

## **The Colonization of the Pacific: The Story According to Human Leukocyte Antigens**

S. W. SERJEANTSON,<sup>1</sup> D. P. RYAN, AND A. R. THOMPSON

### SUMMARY

The human leukocyte antigen (HLA) distributions in 16 Pacific populations have been collated from published and unpublished reports. Gene frequency and linkage disequilibrium relationships among groups show that Australians and Papuans share a common ancestry, that coastal Melanesia has about 16% Austronesian admixture, and that Fiji is truly intermediate between Melanesia and Polynesia. In Polynesia, Cook Islanders show closer affinity with populations of Western Polynesia than with Maoris and Easter Islanders, in contrast to their linguistic affiliations, but otherwise HLA distributions show a clear division between the populations of Eastern and Western Polynesia. This study emphasizes the contribution the HLA system can make to anthropological studies and has provided a version of colonization of the Pacific compatible with theories based on prodigious efforts in many disciplines.

### INTRODUCTION

The human leukocyte antigen (HLA) system, with its cluster of at least five closely linked polymorphic loci, has proved highly informative in the study of interrelationships and migrations between populations in Europe [1, 2]. Here we examine current theories regarding the colonization of Australia, New Guinea, and the Pacific in terms of an HLA map of Oceania.

The earliest arrivals in New Guinea and Australia, at least 50,000 years ago, were speakers of Australoid languages. The Australoid languages are spoken still by Australian Aborigines, but, in New Guinea, these have been overlaid by Papuan languages, introduced from the West about 15,000 years ago [3]. Further waves of

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<sup>1</sup> All authors: Department of Human Biology, John Curtin School of Medical Research, Canberra, 2601, Australia.

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Papuan migration into New Guinea occurred about 10,000 years ago [3], increasing the linguistic and genetic differentiation between New Guinea and Australia and only marginally predating their physical separation by the rising seas at the end of the Pleistocene. The present-day linguistic affiliations of Pacific populations are given in figure 1. Australoid languages are now confined to Australia, whereas languages classified as Austronesian are spoken in most of Indonesia, the Philippines, parts of Malaysia, Vietnam, and Taiwan and have spread east to encompass Micronesia, Polynesia, and island Melanesia [4]. The non-Austronesian, or Papuan, languages, encompass most of New Guinea.

Linguistic and archaeological evidence suggests that Austronesian speakers migrated into Melanesia between 3,500 and 5,000 years ago [4] and intermarried with resident Papuans in the coastal areas of New Guinea, New Hebrides, and New Caledonia. By 3,000 years ago, more groups of Austronesians arrived in Melanesia, moving east to Fiji and West Polynesia and carrying Lapita-style pottery as far as Samoa [5]. These Lapita potters remained in the Samoa area for about 1,000 years before colonizing the Marquesas Islands, 3,000 km to the east; further dispersal to Easter Island, the Hawaiian Islands, and New Zealand occurred 1,200–1,600 years ago.

These theories regarding colonization of Oceania are widely accepted but are not without critics. For instance, Wurm [6] claims, on linguistic grounds, that Papuan speakers did not predate Polynesian speakers in island Melanesia; he argues, rather, that Polynesians were the first settlers in New Hebrides and New

