



The Archaeology of Pig Domestication in Eurasia

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Abstract

The multifaceted behavioral and ecological flexibility of pigs and wild boar (*Sus scrofa*) makes study of their domestication both complex and of broad anthropological significance. While recognizing contextual contingency, we propose several “pathways” to pig domestication. We also highlight the diversity of pig management practices. This diversity complicates zooarchaeological detection of management techniques employed by humans in the early steps of domestication, and we stress the need for multiple lines of evidence. Drawing together the evidence, we review early Holocene human–*Sus* relations in Japan, Cyprus, northern Mesopotamia, and China. Independent pig domestication occurred in northern Mesopotamia by c. 7500 cal. BC and China by c. 6000 cal. BC. In northern Mesopotamia pig domestication followed a combined “commensal and prey” pathway that evolved into loose “extensive” husbandry that persisted as the dominant form of pig management for several millennia. There are not yet enough zooarchaeological data to speculate on the early stages of pig domestication in China, but once that process began, it involved more intensive management (relying on pens and fodder), leading to more rapid selection for phenotypes associated with domestication. Finally, pig domestication “failed” to take off in Japan. We suggest this was related to a number of factors including the lack of domestic crops and, potentially, cultural barriers to conceiving animals as property.

Keywords Pigs · *Sus scrofa* · Domestication · Neolithic · Holocene · Zooarchaeology

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Introduction

The domestication of animals and plants in the Holocene was a major turning point in human history. The adoption of agriculture set the stage for state-level societies, massive population growth, selection for novel phenotypes (e.g., lactase persistence), and unprecedented impacts on the environment. No less significant were the impacts on animals and plants that underwent domestication. They achieved levels of population growth and phenotypic variation otherwise selected against in the wild (Larson and Fuller 2014; Zeder 2015). For these reasons, documenting the processes of domestication and the cultural contexts in which they took place touches on multiple fields of inquiry, from anthropology to zoology (e.g., Frantz et al. 2016; Hide 2003; Mayer et al. 1998).

One of the most unique species to be domesticated is the pig (*Sus scrofa*). Today, pigs are one of the most common livestock animals in the world. Equally significant are long-standing pork taboos, which are emblematic of the foodways of two world religions (Judaism and Islam) and other faiths/ethnic groups (e.g., Ethiopian Orthodox Christians and Yazidis). Pigs also possess several characteristics that differentiate them from other livestock species. They are omnivorous and multiparous (give birth in litters). They are curious and intelligent, able to adapt their behaviors when faced with different social and environmental conditions (e.g., Held et al. 2000, 2002). They are social animals that exhibit high levels of filial imprinting (Dwyer and Minnegal 2005; Graves 1984). These traits evolved in primitive suids millions of years ago, but they became particularly important to human societies in the Holocene when morphologically and behaviorally altered (i.e., “domesticated”) pigs emerged independently in at least two regions, China and northern Mesopotamia.

The diversity of pig management practices and their relationships to broader social, political, gender, ecological, and economic structures in human societies have long interested anthropologists. The natural characteristics of *Sus scrofa* makes it possible for these pigs to intersect with human cultures in various ways. For example, Rappaport (1967) has argued that rapid fluctuations in pig populations, a byproduct of pigs’ natural potential for explosive population growth, articulate with local ecological conditions to dictate the timing of ritual events. Other scholars (e.g., Sillitoe 2001) have noted that in many societies men own pigs but women (their wives) invest all the labor in raising them. It is the unique ability of pigs to thrive on garden crops and household waste, which often fall under the domain of women, that enable these forms of family-level economic alienation. Other scholars have focused on the tendency of lower classes in urban societies to depend more heavily on pig husbandry than members of the upper classes, in ways that create and sustain differential foodways between social status groups (Price et al. 2017; Zeder 2003). Pigs’ unique innate behavioral and physiological traits—their ability to thrive on small plots of land in urban environments and feed off refuse—foster these sociocultural manifestations.

Anthropological interest in pigs is perhaps most prominent among ethnographers working in New Guinea (see Hide 2003). This ethnographic literature

provides fertile ground for archaeologists interested in the origins and evolution of agricultural practices and complex societies (Blanton and Taylor 1995; Kim 1994; Redding and Rosenberg 1998). More recently, zooarchaeologists have conducted their own informant-based research on contemporary pig management practices in a variety of locations, especially in the Mediterranean, where they have furthered scholarly appreciation of the diversity, contingencies, and far-reaching social significance of pig husbandry (Albarella et al. 2007b, 2011; Hadjikoumis 2012; Halstead 2011). These “ethnozooarchaeological” studies (Albarella and Trentacoste 2011) have the benefit of more systemically tracking data relevant to zooarchaeological research.

Although pigs and pig–human relations have long featured in anthropological discussions of social, political, and economic dynamics, there have been relatively few attempts to tie together the diverse threads of archaeological literature on the origins of domestic pigs. In particular, while we can now be (mostly) confident of when and where pig domestication took place, the how and why remain underexplored. These are important questions; unlike other major livestock species (e.g., bovids, camelids), the behavioral and ecological flexibility of pigs makes it possible to hypothesize several “pathways” to domestication, which complicates the zooarchaeological reconstruction of the specific ways in which ancient peoples managed or exploited *Sus scrofa* populations. Several scholars have provided robust syntheses of aspects of pig domestication over the past two decades (Albarella et al. 2006a, 2007a; Nelson 1998; Rowley-Conwy et al. 2012), but much has changed since these articles and books were published, including the addition in recent years of new zooarchaeological, genomic, and isotopic data that allow us to make more informed hypotheses about the processes of pig domestication and their relevance to the study of animal domestication and human–environmental interactions more broadly.

Our review focuses on China and northern Mesopotamia, where pig domestication followed unique trajectories, evolving from other types of human–animal relations, such as commensalism, intensive hunting, and game management, while articulating with other processes, such as feralization and hybridization. Although the end result was categorically identical (i.e., domestic pigs in both regions), there were striking differences in the processes that showcase the variability in the pathways that humans and animals may proceed together toward domestication.

In this review, we evaluate the theoretical concept of domestication, the behavioral and physiological uniqueness of pigs and wild boar, methods to detect the management of pigs and wild boar and their subsequent domestication, examples of intensive hunting or management of *Sus scrofa* in the early Holocene, and the evidence for pig domestication in northern Mesopotamia and China. We lay out potential pathways to pig domestication and present tentative explanations for where it “failed” to occur, such as in Jomon period Japan. These are hypotheses to be tested and reworked with new and improved zooarchaeological, genomic, and isotopic methods. In reviewing the methods currently available to zooarchaeologists, we stress current limitations to interpretation and argue that researchers should exert greater effort in deploying multiple lines of evidence to the study of pig domestication and the forms of human–suid relations that led up to it.

Domestication: Theoretical Considerations and Models for Human–Suid Relations

Domestication is a “concept metaphor” encompassing a range of relationships between humans and other species. There is therefore a long-standing debate on how to conceptualize this process (e.g., Bleed 2006; Clutton-Brock 1992; Ducos 1978; Hemmer 1990; Vigne 2011b; Zeder 2015). Three key issues are, first, how should we differentiate domestication from other human–animal relationships? Second, how do feralization and hybridization, processes that act against domestication, complicate our conceptualization of evolving human–suid relations in the Holocene (Larson and Fuller 2014; Marshall et al. 2014)? Many scholars now recognize that domestication was not a simple, unilateral process, but rather one defined by “failures,” abrupt turns, and complex twists (e.g., Redding 2005). Third, to what extent was human intentionality involved? Traditional conceptualizations of domestication posit it as a process of human domination over nature, a deliberate mastery over animals to create more docile livestock (e.g., Darwin 1868, p. 6). However, some scholars have adopted the opposite perspective, suggesting that plants and animals initiated the process and adapted to human niches (e.g., Rindos 1980). Recently, some have emphasized how intentional human subsistence procurement activities and niche construction can result in unintended consequences (e.g., Zeder 2012).

Disagreement about these fundamental issues has led to experts “talking past one another in a crowded room” (Zeder and Smith 2009). Imprecise use of terminology is a major ongoing problem. For that reason, to tackle the theoretical issues mentioned above, we focus on the definitions of three relationships between *populations* of humans and animals—management, intensive hunting, and commensalism—and their relevance to the study of domestication. These processes are different from individual-level relationships, although we recognize the dialectical relationship between both types. In particular, the ability of people to form close bonds with individual pigs that border on pet-keeping (e.g., the Kubo example below) may have played an important role in the process of domestication.

Management entails exerting control over the reproduction, diet, mobility, social structure, or ecology of a population of wild or domestic animals to enhance its reliability, predictability, and availability as a source of food, clothing, or other product. Many types of behaviors qualify as management: transporting animals to new environments, altering the environments they currently inhabit, providing food, or capturing and raising juveniles. What differentiates it from other, vaguely similar, forms of human activity—e.g., capturing animals and raising them as pets (Serpell 1989; Shipman 2010; Simoons and Baldwin 1982)—is that people practice management strategically and with the principal, though not necessarily exclusive, goal of economic benefit (Clutton-Brock 1989, p. 7).

Intensive hunting is the focused procurement of meat or other products from wild animal populations, often by targeting specific ages or sexes to enhance the

quality and/or quantity of the desired product. Intensive hunting can therefore have a significant impact on an animal population. Often times, intensive hunting alters the natural herd composition and can lead to population decline. But intensive hunting can also select for certain phenotypes, such as smaller horns in bovids hunted as trophy animals or diminished body lengths in heavily exploited fish populations (Sullivan et al. 2017). In economic terms, intensive hunting, like “intensive agriculture” sensu Boserup (1965), involves higher returns at the cost of procurement efficiency, i.e., declining rates of return as labor input increases. Zooarchaeologically, one can detect intensive hunting by changes in the demographic composition of prey species toward younger animals and an increased relative abundance of those prey species in the assemblage. One example is that of gazelle hunting in the Natufian Levant (Davis 2005; Munro 2004).

Finally, *commensalism* is the adaptation on the part of an animal population to human environments in the absence of exploitation. Whereas management involves human intentionality to facilitate the relationship, commensalism takes place largely in the absence of human intentional behavior; humans may tolerate commensalism, but they do not initiate it. Commensalism can be parasitic (e.g., lice and mice) or innocuous (e.g., pigeons) but typically results in selection for unique morphological and behavioral traits similar to those of domestication (e.g., Geiger et al. 2018). For that reason, some scholars categorically lump commensalism with domestication (e.g., Geiger et al. 2018). From a strictly biological perspective, this may be justified, but we prefer to keep the terms separate to highlight the social significance of the changes in human–pig relations (Fuller and Stevens 2017a, b; Vigne 2011b).

This brings us to *domestication*, which we define as the evolutionary process by which a population of organisms develops heritable phenotypes as an adaptation to the selection pressures of living within anthropogenic niches defined by management. These phenotypes distinguish the animal population from its wild progenitors and facilitate exploitation by humans. This biological/ecological change is driven by, and reciprocally drives, a cultural/economic one in which humans’ perception of the organism shifts from prey to livestock—in other words, whereas once people focused on obtaining products of dead animals, now they apply greater attention to acquiring and maintaining live ones. They do so not only to maximize the reliability, predictability, and abundance of desired products but also because the population of live animals becomes a thing of value. While meat and other resources remain major motivating factors in keeping domestic animals, people also tend them for the sake of owning livestock. The process of domestication is co-evolutionary and, although initiated by humans, involves feedback between human and animal partners. Domestication thus impacts humans, sometimes phenotypically (e.g., lactase persistence). Additionally, domestication does not have an endpoint. Indeed, the selection for “improved” breeds in the past three centuries vividly documents the ongoing process of domestication in pigs and other animals. Finally, domestication can be interrupted or suspended, as, for example, when animal populations go feral.

We stress three features of this definition. First, “heritable phenotypes” refer to both physical and behavioral traits, the latter of which are ultimately neurochemical. These traits, which are broadly similar across species, are sometimes referred to as the “domestication syndrome.” Typical phenotypes include coat

color variation, floppy ears, shorter faces, smaller teeth, smaller brains, depressed flight-or-fight response, greater tolerance of stressors, and a general lack of “environmental awareness” (Darwin 1868; Hemmer 1990; Wilkins et al. 2014). Second, in managing animal populations, people significantly interfere in the lives of individuals. People provide food, imprint young animals onto humans, control breeding partners, and attach animals to home ranges that include humans and their settlements (Tani 2017, pp. 3–7). Feedback is a critical part of the process: animal behavior enables novel human behavior, which selects for novel animal phenotypes, which enable newer forms of human behavior, etc. Thus, while domestication is, in essence, management plus phenotypic change, phenotypic change can itself facilitate new types of management.

Third, while it is important to distinguish commensalism, intensive hunting, and management from domestication, these forms of human–animal relationships can evolve into domestication. Commensalism may “prime” certain animal populations for human exploitation by selecting for individuals that can tolerate proximity to humans. This selection for tameness may also cause other phenotypic responses, such as coat color changes or snout length reduction (Geiger et al. 2018; Trut 1999). However, a critical feature of the transition from commensalism to domestication is the change in humans’ perception of animals; for an animal population to transition from commensal to domestic, humans must attempt to gain something from the existing relationship. In doing so, they often select for additional novel phenotypes. For example, by capturing and breeding commensal rodents (house mice and rats) for research, scientists domesticated them, later intentionally selecting for highly specific traits (Arbuckle 2005). An initial commensal relationship may also have played a role in the domestication of pigs.

Intensive hunting can also evolve into domestication when humans modify their behavior towards animals. One can envision a logical progression from intensive hunting to “game management” to “herd management” (or husbandry) as humans become more invested in ensuring the availability, predictability, and reliability of animals (Zeder 2012, p. 249). The transition from intensive hunting to game management involves humans shifting their focus from immediate to delayed returns on animal resources, but without necessarily perceiving of animals as property. This situation may arise when hunters act on the realization that, without management, intensive hunting will result in extirpations of their preferred prey species. Game management might involve, for example, selective culling of males, modifying environments to encourage herd growth, or transporting live animals to new locations. These are effective strategies for ensuring that meat is accessible over the long-term. Herd management, meanwhile, involves an additional and important conceptual flip in which people treat animals as livestock rather than as prey (Meadow 1984). When humans view animals as property, whether communal or private, they shift their focus from the procurement of meat to the propagation of a herd as an end unto itself. As a result, people tend to follow herds more closely and interfere more directly in the lives of “their” animals, adding even greater selection pressures for tameness. The transitions from intense hunting to game management to herd management may be subtle and gradual; they may be difficult to detect zooarchaeologically.

On a general level, selection pressure for “domestication syndrome” phenotypes correlates with increasing investment in animal management. Although any human–animal relationship can select for novel phenotypes, low-intensity game management typically results in minimal phenotypic change or in changes that do not foster additional scaffolding of human–animal relations toward domestication. For example, the introduction of wild boar to island habitats results in size decrease, the so-called “island effect,” but not behavioral ones that would make these populations more amenable to exploitation. Domestication will result only from forms of management that are *both* sufficiently intense and applied for a sufficiently long period of time; they must be applied to populations that are *both* adequately isolated from others of their conspecifics and composed of animals behaviorally and physiologically suitable to adapt to management (Zeder 2012). Needless to say, the devil is in the details. What counts as “sufficiently intense” management or “adequate” sexual isolation remains unclear and, we suspect, highly variable from species to species.

Zeder (2012) has laid out three “pathways to animal domestication” ordered by the amount of human intentionality. The least intentional is the *commensal pathway*, in which populations of organisms adapted first to anthropogenic niches such as predator-free human habitats, waste dumps, stands of cultivated plants, or food stores (e.g., Budiansky 1992; Rindos 1984). Later, humans began exploiting these animals, potentially selecting for additional novel phenotypes. A more intentional *prey pathway* posits that populations of animals adapted to human management, which itself evolved from intensive hunting. Although human intentionality is key here, people need not, and in most instances did not, have a clear conception that they were selecting for rare or novel phenotypes (Bleed 2006; Smith 2007; Zeder 2015). In the most intentional *directed pathway*, humans selectively breed/cultivate only those members of plant and animal populations that express desired traits, directly selecting for novel or rare phenotypes. Such purposeful breeding, such as the experimental domestication of foxes (Trut 1999), is not applicable to the earliest domesticates as it assumes an extant concept of domestication.

