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The origins of the feral pigs on the Auckland Islands

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Abstract At least three releases of pigs (*Sus scrofa*) on the Auckland Islands were made in the early to mid 19th century, the first in 1807 and the third probably in 1842. Initially the releases were to provide food for shipwreck victims and/or sealers and whalers. Whether these pigs were of European, Asian, or Pacific stocks was unknown. As a protection measure for what may now be a rare breed, the Rare Breeds Conservation Society of New Zealand removed 17 of the feral pigs from the main Auckland Island in 1999. Mitochondrial DNA studies were carried out using blood obtained from five of these pigs. Comparisons of D-loop mitochondrial DNA were made among Auckland Island pigs, a range of modern pig breeds, and wild boar from both Europe and Asia. The five Auckland Island pigs sampled are identical over the 394 base pairs studied and are most closely related to European pig breeds, which strongly suggests that they are of European origin.

Keywords Auckland Islands; D-loop; feral pigs; mtDNA; phylogenetics; *Sus scrofa*

INTRODUCTION

A population of feral pigs (*Sus scrofa*) inhabits the largest island in the Auckland Islands, a group of uninhabited subantarctic islands 560 km south of South Island, New Zealand (Fig. 1). Although it is thought that this population derives from pigs released during the 19th century, the original breed or source population, whether European, Asian, or Pacific, is unknown.

While pigs were introduced to many Pacific Islands during prehistoric periods (Allen et al. 2001), they were successfully introduced to New Zealand only after the arrival of Europeans. In the 1770s Captain Cook released Polynesian and Eurasian pigs in New Zealand (Clarke & Dzieciolowski 1991), and by the late 18th and early 19th centuries modified domestic breeds including Asian/European crosses and Polynesian pigs were being carried and released by explorers and mariners.

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Fig. 1 Location of the subantarctic Auckland Islands and Campbell Island. Sequences were derived from 5 of the 17 pigs captured on the east coast of Auckland Island.

The Auckland Islands were discovered in 1806 by Captain Bristow on the vessel *Ocean* while on a whaling voyage south of New Zealand. Although the islands were rarely inhabited for extended periods of time, they have a long history of animal introductions as stock was often left on them for the use of passing whalers and/or shipwrecked sailors. When the Auckland Islands were discovered many types of pigs were being transported in the Pacific; this has raised the question of which breed or breeds were introduced to these particular islands.

History of pig introductions to the Auckland Islands

There are records of continuous pig presence on the main Auckland Island from 1807 until the present, but reports indicate that the population has fluctuated considerably. Charles Enderby in the 1850s noted that there were many pigs, probably of two different breeds, on both Enderby and Auckland Islands (Fig. 1) and his description implied that they were in good health (Taylor 1971). Thus, by the mid 1800s the pig population was well established. By 1885, however, pigs had disappeared from Enderby Island (Taylor 1968). From 1880 to 1927 New Zealand government provisioning visits regularly released mammals such as pigs, goats, sheep, and sometimes cattle to subantarctic islands (Taylor 1971). In addition to these government visits, whaling and sealing companies, who often acted in a secretive manner, released animals on subantarctic islands, although few official records exist. Therefore, while there are three documented releases of pigs on the Auckland Islands, it seems reasonable to assume that this may be an underestimation.

