Paternal Genetic Structure in Contemporary Mennonite Communities from the American Midwest

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ABSTRACT

Over the last 35 years, researchers from the Laboratory of Biological Anthropology at the University of Kansas have been working with Mennonite communities to better understand evolutionary patterns of fission-fusion in relationship to their genetic history and population structure. In this study, short tandem repeat (STR) markers from the nonrecombining region of the Y chromosome (NRY) provided increased resolution of the molecular population structure for these groups. NRY is known to be informative for determining paternal genetic ancestral patterns in recently derived human populations. Mennonites represent a branch of the Anabaptist movement that began in northern and central Europe in the 16th century and maintain a well-documented migration and genealogical history. Provided this historical information, we investigated the genetic relationship of 15 NRY STR loci within five Mennonite communities from Kansas (Goessel, Lone Tree, Garden View, and Meridian) and Nebraska (Henderson). We sought to determine if patterns of fission/fusion along familial lines persisted with paternal genetic information as evidenced through other classical genetic polymorphisms and molecular markers. NRY haplotype information was obtained for 94 individuals, and genetic variation was analyzed and compared across the five study populations and comparative Anabaptist and European populations. NRY haplogroups were assigned using a Bayesian allele frequency approach with 14 STR loci. A total of 92 NRY haplotypes were detected, with none shared across these communities. The most prevalent NRY haplogroup was R1b, which occurred in 56% of the entire sample. Eight additional NRY haplogroups (E1b1b, G2a, I1, I2, J2a1, L, Q, and R1a) were detected in smaller frequencies. Principal component analysis of NRY data, in contrast to mitochondrial DNA data, displayed no patterns of population subdivision of these congregations into communities. These NRY genetic profiles provide additional information regarding the recent migratory history of Mennonite communities and additional evidence for fission along paternal lines after migration to the United States.

Modern Mennonite populations have gone through numerous historical migrations, with some communities settling in the midwestern region of the United States. These migrations are well documented with both historic and genealogical information and provide a unique opportunity to apply anthropological genetic approaches to examine

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Anabaptist population structure. Over the last 250 years, these Mennonite groups have inhabited three distinct geographic regions (western Europe, Ukraine, and the United States). Their experiences at these three locations helped establish a unique cultural identity and a strong sense of shared community, particularly in the Ukraine, where they lived isolated from neighboring Russian and non-Mennonite German settlers (Urry 1989; Stevenson and Everson 2000). Subsequent fissions and migration of these Mennonite groups were also impacted by schisms resulting from differences in religious ideology. Mennonite congregations inhabiting the midwestern United States can be divided into three independent congregations, based on shared religious tenets within the Mennonite religious framework: Alexanderwohl, Holdeman, and Old Colony. All three of these congregations have distinct demographic histories, and a number of their communities have been previously investigated using both classical (Allen 1988; Comuzzie and Crawford 1990; Crawford and Rogers 1982; Crawford et al. 1989; Martin et al. 1996; Rogers 1984) and molecular genetic markers (Demarchi et al. 2005; Melton et al. 2010).

The Anabaptist movement started soon after the Reformation and is characterized by shared religious beliefs in adult baptism, separation of church and state, and pacifism. These groups represented the far left of the Reformation movement and arose in Switzerland, Germany, and the Netherlands (Rogers and Rogers 2000). Anabaptist groups in these three regions were each associated with a charismatic leader and include (a) Mennonites, followers of Menno Simons originating in northern Europe and the Netherlands; (b) Amish, followers of Jacob Amman, formed in Switzerland and southern Germany; and (c) Hutterites, followers of Jacob Hutter, formed in Austria. After these groups formed, a number of small-scale rebellions broke out. Subsequently, local authorities began to view Anabaptists as a threat to social order, resulting in their persecution. These Anabaptist groups were forced to migrate either to underdeveloped areas of eastern Europe or to the Americas. Anabaptist groups that migrated to the United States belong primarily to three distinct groups: Swiss–south German groups, including the Amish; Prussian Mennonites; and Austrian Hutterites. Each of these Anabaptist groups has a different cultural history that may be reflected in the group's population structure. These ethnohistoric events are revealing and can be assessed in terms of their biological impact.

A brief overview of the migration history of these Mennonite communities is as follows. Dutch and German Mennonite refugees immigrated to Polish-controlled areas around Danzig (modern day Gdańsk, Poland), and in 1699 eighteen families formed the Przechova church (Rogers and Rogers 2000; Krahn and Penner 2011). The population increased in size and maintained meticulous genealogical records. In 1821 all but seven families of the congregation moved to Russia and settled in the Ukraine near the Molotschna River. This congregation adopted the name Alexanderwohl, in honor of the Russian czar. Subsequent changes in economic conditions, shifts in Russian governmental policies concerning military exemptions, and internal subdivisions of these groups caused the Alexanderwohl Mennonites to migrate to the United States in 1874 (Rogers and Rogers 2000; Krahn and Penner 2011; Melton 2012). Upon arrival in the United States, the Alexanderwohl group split into two separate divisions: one group settled west of Lincoln, Nebraska, near present-day Henderson, and the other group settled in Kansas, 40 miles north of Wichita, near present-day Goessel. A separate Kansas Mennonite congregation, founded in Ohio in 1858 by John Holdeman, is representative of the Church of God in Christ Mennonites. This congregation is considered a heterogeneous group composed of Pennsylvanian Dutch and Germans mixed with large Mennonite immigrant populations from southern Russia (Crawford et al. 1989). The Holdeman Mennonite community in Meridian, Kansas, further split after the 1980s into the communities of Garden View and Lone Tree.

A number of studies have investigated the genetic history of Mennonites using classical genetic polymorphisms (Crawford and Rogers 1982; Rogers 1984; Crawford et al. 1989; Comuzzie and Crawford 1990; Martin et al. 1996). This research has included blood group systems, serum proteins, and immunoglobulins (Crawford et al. 1989; Martin et al. 1996). More recent genetic studies on these Mennonite communities have focused on molecular markers using apolipoproteins (Demarchi et al. 2005) and mitochondrial DNA (mtDNA) diversity (Melton

et al. 2010). This previous genetic research has demonstrated a fission-fusion pattern characterizing the recent evolutionary history, showing that these new Mennonite communities fission along familial lines (Crawford et al. 1989; Martin et al. 1996; Crawford 2005; Demarchi et al. 2005; Melton et al. 2010). Recent research on mtDNA in the Mennonite communities suggests that molecular genetic data provide a more accurate depiction of Anabaptist history than previously determined through classical genetic markers (Melton et al. 2010). However, mtDNA does not provide a complete genomic profile of a population, and additional evidence from other markers, including those within the nonrecombining region of the Y chromosome (NRY), is warranted.

