16 A genetic perspective on the origins and dispersal of the Austronesians

Mitochondrial DNA variation from Madagascar to Easter Island

Erika Hagelberg, Murray Cox, Wulf Schiefenhövel and Ian Frame

Introduction

This chapter describes the study of one genetic system, mitochondrial DNA (mtDNA), within the Austronesian-speaking world, and discusses whether the patterns of genetic variation at this genetic locus are consistent with the principal models of the settlement and linguistic diversity in this vast geographical region. Mitochondria are the seat of cellular metabolism and have their own complement of DNA. MtDNA is a tiny proportion of the genetic makeup of a human being, and has both advantages and disadvantages in population studies. It is inherited maternally, in contrast with the nuclear chromosomal DNA inherited from both parents. (Note: the mitochondria of the spermatozoon are eliminated from the egg soon after fertilization, so offspring do not inherit paternal mtDNA, although there are exceptions to this rule, as shown by Schwartz and Vissing 2002.) The maternal mode of inheritance permits the study of female lineages through time.

Despite the small size of the mitochondrial genome, each mitochondrion has many thousands of copies of mtDNA, and there are many mitochondria in each cell. The abundance of mtDNA in cells has been exploited in anthropological research on ancient, rare or degraded biological samples, including archaeological bones, old hair samples, or dried blood (Hagelberg 1994). MtDNA accumulates mutations at a relatively fast rate, and so is useful for the investigation of recent evolutionary events. These features have made mtDNA an excellent marker for geneticists interested in human evolutionary history (see Wallace 1995 for review).

Advances in molecular genetics, stimulated by genome sequencing projects, biotechnology and biomedical research, have increased the wealth of available data. There is now a huge amount of mtDNA sequence information on human populations worldwide, used to make inferences about recent human evolution, including migrations and expansions. Researchers claim to have a definitive family tree of human mitochondrial genomes (e.g. Macaulay *et al*. 1999; Herrnstadt *et al*. 2002). Unfortunately, the ease of data acquisition and high

public and scientific interest of human evolutionary studies pressure scientists to publish fast, and generate unnecessary duplications, and conclusions that are sometimes facile or indeed exaggerated. Small sample sizes or inappropriate samples can bias research, and the results of phylogenetic analyses are often presented with insufficient caveats. Moreover, researchers interested in human evolution sometimes forget that mitochondria are not solely provided for the convenience of molecular anthropologists, but are structures of vital importance for the metabolic function of cells, and involved in complex biological processes, as well as in disease and ageing. Most mtDNA studies assume that the patterns of variation in human populations are the result of migration alone, and disregard possible effects of biological selection (Elson *et al*. 2004; Ruiz-Pesini *et al*. 2004). Likewise, paternal mtDNA inheritance and recombination with maternal mtDNA (even if rare phenomena) may have profound consequences for the interpretation of phylogenetic and evolutionary studies, but are generally disregarded by population geneticists (Hagelberg 2003).

Genetic studies often appear convincing, and may fail to be challenged appropriately by archaeologists and linguists, especially if the latter are discouraged by complicated computer analyses or specialist jargon. Conversely, geneticists sometimes lack sophisticated knowledge of the history, culture and subsistence patterns of past human populations. Models drawn from genetic data are frequently bolstered by selective linguistic or archaeological data, rather than interpreted independently, resulting in circular arguments. Genetic data can yield rich insights about human prehistory if interpreted thoughtfully, and this does not necessarily require complicated statistics and computer analysis methods. Fortunately, scholars in different fields are endeavouring to improve mutual intelligibility, as shown by conferences like the one which has led to this book.

The origin of the Austronesian languages

In the present study, we analyzed mtDNA markers in population samples spanning most of the Austronesian world to shed light on the origins and expansion of the Austronesians. Geneticists frequently refer to Austronesian people, or Austronesian genes. But who are the Austronesians, and is there such a thing as an Austronesian gene? The Austronesian language family is perhaps the largest in the world. It comprises about 1000–1200 distinct languages spoken by some 270 million indigenous people distributed more than halfway around the earth, from Madagascar to Easter Island, and from Taiwan to New Zealand. Austronesian languages can be divided into a number of major subgroups, all except one of which are confined to Taiwan, where Austronesian languages are thought to have developed more than five millennia ago. One subgroup of Austronesian languages, Malayo-Polynesian, includes the languages spoken throughout most of Malaysia and Indonesia, parts of Vietnam, some parts of coastal Papua New Guinea (PNG), much of island Melanesia, and Micronesia and Polynesia (Blust 1977, 1999). Although Austronesian language speakers are very diverse culturally and biologically, it is believed that they constitute a family of related peoples. This

is consistent with the view that the Austronesian languages were not acquired by pre-existing static populations, but were spread mainly by colonizers *who shared a common origin*. The dispersal of the Austronesian languages is thought to have been driven by the spread of agriculture from a homeland in southern China, leading eventually to the development of long-range maritime economies in Island Southeast Asia and the Pacific. Scholars believe that while the descendents of the colonizers diversified and adapted to specific local conditions, they retained enough common features to remain a coherent people, often named 'The Austronesians' (Bellwood 1995; Bellwood *et al*. 1995).

Linguistic evidence suggests that there was one single expansion of Austronesian speakers into Oceania (the vast area of the Pacific east of a line drawn through Micronesia and Irian Jaya), where the so-called Oceanic subgroup of the Austronesian language is spoken. The Oceanic subgroup includes all the Austronesian languages of Melanesia (except the very west of New Guinea), most of Micronesia, and all of Polynesia. The only non-Austronesian languages spoken in Oceania, other than the languages introduced after European contact, are the Papuan languages spoken in many parts of New Guinea and island Melanesia. These non-Austronesian or Papuan languages are hugely diverse and number more than 700.

