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# Melanesian and Asian Origins of Polynesians: mtDNA and Y Chromosome Gradients Across the Pacific

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The human settlement of the Pacific Islands represents one of the most recent major migration events of mankind. Polynesians originated in Asia according to linguistic evidence or in Melanesia according to archaeological evidence. To shed light on the genetic origins of Polynesians, we investigated over 400 Polynesians from 8 island groups, in comparison with over 900 individuals from potential parental populations of Melanesia, Southeast and East Asia, and Australia, by means of Y chromosome (NRY) and mitochondrial DNA (mtDNA) markers. Overall, we classified 94.1% of Polynesian Y chromosomes and 99.8% of Polynesian mtDNAs as of either Melanesian (NRY-DNA: 65.8%, mtDNA: 6%) or Asian (NRY-DNA: 28.3%, mtDNA: 93.8%) origin, suggesting a dual genetic origin of Polynesians in agreement with the "Slow Boat" hypothesis. Our data suggest a pronounced admixture bias in Polynesians toward more Melanesian men than women, perhaps as a result of matrilocal residence in the ancestral Polynesian society. Although dating methods are consistent with somewhat similar entries of NRY/mtDNA haplogroups into Polynesia, haplotype sharing suggests an earlier appearance of Melanesian haplogroups than those from Asia. Surprisingly, we identified gradients in the frequency distribution of some NRY/mtDNA haplogroups across Polynesia and a gradual west-to-east decrease of overall NRY/mtDNA diversity, not only providing evidence for a west-to-east direction of Polynesian settlements but also suggesting that Pacific voyaging was regular rather than haphazard. We also demonstrate that Fiji played a pivotal role in the history of Polynesia: humans probably first migrated to Fiji, and subsequent settlement of Polynesia probably came from Fiji.

## Introduction

The colonization of Polynesia which ranges from Hawaii in the north to Easter Islands in the east, Fiji in the west, and New Zealand in the south, is still a matter of debate. According to linguistic evidence, Polynesian languages are closely related to each other and belong to the Austronesian language family that can be traced back to East Asia, in particular to the present-day languages of Taiwanese Aborigines (Blust 1999; Diamond 2000). Furthermore, linguistic evidence (Gray and Jordan 2000) is usually interpreted to support the "Express-train" hypothesis (Diamond 1988), according to which Polynesian ancestors moved rapidly from Eastern Asia into the Pacific without significant admixture with Melanesians (we use the term "Melanesia" in the geographic sense, to include here the mainland of New Guinea and surrounding islands, also referred to as Near Oceania).

Archaeological evidence suggests that western Polynesian islands (Fiji, Futuna, Samoa, Tonga) were settled 2,100–3,200 years ago by people belonging to the so-called Lapita cultural complex that originated 3,000–3,500 years ago in Island Melanesia, in particular the Bismarck Archipelago (Kirch 2000). However, some archaeologists argue that the Lapita cultural complex originated about 6,000 years ago in China and thus associate the spread of Austronesian languages with the Neolithic spread of material culture, including agriculture and Lapita, from East Asia into the Pacific under the Express-train scenario (Bellwood 1978; Diamond and Bellwood 2003), whereas others suggest a strict Melanesian origin of the Lapita cultural complex (White et al. 1988; Terrell 1989; Terrell et al. 2001). Besides the 2 "extreme" models, the "Express train" assuming an Asian origin of Polynesians with no or little admixture of ingenious Melanesians and the "Entangled bank" assuming a long and complex history of human interactions starting from the first occupation of Melanesia in the Pleistocene (Terrell 1988), there are additional "intermediate" models such as the "Triple I" (Green 1991). The Triple I model assumes that components of the Lapita cultural complex are results of Intrusions of nonindigenous Asian components together with the Integration of indigenous Melanesian elements and new Innovations (Green 1991).

In contrast to the clear evidence for an Asian origin of Polynesian languages and a probable Melanesian origin of the Lapita material culture found in Polynesia, the genetic origin of Polynesians is still contentious. Studies of maternally inherited mtDNA markers have favored an Asian origin of Polynesian maternal lineages (Melton et al. 1995; Redd et al. 1995; Sykes et al. 1995; Trejaut et al. 2005) in support of the Express-train hypothesis. In contrast, studies of paternally inherited DNA markers from the nonrecombining portion of the Y chromosome (NRY) have revealed a mostly Melanesian origin of Polynesian paternal lineages (Kayser, Brauer et al. 2000; Capelli et al.

Key words: polynesia, Y chromosome, mtDNA, genetic origins, human population history.

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2001; Underhill, Passarino, Lin, Marzuki et al. 2001; Hurles et al. 2002) supporting the "Slow Boat" hypothesis (Kayser, Brauer et al. 2000). The Slow Boat model assumes that Polynesian ancestors originated in Eastern Asia but mixed extensively with indigenous Melanesians before colonizing the Pacific (Kayser, Brauer et al. 2000). Unfortunately, a similar term "Slow boat to Melanesia" was subsequently used to suggest a Southeast Asian genetic origin of Polynesians in the Pleistocene based on mitochondrial DNA (mtDNA) evidence (Diamond 2001; Oppenheimer and Richards 2001). Studies of autosomal DNA markers suggest different scenarios depending on the markers used, for example, a Melanesian origin of Polynesian hemoglobin genes (Hill et al. 1985, 1987) versus an Asian origin of Polynesian human leucocyte antigen (HLA) genes (Mack et al. 2000; Mack and Erlich 2005).

In this study, we have used NRY and mtDNA markers to investigate the paternal and maternal genetic origin of over 400 individuals from 8 different Polynesian island groups by comparing them with over 900 individuals from Melanesia, Southeast and East Asia, and Australia. This significant increase over previous studies, both in populations and markers analyzed, provides new insights into the history of the human colonization of the Pacific.

## Material and Methods

### Samples

Samples used were described previously (Kayser, Brauer et al. 2000; Kayser et al. 2001; Kayser et al. 2003) except for the following newly sampled groups: Tuvalu in Polynesia—from the 8 islands of Tuvalu (Funafuti, Nanumaga, Nanumea, Niutao, Nui, Nukufetau, Nukulaelae, Vaitupu), (sampled by R.B.R); Futuna in Polynesia from the 2 kingdoms Alo (villages Vele, Mala'e, Taoa, Ono) and Sigave (villages Vaisei, Tavai, Toloke, Fiua, Leava), (sampled by C.M-F); Bereina—a Roro and Mekeo-speaking group (Austronesian) from the south coast of Papua New Guinea (PNG, Central Province) and Kapuna—a Koriki-speaking group (non-Austronesian) from the Gulf Province of PNG (both sampled by W.S. and M.K.); and Sumatra—a Malay-speaking group from the Sungai Pakning village of the Riau Province of Sumatra, Indonesia (sampled by D.G.). These new samples were collected as cheek swabs, and DNA extractions were performed using a salting out protocol (Kayser et al. 2003). In addition, Polynesian blood samples from Fiji, Western Samoa, Cook, Niue, Tokelau, and Tonga, described elsewhere (Trent et al. 1986; Trent, Buchanan et al. 1988), were DNA purified using conventional phenol-chloroform extraction.

