Amer J Hum Genet 24:145–155, 1972

Distribution of the Immunoglobulin Markers at the IgG1, IgG2, IgG3, IgA_2, and κ-Chain Loci in Australian Aborigines: Comparison with New Guinea Populations

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The origins of the aboriginal people of Australia and their relationship to neighboring populations, both historic and prehistoric, are being extensively discussed against a background of increasing archaeological, paleoclimatological, and anthropological knowledge [1, 2]. In recent years, studies on the physical anthropology of the Australian Aborigines have been supplemented by data on blood groups [3–8] and various serum protein polymorphisms, the haptoglobin and transferrin types [6, 9–11], the serum Gc component [12], serum pseudocholinesterase [11], and a range of immunoglobin markers and enzyme groups [6, 13–16]. The immunoglobulin groups, in particular, promise to be of very great value in population studies in general. It is well established that the various immunoglobulin markers are inherited in different combinations in each of the main ethnic groups [17]. These combinations or phenogroups probably arose by rare recombinatory events early in the history of modern man, and it is clearly desirable that the largest possible range of markers be studied in populations of interest.

In this paper we present the results of the typing of sera from selected Australian aboriginal populations for Gm (IgG1, IgG2, and IgG3 loci), Inv (κ-light chain locus), and Am (IgA_2 locus) markers. These results are compared and contrasted

Received July 1, 1971; revised September 30, 1971.

Investigations supported in part by Office of Naval Research contract non R (3656-12) and U.S. Public Health Service research grants AM-08527 and H.E. 10040-01.

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with published and new data from New Guinea populations adjacent to the Australian mainland.

MATERIALS AND METHODS

Populations Studied

Sera were obtained from four populations of Australian Aborigines: 70 samples from the Western Desert (Leonora, Laverton, and Warburton Range) in Western Australia; 46 from Bentinck Island and 130 from Mornington Island in the Gulf of Carpentaria; 52 from Doomadgee on the adjoining mainland; and 28 from Weipa, Cape York Peninsula. The Lardiil of Mornington Island and the Kaiadilt of Bentinck Island have been extensively studied by Simmons et al. [4, 5], Curtain et al. [11], and Tindale [18]. The Weipa populations have been described by Adels and Gajdusek [19] and by Doherty [20], and Galbraith [21]. The locations of these populations are shown on the maps in figures 1 and 2. Also shown are the locations of the New Guinea populations whose Gm markers have been recorded and discussed extensively by Curtain et al. [22]. Selected sera from this survey which had been stored at −70° C were tested for Gm (n) and Am

