Origins of Aleuts and the Genetic Structure of Populations of the Archipelago: Molecular and Archaeological Perspectives

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Abstract   We summarize the results of a field and laboratory research program (1999–2006) in the Aleutian Islands on the origins of the inhabitants of the archipelago and the genetic structure of these populations. The Aleuts show closest genetic affinity to the contemporary Siberian Eskimos and Chukchi of Chukotka and differ significantly from the populations of Kamchatka (the terminus of the archipelago) and Alaskan Eskimos. Our findings support the hypothesis that the ancestors of the Aleuts crossed Beringia and expanded westerly into the islands approximately 9,000 years ago. The Monmonier algorithm indicates genetic discontinuity between contemporary Kamchatkan populations and western Aleut populations, suggesting that island hopping from Kamchatka into the western Aleutian Islands was highly unlikely. The primary determinant of the distribution of genes throughout the archipelago is geography. The most intimate relationship exists between the genetics (based on mtDNA sequences and intermatch/mismatch distances) and geographic distances (measured in kilometers). However, the Y-chromosome haplogroup frequencies are not significantly correlated with the geography of the Aleutian Islands. The underlying patterns of precontact genetic structure based on Y-chromosome markers of the Aleut populations is obscured because of the gene flow from Russian male colonizers and Scandinavian and English fishermen. We consider alternative theories about the peopling of the Americas from Siberia. In addition, we attempt a synthesis between archaeological and genetic data for the Aleutian Islands.

Until the mid-1980s and the development of molecular methods, the reconstruction of human origins was based primarily on archaeological, morphological, linguistic, and genetic data. The genetic characterizations of populations were less informative because they were limited to blood group, serum, and red blood cell protein frequencies, which provided some useful information about population affinities but lacked specific information about sex-related migrations and the

phylogenies of specific genes. It was with the development of DNA sequencing methods, particularly the hypervariable regions of mitochondrial DNA, that the maternal contribution of population movements could be assessed. In addition, the discovery of polymorphic markers on the haploid male-specific portion of the Y chromosome has provided information from the paternal perspective for population processes. Specifically, short tandem repeats (STRs) and single nucleotide polymorphisms (SNPs) on the Y chromosome have helped to distinguish between short- and long-term evolutionary change (Rubicz et al. 2007).

Theories of Aleut Origins

The earliest attempts to reconstruct the origins and population dynamics of Aleut populations were based primarily on anthropometric and craniometric measurements [see Justice et al. (2010) and Ousley and Jones (2010), both in this special issue]. During the 1930s, Aleš Hrdlička's research in the Aleutian Islands focused on cranial remains that he collected throughout the archipelago. He concluded that the Aleuts were not the first occupants of the Aleutian archipelago, having been preceded by another more ancient people identified as the "Pre-Aleuts," with long, narrow, dolichocranic skulls. He posited that at approximately 1000 BP, Pre-Aleut people on Umnak Island were replaced by Aleuts migrating west along the island chain (Hrdlička 1945). His research suggested that two separate movements had occurred along the Aleutian archipelago with replacement of the earlier group by a more recent population. Hrdlička (1945) also noted that the Aleuts were morphologically distinct from the Eskimos but showed affinity to the round-headed, brachycranic "variety" of Siberian Tungusic crania. Hrdlička's protégé, William S. Laughlin, argued against the proposed replacement of the Pre-Aleuts (renamed Paleo-Aleuts) by the Aleuts (renamed Neo-Aleuts) and instead suggested that the temporal discontinuity of craniometric types (i.e., brachycrany versus dolichocrany) actually constituted a gradual differentiation of morphology in situ (Laughlin and Marsh 1951). Laughlin and Aigner (1975) interpreted the archaeological and cranial evidence to signify continuous occupation of the eastern Aleutian Islands by a single population. However, a recent reanalysis and dating of the skeletal materials from the Chaluka, Kagamil, and Ship Rock sites in the Aleutian Islands suggest that the Paleo-Aleut remains are older than 1000 BP, whereas the so-called Neo-Aleut burials date after 1000 BP. Brenner Coltrain et al. (2006) interpreted the skeletal data to signify that the Neo-Aleuts represent a migration of closely related peoples moving westward along the archipelago. Smith et al. (2009), using larger samples, observed an apparent shift in mtDNA haplogroup frequencies in the eastern Aleutians approximately 1,000 years ago and concluded that the data supported an easterly population expansion.