### Genotyping and Sequencing

In total, we analyzed 35 NRY binary markers including 26 as described previously (Kayser, Brauer et al. 2000; Kayser et al. 2001, 2003), with the alteration of M9 and RPS4Y typed here in a multiplex polymerase chain reaction (PCR)-restriction fragment length polymorphism with 56 °C annealing temperature during PCR and 45 °C incubation temperature during restriction enzyme digest. In addition, 9 markers were typed: M226, M254, M296 (identified by P.J.O. at the Stanford Genome Technology Center and first described here); M353, M387 (identified by P.A.U. and A.A.L. and first described here); P34 (Karafet et al. 2005); M177 (Underhill et al. 2000); M214 (Underhill, Passarino, Lin, Shen et al. 2001); and M134 (Cordaux et al. 2004). Typing details for these additional markers are provided in Table S1, Supplementary Material online (except for M134, which was typed as described by Cordaux et al. [2004]). In all, 7 NRY microsatellites (y-chromosomal short tandem repeat polymorphims, Y-STRs) were typed as described previously (Kayser, Brauer et al. 2000), whereas the duplicate DYS385 Y-STR loci were typed separately as described by Kittler et al. (2003). The hypervariable region 1 (HVR1) of mtDNA was amplified using primers L16001 and H16410 (Handt et al. 1996; Cordaux et al. 2003), sequenced using Big Dye chemistry as recommended by the manufacturer (Applied Biosystems, Foster City, CA), and products were separated on an ABI 377 or ABI 3700 DNA Sequencer (Applied Biosystems). Both DNA strands were sequenced separately, and in case of the "C-stretch" in the region 16184–16193, both strands were sequenced twice. Sequences were analyzed using the SeqManII software from the Lasergene software package (DNASTAR Inc., Madison, WI). The mtDNA 9-bp deletion was analyzed as described elsewhere (Redd et al. 1995). The phylogenetic relationships of the NRY and mtDNA markers used here are shown in Figure S1 (Supplementary Material online).

### Statistical Analyses

Median-joining networks were constructed as described previously (Kayser, Brauer et al. 2000) using the software Network (http://www.fluxus-engineering.com/sharenet.htm), also used for age estimation. The software package ARLEQUIN (http://lgb.unige.ch/arlequin/), (Schneider et al. 2000) was applied for various diversity estimations as well as $F_{ST}/R_{ST}$ calculation. The commercially available software packages SPSS and STATISTICA were used for correlation analyses, $\chi^2$ exact test, and multidimensional scaling (MDS) analysis. Bayesian-based coalescence analyses of Y-STR haplotypes were performed using the software BATWING (Wilson et al. 2003) with the following parameter: a gamma distribution was used as a prior distribution for the mutation rate of each STR. The 2 parameters $\alpha$ and $\beta$ of the gamma distribution were assigned based on locus-specific mutation rates estimated from family studies (Kayser, Roewer et al. 2000; Dupuy et al. 2004): DYS19 ($\alpha$ 5, $\beta$ 2763), DYS390 ($\alpha$ 12, $\beta$ 2233), DYS391 ($\alpha$ 10, $\beta$ 2182), DYS392 ($\alpha$ 1, $\beta$ 2182), DYS392 and DYS393 ($\alpha$ 1, $\beta$ 2182), DYS389I ($\alpha$ 5, $\beta$ 2192), and 389II ($\alpha$ 6, $\beta$ 2192). The 2 parameters describing the population growth ($\alpha$ and $\beta$ in the model) have been set as $\alpha$ prior gamma (2,400) and $\beta$ uniform (0.1, 0.2).

## Results and Discussion

### Polynesian Paternal Ancestry

The 35 NRY binary markers analyzed here define 24 NRY haplogroups, of which 18 are found in Polynesia, 13 in Melanesia, 17 in Asia, and 6 in Australia (fig. 1; Table S2, Supplementary Material online). Of the NRY