Recently, anthropological genetic studies applied uniparental molecular genetic markers to examine the biological consequences of migration by the different Anabaptist populations (Pollin et al. 2007; Melton et al. 2010; Pichler et al. 2010). These Anabaptist groups (Amish, Hutterites, and Mennonites) have experienced dynamic histories characterized by several demographic events, which have contributed to their unique genetic structure (Martin et al. 1996; Crawford 2000; Melton et al. 2010; Melton 2012). However, to date few studies have focused on the paternal contribution in these Anabaptist communities by examining NRY polymorphisms (Pollin et al. 2007; Pichler et al. 2010). Short tandem repeat (STR) markers from the NRY are known to be informative for determining paternal genetic ancestral patterns in recently derived human populations, and examining these polymorphisms provides additional insight into their genetic history. Two previous studies investigated the NRY in Anabaptist communities. Pollin et al. (2007) studied NRY variation in the Amish population and found a high correlation between their male genetic lineages and genealogical information based on surname analysis. Pichler et al. (2010) investigated NRY variation in the Hutterite population, compared them with an Austrian population from South Tryol, and found that this population demonstrated a unique genetic profile related to central and eastern European population. However, these studies did not compare Anabaptist populations with one another.

In the present study, we characterized NRY diversity within and between these distinct midwestern Mennonite communities and assessed their biological relationship with other Anabaptist and European populations. Our research aims here were to (a) determine the paternal genetic relationships among five Mennonite communities using NRY polymorphisms, (b) investigate the paternal biological relationship among two different Mennonite congregations and other European populations, and (c) determine if paternal population subdivision within these communities demonstrates patterns of fission-fusion as previously reported for classical genetic polymorphisms, immunoglobulins, and molecular markers.

Materials and Methods

Population Samples

We examined five Mennonite communities inhabiting Kansas and Nebraska (Figure 1), subdivided into two major congregations: Alexanderwohl, which includes the two communities of Goessel, Kansas, and Henderson, Nebraska; and Holdeman, which includes the three Kansas communities of Meridian, Lone Tree, and Garden View. This study included 94 male participants, with samples collected as part of longitudinal multidisciplinary study of midwestern Mennonite communities in the United States. Kansas samples were collected by researchers from the Laboratory of Biological Anthropology, University of Kansas, in 2004, as described previously (Demarchi et al. 2005). Nebraska samples were collected in 1981 as part of a study of biological aging (Crawford 2000). Human ethics approval was approved by the University of Kansas, and signed informed consent was obtained for all participants in both studies.

Collection of blood samples and DNA extraction were performed as previously described (Melton et al. 2010). The 94 male samples used in this analysis comprised 13 individuals from Goessel, 21 from Henderson, 25 from Meridian, 15 from Garden View, and 20 from Lone Tree. To avoid close relatives, we only investigated male participants with different surnames, which were checked against pedigree information to ensure accuracy. Comparative NRY STR data for Hutterites (Pichler et al. 2010), Old Order Amish (Pollin et al. 2007), and eight European populations (Poland, Sweden, Netherlands, Finland, Italy, Russia, Germany, and

FIGURE 1. Mennonite communities of the Midwest. Reprinted with permission from Melton et al. (2010).

Switzerland) were collected from the literature (Table 1).

NRY Analysis

Male participants were characterized for 15 NRY STRs (DYS456, DYS389I and II, DYS390, DYS458, DYS19, DYS385 a/b*, DYS393, DYS391, DYS439, DYS635, DYS392, YGATAH4, DYS437, DYS438, and DYS448). These 15 STRs were analyzed using the AmpFlSTR YFiler kit from Applied Biosystems (Foster City, CA, USA) and multiplexed for fragment analysis on an Applied Biosystems 3130 sequencer at the University of Kansas Natural History Museum DNA Sequencing Laboratory. NRY STRs were assigned using Peak Scanner Software, version 1.0 (Applied Biosystems, Waltham MA, USA). NRY haplogroups were assigned using a Bayesian allele frequency approach using the 15 most informative NRY STR loci (http://www.hprg.com/hapest5/).

Analytical Techniques

Intrapopulation Analysis

NRY STR allelic frequencies, number of haplotypes, and additional diversity indices based on Nei (1987) were analyzed using Arlequin, version 3.5 (Excoffier and Lischer 2010). Haplogroup frequencies were computed based on inferred assigned haplogroups as described above.

Population Structure

Population structure in the five Mennonite communities was tested using analysis of molecular variance (AMOVA) to identify partitions of variance based on NRY STR data, was performed in Arlequin, version 3.5 (Excoffier et al. 1992; Excoffier and Lischer 2010). AMOVA was also performed on previously analyzed mtDNA hypervariable segment I (HVS-I) data (Melton et al. 2010). Initial analyses were performed separating the communities by congregation (Alexanderwohl and Holdeman). An additional AMOVA analysis was performed, with the Alexanderwohl communities of Goessel and Henderson placed in the first group, Meridian and Garden View in the second group, and Lone Tree treated as a third group following results from Melton et al. (2010). Additionally, Mantel tests (Mantel 1967) were performed to determine the correlation between genetic distances and geographic distances. Pairwise distances were computed for NRY STR data (present study; Pollin et al. 2007; Pichler et al. 2010) and for mtDNA data (van der Walt et al. 2005; Melton et al. 2010; Pichler et al. 2010) in Arlequin, version 3.5. Geographic distance matrices were calculated in R, version 3.2 (https://www.r-project.org/), and Mantel tests examining the relationship of Anabaptist NRY STR distances with mtDNA distances, NRY STR distances with geography, and mtDNA sequence distances with geography were performed using the ade4 package (version 1.7-2, http://pbil.univ-lyon1.fr/ADE-4) in R, version 3.2 (Dray and Dufour 2007).

Interpopulation Analysis

Principal coordinate analysis (PCoA) was used to visualize the biological relationships among Mennonite congregations and comparative European populations. Given differences among published NRY STR data sets, a reduced set of six common loci (DYS19, DYS389I and II, DYS390, DYS391, DYS392, and DYS393) were used to construct NRY STR pairwise distances in Arlequin, version 3.5. These distances were used to construct two-dimensional PCoA plots using the APE package (version 3.3, http://ape-package.ird.fr/) in R, version 3.2 (Paradis et al. 2004). Plots were constructed to examine the relationships among the Anabaptist groups and to determine the relationship of these groups to parts of Europe that were briefly home to these refugees based on the historical records.

Results

NRY STR Variation

A total of 94 individuals were characterized in these five Mennonite communities, and 92 different haplotypes were identified (Table 2), with no haplotypes shared between communities. Garden View and Lone Tree were the only two communities where a single haplotype was identified in two individuals with gene diversities (H) of 0.9905 and 0.9947. When the data set excluded loci not found in the comparative literature, the two Alexanderwohl communities of Goessel and Henderson shared two R1b haplotypes. The Holdeman congregation also shared R1b haplotypes among the various communities, and Henderson shared two R1b haplotypes with Meridian.