We argue that the *prey* and *commensal* pathways are appropriate models for initial pig domestication, but we do not think they should be considered in isolation. Variations and combinations of prey and commensal pathways likely shaped the trajectory to pig domestication (Fig. 1).

It is important to recognize the influence of *counter-domestication* processes (Balasse et al. 2016; Larson and Fuller 2014; Marshall et al. 2014), including the interbreeding of wild boar with domestic pigs (*hybridization*) and the readaptation of domestic pig populations to wild conditions in the absence of human management (*feralization*). Both processes may limit the long-term sustainability of domestic phenotypes and significantly complicate any simplified pathways model. In fact, we argue that feralization and hybridization are more applicable to pigs than many other domestic animals because (1) feral pig populations thrive in a number of environmental settings once they gain a foothold; (2) the wide natural distribution of Eurasian wild boar creates more opportunities for hybridization; and (3) wild boar are naturally attracted to human settlements, where they may mate with domestic pigs.

Fig. 1 Possible pathways to pig domestication, based on Zeder (2012; see also Smith 2007). In (1) wild boars' invasion of anthropogenic niches gives humans opportunities to manage *Sus* populations and exert selection pressures that inspire genetic changes coding for novel ("domestic") phenotypes. In (2) the invasion of anthropogenic niches, without subsequent management, creates novel selection pressures that drive genetic/phenotypic change. These changes inspire humans to manage morphologically and behaviorally modified *Sus*, further selecting for novel genotypes/phenotypes. In (3) intensive hunting of wild boar transitions into management and the selection for novel phenotypes. In (4) intensive hunting and commensalism take place side by side, each selecting for new genotypes that are *not* reproductively isolated from one another. The hybridization of commensal and managed wild boar forms the basis of the original domestic population

Hybridization can create a situation that Larson and Fuller (2014) have referred to as "introgressive capture," a process whereby a domestic population originally native to Location A is transported to Location B, where it interbreeds with local B wild boar. These B genotypes are thus "captured" and incorporated into domestic stocks. Drift or selection may result in population-level replacement of A by B genotypes, thus *appearing* to indicate an independent process of domestication in Location B. Several archaeogenetic studies have shown that introgressive capture significantly impacted ancient pig populations (e.g., Larson et al. 2007a; Ottoni et al. 2012).

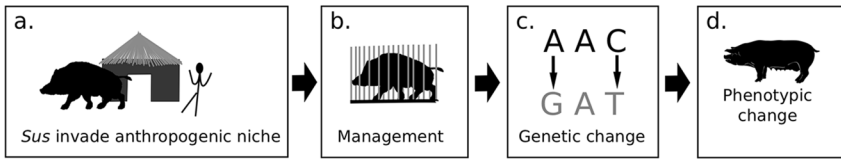
Feralization is not a wholesale return to wild phenotypes. For example, "free-living" or extensively managed pigs in Sardinia have regained both the brain size and olfactory mucosa cell density of wild boar but not the levels of gene expression for proteins associated with olfaction (olfactory marker protein and neuropeptide Y) (Maselli et al. 2014). Kruska and Röhrs' (1974) study of Galapagos feral pigs demonstrated that these animals retained the small brain sizes (encephalization quotients) of their domestic ancestors. Feralization is a complex process patterned and constrained by unique environmental factors. It deserves more investigation by ecologists and zooarchaeologists.

In sum, distinguishing and understanding the connections between domestication and other human–animal relations remain important tasks, theoretically and methodologically. Additionally, the variability of prey, commensal, or combined pathways, as well as the mitigating processes of feralization and hybridization, necessitate that scholars recognize domestication as a highly complex and contextual process. While many would readily agree with this sentiment, one aspect of animal domestication that anthropological zooarchaeologists may neglect is an understanding of animal physiology and behavior. While we do not advocate that zooarchaeologists need zoological training, we do argue that a fundamental familiarity with the evolution, biology, and behavior of an animal species is a *sine qua non* of research into its domestication.

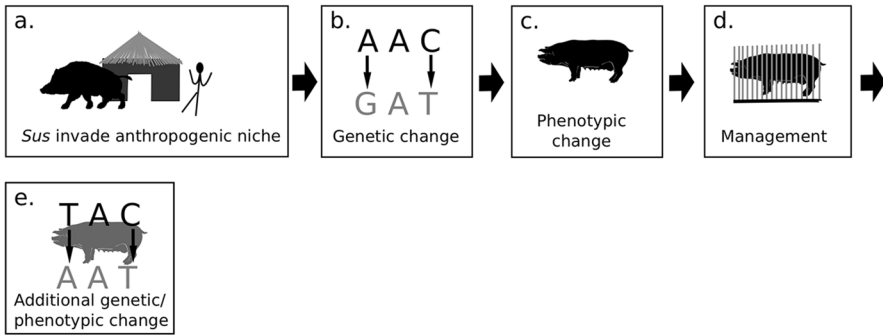
Evolution, Biology, and Behavior of *Sus scrofa*

The genus *Sus* split off from other Old World suids in southeast Asia (*Babyrousa babyrousa*) and sub-Saharan Africa (*Potamochoerus* sp., *Hylochoerus* sp., and *Phacochoerus* sp.) 7–18 million years ago (Frantz et al. 2016; Gongora et al. 2011;

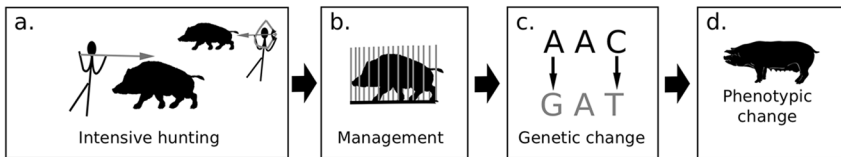
(1) Commensal Pathway 1



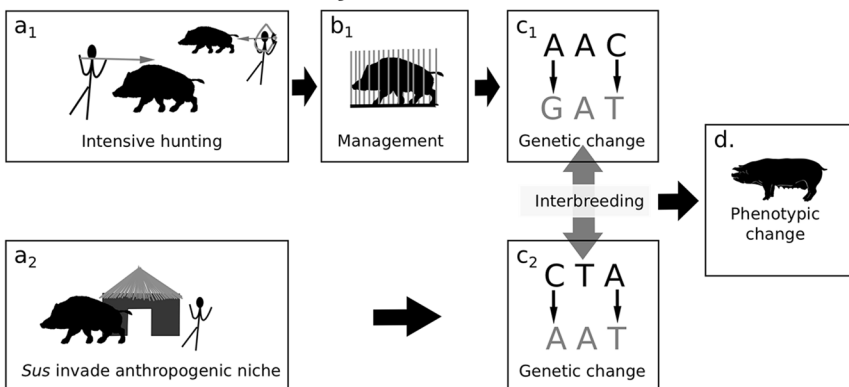
(2) Commensal Pathway 2



(3) Prey Pathway



(4) Combined Pathway



Orliac et al. 2010; Ramos-Onsins et al. 2014). The genus *Sus* evolved in south-east Asia. With the exception of *S. scrofa*, all species of *Sus* exist naturally only in southeast Asia and island southeast Asia. They include *S. celebensis* (Celebes), *S.*

verrucosus (Java), *S. barbatus* (Borneo), and *S. cebifrons* and *S. philippensis* (Philippines) (Frantz et al. 2016; Gongora et al. 2011; Groves 2007; Orliac et al. 2010). Today, *Sus scrofa* maintains natural habitats across Eurasia and parts of North Africa (Barrios-Garcia and Ballari 2012; Groves 1981, 2007).

Wild, feral, and domestic pigs thrive in riparian, lacustrine, marsh, and forest environments. Being nonruminating omnivores, they consume a range of food but exhibit a preference for high-fiber, high-energy, low-protein foods (e.g., Masseti 2007, p. 161). While capable of eating meat and even hunting small animals, the vast majority of their calories come from vegetable foods. Stomach contents of modern wild boar include substantial quantities of fruits, mushrooms, nuts, tubers, and domestic cereals in addition to noninsignificant amounts of grasses, bark, leaves, annelids, insects, small mammals, birds, and reptiles (Gimenez-Anaya et al. 2008; Herrero et al. 2006; Schley and Roper 2003).

Body size in wild boar loosely follows Bergmann's Rule: populations inhabiting higher latitudes exhibit larger average body size (Albarella et al. 2009; Anezaki et al. 2008; Mayer et al. 1998). Similarly, average size diminution in wild boar over the past 15,000 years can be understood as an adaptation to average global temperature increase (Albarella et al. 2009, p. 132; Davis 1981). Body size is also marked by sexual dimorphism. Male and female piglets are the same weight at birth and exhibit nearly identical growth rates until around 1 year old, at which point male growth accelerates. By age two, males weigh roughly 25–40% more than females. Much of the additional mass is concentrated on the forelimbs; male forelimb bone breadth measurements are about 10% larger than those of females (Payne and Bull 1988; Spitz et al. 1998; Online Resource 1, Table S5). Males also have large, permanently growing upper and lower canines, while females' tusks are smaller and develop roots. However, molar and premolar teeth exhibit low levels of sexual dimorphism (1–4%; Online Resource 1, Table S6) (Bull and Payne 1982; Evin et al. 2013, p. 742).

Under optimal husbandry conditions, domestic sows reach sexual maturity before 1 year of age and can produce two litters per year (although double farrowing, which is dependent on level of feeding and weaning age, only occurs regularly in domestic populations under intensive management), with an average gestation time of 114 days (Bazer et al. 2001). Wild boar exhibit the same gestational length, but females often reach sexual maturity significantly later. Spitz et al. (1998, p. 257) report that, on average, wild sows in southern France reached puberty at 21 months. Other studies report wild/feral females reaching sexual maturity before 12 months but typically giving birth for the first time after their first birthday (e.g., Taylor et al. 1998).

Litter sizes are variable and depend on a number of factors including health and age of the sow. On average, wild and feral pigs produce 3–6 piglets per litter (Bazer et al. 2001; Bywater et al. 2010). In improved domestic breeds, which have undergone positive selection for litter size and teat count (Ramos-Onsins et al. 2014), litters of 10 or more piglets are common (Bazer et al. 2001). After birth, young pigs are particularly vulnerable to hypothermia, starvation, and predation (Mount 1968, p. 35). Without proper care, attrition rates of 15–40% are not atypical (Bieber and Ruf 2005; Focardi et al. 2008; Milligan et al. 2002; Sillitoe 2007, p. 338).

In the wild, *Sus scrofa* are weaned at around 3 months of age or as early as 3 weeks under husbandry conditions (Spinka 2009). Wild males leave their natal sow groups (sounders) in 12–18 months (Graves 1984) and become weakly territorial, wandering in and out of sounders, remaining solitary, or forming bachelor herds (Spinka 2009). Typically, sounders comprise 2–5 sows and their young (Taylor et al. 1998). The sows only leave the sounder for a few days around parturition (Curtis et al. 2001, p. 59).

Wild boar and pigs possess cognitive and social behaviors that are unique among livestock species. They are curious and, if prevented from rooting and exploring, develop pathological behaviors associated with boredom (Houpt 2005, p. 101; Studnitz and Jensen 2002; Studnitz et al. 2007). Pigs also display social intelligence. Pigs recognize when another pig has located food and, by following the “informed” individual until it leads them to the source, exploit that knowledge to obtain concrete goals. Meanwhile, “informed” pigs have been shown to exhibit “tactical deception,” recognizing that they are being followed and altering their behavior to minimize competition over access to food (Held et al. 2000, 2002).

Sus scrofa’s social behavior is formed at an early age largely through filial imprinting (Dwyer and Minnegal 2005; Graves 1984). Piglets require social contact; an isolation experiment conducted in the 1960s by Ratcliffe et al. (1969) demonstrated that piglets placed in solitary pens became “withdrawn” after 2–3 weeks, remaining stationary and even showing little interest in food. They also experienced advanced rates of coronary arteriosclerosis. However, while social contact is essential for pigs’ wellbeing, it need not be with other pigs. This offers an opportunity for humans to insert themselves into the social lives of suids via management or pet-keeping.

Dwyer and Minnegal (2005) have shown how different management strategies in New Guinea manipulate the imprinting instinct. A unique example is the Kubo, a mobile group practicing mixed hunting, gathering, and small-scale cultivation of sago palm (*Metroxylan*) in the lowlands near the Strickland River. The relationship begins soon after birth; people track a pregnant wild boar sow (who might already belong to a Kubo woman) in the days leading up to parturition to locate her nesting area. About 2 weeks after the sow has given birth, parties of Kubo will ambush the sow and her nursing litter and distribute the piglets to women, who raise them in isolation from other pigs. The human caretaker fondles the piglet, feeds it premasticated bananas and other soft foods, sleeps in the same house with it, and carries it with her on foraging and gardening trips. After about 3–4 months, the piglet is allowed to forage on its own and may begin associating with other wild boar. However, the piglet often remains attached to its caretaker, returning regularly to her. After 18 months, the caretaker relocates the now fully grown wild boar to an ideal foraging area, such as a swamp. Such attempts sometimes fail; animals frequently return to their humans at night. Even when successful, the bond between human and wild boar remains strong until the animal is slaughtered for its pork. In fact, its caretaker is the only human that the wild boar will allow to approach it.

Human Behavior Toward Pigs: The Diversity of Management

The Kubo are an example of the rich diversity of pig husbandry (“herd management”) arrangements that exist around the globe. We broadly distinguish between two types of management: *intensive*, in which pigs are kept in sties and fed scraps or fodder, and *extensive*, in which pigs are allowed to range more freely and forage their own food, sometimes accompanied by a swineherd. These two forms of pig husbandry exist on a spectrum with other suid exploitation strategies that is defined by increasing labor/resources/infrastructure investment by humans and genotypic/phenotypic impact on pig populations: hunting → intensive hunting → game management → extensive management → intensive management (see Vigne 2011b, p. 173).

Within these two categories, pig husbandry takes on many forms. One can herd pigs to pastures, sometimes over long distances (Albarella et al. 2011; Hamilton and Thomas 2012; Wealleans 2013); allow pigs to free-range in pastures, woodlands, and on the peripheries of settlements (Albarella et al. 2007b; Hadjikoimis 2012; Halstead 2011; Kagira et al. 2010); raise them in sties and feed them household garbage (Fahmi and Sutton 2010); or set them loose in urban environments to feed off sewage and other settlement waste (Jørgensen 2013). While these different forms of pig management exist around the globe, the richest and most vivid ethnographic descriptions of nonindustrial pig production come from New Guinea (Blanton and Taylor 1995; Hide 2003).

Extensive husbandry of *Sus scrofa* in New Guinea exists in the substantial gray area between living in the “wild” and in “domestic” settings. A useful starting point is the work of Kelly (1988), who has referred to extensive husbandry as “forage-based” systems. He describes how villagers rely only on incentivizing free-ranging pigs to return to settlements at (ir)regular intervals, something accomplished by feeding them food scraps and by fondling to imprint piglets onto people so that the animals learn to return regularly. Women are often the primary caretakers of pigs; one iconic image, although not necessarily commonplace, is of women breast-feeding piglets to facilitate imprinting onto humans (Simoons and Baldwin 1982, pp. 427–430).

Under these forms of extensive management, pigs are often owned (usually by men) and are therefore livestock, but their lifestyles after the first few months of life may differ little from those of animals not considered property. In some circumstances, males and females are kept, bred, and turned loose once they are weaned. The pigs stay close to human settlements because human waste and abandoned gardens provide a reliable source of food, but villagers make no attempt to restrict pig movement beyond fencing them out of active gardens and gravesites (e.g., Boyd 1985, p. 123). In other circumstances, pig owners only keep sows, or sometimes sows and castrated males. The animals may be turned loose or kept close to settlements by regular feeding, but the people rely on wild males to service their livestock. Under these forms of extensive husbandry, pig owners apply greater amounts of energy and investment at crucial moments in pigs’ lives. For example, they often carefully monitor and provide daily fodder for pregnant sows

to ensure that the sow and her litter remain in close contact with humans (Boyd 1985, p. 123; Dwyer 1996).