Later, Laughlin et al. (1979) argued for a two-migration model for the peopling of the Americas, with one migration following an inland route through central Beringia that gave rise to American Indians and a coastal expansion spreading

from northern Kamchatka to the Alaska Peninsula, where the ancestral Eskimo and Aleut groups bifurcated. The Aleut populations island-hopped in a westerly direction, whereas the Eskimos continued north along the northern slope of Alaska. If Laughlin's interpretation of the skeletal data is correct, then the Aleuts and Alaskan Eskimos share common ancestry and should exhibit the closest genetic affinity, with both groups differentiating genetically from Native Americans. However, these interpretations are complicated in living populations by possible gene flow from the Eskimos of Alaska.

Szathmary (1979), using blood group frequencies of Siberians, Eskimos, Aleuts, and Northwest Coast Indians, tested several hypotheses about the origins of these circumpolar populations. She first examined the "most current hypothesis," one for which there is archaeological and linguistic support (Szathmary 1979: 185). This hypothesis, originally voiced by Laughlin (1963), states that the Eskimo and Aleut ancestral populations "occupied the shore from Hokkaido to Umnak Island. . . . After the submergence of Beringia, Eskimos spread north along the Alaskan coast, eventually migrating across Canada and into Greenland" (Szathmary 1979: 185). However, this purportedly intimate relationship between the Aleuts and Eskimos was contradicted by a dendrogram that Szathmary generated for 14 populations and 8 blood group loci. Based on these blood group data, the Aleuts showed closest affinity to the Nootka, and the Eskimos constituted a separate branch of the phylogenetic tree. However, this analysis was flawed because of the populations used to represent the Aleuts, namely, the Commander Islands, which were uninhabited until 1825 but forcibly populated by the Russian-American Company. The relocated founding populations of Medni and the Bering Islands consisted of a mélange of Aleuts, Eskimos, Siberian Natives, Gypsies, Russians, and Ainu [see Rubicz et al. (2010) in this issue].

Harper (1980), using seven serum and erythrocytic proteins, measured genetic distances among the Athapaskans, Aleuts, Yupik, and Inupik Eskimos. He concluded that American Indians separated from Siberian populations 15,000 years ago and that Eskimos diverged from Aleuts 8,000 years ago. The Yupik and Inupik Eskimos shared common ancestry only 5,000 years ago. This phylogenetic reconstruction assumed a single migration from Siberia 15,000 years ago, followed by the divergence of Eskimos and Aleuts.

In the 1980s, Laughlin and his research group collected blood specimens from Aleuts of the Pribilof Islands (St. George and St. Paul) and compared them to Kodiak Island Eskimos. The Pribilofs were populated in the 19th century by Aleuts, who were forced to harvest furs for the Russian-American Company. Blood group, serum, and erythrocytic protein variation from the samples collected by Laughlin were described by Majumder et al. (1988). The dendrogram generated from the 16 polymorphic genetic markers failed to separate the Aleuts from the Kodiak Eskimos. Instead, one Kodiak community, Akhiok, diverged from all the other Eskimo and Aleut groups, and the Aleut population of St. Paul clustered with the Kodiak Eskimos. Majumder et al. (1988) cautioned readers about the nature of the sample: There may have been ethnic misclassification because of

the self-reporting of ancestry, and because genealogical information was not col-lected, the statistical methods were not corrected for relatedness. Unfortunately, this one sample from Laughlin's original study (St. Paul Island) was the sole basis for the characterization of mtDNA variation in the Aleutian Islands (Merriwether et al. 1995) until the comprehensive sampling and molecular research by Rubicz et al. (2003). In the study by Merriwether et al. (1995), the St. Paul Aleut sample was described as having haplogroup C (in addition to A and D), which is absent in all other islands of the Aleutian archipelago.

