

The Impact of the Austronesian Expansion: Evidence from mtDNA and Y Chromosome Diversity in the Admiralty Islands of Melanesia

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The genetic ancestry of Polynesians can be traced to both Asia and Melanesia, which presumably reflects admixture occurring between incoming Austronesians and resident non-Austronesians in Melanesia before the subsequent occupation of the greater Pacific; however, the genetic impact of the Austronesian expansion to Melanesia remains largely unknown. We therefore studied the diversity of nonrecombining Y chromosomal (NRY) and mitochondrial (mt) DNA in the Admiralty Islands, located north of mainland Papua New Guinea, and updated our previous data from Asia, Melanesia, and Polynesia with new NRY markers. The Admiralties are occupied today solely by Austronesian-speaking groups, but their human settlement history goes back 20,000 years prior to the arrival of Austronesians about 3,400 years ago. On the Admiralties, we found substantial mtDNA and NRY variation of both Austronesian and non-Austronesian origins, with higher frequencies of Asian mtDNA and Melanesian NRY haplogroups, similar to previous findings in Polynesia and perhaps as a consequence of Austronesian matrilocality. Thus, the Austronesian language replacement on the Admiralties (and elsewhere in Island Melanesia and coastal New Guinea) was accompanied by an incomplete genetic replacement that is more associated with mtDNA than with NRY diversity. These results provide further support for the “Slow Boat” model of Polynesian origins, according to which Polynesian ancestors originated from East Asia but genetically mixed with Melanesians before colonizing the Pacific. We also observed that non-Austronesian groups of coastal New Guinea and Island Melanesia had significantly higher frequencies of Asian mtDNA haplogroups than of Asian NRY haplogroups, suggesting sex-biased admixture perhaps as a consequence of non-Austronesian patrilocality. We additionally found that the predominant NRY haplogroup of Asian origin in the Admiralties (O-M110) likely originated in Taiwan, thus providing the first direct Y chromosome evidence for a Taiwanese origin of the Austronesian expansion. Furthermore, we identified a NRY haplogroup (K-P79, also found on the Admiralties) in Polynesians that most likely arose in the Bismarck Archipelago, providing the first direct link between northern Island Melanesia and Polynesia. These results significantly advance our understanding of the impact of the Austronesian expansion and human history in the Pacific region.

Introduction

Studies of mitochondrial (mt) and nonrecombining Y chromosome (NRY) DNA variation have provided important insights into the colonization of the Pacific (Melton et al. 1995; Redd et al. 1995; Sykes et al. 1995; Kayser et al. 2000, 2006; Capelli et al. 2001; Hurles et al. 2002; Trejaut et al. 2005). The vast majority (94%) of Polynesian mtDNA types are of East Asian origin (Kayser et al. 2006), and a genetic trail for a particular mtDNA HV1 motif (the Polynesian motif [PM]) that is in high frequency (~78%) in Polynesians can be traced back along Island Melanesia and coastal New Guinea to Eastern Indonesia, continuing via the immediate precursor HV1 sequence (lacking the transition at 16247) through the Philippines to Taiwan (Redd et al. 1995; Trejaut et al. 2005). Surprisingly, most (~66%) Polynesian Y chromosomes are of Melanesian origin (Kayser et al. 2000, 2006); this large discrepancy between the mtDNA and NRY ancestry of Polynesians led us to propose the “Slow Boat” model of Polynesian origins (Kayser et al. 2000). According to this model, Austronesians spread from East Asia (perhaps Taiwan), intermixed with people in coastal New Guinea and/or Island Melanesia,

and then continued spreading eastward across the western and southern Pacific. To explain the discrepancy between the mtDNA and NRY in the ancestry of Polynesians, it was proposed that this intermixing was sex biased, involving primarily the occasional union of an Austronesian woman and a non-Austronesian man, as is typical of matrilocality and no other (Hage and Marck 2003); a position we further affirmed by additional Polynesian data (Kayser et al. 2006). Recently, this Slow Boat model has received further genetic support from studies of genome-wide autosomal DNA variation in Polynesians, which indicate a primarily East Asian origin of Polynesians but with nonnegligible genetic contributions from Melanesia (Friedlaender et al. 2008; Kayser et al. 2008).

An important question raised by this scenario is the overall genetic impact of the Austronesian expansion on Melanesia, especially the islands north of mainland New Guinea. We use the term “Austronesian” to refer to the people who brought languages classified as Austronesian into this part of the world, including their current speakers. Northern Island Melanesia represents the area where seafaring, pottery-making people, who most likely spoke an Austronesian language immediately ancestral to Proto-Oceanic, first arrived in Melanesia about 3,400 years before present (y.b.p.) according to archaeological evidence (Kirch 1997, 2000). Because human settlement in this region goes back into the Pleistocene period according to archaeological data (Allen et al. 1988; Pavlides and Gosden 1994; Leavesley et al. 2002; Specht 2005), northern Island Melanesia can

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be assumed as the first regional contact zone for the incoming pre-Proto-Oceanic-speaking Austronesians and the local non-Austronesian inhabitants of Melanesia and presumably reflects the region where the assumed genetic admixture between these 2 groups of people mostly occurred initially. These people then developed in the Bismarcks the characteristic elements of the Lapita cultural complex (most notable highly decorated dentate-stamped pottery) (Green 1991a, 2002, 2003; Spriggs 1997), as well as the Proto-Oceanic language (Lynch et al. 2002). Subsequent voyages distributed Lapita cultural elements further east to Santa Cruz, Reef Island, Vanuatu, New Caledonia, Fiji, and eventually into (western) Polynesia within only about 500 years, whereas the Proto-Oceanic language of the voyagers started to diversify into different Oceanic subgroups finally leading to the approximately 450 Oceanic languages known today (Green 1991a, 1997; Kirch 1997; Blust 1999; Lynch et al. 2002).

To investigate the genetic impact of the Austronesian expansion in Melanesia, we analyzed mtDNA and NRY variation in the Admiralty Islands, located north of mainland New Guinea. The “Admiralties” were first colonized by humans from about 21 to 24,000 y.b.p. onward (Fredericksen et al. 1993; Ambrose 2002; Specht 2005) linking them with similarly old and older sites (40–50,000 y.b.p.) in mainland New Guinea and other parts of northern Island Melanesia (Groube et al. 1986; Pavlides and Gosden 1994; Spriggs 1997; Leavesley et al. 2002; Specht 2005). The human Pleistocene occupation of the Admiralty Islands is quite remarkable as it involved a minimum blind crossing of 60–90 km of open ocean, with no land in sight, in a 200- to 230-km voyage, thus representing one of the few examples of humans crossing water where land was not intervisible prior to the Austronesian expansion across the Pacific (Irwin 1992; Spriggs 1997). Today, the Admiralties are settled by people speaking 30 different Oceanic languages belonging to the Admiralties subgroup of Oceanic within the Austronesian language family (Lynch et al. 2002). The presence of at least 1 (perhaps 3) Lapita site on the Admiralty Islands (Kennedy 1981; Ambrose 1991; McEldowney and Ballard 1991; Spriggs 1997) together with a distribution of obsidian tools from Lou Island to regions outside the Admiralties such as to New Britain, the Solomons and as far as Vanuatu from the Lapita period onward (Spriggs 1997; Summerhayes 2003) suggests that the Admiralties could have played an important role during the Austronesian expansion.

Thus, the Admiralty Islands were already inhabited for about 20,000 years before the Austronesians arrived there. Did the Austronesian newcomers completely replace the local non-Austronesian inhabitants, or can one find either linguistic or genetic traces of these first inhabitants in contemporary Admiralty Islanders? The complete lack of knowledge on the extinct non-Austronesian languages of the Admiralties makes it difficult (if not impossible) to search for their traces in the contemporary Austronesian languages of these islands. Here, we analyze mtDNA and NRY variation in contemporary Admiralty Islanders in order to search for genetic traces of the pre-Austronesian inhabitants and to test if the Austronesian language replacement on these islands was accompanied by a genetic

replacement. Our results provide further insights into the genetic impact of the Austronesian expansion and enhance our understanding of the human colonization of Island Melanesia and the southern Pacific region.