The spread of the Oceanic language speakers has been the subject of intensive study by geneticists using both classical and molecular genetic markers. Genetic research has focused largely on the question of the settlement of Polynesia and generally involves rather simplistic classifications of Oceanic peoples into the three major groups, Polynesian, Micronesian and Melanesian. The main conclusion of these studies is that the so-called Melanesian peoples are genetically diverse, whereas Polynesians are relatively homogeneous. Genetic studies have concluded that the greater genetic diversity in Melanesia, compared to Polynesia, reflects the depth of occupation of the two respective areas (see e.g. Hill and Serjeantson 1989; Cavalli-Sforza *et al*. 1994 for reviews). In this model, New Guinea and island Melanesia are areas where genetic and linguistic diversity are thought to have accumulated gradually by mutation and drift since the time of first settlement, about 50,000 years before the present (Groube *et al*. 1983; Wickler and Spriggs 1988). In contrast, the islands within the Polynesian triangle are believed to be culturally, linguistically, and biologically homogeneous because there was less time for mutations (whether linguistic or genetic) to accumulate since the expansion of a small group of founders. The first human settlement only occurred relatively recently, about 3000 years ago in the case of western Polynesia, and was only concluded with the colonization of New Zealand in the 12th century AD (Anderson 1991).

Scholars have postulated different models for the origin of Oceanic populations, with labels such as the 'express train' (Diamond 1988), the 'entangled bank' (Terrell *et al*. 2001), and alternatives such as the 'slow ~~train~~' hypothesis (~~Kayser *et al*. 2000~~). The term 'express train' was coined by Diamond to explain the rapid spread of Austronesian languages and the Lapita culture to the central Pacific (Fiji, Tonga, and Samoa). In this model, the Austronesian-speaking, Lapita pottery-

boat / Oppenheimer and Richards 2001a

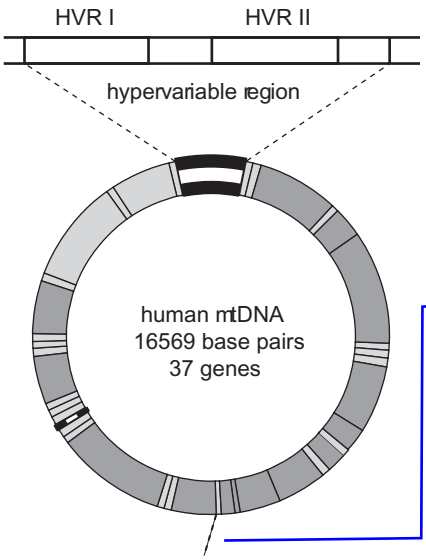
making horticulturalists with developed navigational skills presumably originated in Taiwan, and their eastward expansion into the Pacific was driven ultimately by the emergence of agriculture in southern China (Bellwood 1991). The 'express train' model assumes that the expansion of the proto-Polynesians/Austronesians was rapid and there was little genetic admixture between the recent immigrants and the earlier Melanesian/Papuan settlers of the western Pacific.

Mitochondrial DNA diversity in the Pacific

Genetic studies by Clegg and colleagues, based on globin gene polymorphisms inherited from both parents (Hill *et al*. 1989; O'Shaughnessy *et al*. 1990), indicated that the proto-Polynesians had moved into the eastern Pacific after considerable admixture with Papuan language speakers in Melanesia. These researchers observed that certain globin types causing thalassaemia (an inherited blood disorder), thought to be associated with resistance to malaria in people in malarial regions of coastal and island Melanesia, were also carried at remarkably elevated frequencies by Polynesians (including Tahitians and Maori) from islands where malaria never existed. This finding suggested that the proto-Polynesian immigrants had 'picked up' the thalassaemia genes during their sojourn in Melanesia *en route* to the eastern Pacific. This conclusion was confirmed by more recent studies, based on the male Y chromosome, that indicated that a high proportion of Y chromosomes in Polynesia (Cook Islands and Samoa) appeared to derive from Y chromosomes in coastal New Guinea and island Melanesia (Kayser *et al*. 2000). Both these studies supported an 'entangled bank' model of Pacific settlement.

In contrast, the earliest studies based on mtDNA markers provided strong evidence of the 'express train' scenario. The first mtDNA marker that was useful for research on Pacific peoples was the so-called 9-base-pair (9-bp) deletion, a harmless deletion of one of two copies of a 9-bp tandem repeat, first observed in a proportion of present-day peoples of Asian origin (Wrischnik *et al*. 1987). Hertzberg *et al*. (1989) analyzed present-day human DNA samples from various locations in the Pacific, and observed no instances of the mutation in New Guinea highlanders, while it was found at moderate frequency in peoples of coastal PNG, and at fixation levels (100 per cent frequency) in Polynesians. The 9-bp deletion appeared to be a truly Polynesian genetic marker that linked Polynesians to mainland and Southeast Asia, but not to Papuan speakers.

Shortly after this observation, one of us (E.H.) performed an analysis of mtDNA in human skeletal remains from archaeological sites in the Pacific. Thirty-eight bone samples, including some of the oldest human remains from the Pacific, were surveyed, and 21 yielded results for the 9-bp deletion locus. All the skeletal samples from Polynesian prehistoric sites had the 'Polynesian' 9-bp deletion, while the older samples, from Lapita, post-Lapita, or related sites in the western Pacific, did not have the deletion. Several of the bone samples yielded additional DNA sequence information for a highly informative part of the mitochondrial genome, called the first hypervariable region (Figure 16.1). Prehistoric bone samples from



Note: the diagram has been truncated. Either replace by original diagram or replace the little broken line by an arrow and add in the legend: "The arrow shows the position of the informative 9 base pair deletion".

