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Genetic Evidence for Modifying Oceanic Boundaries Relative to Fiji

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Title: Genetic Evidence for Modifying Oceanic Boundaries Relative to Fiji

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Abstract:
We present the most comprehensive genetic characterization to date of five Fijian island populations: Viti Levu, Vanua Levu, Kadavu, the Lau Islands, and Rotuma, including non-recombinant Y (NRY) chromosome and mitochondrial DNA (mtDNA) haplotypes and haplogroups. As a whole, Fijians are genetically intermediate between Melanesians and Polynesians, but the individual Fijian island populations exhibit significant genetic structure reflecting different settlement experiences in which the Rotumans and the Lau Islanders were more influenced by Polynesians, and the other Fijian island populations were more influenced by Melanesians. In particular, Rotuman and Lau Islander NRY chromosomal and mtDNA haplogroup frequencies and Rotuman mtDNA hypervariable segment 1 (HVS1) region haplotypes more closely resemble those of Polynesians, while genetic markers of the other populations more closely resemble those of the Near Oceanic Melanesians. Our findings provide genetic evidence supportive of modifying regional boundaries relative to Fiji, as has been suggested by others based on a variety of non-genetic evidence. Specifically, for the traditional Melanesia/Polynesia/Micronesia scheme, our findings support moving the Melanesia-Polynesia boundary so as to include Rotuma and the Lau Islands in Polynesia. For the newer Near/Remote Oceania scheme, our findings support keeping Rotuma and the Lau Islands in Remote Oceania and locating the other Fijian island populations in an intermediate or "Central Oceania" region to better reflect the great diversity of Oceania.

In prior work (Shipley et al. 2015), we examined genetic markers in five Fijian island populations (Viti Levu, Vanua Levu, Kadavu, Rotuma, and the Lau Islands), and found that Fiji is not genetically homogenous but rather exhibits significant genetic structure among these populations. In particular, we found significant genetic structure for NRY chromosomal short tandem repeat (NRY-

STR) haplotypes, both with and without the Rotumans, and found that Rotuman mtDNA haplogroup frequencies and HVS1 region haplotypes are much more similar to those of Polynesian populations than those of the other Fijian populations. However, that study was limited by the number and types of genetic markers and the relatively small Rotuman sample size. In the current study, we have examined NRY chromosomal single nucleotide polymorphisms (NRY-SNPs) to determine Y chromosomal haplogroup frequencies, substantially increased the number of Rotuman samples, and applied our findings to the on-going debate over Oceanic boundaries relative to Fiji, both with regard to the traditional Melanesia/Polynesia/Micronesia (MPM) scheme and the newer Near/Remote Oceania (NRO) scheme.

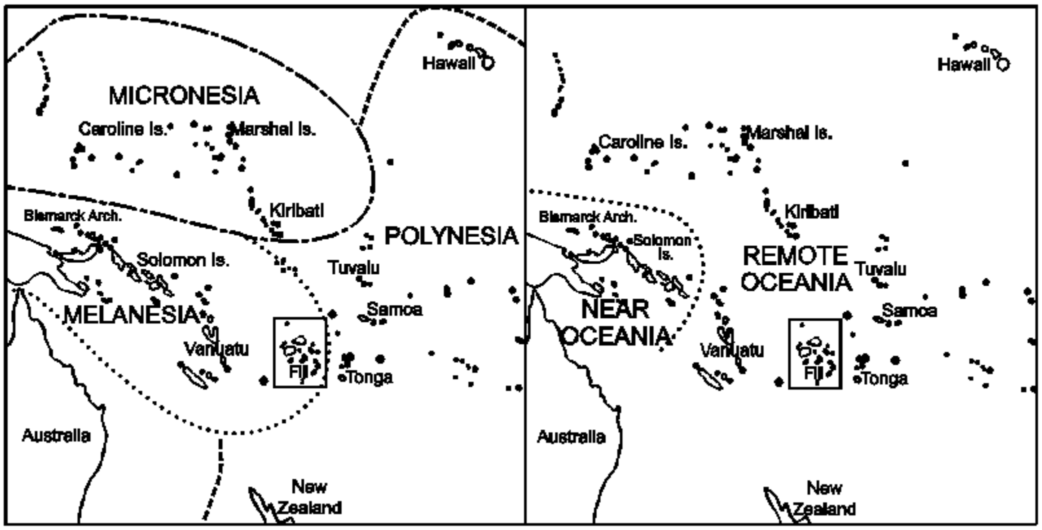

Figure 1. Current Melanesia-Polynesia-Micronesia scheme (left), with Fiji boxed, and current Near-Remote Oceania scheme (right), with Fiji boxed.

The origins of and arguments for and against the MPM and NRO schemes are complex and a full treatment is beyond the scope of this paper, but a short introduction is necessary in order to better understand the significance of our findings and conclusions. The MPM scheme (shown in Figure 1(Left)) resulted from Dumont d'Urville's (1832) initial division of Oceania into three regions (actually four, including Malaysia (Tcherkezoff 2003)). "As geographic referents, the terms Melanesia, Polynesia, and Micronesia have generally neutral connotations," (Clark 2003:157) but, like many such concepts of the period, also carry racial implications. Dumont d'Urville located the lighter-skinned Polynesians (and Malaysians) higher, the Micronesians intermediate, and the darker-skinned Melanesians lower on a socio-evolutionary scale (Clark 2003, citing Dumont d'Urville 1832; Tcherkezoff 2003). Fijians were ranked highest among Melanesian populations because they had been "improved" by contact with Polynesians (Clark 2003, citing Dumont d'Urville 1832). While recognizing the need to divide Oceania into manageable and meaningful regions, some, such as Thomas et al. (1989), have expressed dislike for the MPM scheme because of its tainted beginnings, and have argued for a different scheme that is supported by scientific evidence. Others, such as Sahlins, have argued that assertions that the continued use of the terms "Melanesia" and "Polynesia" perpetuates racism and bigotry can only be sustained if these distinctions have no value whatsoever and are instead nothing more than ideological survivals (Thomas et al. 1989). This second group has noted that work done in all areas of anthropology is "sufficient to explain the continuing anthropological disposition to distinguish Polynesia and Melanesia–*despite rather than because* of the original basis of the contrast, long ago disavowed"–i.e., the MPM scheme *is* supported by scientific evidence (Thomas et al. 1989:37, emphasis in original). A small third group, which includes Guiart (1982) and Spriggs (1984), has argued against what it saw as a racial bias against Melanesia and in favor of Polynesia, and ultimately asserted that there is no legitimate basis for distinguishing between Melanesians and Polynesians or for deriving Polynesians from any place but Melanesia. However, that assertion contradicts strong scientific evidence. In particular, Guiart (1982) seemed primarily concerned with Pan-Pacific nationalism and the "unity of Oceanic peoples" (Guiart 1982:143), and Spriggs (1984) seemed primarily concerned with the political utility of "a Melanesian origin for the Polynesians" (Spriggs 1984:222).