Materials and Methods

A total of 147 samples from the Admiralty Islands of the Manus Province of Papua New Guinea (PNG) were collected (by M.K., D.S., and W.S.) with individual informed consent, the approval of the Medical Research Advisory Committee of PNG, and with support from the Manus Provincial Government in 2005. Samples were sorted according to the paternal grandfather’s birthplace/language for the NRY data analysis and the maternal grandmother’s birthplace/language for mtDNA data analysis. Nine language groups were sampled from different villages, respectively, mostly from Manus, the major island of the Admiralties: Nyindrou from western Manus combined with Bipi from Bipi Island west of Manus because of small sample size; Kurti from northern Manus; Lele from northeastern Manus; Ere and Kele (combined) from southeastern Manus; Nali from southeastern Manus; Mokerang from Los Negros Island east of Manus; Andra–Hus mostly from Andra Island north of Manus combined because of small sample size with the nearby Ponam Island (Ponam language) and Pituluh Island (Leipon language); Titan from Rambutyo Island, M’Buke Island, Nauna Island, and Sanders Island (all southeast of Manus); and Seimat from the Ninigo Island Group and Hermit Islands as well as Wuvulu–Aua from Wuvulu Island—here because of small sample sizes used as a combined Seimat–Wuvulu group (all these islands are west of Manus and considered separate island groups from the Admiralty Islands, but for convenience here they are included with the Admiralty Islands). All language groups sampled belong to the Oceanic branch of the Austronesian linguistic family. The sample size per group is provided in tables 1 and 2 for the NRY and mtDNA data, respectively, and the approximate location of the 9 language groups is indicated in figure 1. A more detailed map of the Admiralties showing all islands sampled is provided in the supplementary figure S1 (Supplementary Material online). A map of the entire study region and its larger geographic context is provided in the supplementary figure S2 (Supplementary Material online) also showing the location of the Wuvulu, Ninigo, and Hermit Islands sampled. Care was taken to include unrelated individuals only, based on self-reported family histories for 3 generations. Distantly related individuals, as indicated by the sampling questionnaires, were excluded from the NRY or mtDNA data analysis whenever the relationship was confirmed by the respective genetic data. We also excluded individuals with a record-based family history from outside of the Admiralty Islands.

DNA was extracted from cheek swab or saliva samples as described elsewhere (Quinque et al. 2006). Overall, we analyzed 44 binary markers and 7 short tandem repeat (STR) loci (microsatellites) from the nonrecombining region of the Y chromosome (NRY), as well as mtDNA hypervariable region 1 (HV1) sequences and the 9-bp deletion

Table 1
NRY Haplogroups in Language Groups from the Admiralty Islands

Language Group	O-M110 ^a	O-M324 ^a	C-M38 ^b	C-M208 ^b	K-M9 ^b	K-P79 ^b	K-M254 ^b	K-M226 ^b	M-P34 ^b	Total
Seimat–Wuvulu (S/W)	4	0	0	1	1	5	0	0	0	11
Titan (Tit)	4	0	0	4	2	1	5	4	1	21
Nyindrou (Nyi)	3	1	0	3	2	0	2	0	6	17
Mokerang (Mok)	0	0	0	0	3	0	1	0	0	4
Ere–Kele (E/K)	1	0	0	0	8	0	3	0	2	14
Lele (Lel)	0	0	0	9	10	0	3	0	1	23
Nali (Nal)	3	0	0	3	7	0	2	2	2	19
Andra–Hus (A/H)	2	0	1	1	5	0	4	5	2	20
Kurti (Kur)	9	0	0	1	2	0	5	0	1	18
Total (Adm)	26	1	1	22	40	6	25	11	15	147
Percent	17.7	0.7	0.7	15.0	27.2	4.1	17.0	7.5	10.2	100.0

^a Assigned as Asian origins.^b Assigned as Melanesian origins.

marker (Redd et al. 1995). HV1 sequences were used to infer mtDNA haplogroups, whereas NRY binary markers were used to characterize NRY haplogroups. The phylogenetic relationships of the NRY and mtDNA haplogroups are provided in the supplementary figure S3 (Supplementary Material online). DNA sequence analysis was carried out, and markers were genotyped as described previously (Kayser et al. 2006) except for P79 and P117, 2 recently identified new subgroups of K-M9 (Scheinfeldt et al. 2006); M110 and M101; 2 previously reported subgroups of O-M119 (Underhill et al. 2000); and M324, a recently identified new subgroup of O-M122 (Shi et al. 2005) as well as M121, M164, M159, and M7—4 subgroups of O-M324 (Underhill et al. 2000; Shi et al. 2005) that were all typed using standard SNaPshot technology. DNA sequences of polymerase chain reaction and extension primers for those loci are provided in the supplementary table S1 (Supplementary Material online). Other samples from Asia, Melanesia, and Polynesia as previously described (Kayser et al. 2006) were typed here for the additional NRY markers listed above, and updated NRY and mtDNA data are provided in the supplementary tables S2 and S3 (Supplementary Material online), respectively. The HV1 sequences of the Admiralty samples used here are available via GenBank (<http://www.ncbi.nlm.nih.gov/Genbank/>) under the following accession numbers EU579532–EU579675.

ARLEQUIN version 3.0 (Excoffier et al. 2005) (available at <http://cmpg.unibe.ch/software/arlequin3>) was used

to calculate haplotype diversity, mean number of pairwise haplotype differences (MPD), F_{st} from haplogroup frequencies, and R_{st} from haplotypes. Multidimensional scaling (MDS) plots and Mann–Whitney U tests were performed with the software package STATISTICA. Median-joining networks (Bandelt et al. 1999) among Y-STR haplotypes within NRY haplogroups were constructed using the software NETWORK version 4.5 (available at <http://fluxus-engineering.com>) with marker weighted according to locus-specific Y-STR mutation rates as described previously (Mona et al. 2007). A Bayesian-based coalescent approach (Wilson and Balding 1998; Wilson et al. 2003), implemented in the software BATWING, was used for demographic inference of NRY haplogroups using Y-STRs and the NRY haplogroup tree topology. The coalescent prior model used for the topology and branch lengths of the gene genealogy was an initial constant population size followed by a demographic expansion (Wilson et al. 2003). The likelihood of the gene genealogy was computed under the stepwise mutation model (Ohta and Kimura 1973). The posterior probability of the gene genealogy, population genetic parameters, and NRY haplogroup dating were approximated through the Metropolis–Hastings algorithm (Metropolis et al. 1953; Hastings 1970). Priors for Y-STRs mutation rates and the coalescent model were applied as described previously (Kayser et al. 2006). To determine the coalescence time of each haplogroup, the gene genealogy was constrained using the known NRY phylogeny

Table 2
mtDNA Haplogroups in Language Groups from the Admiralty Islands

Language Group	PM ^a	B4a ^a	B4b1 ^a	B5b ^a	E1b ^a	M7b ^a	M7c1c ^a	P2 ^b	P4 ^b	Q1 ^b	Q2 ^b	Total
Seimat–Wuvulu (S/W)	10	3	0	0	0	0	0	0	0	0	3	16
Titan (Tit)	10	2	0	0	0	0	0	1	1	1	6	21
Nyindrou (Nyi)	3	3	1	2	0	1	2	0	0	3	1	16
Mokerang (Mok)	3	0	0	0	0	1	0	0	0	2	0	6
Ere–Kele (E/K)	0	3	1	0	0	0	0	2	0	7	0	13
Lele (Lel)	11	0	0	0	0	1	0	1	0	0	1	14
Nali (Nal)	5	5	0	0	2	3	0	0	0	7	1	23
Andra–Hus (A/H)	6	3	0	0	0	0	0	0	1	4	0	14
Kurti (Kur)	5	0	0	1	0	0	0	1	0	14	0	21
Total (Adm)	53	19	2	3	2	6	2	5	2	38	12	144
Percent	36.8	13.2	1.4	2.1	1.4	4.2	1.4	3.5	1.4	26.4	8.3	100.0

^a Assigned as Asian origins.^b Assigned as Melanesian origins.

