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BRIEF COMMUNICATION

Mitochondrial DNA variations in Austronesian-speaking populations living in the New Georgia Islands, the Western Province of the Solomon Islands

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Abstract

Modern Austronesian (AN)-speaking Melanesians are considered to be derived from the admixture of indigenous non-Austronesian (NAN)-speaking people and AN-speaking people from Southeast Asia. In this study, we analyzed mitochondrial DNA (mtDNA) variations in the D-loop region for two AN-speaking Melanesian populations (Munda and Kusaghe) and an AN-speaking Micronesian population (Rawaki) in the New Georgia Islands, the Western Province of the Solomon Islands to examine their genetic similarities to AN-speaking Polynesians in Tonga and NAN-speaking Melanesians, Gidra, in Papua New Guinea. The 'Polynesian motif', which is well-characterized mtDNA marker for Polynesians, was frequently observed in Munda and Kusaghe. Of particular interest, haplogroup E1a2 + 16261, which has been rarely observed in the Solomon Islands, accounted for 12.8% in Kusaghe. It has been reported that the haplogroup E1a2 arose in Island Southeast Asia (ISEA) 9400 ± 2850 years ago. Phylogenetic and principle component analyses for 24 Oceanian populations revealed that Munda and Kusaghe populations were genetically close to Tongan population, but not to Gidra. Rawaki population showed no apparent genetic similarities to populations of Tonga and Gidra. Our results suggest that considerable gene flow from AN-speaking populations originated from Southeast Asia to indigenous Melanesians occurred in the New Georgia Islands.

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Accumulating evidence has demonstrated that major human dispersals into Oceania occurred twice: a Pleistocene migration of non-Austronesian (NAN)-speaking people to Near Oceania and a Late-Holocene one of Austronesian (AN)-speaking people from Southeast Asia. A number of genetic studies have indicated that the AN-speaking people admixed with NAN-speaking indigenous people in Near Oceania when they reached, followed by their rapid expansion into Remote Oceania such as Polynesia [1–6]. Although most present-day AN-speaking populations in Near Oceania appear to be descendants of the admixed populations, the genetic ancestry proportions vary among populations. The detection of AN-speaking Melanesian populations genetically close to Polynesians would be helpful for tracing the migration routes of Polynesian ancestors.

A recent large-scale genetic study on the Solomon Islands argued that the major source of mitochondrial DNA (mtDNA) types in Remote Oceania was the Solomon Islands [1]. The Solomon Islands consist of a chain of six large islands (i.e., Guadalcanal, Choiseul, Santa Isabel, New Georgia, Malaita, and Makira) and approximately 900 small islands. To our

Table 1 mtDNA haplogroup frequency (%) in Oceanian populations

Haplogroup	Population (*n*)				
	Munda (37)	Kusaghe (47)	Rawaki (48)	Tonga (43)[a]	Gidra (59)[a]
B4 + 16261	13.5	12.8	20.8	9.3	
B4a1 + 16311				2.3	
Polynesian motif[b]	70.3	74.5	35.4	79.1	
B4b1			2.1		
B4b1a2i			18.8		
D4m2a			14.6		
E1a2 + (16261)		12.8			
H2a2a1					3.4
L3e1d					1.7
M10a1b					6.8
M27b2	2.7				
M27c	5.4				
M28a				4.7	
M54	5.4				
M66					8.5
M7c1				2.3	
M7c1a4a/M7c1c3[c]			6.3		
P1					11.9
P1d1			2.1		5.1
P3b1					1.7
Q1	2.7				32.2
Q2				2.3	
Q3a1					27.1
U7b1					1.7

[a]Data were obtained from our previous study [6]. Tonga and Gidra people are AN-speaking Polynesians and NAN-speaking Melanesians, respectively

[b]The assembled frequency of the haplogroup having the Polynesian motif, such as haplogroup B4a1a1 and its subhaplogroups