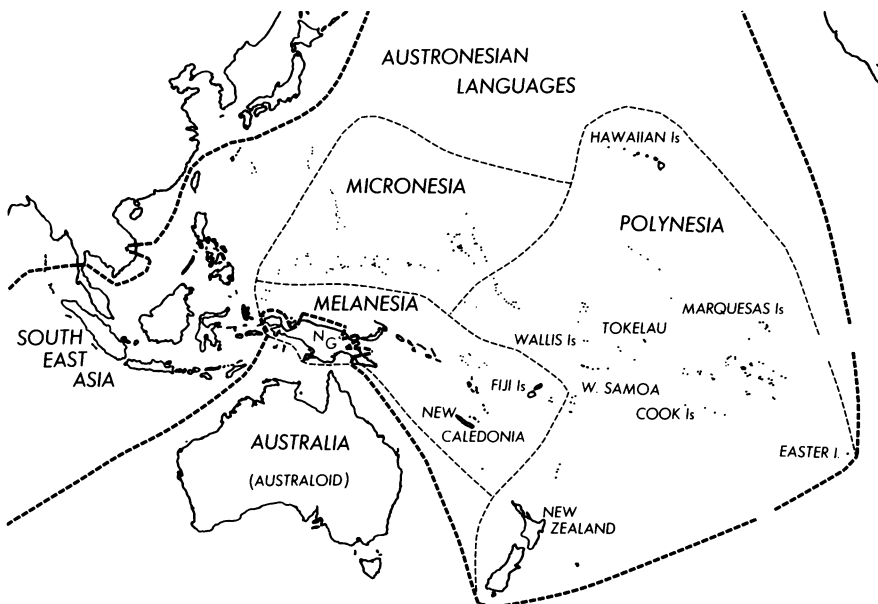


FIG. 1.—Outline of the distribution of Austronesian languages in Southeast Asia, Micronesia, Melanesia, and Polynesia; of Australoid languages in Australia; and of Papuan languages in New Guinea (NG).

Caledonia and were later replaced by Melanesians. Certainly, this may have been the case in Fiji, where archaeological evidence suggests an initial Lapita settlement with later Melanesian intrusion [7]. Another unresolved question is whether the makers of Lapita pottery were derived from the earliest Austronesian-speaking settlers in east Melanesia or represent a second wave of Austronesians who brought with them Lapita-style pottery from eastern Indonesia.

Genetic data can provide valuable additional insights into the history of early Pacific migrations, as shown for non-HLA blood genetic markers [8]. Although the genetic profile of a population is subject to all the evolutionary forces of founder effects, genetic drift, and selection, it cannot be altered radically according to dictates of fashion or expediency, as can language and culture. In addition, the HLA system is a powerful anthropological tool not only because of the extreme polymorphism at each locus, but also because of the close linkage between loci.

When alleles at closely linked loci occur jointly in individuals more often than would be expected by chance, the population is considered to be in linkage disequilibrium. Linkage disequilibrium can arise from founder effects or can be created by population fusion even if there is no disequilibrium in either of the original fusing groups [9]. Linkage disequilibrium decreases in large, randomly mating populations in the absence of selection at a geometric rate dependent on the recombination fraction  $(1 - r)$  per generation [10]. With a recombination fraction of 0.8% between *HLA-A* and *HLA-B* loci [11], 200 generations or about 5,000 years are necessary to reduce any linkage disequilibrium in the founding population by a factor of 5. As it was about 5,000 years ago that the first Austronesian speakers established settlements in coastal Melanesia [4], remnants of the *HLA-A,B* linkage disequilibria relationships resulting from Papuan and Austronesian intermarriages should still be detectable in present-day populations.

The *HLA-B* and *HLA-C* loci are even more closely linked than are *HLA-A* and *HLA-B*, with a recombination fraction of approximately 0.2% [11]. For these loci, 20,000 years of random mating are required to reduce linkage disequilibrium by a factor of 5. The power of linkage disequilibrium in drawing inferences about common ancestral relationships is well illustrated by the strong disequilibrium between *HLA-B13* and *HLA-Cw4* in both Melanesians [12] and Australian Aborigines (H. Bashir, personal communication, 1981), groups known to have been separated for at least 8,000 years [13]. The nonrandom joint occurrence of these two alleles on the same haplotype is unique to these populations. As Feldman and Christiansen [14] caution, linkage disequilibrium is itself subject to all the evolutionary forces of selection, random genetic drift, and migration. On theoretical grounds, there is no greater validity in drawing inferences from linkage disequilibrium relationships than from gene frequency distributions. However, speculation based on both parameters may be undertaken with considerably more confidence than if based on either parameter alone. Here we examine the genetic relationships between 16 Pacific populations with respect to *HLA-A* and *-B* gene frequencies. We then use linkage relationships, where available, to test hypotheses of population fusion and subdivision suggested by the HLA genetic relationships.

## MATERIALS AND METHODS

For New Caledonia, Ouvea, Fiji (Suva), and Wallis Islands, HLA antigen frequencies have been published for persons with abnormal glucose tolerance and controls [12]. As patients and controls showed no consistent significant difference in HLA distributions and since diabetics were ascertained in random surveys in Ouvea and Fiji, data for patients and controls are combined in this report for calculation of gene frequencies. The earlier study pooled data for Uea and Iai speakers on Ouvea (Loyalty Islands) since the HLA profiles for Polynesians (Uea) and Melanesians (Iai) were not significantly different. Here data are provided for the two groups separately.