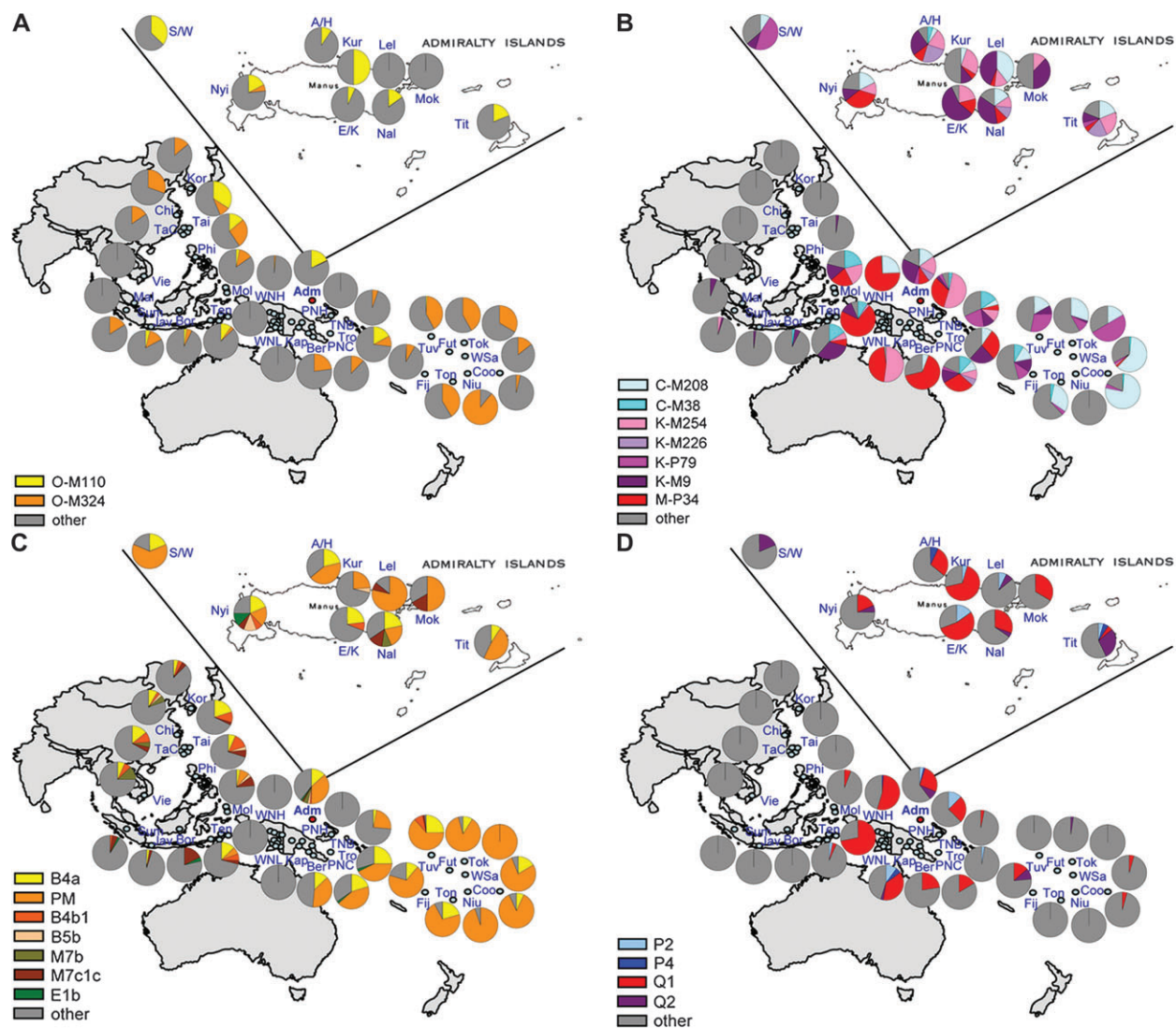


FIG. 1.—Frequencies of NRY (A and B) and mtDNA (C and D) haplogroups of Asian (A and C) or Melanesian (B and D) origin in the Admiralty Islands and in populations from Asia, Melanesia, and Polynesia. Only those haplogroups observed on the Admiralties are shown. Non-Admiralty groups are from our updated previous study (Kayser et al. 2006). For abbreviations, see tables 1 and 2 and supplementary tables S2 and S3 (Supplementary Material online).

(supplementary fig. S3, Supplementary Material online). The final analysis was based on 2 runs of 100 million Marco Chain Monte Carlo (MCMC) generations each with a 10% burn-in period. TRACER (Rambaut and Drummond 2004) (available at <http://tree.bio.ed.ac.uk/software/tracer/>) was used to check for the convergence of the 2 runs and to compute the effective sample size (always >200) and the 95% high posterior density of all the parameters, combining the 2 runs.

Results and Discussion

Correspondence between Genetic, Cultural, and Linguistic Evidence

The geographic origin of the majority of mtDNA and NRY haplogroups in the southern Pacific region can be confidently assigned as either Asian or Melanesian, based

on the frequency distribution of NRY and mtDNA haplogroups as well as their associated Y-STR diversity and HV1 sequence diversity. The presence of Asian NRY and mtDNA haplogroups in Melanesia and the southern Pacific most likely reflects the Austronesian expansion, whereas Melanesian haplogroups are likely to be indigenous to the region, representing earlier inhabitants of Melanesia prior to the Austronesian arrival. On the Admiralty Islands, we observed 9 NRY haplogroups of which 2 are of assumed Asian (O-M110 and O-M324) and 7 are of assumed Melanesian (C-M38, C-M208, M-P34, K-M9, K-P79, K-M254, and K-M226) origins (tables 1 and 2, fig. 1). Furthermore, we observed 11 mtDNA haplogroups in the Admiralties, of which 7 are of assumed Asian (PM, B4a, B4b1, B5b, E1b, M7b, and M7c1c) and 4 are of assumed Melanesian (P2, P4, Q1, and Q2) origins (tables 1 and 2, fig. 1). Overall, 81.6% of the Admiralty Y chromosomes were of Melanesian origin and 18.4% of

Table 3
Average Proportion of Asian and Melanesian NRY/mtDNA Haplogroups in Language Groups from the Admiralty Islands

Language Group	NRY-DNA		mtDNA	
	Asian (%)	Melanesian (%)	Asian (%)	Melanesian (%)
Seimat–Wuvulu	36.4	63.6	81.3	18.8
Titan	19.0	81.0	57.1	42.9
Nyindrou	23.5	76.5	75.0	25.0
Mokerang	0.0	100.0	66.7	33.3
Ere–Kele	7.1	92.9	30.8	69.2
Lele	0.0	100.0	85.7	14.3
Nali	15.8	84.2	65.2	34.8
Andra–Hus	10.0	90.0	64.3	35.7
Kurti	50.0	50.0	28.6	71.4
Total	18.4	81.6	60.7	39.3

NOTE.—For Asian and Melanesian haplogroup assignment, see tables 1 and 2.

Asian origin, whereas 39.3% of the Admiralty mtDNA types were of Melanesian origin and 60.7% of Asian origin (table 3).

Thus, although all the groups in the Admiralties now speak Austronesian languages (belonging to the Admiralties subgroup of Oceanic), our data indicate that there is a significant non-Austronesian genetic component from Melanesia present in contemporary Admiralty Islanders, in addition to the Austronesian genetic traces from Asia, with more Melanesian influence for the NRY than for mtDNA and more Asian influence for mtDNA than for NRY-DNA. This suggests that the incoming Austronesians, bringing with them a language immediately ancestral to Proto-Oceanic (as well as Lapita pottery and oceangoing sailing canoes), influenced the local non-Austronesian inhabitants to give up their local languages. On the other hand, interactions between the local non-Austronesians and the incoming Austronesians may have led to linguistic innovations from pre-Proto-Oceanic to Proto-Oceanic in the Bismarcks (Ross 1996). Moreover, our mtDNA and NRY-DNA data indicate that the incoming Austronesians intermixed genetically mostly with the local non-Austronesian men and less so with local non-Austronesian women. Archaeological evidence suggests a time window of about 300 years between the first arrival of the Lapita people in the Bismarcks (Summerhayes 2007) and their heading off to occupy the western and southern Pacific, which marks the time frame of the assumed initial genetic admixture episode between Austronesians and non-Austronesians in northern Island Melanesia. Recent genome-wide autosomal data further support a nonnegligible amount of admixture (~20%) between Austronesians and non-Austronesians prior to further eastward migration of the Austronesians (Friedlaender et al. 2008; Kayser et al. 2008).