[c]These two haplogroups have the same nucleotide sequences of the D-loop region

knowledge, mtDNA variations have been investigated only for a population, Kolombangara, in the New Georgia Islands, the Western Province of the Solomon Islands so far [1]. Since there are several major islands in the New Georgia Islands besides Kolombangara (Figure S1), populations living in other islands are worthy of investigation to understand the genetic diversity of AN-speaking populations in the New Georgia Islands. In this study, mtDNA variations in the D-loop region were investigated for two AN-speaking Melanesian populations, Munda and Kusaghe, in New Georgia and an AN-speaking Micronesian population, Rawaki, in Arundel of the New Georgia Islands (Figure S1). Since Rawaki villagers migrated from the Gilbert Islands, Kiribati to the current place ~50 years ago, they were regarded as Micronesians in this study. The analysis of mtDNA variations in Rawaki helps us to understand how Munda and Kusaghe are genetically close to Polynesians in Tonga (to be described later).

Peripheral blood was sampled after obtaining informed written consent from each participant. This study was approved by the Health Ethics Committee, Ministry of Health, Solomon Islands, the Ministry of Education and Training, Solomon Islands, the Research Ethics Committee of the Faculty of Medicine, The University of Tokyo, and the Research Ethics Committee of the Graduate School of Science, The University of Tokyo. Genomic DNA was extracted from peripheral blood using a QIAamp Blood Kit (Qiagen, Hilden, Germany). The amplification and sequence determination of the D-loop region of mtDNA were conducted as previously described [6]. The sequences of the D-loop region have been deposited in GenBank (GenBank accession numbers LC270643–LC270774).

First we examined the mtDNA diversity in the New Georgia Islands. Mismatch distributions of mtDNA sequences within populations were shown in Figure S2. The mean numbers of pairwise nucleotide differences for Munda, Kusaghe, and Rawaki were 3.97, 1.61, and 4.37, respectively. Compared to Munda and Rawaki, Kusaghe showed low diversity of mtDNA. This seems to result from small population size of Kusaghe villagers.

Next, the mtDNA haplogroups were assigned to each individual of the Munda, Kusaghe, and Rawaki using the mtDNAprofiler (http://mtprofiler.yonsei.ac.kr/) and the Haplogrep2 webtool [7] based on Phylotree Build 17 [8]. The majority of mtDNA haplogroups in Munda, Kusaghe, and Rawaki originated in Asia (B4, E1a2, M7c1c) [1, 9–11], whereas characteristic haplogroups found in Near Oceania (P1, Q1, and M27) [1, 5, 12] existed at low frequencies (Table 1). The 'Polynesian motif', which is well-characterized mtDNA marker for Polynesians, was frequently observed in Munda (70.3%) and Kusaghe (74.5%). The frequency distributions in these two populations were very close to that in Polynesians in Tonga [6], and were not similar to that in NAN-speaking Melanesians, Gidra, at all (Fig. 1). Rawaki showed the frequency distribution different from Melanesians and Polynesians (Fig. 1). The higher frequency of haplogroup B4 other than Polynesian motif in Rawaki may be the feature of Micronesians. A median joining network [13] of mtDNA sequences in haplogroup B4 was further generated using DNAsp v5 [14] and Network version 5.0.0.1 (fluxus-engineering.com). The major mtDNA sequences in haplogroup B4 were shared among AN-speaking populations in the Solomon Islands, Papua New Guinea [6], and Tonga [6] (Figure S3). The present results support a previous observation that the major source of mtDNA types in Remote Oceania appeared in the Solomon Islands [1].