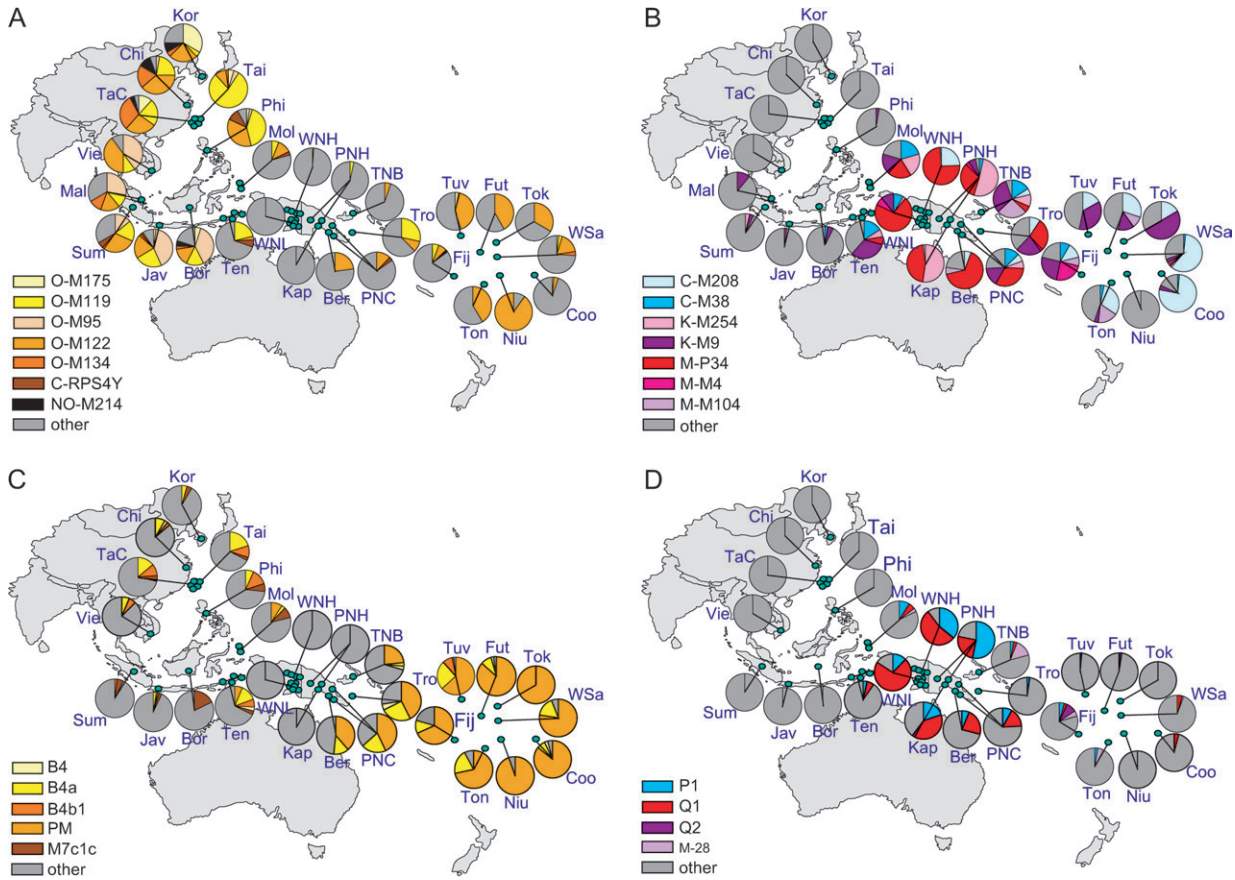


FIG. 1.—Frequency distribution of (*A*, *B*) NRY and (*C*, *D*) mtDNA haplogroups found in Polynesia with a genetic origin in (*A*, *C*) Asia or (*B*, *D*) Melanesia.

haplogroups observed in Polynesia, we had identified previously a Melanesian origin for C-M38, C-M208, and M-M4 (Kayser et al. 2001, 2003). Because P34 and M254 occurred on the background of M4 and M230 (Figure S1a, Supplementary Material online), respectively, both of which have putative Melanesian origins (Kayser et al. 2001, 2003), we assume an origin of M-P34 and K-M254 in Melanesia. Furthermore, a Melanesian origin of haplogroup M-M104 is suggested by its frequency distribution (Table S2, Supplementary Material online; fig. 1), the associated Y-STR haplotype diversity that is higher in Melanesia (1.00 $\pm$ 0.08) than in Polynesia (0.92 $\pm$ 0.05), and its phylogenetic origin on the background of the Melanesian haplogroup M-M4 (Figure S1a, Supplementary Material online). We also inferred a Melanesian origin of Polynesian Y chromosomes belonging to haplogroup K-M9 (and thus lacking any of the other known markers on the M9 background; Figure S1a, Supplementary Material online) because 22 of 27 (81.5%) Polynesian K-M9 haplotypes cluster with Melanesian K-M9 haplotypes in a median-joining network (fig. 2*B*). Asian and Australian haplotypes are not shared with Polynesian haplotypes and appear more distant to Polynesian haplotypes in the network (fig. 2*B*), whereas only one haplotype is shared between Polynesians and Melanesians. Additionally, analyses of the mean number of pairwise differences between Y-STR haplotypes associated with Polynesian K-M9 and Melanesian K-M9, as well as between Polynesian K-M9 and all Asian haplogroups on the background of M9 (O-M175, O-M122, O-M119, O-M134, O-M95, K-M214), support a closer relationship of Polynesian K-M9 with Melanesian K-M9 haplotypes than of Polynesian K-M9 haplotypes with any Asian M9 subgroups (analyses not shown). Thus, Polynesian K-M9 chromosomes are likely to be of Melanesian origin. Overall, 7 NRY haplogroups found in Polynesia are of Melanesian genetic origin: C-M208, C-M38, K-M9, K-M254, M-M4, M-P34, and M-M104 (fig. 1). In summary, 65.8% of the Polynesian Y chromosomes can be traced back to Melanesia, of which 34.5% is accounted for by haplogroup C-M208 and 17.9% by K-M9 (Table S2, Supplementary Material online; fig. 1).

We and others (Su et al. 1999; Kayser, Brauer et al. 2000; Kayser et al. 2001, 2003) have previously identified an Asian origin for the NRY haplogroups O-M175, O-M122, O-M134, O-M95, and O-M119, and an Asian origin was also suggested for haplogroups C-RPS4Y and NO-M214 (Karafet et al. 2002). We observed all 7 Asian haplogroups in Polynesia (Table S2, Supplementary Material online; fig. 1). Altogether, 28.3% of Polynesian Y chromosomes could be traced back to Asia, of which 24.3% is contributed by a single haplogroup, O-M122 (Table S2,

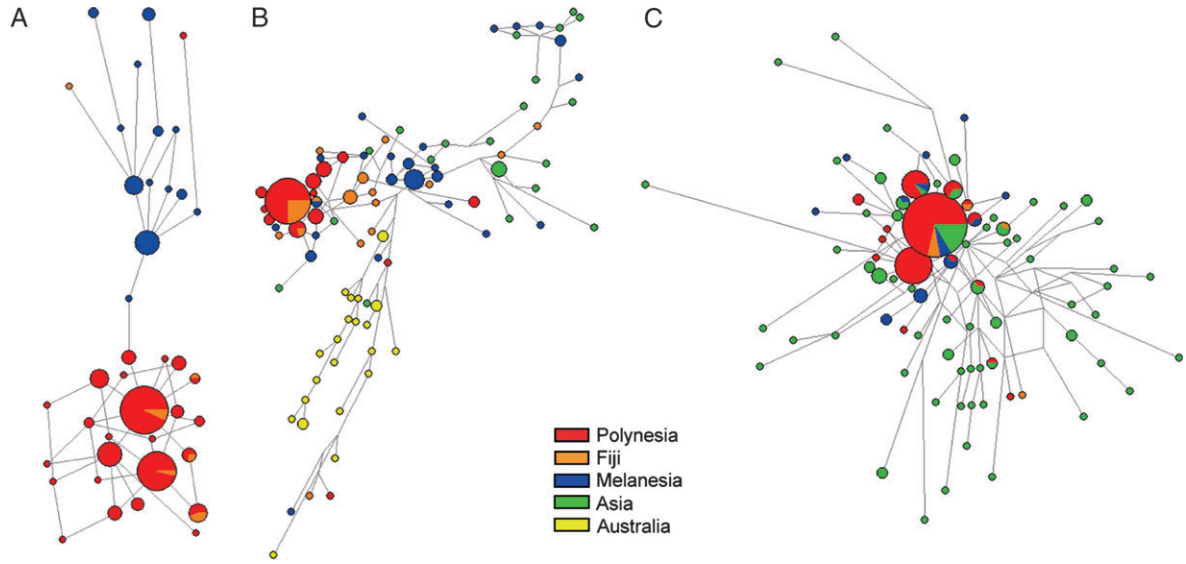


FIG. 2.—Haplotype networks based on 7 Y-STRs associated with 3 major Polynesian NRY haplogroups: (*A*) C-M208, (*B*) K-M9, and (*C*) O-M122. Circles denote haplotypes, with the area of the circle proportional to the number of individuals carrying the particular haplotype. Lines denote mutation steps, and networks were weighted according to Y-STR mutation rates.