Haplogroup Distribution

Several European haplogroups were identified, including R1b (56.3%), R1a and I2 (9.6%), E1b (6.4%), I1 and Q (5.3%), G2a (3.2%), J2 (2.1%), and haplogroup L and an unidentified haplotype (1.1%). The distribution of these haplogroups varied among the communities (Figure 2). R1b (50–63.2%) and R1a (4–26.3%) were the only haplogroups found in all five communities. The Alexanderwohl communities of Goessel and Henderson both exhibited haplotypes belonging to haplogroups G2a and J2a. Goessel exhibited the most haplogroup diversity, with six haplogroups (R1b, 53.8%; I2a, 15.4%; J2a, G2a, R1a, and Q, 7.7%) represented in 13 individuals and the highest mean number of pairwise differences between haplotypes (11.4872). Meridian exhibited the second highest haplogroup diversity, with at least seven NRY haplogroups present (R1b, 56%; E1b1, 12%; I1a and Q, 4%; I2, L, R1a, and one unidentified haplotype, 4%) in 25 individuals and an average number of pairwise differences of 11.22. It was the only community to have haplogroup L present. Lone Tree exhibited the lowest haplogroup diversity, with 63.2% of the individuals belonging to haplogroup R1b, 26.3% belonging to haplogroup R1a, and 5.3% representing haplogroups E1b1a and I2a. Garden View had four haplogroups represented (R1b, 50%; I2, 35.7%; R1b and Q, 7.1%) and exhibited the lowest average number of pairwise differences between haplotypes, 9.8476.

Table 1. Populations Used in This Study

Population / Subpopulation[a]	*n*	Latitude	Longitude
Mennonites[1]	94	NA	NA
Goessel	13	38.2464	–97.3489
Garden View	15	38.0819	–97.5137
Henderson	21	40.7797	–97.8123
Lone Tree	20	38.3054	–97.5464
Meridian	25	38.2275	–97.4165
Hutterites (South Tyrol, Italy)[2,3]	75	46.7341	11.2888
Old Order Amish (Lancaster County, PA)[4,5]	732	40.0467	-76.1784
Sweden[6]	383	NA	NA
Blekinge/Kristianstad	41	NA	NA
Gotland	40	NA	NA
Swedish Saami	38	NA	NA
Skaraborg	45	NA	NA
Uppsala	55	NA	NA
Värmland	42	NA	NA
Västerbotten	41	NA	NA
Österbotten	40	NA	NA
Östergötland/Jönköping	41	NA	NA
Western Russia[7]	575	NA	NA
Archangelskaja	42	NA	NA
Brianskaja	43	NA	NA
Iwanovskaja	40	NA	NA
Lipezkaja	47	NA	NA
Nowgorodskaja	40	NA	NA
Orlovskaja	42	NA	NA
Penzenskaja	81	NA	NA
Ryazanskaja	36	NA	NA
Smolenskaja	42	NA	NA
Tambovskaja	48	NA	NA
Tverskaja	42	NA	NA
Vologodskaja	40	NA	NA
Sverdlovsk[8*]	32	NA	NA
Switzerland[9]	64	NA	NA
Germany[9]	88	NA	NA
Netherlands[9]	88	NA	NA
Poland[10]	208	NA	NA
South Tyrol, Italy[3]	227	NA	NA
East Finland[11]	306	NA	NA
Northern Karelia	22	NA	NA
Northern Ostrobothnia	129	NA	NA
Northern Savo	107	NA	NA
Southern Karelia	48	NA	NA
West Findland[11]	229	NA	NA
Hame	49	NA	NA
Southwestern Finland	50	NA	NA
Southern Ostrobothnia	58	NA	NA
Swedish-speaking Ostrobothnia	25	NA	NA
Satakunta	47	NA	NA

[a] References: 1, Present study, with mtDNA from Melton et al. 2010; 2, Pichler et al. 2009; 3, Pichler et al. 2010; 4, Pollin et al. 2007; 5, van der Walt et al. 2005; 6, Karlsson et al. 2006; 7, Roewer et al. 2008; 8, Trynova et al. 2011; 9, Kayser et al. 2001; 10, Rebala and Szczerkowska 2005; 11, Lappalainen et al. 2006.

Population Structure

AMOVA results for NRY STR and mtDNA variation are shown in Table 3. As with mtDNA, the amount of variation seen among groups is lower than seen within all populations, whereas the amount of variation within populations is high. The amount

