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The Pigs of Island Southeast Asia and the Pacific: New Evidence for Taxonomic Status and Human-Mediated Dispersal



KEITH DOBNEY, THOMAS CUCCHI, AND GREGER LARSON

THE PROCESSES through which the economic and cultural elements regarded as “Neolithic” spread throughout Eurasia remain among the least understood and most hotly debated topics in archaeology. Domesticated animals and plants are integral components of the chrono-cultural and paleoenvironmental data set linked to the earliest farming communities, and their remains are key to understanding the origins and spread of agriculture. Although the majority of research into animal domestication and Neolithic dispersal has focused upon western Eurasia, the Near East, and Europe, where both traditional and new techniques have significantly advanced our ideas regarding the origins and spread of Neolithic farming westward, less emphasis has been placed upon its eastward spread from mainland East Asia to Island Southeast Asia (ISEA).

The close relationship between people and pigs has been a long and varied one for millennia. Pigs have been of great economic and symbolic importance to the tribal societies of ISEA (Banks 1931; Hose and McDougall 1901; Medway 1973; Rosman and Rubel 1989) and, for that reason, wild pigs and their feral and domestic derivatives have been widely introduced as game and/or livestock throughout the region (Groves 1995; Oliver and Brisbin 1993). As a result of this human agency, a diversity of introduced domestic, feral, and possible wild suid forms has arisen.

Continuing debate over the present day taxonomy of these island suids, and even bigger problems with the specific identification of their fossil remains, leave us very little idea as to which species are actually represented in the archaeological record, let alone their past wild, feral, or domestic status. Archaeological evidence demonstrates that wild boar were important prey animals of early hunter-gatherers across wide areas of ISEA. However, during the early Holocene this predator-prey relation evolved into something more complex, as wild boar (and

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some other mammal species) became key players in the advent and subsequent dispersal of Neolithic farmers around the world.

Despite the almost ubiquitous presence of *Sus* remains from many archaeological sites of Holocene date in mainland East Asia, ISEA, and Oceania, comparatively little is known about the temporal context of pig domestication, the actual species involved, and their involvement in the different human diasporas of the region. Although ISEA is perhaps one of the most important and interesting regions to study the range of different relationships between pigs and humans (since it contains the core of *Sus* genus genetic diversity—Groves 1981, 1983), limited fossil and archaeological evidence has meant that little is known about their origin, evolution, past natural distribution, and exploitation (Hardjasmita 1987; Lucchini et al. 2005).

In ISEA, several different endemic pig species (*Sus scrofa*, *S. verrucosus*, *S. barbatus*, *S. celebensis*, *S. cebifrons*, and *S. philippensis*) are found (see Table 1). The high degree of morphological similarity between them adds a significant problem to ascertaining exactly which species of *Sus* is actually present within the zooarchaeological record. To make matters worse, inter-species hybridization between introduced *S. scrofa* and the other indigenous species cited above has been claimed (Blouch and Groves 1990), and is of course something that could have occurred in the past. In fact Groves (1981) has previously claimed that the feral and domestic pigs of New Guinea at the time of European contact were hybrids of *Sus scrofa* and *Sus celebensis*.

Pigs have been linked with some of the principal models of human colonization of Oceania. For example, the “Express Train” model purports that Austronesian-speaking farmers, originating in Taiwan, spread south through Island Southeast Asia and then eastward into the Pacific, taking with them their domesticated animals that included pigs, chickens, and dogs (Bellwood 2001, 2006). Alternative theories, supported by modern human genetic studies (Oppenheimer and Richards 2001), purport that Holocene foragers of ISEA had a longstanding experience of the domestication process (Gosden 1995; Latinis 2000; Spriggs 1996)

TABLE 1. WILD *SUS* OF MAINLAND EAST ASIA AND ISLAND SOUTHEAST ASIA AND THEIR CURRENT GEOGRAPHIC DISTRIBUTION (AFTER GROVES 2007)

SPECIES NAME	COMMON NAME	CURRENT DISTRIBUTION
<i>Sus scrofa</i>	Wild boar	16 subspecies distributed throughout mainland Eurasia, Taiwan, Japan, Peninsular S.E. Asia and offshore islands, Sumatra, the Riau-Lingga archipelago, Java and along the Nusatenggara chain as far as Komodo
<i>Sus barbatus</i>	Bearded pig	Borneo, Sumatra, Bangka, the Riau archipelago, and the Malay peninsula
<i>Sus verrucosus</i>	Javan warty pig	Java, Madura, and Bawean
<i>Sus philippensis</i>	Philippine warty pig	Luzon, Mindanao, Balabac, Samar, Leyte, Bohol, and Catanduanes
<i>Sus cebifrons</i>	Visayan pig	Visayan Islands in the central Philippines (Negros, Panay, and Masbate)
<i>Sus celebensis</i>	Sulawesi warty pig	Sulawesi and offshore islands, including Peleng and Salayar, Halmahera, Timor, Roti and Lendu, Flores, and Simuleue

and so animals such as pigs would have been domesticated locally and spread in complex ways by both hunter-gatherers and farmers alike. This theory appears to be supported in some cases by the study of habitation deposits from caves, where long cultural sequences encompassing the farming transition have indicated long-lived and variable foraging systems rather than a sudden shift to farming associated with the appearance of Neolithic pottery (Anderson 2005; Barker 2005; Latinis and Stark 2005).

However, at other sites such as the well-known caves of Sarawak (Niah, Lobang, and Kudih), preliminary studies of the *Sus* remains have been used to claim the introduction of allochthonous domestic pigs during the Neolithic (Medway 1973). However, what remains to be resolved is whether these pigs represent a local domesticated variety of indigenous wild pig, or ones introduced as part of the Neolithic farming package from elsewhere.

Whatever the species (and their wild or domestic status), pigs clearly were introduced to Near then Remote Oceania by early human settlers, since (with the exception of Sulawesi) none of the islands east of the Wallace Line possessed endemic populations of pigs (Groves 1981, 1983). The limited zooarchaeological evidence that exists from Wallacea suggests that pigs first appear in the Moluccas (Bellwood and White 2005), Flores (Morwood et al. 2004), and Timor (Glover 1986), during the Holocene, and their remains are associated with the arrival of the “Neolithic cultural package.”