Supplementary Material online; fig. 1). Thus, overall 94.1% of Polynesian Y chromosomes analyzed here can be classified as of either Melanesian (65.8%) or Asian (28.3%) origin.

Of the remaining NRY haplogroups found in Polynesia, 2 (R-M173 and F-M89) most likely represent European admixture because comparison of their Y-STR haplotypes to the Y-STR Haplotype Reference Database (http://yhrd.org/index.html) revealed that 83–100% of the matches involved exclusively European haplotypes (data not shown). Haplogroup K-M353 is likely to be of Fijian origin and is described in more detail below. One additional individual from the Cook Islands had the SRY10831a mutation and was ancestral for M9, M89, and RPS4Y, but the y-chromosome alu repeat polymorphism locus could not be amplified after several attempts and for unknown reasons. Unfortunately, the lack of DNA for this sample omitted us from additional genotyping to resolve the Y chromosome lineage of this single individual in more detail.

## Polynesian-Specific NRY Haplogroups

Two NRY markers were restricted to Polynesia. One, M353, was found in 4 Fijians and 1 Futunan and most likely arose in Fiji as the associated Y-STR haplotypes are all different among the 4 Fijians, whereas the single Futunan Y-STR haplotype is identical to a Fijian haplotype. The other marker consists of a triplication event involving the DYS385 microsatellite (which usually exists as duplicated copies) on an O-M122 Y chromosome background. This DYS385 triplication occurred in all 8 Polynesian populations analyzed but not anywhere outside Polynesia (table 1). Separation analysis of the different DYS385 copies according to the procedure of Kittler et al. (2003) revealed that the shortest allele (always 12 repeats in lengths) belongs to the DYS385a copy, whereas the other 2 alleles (mostly 13 and 16 repeats) belong to the DYS385b and the new DYS385c copy (which therefore most likely originated from the DYS385b copy). This consistent pattern, together with the O-M122 association, suggests a single origin of this DYS385 triplication in Polynesia. The Y-STR haplotype diversity associated with DYS385tri/O-M122 was highest in Tuvalu, suggesting that Tuvalu is the likely place of origin (table 1). In addition, a median-joining network of the 10 Y-STR haplotypes observed in the 56 individuals carrying this marker provides evidence for a recent expansion with a widespread most frequent haplotype (occurring in 7 of 8 Polynesian populations with an overall frequency of 50%) and a star-like structure (Figure S2, Supplementary Material online). This Y-STR haplotype (including the 3 DYS385 alleles) was also frequent (20%) in an independent sample of Pacific Islanders, although Y-SNP data were not reported (Shepherd et al. 2004). The age of this lineage is estimated to be 3,700 years (95% credible interval 2,100–6,500 years based on the BATWING analysis; dates based on other methods are given in Table S3, Supplementary Material online). Thus, the DYS385 triplication associated with haplogroup O-M122 provides clear evidence not only for a Polynesian founder effect but also for a recent west-to-east expansion within Polynesia.

## Polynesian Maternal Ancestry

The mtDNA sequence data together with data from the 9-bp deletion allowed us to infer 31 mtDNA haplogroups, of which 10 are found in Polynesia, 12 in Melanesia, and 26 in Asia (Table S4, Supplementary Material online; fig. 1). Five Polynesian mtDNA haplogroups have an Asian origin: B4, B4a, B4b1, Polynesian motif (PM), and M7c1c (Kivisild et al. 2002) resulting in an overall estimate of 93.8% of Polynesian mtDNAs being of Asian origin, of which 77.6% accounted for by a single haplogroup (the PM). In addition, 4 Polynesian mtDNA haplogroups have a probable Melanesian origin: P1, Q1, Q2 (Friedlaender et al. 2005), and M28 (Merriwether et al. 2005), resulting in an overall

**Table 1**
**Frequencies and Associated Y-STR Diversity of the DYS385 Triplication on Haplogroup O-M122**[a]

| Population | *N* | M122/DYS385 Triplication Count (%) | Proportion of Total O-M122 in % | Haplotype Diversity[b] | Haplotype MPD[b] |
|---|---|---|---|---|---|
| Cook | 66 | 1 (1.5) | 33.3 | — | — |
| Niue | 10 | 9 (90.0) | 100.0 | 0.56 ± 0.17 | 0.61 ± 0.60 |
| Tokelau | 6 | 2 (33.3) | 100.0 | 1.00 ± 0.50 | 2.00 ± 0.00 |
| Samoa | 61 | 4 (6.6) | 36.4 | 0 | 0 |
| Tonga | 28 | 12 (42.9) | 100.0 | 0.68 ± 0.15 | 1.17 ± 1.17 |
| Futuna | 50 | 10 (20.0) | 47.6 | 0.20 ± 0.15 | 1.00 ± 2.02 |
| Tuvalu | 100 | 14 (14.0) | 34.1 | 0.76 ± 0.12 | 2.70 ± 2.18 |
| Fiji | 94 | 4 (4.3) | 57.1 | 0.50 ± 0.27 | 2.00 ± 2.19 |

[a] individuals with 3 copies of DYS385 but 2 identical alleles were not included here due to technical problems in unequivocally differentiating those from individuals with 2 copies. Thus, numbers provided are most likely underestimated.
[b] based on 10 Y-STRs.

estimate of 6% of Polynesian mtDNAs with a Melanesian origin. Altogether, we could classify all but one of the Polynesian mtDNAs analyzed as either Asian (93.8%) or Melanesian (6%) in origin (Table S4, Supplementary Material online; fig. 1); the remaining individual belonged to haplogroup T, which likely represents recent European admixture (Macaulay et al. 1999).