Figure 16.1 Diagram of human mitochondrial DNA, showing the position of the informative 9-base pair (9-bp) deletion, a deletion of one of two copies of a 9-bp motif observed frequently in people of Asian origin. The highly variable non-coding region contains most of the sequence variability in the mitochondrial genome.

the Chatham Islands and Hawaii carried nucleotide substitutions that were different to those in previously sequenced DNA of living Europeans and other peoples, at positions 16,217, 16,247, and 16,261 of the reference mtDNA sequence (Anderson *et al*. 1981). These specific substitutions were also observed in four unrelated present-day Tahitians analyzed for comparison. Two other prehistoric individuals, from the Society Islands and Hawaii, had a similar pattern of mutations, with the exception of that at position 16,247. These results confirmed that prehistoric people within the Polynesian triangle had a homogeneous genetic heritage. The same 'Polynesian' mtDNA markers were also detected in 12 prehistoric skeletons from two archaeological sites in Easter Island, supporting the view that the island was settled originally by Polynesian navigators, and not Amerindians (Hagelberg *et al*. 1994).

In contrast, the lack of the 9-bp deletion in bone DNA of prehistoric people associated with presumably 'Austronesian' sites in the western Pacific indicated that they were genetically 'Melanesian' and not 'Polynesian'. While generally supporting the express train scenario, we suggested (with many caveats) that Papuan-language speakers had expanded ~~eastwards towards~~ to central the Pacific before the arrival of the Polynesians. This conclusion uncoupled the Polynesian expansion from the Lapita Cultural Complex (Hagelberg and Clegg 1993). Our subsequent research on present-day Pacific islanders, discussed in this chapter, has tended to confirm the view that the Polynesians do not derive directly from the so-called Lapita people.

These studies on archaeological bone samples may appear trivial compared with the vast number of sequences on modern DNA that can be generated today. However, they represent the earliest application of bone DNA typing to a question of prehistory and, with the study by Rebecca Cann and colleagues on DNA of present-day Pacific islanders, identified for the first time a unique mtDNA sequence type associated with a geographically distinct population group (Lum *et al*. 1994).

This Polynesian mtDNA type, which later became known as the 'Polynesian motif', was characterized by a suite of mtDNA mutations observed in Polynesians, namely the 9-bp deletion, and the substitutions at positions 16,217, 16,247, and 16,261. Interestingly, Redd, Stoneking and colleagues detected the 9-bp deletion, a marker previously considered to be characteristically Asian, in DNA samples of sub-Saharan Africans, and they advised caution in the interpretation of data based on just one mtDNA locus (Redd *et al*. 1995). The 9-bp deletion observed in Africans occurred together with mtDNA sequence types quite distinct from the 'Polynesian motif', suggesting that the deletion had occurred independently in Africa and in Asia. The 'Asian' type of 9-bp deletion was always associated with the Polynesian motif, or with mtDNA variants that had a subset of the nucleotide substitutions of the motif. These Asian variants included the type without the 16,247 mutation observed earlier in Polynesian bone DNA (Hagelberg and Clegg 1993), a third type, with the 16,217 mutation and the 9-bp deletion (identical to a mtDNA variant found in haplogroup B, one of the four mitochondrial lineages A, B, C, and D, previously identified in the Americas by Ballinger *et al*. 1992), and, lastly, a mtDNA variant with a substitution at position 16,189 (Melton *et al*. 1995; Redd *et al*. 1995). The Polynesian motif and related mtDNA types were subsequently observed in present-day individuals in additional locations throughout the Pacific and Southeast Asia (Sykes *et al*. 1995). The studies on mtDNA variation in living Pacific islanders supported an 'express train' mode of settlement, beginning somewhere in Asia and characterized by a rapid eastwards expansion of Austronesian, 9-bp deletion-carrying peoples to reach all corners of the Polynesian triangle.

Redd, Stoneking and colleagues (Melton *et al*. 1995; Redd *et al*. 1995) proposed that the four 'Asian' mtDNA types, variants, or lineages had developed sequentially from an ancestral form, in the following sequence (the number refers to the mtDNA position where an informative mutation is observed):

1 9-bp deletion + 16,189
2 9-bp deletion + 16,189 + 16,217 (present also in the Americas)
3 9-bp deletion + 16,189 + 16,217 + 16,261
4 9-bp deletion + 16,189 + 16,217 + 16,247 + 16,261 (Polynesian motif)

These four types can also be identified using a binomial notation, to indicate the presence (1) or absence (0) of each of the four nucleotide substitutions, on the 9-bp deletion background (identified as haplogroup B):

1 B – 1000
2 B – 1100
3 B – 1101
4 B – 1111 (Polynesian motif)

Polynesian origins in eastern Indonesia?