Farther east in New Guinea, there is still much debate as to precisely when and how pigs arrived (Green 2000; Groves 1997; Lucchini et al. 2005). The broad consensus is that the appearance of pig is a direct consequence of human introduction as a domestic (or at least managed) animal, although there are some who still maintain that pigs might just as easily have arrived early on New Guinea without human assistance (Bulmer 1975, pers. comm.). The broader question of the precise origins (and subsequent dispersal routes through ISEA) of the Neolithic cultures of Near and Remote Oceania remains the subject of much heated debate. Models of the origins and spread of Lapita (the immediate ancestors of the Polynesians and other Oceanic cultures) that focus upon the entire Lapita cultural and ecological package moving from Taiwan to the Pacific with little interaction, are contrasted by others that identify broader regions and possibly multiple origins of the various cultural components including pigs. The degree to which the various cultural and biological elements reflect dispersal has also been questioned, as has the extent to which these various components were dispersed as a single unit (Hurles et al. 2003).

New techniques (principally geometric morphometrics and genetics) mean that animals like the pig—a significant component of Neolithic human dispersal and exchange networks within and beyond ISEA—can now contribute new and important information to this wider biological and archaeological debate.

TOOTH SHAPE, *SUS* TAXONOMY, AND DISPERSAL

Morphological change—principally the differences in size and shape of teeth and bones—has been the traditional zooarchaeological criteria used to separate closely related species and also to detect the early stages of animal adaptation to the human environment, i.e., the domestication process. Of course size can be affected by a range of non-human factors including climate, but where humans

become the principal controlling agent, the picture becomes far more complex. As a consequence, one of the key methodological challenges still facing zooarchaeologists is how to access and separate the phenotypic expression of taxonomic status, and adaptation to the essentially new human environment early in the commensalism/domestication process.

The technique of geometric morphometrics can achieve this by providing detailed mathematical descriptions of biological organism, allowing the separate analysis of the shape component of morphological form (Kendall 1977), which is importantly wholly independent of size. This distinction between the two parameters of morphology (i.e., scale and shape), not possible using traditional biometrical techniques, allows environmental (e.g., diet, climate, temperature, latitude, etc.) and genetic factors (e.g. selective pressure, genetic drift, bottleneck, and founder events) involved in morphological change, to be separated.

Teeth are often the most common (and sometimes the only complete) biological structure recovered from archaeological assemblages. They are formed deep within the jaw and are only exposed to functional stress once mineralized and fully erupted. Unlike bone, once mineralized, enamel cannot be remodeled, so all functional adaptation must be brought into the genome through natural selection (Koenigswald and Pfretzschner 1991). Consequently, tooth morphology is far less influenced by environmental factors than that of bone during development and for that reason will less likely show a wide range of phenotypic variation linked with environmental factors and thus better reflect genetic variation.

Recent use of this approach using outline analyses of molar teeth (Caumul and Polly 2005; Cucchi et al. 2006; Michaux et al. 2007; Renaud et al. 2006; Macholan M. 2006) has shown that these techniques can be used to clearly reveal the genetic component of dental variation in a range of small mammals. This first zooarchaeological application of molar shape analysis has demonstrated that the method is powerful enough to segregate both species and subspecies, as well as revealing a clear phylogeographic component to morphological variation (Cucchi 2005; Cucchi et al. 2002).

In the case of *Sus*, preliminary application of molar shape analysis (using Eigenshape values) has previously been employed to study dental variation (Warman 2000, 2005). However, in this early attempt, results were ambiguous, almost certainly related to the choice of the teeth analyzed (DP₄ and M₁), both of which suffer from important and extreme variation due to both occlusal wear and abrasion from adjacent teeth. Our own research using the lower third molar (M₃), clearly shows that tooth crowns do not just become shorter or narrower, but in fact can radically alter their morphological expression. Thus, to describe in detail the truly complex form of the polycusp molar of *Sus scrofa*, and observe its evolution through time, the classical morphometrical approach based on linear measurements is unfortunately far too crude and largely inappropriate. A detailed study of tooth morphology (using the geometric morphometric technique of outline analysis) was, therefore, employed to further explore the true taxonomic status of Wallacean pigs and to see if specific dental morphotypes could be associated with feral and/or domesticated pigs. Specific objectives were to resolve the status of the so-called “wild” pigs of New Guinea and the Holocene pig remains from Liang Bua cave, Flores.

Among the three permanent molars of *Sus* dentition, the third lower molar

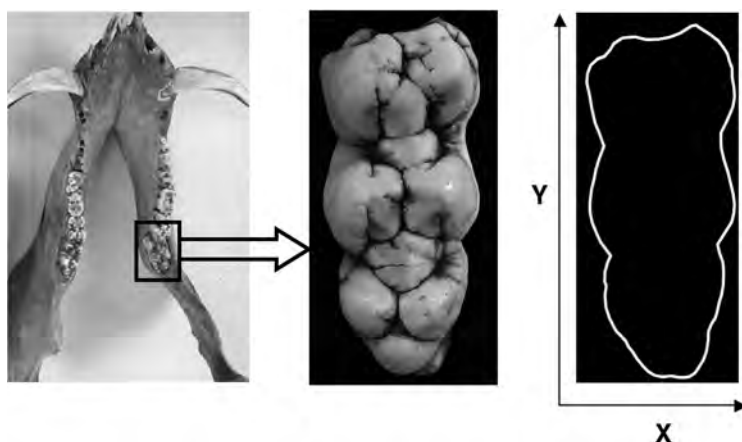


Fig. 1. a: Photo of *Sus* mandibular tooth row showing position of third molar (M_3); b: Occlusal view of complete M_3 ; c: External outline of the two dimensional projection of the M_3 .