The discrepancy between the estimated autosomal non-Austronesians contribution to the Austronesian gene pool of about 20% (Friedlaender et al. 2008; Kayser et al. 2008) versus an estimated NRY contribution of about 66% and an estimated mtDNA contribution of about 6% (Kayser et al. 2006) may reflect sex-biased genetic admixture, perhaps as a consequence of a matrilineal residence pattern

(where a husband moves to or near the place of his wife and her ancestors) and a matrilineal descent system (where an individual is considered to belong to the same descent group as his or her mother) as previously suggested to explain the differences between NRY and mtDNA ancestry of Polynesians (Hage and Marck 2003). As a consequence of matrilineal residence of Proto-Oceanic Austronesians, non-Austronesian men (rather than woman) would have moved to Austronesian villages and a matrilineal structure of their society would have provided a societal environment where paternity is considered relatively unimportant (Hage and Harary 1996). Both effects together would have allowed the accumulation of more non-Austronesian NRY-DNA than mtDNA diversity in the gene pool of the admixed groups, as suggested previously (Hage and Marck 2003). However, as with all nonrecombining markers, genetic drift can have a strong effect in shaping NRY and mtDNA frequency distributions and more genome-wide autosomal data from additional populations, combined with demographic modeling, are required to sort out the relative roles of residence pattern, society structure, amount of admixture, and subsequent migration and drift in shaping the autosomal, NRY, and mtDNA gene pools of Polynesians.

Our data clearly show that the language replacement by Austronesians on the Admiralty Islands was accompanied by an incomplete genetic replacement that was associated more with maternally inherited mtDNA than with paternally inherited NRY-DNA. Our genetic evidence thus suggests that language in this region was transmitted via the Austronesian mothers, perhaps as a consequence of matrilocality and matrilineality, because the language acquired by the next generation was not only that of the mother but presumably also that of the entire village providing the immediate environment for Austronesian language transmission.

The genetic situation in the Admiralties of northern Island Melanesia is thus somewhat similar to that found previously for Polynesia, namely, a higher frequency of Melanesian than Asian NRY haplogroups but a higher frequency of Asian than Melanesian mtDNA haplogroups (supplementary tables S2 and S3, Supplementary Material online) (Kayser et al. 2006). This similarity between the assumed region of initial admixture between pre-Proto-Oceanic-speaking Austronesians and non-Austronesians on the one hand and the most eastern final destination of the Austronesian expansion on the other hand provides further support for the Slow Boat hypothesis of Polynesian origins (Kayser et al. 2000). However, there is 1 important difference: the frequencies of Melanesian NRY and mtDNA haplogroups are both significantly higher in the Admiralty Islands than in Polynesia (NRY: average frequency of Melanesian haplogroups is 79.8% in the Admiralty groups vs. 51.6% in Polynesian groups [excluding Fiji], $P < 0.05$; mtDNA: average frequency of Melanesian haplogroups is 39% in the Admiralty groups vs. 3.6% in Polynesian groups, $P < 0.01$). This suggests the following scenario: pre-Proto-Oceanic-speaking Austronesians arrived in northern Island Melanesia and mixed with the local non-Austronesian inhabitants, albeit in an asymmetric sex-specific manner in accordance with the Slow Boat hypothesis

while forming the characteristics of the Lapita cultural complex and developing the Proto-Oceanic language. These people then continued expanding eastward via Island Melanesia, Fiji, and eventually into Polynesia, leaving Lapita material culture and genetic footprints as well as developing numerous Oceanic languages from their Proto-Oceanic stock. The Oceanic-speaking Austronesians that remained in coastal New Guinea and northern Island Melanesia continued to mix genetically with their non-Austronesian neighbors, thereby increasing the frequency of Melanesian NRY and mtDNA haplogroups in Austronesian groups with respect to those Austronesian groups that ultimately settled in Polynesia. This scenario suggests little if any further contact between Polynesia and Island Melanesia following the initial colonization of Polynesia, as also corroborated by genetic data on at least 1 particular NRY haplogroup (P-79) combined with patterns of Y-STR haplotype sharing, as discussed below.

Although the non-Austronesian languages of the Pleistocene Admiralty Islanders were completely replaced by the Austronesians, this was not the case in other areas of coastal mainland New Guinea (i.e., regions of the north, east, and southeastern coast) and Island Melanesia (e.g., the Bismarck Archipelago) where pockets of non-Austronesian-speaking groups still exist among the more numerous Austronesian-speaking groups (Wurm and Hattori 1981). How much of the gene pool of the Austronesian and non-Austronesian-speaking populations of coastal New Guinea and Island Melanesia can be traced to the Austronesian expansion? We compared the frequencies of Asian and Melanesian mtDNA and NRY haplogroups in the present data from the Admiralties combined with previously published data (Kayser et al. 2006; Scheinfeldt et al. 2006; Friedlaender et al. 2007) for other Austronesian and non-Austronesian groups in this region (fig. 2). Overall, the frequency of Asian mtDNA haplogroups was on average 58.4% in 29 Austronesian groups and 42.1% in 13 non-Austronesian groups, and this difference is not statistically significant (Mann-Whitney U test, $Z = 150$, $P = 0.13$). The frequency of Asian NRY haplogroups was on average 16.1% in 28 Austronesian groups and 1.7% in 7 non-Austronesian groups, a difference that is statistically significant (Mann-Whitney U test, $Z = 3.05$, $P = 0.002$). Thus, the frequencies of Asian mtDNA and NRY haplogroups are both higher (significantly so for the NRY haplogroups) in Austronesian groups than in non-Austronesian groups in coastal New Guinea and Island Melanesia, consistent with the Asian origin of the Austronesians. Moreover, in the non-Austronesian groups of these regions, the frequency of Asian mtDNA haplogroups (42.1%) was significantly higher than that of Asian NRY haplogroups (just 1.7%, $P < 0.05$). This may reflect a strong influence of patrilocality in the non-Austronesian groups of Melanesia on their admixture with the Austronesians, which would favor admixture with Austronesian women rather than Austronesian men. A recent study of genome-wide diversity found a signal attributed to Asian ancestry of up to about 20% in the gene pool of Austronesian-speaking groups of northern Island Melanesia, which was lacking from the regional non-Austronesian groups tested (Friedlaender et al. 2008).

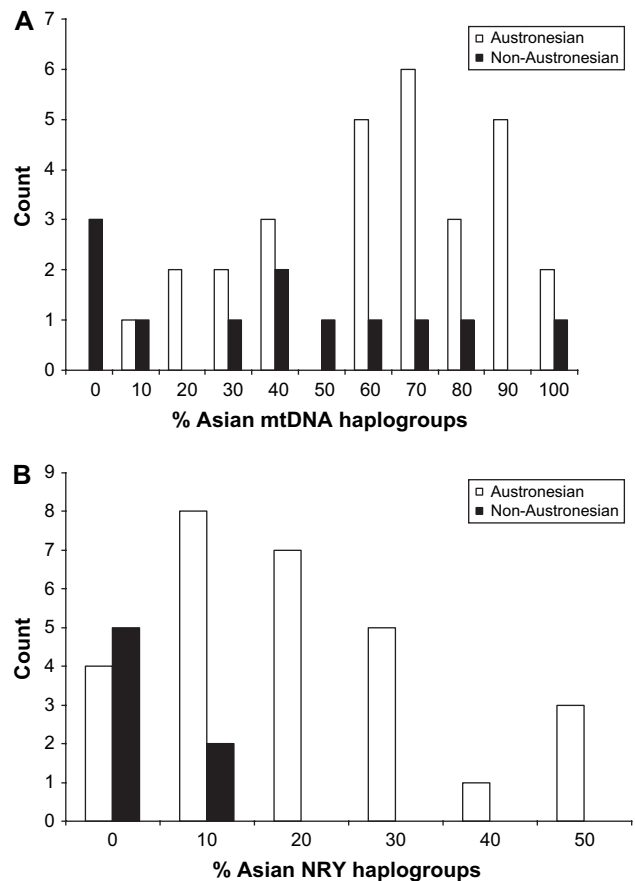


Fig. 2.—Histograms of the frequency of Asian mtDNA (A) and NRY (B) haplogroups in Austronesian and non-Austronesian groups from mainland New Guinea and Island Melanesia. Data are from the present study, our updated previous study (Kayser et al. 2006) (see supplementary tables S2 and S3, Supplementary Material online), and 2 other studies (Scheinfeldt et al. 2006; Friedlaender et al. 2007).

