Immunoglobulin Haplotype Frequencies in Anabaptist Population Samples: Kansas and Nebraska Mennonites and Indiana Amish

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Abstract Anabaptist history is a chronicle of repeated migrations, fissions, and fusions of various subgroups. The effects of these events should be evident in the population biology of the Anabaptist groups. No prior genetic studies have included the polymorphic and highly informative immunoglobulin markers. Here, 685 serum samples representing 1 Amish and 3 Mennonite community samples (7 congregations) were studied for immunoglobulin allotypes. The haplotypes *IGHG*F B, IGHG*A,Z G,* and *IGHG*A,X,Z G* range in frequency from 0.542 to 0.765, 0.123 to 0.290, and 0.075 to 0.170, respectively. *IGK*1* frequencies range from 0.035 to 0.077. All frequencies are within expected ranges for central and western European population samples. There was considerable intergroup variability among the Anabaptist samples that was statistically significant ($\chi^2_9 = 22.63$, $0.005 < p < 0.01$). Principal component analyses, including the immunoglobulin allotype frequencies and published data on ABO, MN, and Rhesus (Dd) markers, demonstrate that the Mennonite congregation samples with close historical ties group together and are distinct from the Amish and Meridian congregation samples.

The Amish and Mennonites are referred to as Anabaptists, a label applied to religious sects that shared certain principles but arose independently of each other during the sixteenth and seventeenth centuries (Hostetler 1980; Smith and Krahn 1981). Amish peoples have received considerable attention from social scientists [e.g., Cong (1992), Hostetler (1980), Hostetler and Huntington (1971), and Kraybill (1989)]. Their distinctive way of life, isolation from the outside world, and lengthy genealogies facilitate research by demographers (Cross and McKusick 1970; Ericksen et al. 1979; Espenshade 1971;

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Hamman et al. 1981; Markle and Pasco 1977; Pollack 1978; Smith 1960), geneticists (Jackson et al. 1968; Juberg et al. 1971; Kostyu et al. 1974; McKusick et al. 1964; McKusick 1978; Morgan et al. 1980; Ward et al. 1972), and others who study such aspects of population structure as group fissioning and inbreeding [e.g., Hurd (1983, 1985a,b)]. Mennonites are examined for the same reasons and are also studied by behavioral scientists [e.g., Boynton (1986) and Redekop (1989)], demographers (Allen and Redekop 1967; Everson et al. 1995; Heaton 1986; Lin and Crawford 1983; Stevenson and Everson 1989, 1990; Stevenson et al. 1989, 1994; Yoder 1985), and geneticists (Allen 1988; Allen and Redekop 1987; Brown et al. 1974; Crawford et al. 1989; Moore 1987; Rogers 1984, 1987; Stevenson et al. 1990).

Interdisciplinary studies that examine ethnohistory relative to the genetic structure of a population are particularly revealing because cultural events can be assessed in terms of their biological impact (Crawford 1973). The best genetic markers for such investigations are easily ascertained, have a simple Mendelian inheritance, and are highly polymorphic (Schanfield 1980). However, only a few studies on Amish and Mennonite populations have provided such detail (Crawford et al. 1989; McKusick et al. 1964; Rogers 1984), and no prior genetic studies included the polymorphic and highly informative immunoglobulin markers. The inherited differences on human immunoglobulins (including the GM and KM markers) are anthropologically useful because many of the haplotypes are able to serve as unique population markers (Schanfield 1980; Schanfield and Fudenberg 1975; Steinberg and Cook 1981). Populations that are in closer proximity are distinguished by less marked differences in haplotype frequencies. The objective here is to present the first immunoglobulin haplotype frequencies for Amish and Mennonite populations and place them in ethnohistorical context.

Populations

The Amish and Mennonite Protestant sects are derived from the Anabaptist movement, which arose during the Reformation in sixteenth-century Switzerland and spread eastward into what is now southern Germany and Austria and northward into the Netherlands and northern Germany (Dyck 1981; Hostetler 1980; Smith and Krahn 1981). Anabaptism initially consisted of many local factions that organized around charismatic personalities, such as Jacob Ammann (Amish) and Menno Simons (Mennonites). All Anabaptists rejected the imposition of a state church, infant baptism, and military conscription, which put them at odds with most European leaders. As a result, their histories are characterized by a series of persecutions and migrations. Figure 1 represents the migrations of the Amish and Mennonites within Europe.

Figure 1. Principal Dutch and northern Germany Mennonite migrations involved in this study. The Alsace and Palatinate areas are sources of the earliest Anabaptist (Mennonites and Amish) migrations to the United States, which began in the late seventeenth and early eighteenth centuries. [Adapted from Bender and Smith (1956, p. 257).]

William Penn, granted a charter by King Charles II of England to form a colony in America, knew of the Anabaptists' suffering and invited them to relocate from the Rhine area to Pennsylvania (Fisher 1908; Peare 1957; Schwieder and Schwieder 1975). The first Anabaptist settlers arrived in 1683, but the Amish immigrated in two waves: 1727–1770 and 1815–1860 (Smith and Krahn 1981). Eventually, the Amish moved west into Holmes County, Ohio, after 1812 and into Lagrange and other counties in Indiana during the 1840s. The Amish of this study represent settlements in the Elkhart and Lagrange counties of Indiana.

Many Dutch, German, and other Anabaptists fled east to Poland-controlled areas around Danzig (Gdansk), and in 1699 eighteen families formed the Przechovka church located 60 miles south of Danzig (Duerksen 1955; Rogers 1984). Prussia took control of the area in 1772 and limited the availability of land and reexamined the exemption from military service (Frie-

sen 1989). Catherine the Great invited Mennonites to settle in southern Russia; migrations began in 1788 and the Chortitza Colony was founded near the Dnieper River. More Mennonites migrated in 1803 and founded the Molotschna Colony in Taurida Province on the Molochnaya River. Almost the entire Przechovka congregation (21 families) joined the Molotschna Colony in 1824 and founded the Alexanderwohl church and settlement (Duerksen 1955; Rogers 1984). Figure 2 reconstructs the fission-fusion processes experienced by the Mennonite populations.