(M_3) was specifically chosen because it is the largest, most morphologically complex molar, exhibiting more variability, particularly in the posterior lobe (talonid); and it is the final permanent tooth to develop and erupt, therefore, retaining its morphological integrity for longer. The morphological variation seen in the M_3 of pigs can be readily described by the two-dimensional projection of the tooth viewed from its occlusal surface (Fig. 1). The outline of this two-dimensional projection can successfully register continuous variation on molariform teeth, as demonstrated by previous studies of murine (Cucchi et al. 2002, 2006; Renaud and Michaux 2004; Renaud et al. 2006) and suid teeth (Larson et al. 2007; Cucchi et al. Forthcoming). In suid molars, the outline form importantly does not vary greatly with occlusal attrition, thus providing a morphological signature that is largely independent of both the age of the individual and the age profile of the population (Renaud 2005).

Modern comparative specimens used in the study consisted of 137 mandibular M_3 specimens from museum collections around the world and included the main *Sus* taxa identified by Groves (1981, 1983, 2001), i.e., *Sus scrofa* sp., *Sus barbatus*, *Sus verrucosus*, *Sus celebensis*, and *Sus philippensis*. Six archaeological pig specimens from Liang Bua Flores were also analyzed (for full details of methodology and specimens used see Larson et al. [2007] and Cucchi et al. Forthcoming).

Two-dimensional images of the M_3 in occlusal view were captured using a digital camera. One hundred equally spaced points on each individual outline were semi-automatically sampled and their coordinates recorded using an optical image analyzer. The starting point of the outline was defined at the junction of the distolingual cusp (entoconid) and the Talonid (hexaconid). An elliptic Fourier transform (EFT) (Crampton 1995; Ferson et al. 1985; Kuhl and Giardina 1982; Rohlf and Archie 1984) was then performed on x - and y - coordinates of the 100 outline points using biostatistics software. This method is based on a separate Fourier decomposition of the incremental changes of the x - and y -coordinates as a function of the cumulative length along the outline. Each function (x - and y -

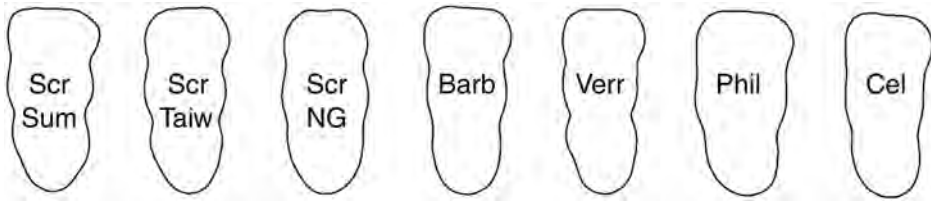


Fig. 2. Reconstructed average M_3 shape of recent ISEA *Sus* species used in the analysis. Scr = *Sus scrofa* (Sum—Sumatra; Taiw—Taiwan; NG—New Guinea). Barb = *Sus barbatus*; Verr = *S. verrucosus*; Phil = *S. philippensis*; Cel = *S. celebensis*.

variations) was decomposed into a sum of trigonometric functions of decreasing wavelength (i.e. harmonics). Hence, each harmonic corresponds to four coefficients: A_n and B_n for x , and C_n and D_n for y , defining an ellipse in the xy -plane. These coefficients are the shape descriptors of the outline and are the input variables for multivariate statistics.

In order to compare molar outline shape variation, information regarding size and orientation must be standardized. Size standardization is performed by division of the coordinates by the square root of the area of the first ellipse defined by the first harmonic. The long axis of this ellipse is also used to standardize the orientation of the different specimens. The coefficients of the first harmonic corresponding to residuals after standardization should not be included in subsequent statistical analyses (Crampton 1995). Shape changes are visually depicted by reconstructed outlines. An outline can be reconstructed from any set of Fourier coefficients following the inverse Fourier method. “Mean outlines,” reconstructed on the averaged Fourier coefficients per taxon, were used to visualize shape differences between the different species groups (see Fig. 2).

Principal components analysis calculated from elliptic Fourier coefficients extracted from third lower molar (M_3) occlusal outlines of the recent pigs have shown a robust separation of tooth shape signatures between the *Sus* specimens from Sundaland and Wallacea, as well as a further complete separation of the pigs from New Guinea (Fig. 3). These tooth shape data confirm that the third-lower-molar shape phenetic relationships are congruent with the available phylogenetic survey of ISEA wild pigs obtained from mtDNA nucleotides (Larson et al. 2005; Lucchini et al. 2005), and confirms the presence of a phylogenetic signature within the morphological variation of *Sus* teeth, a fact previously only observed in rodents such as *Marmota* (Caumul and Polly 2005), *Apodemus* (Renaud 2005), and *Mus* (Cucchi 2005; Macholan et al. 2006).

The significant phenotypic divergence between the so-called “wild pigs” (*Sus scrofa papuensis*) of New Guinea and other Sunda and Wallacean morphotype groups can be readily explained by the large genetic distance between the New Guinea (“Pacific Clade”) and the ISEA pigs revealed by Larson et al. (2005, 2007; and below). It is clear from both the tooth shape and mtDNA data that their phylogeography could not be related to the same natural dispersal process as the Wallacean pigs. Even if pigs are good swimmers, the nearest stepping-stone island to New Guinea during the last glacial maximum (LGM) was 65 km (Golson and Hughes 1980; Green 1994; Voris 2000), which make the proposed natural dispersal of pigs to New Guinea (suggested by e.g., Bulmer 1975) highly