NRY Haplogroup O-M110: A Genetic Signature of the Taiwanese Origin of the Austronesian Expansion

The Asian NRY-DNA evidence in the Admiralties comes almost exclusively from haplogroup O-M110, which is present at an average frequency of 17.7% (table 1, fig. 1) and was observed in all but 2 groups from the Admiralties. O-M110 is a subgroup of O-M119 (Underhill et al. 2000), which was previously associated with the Austronesian expansion (Kayser et al. 2001, 2006). Our new data show that O-M110 was most frequent in Taiwan (34.1%), moderately frequent in the Philippines (12.8%), and less frequent in the central and eastern parts of Island Southeast Asia (2.5–9.7%) but was completely absent from Mainland East and Southeast Asia as well as the western parts of Island Southeast Asia (fig. 1; supplementary table S2, Supplementary Material online). In addition to the Admiralties, O-M110 was also frequent in the Trobriand Islands (frequency = 17.3%), another part of Austronesian-speaking Island Melanesia, but was otherwise absent from mainland New Guinea and only found in very low frequency (~1%) in Fiji and Tuvalu (fig. 1; supplementary table S2, Supplementary Material online). O-M110 also appears nearly absent from Austronesian-speaking (as well as non-Austronesian)

groups from the northwestern part of New Guinea (the Bird's Head region); although not formally tested, this can be assumed because haplogroup O-M119 (the direct ancestor of O-M110) was only observed in a single man from the Austronesian-speaking Wandamen group (Mona et al. 2007). Previously, 2 related studies also reported O-M110 in highest frequency in Taiwan and additionally observed this haplogroup in Thailand, Malaysia, Cambodia, Borneo, Java, and on Majuro Island of Micronesia (Su et al. 1999, 2000). Another previous study found O-M110 in Taiwan, Philippines, Indonesia, and PNG, again with highest frequency in Taiwanese (Karafet et al. 2005). Two additional studies detected the NRY marker M50, which is thought to be a phylogenetic equivalent of M110, in the Christmas Island south of Java (Wise et al. 2005) but not in a large sample of East Asian populations (Xue et al. 2006).

This frequency distribution suggests an ultimate origin of haplogroup O-M110 in Taiwan and a spread in association with the Austronesian expansion, which is corroborated by the Y-STR diversity associated with O-M110 that was highest for Taiwanese Aborigines (Nei's haplotype diversity = 0.890 ± 0.060 ; MPD = 2.62 ± 1.49 ; $N = 14$) and lower in Southeast Asia (0.879 ± 0.060 ; 1.64 ± 1.04 ; $N = 12$) and Melanesia (0.886 ± 0.031 ; 2.01 ± 1.16 ; $N = 36$). Haplogroup O-M110 associated Y-STR haplotypes differ significantly between Asia and Melanesia ($R_{st} = 0.352$; $P < 0.00001$) but not between Taiwan and Southeast Asia ($R_{st} = 0$; $P = 0.838$). The haplotype network also suggests Taiwan as the most likely region of origin (fig. 3), in that only Taiwan haplotypes are found branching off all the central haplotypes in the network. There also was little sharing of O-M110 associated Y-STR haplotypes between the Admiralties and the Trobriands of Island Melanesia (fig. 3), indicating little contact between the islands north and east of mainland New Guinea following the initial arrival of the Austronesians in Melanesia.

Linguistic (Blust 1999) and archaeological (Bellwood 2004; Bellwood and Dizon 2005) evidences strongly suggest a Taiwanese origin for the Austronesian expansion. This hypothesis is also supported by mtDNA evidence, as a genetic trail for the origin of the mtDNA "PM" (via its immediate precursor haplogroup B4a1) can be traced back to Taiwan (Redd et al. 1995; Trejaut et al. 2005), but up until now, a specific source for any of the Asian NRY haplogroups in Southeast Asia and Oceania has not been identified. The evidence detailed above strongly suggests an ultimate Taiwanese origin for O-M110 and thus provides the first direct Y chromosome evidence in support of a Taiwanese origin for the Austronesian expansion. Unfortunately, the NRY marker M110 has not been analyzed previously in other detailed studies of NRY variation in New Guinea or Island Melanesia; further genotyping in this region would be desirable to fully delineate the extent of the spread of haplogroup O-M110. Although O-M110 most likely represents a genetic footprint of the Austronesian expansion into Island Melanesia, surprisingly this paternal genetic signature does not continue much into Polynesia, where the major Asian NRY evidence is haplogroup O-M122 as previously identified (Kayser et al. 2000,

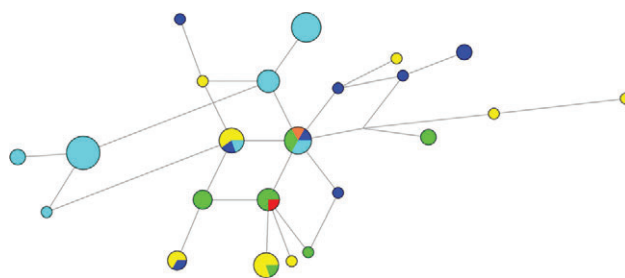


FIG. 3.—Median-joining network of haplogroup O-M110 associated Y-STR haplotypes using data from the present study and our updated previous study (Kayser et al. 2006). Circles denote haplotypes, with the area of the circle proportional to the number of individuals carrying the particular haplotype. Colors indicate the geographic origin of the samples with yellow for Taiwanese Aborigines, green for Southeast Asians, blue for Island Melanesians, (with light blue for Admiralty Islanders and dark blue for Trobriand Islanders), red for Polynesians, and orange for Fijians. Lines denote mutation steps, and the network was weighted according to Y-STR mutation rate differences (for details, see Materials and Methods).

2006; Su et al. 2000); in particular, by a recently identified new subgroup of O-M122 as described below.

Other NRY Diversity in the Admiralty Islands

Haplogroup O-M324* is another NRY haplogroup of Asian origin in the Admiralties but was only found in a single Nyindrou man from Manus (table 1, fig. 1). O-M324 can be associated with the Austronesian expansion because it represents the major subgroup of O-M122 (Shi et al. 2005), previously identified as the major Asian NRY haplogroup in Polynesia (Kayser et al. 2000, 2006; Su et al. 2000). In fact, all O-M122 Y chromosomes from Polynesia, Fiji, and Melanesia described in our previous studies were identified as haplogroup O-M324* in the present study (except 2 Samoans with O-M7, a subgroup of O-M324, see below) (supplementary table S2, Supplementary Material online). Y-STR haplotype diversity associated with haplogroup O-M324* was higher in East Asia (Nei's diversity: 0.991 ± 0.018 , MPD: 3.90 ± 2.04 , $N = 21$) than in Southeast Asia (0.915 ± 0.038 , 2.62 ± 1.44 , $N = 33$), Melanesia (0.921 ± 0.042 , 2.18 ± 1.26 , $N = 20$), and Fiji (0.714 ± 0.181 , 1.86 ± 1.20 , $N = 7$) but was lowest in Polynesia (0.694 ± 0.038 , 1.02 ± 0.69 , $N = 96$) keeping with the assumption of an East Asian origin of haplogroup O-M324* and a subsequent spread by the Austronesian expansion as far as Polynesia. In contrast to the Admiralties, O-M324* was more frequent and widespread among other Austronesian-speaking groups of Island Melanesia and coastal New Guinea (fig. 1; supplementary table S2, Supplementary Material online). In East and Southeast Asians described in our previous study as belonging to haplogroup O-M122 (Kayser et al. 2006), we now observed slightly more NRY haplogroup variation with O-M122* and O-M7, in addition to O-M324* (supplementary table S2, Supplementary Material online). Haplogroup O-M324* has previously been found to be widespread across East Asia, both in northern as well as southern regions (Shi et al. 2005), whereas O-M7 seems to be more restricted to southern parts of East Asia and was also found in Malaysia and Sumatra (Su et al. 1999; Shi et al. 2005; Xue et al. 2006).