The communities flourished until land shortages and the exemption from military service were again jeopardized (Dyck 1981; Duerksen 1955; Rogers 1984; Smith and Krahn 1981). After sending representatives to America in 1873, most of the village of Alexanderwohl emigrated on two separate ships the following year (Sawatzky 1971; Wedel 1974). One group founded the Alexanderwohl Church near Goessel, Kansas. As the church grew and expanded, two daughter churches were established (Duerksen 1955): Tabor Mennonite Church in 1909, built 5 miles southeast of the parent church; and Goessel Mennonite Church, formed in 1920 in Goessel, Kansas. All three congregations are represented in this study.

Another contingent from the Russian Alexanderwohl congregation arrived in Lincoln, Nebraska, and settled about 40 miles west of Lincoln, founding the Bethesda Mennonite Church at the present town of Henderson, a sample of which is represented here (Crawford and Rogers 1982; Rogers 1984; Voth 1975). A second Nebraska Mennonite congregation, the Henderson Mennonite Brethren Church, traces its origins to 1835, when Mennonites in the Chortitza and Molotschna communities were joined by Prussian emigres who had been influenced spiritually by the Moravian Brethren (Crawford and Rogers 1982; Rogers 1984; Dueck 1989). They formed a separate church in 1860 and migrated to America in 1874. In 1876 they founded the Henderson Mennonite Brethren Church in York and Hamilton counties, Nebraska; they are also sampled in this study.

Finally, disputes over doctrinal issues continue, and new congregations often result. In 1858 John Holdeman of New Pittsburg, Ohio, founded the Church of God in Christ Mennonites (Dyck 1981; Smith and Krahn 1981). He recruited his members from descendants of Swiss and southern German Mennonites who had arrived in the United States during the eighteenth and nineteenth centuries. This sect is represented by the Meridian church, located near Hesston, Kansas.

Methods

This study includes blood samples from one Amish and three Mennonite communities, represented by at least seven congregations. Biological relationships were known for the participants of the study, and all first-order

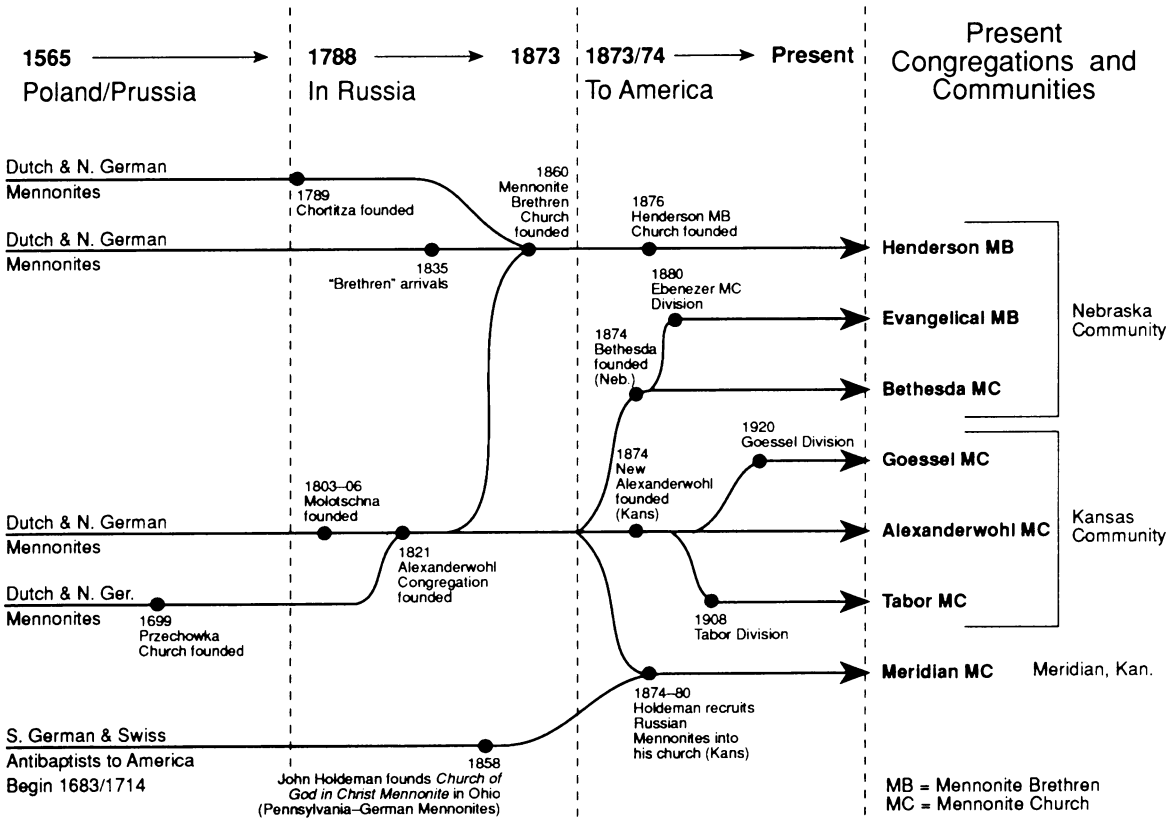

Figure 2. Ethnohistorical dendrogram of the Mennonite congregations included in this study.

Table 1. Reagents Used for Immunoglobulin Allotyping: Specificity

	Amish		*Mennonite*	
Specificity	*Agglutinator*	*Coat*	*Agglutinator*	*Coat*
G1M A	PAN	PET	PAN	PET
F	STA	DAN	STA	DAN
X	ALX	PET	ALX	PET
G3M B0	R-60	PUH	TOL	PUH
B1	KEK	ADA	TOL	HUN
B3	LOG	HUN	LOG	HUN
B4	KEK	HUN	GOEL	HUN
B5	FIE	PUH	FIE	PUH
C3	HEN	422	HEN	ADA
C3 + C5	HAW	422	HAW	ADA
G	R-68	SUL	R-68	SUL
G5	BRO	SUL	BRO	SUL
S	YAR	PUH	YAR	PUH
T	CRA	PUH	CRA	PUH
KM 1	SIN or RUT	PET	SIN	PET

relatives were removed. The 599 blood specimens for the Kansas and Nebraska Mennonites were collected as part of a three-year multidisciplinary study on aging, which is described by Crawford and Rogers (1982). This sample represents almost one-third of the Mennonite citizens of Henderson, Nebraska, almost one-third of the Alexanderwohl congregation, the largest congregation of the town of Goessel, and about one-quarter of the Meridian congregation. The 86 Amish blood samples were collected as part of a two-year study on the association of HLA haplotypes and viral antibody response in a sample of Amish living in Elkhart and Lagrange counties in Indiana (Hsia et al. 1977).