Table 2. NRY Haplogroups Identified in the Five Mennonite Communities

Community / Inferred Haplogroup (Probability)	NRY STR Locus (reduced loci shown in boldface)																Number of Haplotypes Shared																
	DYS19	DYS3891	DYS3891I	DYS390	DYS391	DYS392	DYS393	DYS385	DYS437	DYS438	DYS439	DYS448	DYS456	DYS458	DYS635	Y-GATA_H4	Goessel	Henderson	Garden View	Lone Tree	Meridian	Amish	Hutterites	Western Russia	Sweden	Switzerland	East Finland	West Finland	Germany	Poland	Italy	Netherlands
Goessel																																	
G2a (99.9%)	**15**	**12**	**27**	**21**	**12**	**13**	**14**	14,15	16	10	11	22	14	17	25	12																	
I2a (58.6%)	**14**	**14**	**26**	**26**	**11**	**10**	**13**	12,15	14	10	10	21	17	18	25	12																	
I2b1 (70.9%)	**17**	**14**	**28**	**24**	**10**	**12**	**14**	14,15	15	12	10	20	15	17	22	11																	
J2a1x (90.8%)	**13**	**14**	**30**	**20**	**11**	**10**	**13**	12,15	14	9	12	21	15	16	23	12																	
Q (93.7%)	13	13	27	21	11	10	13	14,15	15	13	13	20	17	16	22	12																	
R1a (93.7%)	16	13	30	25	11	**11**	**14**	12,15	16	11	11	20	15	17	22	13								3					1	1		
R1b (100%)	**14**	**15**	**33**	**26**	**12**	**13**	**13**	12,15	16	13	12	19	17	18	24	11																	
R1b (100%)	**14**	**14**	**25**	**25**	**11**	**9**	**13**	12,15	15	13	12	19	17	16	24	12																	
R1b (100%)	**14**	**14**	**31**	**24**	**11**	**13**	**13**	12,15	15	13	12	19	15	16	23	12		1							3	1							
R1b (100%)	**14**	**14**	**32**	**25**	**11**	**13**	**13**	12,15	15	13	12	19	17	16	26	12																	
R1b (100%)	14	14	32	24	12	13	**13**	14,15	15	13	13	19	15	17	26	11		1															
R1b (83.8%)	15	14	26	**26**	**12**	**11**	**13**	11,12	14	12	13	19	16	17	24	12																	
R1b (97.2%)	14	**11**	**33**	**26**	**10**	**10**	**12**	14,15	14	13	12	20	18	16	24	13																	
Henderson																																	
E1b1a (88.1%)	15	15	32	21	10	**12**	**15**	14,16	14	11	11	20	15	16	22	10																	
E1b1b (93.1%)	16	15	**33**	**24**	**10**	**12**	**13**	15,17	14	11	11	20	16	17	22	10																	
G2a (76.2%)	**15**	**13**	**30**	**23**	**10**	**11**	**13**	14,15	16	11	12	20	15	16	24	12																	
G2a (83.7%)	**15**	**14**	**31**	**20**	**10**	**11**	**14**	12,15	17	13	10	20	17	17	23	13																	
I1 (68.8%)	**14**	**13**	**30**	**23**	**10**	**11**	**13**	12,15	16	11	11	20	15	16	24	11																	
I1 (99%)	**14**	**13**	**29**	**23**	**10**	**11**	**13**	14,15	17	11	10	20	15	16	25	12		1						2	2		2	3				
I1 (99.4%)	14	13	30	23	12	**11**	**13**	14,15	16	11	11	20	16	15	24	10																	
J2a1h (98.1%)	15	14	30	**24**	**10**	**11**	**12**	15,17	14	10	11	21	16	14	24	12								2								
Q (68.8%)	**15**	**14**	**33**	**24**	**10**	**12**	**13**	15,17	15	11	11	20	16	16	22	13																	
R1a (100%)	**16**	**14**	**31**	**26**	**10**	**11**	**13**	14,15	14	12	10	20	17	15	24	13																	
R1b (100%)	**14**	**14**	**32**	**24**	**12**	**13**	**13**	12,15	16	13	14	19	16	18	24	12	1																
R1b (100%)	**14**	**14**	**30**	**25**	**11**	**13**	**13**	12,15	16	13	13	20	17	17	24	13		1			1												
R1b (100%)	**14**	**10**	**31**	**25**	**11**	**13**	**15**	12,15	14	13	12	18	17	17	24	11																	
R1b (100%)	**14**	**14**	**31**	**24**	**10**	**13**	**12**	14,15	15	13	10	19	16	19	23	12																	
R1b (100%)	15	14	30	25	11	13	**13**	12,15	16	13	11	17	17	19	24	12																	
R1b (100%)	14	14	30	24	**12**	**13**	**13**	12,15	15	13	10	19	17	17	24	11										1							
R1b (100%)	**14**	**14**	**31**	**24**	**11**	**13**	**13**	12,15	15	13	12	19	17	16	24	12	1					41			3	1							
R1b (100%)	**14**	**13**	**29**	**24**	**12**	**13**	**13**	12,15	15	13	12	19	17	17	24	12						4											
R1b (100%)	**14**	**14**	**30**	**25**	**11**	**13**	**13**	12,15	15	13	13	21	17	17	25	12		1			1								1				
R1b (77.6%)	14	13	29	23	10	11	**13**	14,15	15	11	12	19	15	16	25	12		1						2	2		2	3				
R1b (99.8%)	**14**	**13**	**30**	**24**	**10**	**14**	**13**	12,15	14	12	11	20	17	16	23	12																	1
Garden View																																	
I2a (74.7%)	17	**14**	**29**	**25**	**11**	**8**	**13**	12,15	15	13	9	19	16	16	24	8																	
I2a (77%)	**15**	**14**	**26**	**24**	**11**	**13**	**13**	13,16	15	10	12	20	15	16	24	12																	
I2a (86.6%)	**15**	**13**	**31**	**24**	**12**	**16**	**13**	12,15	15	11	15	21	15	19	24	12																	
I2a (93.5%)	**14**	**13**	**30**	**24**	**10**	**10**	**13**	12,15	15	10	13	18	16	17	24	12																	
I2a (95.9%)	**14**	**14**	**28**	**24**	**11**	**11**	**13**	12,15	14	8	12	20	16	17	24	12																	
Q (67.7%)	**14**	**14**	**31**	**24**	**11**	**16**	**13**	12,15	15	11	14	20	16	18	25	12																	
R1a (50.2%)	**13**	**14**	**31**	**22**	**11**	**18**	**13**	11,15	14	10	11	20	17	15	23	10																	
R1b (100%)	14	14	25	25	11	13	**13**	12,15	16	12	12	17	17	16	23	12																	
R1b (100%)	15	13	30	25	**11**	**13**	**13**	12,15	16	13	12	17	17	16	24	12																	