Although the Auckland Islands were discovered by Bristow in 1806, he did not land there until the following year, in October 1807, when he returned in command of the *Sarah*. This boat was anchored in Port Ross on the main Auckland Island and pigs were released on shore near Erebus Cove, as a future food source for whalers and shipwreck victims (McNab 1909). In 1840, during an Antarctic Expedition under Sir James Ross, the Auckland Islands and Campbell Island were visited and pigs were landed at Port Ross (McNab 1909). In 1842 a Ngati Mutunga chief, Matioro, took a group of Maori and just under 30 Moriori slaves from the Chatham Islands to the Auckland Islands, where they remained until 1856 (King 1989; Taylor 1971). Upon their arrival, pigs and dogs were released and many were allowed to run wild (Taylor 1971). The Southern Whale Fishery Company established a settlement, governed by Charles Enderby, at Port Ross in 1849 (McNab 1909). It is unclear whether Charles Enderby brought pigs with him. The settlement was unsuccessful and abandoned in 1852 but many pigs, sheep, and cattle were left behind. After several shipwrecks, including that of the *General Grant* in 1866, the provincial government of Southland, New Zealand, sent the ship *Amherst* to search the subantarctic islands for castaways. Several supply depots were left on the Auckland Islands and pigs were released on Campbell Island (McNab 1909). The provincial government of Southland and the state government of Victoria, Australia, provisioned depots and released domestic animals as a service for about 10 years. In 1877 this service was taken over by the New Zealand government and was continued until 1927 (Falla 1975). The *Tutanekei* made a final trip to the Auckland Islands in 1929 and it is thought that the islands were not visited again until World War II. All of the Auckland Islands were made a reserve for native flora and fauna in 1934 (Taylor 1971).

Various qualitative reports indicate that the pig population fluctuated dramatically in size from the 19th century to the present (Challies 1975; Taylor 1975). There is evidence of at least two major population declines. The first occurred in the 1860s (Challies 1975), and Department of Conservation staff observed another in 1995 (A. Cox pers. comm. 2002).

In 1998 the Auckland Islands were made a World Heritage site, in recognition of their rare and unique flora and fauna. There is, therefore, some pressure to remove all pigs from Auckland Island, but there is also interest in preserving the pigs which are believed to be a rare breed. In January 1999 the Rare Breeds Conservation Society of New Zealand mounted an expedition to capture some Auckland Island pigs. The pigs were caught on the east coast of Auckland Island, usually within 50 m of the shore, and were relatively difficult to find. Seventeen were captured and they were described as in light but healthy condition (R. Fraser pers. comm. 2002).

Table 1 The code number assigned to each mitochondrial DNA D-loop haplotype, the breed(s) of pig or boar in which it was found, and the associated GenBank accession numbers.

Haplotype	Breeds represented	Accession numbers
1	Japanese wild boar	AB041469
2	Japanese wild boar	AB041471
3	Japanese wild boar	AB041472
4	Japanese wild boar	AB041467
5	Japanese wild boar	AB059652
6	Japanese wild boar	D42172, D42175, D42177, AB041470, AB041473, AB015084
7	Japanese wild boar	D42174
8	Japanese wild boar	D42178
9	Japanese wild boar	AB015085
10	Japanese wild boar	D42171
11	Japanese wild boar	AB041468, AB015086
12	Satsuma & Okinawa native pig	D42185, AB015092
13	Satsuma	AB015091
14	New Satsuma	D42182
15	Meishan	D42181
16	Meishan & Large White	AB041474, AB041490
17	Meishan	AF304200
18	Ohmini & Pot Belly Miniature	D42183, AB041479
19	Jinhua	AB041476
20	Jinhua	AB041475, AB041477
21	Moncai & Shizuoka Berkshire	AB041480, AB041483
22	Moncai	AB041481
23	Yontsuan & Moncai	AB041478, AB041482
24	Ryukyu wild boar	D42184
25	Ryukyu wild boar	AB015088
26	Ryukyu wild boar	AB015089
27	Ryukyu wild boar	AB015090
28	European wild boar	AB059651
29	Duroc Okayama	AB041487
30	Landrace	AF304202
31	Berkshire & Japanese wild boar	AB059650, D42173, D42176
32	Italian wild boar & European wild boar	AF304201, AB015095
33	European wild boar	AB015094
34	Hampshire, Okayama Berkshire, Pietrain, Large White, Landrace Kanagawa, Swedish wild boar & Landrace	AB041485, AB041488, AB041489, AB041494, AB041495, AB041496, AF304203, AF034253,
35	Landrace/Duroc & Duroc Okayama	D42170, AB041486
36	Landrace Kanagawa	AB041497
37	Landrace Kanagawa	AB041498
38	Landrace	AB041499,
39	Swedish slaughterhouse pig	AJ002189
40	**Auckland Island pig**	**AY237540**
41	Kagoshima Berkshire	AB041484
42	Large White Kanagawa	AB041491
43	Large White	AB041492
44	Large White	AB041493
45	Yucatan miniature	AB015093