The 685 serum samples were typed for immunoglobulin allotypes at the Immunohematology Laboratory of the American Red Cross Blood Services National Headquarters in Washington, DC, in 1981 and 1982. Minimally, all samples were tested for G1M (allotypes *A*, *F*, and *X*), G3M (allotypes *B0*, *B1*, *B3*, *B4*, *B5*, *C*, *G*, *S*, and *T*), and KM1 using previously described methods (Schanfield Polesky et al. 1975). The reagents used are presented in Table 1. In addition, some G1M (allotype *A*) and G3M (allotype *B*) positive sera were tested for G1M (allotype *Z*) (see Table 2).

Haplotype frequencies for the GM system were estimated using the allocation method of Andersson (1985). The *IGK*1* frequencies were determined from the square root of the KM (*1* −) frequency.

A heterogeneity chi-square was used to measure population differences and divergence.

Table 2. Distribution of Immunoglobulin Phenotypes in Anabaptist Congregations and Communities

		Phenotype									
Population	*N*	*G3M: G1M:*	G^a *A*	G^a *A,X*	G^a,B^b *F,A*	G^a,B^b *F,A,X*	B^b *F*	B^b *F,Z,A*	G^a,B^b *A*	B^c,G,S *Z,A*	*Chi-Square*	*Degrees of Freedom*[d]
Amish (Indiana)	86		3	8	21	19	34	0	1	0	0.06	2
Kansas Mennonites												
Alexanderwohl	166		7	2	28	34	92	3	0	0	12.68	3[f]
Goessel	49		1	0	10	9	27	2	0	0	2.52	2
Tabor	83		1	1	20	14	45	1	1	0	3.14	3
Kansas Community[g]	266		8	2	51	53	145	6	1	0	12.89	4[e]
Meridian	60		6	6	16	11	19	0	1	1	3.54	3
Nebraska Mennonites												
Bethesda	189		7	8	54	21	98	0	1	0	2.97	2
Henderson	41		2	1	16	5	17	0	0	0	0.15	2
Nebraska Community[g]	234		9	8	73	28	116	0	1	0	0.76	2

a. GM Z was not tested for but is always associated with GM G.

b. Represents the phenotype GM B0,1,3,4,5.

c. Represents the phenotype GM B0,3,5.

d. Pooled cells if expected frequencies less than 1 and reduced degrees of freedom accordingly.

e. $0.01 < p < 0.025$.

f. $0.001 < p < 0.005$.

g. Numbers reduced if first-order relatives are included in community pool. In addition, the Nebraska Community includes a few Evangelical Mennonite Brethren individuals. Kansas Community represents the Alexanderwohl, Goessel, and Tabor communities. Nebraska Community represents the Bethesda and Henderson communities.

Principal components analyses facilitated the comparison of ethnohistory with genetic structure, and although GM is a highly informative system, the GM data were supplemented by already published data on additional genetic markers. The Mennonite samples of this study have been typed for additional genetic markers (Crawford et al. 1989), but ABO, MN, and Rhesus (Dd) data from another sample of Indiana Amish were used in the principal components analyses. Both principal components analyses took into account population sample sizes.

Principal components analyses were performed using ANTANA (Harpending and Rogers 1984). The program produced orthogonal synthetic gene frequencies that account for the greatest amount of population variation. Two analyses were run, including gene frequencies and sample sizes for 7 and 15 populations, respectively. The 7-population analysis included the following systems: ABO, MN, and Rhesus (Dd) from Crawford et al. (1989) except for the Amish (Juberg et al. 1971) and GM and KM data from this study for all the Amish and Mennonite congregations. The 15-population analysis included GM and KM data for the four Amish and Mennonite communities and ABO, MN, and Rhesus (Dd) from Crawford et al. (1989) for the Mennonites and from Juberg et al. (1971) for the Amish. See Mourant et al. (1976) for the ABO, MN, and Rhesus (Dd) frequency data for the additional 11 European populations excluding the Netherlands (Fraser et al. 1974) and Table 3 for the immunoglobulin haplotype frequencies and references for all the European populations.

Results

Immunoglobulin allotype and phenotype (GM-KM) distributions and haplotype frequencies for the studied Amish and Mennonite populations are presented in Tables 2 and 4. KM 1 distributions and frequencies are given in Table 5. Table 3 presents previously published haplotype frequencies of central European populations for comparison.

The number of phenotypes and the number of haplotypes ranged from five to seven and three to five, respectively. Statistically significant deviations from Hardy-Weinberg expectations were found in the Alexanderwohl sample, which led to significant deviations in the Kansas Community (see Table 4). In the Alexanderwohl and Kansas Community samples (not representing the Meridian congregation) the GM A G and GM A,X,F B,G phenotypes occurred more than expected and the GM A,X G phenotype occurred less than expected.