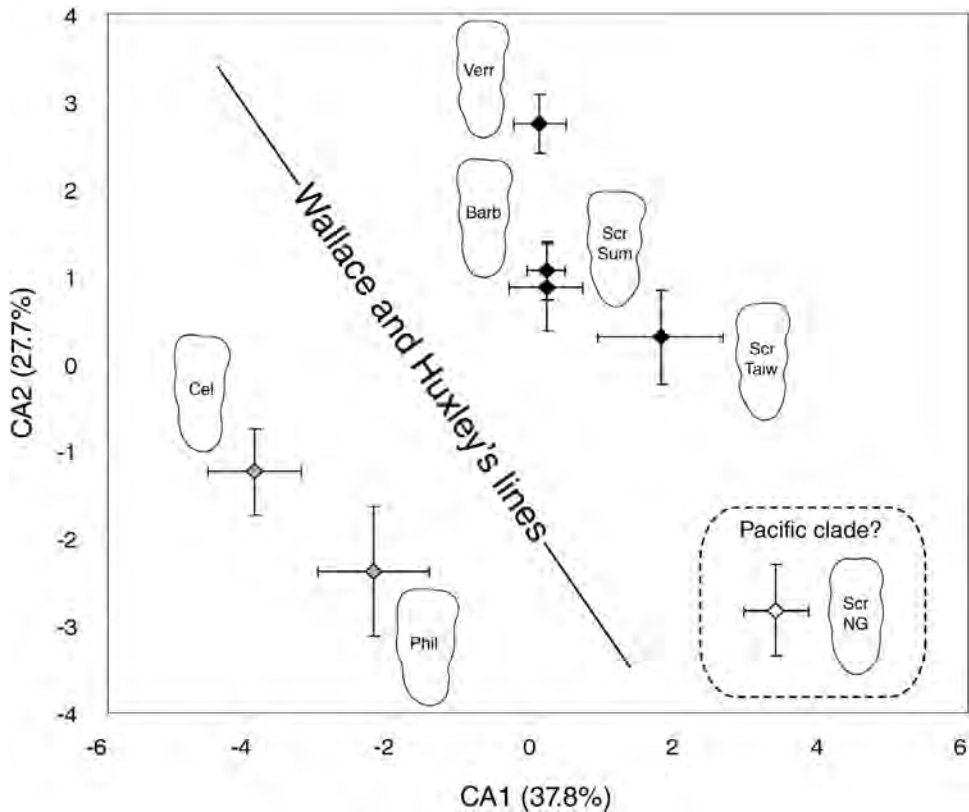


Fig. 3. Shape differentiation of the M_3 of ISEA wild pigs. First and second canonical axes (CA1/CA2) with mean outline for each taxa. Tooth outlines correspond to those in Figure 2.

improbable. On the basis of these data, human agency is clearly the most likely mechanism for pig translocation to New Guinea.

An interspecific hybrid (*Sus scrofa vittatus* × *Sus celebensis*) as the basis to explain the anthropogenic status and morphological divergence of New Guinea pigs (Groves 1983, 1995) is also not supported by our current morphometric data or the modern mtDNA phylogenetic analysis, all of which confirm the maternal affinity of the New Guinea pigs as a form of *Sus scrofa*. So why is the *Sus scrofa* dental morphotype of recent New Guinea pigs obviously different to their *S. scrofa* counterparts from ISEA? We propose that this unique tooth shape reflects the fact that the New Guinea pig populations are descended from introduced primitive domestic stock (Mohr 1960), and that the distinctive enamel crown shape reflects the intense selection pressures associated with the domestication process of their ancestors, i.e., an initial adaptation to an anthropogenic environment in relative breeding isolation (Arbuckle 2005). Their continued isolation from a sufficient migrant flow further prevented their assimilation with the wild *S. scrofa* pool of Sundaland.

Tooth shape analysis of the archaeological pigs from Holocene deposits at Liang Bua, Flores has also thrown further light on the complex story of pig

taxonomy and human mediated dispersal. Comparison with recent *Sus* tooth morphotypes show the presence of two pig taxa at the site, i.e., an endemic Wallacean type and several sharing the unique tooth morphotype of the recent New Guinea pigs (see Fig. 3 in Larson et al. 2007). Tooth shape analysis (Fig. 3) also indicates that the Flores archaeological and recent pigs are most closely related to those from New Guinea. These data show that two separate human introductions of *Sus* to the island of Flores occurred during the Holocene, one involving an endemic *Sus* species (*S. celebensis*), the other involving the arrival of domesticated *S. scrofa*. The discussion of the mitochondrial DNA evidence below provides further indisputable support for these conclusions.

GENETICS, *SUS* TAXONOMY, AND DISPERSAL

A recent phylogeographic study of modern wild, feral, and domestic *Sus* mtDNA across Eurasia (Larson et al. 2005) analyzed an alignment of 663 base pairs of the control region of mitochondrial DNA from 686 wild and domestic pigs from around the world. A consensus tree, built using a Bayesian Monte Carlo-Markov Chain, provided a structure which revealed a remarkably strong phylogeographic signal across the natural range of Eurasian and ISEA *Sus*. The resulting phylogenetic tree revealed 14 clades that were geographically restricted to specific regions of the old world. Over 98 percent of samples from a specific place possessed genetic signatures correlated with that location. Less than 2 percent of samples possessed signatures that violated this correlation, indicating that these were likely the result of human-mediated introgression and/or dispersal, an extremely important observation, and one which provided the impetus for our ongoing studies focused on ISEA and Oceania.

Aside from identifying multiple centers of pig domestication across the globe, these data rather tantalizingly revealed the presence of a unique *Sus scrofa* haplogroup ("Pacific Clade"), which (although limited in overall numbers of samples) included recent museum specimens of pigs collected from Halmahera (in the Moluccas), New Guinea, and several Pacific islands including Hawai'i and Vanuatu. Although it was realized that these unique data had the potential to reveal more about human dispersal trajectories within ISEA and Oceania, the absence from this haplogroup of other species of ISEA *Sus* from Western Indonesia, or any wild or domestic pig specimens from mainland Asia, meant that the origin and dispersal trajectory of this clade could not be identified on the basis of the data collected during the original study.

In order to further investigate the geographic origin of the Pacific Clade and its distribution within ISEA, Near and Remote Oceania, a more extensive study of modern (and some archaeological) specimens was undertaken (Larson et al. 2007). Extraction and sequencing of the same 663 base pairs (bp) of the mitochondrial control region was undertaken from an additional 243 recent wild, feral, and domestic pigs from across ISEA and mainland Southeast Asia. These included 160 from Malaysia, the Greater Sunda islands (Sumatra, Java, Sulawesi, and numerous, smaller adjacent islands) and Lesser Sunda chain (Bali, Lombok, Sumbawa, Sumba, Flores, and Timor), other islands (including the Moluccas); 57 from the Philippines; and 9 from selected Polynesian islands. The 663 bp fragment was also determined for three archaeological pig samples, whilst a further 23 were characterized with three diagnostic ~120 bp fragments using appropriate

ancient DNA methods including independent replication (Cooper and Poinar 2000; Shapiro et al. 2004). An additional 512 pig sequences from GenBank were used in phylogenetic analyses performed with Bayesian Monte Carlo–Markov chain (MCMC) (Ronquist and Huelsenbeck 2003) methodology. Thus, a total of 755 specimens were included in the study.

