Patterns of Y-Chromosome Diversity Intersect with the Trans-New Guinea Hypothesis

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The island of New Guinea received part of the first human expansion out of Africa (>40,000 years ago), but its human genetic history remains poorly understood. In this study, we examined Y-chromosome diversity in 162 samples from the Bird's Head region of northwest New Guinea (NWNG) and compared the results with previously obtained data from other parts of the island. NWNG harbors a high level of cultural and linguistic diversity and is inhabited by non-Austronesian (i.e., Papuan)–speaking groups as well as harboring most of West New Guinea's (WNG) Austronesian-speaking groups. However, 97.5% of its Y-chromosomes belong to 5 haplogroups that originated in Melanesia; hence, the Y-chromosome diversity of NWNG (and, according to available data, of New Guinea as a whole) essentially reflects a local history. The remaining 2.5% belong to 2 haplogroups (O-M119 and O-M122) of East Asian origin, which were brought to New Guinea by Austronesian-speaking migrants around 3,500 years ago. Thus, the Austronesian expansion had only a small impact on shaping Y-chromosome diversity in NWNG, although the linguistic impact of this expansion to this region was much higher. In contrast, the expansion of Trans-New Guinea (TNG) speakers (non-Austronesian) starting about 6,000–10,000 years ago from the central highlands of what is now Papua New Guinea, presumably in combination with the expansion of agriculture, played a more important role in determining the Y-chromosome diversity of New Guinea. In particular, we identified 2 haplogroups (M-P34 and K-M254) as suggestive markers for the TNG expansion, whereas 2 other haplogroups (C-M38 and K-M9) most likely reflect the earlier local Y-chromosome diversity. We propose that sex-biased differences in the social structure and cultural heritage of the people involved in the Austronesian and the TNG expansions played an important role (among other factors) in shaping the New Guinean Y-chromosome landscape.

Introduction

Studies of human Y-chromosome diversity have provided important insights into the origin, history, and relationships of human populations on global and regional levels (Karafet et al. 1999; Rosser et al. 2000; Cruciani et al. 2002; Zerjal et al. 2002), including Oceania (Capelli et al. 2001; Kayser et al. 2001; Hurles et al. 2002). For the latter region, Y-chromosome data together with those from mitochondrial DNA revealed that Polynesians are of mixed East Asian and Melanesian genetic origin (Kayser, Brauer, et al. 2000; Kayser et al. 2006).

The island of New Guinea is interesting for studying human genetic history because it was occupied by anatomically modern humans as long as 35–40,000 years ago (Groube et al. 1986; Pavlides and Gosden 1994; Leavesley et al. 2002; Specht 2005) representing part of the first expansion of modern humans out of Africa. Melanesia (used here as geographic term comprising mainland New Guinea and surrounding islands in the north and east, also referred to as Near Oceania together with most of the Solomon islands) is inhabited today by speakers of 2 kinds of languages. Austronesian-speaking groups have a common ancestral language, Proto-Austronesian, and mostly live on islands around New Guinea as well as on the northeast and southeast coasts of the New Guinea mainland. Non-Austronesian (=Papuan)–speaking groups lack a (recent) common ancestry and include numerous linguistically unrelated groups. Papuan speakers dominate the New Guinea mainland, living inland from Austronesian speakers where such are present, and are also found in a few places around the islands north, northeast, and east of mainland New Guinea where their languages have persisted to modern times (Wurm and Hattori 1981; Specht 2005). These 2 groups of people have a different history in Melanesia: non-Austronesian–speaking groups reflecting the ebb and flow of language that emerged out of the Pleistocene language geography, whereas Austronesian speakers arrived as migrants from East Asia not earlier than 3,500 years ago (Kirch 1997).

Informative genetic markers mostly from the nonrecombining part of the Y-chromosome and from mitochondrial DNA have been identified previously. As expected, markers of East Asian origin are observed more often in Austronesian-speaking groups and more rarely (or not at all) in non-Austronesian–speaking groups of Melanesia, whereas markers that originated in Melanesia prior to the arrival of Austronesian speakers are found with high frequency in non-Austronesian–speaking groups (Stoneking et al. 1990; Merriwether et al. 1999; Kayser et al. 2001; Tommaseo-Ponzetta et al. 2002; Kayser et al. 2003; Kayser et al. 2006; Scheinfeldt et al. 2006).

The genetic history of the New Guinea area prior to the arrival of Austronesian speakers has only recently begun to receive attention. The Trans-New Guinea (TNG) hypothesis proposes a very large family of languages mostly spoken along the central cordillera of New Guinea and in some regions north and south of the cordillera, with outliers in the Timor area of Island Southeast Asia. The TNG hypothesis implies an expansion of people speaking TNG languages

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started about 6,000–7,000 (perhaps as early as 10,000) years ago in the central highlands of what is now Papua New Guinea (PNG), most likely in connection with the expansion of agriculture, and spread both eastwards and westwards (Pawley 1998; Denham et al. 2003; Pawley 2005). So far, the amount of genetic data available from New Guinea was not sufficient to suggest either parallels or discontinuities with the TNG hypothesis. In this study, we address human population history of New Guinea by analyzing Y-chromosome diversity of the Bird's Head as well as the Bomberai Peninsulas and surrounding regions of northwest New Guinea (NWNG) and compare the data with results previously obtained from additional New Guinean regions as well as from East, Southeast Asia, and Polynesia (Kayser et al. 2003; Kayser et al. 2006).