The frequency of haplotype *IGHG*F B* ranges from 0.542 in the Meridian sample to 0.765 in the Goessel sample (see Table 4). The low frequency is lower than what is typical for northwestern Europe (see Switzerland in Table 3), whereas the highest frequency of 0.765 is not unusual relative to

Table 3. Comparative Population Haplotype Frequencies

		Haplotype					
Population	*N*	*IGHG3*:* *IGHG1*:*	*G* *A*	*G* *A,X*	*B* *F*	*IGK*I*	*Source*
Austria (Vienna)	1602		0.185	0.074	0.741	0.083	Mayr and Mickerts (1970)
Croatia	452		0.134	0.035	0.831	0.053	Schanfield, Herzog et al. (1975)
Czech Republic (central Bohemia)	684		0.135	0.079	0.776	0.060	Fraser et al. (1969)
Germany (Freiburg)	772		0.137	0.061	0.728	0.061	Ritter et al. (1964)
Germany (Munich)	131		0.169	0.091	0.740	0.059	Ropartz et al. (1963)
Germany (Rheinland-Pfalz)	386		0.204	0.099	0.697	0.055	Ropartz et al. (1964)
Hungary (Budapest)	182		0.145	0.051	0.777	0.073	Schanfield, Gergely et al. (1975)
Netherlands	792		0.189	0.102	0.709	0.094	Fraser et al. (1974)
Poland (Krakow)	600		0.138	0.056	0.806	0.055	Socha and Kaczera (1968)
Poland (Lower Silesia)	300		0.168	0.065	0.767	0.070	Schlesinger and Luczkiewicz-Mulczykowa (1971)
Switzerland	98		0.253	0.119	0.628	0.080	Steinberg and Cook (1981, p. 43)

typical frequencies of this haplotype in eastern and southern Europe (Steinberg and Cook 1981; Stevenson and Schanfield 1981). Croatia and Poland exhibit slightly higher frequencies (Table 3).

The *IGHG*A,Z G* haplotype frequency ranges from 0.123 in the Goessel sample to 0.290 in the Meridian sample, and the *IGHG*A,X,Z G* haplotype frequency ranges from 0.075 in the Henderson sample to 0.170 in the Amish sample. The highest frequencies of these haplotypes are typically found in northern and western Europe (Steinberg and Cook 1981), and the ranges here (except for the Amish and Meridian samples) are a bit lower and more consistent with what is typical of eastern and southern European populations.

Seventeen individuals exhibit the phenotypes listed in the last three columns of Table 2. These phenotypes cannot be explained solely by the most common European haplotypes [e.g., *IGHG*A,Z G, IGHG*A,X,Z G,* and *IGHG*F B0,1,3,5* (hereafter referred to as *IGHG*F B*)] (Steinberg and Cook 1981). Pedigree analysis is necessary to establish with certainty the haplotypes involved. However, some of the phenotypes are probably the result of

Table 4. Distribution of Haplotype Frequencies in Several Anabaptist Congregations and Communities

		Haplotype Frequency (Standard Error)				
		IGHG3:*	*G*[a]	*G*[a]	*B*[b]	*B*[c]	*B,S*[d]
Population	*N*	*IGHG1*:*	*A*	*A,X*	*F*	*Z,A*	*Z,A*
Amish (Indiana)	86		0.196	0.170	0.628	0.006	0.000
			(0.030)	(0.029)	(0.037)	(0.006)	
Kansas Mennonites							
Alexanderwohl	166		0.131	0.110	0.750	0.009	0.000
			(0.019)	(0.017)	(0.024)	(0.005)	
Goessel	49		0.123	0.092	0.765	0.020	0.000
			(0.033)	(0.029)	(0.043)	(0.014)	
Tabor	83		0.143	0.092	0.753	0.012	0.000
			(0.027)	(0.022)	(0.033)	(0.008)	
Kansas	266		0.131	0.104	0.752	0.013	0.000
Community			(0.015)	(0.013)	(0.019)	(0.005)	
Meridian	60		0.290	0.151	0.542	0.0085	0.0085
			(0.041)	(0.033)	(0.045)	(0.0084)	(0.0084)
Nebraska Mennonites							
Bethesda	189		0.200	0.080	0.717	0.003	0.000
			(0.021)	(0.014)	(0.023)	(0.003)	
Henderson	41		0.254	0.075	0.671	0.000	0.000
			(0.048)	(0.029)	(0.052)		
Nebraska	234		0.210	0.079	0.708	0.003	0.000
Community[e]			(0.019)	(0.012)	(0.021)	(0.003)	

a. GM Z not tested for but always associated with GM G.
b. Represents the haplotype *IGHG*F B0,1,3,4,5.*
c. Represents the haplotype *IGHG*A,Z B0,1,3,4,5.*
d. Represents the haplotype *IGHG*A,Z B0,3,5,S.*
e. Includes a few unrelated representatives of an Evangelical Mennonite Brethren congregation.

Table 5. Distribution and Frequencies of KM 1 and *IGK*1*

Population	*N*	KM 1	*IGK*1*
Amish, N. Indiana	88	2	0.011
Kansas Mennonites			
Meridian congregation	56	3	0.027
Alexanderwohl	101	14	0.072
Goessel	47	7	0.054
Tabor	19	2	0.077
Kansas Community[a]	148	17	0.059
Nebraska Mennonites			
Bethesda	189	16	0.043
Henderson	41	3	0.037
Nebraska Community[a]	234	22	0.048

a. Numbers reduced from simple sum if first-order relatives are included in community pool. In addition, the Nebraska Community includes a few Evangelical Mennonite Brethren individuals.

a combination of one of the three common European haplotypes with haplotypes typically found in other populations, such as the central Asian or African haplotype *IGHG*A,Z B0,1,3,4,5* (hereafter referred to as *IGHG*A,Z B*) and the African haplotype *IGHG*A,Z B0,3,5,S* (hereafter referred to as *IGHG*A,Z B,S*).

The six individuals with phenotypes GM A G,B and the ten individuals with GM A,Z,F B result most likely from the presence of the typically European haplotypes *IGHG*A,Z G* and *IGHG*F B,* respectively, combined with the central Asian or African haplotype *IGHG*A,Z B.* The samples were not tested for the A2M markers, so the central Asian haplotype, associated with A2M 1, cannot be distinguished from the African haplotype, associated with A2M 2 (Stevenson et al. 1985). The *IGHG*A,Z B* haplotype is found in contemporary central Europeans (Stevenson and Schanfield 1981).

