### Pacific 'Babes'<sup>1</sup>: Issues in the Origins and Dispersal of Pacific Pigs and the Potential of Mitochondrial DNA Analysis

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ABSTRACT We explore potential sources of genetic variation in Pacific pigs over the duration of their commensal relationships with Pacific people. Three time periods are identified as critical to understanding the history of pigs in the Pacific region: (1) the late Pleistocene–early Holocene following from human movement into Near Oceania; (2) with Lapita colonization of Remote Oceania beginning ca. 3000 BP, and (3) in Polynesia, shortly after sustained Euro-American contact (ca. late 1700s) when several new breeds were introduced into the region. This paper highlights the important role mitochondrial DNA (mtDNA) work can play in detailing the origins, directions, and frequency of pig transfers, and by extension, the movements of their human carriers. Our preliminary molecular studies identify a hypervariable region of mtDNA in the genus *Sus*, rendering it an ideal taxon for detailed study of the issues we raise herein. Copyright © 2001 John Wiley & Sons, Ltd.

Key words: pig (Sus); mitochondrial DNA; human commensals; molecular archaeology; Pacific

### Introduction

Pig was one of three animal domesticates in prehistoric Polynesia, transported from Near Oceania into Polynesia as far afield as the Hawaiian Islands by the region's earliest colonists. While the evidence suggests that its actual consumption was often infrequent and irregular, pig played a crucial role in rituals, politics, and rites of passage throughout the region (e.g. Ferdon, 1987; Kirch, 1994). In many contexts the development of pig husbandry coincided with the process of agricul-

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tural intensification, with pigs acting as storage mechanisms for surplus starches. Despite the important position of pig in traditional Pacific societies, the taxonomic relationships and historical dispersals of the taxon have been little explored in the Pacific context.

The homeland of Pacific pigs lies in island southeast Asia. This is not only the area of greatest *Sus* diversity, but also a region where animal translocations between islands date back to the late Pleistocene. The antiquity of pig dispersals into Papua New Guinea and island Melanesia is uncertain, but it had been carried into Remote Oceania by at least 3000 BP. There are suggestions that its dispersal may not have been temporally or taxonomically uniform, and we know its persistence on some Pacific islands was variable through time. Soon after western contact, European voyagers introduced new breeds to many Polynesian islands, sometimes with dramatic effects on indigenous pig

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<sup>&</sup>lt;sup>1</sup> *Babe* is the well-known juvenile European White pig who played the lead role in the American Academy Award-winning film of the same title. 'Babes' is also an allusion to the maternal basis of mtDNA transmission.

populations. In at least one case it appears that a unique breed may have developed—the New Zealand *Kunekune* pig. This paper reviews our current state of knowledge and considers how mitochondrial DNA (mtDNA) studies can help resolve questions on the origins, dispersal, and cultural role of pig, particularly in Polynesia, but also in related regions to the west.

Our interest in Pacific pigs was initially an outgrowth of the genetic work of Matisoo-Smith and colleagues (Matisoo-Smith, 1994; Matisoo-Smith et al., 1998a,b) on another human conmensal, the Pacific Rat (Rattus exulans). These studies demonstrate the possibilities of using rat phylogenies to infer the source and dispersal patterns of this rat, and by extension the origins and movements of their human carriers, across the Pacific. Pigs offer the potential to provide a history of human migration and interaction in the Pacific independent from, but complementary to that of the Pacific Rat. Unlike rats, there is little question about the intentionality of pig introductions in the context of colonization (Matisoo-Smith, 1994; Anderson, 1996). Additionally, their large size and high food requirements would have limited the number of individuals that could be carried on any given voyage, which has phylogenetic implications. Their cultural importance would favour their transport in both colonizing and subsequent voyaging expeditions. Genetic studies can inform not only on these issues, but also on a variety of questions relating to pig origins, dispersals, traditional agroecologies, and the impact of western contact. In addition, given the complexity of pig taxonomy in the Asia/Pacific region, molecular identification may allow for unequivocal species identification that may not be possible based on morphology alone.

Herein, we review three main periods in the history of Pacific pigs where we think genetic studies are poised to make significant contributions. This review brings together a diverse body of evidence and poses a series of questions that we think mtDNA analyses are particularly well-suited to answer. While our research is on-going, the degree of genetic variability we have observed thus far indicates both the importance of considering questions of pig origins and dispersals in the Pacific and the potential of ancient mtDNA studies for answering those questions.