The Bird's Head or Doberai Peninsula (Indonesian: Kepala Burung, Netherlands: Vogelkop), named after its distinctive shape, and the Bomberai Peninsula (together referred to as Bird's Head region thereafter) are located in the northwestern part of West New Guinea (WNG) (formerly called Irian Jaya or West Irian, Indonesia). Evidence for the first human occupation of the Bird's Head region goes back at least 26,000 years (Pasveer 2004), consistent with earlier dates from other regions of New Guinea going back 35–40,000 years (Groube et al. 1986; Pavlides and Gosden 1994). Later on, this region was a key point of an extensive network of contacts and exchange (Aplin 1998), connecting the New Guinea area with the neighboring Eastern Indonesian islands. Consequently, the Bird's Head region harbors a high level of cultural (including language) diversity hosting Austronesian- as well as non-Austronesian–speaking groups (Nettle 1999). Regional non-Austronesian languages are mostly spoken on the Bird's Head Peninsula and less so on the more southern Bomberai Peninsula as well as east of the Cenderawasih (formerly Geelvink) Bay. Regional Austronesian languages are distributed at the junction of the Bird's Head and the Bomberai Pensinsulas, in the central and eastern parts of the Bomberai Peninsula, on the islands west of the Bird's Head Peninsula (Waigeo, Batanta, Salawati, and Misool), on Yapen, Biak, and Numfor, with surrounding smaller islands in the Cenderawasih (Geelvink) Bay, as well as on Aru and Kai south of the Bomberai Peninsula (Wurm and Hattori 1981). Notably, the Bird's Head region with surrounding islands hosts almost all Austronesian speakers of WNG.

Most genetic studies on WNG populations employed blood group markers and were often performed on single populations only (Nijenhuis and van der Hoeven 1956; de Vries and Nijenhuis 1960; Nijenhuis et al. 1960; Nijenhuis et al. 1966; Simmons et al. 1967; Gajdusek et al. 1978; Tommaseo et al. 1992). Molecular genetic data for WNG are rare, and only one large set of samples has been analyzed recently for Y-chromosome and mtDNA diversity to investigate population history but included samples from non-Austronesian–speaking groups from the highlands and lowlands of southwest New Guinea (SWNG) (Tommaseo-Ponzetta et al. 2002; Kayser et al. 2003). Only one group from NWNG, that is, the Ayamaru district, has been studied for some Y-chromosome markers (Capelli et al. 2001).

The Y-chromosome data presented here for the Bird's Head and surrounding regions of NWNG combined with our previously published data shed new light on the genetic history of the island. For the first time, we provide genetic parallels to the TNG hypothesis. We also report little genetic differentiation at the Y-chromosome level between Austronesian- and non-Austronesian–speaking groups in NWNG.

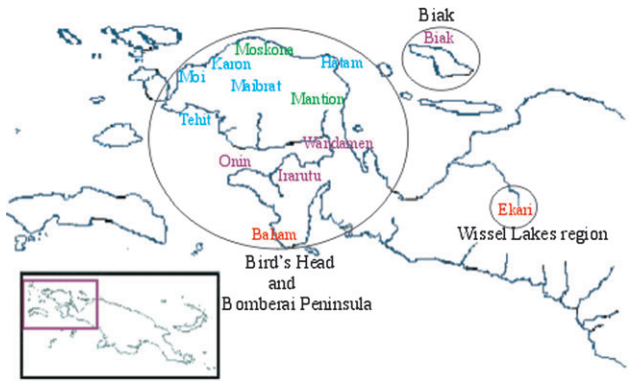

FIG. 1.—Schematic map of NWNG with location of the populations sampled. The Bird's Head region comprises of the Bird's Head or Doberai Peninsula as well as the more southern Bomberai Peninsula. Colors refer to linguistic families: blue, West Papuan; green, East Bird's Head; red, TNG; violet, Austronesian.

Materials and Methods

Samples

In a collaborative project together with the Eijkman Institute for Molecular Biology in Jakarta, Indonesia, M.T.-P. collected mouth swab samples from 162 men under informed consent who belonged to 13 populations from the Bird's Head region, as well as the Wissel Lakes region and Biak Island, all in NWNG (Indonesia). The Bird's Head region includes the Bird's Head or Doberai Peninsula and the more southern Bomberai Peninsula (fig. 1). Four Austronesian and 9 non-Austronesian groups, the latter from 3 different linguistic subgroups (East Bird's Head, West Papuan, and TNG), were sampled. The location of the populations is shown in figure 1, whereas sample size together with the linguistic classification is provided in table 1.

Y-Chromosome Genotyping

In total, 16 binary markers from the nonrecombining region of the Y-chromosome (NRY) here referred to as Y-SNPs (M9, RPS4Y, M38, M208, M230, M254, M226, M4, P34, M104, M175, M119, M122, M74, M214, and M353) were analyzed following protocols described elsewhere (Kayser, Brauer, et al. 2000; Kayser et al. 2001; Kayser et al. 2003; Kayser et al. 2006). The phylogenetic relationship of the markers and respective haplogroups can be obtained from the supplemental material of Kayser et al. (2006). In addition, 7 NRY short tandem repeat or Y-STR markers (DYS19/394, DYS389I, DYS389II, DYS390, DYS391, DYS392, and DYS393) were genotyped following the protocol described elsewhere (Kayser et al. 1997). Additional Y-chromosome data obtained in previous studies for the same markers from various

Table 1
Sample Size and Linguistic Classification of the Populations Studied

Population	Linguistic Classification	Sample Size
Baham	TNG	24
Ekari	TNG	19
Maibrat	West Papuan	24
Moi	West Papuan	8
Tehit	West Papuan	5
Hatam	West Papuan	12
Karon	West Papuan	22
Mantion	East Bird's Head	11
Moskona	East Bird's Head	10
Irarutu	Austronesian	5
Onin	Austronesian	2
Wandamen	Austronesian	10
Biak	Austronesian	10

populations from SWNG, mainland and island PNG, East and Southeast Asia, as well as Polynesia (Kayser et al. 2003; Kayser et al. 2006) were considered for comparative data analyses.