When only sows are kept, only half of the reproductively viable herd is under management and thus selective pressure. But other situations involve even less selective pressure. Several ethnographic accounts from New Guinea depict villages in which all “pigs” are simply captured wild boar, of which every male is castrated. After a period of imprinting, these animals can be turned loose to forage on their own (Dwyer 1996). The example of the Kubo is a unique form of this type of wild-capture management practice (Dwyer and Minnegal 2005). However, in other instances, people raise captured wild animals intensively. In the 1930s, the lowland Keraki confined captured wild boar to pens, castrated all males, and provided them so much fodder that they could no longer rise to their feet (Dwyer 1996, p. 486). Thus, although aspects of intensive management were utilized, such a system could not lead to domestication since there is no selection for heritable phenotypes. That exception aside, more intensive management practices typically apply greater selective pressure for “domestication syndrome” phenotypes.

Increasing management intensity involves greater labor investment. Sillitoe (2001, pp. 177–178) estimates that Wola women spend an average of 28 min and almost 400 calories per day feeding pigs, putting them into stalls, cleaning out their pens, and tending sick animals. Villagers who adopt intensive management construct housing for their pigs, supply them with almost all of their food, and manage their social interactions. Both males and females are kept, and they are bred together. As such, they restrict gene flow from wild-living animals, creating a genetic bottleneck in which “domestication syndrome” phenotypes can accumulate and spread. Kelly (1988) refers to these systems as “fodder-based” because villagers devote a large portion of cultivated foods, especially sweet potatoes (*Ipomoea batatas*), to pig feed (Hide 2003, pp. 55–75). These more intensive management techniques foster more rapid herd growth and weight gain, thus providing more pork and allowing for more frequent or larger feasts. Competitive feasting can directly inspire the transition from extensive to intensive management (Dwyer 1996).

In New Guinea and elsewhere, considerable diversity exists in feeding, control over breeding, and housing. For example, Hide (2003, p. 54) contrasts pig-housing techniques among the Kaluli in the rainforested parts of the southern highlands, who keep pigs underneath their houses, to other groups, such as the Dani, who construct large pig houses with individual stalls. Other groups, such as those living on Manus Island, reportedly keep pigs in small cages (c. $2 \times 1.25 \times 1$ m). Similarly, the amount and types of food provided to pigs varies. While sweet potato are common crops in the highlands, pig caretakers gather and feed their pigs various grasses, leaves, small mammals, lizards, frogs, and earthworms (Hide 2003, p. 56).

Several factors complicate the analytical division between extensive and intensive husbandry. First, the two forms exist on a spectrum and can bleed into one another. The example of the Keraki shows how people can blend elements of intensive and extensive husbandry, exerting considerable control over diet, mobility, social structure, and ecology, but none over breeding. Similarly, many extensive husbandry practices, while allowing pigs to forage in the day, involve elements of intensive husbandry, such as nightly penning and the provisioning of fodder (Boyd 1985; Hide

1981, p. 328; Sillitoe 2007, p. 332). Control over mobility, diet, ecology, reproduction, and social structure exist, in part, independently of one another. This has led to a debate in the New Guinea ethnographic literature about how best to categorize pig husbandry systems. While Kelly (1988) has emphasized control over diet, Baldwin (1978) has focused on control over reproduction, differentiating “pig-rearing” from “pig-breeding” systems. Control over reproduction, degree of contact with humans, maintenance of breeds through selective reproduction, provisioning of fodder, availability of wild foods, proportion of time spent confined to pens or tethered to stakes, the size of pens, and the number of animals kept vary from situation to situation. Ethnographers and zooarchaeologists should record these data separately rather than relying on general categories.

Zooarchaeologists rely on time- and space-averaged deposits (Lyman 2003) and must account for the fact that different management and hunting practices can occur side by side. Interpretation of the ethnographic data suggests that mixed exploitation strategies are commonplace. One of us (Hongo), for example, observed mixed husbandry strategies near Sapa in northern Vietnam in the early 2000s. While some households kept their pigs in pens and fed them scraps of kitchen waste, others kept pigs outside and tethered to posts. Still other pigs appear to have been allowed to wander ad libitum, and the villagers constructed fences around vegetable gardens to prevent pigs from destroying them. Pig exploitation can also undergo rapid transformations, something made possible by pigs’ explosive population growth rates. Thus, members of the Awa village of Irakia decided in 1971 to shift from an extensive system, in which villagers only kept sows and castrated males—which they allowed to free-range and regularly provided small amounts of garden produce—to an intensive one, in which fodder and refuse were collected to feed pigs more frequently, weaned piglets were kept in women’s houses to be “socialized,” and pigs’ mobility was restricted by the construction of a 400-m long wooden “pig barricade” a kilometer away from the village (Boyd 1985, pp. 123–124). These examples highlight the diversity of pig exploitation practices in close temporal and spatial proximity that would become mixed together within depositional palimpsests.

Detecting Pig Domestication: Prospects and Problems

Documenting domestication involves the identification of changes in human behavior reflecting management and genotypic/phenotypic changes in *Sus scrofa* as adaptations to management. Many challenges face researchers interrogating the process of pig domestication, especially those involving equifinality. We stress that multi-method approaches can overcome some of these issues.

Documenting Management

Documenting management is one of the most challenging aspects of studying pig domestication. Intensive hunting, game management, herd management, and commensalism grade into one another and often exist alongside one another. They are

difficult to separate with current zooarchaeological methods. Three main types of methods for reconstructing human–suid relations—demographic profiles, stable isotopes, and pathologies—offer a window into how and under what circumstances humans altered their behavior toward wild boar.

Demographic Profiles

Demographic profiles shed light on the ages and sexes of animals that herders and hunters killed and deposited on-site, allowing scholars to track changes in exploitation strategies (e.g., Bökönyi 1969; Meadow 1989). Methods for assessing age-at-death in pigs are decades old at this point (Bull and Payne 1982; Grant 1975; Silver 1969), but recent papers have improved analytical precision using data from tooth eruption/wear patterns and epiphyseal fusion (Legge 2013; Lemoine et al. 2014; Wright et al. 2014; Zeder et al. 2015). These techniques offer exciting new possibilities for documenting the age and sex composition of exploited suid populations.

One might expect the shift from intensive hunting to game management to go hand-in-hand with a more focused targeting of juvenile males as a means of maintaining high sow-to-boar ratios. This can dramatically increase the size of a wild boar population even within the span of 5–10 years (see Rowley-Conwy et al. 2012, fig. 14). However, because suid populations grow rapidly, a strategy focused on young male kill-off is not as essential to *Sus* management as it is to bovids (e.g., Zeder and Hesse 2000) or camelids (e.g., Mengoni Goñalons 2008). For the latter two, the maintenance of a core group of females ensures herd stability over time; with pigs and wild boar, young male kill-off can quickly lead to a population that has outstripped the carrying capacity of its local environment (Rappaport 1967, pp. 24–25). Thus, even domestic pig managers, while they tend to slaughter males with greater frequency, kill a good number of young females. Depending on the size of their herd and mitigating environmental and social conditions, the ratio of young males to females may approach 50/50. Even herders attempting to increase their livestock numbers would not tend to be overly concerned with keeping more than one female from a litter.

Problems of equifinality are also important to consider in the interpretation of demographic data. Rowley-Conwy et al. (2012, pp. 23–29) spell out how two different hunting practices, which they refer to as “tactical” and “strategic” approaches, can result in nearly identical demographic profiles. As they describe, a “tactical” approach might involve intensive hunting of spring-born piglets in summer and inexperienced 1–2 year old males in the winter. A “strategic” approach, a form of game management, involves hunters attempting to keep wild boar populations at sufficiently large numbers by killing off excess piglets and juvenile males (Rowley-Conwy et al. 2012, p. 26). The demographic profiles reconstructed by a zooarchaeologist would be more-or-less equivalent, despite the fact that the specific human–suid relations that generated them were quite distinct. Similarly, under most forms of pig husbandry, herders keep one reproductive male for every 5–10 sows and cull the majority of pigs between 6 months and 2 years of age (e.g., Hadjikoumis 2012, p. 356). Thus, one could interpret a zooarchaeological assemblage that consisted primarily of animals less than 24 months old along with a few females over 24 months

old as evidence of herd management. However, intensive hunting strategies that focus on females and their young, perhaps dispatching entire sounders in an ambush, would result in nearly identical demographic profiles.

Equifinality also complicates the identification of intensive and extensive management strategies. One could reasonably expect that more intensive forms of husbandry would focus on younger animals, since lower rates of mobility coupled with greater caloric intake would shorten the time between birth and the achievement of a desired slaughter weight. Zooarchaeologists have generally interpreted decreasing average age-at-death as part of a process of husbandry intensification (Çakırlar and Marston 2019; Lemoine et al. 2014; Price 2016). However, this interpretation, while adhering to a calorie-maximizing, cost-effective management system prized under capitalism (e.g., White 2011, pp. 105–108), neglects the important role of other cultural factors that can influence slaughter timing. For example, pig herders in Corsica interviewed by Albarella et al. (2011) traditionally slaughtered their animals between 1 and 3 years old, the time it took to reach a desired weight of 100–200 kg. But in recent years, herders also slaughtered a significant number of animals less than 2 months old (and less than 10 kg) because of a developing trend in the desire for suckling pigs. In other words, the average age of slaughter has declined while husbandry conditions remained more-or-less constant. Thus, taste, in addition to economics, can have a significant impact on the demographic profile.

The growth rates attainable by pig populations enable greater flexibility compared to other animals. Pig breeders therefore can adopt a more diverse range of slaughter practices that reflect cultural structures and personal preferences. In particular, ritual can be a determining factor in slaughter scheduling. In many communities in New Guinea, the decision to slaughter is dictated less by the ages of individual pigs than by the timing of large-scale feasts (Boyd 1985; Rappaport 1968; Sillitoe 2001). These feasts often occur irregularly, prompted by factors such as the death of a community leader or the ability of a leader to organize a large prestige-bolstering event. Rappaport (1967) has even argued that feasts tend to occur when pig populations grow to a size that pushes up against the boundaries of the environmental carrying capacity.

Demographic data are central to zooarchaeological reconstructions of suid exploitation strategies. Nevertheless, the diversity and dynamism of pig exploitation make equifinality a major interpretational hurdle. Analytically indistinguishable demographic profiles can result from very different hunting and management strategies. We suggest a solution to this problem in multiple lines of complementary evidence. For example, a demographic profile that includes a large number of young animals as well as mature sows could, by itself, reflect intensive hunting, game management, or herd management. It could reflect intensive or extensive husbandry. But one could test between these alternatives by reconstructing diet through light stable isotopes (e.g., Balasse et al. 2018), dental microwear (e.g., Wilkie et al. 2006), or plant microfossil preserved in dental calculus (e.g., Weber and Price 2016). One could use morphological data to determine whether the proportions of wild boar, feral pigs, or hybrids in the assemblage, which could indicate the degree of control over reproduction (Balasse et al. 2016; Price and Evin 2019). Or one could use data from analysis of pathologies (e.g., Ervynck et al. 2001) to determine if males and

females experienced different levels of stress, thus potentially indicating different lifestyles/relations to humans for boars and sows. By exploring new types of data and collaborating with specialists in other subfields, zooarchaeologists can investigate human–suid relations in ways that are not possible through demographic data alone.

Light Stable Isotopes

Like demographic profiles, light stable isotopes shed light on human–suid relations, but their most powerful application is in combination with other methods. The most commonly employed analysis is of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in bone collagen. These isotopes reflect dietary parameters. Being omnivores, pigs possess a range of dietary regimes that can be reconstructed through the measurement of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, making them an especially unique animal to study isotopically. Moreover, since herd management almost always involves feeding pigs, although admittedly in small amounts in some cases, one can expect its onset to coincide with dietary change.

Carbon is one of the most useful isotopes for studying pigs. Researchers in China have used the enrichment in $\delta^{13}\text{C}$ as an indicator of millet consumption (Hu et al. 2009; Pechenkina et al. 2005; X. Wang et al. 2018). As a C_4 plant, millet, one of the earliest crops in China, is enriched in $\delta^{13}\text{C}$ c. 15‰ compared to C_3 plants. This leaves a clear signature in the isotopic composition of bone collagen, one suggestive of greater proximity to human settlements and, potentially, foddering. Other scholars have interpreted enrichment in $\delta^{13}\text{C}$ in pigs as indicating the consumption of marine fish (e.g., Müldner and Richards 2007), possibly as a result of foddering practices or of wild-living animals feeding on human settlement waste. Still others have used the enrichment in $\delta^{13}\text{C}$ to test whether people fattened pigs on seasonal nut harvests, a system known in medieval England as *pannage* (Madgwick et al. 2012).

Because pigs and wild boar are flexible omnivores, nitrogen isotopes have the potential to shed light on diverse feeding practices. For example, marine fish and invertebrates are significantly enriched in $\delta^{15}\text{N}$, and some have interpreted higher $\delta^{15}\text{N}$ values as indicating the consumption of marine protein (Minagawa et al. 2005; Matsui et al. 2005). Others have argued that enrichment in $\delta^{15}\text{N}$ reflects the consumption of settlement waste, especially that containing greater amounts of animal protein than typically available to wild-living suids (Hamilton and Thomas 2012; Madgwick et al. 2012). Another especially important source of $\delta^{15}\text{N}$ enrichment in animals is the consumption of plants grown in soils fertilized with manure (Bogaard et al. 2007; Styring et al. 2015, 2017). Finally, some analysts have documented significant depletions in $\delta^{15}\text{N}$ in pigs; one way of explaining this is the reliance on legumes as a major protein source (Hamilton and Thomas 2012; Lösch et al. 2006). However, only with environmental proxy data and paleoethnobotanical evidence can one differentiate between these alternative scenarios.

Some researchers have hypothesized relationships between stable isotopes and management intensity (e.g., Balasse et al. 2018, p. 83). They have suggested that more intensive sty-raising strategies lead to enrichment in $\delta^{15}\text{N}$ as a result of pigs consuming household leftovers (“slop”) that include animal protein. This

relationship remains hypothetical and, in fact, intensive pig husbandry operations need not include much animal protein at all. More important to intensive pig husbandry is grain. Feeding pigs cereal fodder is important for fattening pigs prior to slaughter. So much so, in fact, that Early and Middle Bronze Age texts from Mesopotamia contrasted intensively managed “grain-fed pigs” (*šah-hi-a še*) from their wild-living counterparts (“reed thicket pigs,” or *šah-api/šah (h)apu*; e.g., Lion and Michel 2006, p. 91). Given the importance of grain consumption in pig husbandry, especially under intensive conditions, we suggest that the enrichment in $\delta^{15}\text{N}$ that researchers have observed (e.g., Balasse et al. 2018) reflects not so much the contribution of animal protein to pig diet but the increased contribution of grain grown in manured fields.

While promising, equifinality remains a major problem for stable isotopic research (Makarewicz 2016b, pp. 201–202). Isotopic change indicates a shift in diet, but not necessarily what kind of shift, as the prior examples show. Additionally, processes other than management can cause a dietary shift, such as the exploitation of new habitats by wild boar. Many of the dietary changes observed in early Holocene pig remains might have resulted from commensalism, not management. Indeed, attraction to human settlements as commensals/pests may very well have helped wild boar habituate to humans on the path to domestication (Fig. 1).