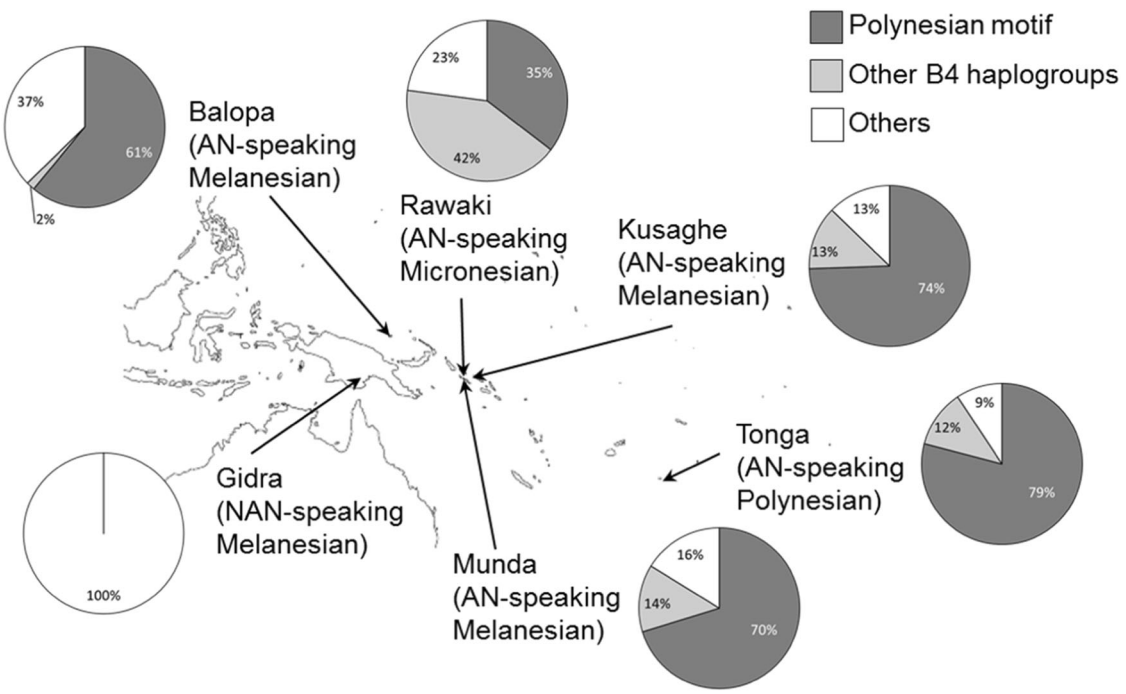

Fig. 1 The distribution of the Polynesian motif and haplogroup B4 in the six Oceanian populations

The geographical distribution of haplogroup E1a2 has been considered to support the Austronesian expansion model from Taiwan to Oceania via the Philippines [15, 16]. Of particular interest, haplogroup E1a2 + 16261 accounted for 12.8% in Kusaghe (Table 1). The haplogroup E1a2 appears to have arisen in ISEA 9400 ± 2850 years ago [11] and has been rarely found in the Solomon Islands so far [1, 11]. It is known that Kusaghe villagers originally lived in a mountainous area and moved to the northern coast. Thus, relatively high frequency of haplogroup E1a2 + 16261 in Kusaghe is not likely to result from recent admixture or back migration of Polynesians.

To further examine the genetic similarity between AN-speaking populations in the New Georgia Islands and Polynesians in Tonga, phylogenetic analysis, and principal component analysis (PCA) were performed based on the frequencies of haplogroups for the three populations in New Georgia Islands together with 21 Oceanian populations previously reported [1, 6]. We calculated pairwise Fst values from mtDNA haplogroup frequency data of 24 populations using the web version of Genepop [17, 18]. Negative Fst values were replaced with zero. Then, a neighbor-joining [20] tree was reconstructed based on the pairwise Fst values by using the MEGA software version 6 [19] (Fig. 2a). A PCA was conducted using R software package (http://www.R-project.org) (Fig. 2b). In both analyses, Munda and Kusaghe populations were located close to populations of Tonga and Polynesian outliers, but far from NAN-speaking Gidra population, suggesting that considerable gene flow from AN-speaking populations that originated from Southeast Asia to indigenous Melanesians occurred in the New Georgia Islands. Kolombangara was not close to Munda and Kusaghe in either phylogenetic tree or PCA plot (Fig. 2) despite that their places of residence were geographically close to each other (Figure S1). It is interesting that there is remarkable difference in the genetic diversity between AN-speaking Melanesian populations in the New Georgia Islands. AN-speaking Micronesian population, Rawaki, was closely located to Bellona population in phylogenetic tree and PCA plot as expected (Fig. 2). Bellona Island is inhabited by Micronesians, as well as Melanesians.

The marked similarity of mtDNA variations between AN-speaking Melanesians in the New Georgia Islands and Polynesians in Tonga suggests that ancestral populations of Polynesians may have passed through the area in the vicinity of the New Georgia Islands before their expansion to Remote Oceania. However, mtDNA variations reflect only the population history of maternal lineage. Further analysis using whole genome single nucleotide polymorphisms is required to fully understand the genetic similarity between AN-speaking Melanesians in the New Georgia Islands of the Solomon Islands and Polynesians.