The overall structure of the resulting phylogenetic tree revealed a polytomy of clades within a basal cluster that included all *Sus* species endemic to ISEA (*S. scrofa*, *S. verrucosus*, *S. barbatus*, *S. celebensis*, and *S. philippensis*). From this, a strongly supported branch (posterior probability of 100) leads to a more derived cluster consisting only of *Sus scrofa* specimens from mainland Asia, and to an additional very strongly supported (posterior probability of 100), group that includes all pigs of the so-called “Pacific Clade” identified by Larson et al. (2005).

While the position of the Pacific Clade on the phylogenetic tree clearly confirmed its taxonomic distinction as *Sus scrofa* and its mainland Asian (not ISEA) origin, the geographic distribution of the specimens within this cluster is perhaps more intriguing (Fig. 4). The most westerly representatives of the Pacific Clade are two wild boar specimens from Viet Nam. In addition, four Pacific Clade pigs are from Sumatra and Java (islands on which indigenous wild populations of *Sus* existed well before the Neolithic), whilst Pacific Clade pigs also make up 15 of 19 specimens from eight islands east of the Wallace Line in the Lesser Sunda chain and the Moluccas, as well as all 17 samples from New Guinea. This relationship clearly indicates that the so-called “wild pigs” of New Guinea are associated with the dispersal of mainland Southeast Asian pigs, thus making them the feral progeny of domesticated Pacific Clade individuals originally introduced by farmers to islands east of the Wallace Line, a conclusion wholly supported by our molar outline data.

Perhaps more important for assessing the trajectories of human-mediated pig dispersal from mainland East Asia into and within ISEA is the fact that no Pacific Clade pigs were identified from Taiwan (even though samples included both native wild and domestic modern pigs and an ancient domestic sample), from the 40 wild samples from the Philippines (identified as endemic *Sus philippensis*), or from the 17 introduced domestic samples from two central Philippine islands (Panay and Cebu).

In order to provide at least some temporal context for pig dispersal in Oceania, ancient DNA was also successfully extracted from five archaeological pig specimens from purportedly pre-European contact sites in Polynesia (from Tubuai, Hanamiai in the Marquesas, and the Tangatatau rockshelter in Mangaia), the Reef Islands (site RF-3), and Mussau (site EKQ). Although somewhat limited in number and geographic and temporal coverage, sequencing revealed all of these specimens to be Pacific Clade pigs, unequivocally linking them with Polynesian dispersal and, by association, with that of the earlier Lapita cultural complex, traditionally associated with the first peopling of Remote Oceania (Kirch 2000).

Analyses of a further six ancient mtDNA sequences extracted from archaeological *Sus* specimens from Liang Bua Cave (Flores) demonstrated two separate human-mediated dispersals of domesticated *Sus scrofa* (Pacific Clade pigs) and one involving an endemic Wallacean *Sus* species (*Sus celebensis*) confirming conclusions drawn from molar shape data. Since *Sus celebensis* is endemic only to Sulawesi (assuming it was not naturally distributed beyond Sulawesi in the early Holocene), its presence at Liang Bua on Flores as early as 7000 B.P. (based upon



Fig. 4. Map showing the geographic distribution of specimens with the “Pacific Clade” haplotype (after Larson et al. 2007). Crosses represent islands on which at least one specimen possessing the haplotype was identified. The cross in mainland Southeast Asia represents the two mainland Asian wild boar samples in Viet Nam that possessed this haplotype. Regions on the map are: Mal—peninsular Malaysia; Bor—Borneo; Sum—Sumatra; Jav—Java; Sul—Sulawesi; F—Flores; T—Timor; Mol—Moluccas Islands; PI—Philippines; Tai—Taiwan; NG—New Guinea. The dashed line labeled WL represents the Wallace Line. The Greater Sunda Islands consist of Sumatra, Java, Borneo, and Sulawesi, though despite reasonable sampling on all four islands, Pacific Clade pigs were only found on Sumatra and Java. The Lesser Sunda Islands consist of the chain of smaller islands extending in an arc to the east of Java toward New Guinea, and Pacific Clade pigs were found on every island in the Lesser Sunda chain from which pig samples were analyzed. The Wallace Line runs between the Lesser Sunda Islands of Bali and Lombok, located just to the east of Java. Lastly, Pacific Clade pigs were identified on three islands in the Moluccas chain located between Sulawesi and New Guinea.

the stratigraphic association of this earliest pig specimen and associated C^{14} dates of charcoal) suggests an early Holocene translocation of this wild species by humans. Perhaps it was even domesticated during the early Holocene, as previously suggested by Groves (1983).

DISCUSSION

Current views place early pig (*Sus scrofa*) domestication in central and southern China (and perhaps even in the upper reaches of the Yellow River) at around 8000 B.P. (Jing and Flad 2002). The subsequent dispersal of early rice agriculturalists into Peninsular Southeast Asia and Taiwan from China has traditionally been

viewed as a wave of immigration from a core region into areas where indigenous hunter-gatherers had existed for millennia (Higham 2002), although empirical evidence for the origins and dispersal of domesticated pigs within these regions is largely absent. Furthermore, the paucity of excavated Neolithic sites in Indonesia, and the limited studies undertaken in the Philippine archipelago, has meant that faunal assemblages in these key regions are yet to contribute significantly to debates surrounding Austronesian expansion and dispersal.