As mentioned above, additional environmental proxy data are particularly valuable to the interpretation of isotopic data. For example, scholars making an argument for pasturing of swine in hardwood forests should seek corroboration in pollen core or other paleobotanical datasets to determine if these habitats existed within the catchment area. Other zooarchaeological data can also be helpful in testing between the alternative scenarios suggested by isotopic evidence. For example, combining demographic/biometrical data with isotopic data can reveal if animals with enriched or depleted in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were predominantly females, something that could be taken as evidence for exclusively sow-keeping strategies. Or one could examine morphological data in combination with isotopic data at sites where domestic pigs are documented to determine if the diets of domestic and wild animals differ. Similarly, one could interpret isotopic evidence for a dietary shift coupled with a demographic profile inconsistent with expectations for management (i.e., lacking juvenile kill-off) as indicative of commensalism.

Analysis of Pathologies

Contact with and especially management by humans exposes livestock to novel stressors, while at the same time removing others. This impacts pig health and incidence of pathologies. Pigs may experience greater or lesser intensities of psychological, health, nutritional, or social stressors from being confined to pens or being herded in large groups. Foddering may alleviate seasonal nutritional stresses, while restricting pigs’ mobility may prevent them from obtaining seasonally available foods (e.g., nuts). At the same time, communicable diseases may become more prevalent through interspecies contact—in fact, the distant genetic split between different tapeworm (*Taenia*) species suggests that pigs contracted *T. solium* and *T. asiatica* from humans, not the other way around (Hoberg et al. 2001). But human

intervention also increases the chances of an animal surviving an injury or illness (Bartosiewicz 2013, p. 51; Bendrey 2014), and housing may prevent weaker animals from falling victim to predators. Thus, the survival rate for stressors is also expected to increase under management.

Taken together, the average rates of skeletal and dental pathologies are expected to increase in managed wild boar and pigs as a result of two seemingly contradictory circumstances: (1) a decline in health status of the population and/or (2) the ability of members of the population to survive stressors. This well-known phenomenon in which physiological markers of stress increase in populations affected by increased survivability and/or an increased incidence of stressors is known as the “osteological paradox” (Wood et al. 1992).

Following the pioneering work of Dobney and colleagues (Dobney and Ervynck 1998, 2000; Dobney et al. 2002; Ervynck and Dobney 1999), zooarchaeological research into pathologies in pigs has focused on hypoplasias, especially linear enamel hypoplasias (LEH). Hypoplasias are localized reductions in enamel thickness that develop when stress hormones trigger ameloblasts to temporarily cease enamel secretion during Phase 1 of amelogenesis. The types of stress are nonspecific but include dietary deficiencies, metabolic abnormalities, localized trauma, disease, and psychological stress (Goodman and Rose 1990; Guatelli-Steinberg 2001; Hillson 1996, p. 165). Although the identification of specific stressors is complicated, the frequencies of hypoplasias can indicate the initial onset of management or changing husbandry conditions (e.g., between extensive and intensive husbandry regimes) (Bertini 2016; Dobney et al. 2007; Ervynck et al. 2001; Price et al. 2017).

Equifinality remains a major shortcoming of pathology studies, and in particular those of hypoplasias. First, the causes of hypoplasias are nonspecific. Second, as the “osteological paradox” dictates, the rate of incidence can be caused by either an increase in the number and intensity of stressors and/or an increase in their survivability. While one could reasonably expect both of these conditions to be met under management, other factors can also be at play, for example, changes in population pressure or changes in habitat, such as those caused by ecological degradation or climatic amelioration at the beginning of the Holocene. Examination of hypoplasias works best in conjunction with other methods, such as demographic profiles and isotopic studies, to determine if management really is the likely culprit for changes in rates of pathologies (e.g., Ervynck et al. 2001).

The study of other types of pathologies is less common in zooarchaeological examinations of pig domestication but may hold promise for future research. Although often remarked upon anecdotally, tooth crowding, interstitial occlusion/wear, and tooth rotation are symptomatic of either the reduction in jaw size or the dietary changes accompanying domestication (Ma and Liu 2017, p. 308). However, dental crowding can be present in wild populations, as Ameen et al. (2017) have shown in wolves. A more systematic study of rates of these dental anomalies in wild, domestic, hybrid, and feral individuals is certainly warranted.

Few researchers have examined pig remains for traces of ancient pathogenic microbes. The promise of extracting ancient microbial DNA trapped in dental calculus, which has been applied to studies of ancient human diseases (e.g., Weyrich et al. 2015), could add a new angle to studies of ancient human–suïd interaction.

Especially pertinent would be uncovering the history of diseases that currently affect pigs, including viruses (e.g., classic swine fever, *Pestivirus*), bacteria (e.g., brucellosis, *Brucella suis*), and helminths (e.g., trichinosis, *Trichinella spiralis*) (Hide 2003, pp. 139–157). Indeed, one pioneering study of soil samples from human graves at Pre-Pottery Neolithic B (eight–seventh millennia cal. BC) sites in Cyprus found the ova of *Ascaris* sp. and *Taenia* sp., two taxa that can be transmitted between humans and pigs (Harter-Lailheugue et al. 2005).

Documenting Genotypic and Phenotypic Change

Domestication is ultimately a biological process of adaptation to management. It is therefore critical that scholars demonstrate genotypic and/or phenotypic change occurring in the same context as or soon after evidence for management. Scholars have employed two types of analysis to detect the evolutionary responses by populations of suids: biometrical approaches (including geometric morphometrics) and ancient DNA analysis.

Biometrics

Scholars have long observed that domestic pigs tend to exhibit smaller body sizes than wild boar and that metrical data are valuable in the study of pig domestication (Albarella et al. 2006a; Albarella and Payne 2005; Flannery 1983; Rüttimeyer 1862; Winge 1900). In the past, biometrical approaches have relied on taking measurements with calipers. Some refer to this approach as “traditional biometrics” (e.g., Evin et al. 2013). More recently, with the aid of modern computer software, scholars have applied geometric morphometrics (GMM) to the study of pig domestication.

Much of the research using traditional biometrics has focused on teeth. Abundant data from modern wild, feral, and domestic pig populations demonstrate empirically that domestic animals exhibit significantly smaller dental metrics, especially in the lengths and breadths of their molars (e.g., Mayer et al. 1998). Scholars debate the biological mechanism for this reduction. It might reflect facial shortening, a hallmark feature of the “domestication syndrome” (see Evin et al. 2017b). Facial shortening likely has a genetic component, but diet and mobility may also play a role. Lieberman (1996) observed experimentally that pigs subjected to less physical activity experienced a loss of cranial robusticity. Although tooth size was not impacted in Lieberman’s study, it is possible that the persistence of less mobile lifestyles in pigs over several generations could lead to smaller dentition as teeth accommodated to reduced jaw size. An alternative explanation for dental size reduction derives from Wilkins et al. (2014), who posit that the selection for tameness impacts neural crest cells, from which are derived, in addition to other types of cells, odontoblasts. If so, then dental size reduction, facial shortening, and other traits are symptoms of this underlying biological process.

Scholars employing traditional biometrics have also made use of measurements of long bone breadths and lengths to study pig domestication. Body size reduction

is a feature of domestication in pigs and other animals. Again, scholars debate the biological significance of this morphological change. Zeder (2001) has made the important critique that at least some of the apparent size reduction in some domestic animals is *demographic*, not phenotypic; that is, it results from a higher proportion of females to males. Meanwhile, Tchernov and Horwitz (1991) have argued that size diminution was a by-product of selection for higher numbers of offspring, a switch toward greater *r*- (as opposed to *K*-) selection. Meadow (1984), on the other hand, has speculated that early domesticates suffered impoverished diets, and that females born from smaller, nutritionally deficient mothers would mature into small sows, and in turn give birth to small piglets that would achieve low adult weights. In other words, reduced body sizes may have been passed down epigenetically rather than genetically. Indeed, researchers studying the inheritance of human stature have posited a strong epigenetic component (Wells and Stock 2011, p. 422). It is possible that an initially epigenetic inheritance of small stature in pigs, dictated by gene expression affecting in hormone levels, was later “fixed” through genetic mutation. Researchers have detected similar examples of fixation in other domestic species; for example, the reduction in the number of auxiliary branches in erect knotweed (*Polygonum erectum*) (Zeder 2018, p. 7).

Several processes unrelated to domestication can initiate size diminution in mammals. The first is Bergmann’s rule, which is important to consider as animal domestication took place in the context of post-Pleistocene global warming (Davis 1981). Another is Foster’s rule, or the “island effect,” which dictates that medium-large mammals inhabiting islands will undergo body size reduction. For example, wild boar (or feral pigs) on Corsica and Ryukyu exhibit some of the smallest biometrics among pigs (Albarella et al. 2009; Evin et al. 2015). Finally, as mentioned above, hunting pressure can select for size change. The magnitude of the impact can be quite large. In a 30-year study on the effect of intensive (trophy) hunting of bighorn sheep (*Ovis canadensis*) in which large males were specifically targeted, Coltman et al. (2004) documented a 29% reduction in average ram body weight from around 85 kg in 1975 to 60 kg in 2002. We have not found comparable data on wild boar. However, except when large boars are hunted as trophy animals, intensive hunting strategies, which typically target juveniles and avoid dangerous males, should have a minimal impact on size.

In addition to traditional biometrical approaches, several researchers have applied 2D geometric morphometrics (GMM) to the study of suid teeth, in particular, upper and lower second and third molars and (e.g., Cucchi et al. 2011; Evin et al. 2013, 2014; for an up-to-date review, see Evin et al. 2017a). Some have also applied 3D GMM techniques to study cranial shape, although so far only in modern specimens (Evin et al. 2017b; Owen et al. 2014). At heart, GMM is a type of biometrical analysis, albeit one with more in-depth computation enabling more precise measurements of the sizes and shapes of biological specimens (Adams et al. 2004; Bookstein 1996; Slice 2007; Zelditch et al. 2004). GMM practitioners compare specimens by identifying standardized morphological “landmarks,” which are points plotted in 2D or 3D at homologous anatomical locations (see Zelditch et al. 2004).

Researchers using GMM report specimen size as “centroid size.” The centroid is the “center of mass” of a 2D or 3D shape; centroid size is the square root of the

sums of the squares of the distances between each landmark and the centroid (Zelditch et al. 2004, pp. 11–13). Several papers have reported size decrease in pig molars during domestication using this technique (Balasse et al. 2016; Cucchi et al. 2009, 2011, 2016; Evin et al. 2013). Centroid size as a method has several mathematical advantages over traditional biometrics (Zelditch et al. 2004, p. 13). On a practical level, centroid size measures the entire specimen (in 2D or 3D), thus giving a more holistic estimate of specimen size than traditional biometrics. Thus, while traditional biometrics of teeth report anterior breadth, posterior breadth, and length separately, centroid size combines these and other measurements along other axes into one metric.

The second feature of GMM is shape analysis. Although not typically quantified, shape analysis is foundational to traditional zooarchaeological and zoological identification of taxon, sex, or population (Zelditch et al. 2004, p. 13). Empirically, molar shape is better able to distinguish populations of suids than size (Cucchi et al. 2017; Evin et al. 2013). Several scholars have analyzed second and third molar shapes using neighbor-joining networks tree, finding clear distinctions between wild and domestic populations (Balasse et al. 2016; Cucchi et al. 2011; Evin et al. 2015; Price and Evin 2019). Nevertheless, some scholars have expressed concern over the biological mechanism by which tooth shape changes. Rowley-Conwy and Zeder (2014, p. 837), for example, point out that there is no clear explanation for why tooth shape might change and how these changes are specifically related to the process of domestication. While similar critiques exist for traditional biometrics, zooarchaeologists using GMM should think carefully and critically about causation. We know of several processes besides domestication (see below) that can account for size change in wild boar. But scholars do not yet understand why tooth shape changes, beyond the general observation that domestication impacts dental anatomy.

GMM is perhaps most powerful in its ability to offer high-resolution perspectives on morphological differences between suid populations today. Thus, Evin et al. (2015) describe the size and shape variation among wild boar, domestic pigs, wild boar bred in captivity, feral pigs, wild boar native to islands, and hybrids. Among the most interesting result was that the reduction in third molar length (and concomitant shape change) was detected in a small sample ($N=4$) of captive wild boar populations that were kept for three or more generations in the historic livestock garden at the Martin Luther University of Halle-Wittenberg (Evin et al. 2015). However, the authors found no such changes in the second molars. This suggests that third molar shape and size are among the first features impacted by the novel selection pressures of anthropogenically altered environments.

One can mitigate the obscuring effects of equifinality by combining biometrical approaches with other methods. For example, Cucchi et al. (2016) combined GMM and light stable isotopes (C and N) to argue that diet and dental size/shape evolved in tandem, likely as a result of husbandry intensification during the Neolithic and Bronze Ages in China. This demonstrates the power of combining datasets reflecting management and phenotypic change to document the evolution of pig husbandry and its effects on morphology. Other studies have also combined GMM with stable isotope analysis and other techniques to examine the dynamics of pig husbandry and evolution along multiple axes (e.g., Balasse et al. 2016).

Genetics

Research on the genetics of modern and ancient *Sus scrofa* has established patterns of gene flow between different populations as well as population movements and turnovers (Frantz et al. 2015; Larson et al. 2005, 2010; Ottoni et al. 2012). Over a decade ago, pioneering research by Larson et al. (2007a) identified two diagnostic regions of mitochondrial DNA (mtDNA) of just 663 basepairs (bp) and 80 bp in length (Larson et al. 2005, 2007a, 2010; Manunza et al. 2013; Ottoni et al. 2012). Since that time, researchers have increasingly utilized ancient DNA to examine human–pig relations.

One limitation of existing ancient DNA studies of pigs is that they have largely utilized mtDNA. Mitochondrial DNA is inherited maternally and without proper interpretive hedging, the results of mtDNA studies can skew the depiction of population structures. A study by Larson et al. (2005) found no mitochondrial distinctiveness in island southeast Asian *Sus* species, despite clear morphological differences between them (Albarella et al. 2009; Cucchi et al. 2009; Larson et al. 2007b). Subsequent whole-genome research (combining mitochondrial and nuclear DNA), showed that those *Sus* populations are, in fact, genetically distinct and more distantly related than previously suggested (Frantz et al. 2016, p. 66). As technological and cost barriers to aDNA research continue to fall, more information derived from whole-genome research promises to reveal previously undetected nuances in early pig/wild boar population dynamics.

Another current limitation is that, while population genetics can document the spread and dynamics of pig populations, they do not detect domestication directly. Ancient DNA has the potential, however, to directly document mutations responsible for phenotypic changes, especially of traits otherwise not detectable by zooarchaeologists. Wilkinson et al.'s (2013) study of modern Chinese and European domestic breeds indicate intense selection for a number of traits associated with body growth, fat accumulation, mammary gland development/teat count, coat color, and bone development (see also Bosse et al. 2014a, b; Frantz et al. 2015; Li et al. 2014; Ramos-Onsins et al. 2014). Other studies have shown radically different levels of brain gene expression between modern domestic pigs and wild boar (Albert et al. 2012; Maselli et al. 2014). Two genes whose expression is particularly affected in pigs and other domesticates (dogs, rabbits, and guinea pigs) are *SOX6* and *PROM1* (Albert et al. 2012). As of yet, no one has studied these mutations or different levels of gene expression in archaeological specimens. However, scholars have studied the MC1R gene, which codes for the melanocortin 1 receptor protein, in ancient pigs. This is a key component of coat color, which varies in domestic but not wild populations (Fang et al. 2009; Krause-Kyora et al. 2013; Meiri et al. 2013).

Late Pleistocene/Early Holocene Interactions with *Sus scrofa*

Hunting wild boar was limited in the Lower and Middle Paleolithic but became more prominent in the Upper Paleolithic, likely facilitated by technological advances such as projectile weapons, nets, and, perhaps most importantly, domestic dogs

(Bar-Yosef 2002b, p. 367; Klein 2009, p. 562). It is probably not a coincidence that evidence for intensive wild boar hunting in the Middle East postdates the arrival of dogs in the Early Natufian (e.g., Davis and Valla 1978). By the early Holocene, several human populations had developed intensive hunting practices, including the targeted hunting of juvenile wild boar. Some experimented with game management, for which the most concrete evidence is the intentional introduction of wild boar and other suids to islands. There is intriguing, though not well dated, evidence for introductions by humans of other species of suids to islands, such *Potamochoerus larvatus* to Madagascar and *Babyrusa* sp. to the Sula and Buru Islands (Cucchi et al. 2009; Frantz et al. 2016, p. 70; Groves 1983; Larson et al. 2007b). Here, we focus on prehistoric intensive hunting and game management on Cyprus and in Japan. While the former was ultimately tied to a process of pig domestication in northern Mesopotamia, Jomon wild boar management did not lead to domestication.