Through the Southland Heirloom Breeds Charitable Trust, who now hold the pigs near Invercargill, New Zealand, we obtained blood samples from 5 of the 17 captured Auckland Island pigs. We analysed nucleotide sequences from the mtDNA D-loop from these samples and compared them with sequences obtained from GenBank (Benson et al. 2002) for a range of Asian and European pigs to identify the origins of the Auckland Island pigs.

MATERIALS AND METHODS

DNA was extracted and purified from whole blood samples (Daiger et al. 1984), resuspended in water, and used as template for the polymerase chain reaction (PCR). We amplified 397 base pairs of the mitochondrial D-loop by using two primer sets: Dlp3 (5′ CGTGAAACCAACAACCCGC 3′), Dlp5 (5′ CATCGWGATGTCTTATTTAAGRGGA 3′), relatively conserved mammalian primers obtained from C. S. Baker, School of Biological Sciences, The University of Auckland (unpubl. data), and pig specific primers PL76 and PH62 (Watanobe et al. 2001). Amplifications were performed in 25 µl reactions containing 2 m*M* $MgCl_2$, 0.1 µ*M* of each primer, 0.25 m*M* of each dNTP, 10 m*M* tris HCl (pH 8.3), 50 m*M* KCl, 1 unit of amplitaq, and 1 µl DNA template. PCR conditions for primers Dlp3 and Dlp5 were an initial cycle of denaturation at 92°C for 2 min, followed by 35 cycles of denaturation at 92°C for 45 s, annealing at 60°C for 1 min, and extension at 72°C for 1 min. A final extension at 72°C for 5 min was performed. PCR conditions for primers PL76 and PH62 were the same as those of Dlp3 and Dlp5 except that the annealing temperature used was 58°C.

The amplified products were purified in sephacryl columns (Microspin S300, from Amersham, Pharmacea, Biotech) and quantified on 2% ethidium bromide stained agarose gels using a low mass ladder. Sequencing was performed at The University of Auckland DNA Sequencing Facility, using the ABI PRISM™ BIG DYE Terminator Sequencing Kit, a Perkin-Elmer Gene Amp PCR System 9700, and an ABI PRISM™ 377 DNA Sequencer XL machine. The 394-bp nucleotide sequences for each sample were constructed by connecting the two overlapping fragments obtained from the different primer sets. This and the alignments were carried out using the software package Sequencher™ (Gene Codes Corporation, Michigan, USA).

A phylogenetic analysis was performed to establish the relationships between the Auckland Island pigs and representatives of both wild boars and domestic pig breeds from Europe and Asia. The 68 pig D-loop sequences obtained from GenBank are described in Table 1. All sequences were aligned to identify the unique haplotypes. We constructed a neighbour-joining (NJ) tree (Saitou & Nei 1987) of these haplotypes using the distance matrix calculated by the Kimura two-parameter model of evolution (Kimura 1980) as implemented in the PAUP* software package v.4.0b10 (Swofford 2001). A bootstrap analysis using 1000 pseudoreplicates was performed on the resulting NJ tree and the tree was arbitrarily rooted at the midpoint.

RESULTS

The sequences obtained for the five Auckland Island pigs were identical across the 394-bp region examined. When compared with the pig sequences from the GenBank database, the Auckland Island pigs represent a unique haplotype (Haplotype 40, Fig. 2). This haplotype, however, contains a motif GCCCAA, at positions 131, 136, 145, 153, 158, and 294, respectively (nucleotide positions numbered as in Okumura et al. (1996)). This motif is closely associated with European domestic pigs and, to a lesser extent, European wild boars (Okumura et al. 1996; Watanobe et al. 2001).