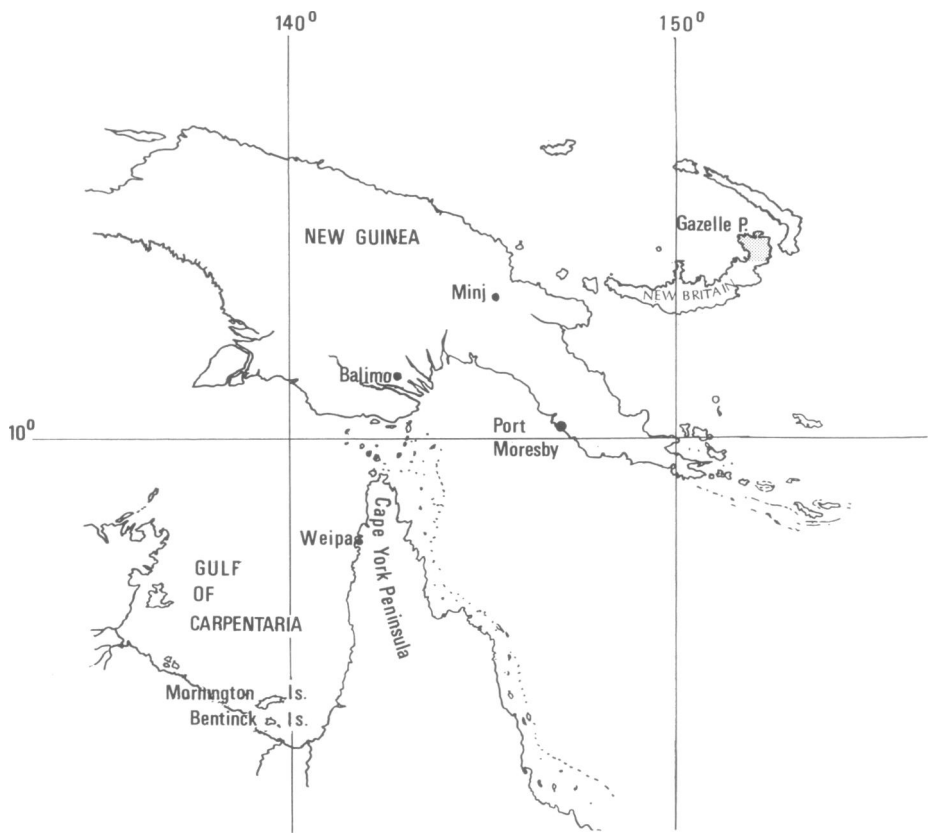

FIG. 1.—Map of northeastern Australia and Papua–New Guinea showing localities from which blood samples were obtained.

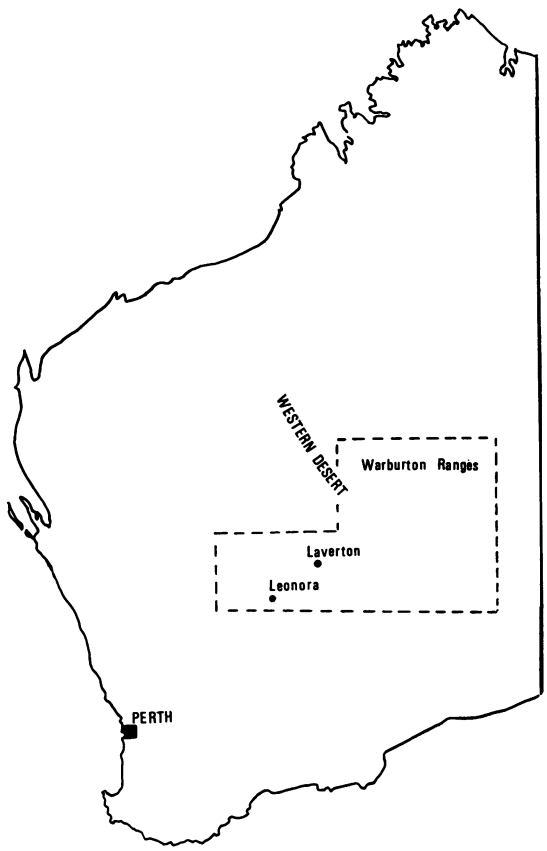

FIG. 2.—Map of Western Australia, showing location of Western Desert aboriginal populations

(1); the reagents for these were not available when the sera were first studied. The aboriginal sera were tested for Gm (a), (x), (f), (z), (n), (g), (b), (s), (t), (c^3) and (c^5), Inv (1), Inv (a), and Am (1).

Gm, Inv, and Am Typing

The reagents used and the methods of typing have been described by van Loghem and Martensson [23], Natvig and Kunkel [24], and Vyas and Fudenberg [25]. The alphabetic nomenclature for the Gm system is used throughout this paper in preference to the numeric nomenclature. The reasons for this were given in the paper by Curtain et al. [22]. The two nomenclatures are set out in table 1.