Cyprus (11,000–9000 cal. BC)

Sus scrofa was not endemic to Cyprus and are absent from the paleontological record. They appear for the first time in *archaeological* deposits dating to the end of the Younger Dryas, indicating that people transported wild boar to the island. These activities qualify as game management, but it is not clear that, once introduced to Cyprus, people continued to manage wild boar populations. Instead, they appear to have practiced intensive hunting. Thus, the data from Cyprus represent game management facilitating future intensive hunting—the “prey pathway” in reverse.

There is ample evidence that wild boar became important sources of food. Several Pre-Pottery Neolithic A (PPNA; 9700–8500 cal. BC) sites in Cyprus have high numbers of wild boar, including Agia Varvara Asprokremnos (46%, 8800–8600 cal. BC) (McCartney et al. 2007) and Klimonas (95%; 9100–8600 cal. BC) (Vigne et al. 2012). But the rockshelter of Akrotiri-Aetokremnos, where wild boar are a small fraction of the faunal remains, provides the earliest evidence (first reported by Reese in Simmons 1999, pp. 164–167). Vigne et al.’s (2009b, p. 16135) reexamination and direct C14 dating of the *Sus* remains revealed that the earliest bones dated to 9700–9400 cal. BC. Nine additional charcoal dates spanning 10,800–9500 cal. BC were taken from an earlier level and associated with six *Sus* phalanges and metapodia (Vigne et al. 2009a, p. S256). While Vigne (2015, pp. 130–131) recognizes that these earlier remains could represent skins or the transportation of a parts of wild boar, a single incisor from a level dating to 9400 cal. BC supports the argument that wild boar were present on the island by the early PPNA (Vigne 2015, p. 131) (Table 1).

Vigne et al. (2009b) provided biometrical data from ten *Sus* phalanges, concluding that the Akrotiri specimens were smaller, on average, than contemporaneous Anatolian wild boar. The specimens were comparable in size to domestic pigs at Pottery Neolithic Gürçütepe and Newe Yam on the mainland. The same was true at PPNA Klimonas, where dental and postcranial metrics were around 15% smaller than those from contemporaneous wild boar in the Levant (Vigne et al. 2014, p. 163). However, the authors pointed out that insular dwarfism among wild-living

Table 1 Approximate dates for Neolithic sequence in Levant and northern Mesopotamia

Period	Approx. Dates (cal. BC)	Major Events
Natufian (Epipaleolithic)	12500–9700	Younger Dryas (10900–9700 cal. BC)
PPNA	9700–8700	
EPPNB	8700–8200	Earliest uncontested evidence for domestic plants
MPPNB	8200–7500	Earliest uncontested evidence for domestic livestock
LPPNB	7500–7000/6700	
Final PPNB (FPPNB or PPNC)	7000/6700–6900/6200	
Pottery Neolithic	7000/6200–5300	Earliest pottery (7000 cal. BC)

Since dates associated with periods differ by subregion, the “/”s separate the earliest and latest dates of each period across all of the Levant and northern Mesopotamia

populations, not domestication, is the likeliest explanation for the small-sized suids on Cyprus (Vigne et al. 2009b, p. 16136).

Based on demographic data, Vigne and colleagues have largely argued in favor of intensive hunting following the initial phases of stocking via game management. However, Vigne et al. (2014, p. 163) note that one could interpret demographic data from Cyprus as evidence of some form of management or intensive hunting in the PPNA. At Klimonas, 40% of the recovered suid jaws contained deciduous fourth premolars, a tooth that is shed no later than 16 months, so almost half were killed before their second birthdays. Excavators at Klimonas also recovered a small number of fetal/neonatal bones (Vigne et al. 2012, p. supp. info. S4). However, Vigne et al. (2012, p. supp. info. S4) argued that, because there were also a good number of old animals in the assemblage, the demographic profile more likely reflects a situation in which hunters focused on sows and their young, rather than management. While the authors have not addressed the possibility of mixed management and hunting strategies, they have shown that the pattern of juvenile culling consistent with an economy singularly focused on husbandry (with a predominant proportion of animals less than 2 years old) did not exist prior to the eighth millennium cal. BC (Vigne 2011a).

Japan (c. 14,500–300 cal. BC)

Archaeologists widely recognize Jomon Japan as constituting a long-standing “barrier” to farming, a context in which hunting and gathering persisted even while agriculture had developed and matured on mainland East Asia (Bleed and Matsui 2010; Crawford 2008; Habu 2004; Kobayashi 2004). Studies of Jomon foodways have emphasized how the rhythms of seasonally abundant resources enabled sedentism and offered an alternative to agricultural production. Scholars have reconstructed a “Jomon calendar” in which foraging and hunting activities varied throughout the year—collecting shellfish in the spring, hunting wild boar

and deer in the winter, and gathering chestnuts and acorns in the autumn (Habu 2004, p. 61; Kobayashi 2004). One question raised by some scholars is whether Jomon hunter-gatherers cultivated plant taxa by around 5000 cal. BC, such as chestnut (*Castanea crenata*), Chinese lacquer tree (*Toxicodendron vernicifluum*), cannabis (*Cannabis sativa*), bottle gourd (*Lagenaria siceraria*), goosefoot (*Chenopodium* sp.), barnyard grass (*Echinochloa* sp.), and beans (*Vigna* sp.) (Matsui and Kanehara 2006; Nasu 2018; Nasu and Momohara 2016; Noshiro and Sasaki 2014). Very small amounts of cultivated rice, barley, and millet might also have been introduced around 3000 cal. BC (Matsui and Kanehara 2006).

If Jomon hunter-gatherers cultivated wild plants, might they also have managed animals? Wild boar was a major source of protein in the Jomon diet along with deer, fish, shellfish, and sea mammals. However, there is no evidence for morphologically domestic pigs until their introduction from China/Korea in the Yayoi period (first millennium BC). There was no diminution in dental or postcranial metrics over time (Hongo et al. 2007). One exception was on the Izu Islands, where *Sus* dental metrical data show a marked diminution, but this is likely indicative of insular dwarfism (Foster's rule) and not domestication (Anezaki et al. 2008). Instead, matching patterns drawn from modern wild boar, Jomon *Sus* dental metrical increase from south to north in compliance with Bergmann's rule (Anezaki et al. 2008; Hongo et al. 2007).

While there is no evidence for autochthonous pig domestication in Japan, it is likely that Jomon hunter-gatherers at least occasionally managed wild boar. Four types of data support this hypothesis. First, during the Initial Jomon (8000–4700 BC), hunters transported wild boar to Hokkaido and the Izu Islands south of Honshu, which were outside the animals' natural range (Bleed and Matsui 2010, p. 361; Hongo et al. 2007, p. 111). Moreover, ancient mtDNA indicates that hunter-gatherers brought wild boar from Honshu to the Izu Island and southern Hokkaido (Hongo 2017; Morii et al. 2002; Watanobe et al. 2004). These examples, comparable to Cyprus, are indications that Jomon hunter-gatherers regularly manipulated wild boar populations, if only to stock islands with favored game. Second, wild boar molars studied from Early (c. 4700–3000 cal. BC), Middle, (c. 3000–2000 cal. BC), and Late (c. 2000–1200 cal. BC) Jomon periods show significantly higher rates of LEH than modern-day wild boar in Japan (Dobney et al. 2007). While many factors can cause an increase in incidence of pathologies in a population, the data are consistent with what one would expect if wild boar were adapting to management by humans and perhaps better able to survive stressors due to human interference.

Third, analyses of demographic data indicate that wild boar were killed primarily between 6 months and 2 years of age at many Jomon sites (Hongo et al. 2007). Except in a handful of examples (e.g., Early and Middle Jomon Tohoku region in northern Honshu), less than 50% of the recovered wild boar mandibles contained third molars, which erupts around 2 years of age (Hongo et al. 2007). At Early Jomon settlements (5000–3500 cal. BC) in the Kanto region, the survival rate beyond one year of age was less than 50%, similar to the example of Hallan Çemi below. However, there is no evidence for a region-wide shift in wild boar survivorship toward younger kill-off over time. Wild boar exploitation strategies were quite

variable, with some communities focusing on older animals and others on younger ones, and hunter-gatherers within each region shifting their strategies considerably from century to century (Hongo et al. 2007).

Isotopic data are another potential indicator of management. Wild boar bones recovered from some sites in Okinawa are enriched in $\delta^{15}\text{N}$. Some have suggested that this reflects the consumption of aquatic resources (Matsui et al. 2005); others, without contradicting that hypothesis, per se, have suggested that $\delta^{15}\text{N}$ enrichment is the result of a managed population of wild boars consuming human waste/leftovers (Bleed and Matsui 2010, p. 362). One cannot rule out the possibility that wild boar foraged in coastal areas on their own, perhaps in areas cleared of predators by humans. It is also possible that shell middens attracted wild boar and that humans living near these middens found the wild boar reliable prey. In fact, large sedentary settlements appeared during the Jomon period, probably opening up a commensal niche for wild boar. However, the evidence for $\delta^{15}\text{N}$ enrichment in Jomon contexts is sporadic and completely absent at other sites.

Changing cultural attitudes towards wild boar coincided with the development of sedentism, which increased between the Initial and Middle Jomon period. In the Middle Jomon (c. 3000 BC), people increasingly represented wild boar in ceramic figures and on vessels. They also buried wild boar with their dead (e.g., Habu 2004, p. 177). This contrasts with the other main hunted terrestrial mammal, deer, which was infrequently depicted in art and did not often figure into rituals. This could be taken as evidence of a perceptual shift in how humans viewed wild boar. It might reflect a tightening relationship between suids and humans, with wild boar becoming more active features of Jomon life.

In many ways, all the pieces appear to have been in place for one or several of the pathways to domestication outlined in Fig. 1. Several lines of evidence indicate the Jomon hunter-gatherers practiced management of wild boar populations, albeit sporadically and unevenly, and the presence of sedentary settlements would have created a commensal niche. And yet, Japan's first domestic pigs appear to have been brought from mainland East Asia along with wet-paddy rice agriculture in the Yayoi period (Hongo 2017, p. 339). There are several potential reasons for the “failure” of pig domestication, or, perhaps better stated, the long-term success of wild boar intensive hunting and game management without domestication. One possibility is that the lack of sedentary communities across Japan until relatively late in the historical sequence. While sedentary villages existed in southern Japan in the Initial Jomon, they became more pervasive in the Early Jomon (4700–3000 cal. BC) and only appeared in substantial numbers and sizes in the Middle Jomon (third millennium cal. BC). This slow evolution of sedentism may have precluded strong long-term relationships from developing between wild boar populations and humans. Management may have been seasonal and/or intermittent, not persistent enough to drive selection.

Another possibility for the lack of evidence for pig domestication in the Jomon is that external cultural factors or aesthetics may have mitigated against the conceptualization animals as property, thus limiting the long-term investment by Jomon hunters in specific suid populations. Indeed, after the introduction of domestic pigs in the Yayoi period, people living in Japan appear to have embraced very extensive

forms of management or even allowed animals to go feral; and during the Kofun period (third to seventh century AD) pig size increased, potentially signaling the widespread abandonment of pig husbandry (Anezaki et al. 2008). With the introduction of Buddhism in the seventh century, taboos on eating mammals and raising livestock limited the success of pig husbandry in Japan even further, and pig husbandry remained rare until contact with European merchants in the 16th century (Hongo 2017).

In addition to these other potential factors, we argue that the lack of an abundance of cultivated crops, especially cereals, prohibited strong relationships from forming between suids and humans in Jomon Japan. While plant cultivation likely existed on some level in Japan, it was not as intensive as in Neolithic China or the Middle East, and there are no definitive examples of domesticated crops until the Yayoi period. Without a surplus of food, long-term herd management of swine may not have been possible. Perhaps additionally, lacking crop surpluses and large cultivated fields, human habitats did not present enough of an attraction to wild boar populations over the long term. With the commensal valve reduced to a trickle, this may have limited the degree to which wild boar experienced selective pressure to adapt to being tolerant of proximity to humans.

Contexts of Pig Domestication

Clear evidence for independent processes of domestication in northern Mesopotamia is present by c. 8700–7000 cal. BC and in China by c. 6600–5000 cal. BC. In addition to these definitive centers, scholars have hypothesized and debated domestication in other locations: the southern Levant (Haber and Dayan 2004; Makarewicz 2016a; Marom and Bar-Oz 2013), western Anatolia (Çakırlar 2012, 2013; Zeder 2017, p. 271), Italy (Albarella et al. 2006a, b; Jarman 1971; Rowley-Conwy et al. 2012), and India/southeast Asia (Larson et al. 2010). However, all of these contexts postdate the appearance of domestic pigs in China and northern Mesopotamia by centuries. We cannot eliminate the possibility that they represent secondary zones.

The zooarchaeology of pig domestication in northern Mesopotamia is better understood than in China, thanks in large part to excavations conducted in Syria and Turkey in the 1980s–present. Zooarchaeological research in China is still developing, but a number of groundbreaking studies have established aspects of the pace and process of pig domestication. New data appear frequently; we recognize that the evolving nature of zooarchaeology in China will likely add considerable nuances to our tentative conclusions in the near future.

Northern Mesopotamia: 8700–7000 cal. BC

Prior to the Holocene, in the Levant and Taurus/Zagros foothills of northern Mesopotamia, the Younger Dryas (Table 2; Fig. 2) interrupted a pattern of increasing sedentism, intensive gazelle hunting, and wild cereal harvesting in the Natufian period (Bar-Yosef 2002a; Munro 2004). The return of warmer conditions at around

Table 2 Natufian, PPNA, and EPPNB sites with proportions of wild boar over 10% (as proportion of identified mammalian taxa)

Site	Period	Region	% <i>Sus</i>	NISP ^a	References
Eynan (Ain Mallaha)	Early Natufian (Niv. II–IV)	S. Levant	14	1425	Ducos (1968, p. 73) ^b
Eynan (Ain Mallaha)	Final Natufian (Niv. I)	S. Levant	17	524	Bridault et al. (2008)
Hallan Çemi	PPNA	N. Tigris	17	2215	Starkovich and Stiner (2009)
Çayönü (Round house)	PPNA	N. Tigris	37	675	Hongo et al. (2009)
Hasanakyef	PPNA	N. Tigris	11	5608	Hongo et al. (n.d.)
Jericho	PPNA	S. Levant	10	559	Clutton-Brock (1979)
Agia Varvara Asprokremnos	PPNA	Cyprus	46	ND	McCartney et al. (2007, p. 73)
Klimonas	PPNA	Cyprus	95	1282	Vigne et al. (2012)
Tell Ain El Kerkh	EPPNB	N. Levant	31	248	Tsuneki et al. (2006)
Shillourokambos (A1)	EPPNB	Cyprus	78	391	Vigne (2011a)
Çayönü (Grill)	EPPNB	N. Tigris	45	653	Hongo et al. (2009)
Boncuklu Höyük	EPPNB-MPPNB	Central Anatolia	48	539	Baird et al. (2018)

^aNISP of mammals identified to family-level only^bDucos (1968) seems to have lumped Early and Late Natufian phases together; Bouchard's (1987, p. 17) tally indicates that Niveau I (Late Natufian) contained 19% *Sus* (NISP = 553) and Niveaux II–IV (Early Natufian) contained 7% (NISP = 1039)

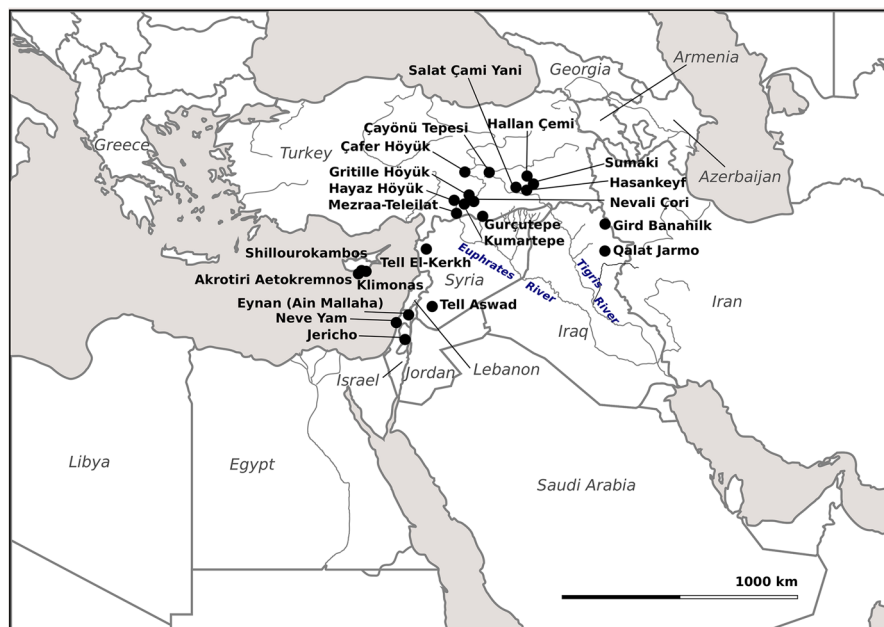


Fig. 2 Map of Middle East showing sites mentioned in text

9700 cal. BC led to the repopulation of village communities in the Pre-Pottery Neolithic A (PPNA). The first appearances in a variety of cultural contexts in the Levant and northern Mesopotamia of domesticated species—chickpeas, emmer and einkorn wheat, barley, bitter vetch, fava beans, lentils, flax, peas, sheep, goats, cattle, and pigs—date to the late ninth and early eighth millennia cal. BC (Arbuckle et al. 2016; Arranz-Otaegui et al. 2016; Bar-Yosef 2011; Peters et al. 2013; Weiss and Zohary 2011; Zeder 2011).

