Immunoglobulin Allotypes in Several North American Eskimo Populations

M.S. SCHANFIELD,[1] M.H. CRAWFORD,[2] J.B. DOSSETOR,[3] AND H. GERSHOWITZ[4]

Abstract   Genetic data consisting of immunoglobulin testing (GM and KM) from 631 Eskimos from 5 populations are reported. These populations are Savoonga, Gambell (St. Lawrence Island), Wales, King Island, and Mckenzie Delta, Baffin Island. The GM and KM haplotypes are analyzed and compared to those occurring in Greenland, Canadian, Alaskan, and Siberian Eskimos and to other Siberian indigenous populations. These analyses suggest that during the peopling of the New World, four separate migrant groups crossed Beringia at various times.

The complex haplotypes of the GM system have proven to be valuable tools in the investigation of human populations, tracing population affinities and demonstrating variation within populations (Schanfield 1980). Previous studies on the immunoglobulin allotypes of Eskimo populations have been limited to the relatively recent reports on the Yupik-speaking St. Lawrence Island Eskimos (Ferrell et al. 1981) and on unidentified Inupik Eskimos from northern Alaska (Matsumoto et al. 1982), and a publication on Inupik-speaking Central Eskimos from Igloolik (McAlpine et al. 1974), with the majority of studies on Eskimos focused on Greenland populations (Nielsen et al. 1971; Persson et al. 1972; Steinberg et al. 1974). This is the first report on the immunoglobulin allotypes of central Alaskan Inupik-speaking Eskimos, Mckenzie Delta Eskimos, and central Eskimos from the Baffin Island area, with additional studies on the Yupik-speaking Eskimos from St. Lawrence Island.

[1]American Red Cross Blood Services, Immunohematology Laboratory, Bethesda, MD.

[2]Department of Anthropology, University of Kansas, Lawrence, KS 66045.

[3]MRC Transplantation Group, University of Alberta, Edmonton, Alberta, Canada.

[4]Department of Human Genetics, University of Michigan, Ann Arbor, MI.

The results of these studies indicate that the Eskimo populations, geographically distributed from Siberia to Greenland, appear to be a single subdivided population with clinal changes in gene frequencies of the aboriginal immunoglobulin haplotypes. These clinal changes may be affected by varying magnitudes of admixture in the different populations. The data indicate that *GM*A G* and *GM*A T* appear to be the only genes present in the ancestral Eskimo populations and that these haplotypes differ from those observed in the Nadene-speaking Indians of Alaska and Canada.

Materials and Methods

The results of testing 631 Eskimos for GM and KM allotype markers are presented. Included are Siberian Yupik speakers of St. Lawrence Island, Eskimos from the villages of Gambell ($n = 167$) and Savoonga ($n = 80$), and the Inupik-speaking Eskimos from the villages of Wales ($n = 67$) and King Island, whose residents now live in Nome ($n = 55$). The data were collected as part of a demographic, morphologic, and genetic study of Alaskan Eskimo populations (Crawford et al. 1981). Data for the Inupik-speaking Mckenzie Delta Eskimos ($n = 202$) from the area of Inuvik, Northwest Territories, were collected as part of a study of HLA antigens in Eskimos (Dossetor et al. 1972). Central Eskimos ($n = 60$) from the Baffin Island area were sampled by A.R. Armstrong, Hamilton Health Association, Ontario, Canada (samples provided by S. Litwin, from the H. Cleve collection of sera, Cornell Medical Center, New York).

All specimens were tested for the allotypic markers G1M A, F, and X, G3M B, G, and T, and KM 1. All samples, except the Mckenzie Delta specimens, were tested for G3M S; selected specimens from St. Lawrence Island and Alaska were tested for A2M 1 and 2; the Central Eskimos from Baffin Island were tested for the new allotypic determinant G1/3M G5. The details concerning the reagents utilized in this research are presented in Table 1. Of the two notations recommended by the WHO workshop on human immunoglobulin allotypes (WHO, 1976) the alphanumeric nomenclature, as modified to follow the recommendations of the International System of Human Gene Nomenclature (ISGN) (Shows et al. 1987) will be utilized throughout this article. Specimens were tested at a dilution of 1/20 in the wells of V-bottom microplates, as previously described (Schanfield 1971; Schanfield and Fudenberg 1975). Plasma specimens were defibrinated by heating diluted specimens at 56°C for 15 min.