RESULTS AND DISCUSSION

Of the markers at the IgG1 and IgG3 loci, only Gm (a), (x), (g), and all of the b factors were found; s, t, c^3 and c^5 were absent. Table 2 shows the Gm (n) and Am (1) types of the various IgG1–IgG3 gene complexes among Australian Aborigines compared with New Guineans. Table 3 shows the frequencies of the various gene complexes in these populations. It can be seen that Am^1 is present in all of the

TABLE 1

COMPARISON OF ALPHABETIC AND NUMERIC NOMENCLATURES OF GM AND INV FACTORS USED IN THIS STUDY

Nomenclature	Gm Specificity															Inv Specificity		
Numeric	1	2	3,4	17	21	11	5,12	10,13	14	...	15	16	6	24		1	2	3
Alphabetic	a	x	f	z	g	b^0	b^1		b^3	b^4	b^5	s	t	c^3	c^5		1	a	b

Australian aboriginal populations, although it is absent in an appreciable number of New Guineans of $Gm^{fa;n;b/fa;n;b}$ genotype (table 2). In the Western Desert Aborigines Gm (n) occurs in low frequency and is found in very high frequency among Bentinck and Mornington Island and Weipa Aborigines of the $Gm^{za;g/za;b}$, $Gm^{zax;g/za;b}$, and $Gm^{za;b/za;b}$ genotypes. In New Guinea, it is mainly found associated with the $Gm^{za;g/fa;b}$, $Gm^{zax;g/fa;b}$, and $Gm^{fa;b/fa;b}$ genotypes. The data in table 2 suggest the presence in the populations studied of six gene complexes: $Gm^{za;n;b}$, $Gm^{za;(n-);b}$, $Gm^{za;(n-);g}$, $Gm^{zax;(n-);g}$, $Gm^{fa;(n-);b}$, and $Gm^{fa;n;b}$. Of these, $Gm^{fa;(n-);b}$ and $Gm^{fa;n;b}$ were absent from the Australian Aborigines and $Gm^{za;(n-);b}$ occurred in the Mornington Island group in very low frequency (.15). Inv (1) together with Inv (a) occurred in variable frequency in all the aboriginal populations studied; the frequencies were 7.7% among the Bentinck and Mornington Islanders, 4.3% at Weipa, and 4.4% among the Western Desert people.

The data reinforce the impression of the occurrence of marked genetic differences between the aborigines of the northern areas of Australia and those in other parts of the continent, particularly of Central Australia and the Western Desert. This impression has emerged from blood group studies (reviewed by Simmons [3]), from consideration of a number of genetic marker systems by Sanghvi et al. [26], and from studies on the Gm and Inv markers. Vos et al. [13] first demonstrated that Gm (c) was absent from Australian Aborigines and that Gm (b) was absent from the Western Desert people, while it occurred in fairly high frequency in people from the Kimberley Ranges. Nicholls et al. [6] found Gm (b) to be virtually absent from the Central Australian populations, while Flory [10] found Gm (b) to be present in some Cape York populations and absent from others. Recently, Steinberg and Kirk [15], after testing 15 Northern Territory aboriginal populations for Gm factors (a), (f), (b), and (c), concluded that the presence of the Gm (b) factors as the Gm^{ab} complex was due to New Guinean admixture, and that up to 30% of the genotypes of the groups they studied could have been derived from New Guinea. Our results confirm and extend these observations for the northern populations and suggest a pattern of considerable complexity. For example, the Lardiil of Mornington Island and the adjoining mainland people have $Gm^{za;g}$ frequencies very similar to those found among the non-Austronesian-speaking people of Minj in New Guinea, while the Kaiadilt of Bentinck Island resemble the non-Austronesian-speaking population at Balimo, on the southwest coast of Papua, in having a high frequency of