The NRO scheme (shown in Figure 1(Right)) was introduced by Pawley and Green (1973) and subsequently refined by Green (e.g., 1991) as an alternative to the MPM scheme. Into Near Oceania they placed New Guinea, the Bismarck Archipelago, and the Solomon Islands east to San Cristobal, almost all of which were settled by Papuan-speaking peoples no later than ~40,000 years ago (Kirch 2000). Into Remote Oceania they placed all of the islands east and north of the Santa Cruz Islands, almost all of which were settled by Austronesian-speaking peoples beginning ~3,200 years ago (Kirch 2000). Pawley and Green (1973) based their bipartite division on such factors as settlement date, material culture, language, island density, and floral and faunal diversity differences, but, importantly, not on genetic or other biological evidence. Perhaps realizing that reducing the already overly inclusive three regions to two regions did an even greater disservice to the great diversity of Oceania, Pawley and Green (1973) further defined an Eastern Pacific division within Remote Oceania, including all of the islands east of Samoa and Niue plus New Zealand and the Chatham Islands, based on material culture differences. Similarly, Finney (1994), though favoring the NRO scheme but perhaps also sensing the unwieldiness of Remote Oceania as a single category, divided Remote Oceania into West Polynesia in which he included Fiji, Tonga, and Samoa, and East Polynesia in which he included the remainder of the original Remote Oceania region. The NRO scheme more accurately reflects the clearly distinct initial settlement dates of the two regions, with parts of Near Oceania having been settled as much as 55,000 years earlier than the remotest islands of Remote Oceania. However, this treats settlement as a single event rather than a process, as though the moment the first Lapitan set foot on previously uninhabited eastern Melanesian lands the act of settling those lands was complete. Just as the process of settling the Americas likely involved multiple waves of settlers over an extended period of time (e.g., Reich et al. 2012), the process of settling eastern Melanesia (or western Remote Oceania), especially a boundary area like Fiji, also spanned a period of time during which admixing occurred with one or more waves of eastwardly migrating Melanesians and westwardly migrating Polynesians.

Although many have argued explicitly against the long-standing MPM scheme (e.g., Thomas et al. 1989; Finney 1996), ambiguously against it (e.g., Kirch 2010, who acknowledged the value of “Polynesia,” and allowed that “Micronesia” was an exception within Remote Oceania, but rejected the usefulness of “Melanesia”), or for it (e.g., Sahlins’ and Stephenson’s comments to Thomas et al. 1989), many continue to use it rather than or alongside the NRO scheme. “There is still little evidence that Dumont d'Urville's tripartite division of the Pacific is in any danger of being replaced…” (Clark 2003:157). Perhaps this is because the tripartite scheme has evolved beyond its original basis and is now supported by meaningful anthropological evidence, or perhaps it is because the bipartite scheme is less reflective of the great diversity of Oceania, especially its genetic diversity. However, both schemes can be improved through boundary adjustments as new information comes to light. In particular, as Sahlins noted, the most disputed boundary between Melanesian Fiji and Polynesian Tonga is likely outmoded and in need of closer examination (Thomas et al. 1989).

Fiji is treated very differently by the two schemes. Under the MPM scheme, Fiji is located at the boundary of Melanesia and Polynesia, which accurately reflects its liminal nature and transitionary characteristics as the “Gateway to Polynesia.” Fijians have traditionally been classified as Melanesian based on their cultural practices and some morphological features (Spriggs 1997), but they share much in common linguistically (Geraghty 1983), phenotypically (Howells and Moss 1933), and genetically (Kayser et al. 2006; Shipley et al. 2015) with Polynesian populations. Tellingly, as many as 35% of Samoan legends connect it with Fiji, including Samoa’s creation story which tells of the simultaneous creation of Samoa, Tonga, and Fiji (Barnes and Hunt 2005). Thus, although originally settled by the Lapitans ~3,100 years ago (Rutherford et al.

2012), modern Fijians are a complex blend of Melanesian and Polynesian characteristics, due at least in part to forward and backward migrations into Fiji during the settlement process (e.g., Kirch 2000; Clark 2003; Barnes 2005; Addison and Matisoo-Smith 2010; Wollstein et al. 2010; Sheppard 2011; Duggan and Stoneking 2014; Shipley et al. 2015). For example, based on an analysis of ~1 million SNPs, Wollstein et al. (2010:1989) found that Fijians were of 65% Polynesian and 35% Near Oceanic ancestry, and have approximately twice as much Near Oceanic ancestry than do Polynesians, “thereby suggesting substantial contact between Fiji and Near Oceania that did not extend to Polynesia.”

The majority of Fijians reside on the larger western islands of Viti Levu, Vanua Levu, and Kadavu, and are culturally, phenotypically, and genetically more influenced by Melanesia (Spriggs 1997), while a significant minority of Fijians reside on the northern island of Rotuma and the eastern Lau Islands, and are culturally (Kirch 2000), phenotypically (Howells and Moss 1933), and linguistically (Geraghty 1986) more influenced by Polynesia. In that light, some have suggested dividing Fiji between Melanesia and Polynesia. For example, in his Outline Map of the South Pacific, Linton (1926) depicted the Melanesia-Polynesia boundary bisecting Fiji, but gave no indication as to which Fijian islands belonged in which region. In his isolation plot of Polynesian islands, Irwin (1990) placed Fiji in a voyaging sphere with western Polynesia (i.e., Samoa and Tonga), but showed Rotuma as being distinct from the rest of Fiji. Burley (2013) identified archaeological support for moving the boundary between Melanesia and Polynesia to within the Fijian group, with Rotuma and the Lau islands being grouped with Polynesia. Others consider all of Fiji to be within Polynesia (Kayser et al. 2006; Mirabal et al. 2012), while still others have characterized western Polynesia as consisting of Tonga, Samoa, and Tuvalu, and left Fiji in Melanesia (Whyte et al. 2005). As Kirch (2000:156) noted, “anthropologists have never quite known how to deal with Fiji. It is a sort of ‘between’ archipelago, situated geographically closer to Western Polynesia…yet usually classified as a ‘Melanesian’ culture…Fiji thus shares an identical foundation culture as Western Polynesia…[but] continued in later millennia to receive both genetic and cultural influences from the west (i.e., from ‘Melanesia’).” Despite this, Fiji has no special significance whatsoever under the NRO scheme, being located approximately 1250 km east of the boundary between Near and Remote Oceania. Even under Pawley and Green’s (1973) and Finney’s (1994) attempts to further subdivide Remote Oceania, Fiji’s non-liminal location within the scheme is incommensurate with its liminal reality.