Statistical Data Analyses

Diversity estimates were computed using the software package ARLEQUIN 2.000 (Schneider et al. 2000). Median-joining networks (Bandelt et al. 1999) among STR haplotypes within Y-SNP haplogroups were constructed using the software NETWORK 4.1.0.0 (available at http://fluxus-engineering.com) with marker weighting according to locus-specific mutation rates. The following weights, obtained from combined locus-specific mutation rate estimates described elsewhere (Heyer et al. 1997; Bianchi et al. 1998; Kayser, Roewer, et al. 2000; Dupuy et al. 2004; Kurihara et al. 2004; Ballard et al. 2005; Budowle et al. 2005; Gusmao et al. 2005), were applied: DYS19:DYS389I:DYS389II:DYS390:DYS391:DYS392:-DYS393 = 4:4:3:3:2:12:10. A Bayesian-based coalescent approach (Wilson et al. 2003) implemented in the software BATWING was used for demographic inferences. BATWING coalescent priors included a model where population size is first constant but later starts an exponential growth to reach its current size. Likelihood of the gene genealogy was computed under the stepwise mutation model. Posterior probability of gene genealogy, population genetic parameters, and Y-SNP haplogroup dating are approximated through the Metropolis–Hastings algorithm (Hastings 1970). Priors for Y-STR mutation rates and coalescent model were applied as in Kayser et al. (2006). The gene genealogy was constrained using the known Y-SNP phylogeny (Kayser et al. 2006), and the time to the most recent common ancestor of each haplogroup was recorded. The final analysis was the result of 2 runs 10^7 Monte Carlo Markov Chain long with 10% burn-in period. TRACER (Rambaut and Drummond 2004) was used both to visualize the generation plot of the likelihood and parameter values (to check for convergence) and to compute the 95% high posterior density of all the parameters combining the 2 runs. Haplogroup coalescent times were estimated for New Guinea in 3 ways: 1) only NWNG populations, 2) only SWNG populations, and 3) only PNG populations to investigate regional differences. Pairwise F_{ST} distances between the populations considered were computed using ARLEQUIN. The distance matrix was then plotted in 2 dimensions by means of multidimensional scaling (MDS) using the commercially available STATISTICA 6.0 software package, which was also used for correspondence analysis of haplogroup frequencies. ARLEQUIN was also used to perform Analysis of Molecular variance (AMOVA).

Results and Discussion

Y-Chromosome Diversity in NWNG

Although the 13 groups from NWNG encompassed much of the linguistic variability of the area, as they belonged to 4 different linguistic families (TNG, West Papuan, East Bird's Head, and Austronesian), this high linguistic diversity is not reflected in the level of Y-chromosome diversity we observed. Y-chromosome diversity found in NWNG (in terms of both Y-SNP haplogroups and Y-STR haplotypes) is relatively low compared with several populations distributed across East/Southeast Asia and Oceania (supplementary table S1 and S2, Supplementary Material online). Interestingly, NWNG populations harbor only 7 of the 13 NRY haplogroups described before in New Guinea populations (Kayser et al. 2006) covering all of NWNG Y-chromosomes. Moreover, 4 of them (M-P34, K-M9, C-M38, and K-M254) account for 95% of all NWNG Y-chromosomes. This result is comparable with that of Capelli et al. (2001), who typed only one population from the Ayamaru region in the Bird's Head and observed 3 haplogroups. Although they only typed a limited number of markers making a direct comparison impossible, our data of the region makes it likely that there is a local correspondence between their haplogroups C, E, and F and our C-M38, M-P34, and K-M9, respectively.

Despite this general low Y-chromosome diversity, it is worth noting that NWNG populations are significantly more diverse than neighboring SWNG populations (Mann–Whitney *U*-test for haplogroups: $Z = 2.367$, P value = 0.018; for haplotypes: $Z = 1.956$, P value = 0.05; after removing groups with a sample size equal to or less than 5). This is not surprising because the reduction of Y-chromosome diversity in SWNG populations (particularly in the highland populations) has been explained by their extreme patrilocal residence pattern (women moving to the place of their husband's family after marriage) together with patrilineal social structure (clans are inherited through the fathers line), polygyny (men having more than one wife), and the practice of male-biased warfare (more men than women are killed during wars) (Kayser et al. 2003). NWNG groups studied here are not highland groups, with the notable exception of Ekari. Indeed, Ekari shows the lowest diversity among all NWNG populations studied (supplementary table S1, Supplementary Material online), with 1 haplogroup (K-M254) at high frequency (73.6%). Furthermore, the low level of associated Y-STRs diversity (supplementary table S1, Supplementary Material online) as well as the network analysis (fig. 3*C*) suggests a bottleneck followed by a recent expansion in Ekari history, a pattern similar to that observed previously in SWNG highland populations, although for different haplogroups (Kayser

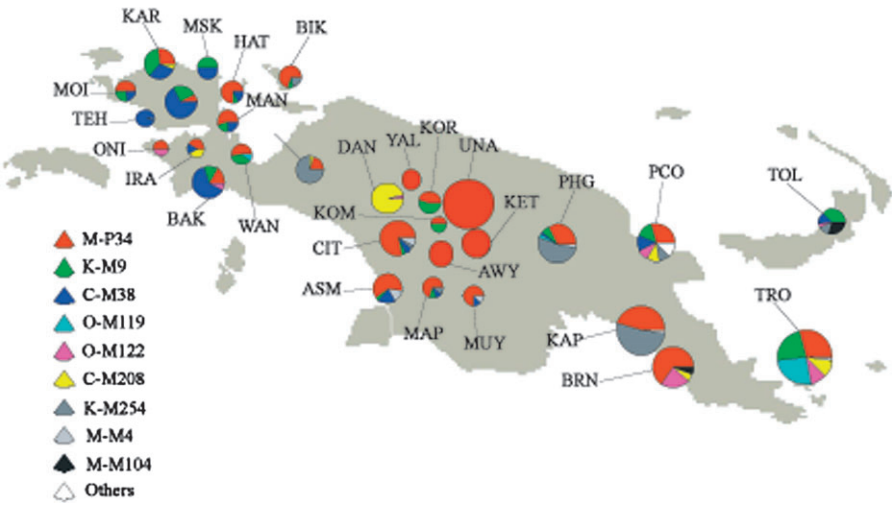

FIG. 2.—Y-chromosome haplogroups and their frequencies in populations from the Bird's Head region and elsewhere in New Guinea. Data from other populations of New Guinea were used from previous studies (Kayser et al. 2003, 2006). Size of the pie charts is according to sample size of the groups. Abbreviations are as in supplementary table S1, Supplementary Material online.

