. scrofa* in the present dataset. Other suids appear mostly as ecological analogues or as wild taxa against which the spread of *S. scrofa* can be measured (Albarella 2007; Larson et al 2010; Ingicco et al 2017). Consequently, from an archaeozoological and genetic standpoint, the domestic suid is effectively synonymous with *S. scrofa*, while other species exemplify alternative human-animal relationships - management, hunting, symbolic use - that never crystallized into full domestication under long-term, global human selection.

Taxonomy and phylogeny in pig domestication. To identify precisely which species contributed to pig domestication, research shows that a rigorous taxonomic and phylogenetic framework is essential. Modern and fossil suid lineages, correctly named and ordered, allow scholars to trace domestication events, hybridization, and introgression through time and space (Iannucci 2022).

Molecular phylogenies of Suidae based on mitochondrial genes and whole genomes consistently recover deep splits between African and Eurasian clades, with the genus *Sus* forming a distinct Eurasian lineage, within which *S. scrofa* and its fossil relatives (e.g., *S. lydekkeri*, *S. arvernensis*, *S. strozzii*) occupy key basal or plesiomorphic positions (Randi et al 1996; Wu et al 2006; Cherin et al 2018; Balint et al 2024; Iannucci et al 2024; Dăescu et al 2025; Petrescu-Mag et al 2025). Such structured trees, supported by both morphology and DNA, make it possible to situate domestic pigs within a wider evolutionary context and to recognize which fossil taxa plausibly lie on the ancestral stem to *S. scrofa* (Randi et al 1996; Cherin et al 2018; Iannucci et al 2024). Detailed systematic work on fossil *Sus* from Europe and Island Southeast Asia highlights how careful anatomical description, standardized terminology, and strict nomenclatural practice are needed to distinguish closely related species and to interpret their role in the diversification of the genus (Cherin et al 2018; Iannucci et al 2024; Pacheco-Scarpitta 2025).

Domestication studies using ancient and modern DNA then build upon this taxonomic scaffold. Multiple independent domestications of *S. scrofa* in the Near East and East Asia, followed by extensive interbreeding with local wild boars and even other suid genera, have been demonstrated only because haplotypes and genomic segments can be mapped unambiguously onto a robust phylogeny and correctly named lineages (Larson et al 2007, 2010; Ottoni et al 2012; Caliebe et al 2017; Frantz et al 2019; Liu et al 2019; Giuffra et al 2000; Zhang et al 2022; Demirbaş et al 2025). These analyses reveal cryptic domestication, genomic turnovers, and introgressions that would remain obscure without consistent, phylogenetically informed nomenclature (Larson et al 2010; Ottoni et al 2012; Amills et al 2017; Frantz et al 2019; Liu et al 2019; Demirbaş et al 2025). Thus, only by respecting the taxonomic order of extant and fossil suids and applying correct names where phylogeny provides sufficient resolution can the true spectrum of species contributing to pig domestication be accurately reconstructed.

Rewilding and hybrid origins of feral pigs. Domesticated pigs (*Sus scrofa domesticus*) that return to free-living conditions and become feral represent a powerful example of “rewilding” driven by both natural and human forces. These feralized populations combine domestic ancestry, wild boar genes, and rapid evolutionary change, giving rise to one of the world’s most successful and damaging invasive mammals (Oroian et al 2014; Petrescu-Mag et al 2014).

Feral pigs almost never derive from “pure” domestic lineages: genomic studies in the USA and elsewhere show that most invasive wild pigs are hybrids between domestic pigs and European wild boar, with mixed ancestry strongly associated with rapid range expansion and high invasiveness (Frantz et al 2013; Smyser et al 2020; Mary et al 2022; Fabbri et al 2023; Barmantlo et al 2024; Smyser et al 2024). In Argentina and Patagonia, feral pigs and wild boar form extensive hybrid swarms with high genetic diversity, which increases their adaptive potential and invasion success (Figueroa et al 2022; Acosta et al 2024; Figueroa et al 2025). Similar patterns of introgression from domestic pigs into wild boar are documented in France, Belgium, Luxembourg, Sardinia and Corsica, often linked to free-range husbandry, restocking, or illegal translocations (Frantz et al 2013; Mary et al 2022; Schleimer et al 2022; Fabbri et al 2023; Fulgione et al 2025). Hybridization introduces domestic alleles affecting morphology, coat colour and reproduction, and some domestic variants show signs of adaptive introgression, improving fitness and population growth in wild contexts (Mary et al 2022; Schleimer et al 2022; Acosta et al 2024; Fabbri et al 2023; Barmantlo et al 2024; Fulgione et al 2025).