Among Fijian island populations, Rotuma probably received its first settlers ~3,000 years ago along with the region generally, and the earliest physical evidence for human occupation was found at Itu’muta and carbon-dated to ~2,000 years ago (Howard and Rensel 2007). After perhaps several hundred years of insignificant contact with other peoples, a backward flow of Polynesians, particularly Samoans and Tongans, from east to west, reached Rotuma (Howard and Rensel 2007). Rotumans' own oral history supports the influence of Samoa, Tonga, and other-than-Fijian influence on their language and culture, as Rotuma was visited by voyagers from Niuafo'ou, Tonga, Futuna, Tuvalu, Tarawa, and Polynesian outliers, and, in turn, early Rotuman voyagers traveled as far as Tikopia and Anuta to the west, and Bora Bora to the east (Howard and Rensel 2007).

HMS Pandora made the first recorded European sighting of Rotuma in 1791, while searching for the mutineers of HMS Bounty. Like many Pacific islands, Rotuma received a number of European and non-European castaways and ship-jumpers, suffered tragic depopulation due to the introduction of foreign diseases, such as measles, and experienced sex-biased outmigration as young men left on European vessels (Howard and Rensel 2007). As a result, there are several potential influences on Rotuman genetics, including (1) an initial founder effect; (2) genetic drift due to small population size; (3) pre-contact gene flow with other Oceanic peoples; (4) post-contact gene flow with Europeans and other non-Oceanic peoples; and (5) one or more potential bottleneck effects due to, e.g., disease or sex-biased migration. Phenotypically, most modern Rotumans are Polynesian in appearance, with light skin, black wavy hair, and Polynesian facial features (Howard and Rensel 2007). Linguistically, Rotuman shares a substantial portion of its vocabulary with Samoan and Tongan (Howard and Rensel 2007). Genetically, Rotumans exhibit the sex-biased admixture which is so distinctive of Polynesia (Shipley et al. 2015).

Similarly, the Lau Islands are located closest to Polynesia and served as a bridge between greater Fiji and Tonga (Kirch 2000). In fact, Tongans established colonies in Lau, and Tongan canoe builders worked in Lau in order to access the larger trees, resulting in "strongly Polynesianized Lauan" society (Thompson 1938:193). The largest island, Lakeba, contains the largest Lapita site found in Fiji and western Polynesia (Best 1984), and historically served as a "Crossroads of the Sea" (Hage and Harary, 1996). Obsidian flakes found on Lakeba and dated to 2,500 years ago have been identified as products of Tonga (Best 1984; confirmed by Reepmeyer and Clark 2010). Linguistically, the Lauan language has been heavily influenced by Tongan and contains a large number of Polynesian loan words (Geraghty 1983).

Materials and Methods

The majority of buccal cell samples were obtained in 2008 from individuals at the University of the South Pacific's main campus in the capital city of Suva, on Vitu Levu. Additional Rotuman buccal cell samples were obtained in 2014 from Suva and the island of Rotuma. DNA was extracted from these samples using the phenol-chloroform method (Sambrook and Russell 2001). Participants whose samples were used for Y chromosome analysis were able to identify their own and at least their father's islands of birth, and those whose samples were used for mtDNA analysis were able to identify their own and at least their mother's islands of birth. All participants gave informed consent, and all samples were obtained and handled in accordance with the human subject research requirements of the University of Kansas and the University of the South Pacific in Fiji.

With regard to the Y chromosome, in addition to the 102 male samples previously reported (Shipley et al. 2015), 16 new male Rotuman samples were similarly processed using an AmpFlSTR® YFILER™ PCR amplification kit (Applied Biosystems) to determine the alleles for 17 NRY-STR loci (DYS19, DYS385a/b, DYS389I, DYS389II-I, DYS390, DYS391, DYS392, DYS393, DYS438, DYS439, DYS448, DYS456, DYS458, DYS635, and YGATAH4). Fragment analyses of the new samples were performed by the University of Arizona Genetics Core (UAGC), and fragment lengths were determined using PEAK SCANNER™ (by Applied Biosystems). Additional NRY-STR data were taken from the literature (Delfin et al. 2012), and additional NRY-STR data for the Polynesian islands of Samoa, Tonga, and Tahiti were provided by AJR. For the Y chromosomal analysis, recognizing the genetically intermediate nature of Eastern Melanesia (or Central Oceania), no Remote Oceanic populations (i.e., the Santa Cruz Islanders and the Vanuatuans) or Polynesian Outlier populations were included in our genetic characterization of Melanesia. The data for Polynesia were limited to alleles for 9 loci (DYS19, DYS385a/b, DYS389I, DYS389II-I, DYS390, DYS391, DYS392, DYS393), so the data for all populations were correspondingly reduced to facilitate analysis. An AMOVA analysis for the five Fijian populations was performed, Slatkin's linearized F_{ST} genetic diversity distances (Slatkin 1996) between the various Melanesian, Fijian, and Polynesian populations were determined using ARLEQUIN 3.11 (by Excoffier and Schneider 2005). Separate analyses were performed in which Polynesian and Melanesian island populations were treated as distinct island populations and in which they were collapsed into two respective regional populations.

Additionally, NRY-SNP haplogroups were determined for 100 of the male Fijian samples using the primers and PCR profiles shown in Table 1. Sequencing was performed by the UAGC, and haplogroup-defining SNP positions were examined in SEQUENCHER 4.8® (Gene Codes Corporation). NRY-SNP haplogroups were characterized as Asian, Asian-descended, Polynesian (i.e., C2a1-P33, which is Melanesian-descended but arose in Polynesia and is characterized as strongly Remote Oceanic by, e.g., Cox et al. (2007) and Delfin et al. (2012)), or Melanesian based on characterizations in the literature (Kayser et al. 2006; Delfin et al. 2012). To facilitate comparison, the NRY-SNP haplogroup frequencies for Melanesia and Polynesia (from Delfin et al. 2012) shown in Table 4 were limited to the same individual haplogroups and haplogroup families determined for the five Fijian island populations as shown in Table 2.

With regard to the mtDNA, in addition to the 107 male and female samples previously reported (Shipley et al. 2015), 19 new male Rotuman samples were similarly processed using light-chain (L) primer L-15996 (5'-ACTCCACCATTAGCACCCAAAGC-3') and heavy-chain (H) primer H-16401 (5'-CACCATCCTCCGTGAAATCA-3') to determine the sequence for a 405 base pairs (bps) fragment from the mtDNA HVS1 region. Sequencing of the new samples was performed by the UAGC. The forward and reverse fragments were visualized using SEQUENCHER® 4.8 (by Gene Codes Corporation), and aligned to the revised Cambridge Reference Sequence. Substitutions within each sequence were examined to ensure proper sequence calling, and a consensus sequence was constructed by merging the two fragments. MtDNA haplogroups were assigned based on substitutions identified in the literature (Friedlaender et al. 2007; Van Oven and Kayser 2009), and each haplogroup was characterized as either Asian or Melanesian based on the origin of the lineage rather than the location where the particular haplogroup may have arisen. For example, we characterized haplogroups B4a1a1 and B4a1a1a as Asian because the B4 lineage originated in Asia, even though B4a1a1 itself may have arisen in Melanesia among Asian-descended peoples (Mirabal et al. 2012) and B4a1a1a is very strongly associated with Polynesia (Redd et al. 1995). Additional mtDNA HVS1 sequences for various Melanesian islands were obtained from GenBank (accession numbers JN017205–JN017907). These sequences were 340 bp long, so the Fijian sequences were correspondingly trimmed to facilitate analysis. The mtDNA HVS1 sequences were analyzed in the same manner as the NRY-STR data. Again, to facilitate comparison, the mtDNA haplogroup frequencies for Melanesia and Polynesia (from Delfin et al. 2012) shown in Table 4 were limited to the same individual haplogroups and haplogroup families determined for the five Fijian island populations as shown in Table 3.