et al. 2003). The Hatam group displays a similarly low level of haplogroup diversity, although Y-STR diversity is somewhat higher (supplementary table S1, Supplementary Material online), and it has been identified as a linguistic isolate, which might explain our genetic findings (Reesink 1996, 1998). Furthermore, NWNG harbors both Austronesian and non-Austronesian groups, whereas SWNG only the latter; the broad association between major linguistic groups and Y-chromosome markers in New Guinea has been already shown (Capelli et al. 2001; Kayser et al. 2001, 2003). Therefore, both in terms of haplogroups and haplotypes, higher diversity in NWNG compared with SWNG is to be expected (although Austronesian-associated Y-chromosomes are rare in NWNG).

Origins of Y-Chromosome Diversity in New Guinea and Demographic Inferences

Five of the seven Y haplogroups found in NWNG, C-M38, C-M208, M-P34, K-M9, and K-M254 are of Melanesian origin (Kayser et al. 2006) and represent 97.5% of all NWNG Y-chromosomes studied (fig. 2 and table 2). The remaining 2 haplogroups, O-M119 and O-M122, are of East Asian origin (Kayser et al. 2001, 2006), reflecting 2.5% of NWNG Y-chromosomes (fig. 2 and table 2). Six additional Y haplogroups were previously observed in mainland and island PNG, albeit in very low frequency, but were not present in this data set from NWNG: M-M4, M-M104, K-M226, K-M230, P-M74, and C-RPS4Y. The first 4 haplogroups most likely originated in New Guinea, whereas the latter 2 were brought there from Asia (Kayser et al. 2006).

C-M38 is the most common haplogroup in NWNG (34.6%, table 2) and the second most frequent haplogroup in New Guinea (average frequency of 12.8%) (fig. 2). A Melanesian origin of this haplogroup was suggested previously (Kayser et al. 2003, 2006), but limited data did not allow identification of a more precise region of origin. With the new data presented here, C-M38 coalescent time estimate suggests its origin in NWNG around 12,375 years ago (6,050–21,325, 95% high posterior density). C-M38 is older and has the highest associated Y-STR diversity in NWNG. All other regions of New Guinea studied (table 3) and Eastern Indonesian as well (Kayser et al. 2006) have lower levels of associated Y-STR diversity. Additionally, Y-STR haplotypes from SWNG and mainland/island PNG appear at

Table 2
NRY Haplogroup Distribution (Counts) in NWNG

Population	*N*	M-P34	K-M9	K-M254	C-M38	C-M208	O-M119	O-M122
Baham	24	4	3		15			2
Ekari	19	4		14		1		
Hatam	12	9	1		2			
Karon	22	6	8		7	1		
Maibrat	24	2	6		16			
Moi	8	4	2		2			
Tehit	5				5			
Mantion	11	6	2		3			
Moskona	10		5		5			
Biak	10	7	1	2				
Onin	2	1						1
Irarutu	5	2			1	2		
Wandamen	10	5	4				1	
Total	162	50	32	16	56	4	1	3

Table 3
Diversity Estimates and Demographic Inferences of the 5 Major Y-SNP Haplogroups with Assumed Melanesian Origin in 3 Regions of New Guinea

Hg[a]	Mean[b]	95% HPD low[b]	95% HPD up[b]	*N*[c]	Ht[d]	Diversity	MPD[e]	Region
M-P34	6,475	3,550	10,450	50	29	0.9600 ± 0.0154	3.339	NWNG
K-M254	3,450	1,475	5,600	16	6	0.6167 ± 0.1347	1.75	NWNG
K-M9	14,575	7,100	23,700	32	20	0.9335 ± 0.0302	3.575	NWNG
C-M38	12,375	6,050	21,325	56	34	0.9636 ± 0.0144	4.641	NWNG
C-M208	[f]	[f]	[f]	4	3	[f]	[f]	NWNG
M-P34	5,875	3,150	9,075	135	41	0.9380 ± 0.0117	3.589	SWNG
K-M254	[f]	[f]	[f]	2	1	[f]	[f]	SWNG
K-M9	11,425	5,425	19,175	10	4	0.5333 ± 0.1801	2.583	SWNG
C-M38	8,050	1,825	16,900	8	5	0.8571 ± 0.1083	3.111	SWNG
C-M208	1,800	725	3,225	23	5	0.6957 ± 0.0727	1.304	SWNG
M-P34	7,356	4,442	10,868	77	45	0.9710 ± 0.0095	4.149	PNG
K-M254	6,291	3,307	9,435	45	18	0.9117 ± 0.0263	4.193	PNG
K-M9	15,127	7,894	24,853	25	21	0.9789 ± 0.0214	5.847	PNG
C-M38	[f]	[f]	[f]	3	3	[f]	[f]	PNG
C-M208	3,513	1,465	5,909	7	4	0.8095 ± 0.1298	3.048	PNG

[a] Hg, haplogroup.
[b] Mean and 95% high posterior density estimates of haplogroup coalescence times (generation time of 25 years).
[c] *N* = sample size.
[d] Ht = number of haplotypes.
[e] MPD = mean pairwise difference between Y-STR haplotypes.
[f] Not estimated for sample size equal to or less than 5. For SWNG and PNG data from Kayser et al. (2006) were used. PNG coast was excluded because it does not represent one location.

derived positions in respect to NWNG haplotypes in a median network analysis (fig. 3*A*), confirming diversity and coalescent time estimate results (table 3). Therefore, all analyses point to an origin of C-M38 in NWNG and a later expansion eastwards toward the other regions of mainland New Guinea and offshore islands as far eastwards as Polynesia (although rarely observed), as well as westwards into Island Eastern Indonesia (Kayser et al. 2006).