Table 1. **Reagents Used for the Detection of Human Immunoglobulin Allotypes**

| Allotype | Specificity[a] | | Coating | |
	Alphanumeric	Numeric	Agglutinator	Antigens
G1M	A	1	Hel[b]	Spr
	A	1	Pan[c,d]	Dwi[c] or Pet[d]
	F	3	Sta	Dul[b] or Dan[c,d]
	X	2	Gey[b]	Har
	X	2	Max[c] or Alex[d]	Pet
G1/3M	G5	28	Bro[d]	Sul
G2M	N	23	R120[e]	Kop
G3M	B0	11	Sch[b]	Sut
	B0	11	Tol[c] or Kek[d]	Puh
	B1	5	Ble[b]	Sut
	B1	5	Tol[c]	Hun
	B3	13	Log[c] or Ree[d]	Hun
	B3 + B5	10 + 13	Pla[c,e]	Hun
	B4	14	G84[c,e] or Kek[d]	Hun
	B5	10	Ste[c]	Hun
	b5	10	Fie[d,e]	Hun
	C3Br	6	Hen[d]	Ada
	G	21	Gha[b]	Egg[e]
	G	21	Gha[b]	Qua
	G	21	Leh[c]	Sul
	G	21	RHu[c] or R68[d]	Sul
	S	15	Gai[c] or Yar[d]	Puh
	T	16	Low[b]	Vai[e]
	T	16	Ros[b,c]	Vai[b,e] or Puh[c]
	T	16	Cra[d]	Puh
A2M	1	1	Far[c,f]	Sch[e,f]
	2	2	Tay[c,f]	Spe[e,f]
KM	1	1	Les[b]	Dul
	1	1	Cla[c]	511A
	1	1	Sim[c,d]	511A
	1	1	Rut[d]	Pet

a. Nomenclature recommended by WHO (1976). Alphanumeric notation will be used throughout this publication.
b. McKenzie Delta Eskimos tested with these reagents.
c. Alaskan and St. Lawrence Island Eskimos tested with these reagents.
d. Central (Baffin Island Area) Eskimos tested with these reagents.
e. Reagent generously provided by A.G. Steinberg, D. Brzier, E. van Loghem, L. Martensson, and R. Wystar.
f. Only selected specimens tested for these specificities.

Haplotype frequencies for the GM system were computed using the maximum likelihood program MAXIM (Kurczynski and Steinberg 1967); the *KM*1* frequencies were calculated from the square root of the KM 1– frequency. Haplotype frequencies were calculated for all populations with a sample size greater than 25. No correction was made for the familial interrelationships of individuals. Goodness-of-fit chi-square values were calculated for all cells with expected values greater than 1.0; all cells with expected values less than 1.0 were pooled to form a residual chi-square. Degrees of freedom for the chi-square test equals the number of expected chi-square values greater than 1.0 minus the number of alleles estimated, less one.

The population structure was analyzed using the *R*-matrix methods of Harpending and Jenkins (1973) and was computed using the ANTANA program (Harpending and Rogers 1984). The *R* (relationship matrix) was used to construct a genetic map, which provides a visual method of comparing gene frequency patterns with predictions based on the history and demography of the subdivided population. This map is a least-squares representation of the relationship matrix. The variance in the *R* matrix is subsumed under the eigenvectors, which are scaled by the square root of the corresponding eigenvalues in order to equalize the scale of projection.

Results and Discussion

The distribution of immunoglobulin phenotypes and haplotypes are presented in Tables 2 and 3. To be consistent with the recommended notation of ISGN 1987 (Shows et al. 1987), phenotypes are represented by the gene name (GM or KM) followed by a space, with allotypes (specificities) at each locus in alphabetical order, separated by a comma. Loci are separated by a space (e.g., GM A G), whereas alleles or haplotypes are indicated by the gene symbol followed by an asterik and then the allotype in the allele, or its shorthand designation, with the entire term either in italics or underlined (e.g., *GM*A G*). To simplify the presentation of data, all sera positive for one or more G3M B reagents are referred to as G3M B positive. All sera positive for the allotypic markers G1M F and G3M B are presumed to carry the Caucasian haplotype *GM*F B0,1,3,4,5* (hereafter referred to as *GM*F B* and not the Southern Asian haplotype *GM*A,F B0,1,3,4,5* (hereafter referred to as *GM*AF B*) (Schanfield and Gershowitz 1973). This is supported by the presence of the phenotype GM F B in one specimen from Wales and three from Inuvik (Table 2). Comparative data from adjacent Asian, Alaskan, and Canadian Indian populations are presented in Table 4.

Table 2. Distribution of Immunoglobulin Phenotypes in Several Inupik and Yupik Eskimo Populations from Alaska and Canada

	Yupik Speakers			Inupik Speakers					
				Alaska		Canada			
	St. Lawrence Island		Total		King	Mckenzie	North Baffin	Total[a] Baffin	Total
Phenotype	Savoonga	Gambell	Yupik	Wales	Island	Delta	Island	Island	Inupik
GM A G	80	29	109	34	31	105	24	46	216
A B[b],G,S,T	57	37	94	24	18	68	4	11	121
A B[b],S,T	14	3	17	0	6	2	0	1	9
A,F B[c],G	4	7	11	5	0	16	0	0	21
A,F B[c],S,T	5	2	7	0	0	8	0	1	9
A,X G	2	2	4	3	0	0	0	0	3
A,X B[b],G,S,T	4	0	4	0	0	0	0	0	0
F B[c]	0	0	0	1	0	3	0	0	4
A,F B[c]	1	0	1	0	0	0	0	0	0
Total	167	80	247	67	55	202	28	59	383
χ^2	7.68	6.10	2.63	6.00	1.68	17.57	0.17	0.16	8.66
P	n.s.	n.s.	n.s.	n.s.	n.s.	0.01	n.s.	n.s.	0.05
KM 1+	81	35	116	27	38	74	15	27	166
1−	86	45	131	40	17	128	13	33	218
Total	167	80	247	67	55	202	28	60	384