Feralization is not a simple return to the ancestral wild state. Comparative genomic, olfactory, dietary and microbiota analyses show that feral pigs form a distinct evolutionary unit, retaining signatures of past domestication while evolving new traits under natural selection in free-living conditions (Petrelli et al 2021). Traits linked to skull formation, neurogenesis, pigmentation, body weight, feeding behaviour, litter size and teat number show evidence of selection under feral conditions (Petrelli et al 2021; Barmantlo et al 2024; Fulgione et al 2025). Historical and global reviews emphasize that biological changes accompanying domestication (high growth and reproduction) often regress partly after feralization, yet invasive feral populations still achieve high densities and wide distributions on continents and islands (Wehr et al 2018; Wehr 2021; Fulgione & Buglione 2022; Gentle et al 2022; McDonough et al 2022).

Ecologically, pig feralization transforms pigs into ecosystem engineers and serious pests. Their rooting, generalist diet and disease reservoir role cause soil disturbance, vegetation damage, crop loss, biodiversity declines and threats to livestock health from the Americas to the Pacific islands and Australia (Wehr et al 2018; Fulgione & Buglione 2022; Gentle et al 2022; McDonough et al 2022; Giglio et al 2024). Human-mediated movement and hunting cultures further shape these populations, both facilitating spread and framing feral pigs as valued game even as management policies seek their control or eradication (Wehr et al 2018; Fulgione & Buglione 2022; Gentle et al 2022; Keil 2023; Giglio et al 2024).

In sum, the return of domestic pigs to the wild produces feral populations that are genetically admixed, evolutionarily dynamic and ecologically disruptive. Feral pigs are not simply wild boar restored, but novel hybrids whose success depends on the interaction of domestication legacies, ongoing hybridization and strong natural selection in human-modified landscapes.

Conclusions. The combined archaeological, genetic, and morphometric evidence clearly demonstrates the unique status of *Sus scrofa* within the Suidae family as the only species that underwent repeated and sustained domestication. This exceptional trajectory is closely linked to its biological and ecological characteristics, including high behavioral plasticity, omnivory, rapid reproduction, and adaptability to a wide range of environments, all of which facilitated its incorporation into diverse human subsistence systems.

Rather than representing a single, linear transition from wild to domestic, pig domestication emerges as a complex, long-term, and regionally variable process. Multiple independent domestication events occurred in different parts of Eurasia, notably in the Near East and East Asia, followed by extensive dispersal, population turnover, and continuous interaction with local wild boar populations. Hybridization and introgression were not marginal phenomena but central mechanisms that shaped the genetic and phenotypic structure of domestic pigs, contributing to their resilience and adaptability.

The evidence further indicates that the boundary between wild and domestic pigs has remained permeable throughout history. In many regions, especially under extensive or free-range management systems, domestic pigs and wild boar formed mixed populations

that are difficult to distinguish morphologically or isotopically. This reinforces the view that domestication should be understood as a continuum encompassing wild, managed, hybrid, feral, and fully domestic forms, rather than as a fixed categorical state.

In contrast, other suid species did not follow similar domestication trajectories. Despite being widely exploited by human populations, they remained primarily within the domains of hunting, opportunistic management, or localized control. This asymmetry underscores that domestication is not an inevitable outcome of human-animal interaction but depends on a specific combination of biological traits, ecological opportunities, and cultural practices.

The integration of taxonomic and phylogenetic frameworks proves essential for accurately reconstructing domestication processes. Robust species identification and well-resolved evolutionary relationships allow for the detection of independent domestication events, cryptic introgression, and lineage replacement, all of which are fundamental to understanding the complex history of pig domestication.

Finally, the phenomenon of feralization highlights the ongoing and reversible nature of domestication. Feral pig populations are not simple returns to a wild ancestral state but represent novel evolutionary entities shaped by admixture, rapid adaptation, and strong selective pressures in anthropogenic environments. Their global spread and ecological impact further demonstrate how domestication and its aftermath continue to influence both evolutionary trajectories and ecosystems.

Overall, the domestication of *Sus scrofa* should be interpreted as a dynamic, reticulate, and context-dependent process, reflecting long-term interactions between humans, animals, and environments. This perspective contributes to a broader understanding of domestication as a multifaceted evolutionary phenomenon rather than a singular historical event.

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

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