M-P34 is the second most frequent haplogroup in NWNG (30.9%, table 2) and the most frequent haplogroup in New Guinea (average frequency 46.8%) (fig. 2). This haplogroup is of Melanesian origin (Kayser et al. 2006), but its distribution is not homogeneous across New Guinea. Unlike C-M38, it reaches its highest associated Y-STR diversity in PNG (table 3). Coalescent analyses suggest that M-P34 arose around 7,356 years ago (4,442–10,868, 95% high posterior density) in what is now PNG (table 3) and spread westwards toward SWNG, NWNG, and Eastern Indonesia as well as eastwards and northwards into Island PNG (Kayser et al. 2006). This scenario is supported by the median network analysis (fig. 3*B*) with the central position of the network occupied by a haplotype most represented in PNG. As expected, PNG haplotypes are scattered through the network.

K-M254 is less frequent than M-P34 in NWNG (9.9%) but shows a pattern similar to that of M-P34 across New Guinea (average frequency of 11.2%) with higher frequency in PNG than in WNG (table 2 and fig. 2). Diversity, time estimates (table 3), and median network analyses (fig. 3*C*) point to an origin of K-M254 in mainland PNG and a spread westwards into WNG and Eastern Indonesia as well as eastwards and northwards into offshore islands (Kayser et al. 2006). However, this haplogroup is younger than M-P34 as its coalescent time for PNG is around 6,291 years ago (3,307–9,435, 95% high posterior density). Interestingly, for NWNG, K-M254 reaches its highest frequency of 73.6% amongst the Ekari. This haplogroup is also the most frequent among PNG Kapuna (a group of people that most likely originated in the highlands but now lives in the lowlands of the Gulf province) and in the PNG highlands implying an ancient link; however, the median network analysis shows both a reduction of diversity in Ekari and a separation between Ekari and PNG haplotypes (fig. 3*C*). Therefore, the most likely explanation is a bottleneck in the Ekari population history followed by an expansion leading to the (random) dominance of K-M254. A similar pattern has been already observed in other highland populations of SWNG leading to the fixation of M-P34 in several groups such as the Una, Ketengban, and Yali (fig. 2) and explained by social structure and lifestyle-associated bottlenecks with subsequent expansions (Kayser et al. 2003).

C-M208 is less informative in NWNG than the previously discussed haplogroups. It is present only in 4 individuals from NWNG (a frequency of 2.5%) (table 2 and fig. 2). C-M208 is of Melanesian origin (Kayser et al. 2006) but showed low frequency everywhere in New Guinea (average 6.8%), except in 2 related groups from the SWNG highlands (Kayser et al. 2003). Given the low sample size for the whole island, or its involvement in a bottleneck with subsequent expansion as in the Dani/Lani from SWNG (Kayser et al. 2003, 2006), it is difficult to infer its more specific geographic origin as well as its coalescent time. Interestingly, C-M208 is the most abundant haplogroup in some Polynesian populations such as the Cook Islanders (77%) and occurs in Polynesia with an average frequency of 34% also displaying a bottleneck signal and subsequent population expansion in Polynesia from network analysis (Kayser et al. 2006). This haplogroup provides the major Y-chromosome evidence for the partial Melanesian origin of the Polynesian gene pool (Kayser et al. 2006).

K-M9 is the third most abundant haplogroup in NWNG (19.8%) and is the most ancient haplogroup in