Table 4
Bayesian-Based tmrca Dates of NRY Haplogroups with Assumed Melanesian origin, Estimated from all Melanesian Groups and Separately from Admiralty Islands samples^a

Melanesia							Admiralty Islands					
Haplogroup	N	tmrca				ESS	N	tmrca				ESS
		Mean	Median	95% low	95% up			Mean	Median	95% low	95% up	
C-M38	73	10,840	10,180	5,061	17,320	336	2	10,800	9,880	4,126	19,950	816
C-M208	59	4,401	4,318	2,778	6,583	437	22	4,543	4,197	1,973	7,746	733
M-P34	276	6,892	6,667	4,450	9,763	318	15	2,312	2,103	818	4,370	900
K-M9*	101	15,260	14,510	7,965	23,380	363	40	14,480	13,580	7,338	23,880	900
K-M226	13	1,906	1,804	668	3,129	548	11	1,364	1,198	397	2,706	779
K-M254	88	6,114	5,802	3,407	8,874	333	25	5,828	5,409	2,726	9,876	767
K-P79	12	4,061	3,911	1,914	7,035	471	6	3,405	3,030	773	6,498	900

^a Only Melanesian haplogroups with overall $N > 10$ are shown, although all haplogroups observed in the respective regions were included in the analysis using data from the present study, our updated previous study (Kayser et al. 2006), and another study (Mona et al. 2007). tmrca, time back to the most recent common ancestor; ESS, effective sample size of the MCMC indicating the convergence of the chain (values >100 are usually considered sufficient for reliable data interpretation).

The additionally typed subgroups of O-M324 (namely O-M121, O-M164, and O-M159) were not observed in any of our samples and were previously found only in single men from China and Cambodia (Shi et al. 2005; Xue et al. 2006). Overall, all the Asian NRY haplogroups that have been found so far in Melanesia as a likely result of the Austronesian expansion were observed on the Admiralties, except O-M119*(xM110), which was frequent in east and Southeast Asia but rare in Melanesia, Fiji, and Polynesia (supplementary table S2, Supplementary Material online). O-M101, an additional subgroup of O-M119* (Underhill et al. 2000), was not found in any of our samples; this marker was originally discovered in a single Chinese (Underhill et al. 2000) but has not been observed in any subsequent studies (Xue et al. 2006; Firasat et al. 2007; Nonaka et al. 2007).

Melanesian NRY-DNA evidence in the Admiralties mainly comes from haplogroups K-M9* (27.2%), K-M254 (17%), and M-P34 (10.2%) (table 1, fig. 1), all of which have a high frequency in mainland New Guinea as well (supplementary table S2, Supplementary Material online) (Kayser et al. 2006; Mona et al. 2007). The latter 2 haplogroups were previously identified as likely markers for the expansion of Trans-New Guinea speakers (Mona et al. 2007). Haplogroup K-M9* (together with C-M38, see below) in Melanesia was previously suggested to reflect earlier local Y chromosome diversity in New Guinea (Mona et al. 2007). The haplogroups C-M208 (15%) and K-M226 (7.5%) also occur at appreciable frequencies in the Admiralties (table 1, fig. 1) but are both rare in mainland New Guinea (supplementary table S2, Supplementary Material online), except for the Dani and Lani from the West New Guinea Highlands, who are almost fixed for C-M208 (Kayser et al. 2003). C-M208 also represents the major Melanesian contribution to Polynesians (Kayser et al. 2006). Haplogroup C-M38 was only found in a single male from Ponam Island north of Manus (table 1, fig. 1). This haplogroup occurs in high frequency in northwestern parts of New Guinea, where it most likely originated (Mona et al. 2007), but otherwise was more rare in mainland New Guinea, Island Melanesia, and eastern Indonesia (supplementary table S2, Supplementary Material online) (Kayser et al. 2006; Scheinfeldt et al. 2006; Mona et al. 2007), and may reflect a marker for the

New Guinean Y chromosome landscape prior to the expansion of Trans-New Guinea speakers (Mona et al. 2007) (see also below). One additional Melanesian haplogroup, P-79, a recently discovered new subgroup of K-M9 (Scheinfeldt et al. 2006), was found on the Admiralties in low average frequency (4.1%) but at high frequency (45%) in the Seimat-Wuvulu group, namely in men from the Ninigo but mostly from Wuvulu Islands in addition to 1 Titan man (table 1, fig. 1). This haplogroup occurred in moderate frequency in New Britain and somewhat less so in New Ireland (Scheinfeldt et al. 2006) but was rare in mainland New Guinea (fig. 1; supplementary table S2, Supplementary Material online). Given that P-79 likely originated in New Britain (Scheinfeldt et al. 2006), it is peculiar that we observed this haplogroup mostly on Wuvulu Island that is most distant from New Britain (supplementary fig. S1, Supplementary Material online) and not on Manus and its directly surrounding islands (with the exception of a single Titan man from M'Buke Island) that are geographically closer to New Britain (supplementary fig. S1, Supplementary Material online). Overall, Melanesian NRY haplogroup diversity was quite high in the Admiralties; only 5 of the 12 currently known NRY haplogroups with an inferred Melanesian origin were not found on the Admiralties. Of these, 3 (K-P117, M-M104/P22, and M-P-87) were previously found mainly in New Britain and New Ireland (supplementary table S2, Supplementary Material online) (Kayser et al. 2006; Scheinfeldt et al. 2006), whereas M-M4* was rare everywhere in New Guinea but more frequent in Fiji and K-M230* was very rare across Melanesia (supplementary table S2, Supplementary Material online) (Kayser et al. 2006).

Do the Melanesian haplogroups in the Admiralty Islands represent their initial Pleistocene occupation, or were they brought by subsequent migration? To investigate this question, we performed Bayesian-based dating of the time back to the most recent common ancestor (tmrca) of the Melanesian NRY haplogroups found in the Admiralties (table 4). These tmrca estimates provide an upper estimate as to when they would have been brought to the Admiralties. With the exception of K-M9*, none of the upper 95% limits for the tmrca estimates for any of the NRY haplogroups exceed the archaeological dates for the initial colonization of the Admiralties during the Pleistocene. Thus,

with the possible exception of K-M9*, all the Melanesian NRY haplogroups found in the Admiralties were brought there after the initial colonization if the earliest archaeological dates for the Admiralties of 24,000 y.b.p. are indeed correct. We also performed this analysis separately using only the data from the Admiralty Islands and the resulting dates very much agree with the overall dates (except for M-P34) (table 4), suggesting no significant bottlenecks in the Admiralty Y chromosome history. The tmrca for haplogroup M-P34 on the Admiralties appears considerably younger than the overall date of this Melanesian haplogroup (table 4), suggesting that this haplogroup was brought to the Admiralties more recently. This is interesting as M-P34 was previously suggested to represent a marker for the Trans-New Guinea expansion starting from the interior of mainland New Guinea 6–10,000 y.b.p. (Mona et al. 2007) and thus would be expected to have arrived in coastal areas of mainland New Guinea considerably later. Overall, the extensive diversity of NRY haplogroups with Melanesian origin in the Admiralties suggests considerable ongoing contact between the Admiralties and mainland New Guinea before the Austronesian arrival, which is supported by archaeological evidence. The Pamwak site in Manus Island revealed a long series of human occupations from its first use about 24,000 y.b.p. until recently with the major period of occupation about 10,000 y.b.p. when new artifact types appeared (Fredericksen et al. 1993; Spriggs 1997; Specht 2005). Archaeological remains from some animal and plant species, which were distributed by humans across the biogeographic boundary between mainland New Guinea and the Bismarcks including the Admiralties (Green 1991b; Allen 2000), suggest several episodes of human Pleistocene contacts between mainland New Guinea and the Admiralties (Summerhayes 2003; Specht 2005) but at most limited human contacts between the Admiralties and the nearby New Britain and New Ireland (Flannery 1995; Specht 2005).