a. Includes North Baffin Island Eskimos and three Labrador Eskimos plus the remainder of Baffin Island Eskimos. One sample was excluded be-
cause the phenotype could not be resolved (Gm[f;b0,1,3,5]).
b. Phenotype is G3M B0,3,5.
c. Phenotype is G3M B0,1,3,4,5.

Table 3.   **Distribution of Immunoglobulin Haplotypes in the Study Populations**

Population	Haplotypes (IgG1, IgG3)					
	GM					
	GM*A G	GM*A T	GM*F B	GM*X G	GM*A−	KM 1
Siberian Yupik speakers						
St. Lawrence Island						
Savoonga	0.643	0.272	0.030	0.018	0.037	0.282
Gambell	0.650	0.281	0.056	0.013	n.d.	0.250
Total	0.651	0.278	0.038	0.016	0.017	0.272
Inupik speakers						
Alaska						
Wales	0.746	0.179	0.052	0.023	n.d.	0.227
King Island	0.727	0.273	n.d.	n.d.	n.d.	0.444
Canada						
Mckenzie Delta	0.728	0.198	0.074	n.d.	n.d.	0.204
North Baffin Island	0.929	0.071	n.d.	n.d.	n.d.	0.319
Total Baffin area	0.873	0.119	0.008	n.d.	n.d.	0.258
Total Inupik speakers	0.753	0.193	0.050	0.004	n.d.	0.246

n.d. indicates that this haplotype was not detected but should have been if present.

The haplotypes *GM*A,Z G* (hereafter referred to as *GM*A G*), *GM*A,Z B0,3,5,S,T* (hereafter referred to as *GM*A T*), and *KM*1* were found to be polymorphic in all the populations tested. The Caucasian marker haplotype *GM*F B* was detected in variable frequencies in all the populations except Wales and north Baffin Island, whereas the haplotype *GM*A,X,Z G* (hereafter referred to as *GM*X G*) (was detected only in Eskimos from St. Lawrence Island and Wales. The origin of the *GM*X G* haplotype in Eskimos is discussed later.

The occurrence of a single serum from Savoonga with the phenotype GM A,F,Z B0,1,3,4,5 suggests the possible presence of a *GM*A,Z−* (hereafter referred to as *GM*A−*) or *GM*A,Z B* haplotype (hereafter referred to as *GM*A B*) in this population. Ferrell et al. (1981) reported the haplotype as *GM*A,Z B*. However, pedigree analysis (Figure 1) indicates that the haplotype would have to be *GM*A Z−* if the purported mother is to remain the biologic progenitor of her children. This suggests that the haplotype has lost either the IgG3 structural gene or the ability to produce IgG3 and may have originated from an unequal crossover with a common *GM*A G* haplotype. Examination of other polymorphic systems does not provide any evidence for maternal exclusion. The maximum likelihood estimate of the haplotype frequency for *GM*A−* was 0.037, whereas the data based on the pedigrees indicate a value of 0.009.

Table 4. **Summary of Eskimo Immunoglobulin Haplotype Frequencies**

Population	n Tested	GM*A G	GM*A G	GM*A T	GM*F B	Others	KM 1	Reference
				Haplotypes (IgG1, IgG3)				
Siberian Yupik speakers								
Siberia								
New Chaplino	100	0.795	n.d.	0.205	n.d.	n.d.	0.206	Sukernik and Ossipova (1982)
Siryeniki	NK	0.815	0.005	0.181	n.d.	n.d.	0.230	Sukernik et al. (1986)
Alaska								
St. Lawrence								
Island Savoonga	148	0.696	0.007	0.287	0.007	n.d.	0.331	Ferrell et al. (1981)
Savoonga	167	0.643	0.018	0.272	0.030	n.d.	0.282	present study
Gambell	73	0.642	0.014	0.331	0.014		0.326	Ferrell et al. (1981)
Gambell	80	0.650	0.013	0.281	0.056		0.250	present study
Inupik speakers								
Alaska								
King Island	55	0.727	n.d.	0.273	n.d.		0.444	present study
Wales	67	0.746	0.023	0.179	0.052		0.227	present study
Mixed	232	0.683	0.011	0.254	0.052		n.t.	Matsumoto et al. (1982)
Canada								
Copper Igloolik	365	0.782	0.005	0.171	0.041		0.269	McAlpine et al. (1974)
Mckenzie Inuvik	202	0.728	n.d.	0.198	0.074		0.204	present study
Baffin Island								
North Baffin	28	0.929	n.d.	0.071	n.d.		0.319	present study
Total Baffin	59	0.873	n.d.	0.119	0.008		0.258	present study
Greenland								
Polor Thule	27	0.944	n.d.	0.056	n.d.		0.212	Persson et al. (1972)
Thule	150	0.879	n.d.	0.121	n.d.		n.t.	Nielsen et al. (1971)
Northwest								
Augpiloktok Island	144	0.656	0.018	0.063	0.264		0.138	Steinberg et al. (1974)
East								
Angmagssalik	65	0.707	0.024	0.183	0.085		0.206	Persson et al. (1972)
Angmagssalik	283	0.804	n.d.	0.191	0.005		n.t.	Nielsen et al. (1971)
Southwest								
Julianehab	55	0.718	0.027	0.209	0.045		0.218	Persson et al. (1972)
Unidentified	215	0.719	0.024	0.108	0.149		n.t.	Nielsen et al. (1971)