Biometrical evidence supports the argument for domestic pigs in the foothills of northern Mesopotamia during the Late PPNB, and probably in the Middle PPNB. This region contained mixed oak woodlands (in xerophilous deciduous steppe-forests and Mediterranean subalpine forests) and riverine ecosystems defined by the deep-cutting northern Tigris and Euphrates Rivers. In this context, populations of wild game would have flourished during the climatic amelioration at the beginning of the Holocene, something hunter-gatherers took advantage of (Peters et al. 2005, 2013; Zeder 2011). People in this region also cultivated legumes such as lentil and vetch in abundance during the PPNA, with domestic cereals increasing in abundance over the course of the PPNB. Also important was nut and fruit exploitation (Arranz-Otaegui et al. 2016). Thus, pig domestication took place in a context defined by the domestication of other animals (sheep, goats, and cattle) and plant (especially legume) cultivation.

Prior to the PPN, hunter-gatherers infrequently targeted wild boar. At only one Natufian site, Ain Mallaha, have zooarchaeologists identified wild boar making up more than 10% of the mammalian fauna (Bouchud 1987; Ducos 1968). In the

Table 3 Approximate dates for occupational phases at Çayönü Tepesi (dating from Erim-Özdoğan 2011; relative abundance data from Hongo et al. 2009)

Building phase	Dates (cal. BC)	Period	% <i>Sus scrofa</i>	NISP
Round	10,400?–8700	PPNA	36	675
Grill	8700–8300	PPNA–EPPNB	45	653
Channeled	8300–8200	EPPNB	38	784
Cobble-paved	8200–7800	MPPNB	31	689
Cell	7500–7300	LPPNB	32	536
Large Room	7200?–6900?	L–FPPNB	22	947
Pottery Neolithic	?	PN	35	460

PPNA, however, a handful of sites in the Levant and northern Mesopotamia contain *Sus scrofa* remains at or above 10% (Table 3). In fact, PPNA communities in the Upper Euphrates and especially Tigris Valleys exhibited considerable diversity in mammalian exploitation, focusing on red deer, sheep, goats, aurochs, and wild boar in highly variable proportions (Arbuckle and Özkaya 2006; Hongo et al. 2009; Rosenberg and Redding 1998; Starkovich and Stiner 2009). The PPNA was therefore a crucial period for evolving human–suid relations, with game or even herd management practiced at some settlements.

The early PPNA site of Hallan Çemi provides evidence of these evolving human–suids relations. Year-round occupation at this mid-10th millennium cal. BC village is indicated by the avifaunal evidence (Zeder and Spitzer 2016). The village consisted of several round structures with stone foundations as well as a large pit (10 m diameter) of possible ritual significance and containing tens of thousands of animal bones, lithics, and fire-cracked rocks (Peasall et al. 1998; Redding and Rosenberg 1998; Rosenberg 1994; Rosenberg et al. 1995; Rosenberg and Redding 1998, 2000). Additionally, excavators recovered the remains of legumes (lentils and vetch), nuts (pistachio and almond), and tubers such as sea clubrush (*Bolboschoenus maritimus*), but not cereals (Peasall et al. 1998, pp. 31–32).

Redding and Rosenberg have suggested that the wild boar at Hallan Çemi were in the early stages of domestication and that the inhabitants of the site practiced forms of herd management similar to sow-keeping husbandry systems in New Guinea (Peasall et al. 1998; Redding and Rosenberg 1998; Rosenberg and Redding 1998). There is no evidence, however, for domestic pigs. Examination of the dental and postcranial metrics from Hallan Çemi has led to the conclusion that small-sized domesticates were not present at the site (Price and Evin 2019). However, one might not expect morphological change to occur at such an early stage in the process of domestication, especially if management practices involved keeping only sows and thus applied weak selection pressures to wild boar populations.

Redding and Rosenberg focused instead on the relatively high proportion of *Sus scrofa* (17%) and demographic data from the large pit. In fact, the demographic data are not unequivocal. The data displayed a high ratio of mature females to males (based on fused pelvises and canine teeth) and high proportion of young animals—around 10% killed before six months and 43% before they were 1 year old (Peasall

et al. 1998, p. 33). Later analyses by other zooarchaeologists have largely corroborated these numbers and also indicated that around 68% were killed before or just after their second birthdays (Lemoine et al. 2014; Price 2016, p. 295). Redding and Rosenberg's (1998) "New Guinea model" is one potential explanation of this pattern. Another hypothesis was put forth by Lemoine (2012), who followed up on Redding and Rosenberg's research by examining the fauna from middens associated with the round structures. Lemoine (2012) found that fetal/neonatal specimens accounted for 44% of the *Sus* long bones and argued that this might reflect the targeted hunting of isolated farrowing sows and their newborn litters. Another possible explanation for the unique demographic profile is that Hallan Çemi hunters targeted entire sounders in the spring, when adult males were away from the group. The latter interpretation has been presented by Leduc et al. (2015) to explain similar demographic patterns of wild boar at the Mesolithic occupation of Les Cabônes Rockshelter in France (9500–7000 cal. BC), where 22% and 46% were killed before 6 months and 1 year of age, respectively (Leduc et al. 2015, p. 477). Such an intensive hunting strategy would minimize many of the risks involved in wild boar hunting and allow hunters to obtain a large amount of meat in one hunt. While it would place demographic pressure on wild boar populations, potentially leading to game depression, it would be sustainable if population sizes were large enough and other predators (e.g., wolves) less frequent.

Despite the issues related to equifinality, we identify three pieces of evidence that support game or even herd management at Hallan Çemi. First, Hallan Çemi was occupied at around the same time that seafaring hunter-gatherers from Anatolia or the Levant were introducing wild boar to Cyprus. People were actively manipulating wild boar populations in the early PPNA, and there is reason to suspect that they may also have done so at Hallan Çemi. Second, Hallan Çemi was occupied in the right time and at the right place; northern Mesopotamia in the PPNA is the context in which one would expect incipient wild boar management to first appear, as pig domestication emerged in this region over the next two millennia. Third, rates of LEH on Hallan Çemi wild boar teeth were comparable to those observed at sites where domestic pigs are known to have been raised; e.g., at Jarmo, where Price (2016, p. 265) has argued pigs were raised under extensive husbandry conditions. However, without new lines of evidence (e.g., from light stable isotopes to detect diet/habitat change) or a careful diachronic examination of these data, zooarchaeologists are unlikely to resolve the question of human–suid relations at Hallan Çemi.

Probably the single most important site for examining the process of pig domestication proper is Çayönü Tepesi. Çayönü is unique in that *Sus scrofa* was the dominant exploited taxon and that the site was continuously occupied from the PPNA to the PN. Data from Çayönü reveal the process of pig domestication along a number of variables: biometrics, age-at-death, frequency of hypoplasias, and stable isotopes. The data also indicate that pig domestication evolved slowly over the course of two millennia, a situation consistent with the interpretation that the selection factors acting on wild boar/incipient domestic pig populations were weak (Ervynck et al. 2001). This adds support to Rosenberg and Redding's (1998) "New Guinea model" of pig domestication based on extensive management.

The biometrical data from Çayönü indicate a decrease in the smallest measurements and in average size over time. Ervynck et al. (2001, p. 62) and Hongo and Meadow (1998, 2000) provide measurements of teeth and long bones. Although morphologically wild boar were abundant in all phases, small-sized specimens appear as early as the PPNA and early EPPNB, but increase in frequency throughout the later EPPNB, MPPNB, LPPNB, and Pottery Neolithic phases. Ervynck et al.'s (2001) examination of dental metrics also shows a minor decrease in average size over the PPNA–PPNB. Breadth measurements of lower first and second molars were, on average .5–1 mm smaller than those at Hallan Çemi in all phases, but lower third molar lengths and breadths were not different. Seen from the level of the *Sus scrofa* population, Ervynck et al. (2001) interpret these data as indicating that the process of domestication was initiated by the EPPNB, but unambiguously morphological domesticates in substantial proportions do not appear until the LPPNB.

Figure 3 and Table 4 show traditional dental metrics from Çayönü and other sites in northern Mesopotamia. The data generally indicate a pattern of dental

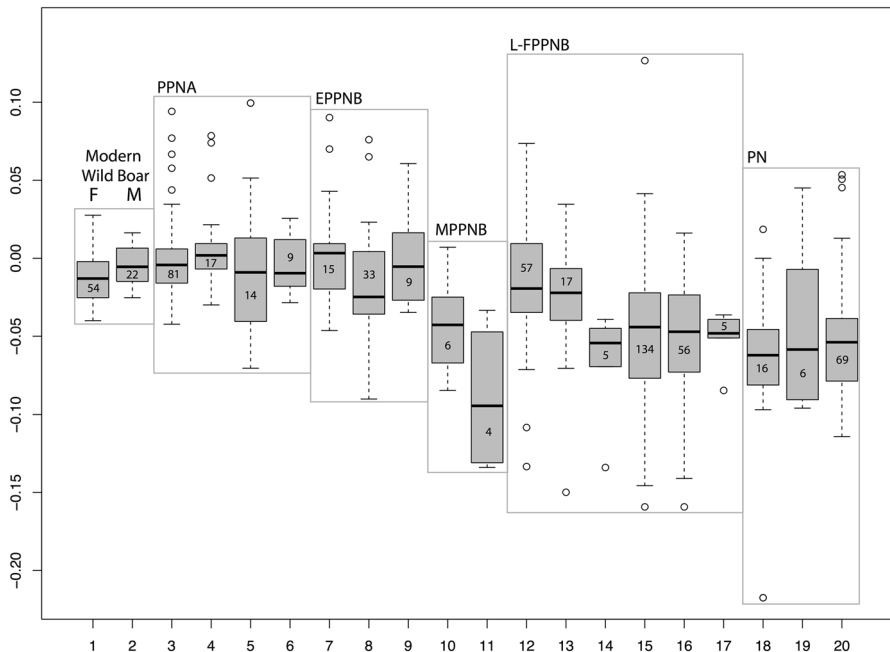


Fig. 3 Boxplot of dental breadth (WA and WP) measurements for upper and lower M1–M3 from PPNA to Pottery Neolithic sites in northern Mesopotamia. Numbers in boxes indicate sample size. Data combined using log-size index (LSI) with using as its standard the Turkish wild boar metrics published by Payne and Bull (1988). 1 and 2—Modern Turkish wild boar (female and male); 3—Hallan Çemi; 4—Hasankeyf; 5—Çayönü (Round); 6—Mureybet; 7—Çayönü (Grill); 8—Çayönü (Channeled); 9—Nevalı Çori (Level III and IV); 10—Çayönü (Cobble); 11—Mezraa-Telailat (MPPNB); 12—Çayönü (Cell); 13—Çayönü (Large Room); 14—Mezraa-Telailat (LPPNB); 15—Hayaz Höyük; 16—Gritille Höyük; 17—Mezraa-Telailat (FPPNB & PN); 18—Kumartepe; 19—Sumaki; 20—Salat Çami Yani (data from Hongo et al. n.d.; Ilgezdi 2008; Kuşatman 1991; Monahan 2000; Payne and Bull 1988; Price and Evin 2019; Joris Peters and Nadja Pöllath, personal communication)

Table 4 Lower molar metrics for Neolithic sites in northern Mesopotamia from the following sources: 1—(Price 2016); 2—(Kuşatman 1991); 3—(Hongo et al. n.d.); 4—(Russell 2010); 5—(this paper)

Site (phase) – Ref.	Date (cal. BC)	Mean measurements in mm			
		M ₁ WA (N)	M ₂ WA (N)	M ₃ WA (N)	M ₃ Length (N)
Hallan Çemi – 1	9500	11.7 (11)	15.5 (12)	18.7 (10)	41.6 (11)
Hasankeyf – 3	9500–9000	11.3 (2)	15.6 (2)	18.0 (4)	40.2 (4)
Çayönü (Round) – 5	10.4 k–8600	ND	15.1 (1)	20.6 (1)	38.5 (1)
Çayönü (Grill and Channeled) – 5	8700–8200	12.2 (5)	15.0 (3)	19.3 (7)	43.2 (7)
Çayönü (Cobble-paved) – 5	8200–7800	ND	13.0 (1)	18.6 (1)	40.5 (2)
Çayönü (Cell) – 5	7500–7300	10.9 (12)	15.8 (6)	18.5 (14)	41.5 (16)
Hayaz Höyük – 2	7500–6500	10.7 (27)	14.0 (15)	17.1 (14)	34.4 (11)
Çayönü (Large Room and PN) – 5	7200–6000	10.9 (3)	14.0 (4)	18.3 (1)	39.1 (2)
Sumaki Höyük – 3	7500–7000	ND	ND	17.6 (4)	33.6 (3)
Gritille Höyük – 2	7000–6500	11.0 (10)	ND	17.5 (1)	30.0 (1)
Qalat Jarmo (PN) – 1	7000–6500	10.8 (23)	14.4 (8)	17.1 (3)	ND
Salat Çami Yani – 3	6800–6300	10.6 (17)	12.6 (6)	15.3 (2)	33.9 (2)
Gird Banahilk – 1	5700–5200	9.6 (4)	12.1 (3)	14.3 (4)	31.5 (4)

size decrease over time, but two features complicate the picture of a continual process of pig domestication. First, a number of small-sized teeth were already present in the Round phase (PPNA) at Çayönü in contrast to Hallan Çemi, whose occupation may have been contemporaneous with that of the Round phase. The reason for this remains unclear, and there is risk of contamination between levels at the site. But it is possible that pressures, anthropogenic or otherwise, were already selecting for smaller teeth and jaws in the PPNA at Çayönü.