The one GM A,Z B,G,S phenotype found in the Meridian congregation is probably due to the European haplotype *IGHG*A,Z G* combined with the predominantly African haplotype *IGHG*A,Z B,S.*

*IGK*1* frequencies are variable in Europe with no apparent cline and range in central European populations from 0.035 in Croatians to 0.253 in the Swiss (Steinberg and Cook 1981; Stevenson and Schanfield 1981). Some of the Kansas Mennonites could not be tested for *IGK*1* because of insufficient blood samples. The gene frequencies range from 0.011 in the Amish sample to 0.077 in the Tabor sample. Overall, frequencies are relatively low compared with frequencies observed in Europe. There is no apparent pattern in the distribution of this allele in Europe.

Contingency chi-square tests were performed on the Kansas ($\chi^2_{(6)} = 2.59$, not significant) and Nebraska ($\chi^2_{(4)} = 0.44$, not significant) Community samples. The absence of statistically significant differences within both communities precluded the need to subdivide either for the contingency chi-square analysis of the Anabaptist population samples. Considerable intergroup variability that was statistically significant was demonstrated (e.g., Amish, Kansas, Meridian, Nebraska samples) ($\chi^2_{(9)} = 22.63$, $0.005 < p < 0.01$).

The principal components analyses are presented graphically in Figures 3 and 4 for seven and fifteen populations, respectively. Five genetic systems are used in these analyses, and populations, taking into account sample size, are plotted by their eigenvectors, each weighted by the multiplication of the square root of the corresponding eigenvalue (Harpending and Jenkins 1973, p. 187). The first three factors account for 51% of the variance.

In Figure 3 the seven population samples are plotted against the first two factors, which account for 45.6% of the variance. The Mennonite congregation samples are relatively close to each other, with the Meridian and Amish samples showing the least affinity with the other Mennonite samples. Alexanderwohl and its offshoot congregations Tabor and Goessel lie closest to each other. Factor 1 separates the Amish from the other samples and is weighted most heavily on *ABO*A* and *IGHG*F B.* Factor 2 separates the

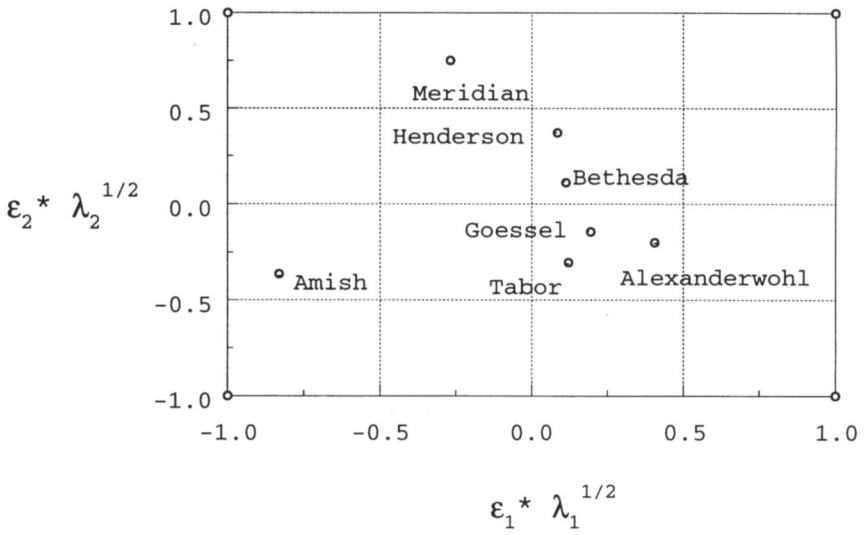

Figure 3. Least-squares reduction genetic map of the seven Anabaptist congregation samples. Frequencies from eight alleles and five genetic loci were used to construct the *R* matrix.

Meridian sample and to a lesser extent the Henderson sample from the Amish and other Mennonite samples and is weighted most heavily on *IGHG*A,Z G* and *ABO*A*. Factor 3 accounts for only another 5.1% of the variance and thus was not included in the genetic map.

Figure 4 represents the results of the principal components analysis of the Amish and Meridian congregations, the Kansas Mennonite Community (Alexanderwohl, Goessel, and Tabor adjusted for removal of first-order relatives) and the Nebraska Mennonite Community (Bethesda, Henderson, and a few unrelated members from an Evangelical Mennonite Brethren congregation), and 11 central European population samples with the same five genetic systems. The first three factors account for 88.5% of the variance. Factor 1 separates the Meridian and Amish samples from all other European samples and from the two Community samples and is weighted on *IGHG*F B* and *IGHG*A,X,Z G*. Factor 2 also separates the Amish and Meridian samples from the other European and Anabaptist population samples and from each other and is weighted on *ABO*A*. Factor 3 is weighted mostly on *ABO*B* and to a lesser extent on Rh *D* and KM and explains only an additional 9% of the variance; therefore it was not included in the genetic map. The Nebraska and Kansas communities are centrally clustered with other European populations.

Discussion

The low numbers of GM phenotypes (5–7) and haplotypes (3–5) for these samples reflect their history of relative isolation. Five to 7 phenotypes

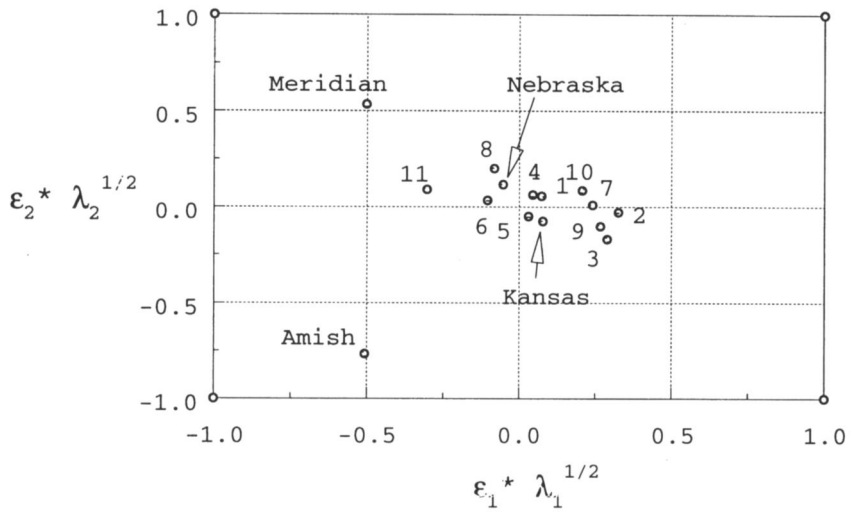

Figure 4. Least-squares reduction genetic map of 4 Anabaptist population samples compared with 11 European population samples. Frequencies from eight alleles and five genetic loci were used to construct the *R* matrix. (1) Austria (Vienna), (2) Croatia, (3) Czech Republic (central Bohemia), (4) Germany (Freiburg), (5) Germany (Munich), (6) Germany (Rheinland-Pfalz), (7) Hungary (Budapest), (8) Netherlands, (9) Poland (Krakow), (10) Poland (Lower Silesia), (11) Switzerland. For references refer to Table 3.