NRY Haplogroup K-P79: A Northern Island Melanesian Genetic Contribution to Polynesia

Analysis of our previously described samples (Kayser et al. 2006) for additional NRY markers reveals that the Melanesian NRY haplogroup K-P79 occurs in Polynesia. In fact, K-P79 was observed at high frequency in some parts of western Polynesia and in Fiji (frequencies of 28% on Tuvalu, 10% on Eastern Futuna, and 11.4% on Fiji) and at lower frequency in other parts of western and in central Polynesia (1.6–3.8% in Samoa, Tonga, and the Cook Islands) (fig. 1; supplementary table S2, Supplementary Material online). The Y-STR diversity associated with K-P79 was significantly higher for Melanesia (Nei's haplotype diversity = 0.900 ± 0.066 ; MPD = 2.86 ± 1.61 ; $N = 13$) than for Polynesia/Fiji (0.623 ± 0.073 ; 0.81 ± 0.59 ; $N = 53$), reflecting an origin of K-P79 in Island Melanesia, as suggested before (Scheinfeldt et al. 2006), and a subsequent spread into Polynesia. Y-STR haplotypes associated with K-P79 differ significantly between Melanesia and Polynesia/Fiji ($R_{st} = 0.610$; $P < 0.00001$) but not between Polynesia and Fiji ($R_{st} = 0.018$; $P = 0.23$). Only 1 out of 16 different haplotypes was shared between the Admiralty Islands (Titan) and Polynesia

and another between New Britain and Fiji. This, together with the observed significant Y-STR differentiation between Melanesia and Polynesia, suggests limited contacts between both regions after the initial settlement of Polynesia and argues against the presence of K-P79 in Polynesia as the result of more recent contacts.

K-P79 is thus the first Melanesian NRY haplogroup in Polynesia that can be assigned to a specific regional source within Melanesia, namely northern Island Melanesia. This is in agreement with linguistic as well as archaeological evidence suggesting that Polynesian (as well as other Oceanic) languages can be traced back to a homeland of Proto-Oceanic in the Bismarcks (Lynch et al. 2002) and that Lapita pottery found in western Polynesia can also be traced back to an origin in the Bismarcks (Kirch 1997, 2000; Spriggs 1997; Green 2002, 2003). Thus, not only were cultural elements, that is, the Lapita cultural complex and Oceanic languages carried from northern Island Melanesia into Polynesia but also genes, at least Y chromosomes belonging to haplogroup K-P79. It appears that the currently known frequency distribution of K-P79 coincides with the distribution of Lapita sites (except for the low frequency of K-P79 in central Polynesia which was settled after Polynesians stopped making pottery). The tmrca for K-P79 suggests that this haplogroup arose before or around the time of the Austronesian arrival in northern Island Melanesia. Haplogroup K-P79 thus might reflect a genetic contribution of northern Island Melanesians to the incoming Austronesians, which the Proto-Oceanic-speaking Lapita people subsequently carried into the western and southern Pacific, hence a genetic marker for Lapita. Additional genotyping of the NRY marker P79 in populations from the western Pacific region, especially Santa Cruz, Vanuatu, and New Caledonia as well as in human skeleton remains from Lapita sites (if DNA preservation allows) would shed further light on the history of this haplogroup.

Moreover, it is possible that all Melanesian genes in Polynesia originated from northern Island Melanesia, since all Melanesian NRY and mtDNA haplogroups observed in Polynesia were also found in the Bismarck Archipelago (Table 1, 2, S2, S3), (Scheinfeldt et al. 2006; Friedlaender et al. 2007). In addition to K-P79, we observed in Western Polynesia and Fiji two other NRY haplogroups, K-P117 and M-M104/P22, with an assumed geographic origin in northern Island Melanesia (Scheinfeldt et al. 2006), although in smaller frequency than K-P79 (Table S2), (Kayser et al. 2006). Furthermore, a fourth NRY haplogroup of assumed northern Island Melanesian origin, M-P87, (Scheinfeldt et al. 2006) was found in moderate frequency in our Fijian although not in the Polynesian samples (Kayser M, Choi Y, Brauer S, Stoneking M, unpublished data). Thus, we see evidence from several NRY haplogroups for an eastward spread of people from northern Island Melanesia as far as Western Polynesia, perhaps associated with the spread of Lapita. However, this scenario is not supported by the absence in Polynesia of several mtDNA haplogroups with an inferred origin in the Bismarcks such as M27, M28, M29, and Q2 (Table S3), (Kayser et al. 2006, Friedlaender et al. 2007). It remains possible that these haplogroups disappeared from the current Polynesian mtDNA gene pool due to genetic drift and bottleneck effects, and/or the respective differences between NRY and mtDNA evidence

reflects the sex-biased admixture between incoming Austronesians and local non-Austronesian in northern Island Melanesia before the eastward spread into Polynesia.

Although, as argued above, the initial genetic admixture between those Austronesians and non-Austronesians that gave rise to the people who further migrated eastward across the Pacific most likely happened in northern Island Melanesia, Austronesians probably arrived earlier in the Bird's Head region of northwestern New Guinea (NWN), as indicated by linguistic data (Lynch et al. 2002). However, this earlier Austronesian arrival in NWN seems to have had only a small genetic impact, though its linguistic impact was much greater (Mona et al. 2007). In particular, although NWN hosts nearly all Austronesian-speaking groups of the western part of New Guinea, the frequency of Asian NRY haplogroups in this region is very low (Mona et al. 2007). Although the genetic influence of early Austronesians to NWN was low, it remains possible that some Melanesian haplogroups were already contributed to Austronesians in the Bird's Head region and then spread by subsequent eastward migration of Austronesians. In particular, NRY haplogroup C-M38 has a high frequency and an assumed origin in the Bird's Head region of NWN (Mona et al. 2007). C-M38 is also more frequent in Austronesian groups (and Fijians) than in non-Austronesian groups of northern Island Melanesia and eastern mainland New Guinea (supplementary table S2, Supplementary Material online) (Kayser et al. 2006; Scheinfeldt et al. 2006). Thus, the Melanesian haplogroup C-M38 might have been distributed at least in part by Austronesians after an early admixture episode with non-Austronesians in the Bird's Head region of NWN. This scenario is less likely for other Melanesian haplogroups based on their frequency distribution.

mtDNA Diversity in the Admiralty Islands

The predominant Asian mtDNA haplogroup in the Admiralties is the PM haplogroup (overall frequency = 36.8%), which was widespread in all 9 Admiralty Island groups. The next most frequent haplogroup was B4a (13.2%), which was moderately frequent in 6 groups but absent from 3 groups (table 2, fig. 1). The PM haplogroup is thought to have originated in eastern Indonesia (Redd et al. 1995), represents the major Asian haplogroup in Polynesia (hence the name), and is also frequent in Austronesian-speaking groups from coastal New Guinea and Island Melanesia (fig. 1; supplementary table S3, Supplementary Material online) (Melton et al. 1995; Sykes et al. 1995; Kayser et al. 2006). Haplogroup B4a, the precursor of the PM haplogroup, occurs at high frequency in Taiwanese Aborigines (20%, fig. 1; supplementary table S3, Supplementary Material online), thus indicating a probable Taiwanese origin for this haplogroup (Redd et al. 1995; Trejaut et al. 2005), and also occurred in moderate frequency in Austronesian-speaking groups from coastal New Guinea and Island Melanesia (fig. 1; supplementary table S3, Supplementary Material online) (Kayser et al. 2006; Friedlaender et al. 2007). Five additional Asian mtDNA haplogroups were also observed in the Admiralties (B4b1, B5b, M7b, M7c1c, and E1b), although not in all groups and in low frequencies (1.4–4.2%, see table 2, fig. 1).

The predominant Melanesian mtDNA haplogroup in the Admiralties (frequency = 26.2%) was Q1, which is also the most frequent Melanesian haplogroup in mainland New Guinea and Island Melanesia (fig. 1; supplementary table S3, Supplementary Material online) (Kayser et al. 2006; Friedlaender et al. 2007). Haplogroup Q2 was on average the second most frequent Melanesian mtDNA haplogroup (8.3%) in the Admiralties, but with a high frequency in only 2 groups (Seimat–Wuvulu with 19% and Titan with 29%) and rare or absent from all other Admiralty groups (table 2, fig. 1). Q2 is rare in mainland New Guinea but more frequent in New Britain and New Ireland (fig. 1; supplementary table S3, Supplementary Material online) (Kayser et al. 2006; Friedlaender et al. 2007). Two other Melanesian mtDNA haplogroups, P2 and P4, also occurred on the Admiralties albeit at low frequencies and on average 3.5% and 1.4%, respectively (table 2, fig. 1). These 2 haplogroups were also rare throughout New Guinea including northern Island Melanesia (fig. 1; supplementary table S3, Supplementary Material online) (Kayser et al. 2006; Friedlaender et al. 2007). Interestingly, the second most frequent mtDNA haplogroup in New Guinea including New Britain and New Ireland, P1 (fig. 1; supplementary table S3, Supplementary Material online) (Kayser et al. 2006; Friedlaender et al. 2007), was not found in the Admiralties. Also missing from the Admiralties were several Melanesian mtDNA haplogroups that are largely restricted to Island Melanesia, such as M27, M28, and M29 (Friedlaender et al. 2007).