### The origin(s) of Pacific pigs

The taxonomy of southeast Asian pigs has a complex and contentious history. Most recently, Groves (1981) identified five species of Sus in this region based on morphology and to a lesser extent, other external characters. These include an older lineage of Sus verrucosus (Javan Warty Hog) and S. barbatus (Bearded Pig) and a more recent lineage of S. celebensis (Sulawesi Warty Pig), S. scrofa (Wild boar), and S. salvanis (Pygmy Hog). Groves' morphological assessments are supported by sympatric distributions between S. scrofa and three other species: S. salvanis (Pygmy Hog), S. barbatus (Bearded Pig), and S. verrucosus (Javan Warty Hog). Additionally, Groves (1983) argued that while S. scrofa  $\times$ S. barbatus crosses are known to produce fertile offspring (e.g. Epstein & Bichard, 1984, p. 147), they do not inter-breed under natural conditions. S. celebensis has an allopatric distribution, while the distinction between S. barbatus and S. verrucosus is based on morphology alone. Groves (1981) also used discriminant function analysis to consider the relationship between 16 characters of skull morphology. The greatest degree of overlap was seen between S. celebensis and S. barbatus, but both were distinct from S. verrucosus and largely so from S. scrofa.

Objections, however, have been raised with respect to the use of cranial morphology as a basis for taxonomic differentiation. Pig cranial morphology in particular appears to be highly affected by its commensal relationship with people. Epstein & Bichard (1984, p. 149) observe that the cranial morphology of domesticated pig has changed more dramatically than any other animal except for the dog. Additionally, cranial morphology can be affected by a variety of factors, including body size, diet, nutrition, and habitat (Epstein, 1971; Mudar, 1986). These concerns point to the potential of DNA studies for evaluating the robustness of taxonomic discriminations made on more traditional grounds. Of particular relevance to anthropological interests, however, is the need to

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identify the pool of genetic variation from which early Pacific colonists may have drawn and the potential of that variation to inform on human migrations and post-settlement patterns of interaction. Our current sampling strategy for pig mtDNA study is directed to this end.

Given the diversity of Sus in island southeast Asia, questions arise as to which species extended eastward into Near Oceania, how they were dispersed, and when. Groves (1983) argues that both S. celebensis and S. scrofa were carried eastward beyond their natural ranges by people. He suggests that the unusual distribution of S. celebensis on several islands offshore from Sulawesi, including Saleyer, Butung, Peleng, and Lembeh, represent human dispersals. Similarly, he argues the 4000-yearold Sus reported by Glover (1986) from Timor represents an exotic introduction, and most likely belongs to S. celebensis (Groves, 1981). In attempting to explain morphological variability in the New Guinea pig, Groves (1983, 1995) argues for a S. celebensis  $\times$  S. scrofa hybrid, which he suggests arose in the Halmahera group. Further afield, he refers to anecdotal accounts that suggest Hawaiian pigs also could be the result of a S. scrofa  $\times$  S. celebensis cross. These accounts, coupled with the high degree of intraspecific morphological variability (see Groves, 1981) and long-term practices of hybridization between wild and domesticate forms (see Yen, 1991), suggest a complex genetic history for Near Oceanic pig.

Limited archaeological data suggests pig (taxon undetermined) on New Guinea by 6000 BP (Golson & Hughes, 1980; Gorecki et al., 1991), and Bulmer (1982, this volume) has long argued an even greater antiquity for pig in the New Guinea highlands, extending back to ca. 10000 BP. More speculatively, shallow basins and 'stake holes' dating to 9000 BP in the Kuk swamp region have been argued to be pig wallows (Golson & Hughes, 1980, p. 299). Two mechanisms could have facilitated pig dispersal at this early date. Bulmer (1975) has argued for a natural dispersal, given that pigs can swim (see also White & O'Connell, 1982: figure 6.8). However, the nearest stepping-stone island to New Guinea even during