is few relative to the 20 or more found in a tri-ethnic hybrid population such as the Black Caribs of Central America (Crawford 1983; Schanfield et al. 1984). At least that many phenotypes are usually demonstrated in European population samples [e.g., Stevenson and Schanfield (1981)]. However, Anabaptist history is a chronicle of repeated migrations and fissions and in some cases fusions of various subgroups.

The Amish became reproductively isolated from most Mennonites early in Anabaptist history. This is forcefully demonstrated by the principal components analyses, in which the Amish are clearly isolated relative to other populations in the three-dimensional plots. They are distinguished by the first and second factors in Figures 3 and 4, respectively. The extremes in gene frequencies [including relatively high frequencies of *ABO*A, MNS*N,* and RH *d* and comparatively low frequencies of *ABO*O, ABO*B, MNS*N,* and RH *D* noted by Juberg et al. (1971)] do not obscure their origins, however. Most of the ancestors of the Amish are derived from Switzerland and southern Germany. The haplotype frequency for *IGHG*F B* is second lowest for the Anabaptist populations of this study and the haplotype *IGHG*A,Z G* frequency is relatively high, but these levels are similar to frequencies in contemporary Swiss and close to frequencies found in contemporary residents of southern Germany and the Netherlands. By contrast, the Amish *IGHG*A,X,Z*

G frequencies are high even relative to contemporary residents of Switzerland, which may partly be due to the small and probably unrepresentative founding population.

Study of the genetic structure of the Kansas and Nebraska Mennonite communities and congregations also suggests parallels with history. The founding group for the Nebraska community included representatives from both the Russian Molotschna and Chortitza colonies, but in general the ethnic origins of both groups are essentially the same. As expected, the GM haplotype frequencies for the Kansas and Nebraska communities are similar to the frequencies for central Europe and are only slightly different from each other.

The Meridian congregation is a melange of Russian and Pennsylvania German Mennonites, although one would expect its genetic structure to be intermediate relative to the Amish and other Kansas Mennonites. This is not reflected in the haplotype frequencies for the GM system. The Meridian congregation displays the the lowest *IGHG*F B,* the highest *IGHG*A,Z G,* and the second highest *IGHG*A,X,Z G* frequencies. This pattern may be due to sample bias but is also suggestive of a unique history.

Overall, these results are consistent with the analyses of Crawford et al. (1989) using red cell antigens and blood proteins. The main difference noted is the increased distinctiveness of the Meridian congregation's genetic structure when GM is included in the analysis.

Conclusions

The presentation of immunoglobulin phenotype and haplotype distributions for the Anabaptist population samples do not reveal any surprises. The patterns in the phenotypic and genotypic frequencies are consistent with expectations based on the central and western European origins of the populations involved. Their relative isolation from outsiders is reflected in the low number of haplotypes and phenotypes.

Contingency chi-square analyses also reveal little heterogeneity within the Kansas and Nebraska Mennonite communities. By contrast, significant heterogeneity is evident when the two communities are part of a contingency chi-square analysis that also includes the Amish and Meridian samples.

Except for the Meridian congregation (which has a unique origin and composition), the Kansas and Nebraska Mennonites group together and are close to other central European populations in graphic representations of the results summarizing the principal components analyses (Figures 3 and 4). The Meridian and Amish samples are outliers in both figures.

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Literature Cited

Allen, G. 1988. Random genetic drift inferred from surnames in Old Colony Mennonites. *Hum. Genet.* 60:639–653.

Allen, G., and C.W. Redekop. 1967. Individual differences in survival and reproduction among Old Colony Mennonites in Mexico: Progress to October 1966. *Eugen. Q.* 14:103–111.

Allen, G., and C.W. Redekop. 1987. Old Colony Mennonites in Mexico: Migration and inbreeding. *Soc. Biol.* 34:166–179.

Andersson, L. 1985. The estimation of blood group gene frequencies: A note on the allocation method. *Animal Blood Groups Chem. Genet.* 16:1–7.

Bender, H.S., and C.H. Smith, eds. 1956. *The Mennonite Encyclopedia, Volume 2.* Scottdale, PA: Mennonite Publishing House.

Boynton, L.L. 1986. *The Plain People: An Ethnography of the Holdeman Mennonites.* Salem, WI: Sheffield Publishing Company.

Brown, S.M., D.C. Gajdusek, W.C. Seyshon et al. 1974. Genetic studies in Paraguay: Blood group, red cell, and serum genetic patterns of the Guayaki and Ayore Indians, Mennonite settlers, and seven other Indian tribes of the Paraguayan Chaco. *Am. J. Phys. Anthropol.* 41:317–344.

Cong, D. 1992. Amish factionalism and technological change: A case study of kerosene refrigerators and conservatism. *Ethnology* 3:205–218.

Crawford, M.H. 1973. The use of genetic markers of the blood in the study of the evolution of human populations. In *Methods and Theories of Anthropological Genetics,* M.H. Crawford and P.L. Workman, eds. Albuquerque, NM: University of New Mexico Press, 19–38.

Crawford, M.H. 1983. The anthropological genetics of the Black Caribs (Garifuna) of Central America and the Caribbean. *Yrbk. Phys. Anthropol.* 26:161–192.

Crawford, M.H., and L. Rogers. 1982. Population genetic models in the study of aging and longevity in a Mennonite community. *Soc. Sci. Med.* 16:149–153.

