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Using pigs as a proxy to reconstruct patterns of human migration

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Abstract

Human beings have been migrating since the dawn of our species. For the vast majority of that time, populations moved across the continents without the aid of domestic animals. In fact, by the time the first animals were fully domesticated, migrating hunter-gatherers had already spread to every continent except Antarctica. Tracing the timing and trajectories of these migratory routes has been a significant anthropological endeavour, and to piece together the palimpsest of human migrations scientists have employed a range of proxies including

modern human genetic signatures, linguistics, and numerous material culture elements. This paper discusses the insights that have been gained by using domestic pigs as a proxy for human movement (post domestication) across western Eurasia and into the Pacific. Pigs have not only informed specific trajectories and timings of migration routes, they have also led to a new general perspective on studies of human migration writ large and have even begun to raise heretofore unexplored questions about the ramifications of human movement for both people and their domestic partners.

Keywords

domestication, Neolithic, mtDNA, phylogeography

Introduction

By the beginning of the Neolithic in the Near East, humans occupied all of the continental landmasses, including Africa, Eurasia, the Americas and Australia. The only continent humans had not yet reached was Antarctica. And humans reached all these places without the advantage of domestic animals, or at least, without the benefit of the full compliment of domestic animals associated with the early Eurasian Neolithic. This record of migration demonstrates that for most regions of the world, people did not need domestic animals in order to travel. Following the domestication of pigs, sheep, goats, and cows, however, farmers travelled extensively with these walking larders and were able to move into areas already occupied by indigenous hunter-gatherers, and onto remote islands inaccessible to people who did not possess domestic animals.

Because farmers often travelled with their livestock, the archaeological remains and genetic signatures of both ancient and modern domestic and commensal animals can be used as a direct proxy for the timing and routes of ancient migration. This has been demonstrated for rats (Matisoo-Smith and Robins, 2004), sheep (Chessa et al., 2009), goats (Fernandez et al., 2006), cows (Edwards et al., 2007) and, of course, pigs (Larson et al., 2007a; Larson et al., 2007b). This paper will focus on the use of pigs as a proxy for human migration first in western Eurasia, and then in the Pacific region, where pigs travelled with people as far east as Hawai'i.

Tracking the migration of farmers into Europe

There is no question that wild boar had been domesticated independently in both the Near East (Ervynck et al., 2001) and in East Asia (Cucchi et al., 2010) by 9,000 cal BP. The degree to which European wild boar were locally domesticated, either independently or as a consequence of the earlier introduction of domestic pigs from the Near East, remains uncertain (Albarella et al., 2006b; Larson et al., 2007a). This uncertainty is the result of the success of *Sus scrofa*'s natural ability to migrate. The natural range of the

wild boar covers most of Eurasia. In this they are unlike sheep and goats, whose wild ancestors are (and likely were) confined to a relatively small geographic region in the Near East. Therefore, any sheep or goat remains found associated with archaeological contexts in Europe are easily identified as domestic specimens (Clutton-Brock, 1999), and thus these two species (along with associated material culture) provide an unambiguous marker of the presence of people whose ancestors migrated from the Near East. By contrast, the ubiquity of wild boar and the significant degree of size variability within wild populations across Eurasia (Albarella et al., 2009) have prevented archaeologists from confidently assigning a wild or domestic status to recovered *Sus* remains, and thus the presence of pig remains on their own cannot be associated with Near Eastern farmers.

In the past, archaeologists lacked the ability to unambiguously ascertain differences between geographically differentiated wild boar populations. Modern genetic studies of pigs have taken advantage of a greater degree of resolution and have confidently identified numerous geographically isolated populations of wild boar that possess distinct genetic signatures. This strong phylogeographic structure has revealed nearly 20 unique genetic groupings of wild boar, even if the relationships between those groupings remain ambiguous (Giuffra et al., 2000; Larson et al., 2005; Larson et al., 2010).

A surprising finding of these publications was the lack of a shared genetic affinity between European domestic pigs and Near Eastern wild boar. The phylogeographic patterning suggested that wild boar from continental Europe differed significantly from those in the Anatolian peninsula and the Near East, and the archaeozoological evidence suggested that though pigs were first domesticated in the Near East, they were later introduced into Europe during the Neolithic. Assuming that the biogeographic boundary between European and Near Eastern wild boar, centred near the Bosphorus, was established well before the origins of domestication, it was reasonable to conclude that the first pigs brought into Europe did not share a genetic affinity with the indigenous wild boar. Because modern European domestic breeds clustered with European wild boar, this result implied that the first pigs introduced by Neolithic farmers had at some point been replaced by European pigs descended, at least maternally, from European wild boar.