Table 1. Primers and PCR profiles for NRY-SNPs.

SNP	HG	Primers	SNP	Profile
RPS4Y	C family	F 5'-CTGTACTTACTTTTATCTCCTC-3'	C→T	*Standard, X = 54°
		R 5'-CAGCAACAGTAAGTCGAATG-3'		
M38	C2 family	F 5’-CAGTTTTTAGAGAATAATGTCCT-3’	T→ G	*Standard, X = 60°
		R 5’-TTAAAGAAAAGAAAAGCAGATG-3’		
M208	C2a family	F 5'-ATAAATACAAAATCACCTGATGGAT-3'	C→T	*Standard, X = 60°
		R 5'-TTAAACAGCGAAATTACTAACAAAA-3'		
P33	C2a1	F 5'-GTGCAAGATAATGACTCTTAT-3'	TT→TC	**P33
		R 5'-GTGCTAGGTCCAAATATG-3'		
M9	K,NO,P,S families	F 5'-GCAGCATATAAAACTTTCAGG-3'	G→C	*Standard, X = 54°
		R 5'-GAAATGCATAATGAAGTAAGCG-3'		
P79	K3	F 5'-TCTTTGCATAAGTTGTGTCCAAT-3'	T→C	*Standard, X = 57°
		R 5'-AAATGAGGCTAATCAATGGAACA-3'		
P256	M family	F 5'-TCTTGGTTTTCCCATTGACC-3'	G→A	*Standard, X = 54°
		R 5'-CATCTCCCAACTTGTCTGTGC-3'		
M4	M1 family	F 5'-TCCTAGGTTATGATTACAGAGCG-3'	T→C	*Standard, X = 60°
		R 5'-TAAAACACTTCTGTGGATGGCA-3'		
M353	M2 family	F 5'-GAATGGCTCATGGCTGAACT-3'	G→A	*Standard, X = 60°
		R 5'-TACTATCAGGGCCCACCAAG-3'		
P117	M3	F 5'-CTGATTATTCTTTTCTACCTTG-3'	C→A	*Standard, X = 53°
		R 5'-CTTAATCTGATGTGTCACTGA-3'		
M175	O family	F 5'-CCCAAATCAACTCAACTCCAG-3'	TTCTC →A	***M175
		R 5'-TTCTACTGATACCTTTGTTTCTGTTCA-3'		
M119	O1a family	F 5'-GAATGCTTATGAATTTCCCAGA-3'	A→C	*Standard, X = 60°
		R 5'-TCCACACAATATACAAGATGTATTCTT-3'		
M268	O2 family	F 5’-CATGCCTAGCCTCATTCCTC-3’	A→G	*Standard, X = 56°
		R 5’-CTGGATGGTCACGATCTCCT-3’		
M122	O3 family	F 5'-GTTGCCTTTTGGAAATGAATAAATC-3'	T→C	*Standard, X = 58°
		R 5'-CACTTGCTCTGTGTTAGAAAAGATAGC-3'		
*Standard profile: DNA: 2.5ng/ml; 95° for 11 min. || (94° for 30 sec.; X° for 30 sec.; 72° for 45 sec.) x 40 cycles || 72° for 10 min.				
**P33 profile: DNA: 5ng/ml; 94° for 3 min. || (94° for 45 sec.; 62° 45 sec. ramp down to 52° in 0.5° increments over first 20 cycles, then hold at 52°; 72° for 45 sec.) x 40 cycles || 72° for 45 min.				
***M175 profile: DNA: 2.5ng/ml; 95° for 10 min. || (94° for 15 sec.; 60° for 45 sec.) x 40 cycles || 60° for 5 min.				

Results

NRY-STR genetic distance data, which is summarized in Table 4, and the resulting multi-dimensional scaling (MDS) plot, seen in Figure 2, show four of the five Fijian populations grouped relatively intermediate between the Polynesian and Melanesian clusters. However, the four central Fijian populations were neither as clearly intermediate between the Polynesian and Melanesian clusters nor as tightly clustered themselves for the NRY-STRs as they were for the mtDNA HVS1 region. The additional Rotuman samples included in the present study shifted Rotuma somewhat closer to the Lau Islands and the Fijian centroid compared to prior results (Shipley et al. 2015). Rotuma had the second lowest number of different haplotypes (17), the lowest gene diversity (0.53 +/- 0.30), and the lowest mean number of pairwise differences (4.75 +/-2.4). These results are almost identical to Samoa at, respectively, 17, 0.53 +/- 0.30, and 4.77 +/- 2.43. AMOVA of the NRY-STR haplotypes of the Fijian populations including Rotuma showed significant genetic structure (*p* = 0.00) and 5.59% variation among populations, and AMOVA excluding Rotuma still showed significant genetic structure (*p* = 0.04) and 3.89% variation among populations. The Lau Islands had the lowest number of different haplotypes (16), the second lowest gene diversity (0.70 +/- 0.38), and the second lowest mean number of pairwise differences (6.18 +/- 3.08).