Position

H	109	110	124	128	131	136	145	153	158	181	185	214	241	248	260	271.1	276	279	288	294	301	302	306	323	387	388	390	405	406	443	452	461	474
1	C	G	A	A	A	-	T	T	G	C	T	T	T	G	C	-	T	C	A	G	C	G	T	T	A	A	T	T	T	A	C	G	C
2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	T	.	.
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4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	G	T	.	.
5	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	T	.	.	.	A	.	.	.	.	.	.	.	.	T	.	.
6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.
7	.	.	.	.	.	.	.	.	A	.	.	.	.	.	T	.	.	.	.	.	.	A	C	.	.	.	.	.	.	.	T	.	.
8	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	A	C	.	.	.	.	.	.	.	T	.	.
9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	C	.	.	.	.	.	.	.	.	.	.
10	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	T	.	.	.	A	.	.	.	.	.	.	.	.	T	.	.
11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	A	.	.	.	.	.	.	.	.	T	.	.
12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.
13	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	A	.	.	.	.	.	C	.	.	T	.	.
14	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	T	.	.	.	A	.	.	.	.	.	.	.	.	.	.	T
15	.	.	.	.	.	.	.	.	.	.	.	.	C	A	.	.	.	T	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.
16	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	T	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.
17	.	.	.	.	.	C	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	T	.	.
18	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	G	T	.	.
19	.	.	.	.	.	.	.	.	.	T	.	.	C	.	.	.	.	T	.	.	.	A	.	.	.	.	.	.	.	.	.	A	.
20	.	.	.	.	.	.	.	.	.	T	.	.	C	.	.	.	.	T	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.
21	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	A	.	.	.	.	.	.	.	.	T	.	.
22	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	C	G	T	.	.
23	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	G	T	.	.
24	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	T	.	.	.	A	C	.	G	.	.	.	.	G	.	.	.
25	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	T	.	T	.	A	C	.	G	.	.	.	.	G	.	.	.
26	.	.	.	.	.	.	.	.	.	T	.	C	.	.	.	.	.	T	.	T	.	A	C	.	G	.	.	.	.	G	.	.	.
27	.	.	.	.	.	.	.	.	.	T	.	C	.	.	.	.	.	T	.	T	.	A	.	.	G	.	.	.	.	G	.	.	.
28	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	T	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.
29	.	.	.	.	.	.	.	.	.	T	.	.	C	.	.	.	.	.	.	.	.	A	.	.	.	.	.	C	.	.	T	.	.
30	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	A	.	.	.	.	.	.	.	.	T	.	.
31	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	T	.	.
32	T	.	.	G	G	C	C	.	.	T	.	.	.	.	.	.	C	T	.	.	.	A	C	C	.	.	C	.	.	G	.	.	.
33	T	.	.	G	G	C	C	.	.	T	.	.	.	.	.	.	C	T	.	.	.	A	C	.	.	.	C	.	.	G	.	.	.
34	T	.	T	.	G	C	C	C	A	T	.	.	.	.	.	.	.	.	.	A	.	A	C	C	.	.	C	.	.	.	.	.	.
35	T	.	T	.	G	C	C	C	A	.	.	.	.	.	.	.	.	.	.	A	.	A	C	C	.	.	C	.	.	.	.	.	.
36	T	.	T	.	G	C	C	C	A	T	.	.	.	.	.	.	.	.	.	A	.	A	.	C	.	.	C	.	.	.	.	.	.
37	T	.	T	.	G	C	C	C	A	.	.	.	.	.	.	.	T	G	.	A	.	A	C	C	.	.	C	.	.	.	.	.	.
38	T	.	T	.	G	C	C	C	A	.	C	.	.	A	.	.	.	.	.	A	.	A	C	.	.	.	C	.	.	.	.	.	.
39	T	.	.	.	G	C	C	C	A	T	.	.	.	.	.	C	.	T	.	A	.	A	C	.	.	.	C	.	.	.	.	.	.
40	**.**	**.**	**.**	**.**	**G**	**C**	**C**	**C**	**A**	**T**	**.**	**.**	**.**	**.**	**.**	**.**	**.**	**.**	**.**	**A**	**.**	**A**	**C**	**C**	**.**	**.**	**C**	**.**	**.**	**.**	**.**	**.**	**.**
41	T	.	.	.	G	C	C	C	A	T	.	.	.	.	.	.	.	.	.	A	.	A	C	.	.	.	C	.	.	.	.	.	.
42	T	.	T	.	G	C	C	C	A	.	.	.	.	.	.	.	C	T	G	A	.	A	C	C	.	.	C	.	C	.	.	.	.
43	T	.	T	.	G	C	C	C	A	T	.	.	.	.	.	.	.	.	.	A	.	A	C	C	.	.	C	C	.	.	.	.	.
44	T	.	T	.	G	C	C	C	A	T	.	.	.	.	.	.	.	T	.	A	.	A	C	C	.	.	C	.	.	.	.	.	.
45	T	A	.	.	G	C	C	C	A	T	.	.	.	.	.	.	.	T	.	A	.	A	C	C	.	.	C	.	.	.	.	.	.