## Dual Genetic Origins of Polynesians

Based on the NRY and mtDNA data, we identified a dual genetic heritage of Polynesians, containing both Melanesian and Asian genetic components. However, these 2 components differed between the paternally inherited Y chromosome and the maternally inherited mtDNA (table 2). Overall in Polynesia, the proportion of Melanesian haplogroups was 11-fold higher for Y chromosomes (65.8%) than for mtDNAs (6%), and of Asian haplogroups was more than 3-fold higher for mtDNAs (93.8%) than for Y chromosomes (28.3%). The proportions of Asian NRY and mtDNA haplogroups in Polynesia were not correlated (Spearman $R = 0.43$, $P = 0.34$, excluding Tokelau due to small sample size), and the correlation for Melanesian haplogroups was somewhat higher but not statistically significant ($R = 0.60$, $P = 0.21$, excluding Niue and Tokelau for small sample size). In addition, no correlation between all NRY haplogroups and mtDNA sequence for Polynesian populations was observed (Mantel test based on $F_{ST}$: $R = 0.243$, $P = 0.25$, excluding Niue and Tokelau). The discrepancy between the amount of Asian versus Melanesian NRY and mtDNA haplogroups of Polynesians could reflect uxorilocal (matrilocal) residence in ancestral Polynesian society (Hage 1998; Hage and Marck 2003), as this would have resulted in more admixture of Asian migrants with Melanesian males than females before their colonization of the Pacific. This explanation finds some support in the proportions of Melanesian and Asian haplogroups in the coastal and island Melanesians included in this study (table 2); those Island Melanesians received a larger contribution of Asian mtDNAs (29.4–72.5%) than of Asian Y chromosomes (5.3–37.7%) from the ancestral Polynesians, as expected given that the respective societies (Tolai, Trobriand Islanders, Bereina-Mekeo) are of virilocal (patrilocal) residence.

Moreover, inferred European genetic components were 15-fold higher for the Y chromosome (4.5%) than for mtDNA (0.3%), in keeping with the expectation that European men would have contributed more genes to Polynesians than European women. The fact that we find lower levels of inferred European ancestry in Polynesia

**Table 2**
**Melanesian and Asian NRY/mtDNA Haplogroups in Polynesia and Island/Coastal Melanesia**[a]

| Region/Population | Asian NRY-DNA | Asian mtDNA | Melanesian NRY-DNA | Melanesian mtDNA |
|---|---|---|---|---|
| Cook | 5.2 | 95.8 | 81.8 | 4.2 |
| Niue | 90.0 | 94.7 | 0 | 0 |
| Tokelau | 33.3 | 100 | 66.7 | 0 |
| Samoa | 25.8 | 94.0 | 69.4 | 6.0 |
| Tonga | 41.4 | 92.3 | 55.2 | 7.7 |
| Futuna | 42.0 | 97.8 | 54.0 | 2.2 |
| Tuvalu | 45.0 | 98.3 | 53.0 | 1.7 |
| Fiji | 14.0 | 79.6 | 78.5 | 20.5 |
| Polynesia (all) | 28.3 | 93.8 | 65.8 | 6.0 |
| Tolai New Britain | 5.3 | 29.4 | 94.7 | 20.6/70.6[b] |
| Trobriand | 37.7 | 72.5 | 62.3 | 2.5/5.0[b] |
| Bereina | 22.9 | 51.6 | 77.1 | 29.0 |
| PNG Coast | 15.2 | 63.3 | 75.8/81.8[b] | 24.5/32.6[b] |
| Island/Coastal Melanesia (all) | 9.0 | 19.0 | 90.0/90.8[b] | 60.6/70.8[b] |

[a] Including haplogroups observed in Polynesia as depicted in figure 1.
[b] Including haplogroups as depicted in figure 1 plus additional haplogroups P2, P3, Q3 (mtDNA), K-M230, and K-M226 (NRY) of Melanesian origin but not found in Polynesia.

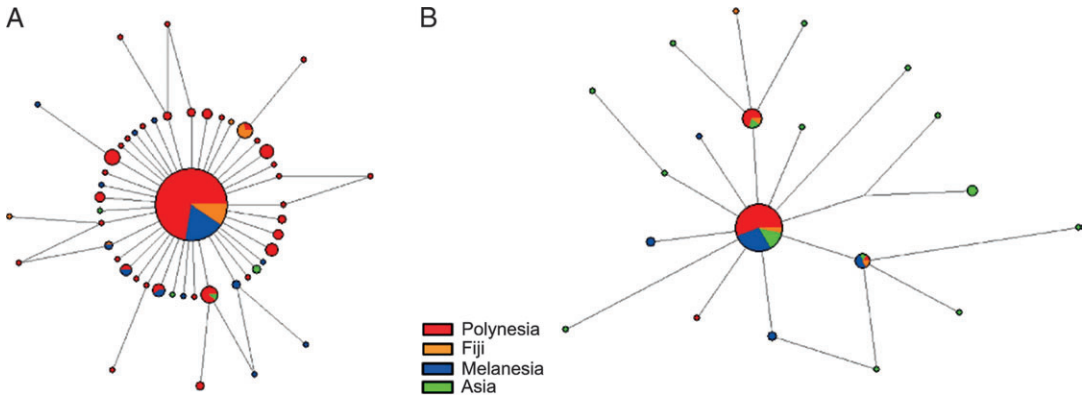


FIG. 3.—Haplotype networks based on mtDNA sequences associated with 2 major Polynesian mtDNA haplogroups: (*A*) PM and (*B*) B4a. Circles denote haplotypes, with the area of the circle proportional to the number of individuals carrying the particular haplotype. Lines denote mutation steps.

than reported in other studies (Hurles et al. 1998; Capelli et al. 2001) may reflect the care taken to exclude individuals whose genealogical history indicated European ancestry. In our study, we only used Polynesian individuals with Polynesian family history in both parental lines (Trent et al. 1986). We also found no evidence for a genetic contribution from the New World as proposed first by Heyerdahl (1950) and identified previously by Y chromosome analysis but interpreted as a recent genetic contribution (Hurles et al. 2003): the most frequent NRY haplogroups in Native Americans are subgroups of haplogroup P-M74/M45(xR-M173) (Lell et al. 2002), which was not observed in our Polynesian samples.