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the lowest of sea levels was 65 km (Golson & Hughes, 1980; Green, 1994). Emerging regional evidence suggest a second mechanism-human agency-as animal translocations in island Melanesia now date to the Pleistocene (but see Gosden, 1992, p. 59). For example, human-aided transfer of the cuscus (Phalanger orientalis) from Papua New Guinea to New Ireland is argued to be as early as 19000 BP (Allen et al., 1989; Flannery & White, 1991). Transfers of wallaby (Thylogale brunii) from Papua New Guinea to New Ireland at 7000 BP are also argued (Flannery & White, 1991). Thus, the transfer of Sus out of island Southeast Asia at this time would be consistent with the developing commensal relationships, voyaging skills and animal translocation abilities of human populations in the region at large. Although many consider the available archaeological evidence for pre-3000 BP pig in Papua New Guinea to be controversial, it can not as of yet be altogether discounted.

Summarizing the foregoing, the available taxonomic evidence suggests that two Sus species were carried between islands of Southeast Asia in the past. Limited archaeological evidence raises the possibility of an undetermined Sus on Papua New Guinea by at least 6000 BP, and perhaps even several millennia earlier. Finally, pig is clearly associated with the arrival of Lapita pottery-bearing populations in Near and Remote Oceania around 3000 BP. This Lapita-age pig could have been derived from extant Near Oceanic pig populations, as has been demonstrated for several other indigenous Near Oceania biota, including domesticated sugar cane, Australimusa banana, and Rattus praetor. Alternatively, Near Oceania may have seen a dual (or even multiple) introduction of Sus from Southeast Asia, one during the late Pleistocene-early Holocene and another coincident with the Lapita-related expansion (a la Kirch, 1997). Similarly, Yen (1991) contemplates dual domestication centres for taro and possibly yam. If the dual introduction of pig is upheld, questions arise as to the taxonomic identity of these two Near Oceanic pig lineages, as well as to those of the pigs carried into Remote Oceania.

# Spatio-temporal distributions of pig in Polynesia

By 3000 BP, pig had been dispersed to West Polynesia (including Fiji) by Lapita-pottery bearing populations, along with dog, chicken, and the Pacific Rat. *S. scrofa vittatus* (the Banded Pig), a highly variable subspecies with a distribution throughout the Indo-Malayan region, is the assumed taxon involved in this transfer (Groves, 1981). But the few, fragmentary and often post-cranial remains of pig from Lapitaage sites can not reliably be assigned to *S. scrofa vittatus*, much less any other specific taxon, based on traditional morphological grounds. Moreover, as suggested above, pigs associated with Lapita could represent more than one species, and/or interspecific crosses.

Also noteworthy, is that pig remains in these early Lapita contexts of Remote Oceania have been quite limited, which has significant implications in terms of the establishment of permanent populations. Remains have now been identified from Niuatoputapu (Kirch, 1988), Fiji (Hunt, 1980), and Tikopia (Kirch & Yen, 1982). But despite extensive work in Tonga, Shutler et al. (1994) have yet to report pig remains of Lapita age, and none of the medium mammal remains from early contexts of the To'aga Site, Manu'a Islands could be reliably assigned to pig based on standard morphological grounds (Nagaoka, 1993). As a whole, the West Polynesian data suggest that relatively small populations of pig were involved in this early period. The evidence raises questions about the security of early establishment, and the possibilities of loss and reintroduction. Multiple introductions, particularly from spatially or temporally separated sources, increase the possibility of distinct mtDNA lineages and the potential to inform on human patterns of interaction.

Gosden (1992) in a broader context, suggests that with the appearance of Lapita pottery, 'What we are charting is not sudden changes due to the influx of new people, but a series of complex social and subsistence changes taking place over millennia' (Gosden, 1992, p. 57). He posits that both Lapita colonists and the colonization process may have been much more heterogenous than generally has been assumed. In this vein, he explores some intriguing if fragmentary and controversial evidence for pre-Lapita explorations of Remote Oceania and the early use of some islands prior to full-fledged settlement. His more general comments reinforce the notion that a single introduction of a genetically uniform pig to Remote Oceania, while possible, should not necessarily be assumed.

Also of interest is the patchy distribution of pig in later Polynesian contexts (Figure 1). There appear to be several cases where pig: (1) was not introduced, died en route, or failed to establish reproductively viable populations; or (2) was introduced and established, only to later disappear from the record. The most well known examples of the former are New Zealand and Easter Island. The long and arduous voyage from central East Polynesia to these islands (Irwin, 1992) may have played a role in the failed transfer of certain human commensals.