However, our data showing the distribution of various *Sus* morphotypes and haplotypes within mainland Asia, ISEA, and Oceania, imply that the existing models of Austronesian dispersal (certainly those involving pigs) are perhaps more complex than previously considered. In particular, the distribution and frequency of Pacific Clade pigs provides an explanation of pig domestication and dispersal that perhaps contradicts some of the existing traditional models. The complete absence of Pacific Clade haplotypes in modern and ancient specimens from mainland China, Taiwan, the Philippines, Borneo, and Sulawesi suggests that any human dispersal from Taiwan to the New Guinea region via the Philippines—as purported by the traditional “Out of Taiwan” model—did not include the movement of domestic pigs from those regions. Thus the origin and trajectory of the pigs associated with both the Lapita cultural complex, and the pigs subsequently transported to Polynesia, clearly reside elsewhere. In this context, the previously mentioned appearance of pigs in the archaeological record of the northern Moluccas after 3500 B.P. (Bellwood and White 2005) is significant. The Neolithic settlers who arrived on these islands and subsequently moved into Oceania must have acquired pigs prior to this date from somewhere other than Taiwan and the Philippines. Our data suggests this most likely occurred in southern Wallacea, a region where significant cultural change appears to have taken place during the initial spread of the Neolithic (Spriggs 2003), and where our data show high frequencies of introduced domestic pigs exclusively possessing the Pacific signature.

The restricted distribution of Pacific Clade pigs in mainland Southeast Asia, Sumatra, Java, the Lesser Sunda Islands, and New Guinea incontrovertibly links the Southeast Asian mainland in the west with Polynesia in the east through the Greater and Lesser Sunda Islands and New Guinea. In view of this, the most parsimonious explanation for such a distribution is a west-to-east dispersal trajectory for domesticated Southeast Asian mainland pigs along this route. The peninsular Southeast Asian origin of the Pacific Clade pigs is further supported by the significant genetic variation present in wild and domestic pigs from the region, a pattern previously employed to propose an independent center of pig domestication in peninsular Southeast Asia (Hongo et al. 2002). In addition, a recent genetic study of modern chickens (Liu et al. 2006)—another key component of the mid-Holocene dispersal and of the Lapita cultural complex—also identified Southeast Asia (specifically Viet Nam, Burma, and Thailand) as a likely geographic center of early chicken domestication. This raises the possibility that the earliest domestic chickens and pigs to arrive in ISEA and Oceania derive from the same broad geographic source, and may perhaps even have formed part of the same Neolithic dispersal complex.

Our data also clearly show that the vast majority of so-called “wild” pigs currently found in the Lesser Sunda chain and New Guinea (East of the Wallace Line) are descendants of introduced domesticated *Sus scrofa* who, in turn, trace

their ancestry to mainland Southeast Asia. Since Pacific Clade haplotypes have been found in almost all archaeological pigs so far sampled from prehistoric and historic sites in Melanesia and Polynesia, Pacific Clade pigs must, therefore, be intimately associated with the Lapita and subsequent Polynesian dispersal episodes into Near and Remote Oceania.

A separate, probably later, human-mediated dispersal involved other mainland East Asian domestic pigs moving through the Philippines to Micronesia (Larson et al. 2007), while a much earlier one (c. 7000 B.C.) involved the translocation of the Sulawesi warty pig (*Sus celebensis*) at least to the island of Flores.

CONCLUSIONS

The ongoing development and implementation of geometric morphometric and biomolecular techniques are providing zooarchaeology with powerful new tools which can be used to re-visit some of the fundamental questions in the field. Perhaps even more significant is the fact that they are underlining and enhancing the role that bioarchaeological data play in addressing more fundamental archaeological questions beyond mere dietary reconstruction and subsistence strategies. Using the remains of one of the most commonly occurring fossil mammals, the pig, we have been able to throw new, and somewhat controversial, light upon the study of human dispersal in ISEA and Oceania. Through such interdisciplinary approaches, zooarchaeology can also strengthen its link with biosystematics and evolutionary biology, enabling us to further understand the complex evolutionary and anthropogenic history of wild pigs, animals that were key components in the development of human societies worldwide.

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REFERENCES CITED

- ANDERSON, D.
2005 The use of caves in Peninsular Thailand in the late Pleistocene and early and middle Holocene. *Asian Perspectives* 44:137–153.
- ARBUCKLE, B. S.
2005 Experimental animal domestication and its application to the study of animal exploitation in prehistory, in *The first steps of animal domestication*, ed. J. D. Vigne, D. Helmer, and J. Peters. Oxford: Oxbow Books.
- BANKS, E.
1931 A popular account of the mammals of Borneo. *Journal of the Malaysian Branch of the Royal Asiatic Society* 9:24.
- BARKER, G.
2005 The archaeology of foraging and farming at Niah Cave, Sarawak. *Asian Perspectives* 44:90–106.