## Genetic Heterogeneity among Polynesian Populations

We analyzed the frequency distributions of the Asian and Melanesian mtDNA and NRY haplogroups in Polynesia (table 2), to ascertain if there is significant genetic heterogeneity among Polynesian groups. With respect to mtDNA, haplogroups PM and B4a vary significantly in frequency ($\chi^2$ exact test: $P = 0.0017$ and $P = 0.03$, respectively, based on 100,000 Monte Carlo simulations). Sample sizes for the remaining mtDNA haplogroups are too small to test for significant differences in frequency (Table S4, Supplementary Material online), although the frequency of Melanesian mtDNA haplogroups is higher in Fiji (20.5%) than elsewhere in Polynesia (0–7.7%) (table 2 and fig. 1). With respect to NRY haplogroups, O-M122, K-M9, M-M104, and C-M208 showed highly significant frequency differences among Polynesian groups ($P < 0.0001$, M-M104: $P = 0.00019$); the other haplogroups either occurred sporadically or only in single populations. Thus, all haplogroups for which sample sizes are sufficient exhibit significant frequency differences among Polynesian groups. This most likely reflects founder events during the colonization of the various islands and/or subsequent genetic drift due to small population sizes. However, many of these haplogroups also show gradients in frequency across the Pacific (fig. 4), with the frequency of one haplogroup (C-M208) significantly and positively correlated with longitude (Spearman's $R = 1$, $P < 0.01$), and the correlations for 2 other haplogroups (K-M9 and PM) approaching statistical significance ($R = -0.77$, $P = 0.07$ and $R = 0.68$, $P = 0.09$, respectively). Such frequency gradients are not expected if founder events occurred at random across the Pacific but instead suggest that there was an increasing tendency for founder events as the more eastern islands were colonized. This interpretation receives further support from the previous observation of an inverse correlation between mtDNA and Y-DNA diversity and the time of colonization of Pacific islands (Hurles et al. 2003). It is also consistent with a study that found a significant association between migration distance from Southeast Asia and loss of heterozygosity for autosomal microsatellite loci, which included a small number of Polynesian groups (Lum et al. 2002). Thus, Pacific voyaging was regular rather than haphazard.

We also noticed striking differences in genetic diversity between groups from different Polynesian islands and for different measures of diversity (Table S5, Supplementary Material online). Diversity of NRY haplogroups and mtDNA HV1 sequences declines from west-to-east (fig. 4), with negative correlations that are approaching statistical significance (Spearman, NRY: $R = -0.77$, $P = 0.07$; mtDNA: $R = -0.71$, $P = 0.07$). Thus, our data provide evidence for a west-to-east settlement of Polynesia with additional evidence from the frequency and diversity distribution of the Polynesian DYS385 triplication and the Polynesian haplogroup K-M353 (see above).

## Time of Migration

Are the different Melanesian and Asian NRY and mtDNA haplogroups in Polynesia today the result of a single wave of migration or multiple migrations? To address this question, we performed network analyses as described previously (Kayser, Brauer et al. 2000), and demographic analyses, for the most frequent Polynesian NRY (C-M208, K-M9, M-M4, O-M122) and mtDNA (PM and B4a) haplogroups using associated Y-STR and mtDNA sequence haplotypes, respectively (figs. 2 and 3). All networks exhibit a consistent pattern with one Polynesian haplotype at high frequency that is shared between all (or almost all) Polynesian groups, and most other Polynesian haplotypes connected via 1 or 2 mutational steps only (figs. 2 and 3; Table S3, Supplementary Material online). This star-like pattern, identified in 4 independent NRY and 2 independent mtDNA haplogroups, indicates a strong founder effect with subsequent population expansion in Polynesia

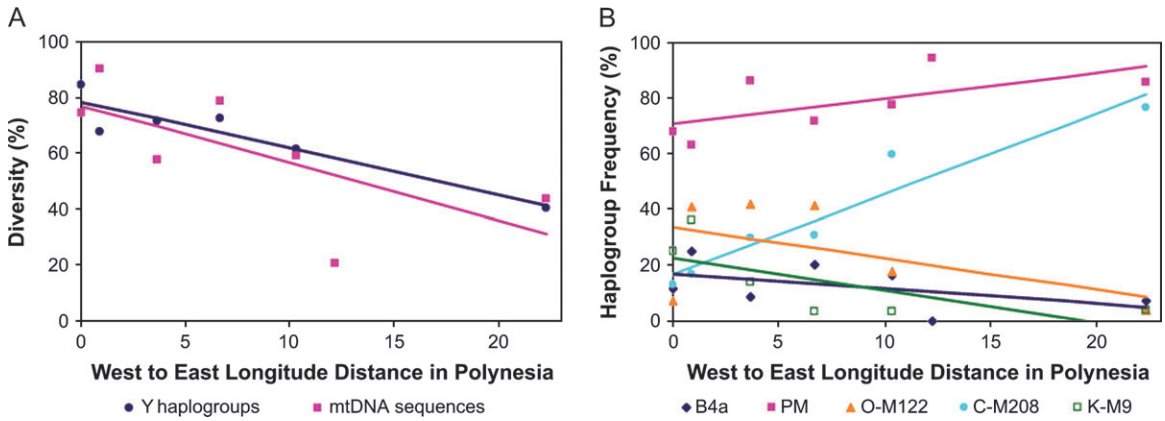


FIG. 4.—Correlation between geographic distances measured as west-to-east longitude within Polynesia and (*A*) the frequencies of major Polynesian NRY/mtDNA haplogroups and (*B*) the overall diversity of NRY haplogroups and mtDNA sequences, for Polynesian populations. Niue (NRY) and Tokelau (NRY, mtDNA) were omitted due to small sample size.

and implies that the number of founding Y-STR and mtDNA haplotypes per haplogroup was low in Polynesia. Evidence for the Polynesian founder effect was also reported previously based on other genetic marker systems (Trent, Mickleson et al. 1988; Flint et al. 1989).

Various methods were used to date the entry of the NRY and mtDNA haplogroups into Polynesia (Table S3, Supplementary Material online). Assuming a generation time of 30 years (males/NRY) or 25 years (females/mtDNA) (Fenner 2005), the time back to the most recent common ancestor (TMRCA) in Polynesia varied from 6,200 to 12,000 years between haplogroups using the Batwing approach for NRY data and 5,500–6,600 using the network approach for mtDNA data (Table S3, Supplementary Material online, also for results of additional dating methods). Because the number of founding mtDNA and Y-STR haplotypes is unknown, the TMRCA reflects an upper bound for the entry time into Polynesia. The BATWING analysis of NRY data also yielded an overall start of expansion time of 5,200 (95% credible interval: 3,300–8,000) years, for all Polynesians across all NRY haplogroups. There is some indication that Y chromosomes belonging to haplogroup K-M9 may have entered Polynesia before all other haplogroups (Table S3, Supplementary Material online); however, the dates for K-M9 should be viewed cautiously because this is an "undifferentiated" paragroup (i.e., defined by the derived allele for the M9 marker and the ancestral allele for all other markers tested on the M9 background) and hence may overestimate the diversity in Polynesia relative to other phylogenetically terminal haplogroups. Otherwise, the dates for both NRY and mtDNA haplogroups are all broadly consistent with each other within the different methods applied, suggesting a single major migration from Melanesia to Polynesia.