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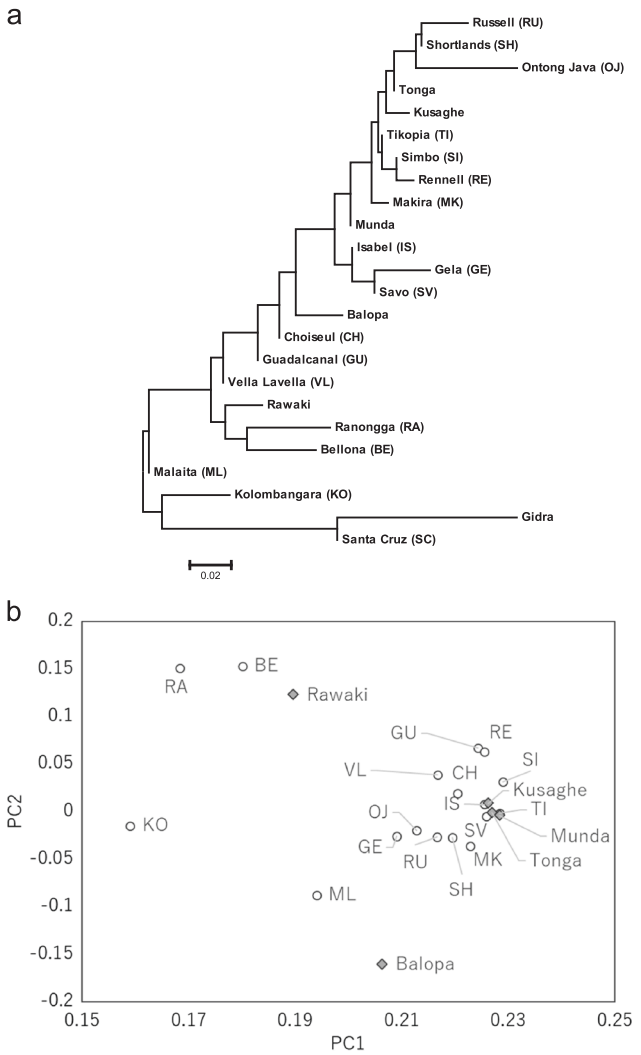

Fig. 2 Neighbor-joining phylogenetic tree and principle component analysis (PCA) plot for 24 Oceanian populations. **a** Neighbor-joining phylogenetic tree for 24 Oceanian populations. The pairwise Fst values computed from mtDNA haplogroup frequencies were used as pairwise genetic distances. Twenty four Oceanian populations were from this study (Munda, Kusaghe, and Rawaki), our previous study (Tonga, Balopa, and Gidra) [6], and Delfin et al. (2012) [1]. **b** Plot of PCA for 24 Oceanian populations based on mtDNA haplogroup frequencies. The contributions of PC1 and PC2 were 0.778 and 0.062, respectively (the cumulative contribution was 0.840). In PCA plot, populations from this study (Munda, Kusaghe, and Rawaki) and our previous study (Tonga, Balopa, and Gidra) [6] are indicated by gray diamonds. Populations from Delfin et al. (2012) [1] are indicated by open circles and abbreviated as follows: *CH* Choiseul, *GE* Gela, *GU* Guadalcanal, *IS* Isabel, *KO* Kolombangara, *RU* Russell, *ML* Malaita, *RA* Ranongga, *MK* Makira, *SV* Savo, *SH* Shortlands, *OJ* Ontong Java, *SI* Simbo, *VL* Vella Labella, *BE* Bellona, *RE* Rennnell, *TI* Tikopia. BE, OJ, RE, and TI are classified as Polynesian Outliers [1]. Gidra [6], and Santa Cruz [1] were analyzed together but were not shown here as they were outliers (their plots are located at $-0.05 < PC1 < 0.1$ and $-0.8 < PC2 < -0.6$)

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Compliance with Ethical Standards

Conflict of interest The authors declare that they have no competing interests.

Informed consent Informed consent was obtained from the patient for publication of this paper.

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