In the case of introduction and loss, however, the available evidence suggests that island size was key in the long-term maintenance of pig populations. Bay-Petersen (1983) argues that extinction of dog and pig occurred primarily on islands under 50 km<sup>2</sup>—a pattern which our further compilation of the ethnographic and archaeological distributions supports. On small islands pigs may have quickly come into direct competition with human populations, as bush areas for natural foraging were unavailable (e.g. Gosden, 1992, p. 60). On Tikopia and Mangaia, for example, Kirch & Yen (1982) suggest that competition led to purposeful extermination, as also was the case on Rotuma in the early 20th century (Howard, personal communication, 1998). Equally plausible, however, is that the high labour costs associated with pig could have led to their extirpation in some contexts (see also Bay-Petersen, 1983). Alternatively, some losses could stem from natural disasters, particularly on small islands which are prone to cyclones.

Importantly for genetic studies, the apparent susceptibility of pig to frequent extirpation, combined with the high cultural value placed on pig flesh, could have effected multiple reintroductions (e.g. Lynch, 1991, p. 427). The

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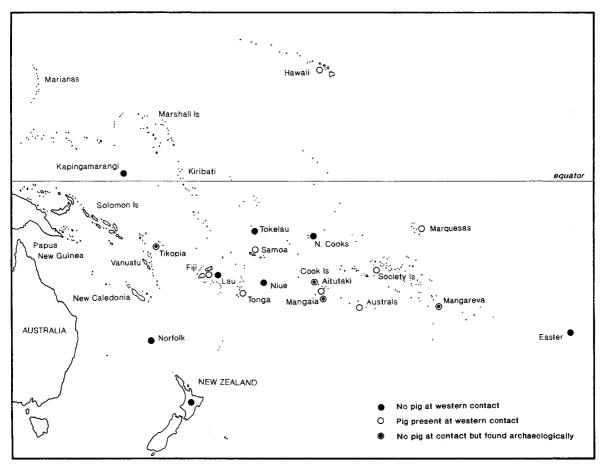


Figure 1. Archaeological and ethnographic discordances in pig distributions in Polynesia.

technologies for long-distance transport of animals were already in place, being part of the cultural repertoire of the original Polynesian colonists. Mitochondrial DNA studies potentially offer one means of assessing multiple introductions of this kind. For example, Matisoo-Smith et al. (in press), recently used mtDNA studies of Chatham and Kermadec Islands Pacific Rat to show relative isolation in the case of the former and multiple contacts in the latter, therein reinforcing other independent archaeological data. Mitochondrial DNA would also be useful in tracking the origin of what have previously been archaeologically invisible components of exchange, specifically commensals and animal products (e.g. tusks and teeth), through their genetic signatures, therein complementing

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Johnson, 1997).

Pacific pigs. Early in the contact period, Europeans began introducing western breeds into the region. Their primary purpose was to establish stock on Pacific islands for use in ship provisioning. However, in most if not all cases, these were not indigenous European breeds but rather European/Asian hybrids developed in the early 1700s or full-fledged Asian breeds (Epstein & Bichard, 1984). Chinese pigs were used quite

geochemical studies of exchange (e.g. Allen &

Influences of Western contact

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early to improve European stock, as they had a greater ability to store fat and matured quickly (Groves, 1983; Epstein & Bichard, 1984). According to Epstein and Bichard, these breeds were imported directly from the Canton District of China and Indo-China, and via Naples and Portugal in the period from 1770 to 1780, and probably before this time. These crosses resulted in dramatic stock improvements and traditional western European breeds were quickly replaced.

European introductions of pig to the Pacific began quite early in the contact period (Ferdon, 1981; Clarke & Dzieciolowski, 1991). In 1774, the Spanish introduced pigs of an unknown affinity to Tahiti (Ferdon, 1981, p. 299). By 1777, David Samwell, travelling with Captain James Cook, observed significant changes in the Tahitian stock, commenting on the surprisingly larger sizes obtained within a 3-year period. These larger breeds not only placed islanders in a more advantageous position with respect to the provisioning of ships, but undoubtedly had a significant impact on native animal husbandry and social practices—although these issues have not yet received anthropological attention.