This narrative rests on the assumption that the natural geographic ranges of wild boar possessing Near Eastern and European signatures have remained static since at least the beginning of the Holocene. If the European genetic motif was naturally present within wild boar populations in the Near East, then Near Eastern farmers could have domesticated this type and a secondary domestication in Europe would no longer be necessary to explain the modern pattern.

At least three different studies (Giuffra et al., 2000; Larson et al., 2005; Ramírez et al., 2009) have independently found what are thought to be European haplotypes in Near Eastern wild boar, though they are present at low frequencies. This pattern has led some authors to suggest that the phylogeographic structure is not as dichotomous as Larson and colleagues (2007a) initially proposed. Ramírez and colleagues (2009), for example, suggested that the occasional inconsistency within the general phylogeographic pattern could be due to the natural admixture of wild boar populations, and need not be a consequence of human-mediated translocation of domestic pigs that subsequently became feral, as has been suggested by Larson and colleagues (2005, 2007a). Ramírez and colleagues (2009) supported their argument with a nuclear microsatellite analysis, the results of which demonstrated that European, Near and Middle Eastern, and North African wild boar populations cluster into a single group, despite the fact that the mitochondrial haplotype frequencies within these samples differ markedly. They argued that since mitochondrial DNA is more prone to extinction on shorter time scales (due to genetic drift), the observed haplotypes frequencies in modern populations could be due to recent demographic events.

Because domestic pigs have been known to become feral (Albarella et al., 2006a), ancient introgression, as suggested by Larson and colleagues (2007a), cannot be ruled out as the cause of the observed discrepancies within the phylogeographic pattern.

A perspective that incorporated only modern DNA would never be able to resolve this issue. The analysis of DNA extracted from ancient remains, however, has become a powerful tool in domestication and migration studies. Though modern DNA analyses allow for a greater resolution than is typically possible through traditional archaeological approaches, they lack any temporal perspective, thus limiting the ability of modern studies to extrapolate their results into the past. Given the complex history of pig domestication, and the inability of modern DNA studies to differentiate between competing historical explanations, ancient DNA studies of archaeological material are the best means with which to resolve the questions discussed above.

As previously mentioned, a great deal of the modern genetic understanding of Near Eastern and European pig domestication rests on the assumption of temporally consistent phylogeographic patterns. By extracting DNA from archaeological material from the Near East to Western Europe, dated from 10,000 years ago to the present, Larson and colleagues (2007a) were able to directly test pig domestication hypotheses and reveal the temporal and geographic pattern of pig haplotypes.

Like the organisms from which it is derived, DNA degrades through time. The rate of that degradation is determined by numerous factors but tends to be faster in hotter climates and in lower latitudes (Binladen et al., 2006). The authors maximized the number of successful samples by identifying a short (~80bp) fragment that contained sufficient changes to enable the sample to be assigned to a Near Eastern or European heritage. Despite this effort, the relatively hotter climates of the Near East had significantly diminished the number of archaeological bones that retained amplifiable DNA fragments even of this size, thus limiting the ability of ancient DNA researchers to compare the DNA of the earliest domestic pigs with those of their European counterparts. Despite this frustration, the preservation of bones from Mesolithic, Neolithic, and later contexts throughout Europe was sufficient to retrieve a continental picture of the shifting patterns of haplotypes from wild and domestic pigs (Larson et al., 2007a).

The evidence firstly demonstrated that no wild boar in Europe dated to a time before the arrival of the Neolithic possessed Near Eastern haplotypes. In fact, the only Mesolithic pigs that did possess a Near Eastern affinity were from the Crimea, suggesting that the biogeographic boundary located near the Bosphorus straits was intact at the beginning of the Holocene. This geographic split between the genetic signatures of wild boar on each side of the boundary then allowed Larson and colleagues (2007a) to directly test whether the first domestic pigs in Europe were brought in from the Near East, or were domesticated from wild boar indigenous to Europe. In several sites in Romania near the Black Sea coast, and the site of Eilsleben in Germany, every pig identified as domestic using morphometric criteria possessed Near Eastern haplotypes, and every wild boar possessed a European genetic signature. The same was true at the Neolithic site of Bercy in France (dated to ~4000 cal BC), except for a single domestic pig that possessed a European haplotype.

From this point to the present, however, all the domestic pigs sampled across Europe possessed European mitochondrial signatures, demonstrating that at least on the continent, the domestic pigs originally introduced from the Near East had been replaced by those who were maternally descended from European wild boar. Some individual medieval and modern pigs from the island of Corsica, however, still retain a Near Eastern maternal genetic affinity, suggesting that they are the sole European pigs to retain the inheritance of the first pigs introduced to the island during the Neolithic. Even more intriguing-

ingly, domestic pigs in the Near East hung onto their Near Eastern ancestry until at least 700 cal BC, after which, they too were replaced by pigs derived from European wild boar. The presence of different haplotypes along the purported northern and southern Neolithic routes into Europe also seemed to suggest that different lineages of pigs were transported along these two routes, but the number of samples was too small to conclusively demonstrate this potential correlation (Larson et al., 2007a).