TABLE 2

GM (n) AND AM (1) TYPES OF VARIOUS IgG1–IgG3 GM GENE COMPLEXES IN AUSTRALIAN ABORIGINES, COMPARED WITH NEW GUINEANS

PROBABLE GM GENOTYPE AND GM (n) PHENOTYPE	GULF OF CARPENTARIA				WESTERN AUSTRALIA	NEW GUINEA				
						New Britain				
	Cape York Weipa $N = 28$	Mornington Island $N = 113$	Mainland $N = 39$	Bentinck Islands $N = 46$	Western Desert Australian Aborigines $N = 70$	Tolai Vunalia MN $N = 48$	Tolai Kuraip MN $N = 39$	Tolai Rakunai MN $N = 17$	Tolai Vunalaka MN $N = 18$	Tolai Nordup MN $N = 40$
za;g/za;g:										
n+	...	...	...	...	2	...	...	...	...	...
n−	2	45	23	...	44	1	2	2	4	...
zax;g/zax;g and *za;g:*										
n+	...	...	...	...	5	...	...	...	...	...
n−	3	9	3	...	19	8	8	7	2	3
za;g/za;b:										
n+	9	41	9	8	...	...	...	...	...	...
n−	...	3	...	...	...	...	...	...	...	...
zax;g/za;b:										
n+	...	6	4	...	...	...	...	...	...	...
n−	...	...	...	...	...	...	...	...	...	...
za;b/za;b:										
n+	14	9	...	38	...	1	...	...	...	...
n−	...	...	...	...	...	...	...	...	...	...
za;g/fa;b:										
n+	...	...	...	...	...	9	2	6	1	1
n−	...	...	...	...	...	2	...	...	...	...
zax;g/fa;b:										
n+	...	...	...	...	...	12	13	1	6	12
n−	...	...	...	...	...	3	2	...	...	3
za;b/fa;b:										
n+	...	...	...	...	...	2	...	...	...	...
n−	...	...	...	...	...	...	...	...	...	1
fa;b/fa;b:										
n+	...	...	...	...	...	10 (10)	12 (8)	1 (1)	3 (3)	17 (14)
n−	...	...	...	...	...	...	...	...	2	3

TABLE 2 (*Continued*)

Probable Gm Genotype and Gm (n) Phenotype	New Guinea								
	New Britain						Mainland		
	Tolai Vairiki MN $N = 56$	Tolai Ralmalmal MN $N = 68$	Tolai Bunamin MN $N = 55$	Tolai Koulon MN $N = 45$	Sulka Mope NAN $N = 54$	Baining Gaulim NAN $N = 43$	Western Highlands Minj NAN $N = 101$	Western District Balimo NAN $N = 99$	Central District Motu MN $N = 38$
za;g/za;g:									
n+	...	...	...	...	...	...	...	...	...
n−	...	3	8	4	1	4	51 (3)	2	...
zax;g/zax;g and *za;g:*									
n+	...	...	...	...	...	...	...	...	...
n−	9	2	9	5	4	24	13	...	...
za;g/za;b:									
n+	...	...	...	...	...	...	25 (1)	12	...
n−	...	...	...	...	...	...	5	2	1
zax;g/za;b:									
n+	...	...	...	...	...	...	3	...	...
n−	...	...	...	...	...	...	...	...	...
za;b/za;b:									
n+	...	...	...	...	...	...	1	80 (11)	1
n−	...	...	...	...	...	...	1	3	...
za;g/fa;b:									
n+	7	19	5	8 (3)	9	5	1	...	...
n−	3	4	1	1	4	...	1	...	1
zax;g/fa;b:									
n+	13	8	23	6 (2)	8 (1)	7	...	...	...
n−	4	4	2	1	2	...	...	...	...
za;b/fa;b:									
n+	...	2[2]	...	1	4	...	...	...	6
n−	...	...	...	...	1	...	...	...	...
fa;b/fa;b:									
n+	20 (20)	23 (16)	7 (4)	19 (19)	20 (20)	3 (3)	...	...	23 (19)
n−	...	3 (1)	...	...	1	...	...	...	7

NOTE.—Combination of new data with results of study by Curtain et al. [22]. Numbers in parentheses relate to number of samples found Am (1) negative. All other samples were Am (1) positive. MN = Melanesian speakers; NAN = non-Austronesian speakers.