- BELLWOOD, P.
 2001 Early agriculturalist population diaspora? Farming, languages, and genes. *Annual Review of Anthropology* 30:181–207.
 2006 Asian farming diaspora? Agriculture, languages, and genes in China and Southeast Asia, in *Archaeology of Asia*, ed. M. T. Stark. Oxford: Blackwell Publishing.
- BELLWOOD, P., AND P. WHITE
 2005 Domesticated pigs in eastern Indonesia. *Science* 309(5733):381; author reply 381.
- BLOUCH, R. A., AND C. P. GROVES
 1990 Naturally occurring suid hybrid in Java. *Zeitschrift für Säugetierkunde* 55:270–275.
- BULMER, S.
 1975 Settlement and economy in Prehistoric New Guinea Highlands. *Journal de la Société des Océanistes* 31:7–75.
- CAUMUL, R., AND P. D. POLLY
 2005 Phylogenetic and environmental components of morphological variation: Skull, mandible and molar shape in Marmots (*Marmota*, Rodentia). *Evolution* 59:2460–2472.
- COOPER, A., AND H. N. POINAR
 2000 Ancient DNA: Do it right or not at all. *Science* 289(5482):1139–1139.
- CRAMPTON, J. S.
 1995 Elliptic Fourier shape analysis of fossil bivalves: some practical considerations. *Lethaia* 28:179–186.
- CUCCHI, T.
 2005 *Le commensalisme murin et les premières sociétés méditerranéennes*. Paris: Muséum National d'Histoire Naturelle 307.
- CUCCHI, T., M. FUJITA, K. DOBNEY
 Forth- New insights into pig taxonomy, domestication and human dispersal in Islands South East coming Asia: Molar shape analysis of *Sus* remains from Niah caves (Sarawak). *International Journal of Osteoarchaeology*.
- CUCCHI, T., A. ORTH, J.-C. AUFRAY, S. RENAUD, L. FABRE, J. CATALAN, E. HADJISTERKOTIS, F. BONHOMME, AND J.-D. VIGNE
 2006 A new endemic species of the subgenus *Mus* (Rodentia, Mammalia) on the Island of Cyprus. *Zootaxa* 1241:1–36.
- CUCCHI, T., J.-D. VIGNE, J.-C. AUFRAY, P. CROFT, AND E. PELTENBURG
 2002 Introduction involontaire de la souris domestique (*Mus musculus domesticus*) à Chypre dès le Néolithique précéramique ancien (fin IX^e et VIII^e millénaire av. J.-C.). English abridged version. *Comptes Rendus Palevol* 1:235–241.
- FERSON, S., F. J. ROHLF, AND R. K. KOEHN
 1985 Measuring shape variation of two dimensional outlines. *Systematic Zoology* 34:59–68.
- GLOVER, I.
 1986 *Archaeology in Eastern Timor 1966–1967*. Canberra: Australian National University Press.
- GOLSON, J., AND P. J. HUGHES
 1980 The appearance of plant and animal domestication in New Guinea. *Journal de la Société des Océanistes* 69:294–303.
- GOSDEN, C.
 1995 Arboriculture and agriculture in coastal Papua New Guinea. *Antiquity* 69:807–817.
- GREEN, R. C.
 1994 Changes over time, in *The origins of the first New Zealanders*: 19–51, ed. D. Sutton. Auckland: Auckland University Press.
 2000 Lapita and the cultural model for intrusion, integration and innovation, in *Australian archaeologist: Collected papers in honour of Jim Allen*: 372–392, ed. A. Anderson and T. Murray. Canberra: Coombs Academic Publishing.
- GROVES, C. P.
 1981 *Ancestors of the pigs: Taxonomy and phylogeny of the genus Sus*. Department of Prehistory, Research School of Pacific Studies, Australian National University, Canberra.
 1983 Pigs east of the Wallace Line. *Journal de la Société des Océanistes* 39:105–119.

- 1995 Domesticates and commensal mammals of Austronesia and their histories, in *Austronesian: Historical and comparative perspectives*: 152–163, ed. P. Bellwood, J. J. Fox, and D. Tryon. Canberra: Australian National University Press.
- 1997 Taxonomy of wild pigs (*Sus*) of the Philippines. *Zoological Journal of the Linnean Society* 120(2): 163–191.
- 2001 Taxonomy of wild pigs of Southeast Asia. *Asian Wild Pigs News* 1.
- HARDJASASMITA, H. S.
1987 Taxonomy and phylogeny of the Suidae (Mammalia) in Indonesia. *Scripta Geol.* 85:1–68.
- HIGHAM, C.
2002 In *Examining the farming/language dispersal hypothesis*, ed. P. Bellwood and C. Renfrew. Cambridge: The McDonald Institute for Archaeological Research.
- HONGO, H., N. ISHIGURO, T. WATANOBE, N. SHIGEHARA, T. ANEZAKI, V. T. LONG, D. V. BINH, N. T. TIEN, AND N. H. NAM
2002 Variation in mitochondrial DNA of Vietnamese pigs: Relationships with Asian domestic pigs and Ryukyu wild boars. *Zoological Science* 19(11): 1329–1335.
- HOSE, C., AND W. MCDUGALL
1901 The relations between men and animals in Sarawak. *The Journal of the Anthropological Institute of Great Britain and Ireland* 31: 173–213.
- HURLES, M. E., E. MATISOO-SMITH, R. D. GRAY, AND D. PENNY
2003 Untangling Oceanic settlement: The edge of the knowable. *Trends Ecol Evol* 18(10): 531–540.
- JING, Y., AND R. K. FLAD
2002 Pig domestication in ancient China. *Antiquity* 76: 724–732.
- KENDALL, D.
1977 The diffusion of shape. *Advances in Applied Probability* 9: 428–430.
- KIRCH, P. V.
2000 *On the road of the winds: An archeological history of the Pacific Islands before European contact*. Berkeley, Los Angeles, and London: University of California Press.
- KOENIGSWALD, W. U., AND H. U. PERETZSCHNER
1991 Biomechanics in the enamel of Mammalian teeth, in *Constructional morphology and evolution*: 113–140, ed. N. Schmidt-Kittler and K. Vogel. Berlin and New York: Springer-Verlag.
- KUHL, F. P., AND C. R. GIARDINA
1982 Elliptic Fourier features of a closed contour. *Computer Graphics and Image Processing* 18: 259–278.
- LARSON, G., T. CUCCHI, M. FUJITA, E. MATISOO-SMITH, J. ROBINS, A. ANDERSON, B. ROLET, M. SPRIGGS, G. DOLMAN, T. H. KIM, E. RANDI, D. DOHERTY, R. AWE DUE, R. BOLT, T. DJUBIAN-TONO, B. GRIFFIN, M. INTOH, E. KEANE, P. KIRCH, K.-T. LI, M. MORWOOD, L. M. PEDRINA, P. J. PIPER, R. J. RABETT, P. SHOOTER, G. VAN DEN BERGH, E. WEST, S. WICKLER, J. YUAN, A. COOPER, AND K. DOBNEY
2007 Phylogeny and ancient DNA of *Sus* provides new insights into Neolithic expansion in Island Southeast Asia and Oceania. *Proceedings of the National Academic Science* 104(12): 4834–4839.
- LARSON, G., K. DOBNEY, U. ALBARELLA, M. FANG, E. MATISOO-SMITH, J. ROBINS, S. LOWDEN, H. FINLAYSON, T. BRAND, E. WILLERSLEY, P. ROWLEY-CONWY, L. ANDERSSON, AND A. COOPER
2005 Worldwide phylogeography of wild boar reveals multiple centers of pig domestication. *Science* 307: 1618–1621.
- LATINIS, D. K.
2000 The development of subsistence system models for Island Southeast Asia and Near Oceania: The nature and role of arboriculture and arboreal-based economies. *World Archaeology* 32: 41–67.
- LATINIS, D. K., AND K. STARK
2005 Cave use variability in central Maluku, eastern Indonesia. *Asian Perspectives* 44: 119–136.
- LIU, Y. P., Q. ZHU, AND Y. G. YAO
2006 Genetic relationship of Chinese and Japanese gamecocks revealed by mtDNA sequence variation. *Biochemical Genetics* 44: 18–28.