What is not in dispute is the complexity of pig domestication and subsequent human migration across western Eurasia. That being said, technological advancements enabling the generation of ever-longer DNA sequences from archaeological material will continue to reveal variability among pig populations in time and space. This increased degree of resolution will only add to our ability to tease apart the complexity, and I suspect that within the next decade the domestic animal proxy model for human migration into Europe will substantially add to our understanding of when and where incoming farmers interacted with indigenous hunter-gatherers and what the ramifications were for the humans and for their domestic animal partners.

Tracking human migrations into the Pacific

The movement of people into Oceania was one of the most extensive human dispersals (Diamond, 2000) and is enormously significant because although hunter-gatherers had travelled over water to reach, for example, Australia, it appears that people were unable to colonise the remote islands of the Pacific without the aid of domestic animals. Though of course the ancestors of the Pacific settlers must have originated in East Asia, uncertainties remain regarding the precise geographic origins of modern populations in Melanesia, Micronesia and Polynesia. A wide variety of scenarios have been suggested, based upon the associated material culture, language, and human genetic signatures, to explain the movement of Neolithic cultures into Near and Remote Oceania (Anderson, 2005; Bellwood, 1998; Bellwood and Diamond, 2005; Green, 2000; Hurles et al., 2003; Kirch, 2000; Oppenheimer, 2004; Terrell et al., 2001). The degree to which the cultural and biological elements used to trace the routes reflect the actual human dispersal has been questioned, as has the extent to which these various components were dispersed as a single unit (Hurles et al., 2003). For example, models of the origins of Lapita (the immediate ancestors of the Polynesians and many other Oceanic cultures) that focus on the entire Lapita cultural and ecological package moving from Taiwan to the Pacific with little interaction differ significantly from those that identify broader regions and possibly multiple origins of the various cultural components (Donohue and Denham, 2010).

Like the European example above, analyses of genetic variation in the domestic and commensal animals which were intimately linked with Neolithic cultures, and which were significant components of human dispersal and exchange networks, can shed light on the origins and routes of the migrating cultures. Pigs, chickens, dogs and rats were introduced to the various islands of Near and Remote Oceania by early human settlers, and studies of Pacific rats (Matisoo-Smith and Robins, 2004) and pigs (Allen et al., 2001; Larson et al., 2005) have demonstrated the potential of these taxa to act as reliable proxies for reconstructing patterns of human dispersal into Oceania. Interestingly, a previous genetic study of pigs in the region (Larson et al., 2005) revealed a unique genetic population of pigs which the authors termed the “Pacific Clade”. Pigs that possessed this signature were found only in Halmahera (in the Moluccas), New Guinea, and several Pacific islands, including Hawaii and Vanuatu, places that have never had an indigenous population of wild boar (Bellwood and White, 2005). The absence of Pacific

Clade haplotypes in any wild or domestic pigs from mainland Asia, or ISEA west of the Wallace Line (Larson et al., 2005), however, meant the geographic origin of the clade could not be identified.

Larson and colleagues (2007b) later investigated the geographic origin of the Pacific Clade and its distribution within ISEA and Near and Remote Oceania by typing mitochondrial control region sequences from more than 200 wild, feral, and domestic pigs from across the region and mainland Southeast Asia, using both museum specimens and archaeological pig remains from several islands. The resulting phylogenetic tree revealed that all of the pigs in ISEA found west of the Wallace Line represented the most basal portion of the tree, suggesting that the genus *Sus* originated in this area. The Pacific Clade pigs, however, clustered with several other clades in East Asia, strongly suggesting that though they are now primarily present east of the Wallace Line, their ancestors did not evolve until wild boar had naturally crossed the Kra Isthmus in modern day Thailand and travelled into peninsular East Asia.