Based on the estimated rate of mutation of mtDNA and statistical analysis of sequence data, Melton *et al*. (1995) and Redd *et al*. (1995) proposed that the 9-bp deletion had originated in mainland Asia about 58,000 years ago (95 per cent confidence interval, CI = 12,000–104,000). An expansion out of Asia was thought to have occurred 27,000 years ago (95 per cent CI = 17,000–65,000) probably through Taiwan, reaching Indonesia but not further east. Lastly, they proposed that the mutation at 16,247 that characterized the full Polynesian motif probably happened in Indonesia about 17,000 years ago, and the early Polynesians expanded out of Indonesia about 5500 years ago (95 per cent CI = 1300–9600) and moved east to colonize the rest of the Pacific. The huge confidence intervals of these calculations make them almost meaningless, and the expansion times of peoples between Taiwan and Indonesia (sometime about 30,000 years ago according to the mtDNA data calculations) seem very large when compared with the linguistic and archaeological evidence of the time of settlement of Taiwan and the expansion of Austronesian languages in island Southeast Asia, thought to have been about 6000 years ago.

The full Polynesian motif mtDNA variant (1111), observed throughout Polynesia in present-day peoples (and in prehistoric remains as far apart as Hawaii, Chatham Islands, and Easter Island), was also detected in the Malagasy (Soodyall *et al*. 1995). Melton *et al*. (1995) observed the motif at high frequency in coastal PNG, and in a small number of Malays, as well as east Indonesian individuals, from the Moluccas and Nusa Tengaras. In east Indonesia, the motif was found in 6 of a total of 55 individuals analyzed, and it is among these 6 individuals that the genetic diversity was highest, suggesting the Polynesian motif was the oldest there. These data were seized by Richards *et al*. (1998), who revised them using a different statistic. They calculated the mean divergence time of the Polynesian motif in the following places: eastern Indonesia (number of subjects, n = 6), coastal PNG (n = 22), Samoa (n = 38), and Cook Islands (n = 48). The divergence times for the Polynesian motif were estimated to have been 17,000 years ago in east Indonesia, 5000 years in coastal PNG, 3000 years in Samoa, and 1000 years in the Cook Islands. While the ages for the expansion of the Polynesian motif in PNG and Polynesia are within the realms of possibility, the date of 17,000 years ago for eastern Indonesia is hard to reconcile with any inferred proto-Polynesian expansion event in that or any other region. Nevertheless, these authors argue strongly for the origin of the Polynesian expansion in the Indonesian archipelago (Oppenheimer and Richards 2001a, 2001b). The conclusion that the proto-Polynesians did not originate in Taiwan or China but in tropical Southeast Asia,

most probably east Indonesia, is founded ultimately on genetic data from six individuals, and must be regarded with caution.

Genetic links between Taiwan and Polynesia

As part of an ongoing collaborative research project on genetic variation in the circum-Pacific region, we performed a comparison between the results obtained from analyses of mtDNA, the male Y chromosome, and nuclear HLA (human leukocyte antigens) loci (Hagelberg *et al*. 1999a). We examined these genetic systems in samples of human DNA from China, Taiwan, Java, PNG highlands, PNG south coast, Trobriand Islands, New Britain, and Western Samoa. The Y chromosome analyses involved microsatellites, or short tandem repeats (Y-STRs), and preceded the development of many of the so-called allelic markers that have been shown to be highly informative in the Pacific. However, one of the Y-STRs (a deletion at the DYS390 locus) was shown to be characteristic of Polynesian male lineages, and was found in the Samoans (70 per cent), and at lower frequencies in coastal PNG (17 per cent), the Trobriands (9 per cent), and New Britain (19 per cent), but not in China, Taiwan, Java, or PNG highlanders. This result undoubtedly linked Melanesian and Polynesian Y chromosomes, and was later confirmed by Kayser *et al*. (2000) using additional Y chromosome markers.

The mtDNA and HLA analyses also showed a link between Polynesia and coastal and island Melanesia. In the case of the HLA analyses, the results were dramatic. A previously described HLA variant, DPB1 0501, known to occur in Asian populations, was found at high frequencies in the Han Chinese (47 per cent), aboriginal Taiwanese (70 per cent), in south PNG (71 per cent), Samoa (70 per cent), and in a staggering 98 per cent of the Trobriand Islanders. The allele was observed in only 13 per cent of PNG highlanders and 14 per cent of Javanese (and is virtually absent in Europeans and Africans) (Zimdahl *et al*. 1999). The HLA analysis showed a connection between China and Taiwan, and coastal PNG, island Melanesia, and Polynesia. Very similar results were obtained from the mtDNA analyses: the coastal and island Melanesians and the Samoans had a very elevated frequency of the mtDNA Polynesian motif (1111), whereas this type was absent in Java and the PNG highlands. The mtDNAs ancestral to the Polynesian motif could be traced back to Taiwan (the 1101 and 1100 types) and ultimately mainland Asia (the 1100 type). Both mtDNA and HLA data showed a link between Taiwan and Polynesia, to the exclusion of Java and PNG highlands, a result consistent with an express train from Taiwan model of settlement.

Mitochondrial DNA variation in the Indonesian archipelago

We extended our mtDNA survey of the Austronesian world by increasing the sample of Han Chinese, and adding new sequence information from other regions, including Tonga, Fiji, several locations in Indonesia, and Madagascar, listed in Table 16.1. All these samples were from present-day individuals, with the exception of Easter Island, where we used previously published ancient DNA sequences,

Table 16.1 List of the population samples of this study, with the number of individuals and observed mitochondrial haplogroups

		mitochondrial DNA types												
		L		*N*								*M*		
		L2	*L3*	*B4*				*B5*	*F*	*P*	*N–other*	*M–Q*	*M–other*	*Not assigned*
Population	*n*			*1111*	*1101*	*1100*	*1000*							
Easter Island	12			12										
Samoa	24			17	7									
Tonga	20			16	1							3		
Fiji	24			11	5					2		4		2
Trobriand Is.	55			26	12	3				1		2	3	8
New Britain	42			9	1					1		7	24	
PNG south coast	23			13	5							2	2	1
PNG highlands	37									11	4	17		5
Ambon	22			1	2			1	2	1			13	2
Lombok	24			2				4	4		1		13	
Manado	22			1				2	1	1	5	1	8	3
Java	53				1	3	2	13	10		1		18	5
Banjarmasin	22				2	1		3	1		2	1	11	1
Taiwan	46				9	3		3	10		2		19	
China	38				3	2		1	6		5		17	4
Madagascar	74	2	19	14							8		30	1
Total	538	2	19	122	48	12	2	27	34	17	28	37	158	32

These data are represented graphically in Map 16.I.

still the only published molecular genetic data on Easter Island (Hagelberg *et al*. 1994). A total of 537 individuals were included in this analysis.