R1b (100%)	16	14	**30**	**26**	**11**	**13**	**13**	12,15	15	13	14	18	16	18	23	12				1		20				1					1
R1b (100%)	**14**	**14**	**30**	**24**	**10**	**13**	**13**	12,15	15	13	14	18	17	16	23	12								1	1	1					
R1b (100%)	**12**	**15**	**24**	**24**	**11**	**13**	**13**	12,15	15	13	12	19	17	17	26	11															
R1b (100%)	**14**	**15**	**32**	**24**	**10**	**13**	**13**	12,15	15	13	12	19	17	17	25	11			1												
R1b (100%)	14	14	30	26	11	13	**13**	12,15	14	13	11	17	16	18	24	11	1														
R1b (100%)	14	14	30	26	**11**	**13**	**13**	12,15	14	13	11	17	16	18	24	11	1														
Lone Tree																															
E1b1b (94.2%)	**13**	**13**	**30**	**25**	**10**	**12**	**13**	12,16	15	8	13	21	18	17	24	11															
I2a (88%)	15	13	29	24	10	**11**	**13**	10,15	17	13	12	20	15	15	21	11				3											
R1a (100%)	16	**14**	**32**	**26**	**10**	**11**	**13**	11,19	15	12	11	19	17	15	24	12			1												
R1a (100%)	**16**	**15**	**32**	**26**	**10**	**8**	**13**	12,16	14	12	11	20	17	15	24	13															
R1a (100%)	**16**	**14**	**32**	**26**	**10**	**11**	**13**	12,15	14	12	11	19	17	15	23	12			1												
R1a (100%)	**16**	**13**	**31**	**26**	**10**	**11**	**13**	13,15	14	12	11	20	16	15	24	13															
R1a (93.1%)	**16**	**14**	**32**	**25**	**10**	**18**	**13**	21,25	14	11	13	20	16	15	24	11															
R1b (99.4%)	**14**	**14**	**24**	**24**	**11**	**15**	**13**	12,15	16	13	13	23	16	16	24	13															
R1b (100%)	14	13	30	24	10	13	13	11,12	14	13	13	19	16	16	23	11			2				4			1			1		1
R1b (100%)	**14**	**13**	**30**	**24**	**10**	**13**	**13**	12,15	15	13	12	18	16	17	24	12			2				4			1			1		1
R1b (100%)	**14**	**14**	**30**	**24**	**10**	**13**	**13**	12,15	14	12	10	19	17	18	23	11		1				20		1	1	1					1
R1b (100%)	**14**	**14**	**32**	**24**	**11**	**13**	**13**	12,15	15	13	12	20	16	17	24	12															
R1b (100%)	**14**	**15**	**32**	**24**	**11**	**13**	**13**	12,15	15	13	12	19	17	17	25	11			1												
R1b (100%)	**14**	**13**	**30**	**24**	**10**	**13**	**13**	12,15	15	13	12	18	16	17	24	12			2				4			1			1		1
R1b (100%)	14	15	32	24	11	13	13	12,15	15	13	12	19	16	17	24	11			1												
R1b (82.7%)	15	13	30	24	**10**	**16**	**13**	11,13	16	12	8	20	15	17	22	11															
R1b (96.4%)	15	14	**26**	**24**	**10**	**15**	**13**	14,15	14	13	11	20	16	16	24	12															
R1b (98.7%)	**14**	**13**	**29**	**23**	**10**	**10**	**13**	12,15	16	11	12	20	15	17	23	11															
R1b (99.5%)	**16**	**14**	**32**	**25**	**10**	**13**	**13**	12,15	15	13	13	19	16	17	23	10															
R1b (99.9%)	**15**	**14**	**24**	**24**	**10**	**9**	**13**	11,17	15	9	14	19	16	17	24	11															
Meridian																															
E1b1b (81.2%)	**16**	**13**	**32**	**23**	**10**	**12**	**13**	15,17	16	11	12	20	17	16	22	11															
E1b1b (99.8%)	**13**	**14**	**32**	**23**	**10**	**10**	**13**	12,15	14	10	12	20	17	15	23	12															
E1b1b (89.1%)	**13**	**15**	**32**	**24**	**13**	**11**	**13**	15,17	15	13	13	22	15	18	24	11															
I1 (72.6%)	**14**	**13**	**29**	**23**	**10**	**12**	**12**	12,15	16	12	11	20	14	15	24	11				1											
I1 (99.2%)	**14**	**13**	**29**	**23**	**10**	**12**	**12**	12,15	16	12	11	20	14	15	22	11				1											
I2a (93.4%)	**15**	**13**	**27**	**23**	**11**	**12**	**13**	12,15	14	11	13	21	15	14	25	12															
L (99.6%)	13	14	27	23	10	15	13	15,17	16	10	14	20	15	17	24	12															
Q (76.7%)	13	13	31	23	12	**14**	**13**	12,15	14	10	13	22	15	18	24	13															
Q (97%)	13	13	29	**25**	**10**	**11**	**13**	15,17	15	12	13	21	14	18	25	12															
R1a (99.6%)	13	**14**	**33**	**27**	**11**	**11**	**13**	12,15	14	10	10	21	17	17	24	11															
R1b (100%)	**14**	**14**	**30**	**24**	**11**	**10**	**13**	12,15	15	13	14	19	15	19	24	12															
R1b (100%)	**14**	**14**	**30**	**24**	**11**	**13**	**13**	12,15	15	13	11	19	17	17	23	12			1				1	3	1		2	3		1	1
R1b (100%)	15	14	31	26	11	13	13	12,15	16	13	12	18	17	17	23	11															
R1b (100%)	14	14	30	25	11	**13**	**13**	12,15	15	12	12	20	15	16	23	13		2													
R1b (100%)	14	14	**29**	**24**	**11**	**13**	**13**	12,15	16	13	12	19	17	17	23	13						2								1	
R1b (100%)	**14**	**13**	**26**	**20**	**10**	**12**	**13**	11,13	14	13	14	20	16	16	23	12															
R1b (100%)	**13**	**11**	**32**	**20**	**13**	**12**	**14**	12,15	15	12	12	20	15	16	25	12															
R1b (100%)	**14**	**14**	**30**	**26**	**11**	**10**	**13**	12,15	14	13	11	18	15	18	23	11															
R1b (100%)	**14**	**14**	**30**	**26**	**11**	**13**	**13**	12,15	16	13	11	20	15	18	23	11	2														
R1b (100%)	**14**	**14**	**30**	**24**	**11**	**13**	**13**	12,15	15	13	15	20	15	19	24	12			1				1	3	1		2	3		1	1
R1b (84.0%)	**15**	**12**	**29**	**20**	**12**	**13**	**13**	12,15	15	13	13	20	16	16	22	12															
R1b (96.2%)	**12**	**14**	**31**	**23**	**11**	**14**	**13**	12,15	15	11	14	20	17	16	25	12															
R1b (99.8%)	**13**	**14**	**33**	**21**	**12**	**13**	**13**	12,15	15	13	14	20	15	16	25	12															
R1b (99.8%)	**16**	**13**	**31**	**21**	**11**	**13**	**12**	12,15	14	13	14	20	16	16	24	11															
Unclassified	**16**	**13**	**30**	**21**	**12**	**13**	**13**	12,15	13	12	14	20	14	16	23	12															

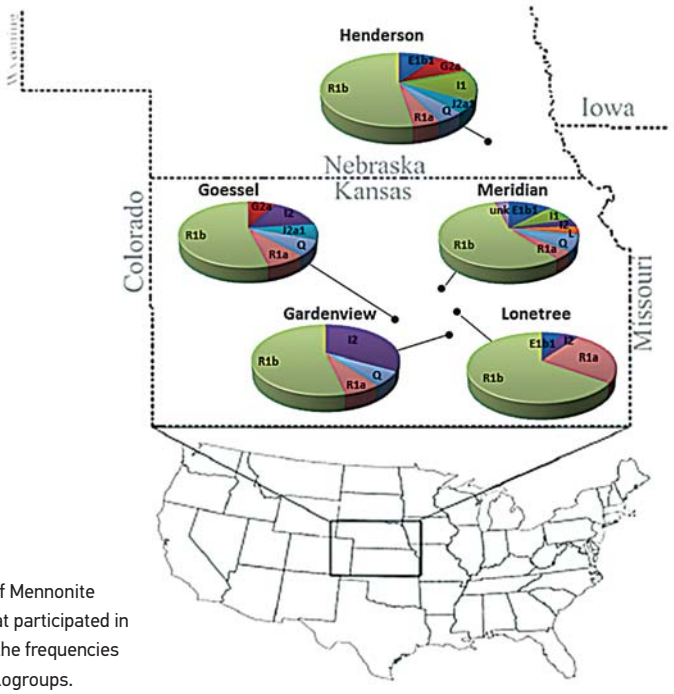

FIGURE 2. Map of Mennonite communities that participated in this study, with the frequencies of predicted haplogroups.

of variation seen within populations is higher in mtDNA than in NRY STR data. The amount of NRY STR variation explained among communities within each grouping is lower (6.12% vs. 7.57%) when Lone Tree is treated as a separate group from the other Holdeman communities. When Mantel tests are applied to these data and geographic proximity, geography and NRY variation are negatively correlated with mtDNA variation (Table 4). This is particularly true of NRY STR and mtDNA distances ($r = -0.5531$); however, neither of these results gave significant p-values. There is a slight correlation ($r = 0.1283$) of geography by NRY STR distance, but these results are also nonsignificant.