An additional 11 populations with HLA data available have been included in the analysis. A criterion of minimum sample size of 50 was established so that studies with small numbers tested, as for the Dani of Irian Jaya [15], were excluded from analysis. In Australia, the work of Cross et al. [16] encompassed a large number of Australoid linguistic groups and was included in preference to the study of Walbiri families [17]. Similarly, in Papua New Guinea, the study by Ting et al. [18] tested individuals from many coastal areas and was considered more representative of coastal Papua New Guinea as a whole than the report for Karkar Island [19]. For the Pacific, all published material for Melanesia and Polynesia has been included, although only family data were available for Mauke [20] and Easter Island [21]. Descriptions of individual study populations are provided in the original reports, which are referenced in table 1. For the Western Samoan data from Crosier and Douglas [22], the gene frequencies have been recalculated.

Many of the studies included in the present analysis were undertaken in 1972 when definition of the HLA system was in its infancy. Therefore, for comparative purposes, information regarding new subtypes (such as A26 and Aw34 within the broad antigen class of A10) have necessarily been ignored in this analysis. Also, only the most recent studies have provided *HLA-Cw* and *-DR* gene frequencies, so the phylogenetic relationships generated here are based on *HLA-A* and *-B* loci alone. *HLA-A* and *-B* alleles occurring at very low frequency have been combined for analysis and are listed as "others" in tables 1 and 2. Combined antigens are A1, A3, and A19 for *HLA-A* and B5, B7, B8, B12, B17, Bw21, and Bw35 for *HLA-B*.

The data suffers from the inevitable inadequacies that are encountered when pooling material from various sources. One inadequacy arises from the absence of published haplotype frequencies in many reports so that genetic kinship was calculated here from gene frequency data. This has resulted in loss of information regarding linkage disequilibrium and in the more serious problem of *HLA-A* and *-B* loci not being independent as assumed by the genetic distance model.

Genetic distances between populations were determined using Morton's [27] method of bioassay, such that the kinship ( $\phi_{ij}$ ) between two populations *i* and *j* is:

$$\phi_{ij} = \left\{ \sum_{k=1}^h (q_{ki} q_{kj} / Q_k) - 1 \right\} (h - 1) ,$$

where  $q_{ki}$ ,  $q_{kj}$  are the frequencies of the *k*th allele in populations *i* and *j*;  $Q_k$  is the mean frequency; and *h* is the number of alleles at the locus.

Dendrogram and eigenvector representations of phylogenetic relationships were generated by the computer programs PHEIGEN and ARBOR [28]. Linkage disequilibrium values were estimated according to the method of Mittal et al. [29], with significance tested by chi-square. Levels of significance were not corrected for the number of haplotypes tested.

## RESULTS

Table 1 lists *HLA-A* gene frequencies for 16 Pacific populations. *HLA-A9* is the most common *A* locus antigen in nearly all groups and maintains a gene frequency greater than .45 in Melanesians and less than .45 in Polynesians.

TABLE I  
HLA-A GENE FREQUENCIES IN PACIFIC POPULATIONS

Population	No. tested	A2	A9	A10	All	Others	Blank	Reference
Ouvea-Polynesian .....	75	.041	.411	.136	.261	.034	.118	...
Ouvea-Melanesian .....	76	.041	.584	.069	.225	.007	.074	...
New Caledonia .....	82	.046	.575	.139	.180	.043	.016	...
Fiji-Suva .....	177	.120	.487	.231	.118	.022	.021	...
Fiji-Nadi .....	76	.080	.590	.200	.130	.000	.000	[23]
Wallis Islands .....	131	.260	.364	.146	.182	.023	.025	...
Mauke Islands .....	157	.201	.458	.183	.138	.016	.004	[20]
Cook Island .....	50	.202	.401	.050	.163	.010	.173	[24]
Western Samoa .....	492	.268	.283	.034	.128	.044	.243	[22]
Samoa-New Zealand .....	100	.300	.238	.146	.146	.051	.120	[25]
Tokelau .....	142	.21	.46	.08	.13	.00	.12	[26]
Maori-New Zealand .....	50	.379	.053	.165	.187	.143	.073	[24]
Easter Island .....	69	.230	.390	.000	.270	.110	.000	[21]
Papua New Guinea Coast .....	247	.037	.438	.135	.168	.020	.202	[18]
Papua New Guinea Highlands .....	214	.000	.763	.042	.046	.027	.122	[19]
Australian Aborigines .....	273	.146	.254	.028	.002	.000	.570	[16]