All ~~DNA~~ subjects were surveyed for the mtDNA 9-bp deletion and hypervariable region. With the exception of the previously published Easter Island sequences, the first hypervariable segment of mtDNA (HVRI) was sequenced as described earlier (Hagelberg *et al*. 1999a, 1999b). Typically, fragments of 400 base pairs of HVRI were obtained for both DNA strands, between position 16,000 and 16,400 of the mitochondrial genome. A subset of the individuals was tested for three different informative restriction fragment length polymorphisms (RFLPs), at positions 3,594, 10,398, and 10,400, and for a base substitution at position 16,390, to help assign them to known world mtDNA haplogroups (Quintana-Murci *et al*. 1999). The results are summarized in Tables 16.1 and 16.2 and shown graphically in ~~the map in~~ Map 16.I.

The population samples of Fiji, Tonga, and Samoa were characterized by a high frequency of the Polynesian mtDNA types 1111 and 1101 (known in the literature as B4 or B4a). A small proportion of individuals, both in Fiji and in Tonga, had mtDNA type Q (part of the major world haplogroup M), a previously described 'Papuan' mtDNA type. One of the Fijians had an unknown mtDNA sequence, identical to that observed in six Trobriand Islanders (n = 55). The Asian mtDNA type F was also detected in two Fijians (n = 24). Asian type F is abundant in China, Taiwan, and Indonesia (particularly Java and Lombok). Polynesian mtDNA types (1111 and 1101) were present at low frequencies throughout the Indonesian archipelago but, in agreement with previous studies, the full Polynesian motif was only found in east Indonesia (Ambon, Lombok, and Manado).

We detected an mtDNA type characterized by the 9-bp deletion and a substitution at mtDNA position 16,140 (sometimes accompanied by 16,217) in all our Indonesian samples. This mtDNA type, known sometimes as B5, was abundant in Java and Lombok, and observed in Borneo, Manado, and Ambon, as well as in Taiwan and China (confusingly, some authors, like Kivisild *et al*. 1999, and Jin *et al*. 2005, call it B4, as the Polynesian motif, although it appears to be quite a different haplogroup, and restricted to East Asia and Island Southeast Asia, not the Pacific). This B5 type (shown in yellow in Map 16.I) might be a signature of the Austronesian expansion southwards from Taiwan to the Indonesian archipelago.

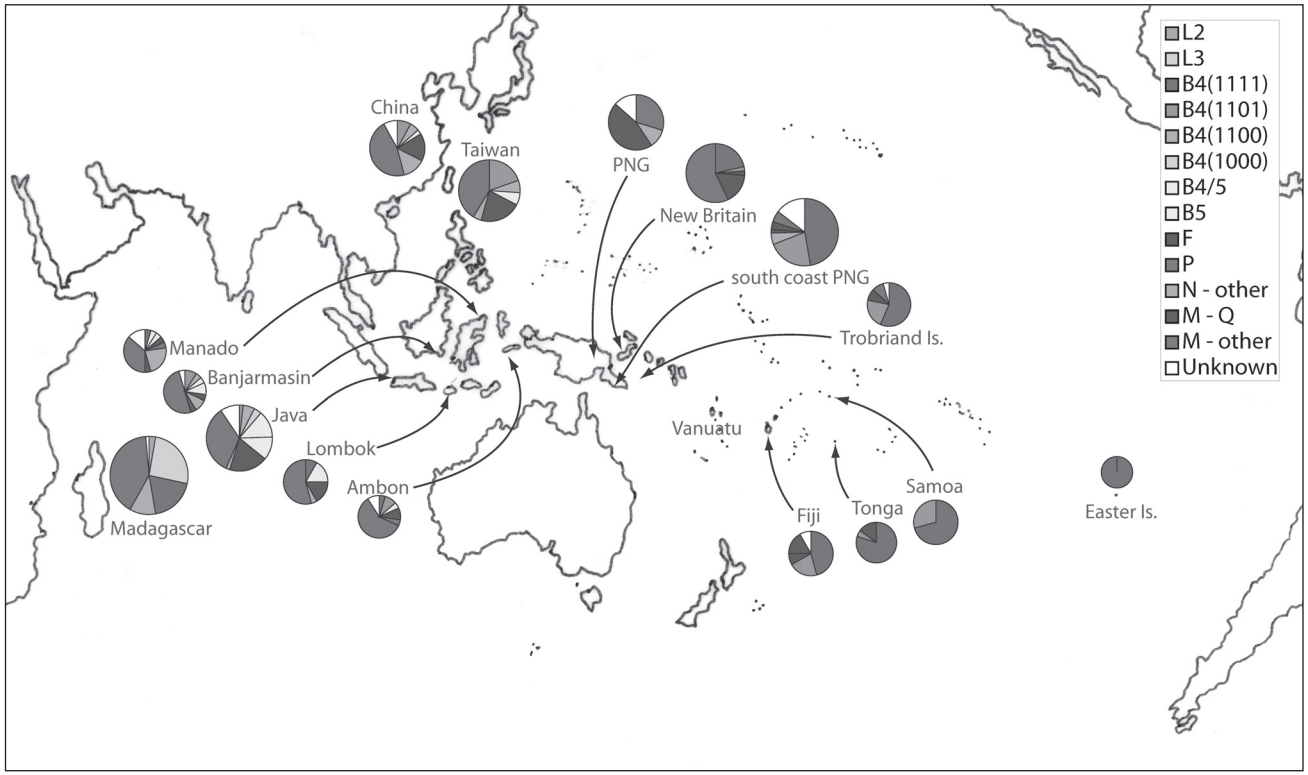
The mtDNA diversity in present-day Taiwanese aboriginals was low, just 24 different mtDNA sequence types in a sample of 46 individuals of 4 tribal groups, suggesting that these people were relatively isolated or endogamous in recent history. The view that Taiwanese have been isolated from other Asian populations is supported by other studies of mtDNA and nuclear DNA variation (Melton *et al*. 1998). Nevertheless, we observed a relatively high degree of similarity, indeed overlap, between the mtDNA types of Taiwan and the Indonesian archipelago.