Patterns of haplotype sharing do indicate some differences between haplogroups of Asian and Melanesian origin. A number of Y-STR haplotypes on the background of O-M122 (of Asian origin) are shared between Polynesia and Asia (8.0%), Polynesia and Melanesia (16%), as well as Melanesia and Asia (4.1%), including 2 haplotypes (2.4%) shared between all 3 geographic regions (Table S3, Supplementary Material online; fig. 2), reflecting the somewhat recent spread of O-M122 Y chromosomes from Asia to Melanesia and Polynesia. However, no haplotype sharing between geographic regions was observed for haplogroups C-M208 and M-M4, which are of Melanesian origin, and only one haplotype (2%) was shared between one Fijian and one Melanesian for K-M9, suggesting a more ancient spread of those NRY haplogroups from Melanesia to Polynesia. With respect to mtDNA haplogroups, there is again sharing of haplotypes between Polynesians and Melanesians for Asian haplogroups B4a and PM (Table S3, Supplementary Material online), whereas there is no sharing of haplotypes between Polynesians and Melanesians for the Melanesian haplogroup M28 (although the sample size for M28 is low, see Table S4, Supplementary Material online), suggesting a more recent spread of mtDNAs from Asia into Polynesia and a more ancient spread of mtDNAs from Melanesia into Polynesia.

If Polynesian ancestors did migrate to coastal/island Melanesia from Asia, mixed with coastal/island Melanesians (thereby obtaining Melanesian Y chromosomes and mtDNA types and leaving behind "Asian" Y chromosomes and mtDNA types), and then left Melanesia and colonized Polynesia, then the degree of haplotype sharing should be the same for haplogroups of Asian versus Melanesian origin because there was a single "separation" of an ancestral group of Polynesians from ancestral Melanesians. The fact that there is extensive sharing of Asian haplotypes, but not Melanesian haplotypes, between Polynesians and Melanesians today, therefore, could indicate that Melanesian haplotypes were present earlier in Polynesia (perhaps in Fiji), leading to greater divergence between Polynesians and Melanesians for haplogroups of Melanesian origin than for haplogroups of Asian origin. However, there are large gaps in the sampling of coastal/island Melanesians, which would need to be filled in before one could be certain that there is truly a difference in patterns of haplotype sharing between Polynesians and Melanesians for haplogroups of Asian versus Melanesian origin.

## Fijian Genetic History

Fiji represents the most western islands of Polynesia, and Fijians share some features of physical and cultural

traits with Melanesians (for overview see Frost 1979), whereas the Fijian dialects are closely related to Polynesian languages (Ross et al. 2003). The NRY and mtDNA data also indicate a closer relationship between Fijians and Melanesians than between other Polynesians and Melanesians. This is evidenced by the following: 1) the highest overall frequency of mtDNA haplogroups of Melanesian origin in Polynesia (20.5%) is observed in Fiji—it is also the only Polynesian group where all 4 Melanesian mtDNA haplogroups observed in Polynesia are found (table 2 and fig. 1); 2) Fiji displays the highest diversity of Melanesian NRY haplogroups in Polynesia and shows the second highest frequency of Melanesian haplogroups (78.5%) in Polynesia with all 5 major haplogroups being present (table 2 and fig. 1); 3) in the K-M9 network, most Fijian haplotypes are more closely associated with Melanesian than with Polynesian haplotypes (fig. 2*C*); 4) Fiji displays the highest frequency of M-M4 (24.3%), which elsewhere only exists in Melanesia (2%), where it most likely originated but today mostly occurs as subgroup M-P34 (28–74%). Thus, M-M4 in Fiji represents an old Melanesian lineage that left Melanesia prior to the M-P34 mutation rising in appreciable frequency. On the other hand, there is also a strong Polynesian association of Fijians: 1) in the C-M208 network, all but one of the Fijian haplotypes are shared with Polynesians (fig. 2*A*); 2) in the O-M122 network, 2 Fijian haplotypes (5 of 7 men) are shared with other Polynesians (fig. 2*B*); 3) the DYS385 triplication, for which a Polynesian origin is assumed, was observed in Fiji but not in Melanesia (table 1); 4) some M9 haplotypes are shared with other Polynesians (fig. 2*C*); 5) the Polynesian haplogroup K-M353 was only observed in Fiji and Futuna (but not in Melanesia) and probably arose in Fiji. Moreover, Fijians appear between the Polynesian cluster and the Coastal/Island Melanesian cluster in the $F_{ST}$-based 2-dimensional MDS plots from mtDNA haplotypes as well as from NRY haplogroups (fig. 5), although the latter MDS plot should be interpreted more carefully as indicated by the relatively high stress value. In addition, Fiji shows the highest overall genetic diversity from all Polynesian groups for both Y chromosome and mtDNA markers.

These results indicate the central role of Fiji in further Polynesian migrations; the fact that Fiji has the highest genetic diversity, and that all Polynesian groups have a subset of the diversity in Fiji, indicates that humans probably first migrated to Fiji and that subsequent settlement of Polynesia probably came from Fiji. This is in agreement with archaeological evidence showing that the oldest findings of Lapita pottery in Polynesia are from Fiji (3,200 years ago). Having originated from the Bismark Archipelago in Island Melanesia, Lapita was first introduced to Polynesia in Fiji, and there was a rapid expansion of the Lapita cultural complex from Fiji eastward into other parts of Polynesia (Futuna, Tonga, Samoa) as suggested indirectly by finding younger Lapita dates elsewhere in Polynesia (2,900–2,100 years ago), but also directly, for example, by the presence of Fijian potsherds in Tonga (Kirch 2000).

An alternative explanation is that following initial colonization, Fiji continued to receive migrants and genes from Melanesia and that humans continued to disperse from Fiji to Polynesia. Although there is archaeological evidence to support this view (for summary see Kirch 2000), the genetic results do not suggest substantial ongoing contact between Fiji and Melanesia, as separate expansions of Y haplogroups C-M208 and K-M9 (both of Melanesian origin) in Fiji/Polynesia versus Melanesia are evident in the networks (fig. 2*A* and *B*). Ongoing contact between Melanesia and Fiji should result in more sharing of haplotypes between Melanesia and Fiji, which is not observed. Moreover, Y haplogroup M-M4 (of Melanesian origin) has its highest frequency in Fiji and exists in Melanesia mostly as its derived subgroup M-P34; ongoing contact should have brought more M-P34 chromosomes to Fiji. However, the low frequency elsewhere in Polynesia of other Melanesian Y and mtDNA haplogroups existing in Fiji precludes definitive conclusions, and additional sampling between mainland New Guinea and Fiji (e.g., from the Solomon Islands, Vanuatu, and New Caledonia) is needed to further investigate the amount of ongoing genetic contact between Melanesia and Fiji.