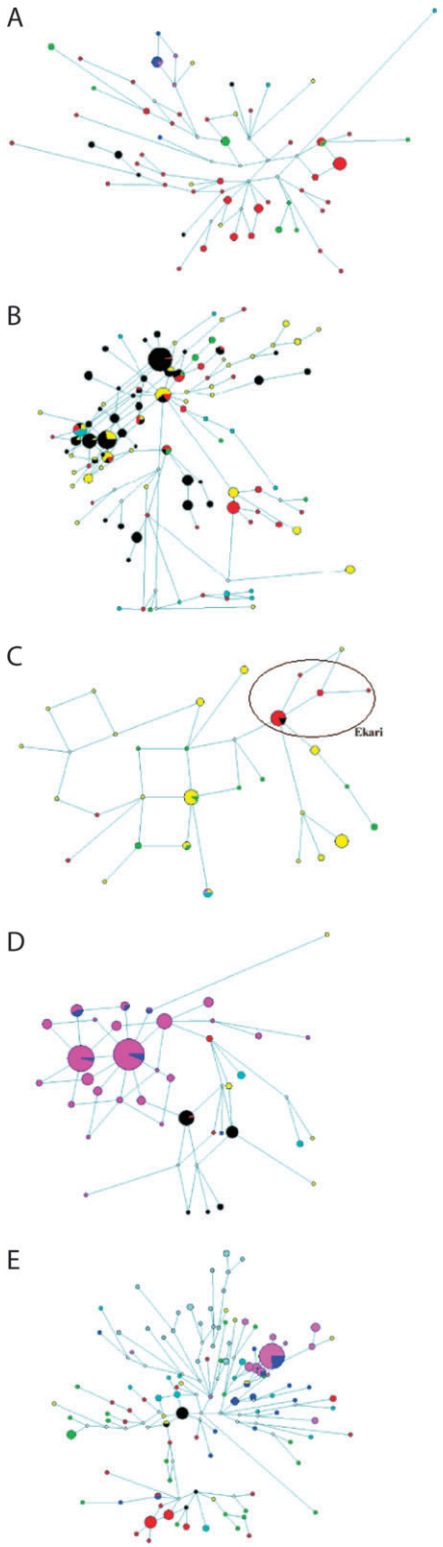

FIG. 3.—Median-joining networks of associated Y-STR haplotypes for the major Y-SNP haplogroups in New Guinea: C-M38 (*A*), M-P34 (*B*), K-M254 (*C*), C-M208 (*D*), and K-M9 (*E*). Node diameter is proportional to Y-STR haplotype frequency. Haplotypes are highlighted in colors according to their geographic regions with red, NWNG; black, SWNG; yellow, mainland PNG; light blue, island PNG; violet, Polynesia; blue, Fiji; green, South East Asia; gray, Australia, white, median vectors. Data from additional populations were used from previous studies (Kayser et al. 2003, 2006).

all New Guinea regions and oldest in PNG (fig. 2 and tables 2 and 3). It occurs with an average frequency of 11.9% in New Guinea. K-M9 Y-chromosomes were contributed from Melanesia to Polynesia (Kayser et al. 2006). The K-M9 network shows regional clustering of haplotypes, which suggests the existence of additional Y-SNPs either not included in our study or, more likely, still unknown (fig. 3*E*). It should be noted that K-M9 Y-chromosomes as described here have been tested and excluded for all markers characterizing known M9 sublineages and being expected in the study populations (M4, M214, M74, M230, and M353). The 2 recently reported new M9 sublineages, K-P79 and K-P117, are not expected to occur in relevant frequencies in NWNG populations studied here because both are highly specific to northern Island Melanesia (i.e., the Bismarck Archipelago and Bougainville) and were very rarely or not observed in individuals from mainland PNG (Scheinfeldt et al. 2006). However, K-M9 is probably still a paraphyletic group, and the discovery of new SNPs on the background of M9 in the future might allow characterizing new M9 sublineages. Noteworthy, in a worldwide study considering 167 Y-SNPs, samples from New Guinea showed by far the highest frequency (30%) of K-M9 Y-chromosomes without any further resolution when tested for all known M9 sublineages (Underhill et al. 2001). At present, all data suggest that K-M9 Y-chromosomes from New Guinea were present well before the Austronesian expansion, but it is still not possible to determine whether they originated in Melanesia or they were brought there during the first peopling of Sahul.

Y-Chromosome and Linguistic Relationships in New Guinea

Y-chromosome markers of Asian origin that were previously associated with the Austronesian expansion out of East Asia into the Pacific, O-M122 and O-M119 (Kayser et al. 2001, 2006), are found in 7.4% of the NWNG Austronesian speakers but only in 1.5% of the non-Austronesian speakers of NWNG (table 2 and fig. 2) and all together in 2.5% of all NWNG Y-chromosomes studied. However, the only non-Austronesian–speaking group from NWNG where O-M122 was observed (but only in 2 individuals) is the Bahams who lives geographically close to Austronesian-speaking groups such as the Onin, Irarutu, and Wandamen studied here (fig. 1). Thus, Austronesian-associated markers in non-Austronesian groups can be attributed to genetic contribution from surrounding Austronesian groups at least in NWNG (and is to be expected elsewhere in New Guinea). What is surprising is the low frequency of Austronesian-associated Y-chromosome markers in Austronesian-speaking groups from NWNG (7.4%) together with the high frequency of Y haplogroups that occurred in Melanesian prior to the Austronesian arrival in the same groups (92.6%). Consequently, AMOVA showed that the Y-chromosome difference between Austronesian- and non-Austronesian–speaking groups in NWNG is not statistically significant (for haplogroups: variance among groups = 7.3%, P value = 0.20; for haplotypes: variance among groups = 0%, P value = 0.58; values obtained after removing groups

with sample size equal to or less than 5). Thus, although Austronesian-associated Y-chromosome markers are observed in NWNG and occur more often in Austronesian than non-Austronesian speakers, the Austronesian expansion had only a small impact on shaping NWNG Y-chromosome diversity. A similarly low Y-chromosome impact of the Austronesian expansion to a different region of New Guinea was found recently in northern Island Melanesia (i.e., Bismarck Archipelago and Bougainville Island) with low frequencies of O-M119 and O-M122 in regional Austronesian-speaking groups (9.7%) and, as expected, lower in regional non-Austronesian–speaking groups (0.9%) with no significant differences between the language groups with respect to Y-chromosome diversity (Scheinfeldt et al. 2006). However, other Austronesian-speaking groups from mainland PNG and surrounding islands show a much higher frequency of O-M119 and O-M122 Y-chromosomes, for example, Bereina from the south coast of PNG (23%) or the Trobriand Islanders east of mainland PNG (38%) (Kayser et al. 2006) demonstrating either regional differences in the original Austronesian Y-chromosome contribution to New Guinea, genetic drift effects, or both.

To further investigate relationships between populations from New Guinea, we performed a correspondence analysis from haplogroup frequencies (fig. 4*a*) and a MDS analysis on pairwise F_{ST} values computed from haplogroup frequencies (fig. 4*b*). The correspondence analysis highlights the presence of geographic clines of haplogroup frequencies: NWNG populations are mostly differentiated by C-M38 and K-M9 Y-chromosomes, whereas SWNG mostly by P-34. This cline is determined by the decreasing frequencies of C-M38 and K-M9 and the increasing frequency of M-P34 going from NWNG toward PNG. Interestingly, Ekari, Kapuna, and PNG highlands do not join this cline as they are characterized by a very high frequency of K-M254 (see above). Also, the Tolai from New Britain, the Trobriand Islanders, and the group from PNG Bereina—all Austronesian speakers—are somewhat outside the cline most likely due to their frequencies of Austronesian-associated O-M119 and/or O-M122. Unfortunately, total inertia is relatively low (52%). MDS analysis confirmed at a broad scale the relationship found using the correspondence analysis. In the MDS plot, a cline differentiating NWNG and SWNG is still present, although somewhat less evident than in the correspondence analysis; Ekari, Kapuna, and PNG highlands are also differentiated from all other populations (due to the high frequency of K-M254).