TABLE 2  
HLA-B GENE FREQUENCIES IN PACIFIC POPULATIONS

Population	No.	B13	B15	B16	B18	Bw22	B27	B40	Others	Blank
Ouvea-Polynesian	75	.076	.062	.034	.027	.434	.062	.192	.041	.072
Ouvea-Melanesian	76	.034	.075	.034	.027	.372	.054	.302	.013	.089
New Caledonia	82	.060	.120	.054	.006	.353	.094	.272	.041	.000
Fiji-Suva	177	.047	.127	.012	.037	.411	.032	.269	.014	.051
Fiji-Nadi	76	.040	.190	.110	.040	.250	.020	.210	.110	.120
Wallis Islands	131	.025	.125	.034	.054	.344	.031	.352	.027	.008
Mauke Islands	157	.019	.023	.128	.003	.389	.062	.244	.023	.109
Cook Island	50	.020	.060	.060	.000	.159	.054	.421	.040	.187
Western Samoa	492	.039	.020	.008	...	.265	.013	.439	.042	.174
Samoa-New Zealand	100	.051	.000	.046	.000	.200	.015	.400	.117	.170
Tokelau	142	.05	.00	...	...	.13	.00	.67	.11	.04
Maori-New Zealand	50	.000	.030	.081	.000	.224	.000	.229	.172	.264
Eastern Island	69	.000	.000	.140	.000	.200	.000	.500	.110	.050
Papua New Guinea Coast	247	.151	.071	.000	.105	.168	.062	.183	.055	.205
Papua New Guinea Highlands	214	.077	.287	.005	.000	.294	.066	.230	.002	.041
Australian Aborigines	273	.058	.080	.000	.000	.220	.000	.441	.000	.201

The HLA-A2 distribution is of particular interest. HLA-A2 does not occur in the large sample from the Eastern Highlands of Papua New Guinea [19], and this finding has been confirmed [15] in a smaller series from the Fore. HLA-A2 is lacking also in the Dani or Irian Jaya [15]. Surprisingly, however, HLA-A2 reaches appreciable frequencies in the group of Australian Aborigines included in this study, as it does in another Aboriginal group, the Walbiri [17]. In general, the Australoid genome is a subset of the Papuan genome, with the Aborigine lacking, for instance, the S blood group antigen of the *MNS* system and generally lacking the B antigen of the *ABO* system [30]. Australoid speakers do have some unique genetic variants such as red cell enzyme variants  $CA_1^{2\text{ Aust}}$ ,  $CA_1^{4\text{ Aust}}$ , and  $CA_2^4$  of carbonic anhydrase [31], and these are presumed to have arisen from mutation [32]. HLA-A2 in Aborigines is unlikely to have arisen as a recent mutation or from recent Caucasoid admixture since it is relatively randomly distributed on haplotypes [17]. It seems more likely that the Papuan invaders of New Guinea lacked the A2 antigen, and the Australoid A2 was lost in genetic drift. Whereas HLA-A2 is in significant positive linkage disequilibrium with HLA-B40 in New Caledonia and the Wallis Islands [12] and also in Western Samoa [22], HLA-A2 and -B40 tend to be negatively associated in Aborigines [17]. This implies a different source of origin for the Australoid A2 antigen compared with the coastal Melanesian A2.

The gene frequency of HLA-A2 ranges from 4%–8% in coastal and island Melanesia, at intermediate frequencies of 8%–12% in Fiji, and then increases appreciably in Polynesia to 18%–30%. The absence of the A2 allele in Papuans permits preliminary estimation of the degree of Austronesian admixture in Melanesian populations of the Pacific. The unweighted mean gene frequency of *HLA-A2* in eight Polynesian populations is .253, and, using this value, the estimated Austronesian admixture in coastal Papua New Guinea is 15%; in Ouvéa, 16%; in New Caledonia, 18%; and in Fiji, 43%.

Table 2 gives *HLA-B* gene frequencies for the same 16 Pacific populations. Alleles *HLA-Bw22* and *-B40* are the most frequent in all populations in the Pacific, and *HLA-Bw22* decreases in a cline from Melanesia to Polynesia while *HLA-B40* increases.

Table 3 is a matrix of kinship values within and between 16 populations with respect to *HLA-A* and *HLA-B* gene frequencies. The highest kinship values are within Australian and Papua New Guinea highland groups, reflecting the isolation of these populations from others in the sample and indicating that they were impervious to Austronesian influences. Australia has high kinship values with Papua New Guinea highland and coastal groups, as expected, but has inflated kinship with Western Samoa. This pseudo-relationship has arisen by chance as will be shown in analyses of haplotype frequencies and linkage disequilibrium values.