- LUCCHINI, V., E. MEIJAARD, C. DIONG, C. P. GROVES, AND E. RANDI
 2005 New phylogenetic perspectives among species of Southeast Asian wild pig (*Sus* sp.) based on mtDNA sequences and morphometric data. *Journal of Zoology* 266:25–35.
- MEDWAY, L.
 1973 The antiquity of domesticated pigs in Sarawak. *Journal of the Malaysian Branch of the Royal Asiatic Society* 46:169–178.
- MICHAUX, J., T. CUCCHI, S. RENAUD, F. GARCIA-TALAVERA, AND R. HUTTERER
 2007 Evolution of an invasive rodent on an archipelago as revealed by molar shape analysis: The house mouse in the Canary Islands. *Journal of Biogeography* doi: 10.1111/j.1365-2699.2007.01701.x:
- MOHR, E.
 1960 Wilde schweine. *Neue Brehm-Bucherei* 247:139.
- MORWOOD, M. J., R. P. SOEJONO, R. G. ROBERTS, T. SUTIKNA, C.S.M. TURNER, K. E. WESTAWAY, W. J. RINK, J. X. ZHAO, G. D. VAN DEN BERGH, R. A. DUE, D. R. HOBBS, M. W. MOORE, M. I. BIRD, AND L. K. FIFIELD
 2004 Archaeology and age of a new hominin from Flores in eastern Indonesia. *Nature* 431(7012):1087–1091.
- OLIVER, W.L.R., AND I. L. BRISBIN
 1993 Introduced and feral pigs: Problems, policy and priorities, in *Pigs, peccaries and hippos status survey and action plan*, ed. W.L.R. Oliver. IUCN.
- OPPENHEIMER, S., AND M. RICHARDS
 2001 Fast trains, slow boats, and the ancestry of the Polynesian islanders. *Science Progress* 84:157–168.
- RENAUD, S., AND J. MICHAUX
 2004 Parallel evolution in molar outline of murine rodents: The case of the extinct *Malpaisomys insularis* (Eastern Canary Islands). *Zoological Journal of the Linnean Society* 142:555–572.
- RENAUD, S., J.-C. AUFRAY, AND J. MICHAUX
 2006 Conserved phenotypic variation pattern, evolution along lines of least resistance, and departure due to selection in fossil rodents. *Evolution* 60(8):1701–1717.
- ROHLF, F. J., AND J. W. ARCHIE
 1984 A comparison of Fourier methods for the description of wing shape in mosquitoes (Diptera: Culicidae). *Systematic Zoology* 33.3:302–317.
- RONQUIST, F., AND J. P. HUELSENBECK
 2003 MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19(12):1572–1574.
- ROSMAN, A., AND P. G. RUBEL
 1989 Stalking the wild pig: hunting and horticulture in Papua New Guinea, in *Farmers as hunters: The implication of sedentism*: 27–36, ed. S. Kent. Cambridge: Cambridge University Press.
- SHAPIRO, B., A. J. DRUMMOND, A. RAMBAUT, M. C. WILSON, P. E. MATHEUS, A. V. SHER, O. G. PYBUS, M.T.P. GILBERT, I. BARNES, J. BINLADEN, E. WILLERSLEV, A. J. HANSEN, G. F. BARYSHNIKOV, J. A. BURNS, S. DAVYDOV, J. C. DRIVER, D. G. FROESE, C. R. HARRINGTON, G. KEDDIE, P. KOSINTSEV, M. L. KUNZ, L. D. MARTIN, R. O. STEPHENSON, J. STORER, R. TEDFORD, S. ZIMOV, AND A. COOPER
 2004 Rise and fall of the Beringian steppe bison. *Science* 306(5701):1561–1565.
- SPRIGGS, M.
 1996 Early agriculture and what went before in Island Melanesia: Continuity or intrusion?, in *The origins of spread of agriculture and pastoralism in Eurasia*: 524–537, ed. D. R. Harris. London: UCL Press.
 2003 Chronology of the Neolithic transition in Island Southeast Asia and the Western Pacific. A view from 2003. *The Review of Archaeology* 24(2):57–80.
- VORIS, H. K.
 2000 Maps of Pleistocene sea levels in South East Asia: Shorelines, river systems and time durations. *Journal of Biogeography* 27:1153–1167.

WARMAN, S. M.

- 2000 *Morphometric investigation of dental variation to examine genetic relationship between pig populations*. London: University College London, 500.
- 2005 Two novel methods for the study of dental morphological variation in *Sus scrofa*, in order to identify separate breeding groups within archaeological assemblages, in *The first steps of animal domestication*: 61–78, ed. J. D. Vigne, D. Helmer, and J. Peters. Oxford: Oxbow Books.

ABSTRACT

This paper undertakes a major survey of the genus *Sus* from Island Southeast Asia and specifically attempts to re-examine the taxonomic status of the pigs of Wallacea, in order to re-evaluate the complex evidence for human mediated dispersal. This was undertaken using the combined approach of tooth outline and mitochondrial DNA analysis. The data provide clear evidence for three dispersal events: The first involved domesticated pigs, originating from wild *Sus scrofa* stock in mainland Southeast Asia, being introduced to the Greater and Lesser Sunda Islands, to the Mollucas, New Guinea, and Oceania. Archaeological specimens clearly link these pigs with the Lapita and subsequent Polynesian dispersals. Since the pigs on New Guinea are specifically linked with this dispersal, it follows that the current wild populations of the island must be the feral descendants of introduced domestic pigs from mainland Southeast Asia, which came into New Guinea via the Lesser Sunda Islands. A second dispersal event also involved domesticated pigs (this time from wild *Sus scrofa* populations from mainland East Asia), introduced to the Philippines and Micronesia, while a third involved the endemic warty pig of Sulawesi (*Sus celebensis*), which data from Liang Bua cave shows was introduced to Flores perhaps as early as 7000 B.C.