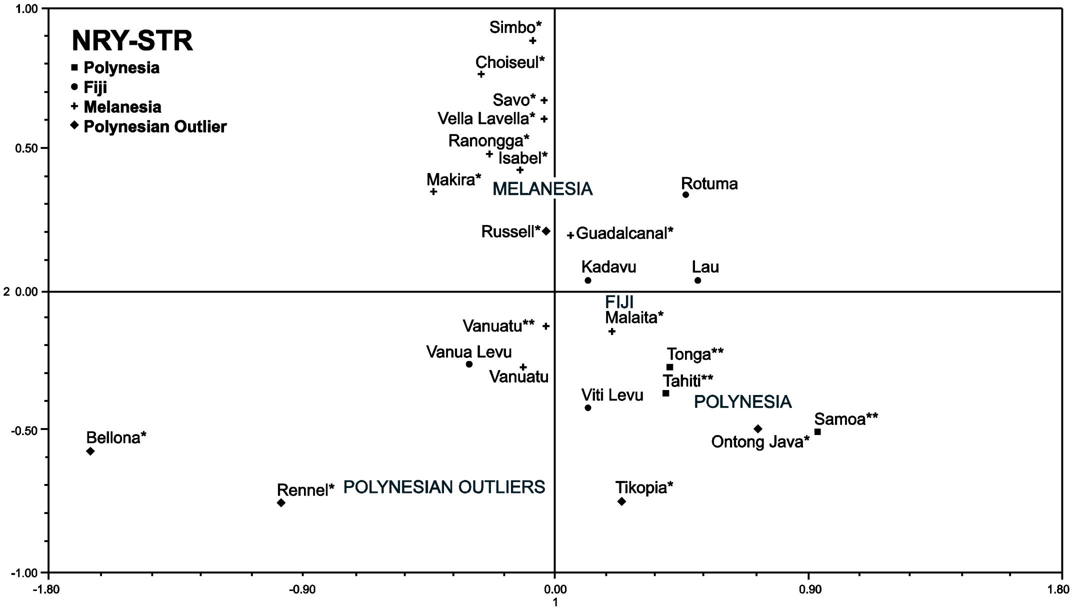

Figure 2. Two-dimensional monotonic MDS plot of Slatkin's linearized F_{ST} genetic distance values based on nine NRY-STRs: 19, 385a, 385b, 389I, 389II, 390, 391, 392, and 393. "*" denotes NRY-STR data from the literature (Delfin et al. 2012); "" denotes NRY-STR data provided by AJR. Final stress = 0.15; r = 0.90.**

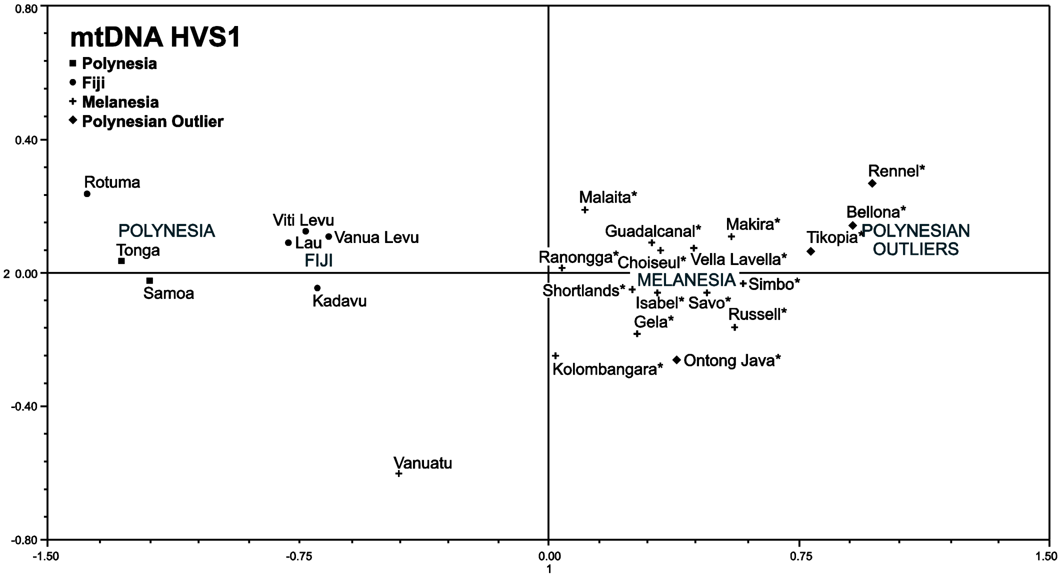

Figure 3. Two-dimensional monotonic MDS plot of Slatkin's linearized F_{ST} genetic distances based on mtDNA HVS1 sequences. "*" denotes mtDNA data from the literature (Delfin et al. 2012). Final stress = 0.10; r = 0.89.

NRY-SNP haplogroup frequencies, which are summarized in Table 2, show that, among specific Asian haplogroups, the O3 family had the highest frequency (accounting for 51.2% of Asian haplogroups), while among specific Melanesian haplogroups, the Melanesian M1 family had the highest frequency at 27.2%. However, an examination of individual island populations revealed substantial heterogeneity, with the western islands of Viti Levu (7.0% Asian, 93.0% Melanesian), Vanua Levu (25.0% Asian, 75.0% Melanesian), and Kadavu (25.0% Asian, 75.0% Melanesian) exhibiting relatively higher frequencies of Melanesian NRY-SNP haplogroups, and the northern island of Rotuma (81.0% Asian, 19.0% Melanesian) and the eastern Lau Islands (50.0% Asian, 50.0% Melanesian) exhibiting relatively higher frequencies of Asian NRY-SNP haplogroups. Further, Viti Levu exhibited a remarkably high frequency, 30.2%, of Melanesian M1 family NRY-SNP haplogroups, while Rotuma exhibited a remarkably high frequency, 76.2%, of Asian O3 family NRY-SNP haplogroups.

Table 2. NRY-SNP haplogroup frequencies for five Fijian island populations. Characterizations of haplogroups as Asian, Asian-Descended, Polynesian, and Near Oceanic Melanesian are based on Kayser et al. (2006) and Deflin et al. (2012).

Population	N	Frequencies of Asian and Asian-Descended Haplogroups		Freq. of a Melanesian-Descended Polynesian Haplogroup	Frequencies of Near Oceanic Melanesian Haplogroups						
		O1a family-M119	O3 family-M122	C2a1-P33	K, NO, S family, or P family; K-M9*(xP256, P79, M175)	K3-P79	M-P256*(xM4, M353, P117)	M1 family-M4	M2 family-M353	M3-P117	C2-M38*(xM208)
Viti Levu	43		0.047	0.023	0.163	0.047	0.093	0.302	0.070		0.256
Vanua Levu	12		0.083	0.167	0.333				0.333		0.083
Kadavu	8	0.250			0.500			0.125			0.125
Lau Islands	16	0.063	0.250	0.188	0.125	0.063	0.063	0.063		0.063	0.125
Rotuma	21		0.762	0.048	0.143	0.048					

Table 3. MtDNA haplogroup frequencies for five Fijian island populations. Characterizations of haplogroups as Asian, Asian-Descended, and Melanesian are based on Friedlaender et al. (2007) and Van Oven and Kayser (2009).