The Melanesian populations have positive kinship values with each other and, in general, negative values with the Polynesian groups. The only exception to this is Mauke, a Polynesian isolate that has positive kinship values with five of the six Melanesian populations. Mauke is a small isolate in a remote location and there-

TABLE 3  
KINSHIP ( $\times 10^{-2}$ ) BETWEEN 16 PACIFIC POPULATIONS: HLA-A AND HLA-B

	MELANESIAN										POLYNESIAN					
	AUS- TRALIAN	PNGH	PNGC	NCAL	OUVM	OUVP	FIJS	FIJN	WALL	SAMZ	WSAM	TOKL	COOK	MAUK	NEWZ	EAST
Australia .....	22.65	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Papua New Guinea	2.67	22.91	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Papua New Guinea																
Coast.....	3.31	5.08	7.00	...	...	...	...	...	...	...	...	...	...	...	...	...
New Caledonia .....	-6.03	7.18	-0.74	3.76	...	...	...	...	...	...	...	...	...	...	...	...
Ouvea-Melanesian .....	-2.36	4.68	0.64	2.15	3.01	...	...	...	...	...	...	...	...	...	...	...
Ouvea-Polynesian .....	-1.56	4.51	1.15	1.38	1.45	1.97	...	...	...	...	...	...	...	...	...	...
Fiji-Suva .....	-4.52	2.67	-0.41	1.76	0.90	0.54	2.89	...	...	...	...	...	...	...	...	...
Fiji-Nadi .....	-7.04	8.04	-0.61	2.52	0.87	-0.07	1.97	6.03	...	...	...	...	...	...	...	...
Wallis Islands .....	-4.17	2.86	-1.65	0.38	-0.06	-0.57	1.51	0.94	3.24	...	...	...	...	...	...	...
Samoa-New Zealand .....	0.87	-1.00	-1.53	-2.98	-2.79	-2.18	-2.05	-2.46	-0.30	3.60	...	...	...	...	...	...
Western Samoa .....	7.62	-1.16	-0.44	-3.43	-1.65	-1.66	-2.55	-4.61	-0.55	2.37	5.03	...	...	...	...	...
Tokelau .....	0.65	3.36	-1.84	-0.47	-0.18	-2.45	-0.56	-0.70	0.74	-0.36	0.79	6.59	...	...	...	...
Cook Island .....	3.83	0.75	-0.31	-1.74	-0.35	-1.51	-2.10	-2.19	-0.78	0.83	2.43	0.92	2.44	...	...	...
Mauke Islands .....	-4.98	6.71	-1.37	2.22	1.01	0.91	2.95	2.73	2.28	0.90	-1.11	-0.81	0.06	7.30	...	...
New Zealand .....	-1.64	-3.87	-2.73	-3.89	-4.62	-2.45	-2.36	-2.78	0.84	5.97	3.67	-3.52	0.99	2.25	15.47	...
Easter Island .....	-6.72	-5.06	-4.92	-1.46	-2.00	-3.29	-3.78	-1.30	-0.33	1.18	-0.24	0.88	0.08	-0.36	5.04	8.15



fore particularly subject to the forces of genetic drift. The effects of random drift have no doubt been accentuated by sampling techniques in Mauke as, although one-quarter of the total population was tested, most individuals were members of nine major families [20].

Within Polynesia, the kinship coefficients tend to be positive, reflecting the genetic similarity of these groups. There are high kinship values within and between the Maori and Easter Island populations, a result of their geographic and genetic isolation from other groups in this study and providing evidence for close common ancestry.

Figures 2 and 3 provide schematic representation of the kinship values in a dendrogram (fig. 2) and eigenvector representation (fig. 3). The dendrogram shows a particularly close cluster between Melanesian and Polynesian speakers of Ouvea, suggesting that the arrival of Polynesian immigrants in Ouvea had a far greater impact on language than on genetics, a situation not uncommon in Melanesia [33]. The Ouvea populations are closely related to Melanesians of New Caledonia, as might be expected from their geographic proximity. The two Fiji series show a preference to cluster with Wallis Islands and Mauke populations before grouping with the rest of Melanesia, and this would confirm the estimate given earlier in this paper of a high Austronesian admixture (43%) in Fijians. The Polynesian groups from Western Samoa, Cook Islands, and Tokelau cluster together, but are well separated from the Easter Island-Maori group. The genetic distance separating the