Intrapopulation Analyses

PCoA was used to determine the relationship of the Mennonite congregations with other Anabaptist groups using a reduced number of loci. The PCoA of Mennonite communities (Figure 3) plots 77.5% of the NRY variation on the first two axes and shows that these Mennonite communities are more similar to one another than they are to either the Old Order Amish or Hutterite Anabaptist populations. However, this PCoA also shows that Mennonite communities do not cluster by their original congregations of Alexanderwohl and Holdeman, and the community of Garden View pulled the farthest from the Mennonite communities in the plot. There is no sharing of paternal haplotypes among the Mennonite communities based on an expanded set of 15 NRY STRs, but with a reduced locus set of six STRs, sharing of haplotypes does

Table 3. AMOVA Results for NRY STRs and mtDNA Sequences

Source of Variation	% Variation	df	Sum of Squares	Variance Components	% Variation
NRY STR					
Among groups	9.89	4	102.343	0.22122	11.29
Among populations w/in groups	7.57	2	7.416	0.12002	6.12
W/in populations	82.54	816	1321.018	1.61889	82.59
Total		822	1430.776	1.96013	
Fixation indices:					
$F_{SC} = 0.06902$					
$F_{ST} = 0.17409$					
$F_{CT} = 0.11286$					
mtDNA					
Among groups	9.48	4	23.029	0.19586	10.12
Among populations w/in groups	1.25	2	3.028	–0.01224	–0.63
W/in populations	89.28	111	194.351	1.75091	90.51
Total		117	220.407	1.93453	
Fixation indices:					
$F_{SC} = -0.00704$					
$F_{ST} = 0.09492$					
$F_{CT} = 0.10125$					

occur (Table 5). All of the shared paternal haplotypes among the communities belong to the most common and widespread western European NRY haplogroup, R1b. The sharing of paternal haplotypes also includes four R1b haplotypes shared with the Old Order Amish, with at least one of these haplotypes found in each of the Mennonite communities. However, no Mennonite communities shared haplotypes with Hutterite populations included in this analysis, and this group is the farthest outlier within this plot.

A second PCoA plot was constructed comparing Anabaptist groups with other European populations using the reduced locus set of six NRY STRs, which represents 46.2% of the observed NRY STR variation (Figure 4). The Mennonite communities plot nearest to Swiss, Italian, Dutch, German, and western Russian populations. All Mennonite communities share reduced haplotypes with Swiss and German groups, six of the 94 Mennonite paternal haplotypes are shared with the Dutch, and five haplotypes are shared with South Tyrol group from the Italian/Austrian border. The Hutterites are located to the far right of the plot, nearest to western Russian and Swedish populations.

Table 4. Mantel Tests of Geographic Proximity, mtDNA, and NRY STR Diversity

Mantel Test	*r*	*P*-Value
Geography × mtDNA	–0.03549	0.5345
NRY STR diversity × mtDNA	–0.55531	0.9932
Geography × NRY STR diversity	0.128335	0.4427

Discussion

Population genetic studies examining religious isolates have long been known to be informative for the study of rare genetic disorders, due to their unique population structure (Pollin et al. 2007; Pichler et al. 2010). However, very few studies have examined molecular genetic data to understand the diaspora of Anabaptist populations following the Reformation. The primary focus for the present study was to determine the paternal genetic relationships among five Mennonite communities using NRY STR data and to determine if these data support the history of fission-fusion that occurred in these groups. Despite a shared history originating after the Reformation, there is no sharing of paternal haplotypes among Mennonite communities. The high level of paternal haplotype diversity seen in this sample may be explained by the small male sample size, the exclusion of individuals with the same surname within each community, and the design of the YFiler kit that is utilized in forensics to distinguish individuals. AMOVA analysis revealed that most of the paternal genetic variation observed in these groups is found within populations. This is not unexpected, as NRY diversity among populations tends to be higher than that seen in mtDNA studies (Jorde et al. 2000;

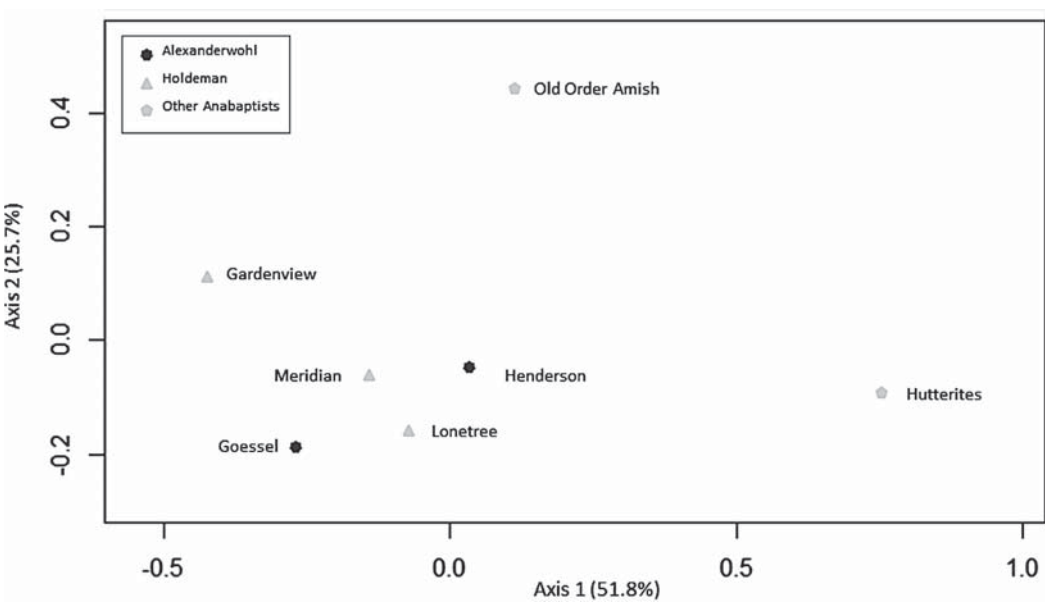

FIGURE 3. Principal coordinate analysis of Anabaptist groups, including the five Mennonite communities, Hutterites, and Old Order Amish.