n.d. indicates that the haplotype should have been detected if present.   NK indicates that the sample size was not indicated.
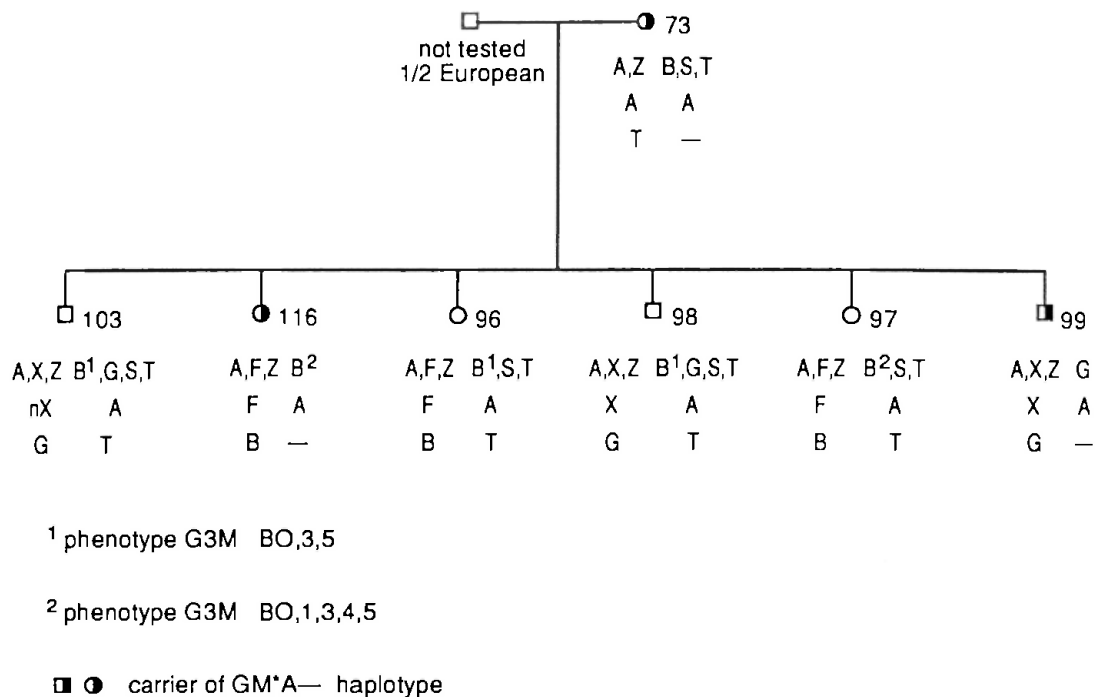
n.t. indicates that the marker was not tested for.

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                                    ☐─────────┬────────● 73
                                  not tested         A,Z  B,S,T
                                  1/2 European         A    A
                                                       T    —


      ☐ 103           ◑ 116          ○ 96           ☐ 98           ○ 97          ◾ 99

    A,X,Z B¹,G,S,T   A,F,Z B²      A,F,Z B¹,S,T   A,X,Z B¹,G,S,T  A,F,Z B²,S,T   A,X,Z G
     nX    A          F   A         F    A         X    A          F    A        X    A
     G     T          B   —         B    T         G    T          B    T        G    —
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[1] phenotype G3M   BO,3,5

[2] phenotype G3M   BO,1,3,4,5

◾ ◑   carrier of GM*A— haplotype

Figure 1. Pedigree demonstrating the probable $GM^*A\,Z-$ haplotype in Savoonga, St. Lawrence Island.

Because the mother (#73) has no full sibs and her mother is adopted, the origin and frequency of the deleted haplotype is unknown but is probably closer to the pedigree frequency than to the maximum likelihood estimate.