It is noteworthy that the frequency distribution of the 4 haplogroups C-M38, P-M34, K-M254, and K-M9 together with their associated Y-STR haplotype diversity and resulting age estimates directly parallel with the TNG hypothesis (Pawley 1998, 2005). This hypothesis suggests that speakers of TNG languages spread from the central highlands of what is now PNG along the central cordillera both eastwards and westwards (also reaching the islands of Timor, Alor, and Pantar in Eastern Indonesia) as well as southwards (Pawley 2005; Ross 2005). Archaeological findings suggested an independent origin of agriculture in New Guinea as long as 9,000–10,000 years ago with more intensive cultivation of various species by 6,500–7,000 years

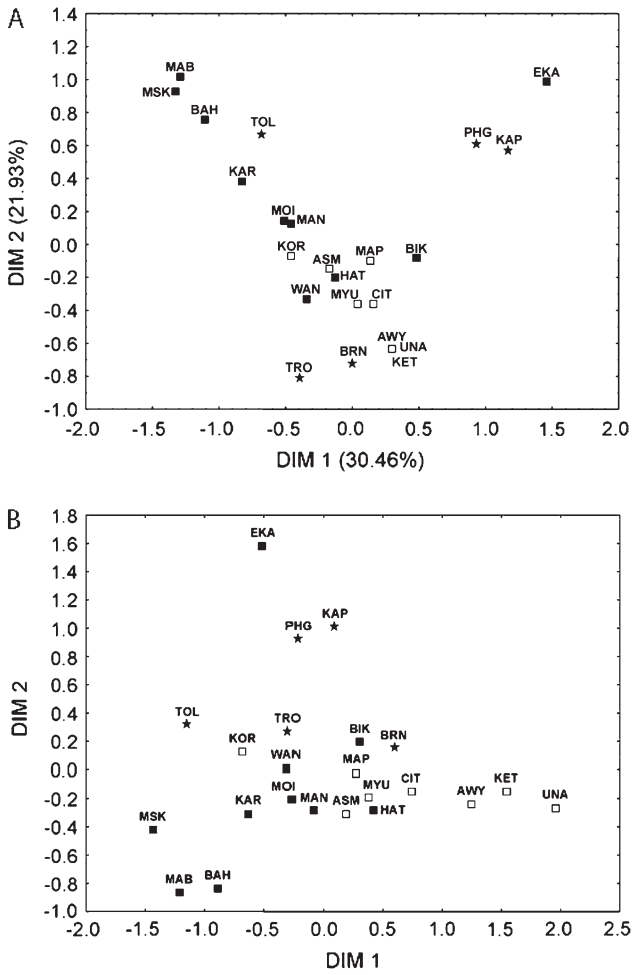

FIG. 4.—Population relationship analysis of New Guinea by means of correspondence analysis of haplogroup frequencies (*a*) and MDS analysis on pairwise F_{ST} values (stress = 0.10) (*b*). Filled squares indicate NWNG groups; nonfilled squares indicate SWNG groups; and stars indicate PNG groups. Data from additional populations were used from previous studies (Kayser et al. 2003, 2006). Groups with sample size equal to or less than 5, "PNG coast" group, and the Dani/Lani were not considered (the former is not a population group; the latter is fixed for C-M208). Abbreviations of population name are as in supplementary table S1, Supplementary Material online.

ago in the Kuk Swamp of the Wahgi Valley of what is now PNG (Golson 1990; Denham et al. 2003; Denham 2005). Pawley (2005) finds it reasonable to assume that an early branch of TNG speakers was established in the Wahgi Valley, and he suggested that the expansion of TNG languages was driven by agriculture. Denham (Denham et al. 2003; Denham 2005) concludes that the archaeological and palaeoecological data support Pawley's model of an early TNG expansion driven by agriculture. Thus, the shift from hunter–gatherer to agricultural societies in New Guinea might have promoted the population expansion of groups speaking TNG languages.

Remarkably, K-M254 and M-P34 show a pattern of diversity as expected under the TNG hypothesis: they both originated in what is now PNG more than 6,000 years ago and spread through the rest of New Guinea and to surrounding islands in Melanesia and Eastern Indonesia (Kayser

et al. 2006). Time estimates are also compatible with the TNG hypothesis and the origin of agriculture in New Guinea, which promoted population expansion in PNG and thus favored the fixation of Y-SNP mutations (haplogroups). Therefore, we propose that the expansion of TNG speakers around New Guinea and beyond seems to have directly determined the distribution of M-P34 and K-M254 (fig. 2).

Haplogroups C-M38 and especially K-M9 are older than the putative start of the TNG expansion and might reflect Y-chromosome diversity prior to the TNG expansion. Their clinal pattern in the opposite direction (starting in NWNG and declining eastwards) might simply be the indirect consequence of the expansion of M-P34 and K-M254 in association with the spread of Trans-New Guinea (TNG) speakers and/or reflect an early expansion of people from the Bird's Head region eastwards into New Guinea.