Table 5. Percentage of NRY Haplotypes Shared between Comparative Populations

	Goessel	Garden View	Henderson	Lone Tree	Meridian	Old Order	Hutterites	Western Russia	Sweden	Switzerland	East Finland	West Finland	Germany	Italy	Netherlands
Goessel			9.52			5.60		0.55	0.52	0.67			0.31		
Garden View				5.00	4.00	2.73			0.26	0.67	0.33		0.31		1.14
Henderson	15.38				4.00	6.15		0.55	1.04	1.34	0.98	1.31	0.31	0.44	1.14
Lone Tree		6.67				2.73		0.55	1.31	0.67	0.33		0.62	0.44	2.27
Meridian		13.33	9.52			0.27		0.18	0.78	1.34		0.87	0.93	0.88	2.27
Old Order	7.69	6.67	9.52	5.00	4.00		21.33	2.57	12.27	18.12	0.98	3.49	10.56	3.96	7.95
Hutterites						21.86		8.44	18.28	13.42	5.88	9.61	9.01	4.41	3.41
Western Russia			14.29	0.05	4.00	23.22	45.33		**51.96**	26.85	25.82	41.92	41.61	11.01	17.05
Sweden	7.69	6.67	19.05	20.00	4.00	**50.82**	**65.33**	**44.40**		49.66	32.68	47.16	37.89	13.66	**27.27**
Switzerland	7.69	6.67	9.52	5.00	4.00	**50.96**	**57.33**	17.43	37.08		10.13	16.59	31.06	11.45	22.73
East Finland		6.67	14.29	5.00		25.96	**62.67**	31.56	43.60	19.46		41.48	15.22	4.41	6.82
West Finland			9.52		4.00	25.27	**62.67**	29.91	49.09	20.81	32.03		24.53	6.61	11.36
Germany	7.69	6.67	4.76	20.00	4.00	46.99	**80.00**	**54.86**	43.08	**51.01**	12.09	24.45		18.06	46.59
Italy			4.76	15.00	4.00	**69.81**	**86.67**	18.90	40.47	37.58	8.17	17.47	29.19		21.59
Netherlands		6.67	4.76	20.00	8.00	30.60	**57.33**	7.71	30.81	35.57	6.86	16.16	27.64	9.69	
Total no. of haplotypes	13	15	21	20	25	732	75	545	383	149	306	229	322	227	88

Boldface numbers indicate that over half of the haplotypes are shared between the two populations.

Pereira et al. 2001). NRY haplotypes tend to be more geographically specific due to differential genetic contributions of males versus females and kin migration (Mielke and Fix 2006). Despite this, some sharing of haplotypes may be expected due to the common origin of Mennonite groups. The PCoA plot of Anabaptist populations (Figure 3) demonstrates that Mennonite communities, while more closely related to one another than to other Anabaptist groups (Hutterites, Old Order Amish), do not cluster by congregation (Alexanderwohl vs. Holdeman). These results may first appear to imply that belonging to a specific Mennonite congregation is not indicative of the NRY variation represented in this study. However, the history of these communities can be used to explain the

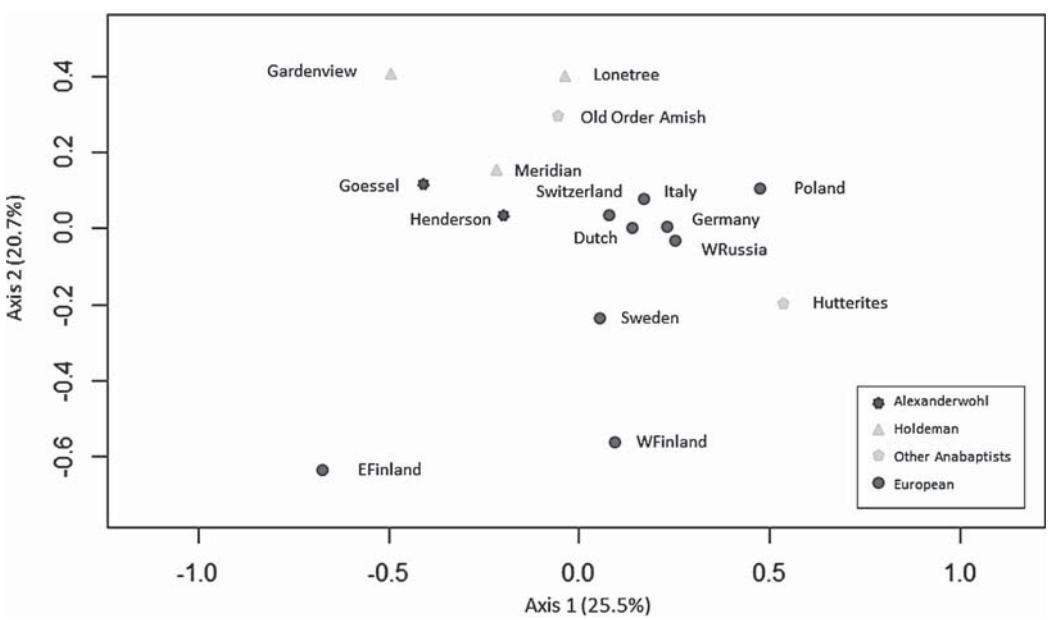

FIGURE 4. Principal coordinate analysis of Anabaptist groups with other European populations.

distribution of NRY haplotypes and haplogroups seen in these Mennonite congregations.

As previously stated, the Alexanderwohl congregation migrated from the Ukraine to the United States in 1874. Upon arrival, this congregation split into two communities, located in Henderson, Nebraska, and Goessel, Kansas. This split was caused by differences in religious ideology, the availability of resources, and additional economic factors (Rogers and Rogers 2000). While there is an absence of paternal haplotype sharing between these two settlements, there is evidence of a shared genetic ancestry. First, both communities demonstrate high frequencies of haplogroup R1b (Goessel, 53.8%; Henderson, 52.4%) and low frequencies of haplogroup R1a (7.7% and 4.8%, respectively), and both are the only Mennonite communities with Y haplogroups J2 and G2a. Furthermore, while there was no sharing of 15-locus NRY STR haplotypes, two six-locus R1b haplotypes are shared between the communities. There are also distinct differences in the paternal haplogroup distribution between these communities. The community of Goessel had two NRY haplogroups, I2a (15.4%) and Q (7.7%), that are not found in the Henderson community, while the Henderson sample had individuals belonging to haplogroup E1b1 (9.5%). These differences support the idea that related individuals tended to remain together (i.e., kin migration) when fission occurred between communities, and this is more pronounced along related male lineages.