Large scale genetic typing of pigs in peninsular East Asia and throughout South Asia, China, the Koreas, and Mongolia, has recently revealed at least five individual wild boar samples whose genetic signatures match those of the Pacific Clade (Larson et al., 2010). These specimens, found in Vietnam, Laos, and Yunnan province, China, suggest that the Pacific Clade likely evolved in peninsular Southeast Asia. In addition to the peninsular East Asian specimens, museum samples possessing Pacific Clade haplotypes were also identified in Sumatra and Java and eight islands east of the Wallace Line in the Moluccas and Lesser Sunda chains, including New Guinea. Despite a reasonable sampling effort, however, no Pacific Clade pigs have yet been found either in Taiwan or on the Philippine Islands, despite the fact that archaeological evidence strongly implies that people travelled with pigs from Taiwan to at least Luzon, the northernmost Philippine island in the archipelago (Piper et al., 2009). None of the islands in Wallacea (with the exception of Sulawesi) possessed endemic populations of *S. scrofa* (Morwood et al., 2004). In fact, archaeological investigations on Flores (Morwood et al., 2004), Timor (Glover, 1986) and the northern Moluccas (Bellwood and White, 2005) have demonstrated that the first appearance of pigs only occurs in Holocene deposits associated with the arrival of the Neolithic “cultural package.” The total of the archaeological evidence, then, seems to suggest that a separate population of pigs, unrelated to the Pacific Clade, were brought south from Taiwan to the Philippines, and because the modern Pacific Clade pigs in Wallacea and New Guinea match those in peninsular Southeast Asia, that perhaps it was in this region that pigs were domesticated before being transported through ISEA.

This narrative works nicely, except when one considers the archaeological record in peninsular Southeast Asia, where there is currently no indication that domestic pigs were present before the end 5th millennium BP, when they appear alongside the first evidence of sedentary agriculture (Higham, 1975; Higham, 2002). This suggests that these domestic pigs were not the result of a process involving local wild boar and that they should not have Pacific Clade haplotypes, though this has not yet been tested. In addition, no modern domestic pigs possessing Pacific Clade haplotypes have yet been found in mainland Asia.

These two facts seem to contradict a narrative that starts in peninsular Southeast Asia and ends in the Pacific. It may be possible, however, that earlier evidence for local domestication of Pacific Clade pigs in this understudied region may yet be uncovered. The lack of modern Pacific Clade pigs could be a consequence of a replacement of native domestics by pigs later introduced from Central China during several possible demographic expansions of agricultural populations into the region, including Austronesian speakers through ISEA and parts of the mainland coastal regions (Pawley, 2003), post-Neolithic expansions of Sino-Tibetan speakers (Pawley, 2003; Van Driem, 1998), and Austro-Tai or Miao-Yao groups from Southern China (Blench, 2005). This possibility is analogous to the temporal replacement

of several domestic animals including chickens in the Pacific (Gongora et al., 2008) and Near Eastern pigs during later prehistory (Larson et al., 2007a).

Intriguingly, there is substantial genetic and morphological evidence that people were transporting another suid species (*Sus celebensis*) within ISEA many thousands of years before the Pacific migrations. A single modern specimen and seven archaeological Liang Bua Cave specimens possessed a unique haplotype that clusters with *Sus celebensis* specimens from Sulawesi. ISEA and Island Melanesia possess a long history of animal translocation (Flannery and White, 1991; Heinsohn, 2003; Spriggs, 1997), and since *Sus celebensis* is endemic only to Sulawesi, its presence on Flores as early as 7,000 BP (based upon the stratigraphic association of the earliest pig specimen and associated ¹⁴C dates of charcoal) suggests an early translocation of this species by humans. Independent verification of the distinctiveness (and also probable domesticated origin) of pigs with the Pacific mtDNA signature is shown by morphometric analysis of the lower third molar from the modern New Guinea and Flores pigs, as well as archaeological pigs from the site of Liang Bua on Flores.

Though the density of sampling in the region needs to be improved, the data thus far support human-mediated dispersals of *Sus* species not only from Asia into the Pacific, but also within Wallacea. The archaeological evidence in the northern Philippines (Piper et al., 2009) as well as the genetic evidence from the Lanyu island off the coast of Taiwan (Luetkemeier et al., 2010; Wu et al., 2007) suggests that people may well have been migrating with yet another genetically and regionally distinct domestic pig, even if that subpopulation was not subsequently carried into the Pacific. What is clear is that the different components of the Neolithic cultural complex may therefore have different origins and trajectories to Near Oceania, where they finally came together and are identified archeologically as Lapita. Knowing that the pigs may have had a different route than the people, or at least did not have the identical route helps researchers to unravel a complicated migration pattern (Donohue and Denham, 2010; Wollstein et al., 2010).

All of these narratives, both in the Pacific and in Europe, demonstrate the complexities of human movement and the dangers of layering an overly simple explanation over large spatial and temporal distances. People were likely involved in different degrees of pig domestication across the Old World and when they migrated, these different populations of people and pigs could easily have mated, creating hybrid populations with hybrid genomes. The extent to which domestic pigs introgressed with wild boar of the same or different species as a consequence of human migration remains unknown, and it is unlikely that we will be able to find out using modern DNA alone. Ancient DNA, derived from the bones of archaeological pig remains, however, could provide the necessary temporal framework to reveal not only the genetic affinities of individual populations of domestic pigs, but also whether or not the processes of domestication across the Old World were truly independent or facilitated by human migration and the introduction of foreign domestic pigs.

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