In 1999, we began an eight-year research program (funded by the National Science Foundation) in the Aleutian Islands and on Kamchatka. We posed the following questions: (1) Who are the inhabitants of the Aleutian archipelago? (2) Where did they come from? (3) Were they the result of a single or multiple migra-tions into the Americas? (4) What was the chronology of the settlement? (5) What is the phylogenetic relationship of the Aleuts to the Eskimos, Na-Dene speakers, and Native Siberians? (6) Given the relocations, depopulation, and genetic bottle-neck following Russian contact, is the genetic structure of the Aleutian popula-tions still detectable?

Materials and Methods

Our research objectives included (1) determining the most likely origins of the Aleuts in Siberia by measuring genetic affinities with contemporary Native Siberians, (2) measuring DNA variation in contemporary populations on all the is-lands currently inhabited by Aleuts, (3) assessing the relationship between genetic distances and geography, (4) examining the genetic sequelae of Russian contact in the 18th and 19th centuries, and (5) determining the symmetry or asymmetry between genetic distances based on maternal versus paternal genetic markers.

From 1999 to 2006, we sampled 11 Aleutian populations. These were Aku-tan, Atka, Bering, False Pass, King Cove, Nelson Lagoon, Pribilof Islands (St. George and St. Paul), Sand Point, Umnak, and relocated Aleuts in Anchorage (see Figure 1, a map of the Aleutian archipelago). Buccal swabs and mouth rinses were collected from volunteers on the U.S. side of the archipelago; the volunteers had agreed to participate after providing informed consent. On the Russian side, volunteers were willing to provide blood samples, which were transported for analysis to the University of Kansas. It should be noted that for small island popu-lations, such as the communities in the Aleutian archipelago, it was not possible to obtain adequate samples of unrelated individuals, because everyone is related to varying degrees. However, because demographic pro formae were administered, we were able to eliminate close relatives from our analysis. The genetics of these Aleut settlements were compared to several populations of Kamchatka, the ter-minus of the archipelago. DNA samples were obtained from Evens and Koryaks, who were selected as representative native populations of Kamchatka.

In the field, DNA was extracted on a daily basis using Chelex resin proce-dures. Standard chloroform-phenol methods were used for the blood or buccal
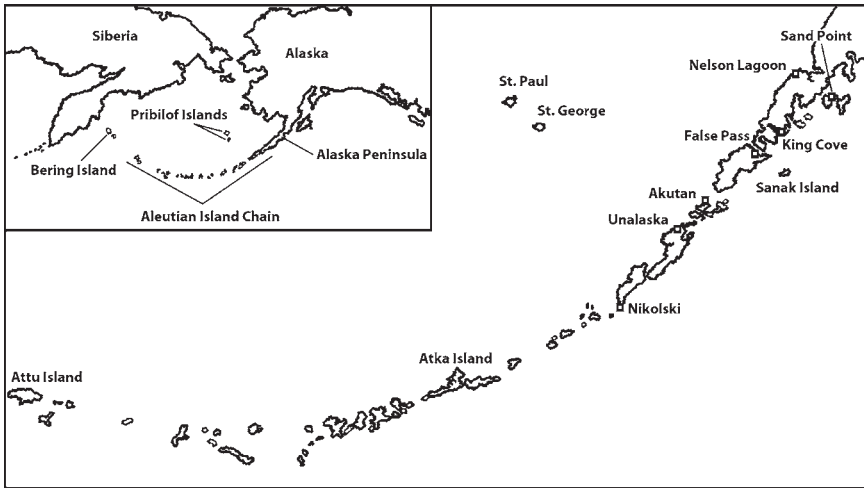
Figure 1. The Aleutian Islands, eastern Siberia, and western Alaska.

smears brought to the Laboratory of Biological Anthropology at the University of Kansas. The DNA samples were analyzed for diagnostic RFLPs of the five major Native American mtDNA haplogroups (see Rubicz et al. 2003). Sequences of the HVS-I region (nucleotide positions 16000–16400) of mtDNA were determined using Big Dye Terminator kits (PR-Applied Biosystems, Foster City, California) with the primers and conditions specified by Schurr et al. (1999).