Clarke & Dzieciolowski (1991) suggest that the first pigs to become established in New Zealand, the 'Captain Cookers', were S. scrofa vittatus brought by Captain Cook from Tonga and Huahine in 1773. They also record early 1800 introductions of three 'English' breeds (two developed from wild European pigs and a third from a S. scrofa cristatus  $\times$  S. scrofa moupinenesis cross in the 18th century). The introduction of S. barbatus to the Bay of Islands by D'Surville in 1769 is also reported (Clarke & Dzieciolowski, 1991, pp. 240, 245). It is uncertain which, if any, of these introductions gave rise to the distinctive New Zealand Kunekune pig-a question of considerable interest to some Maori iwi who consider Kunekune a traditional commensal and to Kunekune breeders (Tipene, 1980).

The *Kunekune* breed are distinguished by their well-developed 'tassels', or hairy tubular appendages, which hang from their lower jaw and are about 40 mm in length (Tipene, 1980). Their small but robust body forms and short legs are also distinctive. Clarke & Dzieciolowski (1991) argue that *Kunekune* arose from introductions made to the East Cape region of the North Island between 1795 and 1840, by Spanish and Portuguese sailors en route from China. They suggest *Kunekune* developed out of *S. scrofa moupinensis*, although other breeds like the Irish Greyhound and the Poland–China breed also have tassels.

The review of Clarke & Dzieciolowski (1991) is dramatic testimony to the number and wideranging sources of breeds that were introduced to the Pacific region relatively early in the historic period. The impacts of this facet of culture contact on traditional animal husbandry systems, island environments, and cultural rituals and prestations are largely unexplored but the timing and direction of transfers are amenable to mtDNA study. Moreover, ample samples from historic contexts are available, particularly in New Zealand and Hawaii, but also elsewhere in the Pacific.

#### **On-going mtDNA studies**

Our first step in addressing the issues presented above has been to explore the potential variation in Pacific pigs across these three time periods-that is, to attempt to identify both within and between species variation. Initially, we designed polymerase chain reaction (PCR) primers to amplify an approximately 200 base pair fragment of the mitochondrial control region. These primers (PP1 and PP2) were based on modern European pig mtDNA sequences from the GenBank database. The identified region of mtDNA contained a number of variable sites and length mutations between Large White and Meishan breeds. We found these primers also worked well with DNA extracted from a pig liver (obtained from a local Auckland butcher) and from tissue, blood, and teeth of New Zealand Kunekune pigs. Using ancient DNA extraction methods described elsewhere (Matisoo-Smith et al., 1997) we also extracted and sequenced DNA from a tusk of a modem wild pig from the Jimi Valley, northern highlands, Papua New Guinea (collected in 1973 by Sue Bulmer). Bulmer (personal communication, 1998) had suggested that this Jimi pig could be

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either an indigenous highland pig, a more recent European breed, or a hybrid between the two. The DNA sequences for these samples were aligned and are shown in Figure 2. It is significant that these three modern pigs produced hypervariable sequences.

Unfortunately, the primers we designed did not work on archaeological pig samples from Polynesian sites. When primers fail to amplify, there are usually two possible explanations. First, DNA may be lacking in the samples. This is particularly likely in the case of archaeological samples. Lack of DNA could be the result of either the age of the samples or their state of preservation. Second, the mtDNA control region in prehistoric Pacific pigs might be significantly different from European breeds, and as a result, the primers do not anneal to the Pacific pig DNA.

To further address this possibility, we attempted amplification of another fragment of mtDNA d-loop, using standard mammalian primers. These new primers (Dlp3 and Dlp5) amplify a more conserved region, and successfully amplify mtDNA from a range of mammalian species. Amplification using Dlp3 and Dlp5 was successful for all samples extracted thus far. The aligned sequences are shown in Figure 3. The resulting variation is very interesting. First, it appears that there is a clear distinction in this region of mtDNA between Pacific pigs (from the Marguesas and New Guinea), European pigs, and Kunekune. In addition, there appears to be variation within Kunekune pigs, with the K4 sample being distinct from the other three Kunekune, differing at two sites (sites 37 and 85 on Figure 3). This degree of variation may the result of admixture between Kunekune and some other breed in the K4 lineage, in which case it highlights some of the potential problems of taxonomic classification based on morphology alone. As Kunekune breeders keep detailed records of pedigree, we will be tracking the family history of the K4 pig to address this possibility. Alternatively, it may indicate that Kunekune are indeed a variable species, which could be the result of ancient origins, a highly variable source population, or a much more complex history for the breed.