Crawford, M.H., D.D. Dykes, and H.F. Polesky. 1989. Genetic structure of Mennonite populations of Kansas and Nebraska. *Hum. Biol.* 61:493–514.

Cross, H.E., and V.A. McKusick. 1970. Amish demography. *Soc. Biol.* 17:83–101.

Dueck, A.J. 1989. Mennonite churches and religious developments in Russia, 1850–1914. In *Mennonites in Russia, 1788–1988: Essays in Honour of Gerhard Lohrenz,* J. Friesen, ed. Winnipeg, Manitoba: CMBC Publications, 149–181.

Duerksen, J.A. 1955. Przechowka and Alexanderwohl: Beginnings of Alexanderwohl, Tabor, Hoffnungsau, and other churches. *Mennonite Life* 8:76–82.

Dyck, C.J. ed. 1981. *An Introduction to Mennonite History.* Scottdale, PA: Herald Press.

Ericksen, J.A., E.P. Ericksen, J.A. Hostetler et al. 1979. Fertility patterns and trends among the Old Order Amish. *Popul. Stud.* 33:255–276.

Espenshade, T.J. 1971. A new method for estimating the level of natural fertility in populations practicing birth control. *Demography* 8:525–536.

Everson, P.M., J.C. Stevenson, and L. Rogers. 1995. Mortality in a migrating Mennonite church congregation. *Hum. Biol.* 67:69–86.

Fisher, S.G. 1908. *The Making of Pennsylvania.* Philadelphia, PA: J.B. Lippincott.

Fraser, G.R., P. Grunwald, F.D. Kitchin et al. 1969. Serum polymorphisms in Yugoslavia. *Hum. Hered.* 19:57–64.

Fraser, G.R., W.S. Volkers, L.F. Bernini et al. 1974. Gene frequencies in a Dutch population. *Hum. Hered.* 24:435–448.

Friesen, J. 1989. Mennonite churches and religious development in Russia, 1789–1850. In *Mennonites in Russia, 1788–1988: Essays in Honour of Gerhard Lohrenz,* J. Friesen, ed. Winnipeg, Manitoba: CMBC Publications, 43–74.

Hamman, R.F., J.I. Barancik, and A.M. Lilienfeld. 1981. Patterns of mortality in the Old Order Amish. 1. Background and major causes of death. *Am. J. Epidemiol.* 114:845–861.

Harpending, H., and T. Jenkins. 1973. Genetic distance among southern African populations. In *Methods and Theories of Anthropological Genetics,* M.H. Crawford and P.H. Workman, eds. Albuquerque, NM: University of New Mexico Press, 177–199.

Harpending, H., and A. Rogers. 1984. *ANTANA: A Package for Multivariate Data Analysis.* Bosque Farms, NM: Harpending and Rogers Press.

Heaton, T.B. 1986. Sociodemographic characteristics of religious groups in Canada. *Soc. Anal.* 47:54–65.

Hostetler, J.A. 1980. *Amish Society,* 3d ed. Baltimore, MD: Johns Hopkins University Press.

Hostetler, J.A., and G.E. Huntington. 1971. *Children in Amish Society: Socialization and Community Education.* Fort Worth, TX: Holt, Rinehart & Winston.

Hsia, S., D.N. Howell, D.B. Amos et al. 1977. Studies of viral antibody responses among Amish families. *J. Immunol.* 118:1659–1664.

Hurd, J.P. 1983. Kin relatedness and church fissioning among the "Nebraska" Amish of Pennsylvania. *Soc. Biol.* 30:59–66.

Hurd, J.P. 1985a. Kissing cousins: Frequencies of cousin types in "Nebraska" Amish marriages. *Soc. Biol.* 32:82–89.

Hurd, J.P. 1985b. Sex differences in mate choice among the "Nebraska" Amish of central Pennsylvania. *Ethol. Sociobiol.* 6:49–57.

Jackson, C.E., W.E. Symon, E.L. Pruden et al. 1968. Consanguinity and blood group distribution in an Amish isolate. *Am. J. Hum. Genet.* 20:522–527.

Juberg, R.C., W.J. Schull, H. Gershowitz et al. 1971. Blood group gene frequencies in an Amish deme of northern Indiana: Comparison with other Amish demes. *Hum. Biol.* 43:477–485.

Kostyu, D., D.B. Amos, S. Harris et al. 1974. HL-A antigens of the Indiana Amish. *Tissue Antigens* 4:415–418.

Kraybill, D.B. 1989. *The Riddle of Amish Culture.* Baltimore, MD: Johns Hopkins University Press.

Lin, P.M., and M.H. Crawford. 1983. A comparison of mortality patterns in human populations residing under diverse ecological conditions: A time series analysis. *Hum. Biol.* 55:35–62.

Markle, G.E., and S. Pasco. 1977. Family limitation among the Old Order Amish. *Popul. Stud.* 31:267–280.

Mayr, W.R., and D. Mickerts. 1970. Der menschliche gammaglobulin polymorphismus. *Acta Biol. Med. Ger.* 25:473–482.

McKusick, V.A., ed. 1978. *Medical Genetic Studies of the Amish.* Baltimore, MD: Johns Hopkins University Press.

McKusick, V.A., J.A. Hostetler, J.A. Egeland et al. 1964. The distribution of certain genes in the Old Order Amish. *Cold Spring Harbor Symp. Quant. Biol.* 99:99–114.

Moore, M.J. 1987. Inbreeding and reproductive parameters among Mennonites in Kansas. *Soc. Biol.* 34:180–186.

Morgan, K., T.M. Holmes, J. Schlaut et al. 1980. Genetic variability of HLA in the Dariusleut Hutterites: A comparative genetic analysis of the Hutterites, Amish, and other selected Caucasian populations. *Am. J. Hum. Genet.* 32:246–257.

Mourant, A.E., A.C. Kopec, and K. Domaniewska-Sobczak. 1976. *The Distribution of Human Blood Groups and Other Polymorphisms.* London, England: Oxford University Press.