TABLE 3

FREQUENCIES OF GENE COMPLEXES AT IgG1, IgG2, AND IgG3 LOCI IN AUSTRALIAN ABORIGINES COMPARED WITH NEW GUINEANS

	za;(n—);g	*zax;(n—);g*	*za;(n—);b*	*za;n;b*	*fa;(n—);b*	*fa;n;b*
	Australian Aborigines					
Mornington Island	.631	.068	.015	.286	.000	.000
Bentinck Island	.087	.000	.000	.913	.000	.000
Mainland	.742	.091	.000	.167	.000	.000
Weipa	.281	.059	.000	.660	.000	.000
Western Desert*	.797 (.019)	.152 (.032)	.000	.000	.000	.000
	New Guineans					
New Britain:						
Tolai Vunalia (MN)	.183	.275	.000	.042†	.086	.414
Tolai Kuraip (MN)	.118	.357	.000	.000	.054	.471
Tolai Rakunai (MN)	.451	.285	.000	.000	.000	.265
Tolai Vunulaka (MN)	.289	.238	.000	.000	.152	.321
Tolai Nordup (MN)	.017	.258	.013†	.000	.228	.484
Tolai Vairiki (MN)	.128	.274	.000	.000	.124	.474
Tolai Ralmalmal (MN)	.225	.106	.000	.015†	.180	.474
Tolai Bunamin (MN)	.248	.342	.000	.000	.038	.371
Tolai Koulon (MN)	.231	.147	.000	.011†	.063	.549
Sulka Mope (NAN)	.165	.141	.039	.007	.158	.490
Baining Gaulim (NAN)	.307	.483	.000	.000	.000	.209
Western Highland:						
Minj (NAN)	.724	.083	.036	.147	.006	.005
Western District:						
Balimo (NAN)	.091	.000	.164	.745	.000	.000
Central District:						
Motu (MN)	.013	.000	.000	.105†	.437	.445

NOTE.—MN = Melanesian speakers; NAN = non-Austronesian speakers.

* The frequencies given in parentheses are for *za;n;g* and *zax;n;g*, respectively, which were found only in this population.

† A gene complex carrying the opposite Gm (n) type may occur, although there is no evidence for it.

$Gm^{za;n;b}$ although they do not possess the $Gm^{za;(n-);b}$ complex. Indeed, the presence of $Gm^{za;n;b}$ in high, or appreciable frequency in all of the populations except New Britain groups (0–.042) and the Motu (.105) is of very great interest, since it has not occurred in any other population so far studied. The data of Steinberg and Kirk [15] and our present results suggest that the $Gm^{ja;(n-);b}$ and $Gm^{ja;n;b}$ complexes which are present in the Melanesian-speaking populations so far studied are absent from Australia. We have suggested previously [22] that the distribution of the Gm markers could be explained by postulating that the southwest Pacific was initially populated by people possessing only $Gm^{za;g}$ and $Gm^{zax;g}$, and that further migrations brought first $Gm^{za;b}$ and then $Gm^{ja;b}$ into the area. We would therefore expect populations isolated either culturally, as in the case of the Baining of New Britain, or geographically, as in the case of the Kuman of Minj or the Western Desert Aborigines, to have a high frequency of $Gm^{za;(n-);g}$ and $Gm^{zax;(n-);g}$. The $Gm^{za;n;b}$ which we found in the Weipa and Bentinck and Mornington Island populations and in the non-Austronesian-speaking New Guinea populations was presumably brought into the area by migrants from the early Southeast Asian Neolithic complex. The Lardiil and Kaiadilt of Bentinck and Mornington Islands are of considerable interest in this connection, since they differ markedly in their blood groups and other markers from the mainland aboriginal populations and from each other [5, 11]. For example, the Kaiadilt lack blood group A and have a B frequency of .224, the highest found in northeastern Australia.

In a detailed discussion of the background of these populations, Simmons et al. [4] suggested an earliest date of 3,500 years ago for the last colonization of Bentinck Island, the more isolated of the two. By then, populations with blood group B and also $Gm^{za;n;b}$ would have been established in the region, and it is probable that the Kaiadilt population was derived from a small group of these people. The very high frequency of the $Gm^{za;n;b}$ complex was probably brought about by the effect of random genetic drift or selection upon a small population whose effective breeding size, as judged from the demography of the population in recent years [18], could often have been as low as 20. The absence of Gm (f) from the Kaiadilt further reinforces the argument by Simmons et al. [4] that their high frequency of blood group B could not be due to more recent contact with Malay trepangers or Europeans since both of these groups have this marker—the former in the complex $Gm^{ja;n;b}$ and the latter as $Gm^{j;n;b}$ or $Gm^{j;(n-);b}$.