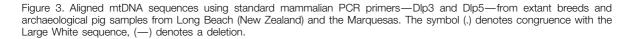
Another interesting result is the molecular identification of a pig tooth obtained from the Otago Museum in 1997. This tooth was recovered from faunal collections from the Long Beach site (S164/20), located just north of Dunedin, excavated by Hamel & Leach (1977). The tooth was labelled as coming from Layer 2,

		10	20	30	40	50		
Butcher Meishan Large White Kunekune Jimi	CNCACAAACATACAAATATGTGACCCCCAAAAATTTTACCATTGAAAACCA							
			c	A A A	т тА			
		60	70	80	90	100		
Butcher Meishan Large White Kunekune			 .G	ACGTCGTGCA	T	•••		
Jimi		T	.G					
Butcher Meishan Large White Kunekune Jimi	CCCCATGC	110 ATATAAGCAT	120 GTACAT					

Figure 2. Aligned mtDNA sequences, using PCR primers—PP1 and PP2—from four extant breeds: European White, Meishan, Papua New Guinea (Jimi) pig and New Zealand *Kunekune*. Sequences are aligned against a sequence from a pig liver obtained from a local Auckland butcher. The symbol (.) denotes congruence with the Butcher pig sequence, (–) denotes a deletion.

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		10	20	30	40	50
White PigLiverl KuneKune0972 KuneKune1 KuneKune2 KuneKune4 Jimi LongBeach Marquesas6	TTCTCGCT	· · · · · · · · · · · · · · · · · · ·	T T T		GATGAACTTT	· AA · · · · · ·
		60	70	80	90	100
White PigLiver1 KuneKune0972 KuneKune1 KuneKune4 Jimi LongBeach Marquesas6	CAGGCATC	110	120	атстсасста	AATCGCCCA	.CT    
White PigLiver1 KuneKune0972 KuneKune1 KuneKune4 Jimi LongBeach Marquesas6	· · · · · · · · · · · · · · · · · · ·	TTAAATAAGA	CATCTCGAT A A A A			



which is dated to around 1600 AD (Hamel & Leach, 1979). The tooth clearly came from a European pig, as the sequence is identical to that obtained from a pig liver purchased from a local Auckland butcher. This result strongly suggests that there has been disturbance at the Long Beach site, with intrusion of historic period materials at least as deep as Layer 2, which confirms the interpretations of Leach & Hamel (1981).

Our positive result using the standard mammalian primers is evidence that there is indeed ancient DNA remaining in the archaeological Pacific pig samples. This suggests that the inability to amplify mtDNA from the archaeological samples using the original primers, PP1 and PP2, is likely due to the inability of the primers to anneal, thus suggesting variability within Pacific pigs. We are currently redesigning

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primers for the more hypervariable region of the d-loop in order to further investigate the degree of variation within Pacific pigs. In addition to locating and obtaining archaeological pig specimens from the Asia/Pacific region, we are also in the process of obtaining bone and tooth samples from the potential source species, *S. celebensis, S. scrofa, S. verrucosus, S. barbatus* and S. *salvanis,* which will be valuable as comparative samples.

### Conclusions

While the 'Pacific Babes' project is still in its infancy, our preliminary results are promising. Based on mtDNA variation, we are currently able to distinguish Pacific pigs from European breeds. This is applicable and extendable to the

other Sus species present in the Asia/Pacific region, and offers a tool with which to address issues in pig taxonomy. We have shown that Kunekune pigs are distinct from both Pacific pigs, and a range of common European breeds, and we are thus one step closer to identifying the mysterious origin of this breed. Finally, we have indications that there may be enough variation within the pigs introduced into the Pacific during the prehistoric period to allow phylogenetic analyses which may be valuable for tracking migration, mobility and trade in the region. These results show the potential of this approach to address the numerous and varied issues raised in this paper, all of which will further our understanding not only of animal/ human interactions, but also of interaction between human populations in the Pacific region.

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