Some difficulty was encountered in typing for A2M 1 and A2M 2 because of the presence of antibodies against the IgA coated red blood cells. Results of testing 165 specimens from Savoonga and Gambell indicate that the haplotype $GM^*A\,G$ was found to be A2M 1 positive 9 times as often as A2M 2 positive, whereas the haplotype $GM^*A\,T$ was found to be A2M 2 positive 2.5 times as often as A2M 1 positive. The haplotypes $GM^*F\,B$, $GM^*X\,G$, and GM^*A- were only associated with A2M 1. These results are consistent with the association of A2M 1 with $GM^*A\,G$ and A2M 2 with $GM^*A\,T$, as previously reported by Schanfield and Fudenberg (1975).

This is the first report of testing Eskimos for the new allelic marker G1/3M G5. Although a limited number of specimens were tested in this study, these data together with Schanfield's (1990) unpublished observations, indicate that G1/3M G5 occurs with the $GM^*A\,G$ haplotype, as has been reported previously (Rivat et al. 1978; Blanc et al. 1976). The actual haplotype should be referred to as $GM^*A,Z\,G,G5$.

It has previously been suggested that *GM*XG* does not exist in unadmixed Eskimo populations (Nielsen et al. 1971). From Tables 3 and 4 it is evident that *GM*XG* occurs only in populations with *GM*FB*, thus supporting the concept that admixture may be the source of *GM*XG*. The differences in frequencies observed for *GM*XG* and *GM*FB* can probably be attributed to the genotypes of those individuals adding genes to the population and the reproductive success of their children.

One area of active debate in the literature concerns the origin of the Eskimos. Two hypotheses have been proposed for the origins of the Nadene and Eskimo populations. The first states that a single population arrived 9000–10,000 years B.P. and adapted to two different ecosystems, the coastal and the arboreal. These two populations differentiated when the Alaskan area arborealized and the Nadene speakers expanded southward and genetically differentiated from the cold-climate coastally adapted population (Szathmary and Ossenberg 1978).

The second hypothesis is that 9000–10,000 years B.P. two distinct populations entered the New World by slightly different routes. The ancestors of the Eskimos followed the coast northward, and the Nadene speakers came through central Alaska into the boreal interior (Szathmary and Ossenberg 1978; Harper 1980; Williams et al. 1985). Szathmary and Ossenberg (1978) proposed that the differences between these two hypotheses could not be resolved on the bases of available data. However, Williams et al. (1985) provided support for the hypothesis that there were two founding populations. In an attempt to determine whether additional evidence could be gathered to evaluate these two hypotheses, we combined the data presented in this report with the available information from the literature (Table 5). Thus these two theories are considered on the bases of the immunoglobulin variation in the Arctic.

The data presented in Table 5 indicate that the Nadene (Athabaskan) speakers have the haplotypes *GM*AG*, *GM*XG*, and *GM*AT*, whereas the Eskimos only exhibit *GM*AG* and *GM*AT*. Thus, under the first hypothesis, all three haplotypes would have to be present in the original population, with the Eskimos losing the *GM*XG* haplotype as a result of drift or selection. Alternatively, it is conceivable that neither population had *GM*XG* and that the Nadene speakers acquired it from the more ancient Amerindian populations who were already in the New World.

Unfortunately, the best data to test the latter hypothesis would have to come from non-Athabaskan populations adjacent to Athabaskan populations. The only area with known GM frequencies where this occurs is Alberta and the Yukon Territory, Canada. Non-Athabaskan speakers from this part of Canada have low or nondetectable frequencies

Table 5. **Reference Asian and North American Immunoglobulin Haplotype Frequencies**

Population	Number Tested	GM*A,Z G	GM*A,X,Z G	GM*A,Z T	GM*F B	Others	KM 1	Reference
Siberia								
Chukchi, central	403	0.731	0.109	0.153	0.006		0.153	Sukernik et al. (1982)
Chukchi, coastal	111	0.859	0.022	0.099	0.018		0.200	Schanfield et al. (1990)
Japan								
Ainu	407	0.563	0.093	0.252		0.093	0.218	Matsumoto and Miyazaki (1972)
Nadene/Athabaskan speakers								
Alaska								
Unknown	64	0.623	0.198	0.156	0.024		n.t.	Steinberg (1965)
Mixed	108	0.468	0.333	0.143	0.056		n.t.	Matsumoto et al. (1982)
Canada								
Dogrib	156	0.790	0.066	0.135	0.066		0.596	Szathmary et al. (1983)
Slave/Beaver	115	0.839	0.022	0.121	0.017		0.604	Schanfield et al. (1990)
Chipewyan	92	0.713	0.022	0.158	0.038		0.280	Schanfield et al. (1990)
Haida	84	0.734	0.093	0.036	0.137		0.458	Field et al. (1988)
Bella Coola	110	0.737	0.159	0.023	0.082		0.445	Field et al. (1988)
Algonkian speakers								
Northern Cree	231	0.981	n.d.	0.015	0.065	0.002	0.435	Schanfield et al. (1990)
Plains Cree	485	0.904	0.005	0.029	0.062		0.420	Schanfield et al. (1990)
Ojibwa	100	0.858	0.072	0.070	n.d.		0.286	Szathmary et al. (1974)
Ottawa	105	0.717	0.074	0.005	0.204		0.368	Szathmary et al. (1974)
Siouan speakers								
Assiniboin	88	0.943	n.d.	0.028	0.028		0.343	Schanfield et al. (1990)

n.t. indicates that the marker was not tested for.