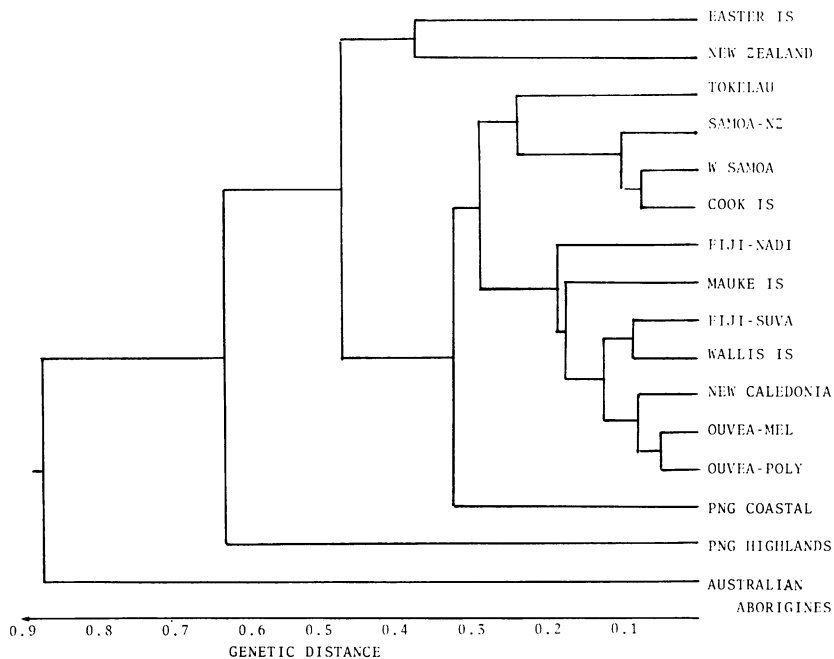


FIG. 2.—Dendrogram from the kinship matrix for 16 Pacific populations

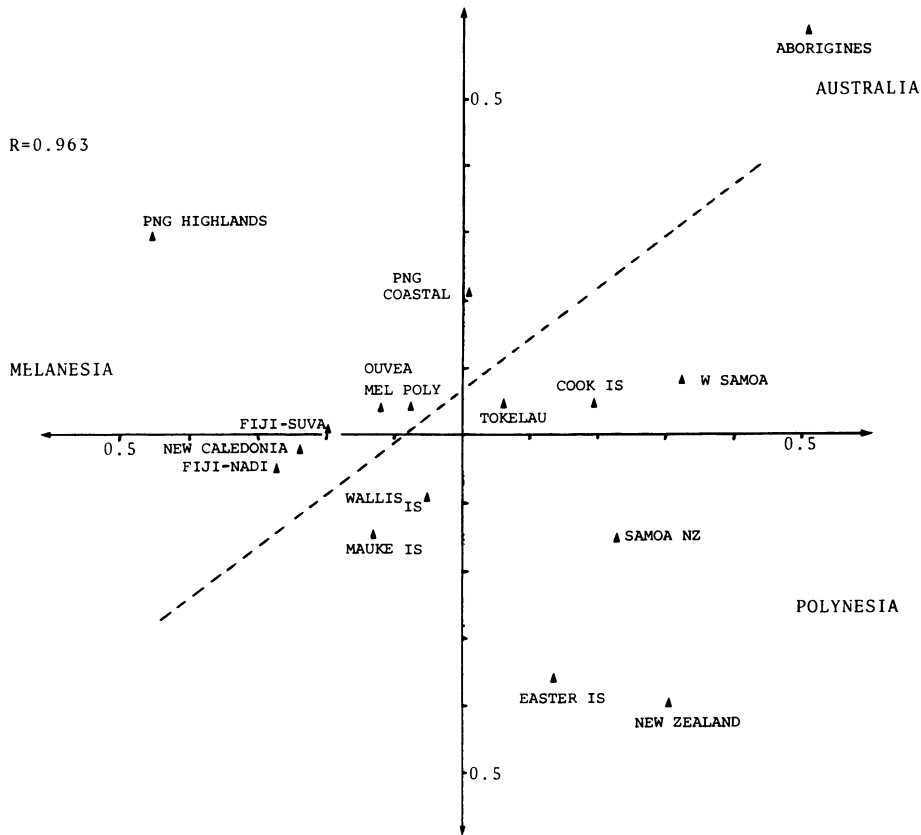


FIG. 3.—Eigenvector representation of the kinship matrix for 16 Pacific populations

two major Polynesian branches is totally compatible with archaeological, linguistic, and cultural evidence [4] that colonists left the Samoa area 2,000 years ago but spent some 400–800 years in East Polynesia before further dispersion to New Zealand and Easter Island.