The Asian M, F, and B5 types are distributed all the way from China and Taiwan to Indonesia. Indonesia has also a small proportion of the 'Papuan' Q (M) and P (N) mtDNA types in the east, as well as the Polynesian types, but the predominant haplogroups throughout the archipelago are the various subgroups of the major group M, and to a lesser extent the N subgroups F and B5, found also in Taiwan,

Table 16.2 Summary of the population statistics calculated in each population on mtDNA sequences between positions 16,081 and 16,380

	n	*9-bp %*	*No. of haplotypes*	*Haplotype diversity*	*SD*	*Mean pairwise difference*	*SD*	*Nucleotide diversity*	*SD*	*Tajima D*
Easter Island	12	100	3	0.44	0.16	0.48	0.45	0.002	0.002	–0.85
Samoa	24	100	4	0.59	0.08	0.70	0.55	0.002	0.002	–0.41
Tonga	20	85	7	0.52	0.13	4.24	2.20	0.014	0.008	–1.20
Fiji	24	67	12	0.85	0.06	5.95	2.94	0.020	0.011	–0.53
Trobriand Is.	55	75	15	0.82	0.05	4.36	2.19	0.015	0.008	–1.07
New Britain	42	24	16	0.81	0.05	7.11	3.40	0.024	0.013	0.04
PNG south coast	23	78	7	0.65	0.10	4.92	2.49	0.016	0.009	–0.64
PNG highlands	37	0	28	0.98	0.01	10.95	5.09	0.037	0.019	–0.82
Indonesia – Ambon	22	14	17	0.94	0.05	7.23	3.52	0.024	0.013	–1.51
Indonesia – Lombok	24	25	19	0.97	0.02	7.45	3.61	0.025	0.013	–1.05
Indonesia – Manado	21	14	18	0.99	0.02	8.93	4.29	0.030	0.016	–1.40
Indonesia – Java	53	36	38	0.99	0.01	9.06	4.23	0.030	0.016	–1.27
Indonesia – Banjarmasin	22	27	21	1.00	0.02	8.36	4.03	0.028	0.015	–1.21
Taiwan	46	33	24	0.94	0.02	7.57	3.60	0.025	0.013	–0.81
China	38	16	35	1.00	0.01	9.02	4.25	0.030	0.016	–1.45
Madagascar	75	21	16	0.90	0.01	6.65	3.18	0.022	0.012	–0.11
Andamans	85	0	7	0.68	0.03	2.83	1.51	0.009	0.006	0.27

Notes
The Arlequin program (Schneider *et al*. 2000) was used; SD: standard deviation; the haplotype diversity gives an estimate of the variation in each population, taking into account the sample size and the number of different haplotypes observed in the sample. The mean pairwise difference between sequences was calculated using the Tamura and Nei substitution model, assuming a gamma distribution alpha = 0.4.



Map 16.1 Map of the Pacific showing the frequency of mitochondrial DNA haplogroups in the locations including in our study. The size of the circles reflects the sample size, shown in Table 16.1.

Note: this Map should be in colour and become a Plate

reflecting millennia of human interaction within Island Southeast Asia, and the wide distribution of Austronesian languages within the region. Only haplotype B4 1101, observed in 15 per cent of our Taiwanese sample, provides a clear-cut link between the mitochondrial types in Taiwan and Polynesia (not forgetting the previously typed HLA-DPB1 type 0501, which also connects Taiwan and Polynesia), consistent with an origin of the proto-Polynesians in Taiwan, and not east Indonesia, as suggested by others (Richards *et al*. 1998; Oppenheimer and Richards 2001a, 2001b).

Interestingly, our previously published genetic data on the Andaman Islanders of the Bay of Bengal, peoples who speak languages that have no relation to the Austronesian languages or other known languages of mainland and Southeast Asia, showed that these people carried mtDNA types solely belonging to a subtype of M haplogroup distinct to the types seen in the Austronesian world, and no N types, including F or B (Thangaraj et *al*. 2003).