n.d. indicates that the haplotype should have been detected if present.

of *GM*XG*, suggesting that the Athabaskan speakers did not acquire *GM*XG* from their neighbors. Furthermore, although the Canadian and southern Athabaskan speakers also have relatively low frequencies of *GM*XG*, it appears to be higher than those found in the adjacent non-Athabaskan populations. The highest North American frequencies of *GM*XG* appear to be in Athabaskan speakers from northern Alaska. Unfortunately, there are no data available on immunoglobulin allotype frequencies from central Alaska. These points suggest that the Athabaskan speakers arrived in the New World with the *GM*XG* haplotype. The pattern of GM haplotypes for the occurrence of *GM*AG*, *GM*XG*, and *GM*AT* is found in all northern Siberian populations (Sukernik and Crawford 1984). This pattern is apparently common in the late-evolving northern Mongoloids.

The pattern observed in Eskimo populations (*GM*AG* and *GM*AT*) from Siberia to Greenland appears to be unique. One could argue that the Eskimos evolved from non-Athabaskan populations in the New World. However, when the distributions of GM haplotypes in the non-Athabaskan-speaking North American Indians are considered, it becomes apparent that as a group they are "GM impoverished" (Schanfield et al. 1990) because they all have relatively low frequencies of *GM*XG* and *GM*AT*. "Creating" Eskimos from non-Athabaskan Indians requires the action of considerable natural selection or genetic drift. A pattern characteristic of South American Indians (i.e., *GM*AG* and *GM*XG* with little or no *GM*AT*) does not occur with regularity except in central Mexico (Schanfield 1976). These data suggest that there were perhaps four groups of immigrants moving into the New World, reflecting changing patterns in the paleo-Mongoloid populations. The oldest pattern, reflected in the South American Indians, had no *GM*AT* and exhibited only *GM*AG* and *GM*XG*. A transitional population had high *GM*AG* and low levels of *GM*XG* and *GM*AT*. A late population of terminally evolved northern Mongoloids (the Nadene speakers) exhibited high frequencies of *GM*AG* and moderate frequencies of *GM*XG* and *GM*AT*. The questions that cannot be readily answered are, (1) Did the Eskimos evolve in Alaska from a peripheral, isolated population and migrate back to Siberia? and (2) Were the Eskimos an isolated Siberian population that developed a maritime hunting and gathering culture, together with its relatively unique GM haplotype profile? It is hypothesized that, because of this cultural adaptation to the maritime ecology, these Eskimos expanded along the coastal areas from Alaska all the way to Greenland. However, the Athabaskan speakers expanded eastward and southward, utimately reaching the southwestern United States.

Although the gene maps based on R-matrix analyses of GM and KM haplotypes in the Arctic and Subarctic populations fail to resolve the alternative hypotheses dealing with the origins of New World populations, these maps provide useful information on the genetic structure of contemporary groups. In Figure 2 the Ojibwa and Chipewyan Amerindian groups show close affinities with most of the Inupik-speaking populations, with the exception of two Greenland samples (both from the western portion) and King Island. Judging from the high incidence of $GM*FB$, it is likely that the west Greenland Eskimos are admixed with the Europeans. However, in the case of King Island there is little racial admixture. The unique position of King Island in the gene map is probably due to the small sample size that was obtained to represent the population and the extreme geographic isolation, which may have contributed to its genetic differentiation.

The first scaled eigenvector (Figure 3) reflects European admixture. This is supported by the presence of $GM*FB$ at relatively high frequencies in the two Greenland Eskimo populations and in the Ottawa and Northern Cree Algonkian speakers. This first eigenvector subsumes 63.4% of the observed variation, whereas the second eigenvector contains 26.4% of the variation. Thus this genetic map includes 89.8% of the observed genetic variation for the GM locus. The Yupik-speaking Eskimo cluster in this map includes the St. Lawrence Island population and their Asian mainland counterparts. The Alaskan Athabaskan populations, on the basis of the incidence of $GM*XG$, appear to resemble genetically the Siberian Nentsi peoples. In contrast to most theories surrounding the origins of the New World Amerindians, this result could be used to argue for a common ancestor of the Nentsi and Athabaskans' peopling of the boreal regions of the North America. However, multivariate assessments based on blood group and protein marker frequencies consistently fail to join the Nentsi and Athabaskans.

The addition of the KM haplotype frequencies to the construction of a genetic map based on immunoglobulins does not significantly modify the observed genetic affinities. The Canadian Indian populations remain clustered, as do the Athabaskan groups. The Inupik groups show much greater variation than do the Yupik populations. This does not appear to be a function of geography and isolation but admixture.