We used a number of analytical procedures to characterize the genetic structure of the populations of the Aleutian archipelago. Because each of these methods is described fully in the literature and because space is at a premium here, we have limited our descriptions to an appropriate citation of the representative article or computer program for each analytical procedure. The methods we used were the following: (1) multidimensional scaling and *R* matrix analyses [NTSYS program and Harpending and Jenkins (1973)]; (2) mismatch-intermatch distributions (Rogers and Harpending 1992); (3) phylogenetic network analysis (Bandelt et al. 1999); (4) Mantel correlations of matrices of genetic distances (Mantel 1967); (5) neighbor-joining trees (PHYLIP program); (6) residual genetic distance interpolation analyses (Miller et al. 2006); (7) SAMOVA (Dupanloup et al. 2002); (8) admixture estimates (Admix 3.1 program); (9) chronometric techniques applied to sequence data, specifically the *p* statistic (the average pairwise difference between a cluster of sequences to a designated root) computed in Network, version 4.0, and calibrated to a rate of 20,180 years per mutation to obtain time estimates (Forster et al. 1996); and (10) spatial autocorrelations computed on the basis of mtDNA sequences (Bertorelle and Barbujani 1995).

Table 1. Frequencies of mtDNA Haplogroups and Subhaplogroups in Aleut Populations and in Beringia (Rubicz et al. 2003)

		mtDNA Haplogroup					
Population	n	A (%)	B (%)	C (%)	D (%)	Other (%)	Reference
Itel'men	47	6.4	0	14.9	0	78.7	Schurr et al (1999)
Koryak	155	5.2	0	36.1	1.3	57.4	Schurr et al (1999)
Chukchi	24	37.5	0	16.7	16.7	29.2	Torroni et al. (1993b)
Siberian Yupik	50	80.0	0	0	20.0	0	Torroni et al. (1993b)
Inuit	30	96.7	0	0	3.3	0	Lorenz and Smith (1996)
Aleut	179	28.5	0	0	71.5	0	This study
Aleut (Pribilof Islands)	78	25.0	0	1.4	66.7	6.9	Merriwether et al. (1995)
Dogrib	42	100	0	0	0	0	Lorenz and Smith (1996); Torroni et al. (1992)
Haida	25	96.6	0	0	3.4	0	Lorenz and Smith (1996); Torroni et al. (1993a)
Bella Coola	36	50.0	5.6	13.9	25.0	5.6	Lorenz and Smith (1996); Torroni et al. (1993a)
Nuu-Chah-Nulth	15	40.0	6.7	13.3	26.7	13.3	Torroni et al. (1993a)

Results

Five mtDNA haplogroups—A, B, C, D, and X—observed both in Siberia and the Americas, are the likely founding lineages brought from Siberia during the early peopling of the Americas. According to Rubicz et al. (2003), RFLP analyses and sequencing of the HVS-I of the mtDNA in Aleuts revealed the presence of only two founding haplogroups (A, 28.5%; and D, 71.5%) in the Aleutian Islands (Table 1). Volunteers in this study, who identified the ethnicity of their mothers and grandmothers as Aleut, exhibit only the Siberian or Amerindian founding haplotypes. Based on only mtDNA, it appears that the Aleut populations experienced little or no admixture with Russians and other European groups.

The presence of haplogroup C (1.4%), reported in an aggregated Aleut population of St. Paul by Merriwether et al. (1995), is most likely the result of Na-Dene gene flow into the community. In our sample of St. Paul, one haplogroup C individual was found, but interviews revealed that he was a Na-Dene Native American who came to that island as an administrator. Derbeneva et al. (2002) found that haplogroup D was fixed and that only a single D2 subhaplogroup was present in a small sample of Aleuts ($N = 30$) on Bering Island.