The other pattern we note is average tooth size *increased* in the LPPNB. Although small-sized specimens (“domesticates”) remained, the inhabitants at Çayönü apparently targeted morphologically wild boar more heavily during the last phases of the PPNB. This pattern contrasts with other contemporaneous sites (Fig. 3) and may reflect several possibilities. First, it is possible that hunting wild boar increased in popularity as a method for obtaining pork alongside that of husbandry. This might be related to new cultural features (e.g., the connection of boar hunting with masculinity) or because domestic herds were insufficient at meeting the inhabitants’ demands. Second, it might also reflect higher rates of killing wild boar “pests,” itself symptomatic of increasing cereal cultivation and storage. Third, it could reflect increased rates of hybridization, perhaps intentional capturing of wild boar to use as breeding stock because of the more limited fertility rates of inbred domestic animals. If the first or third explanations are correct, this could be an indication of the failure of domestic pig husbandry to produce robust or stable enough populations to meet the demands of the inhabitants of Çayönü, even while it was sufficient at other LPPNB settlements, such as Gritille Höyük.

This would force us to reconsider pig domestication. Rather than a “snowballing” process that gained momentum as time went on, it remained fragile for millennia, fraught with risks presented by low productivity, catastrophic herd loss, the popularity of hunting, and the deleterious effects of inbreeding.

Demographic data provide indications for management at Çayönü evolving slowly over time. The inhabitants of Çayönü targeted young animals from the earliest phases, with dental eruption and wear data indicating 57% were killed prior to 1 year of age in the PPNA and early EPPNB phases (Ervynck et al. 2001, p. 54). That pattern is broadly similar to that of Hallan Çemi, but with an even greater proportion of young animals. In fact, the 1-year kill-off rate remained stable over time at Çayönü, with over half of pigs between the PPNA and L–FPPNB killed prior to their first birthdays (57–53%). However, the proportion of pigs killed prior to their second birthdays increased from 62% in the PPNA/early EPPNB (compare to 68% at Hallan Çemi) to 77% in the E–MPPNB to 84% in the L–FPPNB (Ervynck et al. 2001, p. 54). This indicates increasing focus on the targeted slaughter of subadult animals.

Rates of hypoplastic defects (LEH) add support to the argument that management evolved and grew in intensity at Çayönü over the course of its occupation. Hypoplasias affected 22% of teeth in the PPNA–EPPNB phases, a rate similar to that of Hallan Çemi (21%) (Price 2016). It increased to 43% in the E–MPPNB and then fell back down to 30% in the LPPNB and FPPNB, a period in which the metrical data reflect an increased proportion of wild boar in the assemblage. LEH rates then increased again to 58% in the PN (Ervynck et al. 2001, p. 63).

Light stable isotopes provide another piece of evidence for suid management at Çayönü. A sample of 72 *Sus scrofa* bones showed a minor but steady decrease in $\delta^{15}\text{N}$ over time: $\delta^{15}\text{N}$ values averaged $>6\text{‰}$ in the PPNA, but steadily decreased over time to $<5.5\text{‰}$ in the LPPNB Cell subphase (Pearson et al. 2013, p. 187). The same slight, but consistent, depletion in $\delta^{15}\text{N}$ also affected caprines and cattle but not red deer (Hongo et al. 2009; Pearson et al. 2013, p. 187). Although the magnitudes of the differences are small, the isotopic data appear to reflect a dietary shift in those animals undergoing domestication. One possible explanation is that managed animals were fed legumes. Legumes, especially vetch (*Vicia* sp.), are abundant in the Çayönü botanical assemblage (van Zeist and de Roller 1991/1992). These plants maintain, on average, lower $\delta^{15}\text{N}$ values than nonnitrogen-fixers; an increase in their contribution to the diet generally causes a depletion in $\delta^{15}\text{N}$ in animal tissues (DeNiro and Epstein 1981; Lösch et al. 2006).

Data from other sites in northern Mesopotamia point to the Early and Middle PPNB (i.e., 8700–7500 cal. BC) as critical periods in the domestication of pigs. First, the Early and Middle PPNB witnessed an increase in the relative abundance of *Sus scrofa* at several sites. For example, the proportion of *Sus* remains increased substantially between the EPPNB and MPPNB deposits at Nevalı Çori (8–18%) and Cafer Höyük (5–28%) (Helmer 2008; Peters et al. 2005). Second, as Fig. 3 shows, the reduction in the size of suid dentition was a gradual process. Although the small sample sizes make assessment difficult, average dental size appears to have decreased at this time. There also were small numbers of small-sized animals that fall below the lowest size of measurements for wild boar. In addition, we need a

larger sample of early Holocene wild boar metrics, as animals with reduced dentitions might appear as early as the PPNA at Çayönü (though there is potential stratigraphic mixing) and increase in frequency in the Early and Middle PPNB. Postcranial and dental metrics at Çayönü also indicate that smaller-sized suids were present in low proportions in the EPPNB levels at Çayönü (Hongo and Meadow 2000). Similarly, postcranial biometrics falling below the accepted lower limits of early Holocene wild boar have been interpreted as evidence for the appearance of morphologically domestic pigs at Tell Aswad, Mezraa-Teleilat, and Cafer Höyük in the MPPNB (Helmer 2008; Helmer and Gourichon 2008, 2017; Ilgezdi 2008).

Despite these clues, we highlight two caveats, in addition to small sample sizes, that make our identification of domestic pigs by the MPPNB tentative. First, none of the small specimens have been directly radiocarbon dated. This is particularly problematic at the multiperiod Çayönü, where bones could have been mixed between layers. Second is the lack of published raw biometrical data. Notably absent are published raw metrics for dental breadths and lengths, astragalus lengths, and tibia distal breadths—the metrics Albarella and Payne (2005) identify as the most useful for differentiating domestic pigs from wild boar (see also Rowley-Conwy et al. 2012).

We are confident that morphologically domestic pigs were present at sites across northern Mesopotamia in the LPPNB (c. 7500–7000 cal. BC; Fig. 3). Significant numbers of small-sized pigs constitute substantial portions of the large faunal assemblages from Hayaz Höyük and Gritille Höyük, where radiocarbon dates indicate occupations in the late eight millennium or perhaps very beginning of the seventh millennium cal. BC (Roodenberg 1989; Voigt 1988). By this time, pig husbandry was an established component of the Neolithic way of life at communities in both the Upper Euphrates and Tigris River valleys. Domestic pigs consistently make up 10–25% of the faunal remains at LPPNB, FPPNB, and initial PN sites—Çayönü Large Room-PN, 22–35% (Hongo et al. 2009), Gritille, 17% (Monahan 2000), Mezraa-Teleilat LPPNB–PN, 12–15% (Ilgezdi 2008, p. 85), Hayaz Höyük, 20% (Peters et al. 1999), and Gurgütepe, 19% (Peters et al. 1999). Even at sites where *Sus scrofa* was less common, domestic-sized pigs were nevertheless present. At the PPN–PN transitional site Jarmo, where *Sus scrofa* represent less than 10% of the fauna, small-sized domesticates appeared by around 7000 cal. BC at the latest (Flannery 1983; Price and Arbuckle 2015).

Several features allow us to speculate that domestication proceeded via a *combined pathway* (model 4 of Fig. 1). Zooarchaeologists have traditionally focused on the prey route of a combined pathway (Ervynck et al. 2001; Redding and Rosenberg 1998; Vigne et al. 2009b). For example, the introduction of wild boar to Cyprus at around 9400 cal. BC or earlier indicates that humans were manipulating wild boar populations by the PPNA. Demographic data also indicate that intensive hunting and potentially management were present at Hallan Çemi and in the early levels at Çayönü, while data from Çayönü show how these exploitation strategies evolved over time and, importantly, how this evolution went hand in hand with morphological adaptation.

Zooarchaeologists have not explored the commensal route of a combined pathway in detail. However, we suggest that the presence of villages occupied year-round by the PPNA close to the habitats of wild boar would have brought specific populations

of humans and wild boar into regular contact. Early commensal relations between wild boar and humans may have begun very infrequently prior to the PPNA. One potential line of evidence is the unusually high NISP of *Sus scrofa* at Eynan/Ain Mallaha, especially in the Final Natufian phase, 17% (c. 10,000 cal. BC). Ain Mallaha contained preserved architecture, including a possible communal structure, and was one of the largest Natufian base camps (c. .2 ha). It is the only Natufian site with clear evidence for storage (Bridault et al. 2008; Kuijt 2009; Valla 1988). In addition, Ain Mallaha was located near an ideal environment for *Sus scrofa*, the swampy Hula Valley. If there was one settlement where incipient suid commensalism may have developed prior to the Holocene, Ain Mallaha is a good candidate.

However one interprets the evidence from Ain Mallaha, the increase in human populations and their settlement into sedentary villages in the PPNA was pivotal. Archaeological evidence from well-surveyed areas, such as the Levant, indicates that the number of sites, the average size of sites, the depth of occupational deposits, and the density of sites all increased substantially in the PPNA (Kuijt 2000). This would have increased opportunities for wild boar to enter anthropogenic environments as commensals, especially for younger and less wary animals, who would have been attracted to food stores or large waste deposits (e.g., the pit at Hallan Çemi). Wild boar also would have been attracted to gardens and stands of legumes/cereals tended by humans, who may, like horticulturalists in New Guinea (Lemonnier 1986), have had to construct fences or traps to keep these pests at bay.

Throughout the process of domestication, human management of pigs remained extensive. There is little evidence of penning or sexual isolation from wild boar, in the form of higher rates of LEH, architectural traces of pens, or dramatic size reduction, prior to the Late Neolithic (late seventh–sixth millennia cal. BC) (Price 2016; Price and Evin 2019). Instead, the slow rate of morphological change at Çayönü is indicative of a gradual and perhaps multifaceted transition from intensive hunting to extensive herd management. The specific management practices remain unclear, but we can hypothesize, based on ethnographic analogy, that Pre-Pottery Neolithic pig husbandry involved only occasional penning, perhaps limited to farrowing sows and “troublesome” pigs, but with regular allotments of food, especially legumes, that would have kept pigs close to their owners (Sillitoe 2001, pp. 172–178). Pig owners may not have even categorically distinguished between wild and domestic suids on biological criteria (e.g., Descola 1994; Ingold 2000, pp. 77–88), perhaps only differentiating between “owned” and “not-owned” animals. Hybridization and intentional incorporation of wild boar into managed herds was likely a regular feature of Çayönü husbandry, something attested to by the “rebounds” in average suid size in the MPPNB and LPPNB.

We can also speculate that cultivated plant foods played a critical role in the process of pig domestication. As the examples from New Guinea indicate, even in those management systems that Kelly (1988) designates as “forage-based,” the availability of a surplus of food to attract pigs to settlements is crucial to the survival of the human–pig bond. It is probably no coincidence that the first appearance of domesticated pigs and other livestock postdated that of cereals and legumes, of which the latter appear to have been the most important horticultural crop in northern Mesopotamia early on (Arranz-Otaegui et al. 2016). Indeed, the depletion in $\delta^{15}\text{N}$ over time

from Çayönü might reflect a process of increasing amount of legumes in the diets of pigs, sheep, goats, and cattle and the use of these animals as “on-the-hoof” storage of otherwise unused cultivated plant calories for burgeoning Neolithic populations (Meadow 1989, p. 81).

Our current state of knowledge of pig domestication in northern Mesopotamia leaves several important avenues open for future research. Research should investigate changing suid diet in more detail, isotopically or through other means (e.g., dental calculus). In addition, more data are needed from demographic data, biometrics, rates of pathologies, and, what is perhaps most exciting, ancient DNA investigations of alleles associated with the “domestication syndrome,” especially in the critical period stretching from the PPNA to MPPNB. Ideally, zooarchaeologists should employ these data in concert in an effort to paint a holistic image of incipient suid management practices.

The Yangtze and Yellow River Valleys in China: 6600–5000 cal. BC

The river valleys of China were another major center of agriculture and sedentary life in the Holocene (Fig. 4). Pottery predated agriculture in the region, but the Neolithic began around 7000 cal. BC with the emergence of sedentary communities

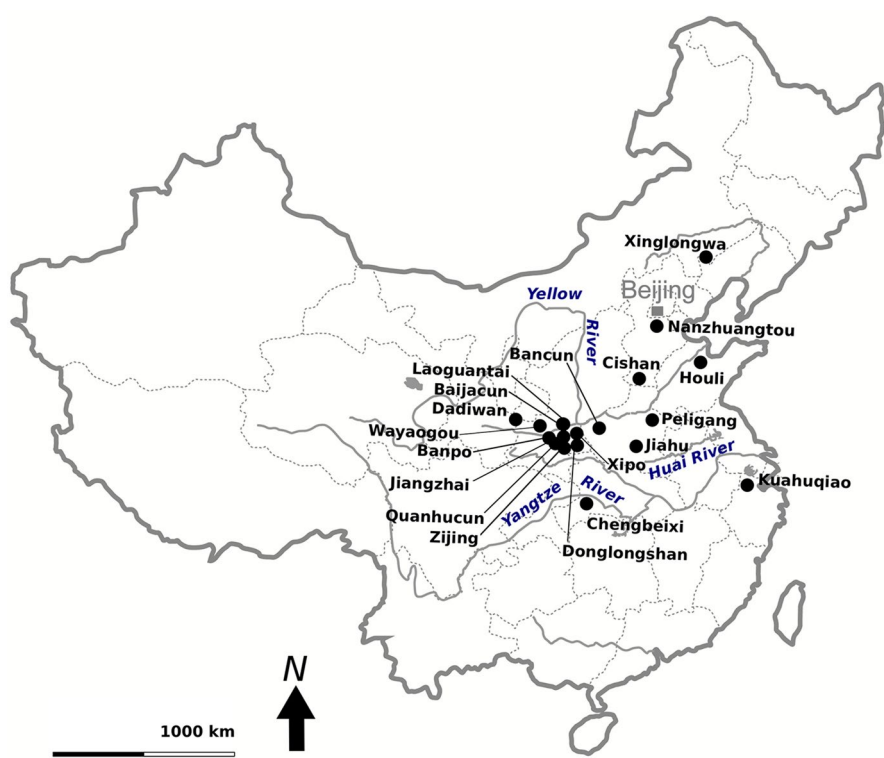


Fig. 4 Map of China showing sites mentioned in text

with distinct pottery traditions along the Yellow River (e.g., Dadiwan I, Laoguantai, Peiligang, Houli, Cishan) and Yangtze River (e.g., Kuahuqiao and Chengbeixi) (Liu 2005). Another important site, Jiahu, lies along the Huai River. People in the Yellow River valley may have cultivated millet as early as 8000 cal. BC, with the earliest reliable evidence for domestic cereals dating to around 6000 cal. BC at Dadiwan and Cishan (Bar-Yosef 2011; Bettinger et al. 2010). At roughly the same time, rice underwent domestication in the Yangtze Valley (Chi and Hung 2010; Fuller 2011).

Zooarchaeological data from these settlements are only partially published. Yuan and Flad (2002, pp. 728–729) list relative abundance data (in %NISP and %MNI) for *Sus scrofa* at sites in the Yellow River valley, where wild boar and deer were the dominant taxa. Wild boar frequencies vary among the earliest Neolithic sites—Bancun I (43%), Zijing I (14%), Baijacun (36%), and Nanzhuantou (6%)—but the relative abundance of *Sus scrofa* tends to increase over time, especially after around 4000 cal. BC (Yuan et al. 2008, p. 357). At Bancun, the relative abundance of *Sus scrofa* increased from 43% to 60% between 6000 and 2200 cal. BC and at Zijing, 14% to 60% between 6000 and 2090 cal. BC (Yuan and Flad 2002). Similarly, the relative abundance of *Sus scrofa* generally increased over time in the Yangtze River valley. However, unlike the Yellow River valley, pigs remained a secondary source of meat at many sites until the fourth millennium cal. BC (Yuan et al. 2008). At Neolithic Kuahuqiao, *Sus scrofa* remains decreased from 27% to 9% between 6200 and 5000 cal. BC (Yuan et al. 2008, p. 354). Pigs became dominant among the mammalian fauna in the Yangtze Valley only around 2000 cal. BC.