The Australian Aborigine and the Papua New Guinea highlander are shown to be well separated from the remainder of the populations studied, both in the dendrogram and the eigenvector plot. The Papua New Guinea coastal group, however, shows closer affiliation with Austronesian-speaking Melanesians than with Papua New Guinea highlanders, and this is compatible with our estimate of 15%–18% Austronesian admixture in all non-Fijian coastal Melanesians in the Pacific.

The eigenvector represents virtually all the HLA genetic variation between populations, with the cophenetic correlation,  $R$ , equal to .963. There is a clear-cut separation between Polynesia and Melanesia, and most populations are distributed from left to right across the dendrogram in much the same way as they are distributed from west to east across the Pacific.

Although the *HLA* gene frequency data has produced a set of relationships between Pacific populations that fits remarkably well with knowledge of interrelationships and migrations gleaned from other disciplines, it is pertinent to ask what additional information can be obtained from studies of *HLA-A* and *-B* linkage disequilibrium relationships. Unfortunately, for most of the published material, haplotype relations are not provided. Table 4, however, provides haplotype frequencies (HF) and linkage disequilibrium values ( $\tilde{\Delta}$ ) for two linkage groups in five representative populations. The  $\tilde{\Delta}$  values for the Aboriginal group, the Walbiri, are calculated from the data provided by Bashir [17], and those for Western Samoa are from Crosier and Douglas [22]. The New Caledonia, Fiji, and Wallis Islands values are calculated from data given by Serjeantson et al. [12].

In table 4, the haplotype frequency of *HLA-A11,B40* is highest in Australian Aborigines, with significant and positive linkage disequilibrium between the two alleles. Positive linkage between *HLA-A11,B40* persists in Melanesians also in both New Caledonia and Fiji, but there is no association between *A11* and *B40* in Polynesians. In contrast, *HLA-A9,Bw22* are in significant positive linkage disequilibrium in Polynesians from both Western Samoa and the Wallis Islands and also in Melanesians from Fiji. However, even though both *A9* and *Bw22* occur at appreciable frequencies in New Caledonia and Australia, they are not in linkage disequilibrium.

Table 4 is of particular interest if one compares haplotype frequencies alone, for the frequencies of *A11,B40* and *A9,Bw22* in Australia are most similar to those in Western Samoa. This phenomenon has contributed to the high overall kinship value of .076 between Australia and Western Samoa given in table 3. However, the  $\tilde{\Delta}$  values in table 4 suggest that this pseudo-relationship is a chance occurrence, for *A11,B40* is an Australoid/Papuan haplotype whereas *A9,Bw22* is of Austronesian origin. This situation emphasizes the additional information that can be provided by knowledge of linkage disequilibrium in populations with similar gene and haplotype frequencies.

The concept that Fiji is an admixture of Melanesian and Polynesian influences is verified by the  $\tilde{\Delta}$  values in table 4. Fiji has both the Australoid *A11,B40* and the Polynesian *A9,Bw22* haplotypes, and, in addition, the  $\tilde{\Delta}$  values for these haplo-

TABLE 4  
HAPLOTYPE FREQUENCIES (HF) AND LINKAGE DISEQUILIBRIUM VALUES  
( $\tilde{\Delta}$ ) PER 1,000 IN SELECTED PACIFIC POPULATIONS

POPULATION	A11,B40		A9,B22	
	HF	$\tilde{\Delta}$	HF	$\tilde{\Delta}$
Australia .....	89	51*	126	25
New Caledonia .....	18	65	236	32
Fiji .....	29	61*	251	74*
Wallis Islands .....	28	-22	179	59*
Western Samoa .....	41	6	105	59*

\*  $P < .05$ .

types are accentuated. As Degos and Dausset [9] point out on theoretical grounds, when two populations fuse and when a positive  $\Delta$  exists in one of the original populations, the  $\tilde{\Delta}$  value is enhanced. This appears to be the case in Fiji, where the Australoid  $\tilde{\Delta}$  value is statistically significant but has declined below 5% significance in New Caledonia.

#### DISCUSSION

This study shows the remarkable power of the HLA system in describing phylogenetic relations in the Pacific, although this power could not be exploited fully because of the inclusion of data from many sources that necessitated, for comparative purposes, omission of information on new antigen subtypes and newly defined *HLA* loci. Schanfield [34] argues that the immunoglobulin system, *Gm*, is more informative than *HLA*, but his arguments are suspect since he compares *Gm* allotypes with *HLA* alleles rather than with haplotypes.