Table 16.2 shows some simple population statistics for our samples, calculated using the Arlequin computer program (Schneider *et al*. 2000). The haplotype diversity is an estimate of the variation of a population and takes into account the sample size and the frequency of each haplotype. It is lowest in Easter Island, followed by the rest of Polynesia and our PNG south coast sample (and the Andaman Islands). The nucleotide diversity is also lowest in these locations, and highest in the PNG highlanders, followed by Han Chinese and Indonesians, reflecting the greater time depth of these populations. The Tajima D statistic is a rough measure of population growth and is negative in growing populations, and positive or near zero in static or contracting populations, like the Andamanese. The errors of these estimates are high due to the small size of our samples.

Mitochondrial DNA variation in Madagascar

We analyzed 74 individuals from Madagascar, from the groups Merina, Betsileo, Sihanaka, and Bezanozano. Madagascar is of particular interest to Austronesian scholars because ~~it has been claimed that~~ the first permanent settlements ~~were~~ associated with incursions from Southeast Asia in the ~~2nd century AD (Burney 1993; Burney *et al*. 2004), although the more usual dates are~~ 5th–7th century (Dewar 1994). Malagasy ~~is Austronesian and Dahl (1991) claimed it was most closely related~~ to the South Barito group of languages spoken in Borneo, although more recent research ~~has linked it to~~ Sama-Bajaw (Blust 2005).

Previous studies have shown that present-day Malagasy derive from both Southeast Asian and African ancestors (Buettner-Janusch *et al*. 1973; Hewitt *et al*. 1996; Migot *et al*. 1995). Soodyall and colleagues showed that the 9-bp deletion was present in a high frequency of Malagasy in association with the Polynesian motif (Soodyall *et al*. 1995, 1996). A study by Hurles *et al*. (2005) indicated that the mtDNA and Y chromosome lineages in Malagasy groups show affinities to Southeast Asia and Africa. Their study included just 33 individuals of precisely the same sample collection as our study.

appear to be to (B) (Dahl 1991) people

(A) or at least in the 2nd century AD (Burney 1993; Burney et al. 2004)

(B) belongs to the Austronesian family, and is claimed to be closest

(C) links it to another Austronesian dialect,

We detected 16 different mtDNA sequences among our 74 Malagasy, a relatively low genetic diversity (Table 16.2). In common with Hurles *et al*. (2005), we detected both African and Southeast Asian mtDNA lineages. Slightly less than a third of the maternal lineages were African types L2 and L3, and the rest were of Asian origin, while approximately half of the male lineages were African, and half Asian (Plate 16.I). A total of 14 (19 per cent) individuals carried the full Polynesian motif (1111), but none had the ancestral B4 types or B5 types with the 9-bp deletion, or the F type, observed throughout Southeast Asia. The other N or M Asian types were similar to other sequences found in Southeast Asia, but only one haplotype, found in 8 of the Malagasy, matched precisely a mtDNA type (M/D) found at low frequency in Java, Lombok, Manado, and Taiwan samples. Our results confirm that Malagasy have both Southeast Asian and African biological influences, but the high frequency of the Polynesian motif is intriguing, as this mtDNA type is not frequent in Indonesians, the presumed Southeast Asian source population of the Malagasy. We believe that this finding, together with the observation of high frequencies of the full Polynesian motif in parts of coastal New Guinea and island Melanesia, merits serious consideration.

Polynesian outliers in coastal and island Melanesia

The vast majority of the mtDNA types we observed in the Trobriand Islands and southern PNG were Polynesian (1111 and 1101), and identical to the types found by us and others throughout the Pacific triangle, as far as New Zealand (Murray-McIntosh *et al*. 1998). The presence of the Polynesian motif in island and coastal Melanesia might be compatible with an entangled web scenario of settlement, with Austronesian newcomers with the Polynesian motif (from a presumed homeland in east Indonesia) intermingling with resident Melanesians, followed by a genetic bottleneck in Melanesia (Melton *et al*. 1998; Oppenheimer and Richards 2001a, 2001b). However, we find this conclusion unlikely. We previously suggested that the Polynesian mtDNA type might have been carried from east Polynesia westwards towards island and coastal Melanesia. The low levels of genetic diversity observed at both the mtDNA and HLA loci in island and coastal Melanesia argue for a recent expansion of people into these areas (Hagelberg *et al*. 1999a). Looking at the genetic data alone, there is a strong argument for a relatively recent influx of Polynesians (not proto-Polynesians), and the question remains whether there is sufficient archaeological or linguistic evidence, or other genetic evidence, to support the contention of a recent east to west expansion.

An extensive study of mtDNA diversity in the Solomon Islands revealed relatively high frequencies of the Polynesian motif in both Austronesian and in many of non-Austronesian-language-speaking parts of island Melanesia, with the exception of the most remote non-Austronesian-speaking areas. The study concluded that Austronesians arriving *from the west* about 3500 years ago had carried the 9-bp deletion into Bougainville and New Britain (Merriwether *et al*. 1999; Friedlaender *et al*. 2002). When we surveyed ten different islands in Vanuatu, we also found the Polynesian motif in most of that Melanesian

archipelago (Hagelberg *et al*. 1999b; Hagelberg unpublished observations). However, the Polynesian component of the population of these islands appeared evolutionarily younger than would be expected if derived from an Austronesian/ Lapita expansion 3500 years ago. Rather than relics of a west to east settlement of early Austronesian seafarers, many parts of island and coastal Melanesia appear to be 'Polynesian outliers', or pockets of Polynesia in Melanesia. As mentioned previously (Hagelberg *et al*. 1999a), the presence of the Polynesian *kava* (a Pacific shrub, *Piper methysticum*, used to make an intoxicating beverage known by the same name) as far west as Fly River, suggests that contacts with Polynesia extend considerably westwards along the PNG coast.