Fig. 2 Base substitutions at the variable sites in the mitochondrial DNA D-loop haplotypes. H, haplotype number. Positions follow Okumura et al. (1996). The symbol (.) denotes congruence with haplotype 1; –, denotes a deletion; and position 271.1 represents an insertion between bases 271 and 272. The nucleotides within the boxes represent the European domestic pig motif. Auckland Island pig (Haplotype 40) in bold.

The phylogenetic tree of sequence haplotypes (Fig. 3) indicates marked differentiation between animals of European and Asian origin with strong (84%) bootstrap support for two major clades. In the Asian clade, the wild boars are present in a well-supported basal clade comprising Ryukyu wild boars and several other, generally separate, clades of Japanese wild boars. Domestic pigs of Chinese, Japanese, and Okinawan origin are interspersed among the Japanese wild boar clades. Also interspersed among the essentially Asian haplotypes were two haplotypes (21 and 29) also found in European × Asian cross breeds, three haplotypes (16, 30, 31) also found in European domestic pigs, and one haplotype (28) reported from European wild boar.

In the European clade, a strongly supported group (bootstrap support 95%) of European wild boar haplotypes is distinguished from a second European group (bootstrap support 76%) comprising haplotypes predominantly from Europe and New World domestic pigs. Several haplotypes in this "European domestic" clade were found exclusively in European × Asian cross breeds (36, 37, 41, and 42). One haplotype (35) occurred in both European pure and cross bred pigs and one haplotype (34) occurred both in European pure and cross bred pigs