Available biometric data can be taken as an indication that pig domestication was underway in the seventh millennium cal. BC, possibly in multiple locations. On the Yellow River, Yuan and Flad (2002) argue that the earliest domestic pigs date to around 6000 cal. BC in and around the site of Cishan. They based their

Table 5 Lower M3 metrics for Neolithic and Bronze Age sites in China, data from the following sources: 1—Yuan and Flad (2002, p. footnote 1); 2—Ma (2005, p. 64); 3—Wang et al. (2015)

Site – Ref.	Date (cal. BC)	Mean WA (mm)	Mean length (mm)	N
Paleolithic Sites – 1	>7000	ND	45.0	ND
Cishan – 1	6000	18.3 mm	41.4	ND
Shishanzi – 1	5000	16.3 mm	38.3	ND
Wayagou – 1	4320–3710	17.1 mm	39.1	18
Jiangzhai – 2	4100–3600	ND	36.1	13
Jiangzhai – 1	4000–2000	17.5 mm	36.2	ND
Xipo – 3	4000–3500	15.9 mm	35.0	22
Shouling – 1	4000–2500	15.9 mm	38.0	ND
Banpo – 1	4000–2500	16.3 mm	35.8	ND
Quanhucun – 2	3850–3550	15.6 mm	33.5	18
Zhukaigou – 1	2000	ND	32.8	ND
Donglongshan – 2	2000–1600	15.0 mm	33.0	33
Yinxu – 1	1400	14 mm	31.4	ND

argument on the size of the third molars from Cishan (mean length 41.4 mm) compared to Paleolithic wild boar (mean length 45 mm) (Table 5). However, there has not yet been published a comprehensive treatment of wild boar metrics from Paleolithic China. Tooth size continued to decrease after 6000 cal. BC. At sites located along the Wei River, a tributary of the Yellow River, H. Wang et al. (2015) showed a clear and continuous decrease in lower molar breadths and lengths at Wayaogou, Jiangzhai I and II, Quanhucun, and Donglongshan, which were occupied from roughly 4320 to 1600 cal. BC. Mean measurements on molars from all of these sites fall below those reported for Cishan (Table 5). *Sus* molars from these sites, as well as another Wei Valley Neolithic site, Lingkou (5130–4500 cal. BC), also displayed higher rates of LEH than in modern Chinese wild boar (H. Wang et al. 2012). The rates of LEH increased over time, especially on the first molar (H. Wang et al. 2012).

In the Yangtze Valley, metrical data also indicate domestication, perhaps by the sixth millennium cal. BC. Although Ma and Liu (2017, p. 308) state that third molar lengths decreased over time at Kuahuqiao (c. 6200–5000 cal. BC), an examination of metrical data complicates their argument. Mean lower third molar lengths decreased only by around .5 mm between the early and late phases of the site, and first-third lower molar breadths showed minimal decrease or even a slight increase (<1 mm) over time (Yuan and Yang 2004). On the other hand, the *minimum* measurements in each phase tended to decrease; minimum lower M3 length and WA decreased 38.6–36.6 mm and 18.1–16.9 mm, respectively. We interpret this as evidence for the development of a domestic population that existed alongside and perhaps not in isolation from wild boar, which the people of Kuahuqiao continued to hunt. Ma and Liu (2017, p. 308) also noted that three *Sus* mandibles from Kuahuqiao showed evidence of dental crowding—a potential but not unambiguous indicator of domestic pigs.

Morphometric analysis of *Sus* remains from Jiahu in the Huai Valley also indicates a process of domestication, perhaps as early as the mid-seventh millennium cal. BC (Cucchi et al. 2011, 2016). Using GMM to assess the lower second molar, Cucchi et al. (2011) found that lower second molar centroid sizes were significantly smaller those of modern wild boar but larger than those of modern domestic pigs and those at fifth millennium cal. BC Xishui in Henan Province. These smaller second molars included a single specimen dating to the earliest phase of the site (Jiahu 1; c. 7000–6600 cal. BC). However, while specimens were smaller than those of modern wild boar, there was no apparent change in size over time at Jiahu (Cucchi et al. 2011, 2016).

One could interpret the centroid size data as evidence *against* a process of domestication. Analysis of the lower second molar shapes, however, revealed a more complex pattern. Cucchi et al.'s (2011) neighbor-joining algorithm identified that tooth shapes from Jiahu 2 (6600–6200 cal. BC; $N=6$) and Jiahu 3 (6200–5800 cal. BC; $N=8$) clustered with both modern domestic pigs ($N=6$) and those from fifth millennium cal. BC Xishui ($N=35$). Meanwhile, modern wild boar ($N=17$) clustered with specimens from both northern (Xinglongwa; 6100–5300 cal. BC; $N=36$) and southern China (Zengpiyan; 8000–?5000 cal. BC; $N=5$). The single specimen from Jiahu 1, however, fell in between the two groupings. Based on the robust sample

sizes and the fact that wild boar from multiple regions throughout China and over time appear to cluster together, Cucchi et al. (2011) concluded that morphological change indicative of domestication was underway at Jiahu by 6600 cal. BC.

We reiterate, however, that the connection between second molar shape change and the other features of the “domestication syndrome” remains unclear. GMM studies of *Sus* dentition are still relatively new. We therefore add a grain of salt to the interpretation that domestication was underway in the Huai River valley by 6600 cal. BC until more dental shape data can be brought to bear on the problem. This is especially important as the Jiahu data represent the earliest scientifically argued date for pig domestication in China. A recent study by Cucchi et al. (2016), which included additional specimens from other sites, revealed a more complex pattern. Specifically, the authors found that the suids from Jiahu 2 and 3 clustered more closely with (although were clearly distinct from) two subspecies of modern wild boar, *Sus scrofa ussuricus* and *S. s. moupinensis*, than with domestic pigs from Xiaawanggang (4600 cal. BC–AD 200).

Isotopic data have played a much larger role in documenting pig domestication in China than in northern Mesopotamia due to the presence of a C4 domesticate (foxtail millet). As a C4 plant, the $\delta^{13}\text{C}$ values of millet and the animals that ate it are enriched c. 10–15‰ compared to C3 plants and their consumers. Taking advantage of this, beginning in the early 2000s, studies relying on small (< 10) samples of pig, dog, and human remains from archaeological sites dating to periods no earlier than c. 4000 cal. BC documented high $\delta^{13}\text{C}$ values. This indicated that all three mammals consumed millet in significant proportions (Hu et al. 2009; Pechenkina et al. 2005). Recent studies with larger sample sizes have corroborated these initial assessments and have extended the data into earlier periods. For example, Barton et al. (2009) collected C and N data from 36 *Sus scrofa* specimens from two phases at Dadiwan in northern China: pre-Yangshao (c. 5900–5200 cal. BC) and Yangshao (4500–2900 cal. BC). They found that suids in the pre-Yangshao had relatively low values of $\delta^{13}\text{C}$ (c. -19‰), indicating a primarily C3 diet that largely overlapped with wild ungulates (deer and aurochs), as well as $\delta^{15}\text{N}$ values ranging from c. 5.5 to 7‰. But in the Yangshao phase, the majority of suids had values of $\delta^{13}\text{C}$ between -11 and -6‰ and $\delta^{15}\text{N}$ between 7.5‰ and 10‰, with both C and N values falling within the range of domestic dogs. The authors interpreted this major shift in diet as evidence of provisioning pigs with millet (causing enrichment in $\delta^{13}\text{C}$) and meat from table scraps (enrichment in $\delta^{15}\text{N}$). Although we interpret the nitrogen data somewhat differently (see below), the data clearly indicate a dramatic change in suid diet by the fifth millennium cal. BC.

Studying long-term changes in isotopes and biometrics, Cucchi et al. (2016) sampled 36 pig remains from Xiaawanggang in Henan Province, which was occupied from the Neolithic through the Han Dynasty (c. 4500 cal. BC–AD 200). From the earliest Yangshao phase, the authors documented the presence of pigs with higher “mixed C3/C4” $\delta^{13}\text{C}$ (c. -18.5‰ to -13‰) as well as those with lower “open C3” values (-21.5‰ to -18.5‰) and $\delta^{15}\text{N}$ values between 2.5‰ and 6‰. But later, in the Longshan phase (c. 2600–1900 cal. BC), the isotopic data revealed two distinct groups. The group identified as domestic based on small third molar size was enriched in $\delta^{13}\text{C}$ ($>-14\text{‰}$) and $\delta^{15}\text{N}$ ($>6\text{‰}$), indicating consumption of C4

plants (millet) and perhaps, organic waste. By the Erlitou, Western Zhou, and Han Dynasty periods, this C4-based, $\delta^{15}\text{N}$ -enriched group was dominant among the small-sized pigs, indicating an intensification of foddering regimes over time.

Although providing clear evidence for shifting diets in *Sus scrofa*, the interpretation of these data requires some caution, as equifinality remains a major concern. The oft-repeated assumption that $\delta^{15}\text{N}$ enrichment reflects feeding on waste or meat-rich table scraps is particularly problematic. An alternative, and more plausible, explanation is that pigs were foddered with crops grown in fertilized soils (Bogaard et al. 2007). Manuring would have enabled intensive cereal production and one can imagine a “recycling” scenario in which people provisioned pigs with millet and collected their feces to manure millet fields. There is evidence for such an economic system. In a recent paper, X. Wang et al. (2018) examined the isotopic composition of millet seeds and pig bones from five Late Neolithic (3500–1500 cal. BC) sites in the Baishui Valley of Shaanxi Province. The authors identified elevated $\delta^{15}\text{N}$ values in both seeds and bones, with the latter also showing elevated $\delta^{13}\text{C}$, reflecting C-4 plant consumption. These data fit expectations for pigs eating $\delta^{15}\text{N}$ -enriched millet and, in turn, millet being fertilized with dung, perhaps from the pigs themselves.

A second problem with the interpretation of isotopic data involves the enrichment of $\delta^{13}\text{C}$. While high $\delta^{13}\text{C}$ values almost certainly reflect consumption of millet by Neolithic *Sus scrofa*, it is not clear how pigs/wild boar came to eat millet. Many studies interpret $\delta^{13}\text{C}$ enrichment as evidence of foddering. This is a likely explanation, especially in later periods. But it is also possible that wild boar or free-living/feral pigs were attracted to stands of millet, perhaps raiding crops or being allowed to feed on post-harvest stubble. As in northern Mesopotamia, the attractiveness of cultivated plants may have pulled *Sus scrofa* closer into the human niche.

Two key questions stand at the center of research on pig domestication in China. First, it remains unclear to what extent the prey, commensal, or combined pathways were involved in the process of pig domestication in China. Compared to northern Mesopotamia, there are fewer published zooarchaeological data from the earliest phases of the Neolithic and, especially, pre-Neolithic periods. The hunting and management strategies employed by people to wild boar populations at the dawn of domestication is almost entirely unexplored. Second, did people in both northern millet-producing regions (Yellow and Huai Rivers) and southern rice-producing regions (Yangtze) independently domesticate pigs? The area over which pig domestication appears to have taken place in China is much larger and may have involved independent (or semi-independent) trajectories in two or three different river valleys. New aDNA evidence can be interpreted as evidence for a multiregional process of domestication (Xiang et al. 2017). However, we cannot objectively conclude a multiregional process of pig domestication without a clear radiocarbon chronology, additional and reliable zooarchaeological data, and solid evidence for early Holocene wild boar ecology and human–suid relations.

Although we do not know much about early Holocene human–suid interactions, the available data from the seventh millennium BC onward give the impression that pig domestication in China was more rapid, perhaps involving the application of intensive management strategies (penning and foddering) earlier on in the process

compared to northern Mesopotamia. Evidence for this includes the more rapid rate of biometrical change in China, which could be indicative of stronger selection pressures and/or sexual isolation from wild boar. Thus, lower third molar measurements of Chinese pigs in Table 5 show a decrease of around 15% from the seventh–fifth millennia cal. BC, compared to the 5–10% size reduction in teeth at Çayönü from the 10th–seventh millennia cal. BC (Ervynck et al. 2001; Hongo and Meadow 1998). Additionally, the frequency of tooth crowding at sixth millennium Kuahuqiao and other sites (Ma and Liu 2017, p. 308) could indicate that facial length decreased at a faster pace than even tooth size, which in turn might reflect greater selection pressures or softer diets in Chinese Neolithic pigs. Finally, if the enrichment in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ does indeed reflect foddering, the isotopic data from China indicate the presence of intensive food provisioning strategies early on in the Neolithic. The sudden shift in isotopic values at Dadiwan in the fifth millennium BC, for example, might show the rapid adoption of such strategies (Barton et al. 2009). These patterns contrast with the more subtle changes at Çayönü, where we have suggested that the slight reduction in $\delta^{15}\text{N}$ over time is evidence for people gradually adding more legumes to their pigs' diets.

Conclusions and Unanswered Questions in Pig Domestication

The ecological and behavioral flexibility of *Sus scrofa* make them adaptable to a number of different types of relationships with humans. This makes understanding the first steps in their domestication complex, but it also presents an opportunity for scholars to push into new theoretical domains in understanding human–animal relations. In particular, pig domestication challenges scholars to think critically about the specific and diverse ways that humans, intentionally or not, applied novel selection pressures to local faunal populations in the Holocene.

Accepting the challenge of documenting pig domestication requires a multi-pronged methodology. Many of the techniques currently employed by zooarchaeologists and other scholars are in dire need of refinement and testing on actualistic data. Additionally, although the impact of archaeogenetics already is impressive, its potential to inform us about specific phenotypic changes has barely been tapped. Documenting ancient allele frequencies and, perhaps, gene expression will illuminate the ways in which pigs adapted to “living in the human niche” (Bleed 2006).

At the moment, we can identify two independent centers of pig domestication. In northern Mesopotamia, domestic morphologies developed by 7500 cal. BC at the latest, and probably closer to 8200 cal. BC. We have suggested that pigs followed a “combined pathway” to domestication in which (1) wild boar were attracted to permanent human settlements, their garbage, and their cultivated foods in the early Holocene and (2) hunter-gatherers began to practice game management and eventually herd management of populations of wild boar. It is likely that commensal and managed populations regularly interbred, swapping genes and epigenetic traits. If we are correct, then the mutations selected for during the domestication process arose from relationships initiated both by humans (management) and wild boar themselves

(commensalism). This adds even greater complexity to the issue of intentionality in the process of domestication.

The situation is less clear in China, where convincing evidence for domestic pigs is present in contexts dating to about 6000 cal. BC, possibly in several (independent?) regions. We have posited that pig domestication in China involved a more rapid progression from extensive to intensive husbandry practices, which resulted in drastic size reduction and large-scale shifts in diet. However, we do not yet have a clear picture of the specific pathways along which pigs and humans proceeded to domestication. Understanding human–suid relations more fully and providing a more concrete framework for the interactions between different river valleys should be among the top research directives into the issue of animal domestication in China.

Revealing are the contexts in which pig domestication did not occur. Why weren't pigs domesticated in Japan? Perhaps, in contrast to the river valleys of northern Mesopotamia and China, human population density was not high enough—or human interference in the lives of wild boar simply not strong enough—to develop the critical mass necessary for the sustained buildup of “domestication syndrome” alleles in *Sus scrofa* populations. One key feature is the conceptualization of animals as property (probably communal property, initially), which would create incentives for long-term investment in specific suid populations and propel selection for tameness. Cultural barriers to such conceptions of animals may well have tapped the brakes on incipient domestication processes. Another key feature is the availability of cultivated crops. While game management strategies are likely to take place without provisioning animals, even the most extensive ethnographic examples of herd management involve feeding pigs. It is possible that, without domestic cereals or large stands of cultivated crops, Jomon suid management was never able to reach the level in which a large enough proportion of the population of suids was dependent enough on humans for domestication to take place.

Understanding the contexts of domestication, as well as those in which it did not occur, forces scholars to think critically about the types and intensities of selection mechanisms at play in the domestication process. As intriguing as the documentation of phenotypic/genotypic changes in ancient pigs is, anthropological archaeology demands a commitment to the study how humans and suids interacted in different contexts and the factors that caused these relationships to change. Testing the alternative scenarios presented in Fig. 1 will allow us to peer more deeply into the complex history of pigs and people in the Holocene.

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