Figure 2 shows the distribution of mtDNA frequencies in the Aleutian Islands and demonstrates the existence of clinal variation in the frequency of haplogroup A, which reaches its highest incidence in Alaska and the eastern Aleutians and has a gradual diminution in the western islands and Siberia.
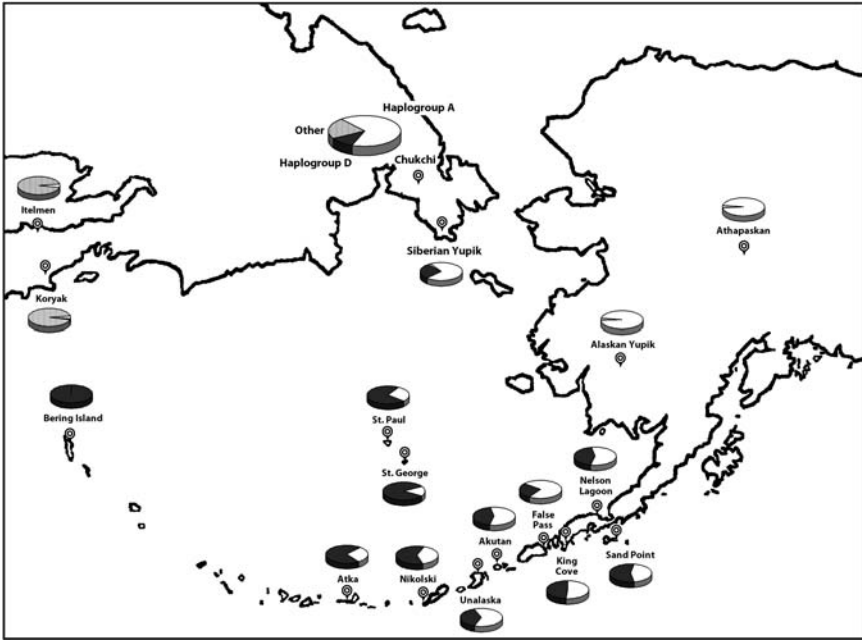
Figure 2.   The Aleutian Islands showing the distribution of mtDNA haplogroup frequencies (Crawford 2007).

Table 2 lists the frequencies of the mtDNA haplogroups in the 11 Aleut populations. The sample sizes from some islands are relatively small; for example, only 10 individuals from the total of 36 residents of Nikolski claimed Aleut ethnicity and agreed to participate. However, this sample size constitutes almost 28% of the total population. With the addition of the eastern Aleutian Island samples (which exhibit high frequencies of haplogroup A), the overall frequencies of haplogroups A and D across the archipelago are 41.6% and 58.4%, respectively. These results differ significantly from the original frequencies (A = 28.5% and D = 71.5%) based primarily on central and western islands (Rubicz et al. 2003).

What distinguishes Aleut mtDNA from other circumpolar populations? Figure 3 provides a schematic phylogeny of mtDNA haplogroups A and D. Subhaplogroups A4 and D4 represent the Asian ancestral roots for the two founding Amerindian haplotypes (Zlojutro et al. 2006). Haplogroup subtype A7 [termed A2a1a by Helgason et al. (2006) and Gilbert et al. (2008)], with a C to T transition at np 16212 relative to subhaplogroup A3, is found only in Aleut populations. In addition, subhaplogroup A2b (16192T in Helgason's designation) occurs at a frequency of 66% in eastern Greenland but is entirely absent among Aleuts. The coalescence time for the A2b clade has been estimated as 3084 ± 1781 years (De-

Table 2. Mitochondrial DNA Haplogroup Frequencies in 11 Aleut Populations (Zlojutro 2008)

Population	Number	Haplogroup A	Haplogroup D
Akutan	16	0.563	0.438
Atka	17	0.294	0.706
Bering	35	0.000	1.000
False Pass	11	0.727	0.273
King Cove	33	0.515	0.485
Nelson Lagoon	16	0.563	0.438
Nikolski	10	0.400	0.600
Sand Point	38	0.447	0.553
St. George	28	0.179	0.821
St. Paul	35	0.286	0.714
Unalaska	28	0.607	0.393
Total	267	0.416	0.584

renko et al. 2007). However, the coalescence time for the entire subhaplotype of A2 suggests greater antiquity: $8,077 \pm 2,435$ years.