Population	**N**	**Frequencies of Asian and Asian-Descended Haplogroups**			**Frequencies of Melanesian Haplogroups**					
		B4b1	**B4a1a1**	**B4a1a1a**	**P1e**	**Q1**	**Q1a2**	**Q2**	**M28**	**M28a**
Viti Levu	22		0.136	0.636			0.045	0.136		0.045
Vanua Levu	21			0.762	0.095	0.095		0.048		
Kadavu	21		0.095	0.619						0.286
Lau Islands	22		0.136	0.682		0.045		0.091	0.045	
Rotuma	39	0.077	0.051	0.821						0.051

MtDNA HVS1 genetic distance data, which is summarized in Table 4, and the resulting MDS plot, seen in Figure 3, show four of the five Fijian populations grouped clearly intermediate between the Polynesian and Melanesian clusters, with the Rotumans clearly grouping with the Polynesians. In particular, the four core Fijian island populations were much more clearly intermediate between the Polynesian and Melanesian populations and much more tightly clustered for the mtDNA HVS1 region than they were for the NRY-STRs. The additional Rotuman samples did not significantly shift Rotuma relative to the Fijian centroid compared to prior results (Shipley et al. 2015). Specifically, Rotuma grouped strongly with Polynesia (Rotuma-Polynesia F_{ST} = 0.00, Rotuma-Melanesia F_{ST} = 0.46), while the other four Fijian populations formed a close group between Polynesia and Melanesia (Fijian Group-Polynesia F_{ST} = 0.10, Fijian Group-Melanesia F_{ST} = 0.25). AMOVA of the mtDNA HVS1 haplotypes of the Fijian populations including Rotuma showed significant genetic structure ($p = 0.03$) and 3.91% variation among populations, but AMOVA excluding Rotuma did not show significant genetic structure ($p = 0.45$) and -0.29% variation among populations.

MtDNA haplogroup frequencies, which are summarized in Table 3, show that, among specific Asian haplogroups, B4a1a1a had the highest frequency (accounting for 85.6% of all Asian haplogroups), while among specific Melanesian haplogroups, Q2 had the highest frequency (accounting for 51.5% of Melanesian haplogroups). Again, however, an examination of individual island populations revealed substantial heterogeneity, with the western islands of Viti Levu (77.3% Asian, 22.7% Melanesian), Vanua Levu (76.2% Asian, 23.8% Melanesian), and Kadavu (71.4% Asian, 28.6% Melanesian) exhibiting relatively higher frequencies of Melanesian NRY-SNP haplogroups, while the northern island of Rotuma (94.9% Asian, 5.1% Melanesian) and the eastern Lau Islands (81.8% Asian, 18.2% Melanesian) exhibiting relatively higher frequencies of Asian mtDNA haplogroups. Further, Kadavu exhibited a remarkably high frequency, 28.6%, of the Melanesian M28a mtDNA haplogroup, while Rotuma exhibited the highest frequency, 82.1%, of the Asian B4a1a1a mtDNA haplogroup.

Discussion

With this paper, we present the most comprehensive genetic characterization to date of five Fijian island populations: Viti Levu, Vanua Levu, Kadavu, the Lau Islands, and Rotuma, including NRY and mtDNA haplotypes and haplogroups, all of which is summarized in Table 4. Our findings confirm that, as a whole, Fijians are genetically intermediate between Melanesians and Polynesians, which reflects a settlement process involving genetic admixture over time. Our data also show that individual Fijian island populations exhibit significant genetic structure reflecting different settlement experiences in which Rotumans and the Lau Islanders were more heavily genetically influenced by Polynesians, while Viti Levuans, Vanua Levuans, and Kadavuans were more heavily genetically influenced by Melanesians. In particular, Rotumans and Lau Islanders have, respectively, 81.0% and 50.0% Asian (or Asian-descended) or Polynesian NRY-SNP haplogroups, which is more similar to Polynesians (77.0% (Delfin et al. 2012)), while Viti Levuans, Vanua Levuans, and Kadavuans have, respectively, 7.0%, 25.0%, and 25.0% Asian (or Asian-descended) or Polynesian NRY-SNP haplogroups, which is more similar to Near Oceanic Melanesians (15.5% (Delfin et al. 2012)). Further, Rotumans and Lau Islanders have, respectively, 94.9% and 81.8% Asian (or Asian-descended) mtDNA haplogroups, which is again more similar to Polynesians (96.4% (Delfin et al. 2012)), while Viti Levuans, Vanua Levuans, and Kadavuans have, respectively, 77.3%, 76.2%, and 71.4% Asian mtDNA haplogroups, which is again more similar to Near Oceanic Melanesians (60.6% (Delfin et al. 2012)). Additionally, Rotuman mtDNA haplotypes group much more strongly with Polynesian mtDNA haplotypes than any other Fijian island population. On the other hand, Rotuman NRY-STR haplotypes group closer to Melanesian than to Polynesian mtDNA haplotypes. However, this anomaly is likely due to the fact that genetic drift has an inherently stronger effect on the Y chromosome.

Table 4. Summary of genetic marker characterizations for five Fijian island populations, Melanesia, and Polynesia. Data for Melanesia and Polynesia are from Delfin et al. (2012).

Population	**NRY**				**MtDNA**			
	Asian, Asian-Descended, & Polynesian NRY-SNP Haplogroup Frequencies	**Near Oceanic Melanesian NRY-SNP Haplogroup Frequencies**	**NRY-STR F_{st} Distance**		**Asian & Asian descended mtDNA Haplogroup Frequencies**	**Melanesian mtDNA Haplogroup Frequencies**	**MtDNA F_{st} Distance**	
			From Polynesian Centroid	**From Melanesian Centroid**			**From Polynesian Centroid**	**From Melanesian Centroid**
Melanesia	*0.155*	*0.845*	---	---	*0.606*	*0.394*	---	---
Viti Levu	0.070	0.930	0.108	0.207	0.773	0.227	0.080	0.257
Vanua Levu	0.250	0.750	0.270	0.177	0.762	0.238	0.069	0.230
Kadavu	0.250	0.750	0.118	0.017	0.714	0.286	0.185	0.261
Lau Islands	0.500	0.500	0.119	0.131	0.818	0.182	0.043	0.261
Rotuma	0.810	0.190	0.261	0.088	0.949	0.051	0.000	0.456
Polynesia	*0.770*	*0.230*	---	---	*0.964*	*0.036*	---	---

Non-genetic evidence of the relative influences of Melanesia and Polynesia on Fiji as a whole and on the various Fijian island populations and non-genetic evidence for modifying the regional boundary relative to Fiji were discussed in the introduction. Our findings support the notion that Fiji is a special place–a “between place” (Kirch 2000:156)–between two great regions, and support non-genetic evidence and arguments for adjusting the Melanesia-Polynesia boundary line, and, in the interest of completeness, creating an intermediate or “Central Oceania” region within the NRO scheme to bring it into greater accordance with the field of genetic anthropology. As summarized in Figure 4, for the MPM scheme our data support moving the boundary so as to include Viti Levu, Vanua Levu, and Kadavu in Melanesia and so as to include Rotuma and the Lau Islands in Polynesia. For the NRO scheme, our data support locating Viti Levu, Vanua Levu, and Kadavu in Central Oceania (which would presumably extend westward to abut the traditional Near Oceania border), and locating Rotuma and the Lau Islands in Remote Oceania. This remedies the untenable situation of, for example, categorizing the populations of, e.g., the Santa Cruz Islands, Vanuatu, and western Fiji with the genetically very different populations of the eastern Pacific. More work is needed to more accurately characterize the genetics of the Pacific, and the adjustment we espouse may be further supplemented based on subsequent work. For example, while Rotuma is clearly genetically very similar to Polynesia, the Lau Islands are somewhat more genetically intermediate between Fiji and Polynesia and additional work could better determine its regional relationships and affiliation. Equally clear, however, is that regional definitions that do not take genetics into account will not accurately reflect all anthropological evidence.