The most serious reservation about HLA as an anthropological tool is that the HLA system has probably been under considerable selection pressure as suggested by numerous HLA antigen associations with disease [35]. The presently observed distributions may reflect not only founder effects and migration, but congruent selection coefficients in different populations. Selection for favorable *HLA* alleles can affect linkage disequilibrium [36] as well as gene frequency relationships between populations.

Despite these reservations, the HLA data permit reassessment of theories regarding the "peopling" of the Pacific. Archaeological evidence shows that New Guinea and Australia were settled more than 50,000 years ago. These early Australoid populations must have continued their contact with each other or else continued to receive new arrivals from a common source for at least another 20,000 years. This seems evident from the maintenance of *HLA-B13, Cw4* and *HLA-A11, B40* linkage relationships in present-day Australians and Melanesians. The linkage disequilibrium values are, however, compatible with a time of separation of about 8,000 years; Golson [13] reports that the pig reached New Guinea about 8,000 years ago but did not enter Australia, which had been geographically isolated at the end of the Pleistocene.

Between 5,000–3,500 years ago, Austronesian speakers arrived in Melanesia and intermarried with resident Papuans in coastal areas. These Austronesians carried *HLA-A2* into Melanesia on the haplotype *HLA-A2, B40*. The positive linkage disequilibrium still persists in these groups, and the frequency of *HLA-A2* provides an estimate of Austronesian admixture in coastal Melanesia of 15%–18%. Austronesian genetic elements have not penetrated into the highlands of New Guinea, although numerous Austronesian loan words have been incorporated into Papuan languages in the New Guinea interior [3].

By 3,000 years ago, the Austronesian-speaking Lapita pottery makers arrived in Melanesia, Fiji, and Samoa. These groups were virtually uninfluenced by Melanesian genes, having neither of the Australoid/Papuan haplotypes, *HLA-B13, Cw4* nor *HLA-A11, B40*. In these later Austronesian migrants, *HLA-A9* and *-Bw22* were in marked linkage disequilibrium, as well as were *HLA-A2* and *-B40*. The HLA

data do not support the theory of Polynesian evolution within east Melanesia, but indicate a Mongoloid wave of migration that is compatible with the time of introduction of Lapita-style pottery, about 3,000 years ago. It is of particular interest that, in Japan, the only Mongoloid population with extensive HLA data available, haplotypes *HLA-A2,B40 (A2,Bw60)* and *HLA-A9,Bw22 (Aw24, Bw54)* also show significant linkage disequilibrium [37].

The Lapita-making Austronesians carried the *HLA-A9,Bw22* haplotype into West Polynesia and left this influence in Fiji. Fiji shows its truly intermediate position in Oceania, with both Australoid and Polynesian linkage relationships and an intermediate frequency of *HLA-A2*.

About 2,000 years ago, colonists left the Samoa area for Eastern Polynesia and settled in the Marquesas until 1,200–1,600 years ago, when further population division occurred with migration to Easter Island and New Zealand. The dendrogram based on *HLA* gene frequencies clearly shows the split between the Samoa-Cook Islands-Tokelau branch and the Easter Island-New Zealand branch. The clustering of Cook Islands with Samoa and Tokelau rather than with New Zealand-Maoris is not consistent with linguistic analysis [38] that classifies both Cook Islanders and Maoris as speakers of the Tahitic subgroup of Polynesian languages. However, as pointed out by Clark [39], the linguistic cognate percentages separating Polynesian subgroups are minimal. The Maori population does not show close affiliations with any other population in the sample, mainly because of its uniquely low frequency of *HLA-A9*, but clusters eventually with the Easter Island group in reflection of their common ancestry in Eastern Polynesia.

The HLA data are compatible with current theories regarding voyages into the Pacific, theories based on prodigious efforts in the disciplines of linguistics, cultural and physical anthropology, and archaeology.

The HLA data are compatible also with recent theories based on non-HLA genetic evidence [8] but less so with the early conclusions of Simmons et al. and Simmons and Graydon [40, 41], who, on the basis of blood groups, claimed Polynesians were closely related to American Indians and showed no similarity with Melanesians and Indonesians. It reflects the power of HLA as an anthropological tool in that this small segment of the human genome can describe in such detail the interrelationships and migrations among peoples. Future studies of HLA distributions in Oceania and Southeast Asia, especially studies that incorporate information on newly defined loci and antigenic subtypes, may well permit clear definition of the source of origin of the Pacific colonists and the complexity of their Pacific voyages.

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