The question of Polynesian outliers in Melanesia is not new. As early as 1938, Peter Buck commented on the existence of Polynesian-looking people with a Polynesian culture and Polynesian dialects on many small Melanesian islands. He wrote: 'the "Polynesian outliers" are not stopping places on the route from New Guinea to Fiji but rather colonies which have been established by movements from the east and the north' (Buck 1938: 45). Buck argued for a northern trajectory of Polynesian settlement through Micronesia, with subsequent interactions between Polynesia, Micronesia and small Melanesian islands. As pointed out by Irwin (1992), the pattern of winds and currents supports this proposition, and archaeological evidence suggests multiple contacts throughout these islands. Irwin suggests that Polynesian inroads in many Melanesian islands were highly probable, but that local differences in population size and degree of isolation must have determined the degree of cultural or biological replacement and whether the Polynesian settlements lasted. He refers to Terrell (1986), who believed that, rather than being marginal phenomena, the kind of interactions that produced these apparent outliers were characteristic of Pacific prehistory.

East to west navigation in the Pacific is extremely efficient (Horridge 1995), as demonstrated by Lieutenant Bligh and other survivors of the *Bounty* mutiny, who sailed in an open boat from the central Pacific directly through the Torres Strait to Timor in east Indonesia. If Europeans could achieve this in the 18th century, why not Polynesian seafarers? Moreover, if sailing through the Torres Strait towards Indonesia was feasible, it is likely that the Polynesians would have done so. This could explain why the Polynesian motif is found in east Indonesia, but not in the west of the Indonesian archipelago, areas more inaccessible from the eastern Pacific.

This conclusion raises important questions. What proportion of the Austronesian genetic signature in coastal and island Melanesia is due to recent back-migrations? If the Polynesian mtDNA motif did not originate in east Indonesia but was taken there in recent centuries by Polynesians, where did it originate? If the ancestors of the Polynesians indeed expanded out of Taiwan, which route did they take into the Pacific? Is it possible that proto-Polynesian navigators might have taken a northern route, via Micronesia (as favoured by earlier ethnographers, discussed by Buck 1938)? These questions will not be answered by molecular genetics, however powerful its techniques, but will require the combined efforts of archaeologists, linguists, and biologists.

Conclusions

The vast majority of the maternal lineages of the inhabitants of the Polynesian triangle east of Samoa are of one single type, characterized by the so-called Polynesian mtDNA motif. The diversity of the DNA sequences is very low, suggesting a recent evolutionary history. This agrees with archaeological evidence of a recent settlement of Polynesia, and the homogeneity of the languages within Polynesia. The Polynesian mtDNA motif derives from mitochondrial types that are present in Asia. There is a clear link between the Polynesian motif and an ancestral but closely related type found in Taiwanese aboriginals (15 per cent). The full Polynesian motif and ancestral type are rare in Indonesia, being mostly confined to east Indonesia. However, these types are found at remarkably high frequencies in island and coastal PNG, accounting for 70 per cent of the mtDNA types in the Trobriand Islands, and 78 per cent in the south coast of PNG. We suggest that these sequences are not relics of the Austronesian settlement of the Pacific, but were carried in recent centuries by Polynesians into island Melanesia and coastal PNG, and as far as east Indonesia, to make these essentially Polynesian outliers.

In highland PNG there are two major mtDNA lineages, M (Q) and N (P). These lineages are ancient, and split from each other before the settlement of New Guinea. They form very distinct clusters in a phylogenetic tree of Southeast Asia and the Pacific, suggesting comparative isolation from the Indonesian archipelago. Mitochondrial types related to these 'Papuan' lineages are found in the Pacific throughout the Solomons and Vanuatu and as east as Fiji, and also westwards in Indonesia. The M and N types in Southeast Asia are related to the types found in PNG, notwithstanding the ancient split, and are found in areas where Austronesian languages are spoken today.

In Madagascar, about a third of the maternal lineages derive from Africa, and the rest from Southeast Asia. Many of the Southeast Asian mtDNA types in Madagascar are similar to those found in Indonesia. About 20 per cent of Malagasy carry the full Polynesian motif, found only at low frequencies in east Indonesia, and absent in the presumed Austronesian source population in Borneo. We suggest that the Malagasy Polynesian motif is indeed ultimately of Polynesian origin, and was carried to Madagascar not by Polynesians, but by the Malay settlers, who presumably acquired the motif through intermarriage with the descendants of the Polynesians in east Indonesia and coastal PNG. The very high proportion of the motif is tantalizing, and should not be dismissed as a genetic curiosity, but taken as possible evidence of long-range trade incursions, possibly associated with slave raids, from the Indonesian archipelago into coastal New Guinea.

The distribution of the Asian mtDNA F, and B5 haplotypes and some of the M types suggest the expansion of peoples from East Asia to Taiwan and Indonesia, with an active network of interactions that contrasts with the comparative isolation of New Guinea, which only has two principal, although ancient, mtDNA lineages. The Polynesian motif seems to be derived from an ancestral type in Taiwan,

and its exact time of entry into the Pacific is unclear, but the genetic evidence is consistent with a route of migration through the Philippines and Micronesia. The Polynesian expansion seems considerably more recent than the Lapita complex. We suggest the Polynesians continued their expansion westwards, replacing many maternal lineages in island Melanesia and the east and south coast of PNG, and reaching as far as east Indonesia. The picture suggested by mtDNA data is one of high mobility and complex interactions in the Pacific and Indian Ocean, including trade networks that continued until they were disrupted by competing Portuguese, Dutch, English, and French trading interests.

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