Figure 4 is a plot of sequences from haplogroup D using median network analysis. The haplogroup D network has a structure similar to that seen for haplogroup A, but it has fewer nodes (Rubicz et al. 2003). The two major nodes represent subtypes D1 and D2 with less frequent D3 and are shared by Chukchi, Siberian Eskimos, and Aleuts. The recently sequenced mtDNA extracted from hair of a 4,000-year-old Paleo-Eskimo from Greenland, belonging to the Saqqaq culture, shares a unique D2a1 haplotype previously found among the Aleuts (Gilbert et al. 2008). In the haplotype A network analysis (not shown), subtype A3 is the nodal Aleut-specific 16212 sublineage.

Figure 5 provides a multidimensional scaling plot (based on intermatch-mismatch distances) of 10 Aleut populations. The first dimension separates the Bering, False Pass, and Nikolski populations from the other Aleut groups. The second dimension separates the populations geographically, with the Bering group being the most westerly and the Nelson Lagoon, King Cove, Sand Point, and False Pass groups representing the easternmost populations off the coast of the Alaska Peninsula.

Figure 6 combines in a single plot a multidimensional scaling based on intermatch-mismatch distance matrices with a SAMOVA [developed by Dupanloup et al. (2002)] that is used to identify genetic barriers corresponding to a predefined number of population groupings (k) that maximizes the proportion of total genetic variance resulting from differences between groups. The genetic barriers revealed by the SAMOVA are (1) between Kamchatkan populations and the remainder of the circumpolar groups; (2) between the Alaskan-Yupik population and the Athapaskan, Chukchi, Siberian Yupik, and the Aleut populations; and (3) between the western Aleuts and the Bering, Atka, and Pribilof Islands, which cluster together and are separated from eastern Aleut groups. The Itel'men and
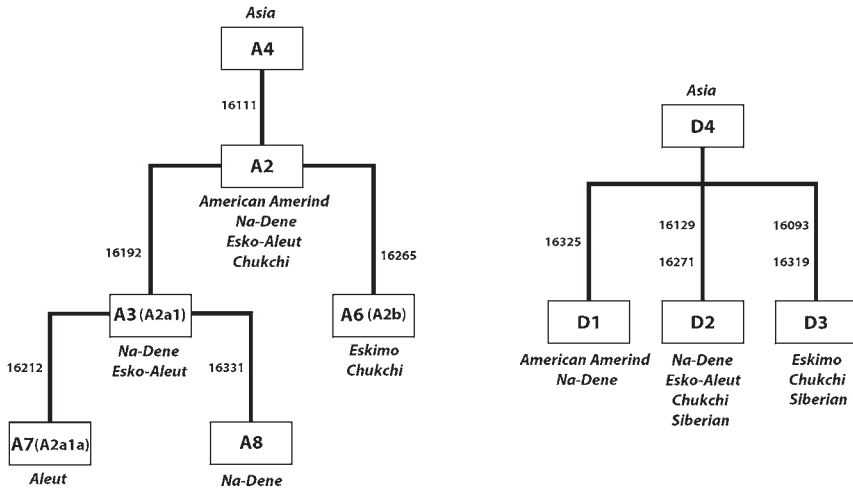
Figure 3. Schematic phylogenetic reconstruction of the relationship among haplotypes of mtDNA haplogroups A and D (Zlojutro et al. 2006). For some subhaplogroups of haplogroup A (in parentheses), the commonly used designation is provided (e.g., A2a1a for the A7 lineage (Gilbert et al. 2008; Helgason et al. 2006).

Koryak populations of Kamchatka are most distant from the other populations and contribute evidence against a theory that some peopling of the Aleutian Islands came from the west in an easterly direction. Interestingly, the Athapaskans cluster with the Chukchi and Siberian Eskimos (Crawford 2007).

Time Estimates.   Table 3 summarizes the estimates of Aleut mtDNA clusters, defined by specific mutations. We converted the p statistic to time, using the rate provided by Forster et al. (1996) of 20,180 years per mutation. The dates for sub-haplogroups A7, also known as A2a1a (specific Aleut mutation 162126G), and D2 overlap and suggest that they are the result of a similar demographic process. The standard errors in all these estimates are high; therefore the chronology must be interpreted cautiously. Other methods of estimating time, such as τ or π, give coalescent dates that are fairly consistent, with a few exceptions. For example, dates for haplogroup A range from 25,225 BP for p to 15,000 BP for estimates based on $\theta\pi$ (Zlojutro et al. 2006).