We also note that while examining parental origins to identify samples for analysis, we found what appears to be exceptionally strong patrilocality among at least two of the Fijian populations. Specifically, of all the samples for which we knew both the mother’s and father’s birthplaces, for Kadavuans, 100% of fathers but only 42% of mothers were from Kadavu, and for Lau Islanders, 100% of fathers but only 57% of mothers were from the Lau Islands. In contrast, for Viti Levuans, 83% of fathers and 74% of mothers were from Viti Levu, and for Vanua Levuans, 96% of fathers and 91% of mothers were from Vanua Levu. For Rotumans, 98% of both fathers and mothers were from Rotuma, but this may reflect Rotuma’s greater geographical isolation and correspondingly lower access to partners from other populations.

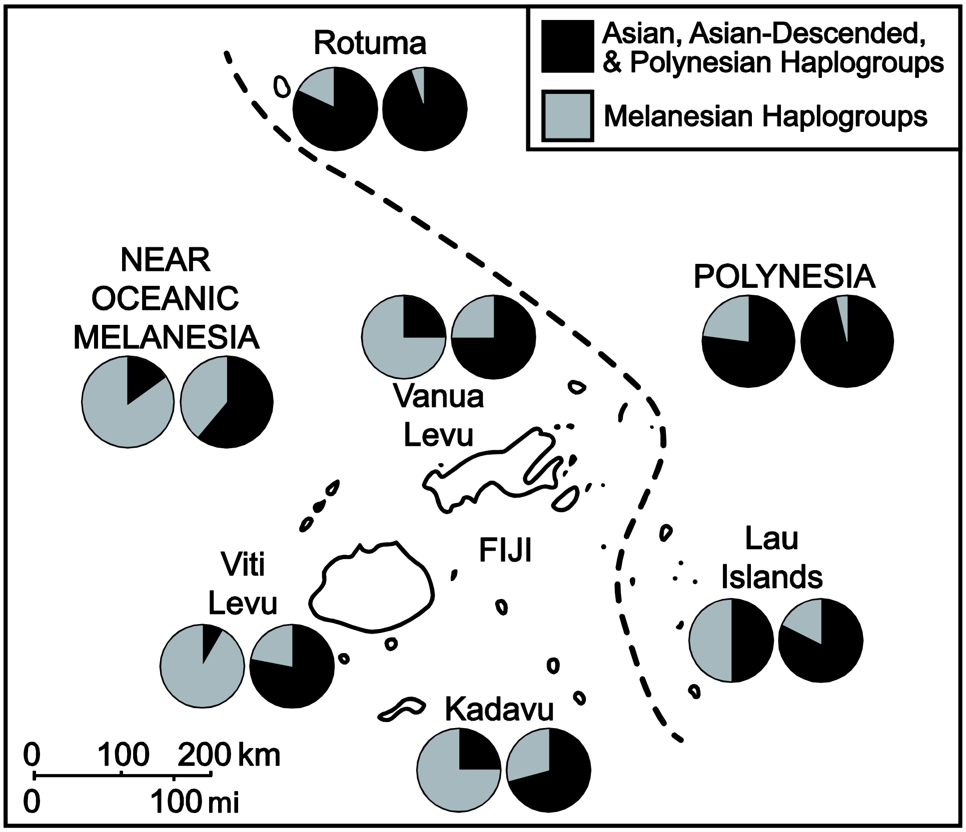

Figure 4. Proposed change to the boundary between Melanesia and Polynesia relative to Fiji (or the eastern boundary of a proposed Central Oceania region), showing NRY-SNP (left pie charts) and mtDNA (right pie charts) haplogroup frequencies for five Fijian island populations. Near Oceanic Melanesian and Polynesian data are from Delfin et al. (2012).

Our study has several limitations. First, although we increased our sample size for Rotuma, samples sizes for other populations could be larger. For the NRY-STR analysis in particular, N < 20 for four of the five island populations, and N = 10 for the Kadavuans. Second, most of our samples were collected from individuals on the campus of the University of the South Pacific in Suva, and these individuals may not be fully genetically representative of their home island populations. Third, our examination was limited to specific genetic markers on the Y chromosome and the HVS1 region of the mtDNA genome, and an examination of other markers and other regions of the human genome might yield different results. For example, we note that A16247G in the HVS1 region, which we used to distinguish between the B4a1a1 and B4a1a1a haplogroups, has been found to back-mutate, (Duggan et al. 2013; Duggan et al. 2014), so some small portion of the participants identified as belonging to B4a1a1 may actually belong to B4a1a1a. Even if this is the case it would not change our conclusions, but sequencing and analyzing other portions of the mtDNA genome would clarify these haplogroup assignments. Relatedly, the diagnostic mutation for B4a1a1a recently changed to A6905G, but this is not within the HVS1 region so we have continued to use A16247G. Further, more work needs to be done to characterize autosomal markers in Pacific populations. With regard to Fiji, only one study has examined autosomal STRs, and it found that Fiji as a whole was most similar to Samoa, Hawaii, and Pohnpei (Lum et al. 1998), which supports to our broader findings and conclusions.

The results of this study contribute to understanding genetic structure among the Fijian island populations and the process of settling the region. Although prior studies treated the Fijians as genetically homogenous, we found important genetic differences among the various island populations that support non-genetic evidence for moving regional boundaries to within the Fijian archipelago. Data collection that does not take these differences into account could yield unreliable results, and regional boundaries that do not take them into account will not reflect all anthropological evidence. Thus, our findings support the continuing need for additional examination of individual island populations within Fiji in order to better understand the process of settling Fiji and of the surrounding regions.

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Literature Cited

Addison, D. J., and E. Matisoo-Smith. 2010. Rethinking Polynesians origins: A West-Polynesia Triple-I model. *Archaeol. Oceania* 45:1–12.

Barnes, S. S., and T. L. Hunt. 2005. Samoa's pre-contact connections in West Polynesia and beyond. *J. Polyn. Soc.* 114:227–266.

Best, S. 1984. *Lakeba: The prehistory of a Fijian island.* Ph.D. dissertation, Department of Anthropology, University of Auckland.

Burley, D. V. 2013. Fijian polygenesis and the Melanesian/Polynesian divide. *Curr. Anthropol.* 54:436–462.

Clark, G. 2003. Dumont d'Urville's Oceania. *J. Pac. Hist.* 38:155–161.

Cox, M, A. J. Redd, T. M. Karafet et al. 2007. A Polynesian motif on the Y chromosome: Population structure in Remote Oceania. *Hum. Biol.* 79:525–535.