## Conclusions

Our study provides evidence for a dual genetic origin of Pacific Islanders in Asia and Melanesia. This is in agreement with the Slow Boat hypothesis of Polynesian origins (Kayser, Brauer et al. 2000) according to which Polynesian ancestors originated in Asia, moved eastward, and mixed extensively with local Melanesians before colonizing the Pacific Islands. Although dating methods revealed somewhat similar entries of NRY/mtDNA haplogroups into Polynesia, haplotype sharing suggests that haplogroups of Melanesian origin may have appeared earlier in Polynesia than those of Asian origin, although more extensive sampling in Melanesia is needed to confirm this observation. The striking difference observed here between Asian and Melanesian contributions to the paternal and maternal gene pool of Polynesians suggests an admixture bias toward more Melanesian men, perhaps as result of uxorilocal (matrilocal) residence and matrilineal descent in ancestral Polynesian society (Hage and Marck 2003). The identified east-west gradient in the frequency distribution of some NRY/mtDNA haplogroups suggests an increasing tendency for founder events as the more eastern islands were colonized and also implies that Pacific voyaging was regular rather than haphazard. The gradual west-to-east decrease of overall NRY/mtDNA diversity in addition to the frequency distribution of the Polynesian DYS385 triplication provide genetic evidence for a west-to-east settlement of Polynesia. Fiji has played a pivotal role in the history of Polynesia either by having had received an earlier migration wave from Melanesia or by subsequent intensive contacts with Melanesia. In order to differentiate between these scenarios, additional sampling between mainland New Guinea and Fiji (e.g., from the Solomon Islands, Vanuatu, and New Caledonia) is needed. Based on the data presented here, Polynesians can be regarded as an admixed population (especially Fijians), although it should be pointed out that autosomal data are needed in addition to the Y/mtDNA data presented here for a more comprehensive estimate of Polynesian genetic admixture. Nevertheless, we predict that Polynesians should be of interest for admixture mapping of

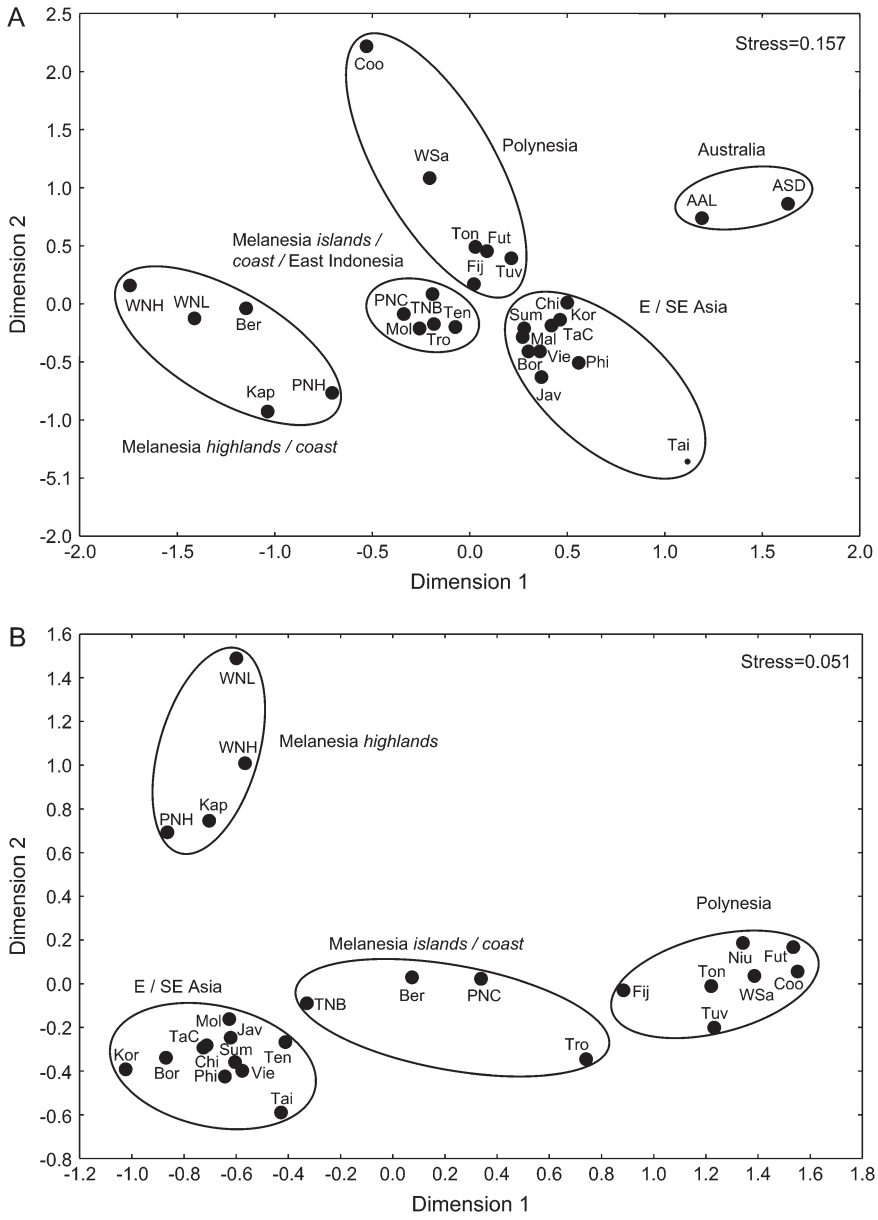


FIG. 5.—Two-dimensional plots from multidimensional scaling analyses based on $F_{ST}$ distances from (*A*) NRY haplogroup frequencies and (*B*) mtDNA sequence haplotypes. NRY haplogroups R-M173 and F-M89 were omitted due to their assumed European origin; Niue (NRY) and Tokelau (NRY, mtDNA) were omitted due to small sample size. For population abbreviations, see Table S5(Supplementary Material online). Geographic regions are highlighted.

disease genes. For example, Polynesians have an extraordinarily high frequency of Type 2 diabetes (Zimmet et al. 1990), which may reflect past selection on genes involved in nutrition metabolism for a "thrifty genotype" (Neel 1962). Polynesians thus may prove of interest not only because of their fascinating history and extraordinary accomplishments in colonizing the Pacific but also from what we may learn about complex diseases that affect other populations.

## Supplementary Material

Supplementary Tables S1–S5 and Figures S1 and S2 are available at *Molecular Biology and Evolution* online (http://www.mbe.oxfordjournals.org/).

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