The high frequency of Gm (b) in the Weipa population may also be explained on the basis of gene flow from New Guinea and the effect of genetic drift or selection. A striking difference between the Weipa and Bentinck Island populations is found in the former's blood group B frequency which was found by Simmons et al. [27] to be only .03. There is thus no connection between the blood group and Gm frequencies in these two populations.

Turning to the New Guinea data, the results for Gm (n) and Am (1) further emphasize the difference already noted [22, 28, 29] between the Melanesian-speaking and non-Austronesian-speaking populations tested: the former possess the gene

complex $Gm^{(fa;n;b)}$; $Am^{(1-)}$ in high frequency, while it is absent from the latter, except in New Britain (Sulka, .343; Baining, .067).

The IgA_2 marker Am (1) described by Vyas and Fudenberg [25] and Am (2) described by Kunkel et al. [30] seem to be identical. The Japanese families studied by van Loghem et al. [31] for Am (2) were retyped by us with reagents for Am (1) with identical results. Van Loghem et al. [29] found the complex $Gm^{fa;n;b}$; $Am^{(1-)}$ to be common among Japanese and have concluded that it is common among other Mongoloids. Caucasian individuals negative for Am (1) [or Am (2)] are very rare, most negative individuals being found in Negroid populations. The IgG_2 marker Gm (n) does not occur in any of the gene complexes common in Negroes, so that in Negroes Am^1 is associated with $Gm^{(n-)}$. The new gene complex $Gm^{za;n;b}$ found in the present study occurred in very high frequencies in Balimo, Bentinck Island, and Weipa, and was found either with or without Am^1. Clearly, the results obtained from a study of the immunoglobulin markers promise to make a considerable contribution to our understanding of the relationships between the southwest Pacific populations and the effects of gene flow and drift on their present composition. The fulfillment of this promise will require surveys more numerous and more extensive than those so far reported and should include the surrounding populations.

SUMMARY

Sera from aboriginal populations in northeastern Australia and the Western Desert of Western Australia were tested for Gm (a), (x), (f), (z), (n), (g), (b), (s), (t), (c^3), (c^5), Am (1), Inv (a), and Inv (1). The populations were the Lardiil of Mornington Island; the Kaiadilt of Bentinck Island; the Weipa Aborigines on the Cape York Peninsula; and the Western Desert Aborigines from Leonora, Laverton, and the Warburton Range of Western Australia. All the subjects were Am (1+), and Gm (f), (s), (t), (c^3), and (c^5) were not found. Inv (a) occurred in low frequency (4.3%–7.3%) in the three groups. The gene complexes $Gm^{za;n;b}$, $Gm^{za;(n-);g}$, $Gm^{zax;(n-);g}$, and $Gm^{za;(n-);b}$ occurred in the northeastern populations, the last complex being in very low frequency in the Lardiil only. Only $Gm^{za;(n-);g}$ and $Gm^{zax;(n-);g}$ occurred in the Western Desert population. Both the Weipa and Bentinck Island populations had very high frequencies of Gm (b), and it was suggested that these may have arisen by a combination of gene flow from New Guinea and genetic drift. These results were compared with data from New Guinea where six gene complexes were found: $Gm^{za;n;b}$, $Gm^{za;(n-);b}$, $Gm^{za;(n-);g}$, $Gm^{zax;(n-);g}$, $Gm^{fa;n;b}$, and $Gm^{fa;(n-);b}$. A high frequency of the complex $Gm^{fa;n;b}$; $Am^{(1-)}$ was found among the Melanesian-speaking New Guinea populations, while it was absent from the non-Austronesian speakers, except those in New Britain. This finding further emphasizes the differences already observed between the Melanesian- and non-Austronesian-speaking populations of New Guinea with respect to the immunoglobulin markers. Finally, the $Gm^{za;n;b}$ complex appears to be unique so far to New Guinea and the northern Australian aboriginal populations.

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