Delfin, F., S. Myles, Y. Choi et al. 2012. Bridging near and remote Oceania: MtDNA and NRY variation in the Solomon Islands. *Mol. Biol. Evol.* 29:545–564.

Duggan, A. T., B. Evans, F. R. Friedlaender et al. 2014. Maternal history of Oceania from complete mtDNA genomes: Contrasting ancient diversity with recent homogenization due to the Austronesian expansion. *Am. J. Hum. Gen.* 94:721–733.

Duggan, A. T. and M. Stoneking. 2013. A highly unstable recent mutation in human mtDNA. *Am J. Hum. Genet.* 92:279–284.

Duggan, A. T. and M. Stoneking. 2014. Recent development in the genetic history of East Asia and Oceania. *Curr. Opin. Genet. Dev.* 29:9–14.

Dumont d'Urville, J.-S.-C. 1832. Sur les ıles du Grand Ocean. *Bulletin de la Societe de Geographie* 17:1–21.

Excoffier, L., and S. Schneider. 2005. Arlequin Ver. 3.0: An integrated software package for population genetics data analysis. *Evol. Bioinform. Online* 1:47–50.

Finney, B. 1994. The other one-third of the globe. *J. World Hist.* 5:273–297.

Finney, B. 1996. Colonizing an island world. *Transactions of the American Philosophical Society, New Series* 86:71–116.

Friedlaender, J., F. Friedlaender, J. Hodgson et al. 2007. Melanesian mtDNA complexity. *PLoS One* 2:e248.

Geraghty, P. A. 1983. The history of the Fijian languages. *Oceanic Linguistics Special Publication, No.* 19:1–483.

Geraghty, P. A. 1986. The sound system of Proto-Central-Pacific. In *FOCAL II: Papers from the Fourth International Conference on Austronesian Linguistics*, P. Geraghty, L. Carrington, and S. A. Wurm, eds. Canberra, Australia: The Australian National University, 289–312.

Green, R. C. 1991. Near and Remote Oceania: Disestablishing 'Melanesia' in culture history. In *Man and a Half: Essays in Pacific Anthropology and Ethnobiology in Honour of Ralph Bulmer*, A. K. Pawley, ed. Auckland, New Zealand: The Polynesian Society, 491–502.

Guiart, J. 1981. A Polynesian myth and the invention of Melanesia. *J. Polyn. Soc.* 91:139–144.

Howard, A., and J. Rensel. 2007. *Island Legacy: A History of the Rotuman People*. Victoria, Canada: Trafford Publishing.

Howells, W. W., and W. L. Moss. 1933. *Anthropometry and Blood Types in Fiji and the Solomon Islands*. New York, NY: American Museum of Natural History.

Irwin, G. 1990. Human colonization and change in the Remote Pacific. *Curr. Anthropol.* 31:90–94.

Kayser, M., S. Brauer, R. Cordaux et al. 2006. Melanesian and Asian origins of Polynesians: MtDNA and Y chromosome gradients across the Pacific. *Mol. Biol. Evol.* 23:2234–2244.

Kirch, P. 2000. *On the Road of the Winds: An Archaeological History of the Pacific Islands before European Contact*. Berkeley, CA: University of California Press.

Kirch, P. 2010. Peopling of the Pacific: A holistic anthropological perspective. *Annu. Rev. Anthropol.* 39:131–148.

Linton, R. 1926. Ethnology of Polynesia and Micronesia. Guide, No. 6:1–3, 5–187, 189–191. Chicago, IL: Field Museum of Natural History.

Lum, J. K., R. L. Cann, J. M. Martinson et al. 1998. Mitochondrial and nuclear genetic relationships among Pacific island and Asian populations. *Am. J. Hum. Genet.* 63:613–624.

Mirabal, S, K. J. Herrera, T. Gayden et al. 2012. Increased Y-chromosome resolution of haplogroup O suggests genetic ties between the Ami aborigines of Taiwan and the Polynesian Islands of Samoa and Tonga. *Gene* 492:339–348.

Pawley, A. and R. Green. 1973. Dating the Dispersal of the Oceanic Languages. *Oceanic Linguistics* 12:1–67.

Reepmeyer, C., and G. Clark. 2010. Post-colonization interaction between Vanuatu and Fiji reconsidered: The re-analysis of obsidian from Lakeba Island, Fiji. *Archaeometry* 52:1–18.

Redd, A., N. Takezaki, S. Sherry et al. 1995. Evolutionary history of the COII/tRNALys intergenic 9 base pair deletion in human mitochondrial DNAs from the Pacific. *Mol. Biol. Evol.* 12:604–615.

Reich, D., N. Patterson, D. Campbell et al. 2012. Reconstructing Native American population history. *Nature 488*:370–374.

Rutherford, J. S., M. J. Almond, and P. D. Nunn. 2012. Analysis of pottery samples from Bourewa, the earliest known Lapita site in Fiji. *Spectrochim. Acta A* 85:155–159.

Sambrook, J., and D. W Russell. 2001. *Molecular Cloning: A Laboratory Manual*. New York, NY: Cold Spring Harbor Laboratory Press.

Sheppard, P. J. 2011. Lapita colonization across the Near/Remote Oceania boundary. *Curr. Anthropol.* 52:799–840.

Shipley, G. P., D. A. Taylor, A. Tyagi et al. 2015. Genetic structure among Fijian island populations. *J. Hum. Genet.* 60:69–75.

Slatkin, M. 1995. A measure of population subdivision based on microsatellite allele frequencies. *Genetics* 139:457–462.

Spriggs, M. 1984. The Lapita cultural complex: Origins, distribution, contemporaries and successors. *J. Pac. Hist.* 19:202–223.

Spriggs, M. 1997. *The Island Melanesians*. Oxford, United Kingdom: Blackwell.

Tcherkezoff, S. 2003. A long and unfortunate voyage towards the 'invention' of the Melanesia/Polynesia distinction 1595-1832. *J. Pac. Hist.* 38:175–196.

Thomas, N., A. Abramson, I. Brady et al. 1989. The force of ethnology: Origins and significance of the Melanesia/Polynesia division [and comments and replies]. *Curr. Anthropol.* 30:27–41.

Thompson, L. 1938. The Culture History of the Lau Islands, Fiji. *Am. Anthropol., New Series* 40:181–197.

Van Oven, M. and M. Kayser. 2009. Updated comprehensive phylogenetic tree of global human mitochondrial DNA variation. *Hum. Mutat.* 30:E386–E394.

Whyte, A. L. H., S. J. Marshall, and G. K. Chambers. 2005. Human evolution in Polynesia. *Hum. Biol.* 77:157–177.

Wollstein, A., O. Lao, C. Becker et al. 2010. Demographic history of Oceania inferred from genome-wide data. *Curr. Biol.* 20:1983–1992.