However, the TNG hypothesis would also predict that the 2 putatively associated markers, K-M254 and M-P34, should display similar coalescent times in the various New Guinea regions because—if true—they were putatively distributed by the same population expansion. Unfortunately, K-M254 is younger than M-P34 in NWNG (K-M254 has almost been erased in SWNG), which would not agree with a single period of expansion from what is now central mainland PNG involving both types of Y-chromosomes. However, when estimating the coalescence of a haplogroup in a region, its starting diversity of associated Y-STR haplotypes is assumed to be zero (one common ancestor), and any starting Y-STR diversity brought into the region concerned would predate the regional haplogroup origin. Consequently, differences between haplogroup estimates could also be influenced by differences in the amount of starting diversities of associated Y-STRs. It is also worth noting that K-M254 has a smaller sample size compared with M-P34; this difference can contribute to the observed discrepancies of the coalescent time estimates of the 2 haplogroups. In addition, demographic events such as population bottlenecks and subsequent expansions have complicated the pattern initiated by cultural and social processes and led to partial confusion of the clinal distribution of Y-chromosome haplogroup frequencies. This is most obvious in the highland SWNG groups that until very recently (partly still today) had strict patrilocal residence patterns and patrilineal clan systems, high degrees of polygeny, and practiced male-biased warfare. Consequently, Y haplogroups appear in fixation together with highly reduced associated Y-STR diversity (Kayser et al. 2003). That the male-biased culture and social structure is responsible for the reduced Y chromosomal diversity in this region is underlined by the fact that mitochondrial DNA diversity is not reduced in those very same SWNG groups (Kayser et al. 2003).

Furthermore, our results suggest that the expansion of TNG speakers had a more pronounced effect on the Y-chromosome diversity of New Guinea populations than the effects of the Austronesian expansion. One explanation for this finding might be that the TNG expansion is at least twice as old as the Austronesian expansion in New Guinea, therefore allowing a wider spread of TNG-associated markers than Austronesian-associated markers through male expansions. Moreover, Trans-New Guinean speakers expanded mostly across the New Guinea highlands that are free of malaria, whereas Austronesians speakers expanded from the islands and mainland cost (because they arrived via sea migration) with high incidence of malaria, probably lowering the effective population size of Austronesian Y-chromosomes. However, a third factor, namely, the social structure and cultural heritage of the people involved, is likely to have had a bigger influence on the observed genetic pattern. TNG societies are mostly patrilocal in their residence and have patrilineal clan systems, whereas Austronesian societies in Oceania seem anciently matrilocal in residence (men move to their wife's land) and matrilineal in descent (clans are inherited through the mothers line) (Hage 1998; Hage and Marck 2003) and often remain matrilocal or at least matrilineal today. This might explain why the Y-chromosome diversity was more influenced by the TNG expansion (i.e., by the expansion of patrilocal and patrilineal groups) than by the Austronesian expansion (i.e., by the expansion of matrilocal or matrilineal groups). One indication for such an effect comes from a previous study on the origins of Polynesians (Kayser et al. 2006) where it was shown that Polynesian ancestors were Austronesian speakers originating from East Asia but genetically mixed with local New Guineans before the colonization of the Pacific, while keeping their language, but incorporating many local Y-chromosomes. This genetic admixture was most likely male biased involving mostly Austronesian women and, over time, mostly New Guinean men, resulting in a higher proportion of Melanesian than Asian Y-chromosome together with a higher proportion of Asian than Melanesian mtDNAs as observed in contemporary Polynesians (Kayser et al. 2006). This sex-biased genetic admixture was likely the result of the Polynesian ancestors' matrilocal residence (Hage 1998; Hage and Marck 2003). Although the colonization of Polynesia most likely went through numerous founder effects and subsequent episodes of bottlenecks that can have contributed to the observed pattern of genetic diversity (by chance only), it is difficult to explain the strong differences between geographic origins of Polynesian Y-chromosomes and mitochondria solely by genetic drift.

Conclusions

The Y-chromosome history of New Guinea is essentially a local history, with some external contribution, but has been influenced by numerous bottlenecks due to migratory and other cultural and social processes. Almost all Y-chromosome diversity of NWNG (97.5%) and about 93% of all New Guinean Y-chromosomes (according to available data) arose locally in New Guinea. It is likely that the expansion of TNG speakers starting from the highlands of what is now PNG about 6,000–7,000 (perhaps as early as 10,000) years ago, presumably in association with the expansion of agriculture, had a great impact on shaping New Guinean Y-chromosome diversity as seen today. The Y-chromosomal haplogroups M-P34 and K-M254 are possible markers of this expansion. Haplogroups C-M38 and K-M9 were either erased by the TNG expansion and reflect the earlier Y-chromosome diversity of New

Guineaor indicate an older expansion starting in NWNG, that is, the Bird's Head region. On the other hand, agricultural people from the East Asian mainland speaking Austronesian precursor language emerged onto Taiwan about 5,500 years ago, and elements of the population were moving on toward the Philippines about 4,000 years ago. Arrival to the Bismarck Archipelago north of New Guinea is now known to be as early as 3,400 years ago with subsequent dispersal into coastal regions of northwest mainland New Guinea. This Austronesian expansion had considerable impact on the linguistic diversity of NWNG, but its impact on the Y-chromosome diversity of this region was low (2.5–7.4%). However, the frequency of Austronesian-associated Y-chromosomes (O-M119 and O-M122) is considerably higher in populations from other regions of New Guinea (on average 21% in Austronesian-speaking groups and 7% in non-Austronesian–speaking groups). It is intriguing to observe that the Austronesian and TNG expansions apparently had such diverse impact on the Y-chromosome diversity of New Guinea (with the latter being much more important than the former). We propose that sex-biased differences in the social structure and cultural heritage of the people involved in the 2 different expansions played an important role (among other factors) in shaping the New Guinean Y-chromosome landscape. Further sampling particularly around mainland PNG (i.e., across the central highlands and in the Sepik–Ramu basin) is needed to shed more light on the overall genetic history of New Guinea.

Supplementary Material

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

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