Conclusions

The immunoglobulin patterns and distributions in the New World suggest that there may have been four groups of immigrants crossing the land bridge in the Bering Straits. The earliest group, reflected by the
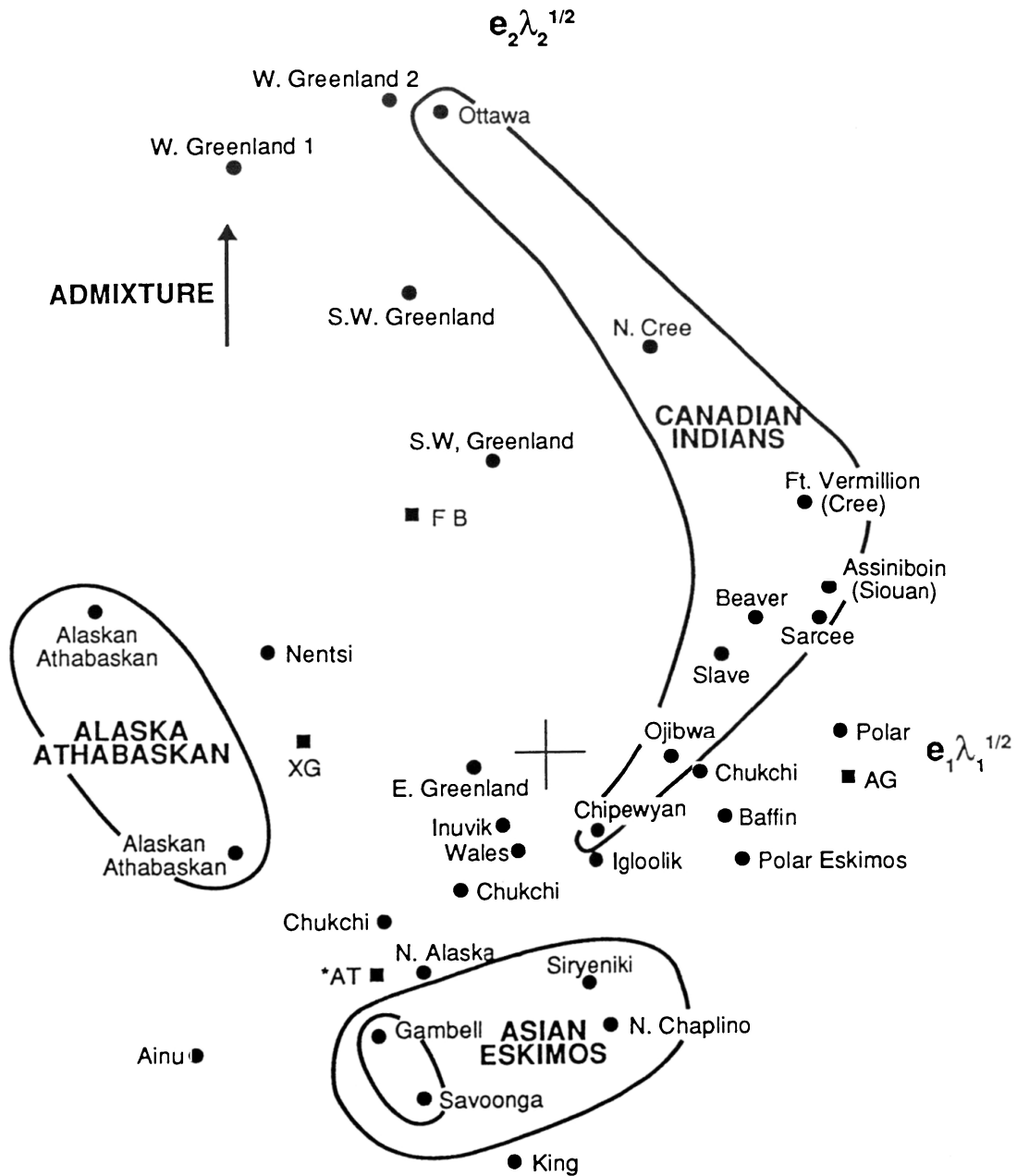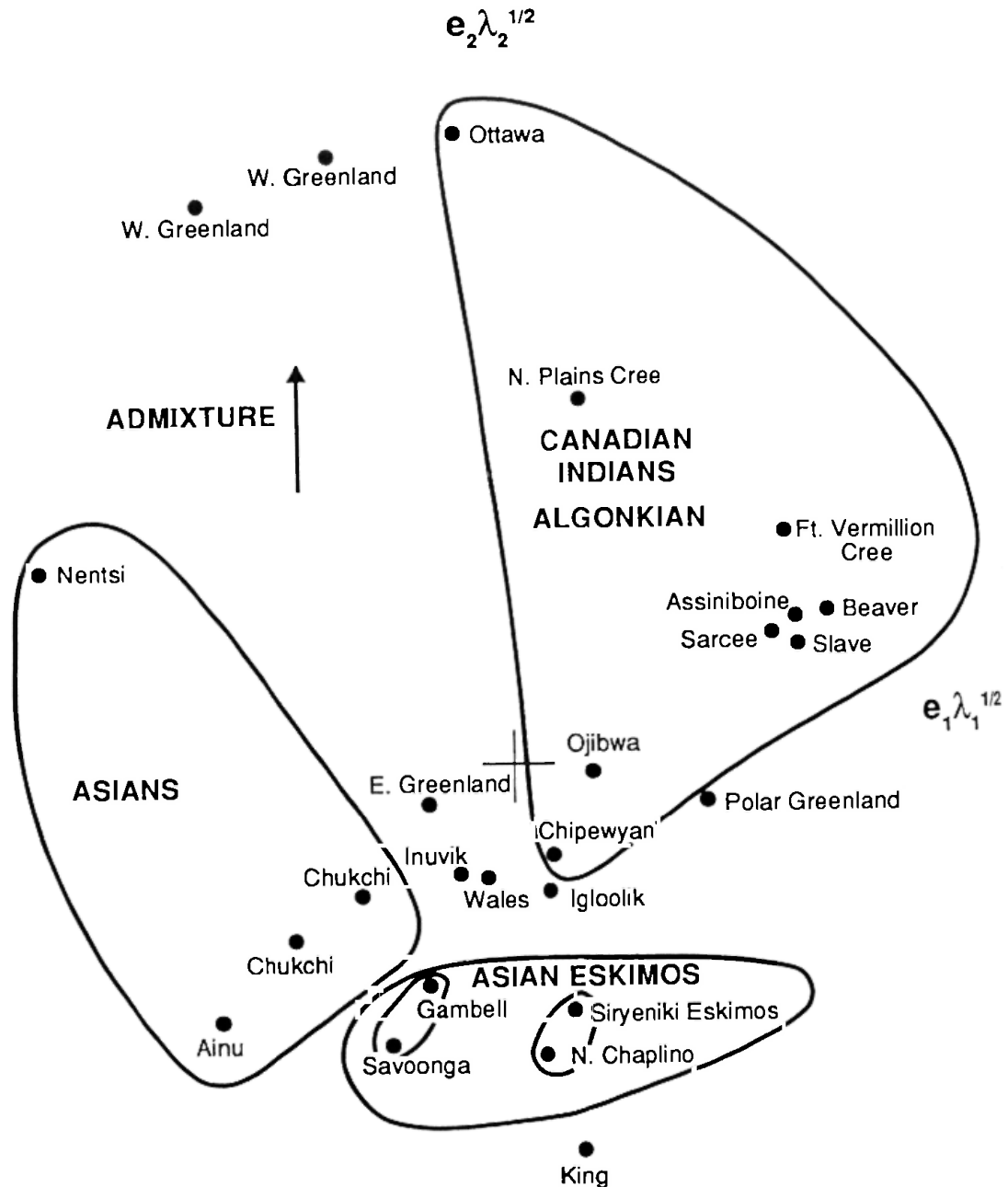
Figure 2. Least-squares reduction genetic map of the Eskimo, Amerindian, and Siberian indigenous populations based on GM allelic frequencies. ■, haplotypes; •, populations. Arrow indicates European admixture gradient.