The Holdeman communities of Kansas are the descendants of a heterogeneous group of Pennsylvania Dutch and Germans that came to Ohio in 1858 and mixed with Kleine Gemeinde Mennonites that migrated from southern Russia in 1874 (Hiebert and Hiebert 1989). This heterogeneity is evident in the NRY STR data, as the original settlement of Meridian has the highest haplogroup diversity compared with the other Mennonite communities examined. However, when these three Holdeman communities, Meridian, Garden View, and Lone Tree, are compared with one another, they share no NRY STR haplotypes and have very distinct paternal haplogroup compositions. Both Garden View and Lone Tree split from Meridian recently, and the result of this founder effect can be seen in the different distributions of non-R1b haplogroups. Garden View and Lone Tree contain NRY haplogroups I2 and R1a, but in Garden View the frequency of these haplogroups is 35.7% and 7.1%, whereas in Lone Tree the frequencies are at 5.3% and 26.3%. Both communities have haplogroups that were not represented in the other, with the presence of haplogroup Q (7.1%) in Garden View and haplogroup E1b1 (5.3%) in Lone Tree. As with the Alexanderwohl congregation, this distribution of haplogroups can be the result of more related male individuals staying together when the group formed new communities away from Meridian.

The results from the NRY STR data from both Mennonite congregations indicate the movement of male lineages to new settlements in related groups of men, or kin-structured migration (Mielke and Fix 2006). Kin-structured migration, patrilocal residence patterns, and the STR kit design can explain why no Mennonite NRY STR haplotypes are shared among these five Mennonite communities. Melton et al. (2010) also noted that in these Mennonite communities only 17 of the 87 surnames were found in more than one community, a result similar to an isonomy study of Mennonites by Rogers (1984). As surnames and NRY markers are both passed through paternal lineages in western European societies, this unequal distribution of surnames and NRY haplotypes provides further evidence for kin-structured fission in Mennonite populations.

Examination of the paternal biological relationship among the Mennonite congregations and other European populations provides additional genetic history of these communities. The unrest following the Reformation led to the dispersal and splintering of Anabaptist groups. Mennonites from the Netherlands and Germany migrated to Prussia between 1527 and 1539. Later unrest led Mennonite communities to flee to eastern Europe, into Poland, in 1699, and later to the Ukraine (Rogers and Rogers 2000). Despite having inhabited areas of eastern Europe, Mennonites have a typical western/northern European genetic makeup, with high frequencies of R1b (56.4%) and a lower frequency of haplogroups I2 and R1a (9.6%). All Mennonite communities shared six NRY haplotypes with Old Order Amish, Sweden, Switzerland, and Germany. At least three communities shared haplotypes with the Netherlands, western Russia, Finland, and Italy, indicating a primary affinity with northern and central European countries. This relationship is

further illustrated in the PCoA plot of Figure 4, where Mennonite groups are most closely associated with Switzerland, Germany, Italy, and the Netherlands. Despite this, the Mennonite groups are distinct from their European source populations. Similar studies of other Anabaptist groups (Pichler et al. 2010; Pollin et al. 2007) have shown that, as these groups migrated from one region to another, there was relative isolation followed by periods of admixture. This movement and splintering of the Mennonite communities as a response to unrest led to bottlenecks in the various groups, followed by periods of genetic isolation from their host communities and later admixture with other Mennonite groups.

A final aim of this study was to determine if the paternal population subdivision within these communities demonstrates patterns of fission-fusion seen in previous studies and to determine if molecular markers provide better subdivision among communities and congregations. Early studies of blood group polymorphism, serum proteins, and immunoglobulins showed mixed results. A study by Crawford et al. (1989) using 19 polymorphic classical markers showed a common history of the Alexanderwohl communities of Goessel and Henderson, with more similarities between these two communities than between either community and the Holdeman community of Meridian. When the study was expanded to include 44 allele frequencies and 15 classical genetic markers, a different result emerged, with the Kansas communities of Meridian and Goessel appearing more similar to each other than they were to the Nebraska community of Henderson. This result countered that from the historical record but could be explained through kin-structured migration (Crawford 2000). The Nebraska community was found to have a unique Rhesus blood group (RH_R) haplotype that distinguished it from the Kansas communities, indicating that founder effect may have contributed to the observed differences. These results are more similar to those seen in the present study, where clustering by congregation did not occur. Martin et al. (1996) utilized variation in immunoglobulins, genetic markers with higher resolution and more population specificity than blood group polymorphisms, to better understand the genetic relationship of three Mennonite communities (Goessel, Henderson, and Meridian). These studies identified small differences in haplotype frequencies among Mennonite communities, variation that could be explained by nonrandom fission along familial lines.

The mixed results of early molecular markers illustrated the need to apply higher-resolution molecular genetic techniques to better understand the patterns of fission-fusion seen in the Mennonites. Melton et al. (2010) used mtDNA HVS-I sequence variation in these same five Mennonite communities to provide higher resolution of the maternal genetic variation and to provide a female history to Mennonite migration. As with the earlier study of classical polymorphisms (Crawford et al. 1989), mtDNA variation could be attributed to genetic ancestry based on congregational affiliation. That study suggested that maternal variation split along familial lines but that these lineages were more related to one another within congregations than were some of the other variants examined. Again, these findings are different from those seen in the present study of NRY markers for these groups, yet some similarities remain. Both sets of molecular markers show high genetic diversity values indicative of low inbreeding, despite the tendency to select mates that were also Mennonites. This is supported by marriage records collected by Stevenson and Everson (2000) that found that Mennonite marriages outside of congregational affiliations were relatively high during the 1700s to early 1800s, with mates found from other congregations 20–50% of the time. Once in Russia, these rates dropped below 2%. However, reproductive isolation of Mennonite congregations has reduced since the 1930s, with mate selection occurring outside of the congregation (Stevenson and Everson 2000). The differences of clustering when comparing Mennonite mtDNA sequences and NRY STRs may be explained if fission occurred along male and female lines when communities were formed in the United States, but women might have been more likely to move between communities within the same congregations, a patrilocal residence pattern common among Anabaptist populations. These results demonstrate the utility of using uniparental molecular markers, as they give a more accurate picture of the history of the Mennonites of the Midwest that is consistent with documented historical and genealogical records.

Conclusion

This study investigated NRY STR markers in five Mennonite communities and related populations to examine kin-structured migration in paternal lineages for these groups. In contrast to evidence from mtDNA and some classical genetic polymorphisms, NRY variation does not segregate these Mennonite communities by their associated congregation but suggests that male relatives migrate and settle together when new communities are formed. These results demonstrate clear evidence that Mennonite groups share genetic affinities with central and northern Europe, areas in which they originated. However, these groups underwent a series of fission and fusion events in their recent evolutionary history, resulting in the NRY variation observed here, where fissions appear to have occurred recently along paternal lines after migration to the United States. Provided this short time frame and the use of uniparental markers that are susceptible to kin-structured migration, additional evidence from genome-wide autosomal markers may provide a more balanced examination of Mennonite genetic ancestry.

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