Peare, C.O. 1957. *William Penn: A Biography.* Philadelphia, PA: J.B. Lippincott.

Pollack, R. 1978. Genetic demography of an Amish-Mennonite population. *Am. J. Phys. Anthropol.* 48:427.

Redekop, C. 1989. *Mennonite Society.* Baltimore, MD: Johns Hopkins University Press.

Ritter, H., C. Ropartz, P.Y. Rousseau et al. 1964. Studies on the formal genetics of the gammaglobulin polymorphism Gm [characters Gm(a), Gm(b), Gm(x)]. *Vox Sang.* 9:340–348.

Rogers, L. 1984. Phylogenetic identification of a religious isolate and the measurement of inbreeding. Ph.D. thesis, University of Kansas, Lawrence.

Rogers, L. 1987. Concordance in isonymy and pedigree measures of inbreeding: The effects of sample composition. *Hum. Biol.* 59:753–767.

Ropartz, C., L. Rivat, P.Y. Rousseau et al. 1963. Les systemes Gm et Inv Europe. *Acta Genet.* 13:109–123.

Ropartz, C., H. Walter, A. Arndt-Hanser et al. 1964. On the frequency of the Gm- and Inv-serum groups in southwestern Germany. *Acta Genet. Stat. Med.* 14:298–308.

Sawatzky, H.L. 1971. *They Sought a Country.* Berkeley, CA: University of California Press.

Schanfield, M.S. 1980. The anthropological usefulness of highly polymorphic systems. In *Current Developments in Anthropological Genetics,* v. 1, *Theory and Methods,* J.H. Mielke and M.H. Crawford, eds. New York: Plenum Press, 65–85.

Schanfield, M.S., and H.H. Fudenberg. 1975. The anthropological usefulness of the IgA allotypic markers. In *Biosocial Interrelations in Population Adaptation,* E.S. Watts, F.E. Johnston, and G.W. Lasker, eds. The Hague, Netherlands: Mouton, 105–114.

Schanfield, M.S., R. Brown, and M.H. Crawford. 1984. Immunoglobulin allotypes in the Black Caribs and Creoles of Belize and St. Vincent. In *Black Caribs: A Case Study in Biocultural Adaptation,* M.H. Crawford, ed. New York: Plenum Press, 365–380.

Schanfield, M.S., J. Gergely, and H.H. Fudenberg. 1975. Immunoglobulin allotypes in European populations. I. Gm and Km (Inv) allotypic markers in Hungarians. *Hum. Hered.* 25:370–377.

Schanfield, M.S., P. Herzog, and H.H. Fudenberg. 1975. Immunoglobulin allotypes of European populations. II. Gm, Am, and Km (Inv) allotypic markers in Czechoslovakia. *Hum. Hered.* 25:382–392.

Schanfield, M.S., H.F. Polesky, and E.B. Sebring. 1975. Gm and Inv testing. In *Paternity Testing,* H.F. Polesky, ed. Chicago, IL: American Society of Clinical Pathologists, Division of Educational Media Services, 45–54.

Schlesinger, D., and A. Luczkiewicz-Mulczykowa. 1971. The Gm(1), Gm(2), and Gm(4) factors in the Polish population. *Arch. Immunol. Ther. Exp.* 19:703–708.

Schwieder, E., and D. Schwieder. 1975. *A Peculiar People: Iowa's Older Order Amish.* Ames, IA: Iowa State University Press.

Smith, C.H., and C. Krahn. 1981. *Smith's Story of the Mennonites.* Newton, KS: Faith and Life Press.

Smith, E.L. 1960. *Studies in Amish Demography.* Harrisonburg, VA: Research Council of Eastern Mennonite College.

Socha, W., and Z. Kaczera. 1968. Studies on gamma-globulin systems in the Polish population. *Folia Biol. Krakow* 16:145–165.

Steinberg, A.G., and C.E. Cook. 1981. *The Distribution of the Human Immunoglobulin Allotypes.* Oxford, England: Oxford University Press.

Stevenson, J.C., and P.M. Everson. 1989. The cultural context of fertility transition in immigrant Mennonites. In *Fertility and Resources,* J. Landers and V. Reynolds, eds. Cambridge, England: Cambridge University Press, 47–61.

Stevenson, J.C., and P.M. Everson. 1990. Initiation of fertility decline in Kansas-Nebraska Mennonites and North American Hutterites. *Colleg. Antropol.* 1:17–24.

Stevenson, J.C., and M.S. Schanfield. 1981. Immunoglobulin allotypes in European populations. III. Gm, Am, and Km allotypes in people of European ancestry in the United States. *Hum. Biol.* 53:521–542.

Stevenson, J.C., P.M. Everson, and M.H. Crawford. 1989. Mennonite fertility in three Midwest communities: Changes in completed family size and reproductive span. *Hum. Biol.* 61:99–115.

Stevenson, J.C., P.M. Everson, and L. Rogers. 1994. Changes in fertility relative to starting, stopping, and spacing behaviors in a migrating Mennonite community, 1775–1889. *Soc. Biol.* 41:83–95.

Stevenson, J.C., M.S. Schanfield, and S.G. Sandler. 1985. Immunoglobulin allotypes in Jewish populations living in Israel and the United States. *Am. J. Phys. Anthropol.* 67:195–207.

Stevenson, J.C., M.S. Schanfield, M.H. Crawford et al. 1990. Immunoglobulin haplotypes: Markers of reproductive success? *Hum. Biol.* 62:479–489.

Voth, S.E. ed. 1975. *Henderson Mennonites: From Holland to Henderson.* Henderson, NE: Henderson Centennial Committee, Service Press Inc.

Ward, F.E., W.B. Bias, E.G. Reisner et al. 1972. HL-A specificities among Old Order Amish: A genetic isolate. In *Histocompatibility Testing 1972,* J. Dausset and J. Colombani, eds. Baltimore, MD: Williams and Wilkins, 93–98.

Wedel, D.C. 1974. *The Story of Alexanderwohl.* North Newton, KS: Mennonite Press.

Yoder, M.L. 1985. Findings from the 1982 Mennonite census. *Mennonite Q. Rev.* 59:307–349.