South American Indians, had no *GM*A T,* only *GM*A G* and *GM*X G.* The second migrant group to enter North America could be characterized by a high frequency of *GM*A G* and low levels of *GM*X G* and *GM*A T.* The Nadene speakers had a high frequency of *GM*A G* and moderate frequencies of *GM*X G* and *GM*A T.* The Eskimo gene pool probably contained *GM*A G* and *GM*A T.* These studies again demonstrate the

$$e_2\lambda_2^{1/2}$$

● Ottawa

● W. Greenland

● W. Greenland

↑
ADMIXTURE

N. Plains Cree
●

CANADIAN
INDIANS

ALGONKIAN

● Ft. Vermillion
Cree

● Nentsi

Assiniboine ● ● Beaver

Sarcee ● ● Slave

$$e_1\lambda_1^{1/2}$$

ASIANS

Ojibwa
●

E. Greenland
●

● Polar Greenland

Chipewyan

Inuvik
Chukchi ● ●
Wales ● ● Igloolik

Chukchi
●

ASIAN ESKIMOS

● Gambell
Siryeniki Eskimos ●

● N. Chaplino

Ainu
●

●
Savoonga

●
King

Figure 3. Genetic map of Holarctic indigenous populations based on both GM and KM allelic frequencies. Clusters demarcated on the basis of geography and culture. In the Canadian Indian cluster, the Beaver, Slave, and Chipewyan groups are Athabaskan speakers.

usefulness of the immunoglobulins in the reconstruction of the affinities and origins of human populations.

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