Population Relationship of Admiralty Islanders

The mixed Asian and Melanesian genetic heritage of the Admiralty Island groups was reflected in their position in MDS plots based on pairwise F_{st} values as generated using the present data, our previously published (Kayser et al. 2006) but updated data (supplementary tables S1 and S2, Supplementary Material online), and data from 2 other studies (Scheinfeldt et al. 2006; Friedlaender et al. 2007). For NRY haplogroups (fig. 4A), all Admiralty groups (except Seimat–Wuvulu) were somewhat surrounded by a cluster of other Island Melanesian groups, a cluster of mainland PNG groups, and a cluster of East and Southeast Asian groups, whereas Polynesians mostly appear between Melanesians and Asians (with the exception of Niue, which may reflect the small sample size). The Seimat–Wuvulu group from the Ninigo, Wuvulu, and Hermit Islands appeared somewhat separated from the Admiralty groups (because of the K-P79 frequency). The MDS plot for mtDNA haplogroups (fig. 4B) was different, with less clear regional clustering of groups (except perhaps for Asians and Polynesians, respectively). The Admiralty groups were scattered across almost the entire plot and appeared intermingled with other Island Melanesian and mainland PNG groups, Micronesians and Fijians, but somewhat more distant to Asians and Polynesians.

Conclusions

The observed higher frequencies of Asian than Melanesian mtDNA haplogroups in the Admiralty Islanders,

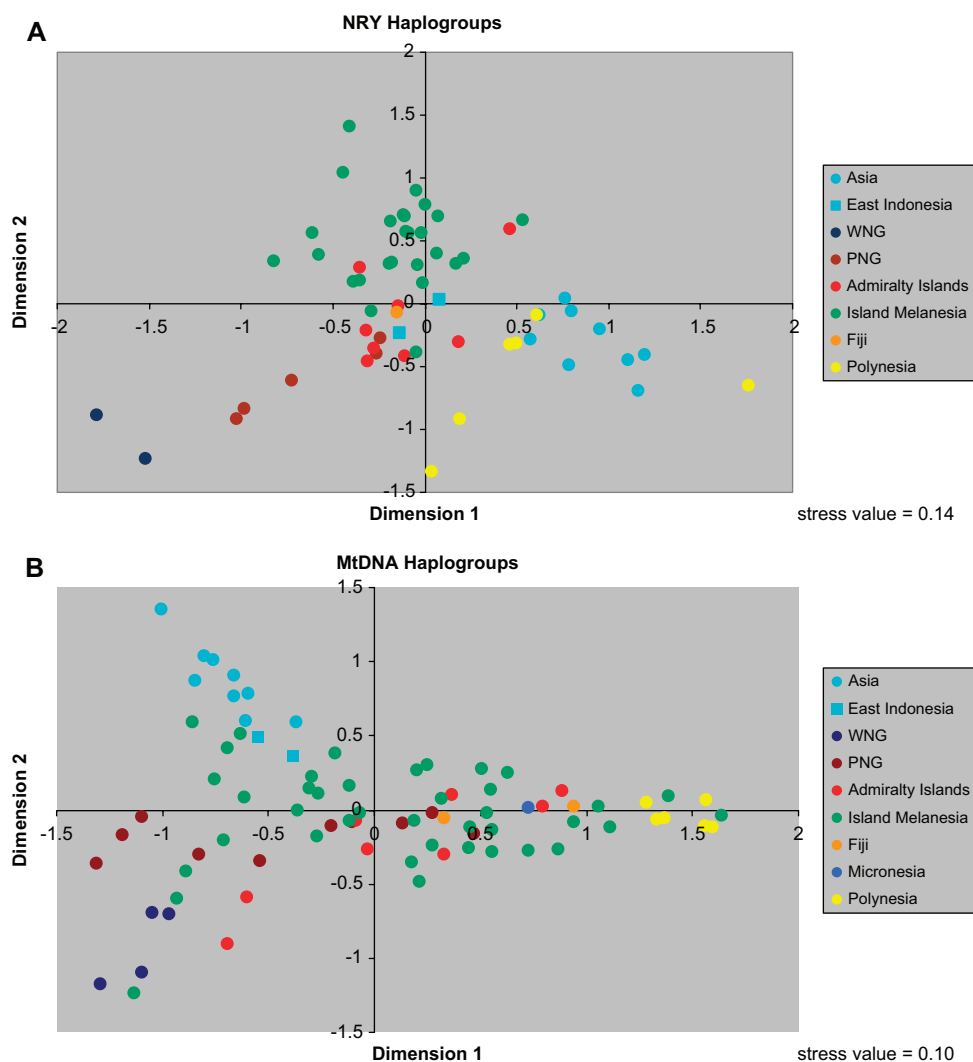


FIG. 4.—Two-dimensional plots from MDS analysis of F_{st} values from NRY haplogroup frequencies (A) and mtDNA haplogroup frequencies (B) using data from the present study, our updated previous study (Kayser et al. 2006), and 2 other studies (Scheinfeldt et al. 2006; Friedlaender et al. 2007); groups with sample sizes less than 10 were excluded.

together with their higher frequencies of Melanesian than Asian NRY haplogroups, suggest sex-biased genetic admixture between the incoming Austronesians and the local non-Austronesians inhabitants of northern Island Melanesia. Thus, the data presented here provide additional support for the Slow Boat model of Polynesian origins because the genetic findings concerning the Admiralties of northern Island Melanesia, the region of assumed first contact between the incoming pre-Proto-Oceanic-speaking Austronesians and the local non-Austronesian inhabitants of Melanesia were similar to those from Polynesia, the final eastern destination of the Austronesian expansion. The observation of more Asian mtDNA haplogroups than Asian NRY haplogroups on the Admiralty Islands as well as in other Austronesian-speaking groups from coastal New Guinea and Island Melanesia suggests that the Austronesian language replacement in Melanesia was driven by Austronesian women rather than men, perhaps as a consequence of a matrilineal residence pattern in combination with a matrilineal social structure. Sex-biased admixture is also

observed in those groups speaking non-Austronesian languages in coastal New Guinea and Island Melanesia, but here there was a much bigger contribution inferred for Austronesian women than for Austronesian men, in keeping with the patrilineal residence and patrilineal social structure of non-Austronesian (Papuan) groups in Melanesia. The major Asian NRY haplogroup on the Admiralties (O-M110) can be ultimately traced back to Taiwan, which provides a genetic parallel to mtDNA data evidence and strikingly intersects with linguistic and archaeological evidence for a Taiwanese source of the Austronesian expansion. Furthermore, our genetic data are in line with archaeological evidence suggesting human Pleistocene contacts between mainland New Guinea and the Admiralties, as we found most known NRY and mtDNA haplogroups with an inferred origin in mainland New Guinea on the Admiralties, as well as with other archaeological data proposing at most limited human contacts between the Admiralties and the nearby New Britain and New Ireland, as we found many mtDNA and NRY haplogroups with an inferred origin in

New Britain/New Ireland absent or nearly so in the Admiralties. Finally, we showed that the Melanesian NRY haplogroup K-P79 was most likely contributed to Polynesia from New Britain/New Ireland, and in fact northern Island Melanesia may have been the source of all the haplogroups of Melanesian origin found in Polynesia. Thus, the work reported here substantially advances our knowledge on the genetic impact of the Austronesian expansion and human history in the western and southern Pacific region.

Supplementary Material

Supplementary tables S1–S3 and figures S1–S3 are available at *Molecular Biology and Evolution* online (<http://www.mbe.oxfordjournals.org/>).

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