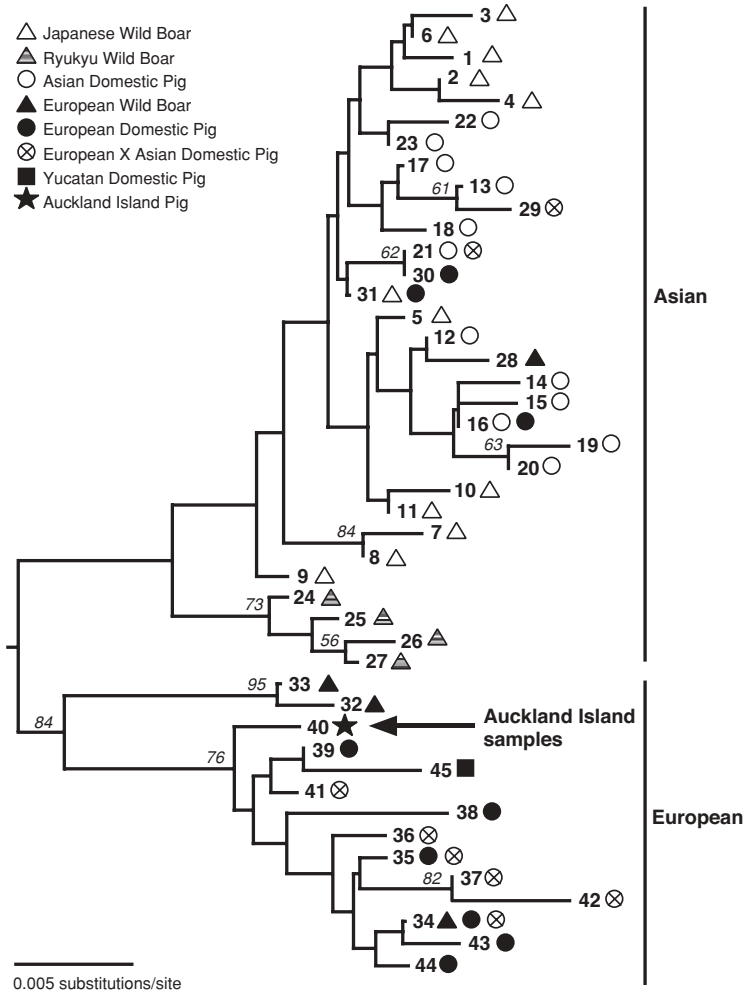

Fig. 3 Midpoint neighbour-joining phylogenetic tree of mitochondrial DNA D-loop haplotypes from Auckland Island pigs and from European and Asian wild boars and domestic pigs. Haplotypes are numbered in bold (Table 1). Where the bootstrap support for individual clades is greater that 50% it is given in italics. Symbols indicate the type of pig or boar in which a haplotype was found.

and in European wild boars. A haplotype (45) found in pigs from Central America (Yucatan) nested deeply within the European clade. The single haplotype (40) found in the Auckland Island pigs also clustered basally within this European domestic clade.

DISCUSSION

Our results suggest that the Auckland Island pigs are probably a single breeding population. Free interbreeding is certainly possible, since boars are known to travel up to 30 km a night and this is sufficient to enable them to cover the whole island (R. Fraser pers. comm. 2002). Since there have been major fluctuations in the population size in its 194-year history it is not surprising that we have found no sequence diversity. Our analysis supports a European origin for the current population of these pigs. The Auckland Island haplotype (40) exhibits the

motif seen in the pigs of known European origin (haplotypes 34, 35, 38, 43, 44, and 45) and in the phylogenetic analysis this haplotype clusters within the European pig clade. Although the basal position within the clade is not strongly supported, i.e., by a bootstrap value greater than 50%, it is suggestive of an older breed and thus an early introduction. It is possible that other breeds were also introduced to the Auckland Islands but did not survive the severe population bottlenecks that have occurred.

It has been observed previously that some European pig breeds exhibit both Asian and European characteristic haplotypes, e.g., Large White (Watanobe et al. 1999), and Landrace and Duroc (Kijas & Andersson 2001). Our analysis confirms these observations. Both Asian and European haplotypes were found in the breeds Landrace (30, 34, and 35), Large White (16, 34, and 35), and Berkshire (31 and 41). This transfer of haplotypes probably arose from the 18th and 19th century interbreeding of Asian and European stocks (Kijas & Andersson 2001). In addition, Clarke & Dzieciolowski (1991) stated that European domestic pigs (*Sus scrofa scrofa*) were cross bred with Chinese (*Sus scrofa moupinensis*) and Indian pigs (*Sus scrofa cristatus*) and that these modified breeds, together with others, were carried on 18th and early 19th century voyages to New Zealand and beyond. One putative European wild boar sequence (haplotype 28) has none of the European motif nucleotides and clusters with the Asian clade. Although this sequence was retrieved from GenBank (accession number AB059651), it has not been published in a peer-reviewed journal and may reflect a data entry error, or a misnamed sample.

The topology of our phylogenetic tree, with its major split into European and Asian types and its further division into four clades, separating the Ryukyu wild boars from the other Asian pigs and separating the European wild boars from the European domestic pigs, is wholly consistent with those published by Watanobe et al. (2001, 2002).

This study builds on the work of the "Pacific Babes" project (Allen et al. 2001) and further highlights the usefulness of mtDNA analysis to investigate the origins and dispersal of pigs in both New Zealand and the wider Pacific. Our analysis strongly supports a European origin for the Auckland Island pigs and, while not sufficient evidence alone, the unique haplotype is suggestive of a rare breed.

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