Based on a neighbor-joining tree constructed for mitochondrial DNA sequences (Figure 7), the genetic structure preserved along the archipelago reflects the action of evolutionary forces and demographic and unique historical events (see Figure 6). The Siberian populations (Koryaks and Itel'men) and Alaskan populations (Yupik Eskimos and Athapaskan) form separate branches. The eastern Aleuts are closest to the Chukchi and Siberian Yupik, whereas the western and newly established populations (St. Paul, St. George, and Bering) form another
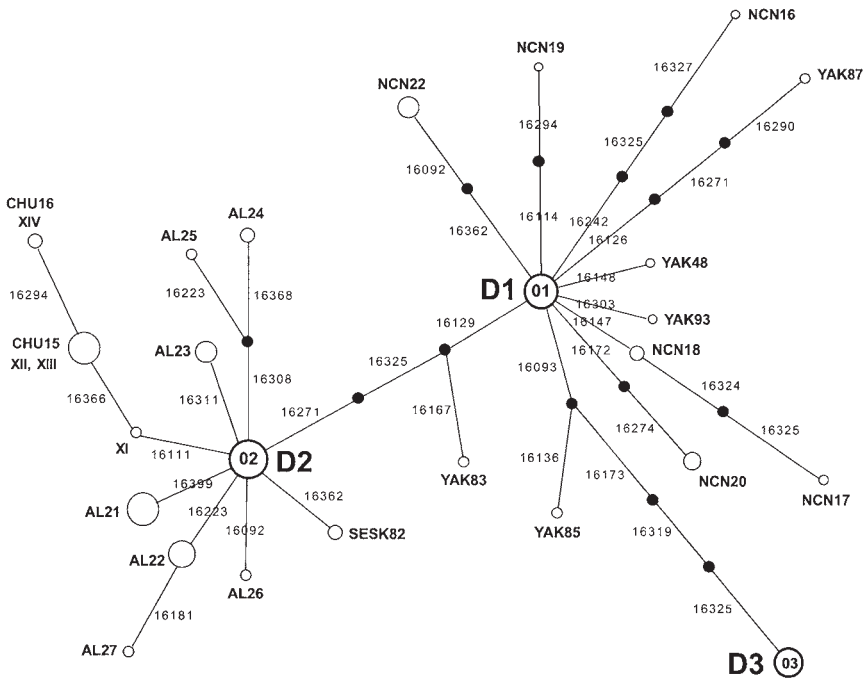
Figure 4. Median network analysis of HVS-I sequences of D haplotypes for Bering populations. AL, Aleuts; CHU, Chukotan; KAM, Kamchatkan; GESK, Greenland Eskimo; SESK, Siberian Eskimo; NCN, Nuu-Chah-Nulth; YAK, Yakima (Rubicz et al. 2003).

branch of the unrooted tree. Bering Island is the most distinctive of the Aleut populations because of the fixation of haplogroup D [see Rubicz et al. 2010 (this issue)]. Figure 8 presents a plot on a map of the Aleutian Islands based on Monmonier's (1973) maximum difference algorithm, which identifies triangulation genetic boundaries, namely, geographic zones where differences were largest (Barrier, version 2.2).

Y-Chromosome Markers. Both SNPs and STRs were typed on 134 Aleut Y chromosomes (see Rubicz et al. 2007) to identify specific haplogroups and haplotypes. Nine Y-chromosome haplogroups were identified: E3, I, I1a, J, N, Q, Q3, R1a, and R1b (Figure 9). These haplogroups were defined by the presence of specific mutations found in Europe, Central Asia, Siberia, and the Americas. Only about 15% of the Y chromosomes from the male participants from the Aleutian archipelago were designated as either Q or Q3, which are considered Native American paternal lineages. Thus most of the Aleut Y chromosomes appear to be of Russian, European, and/or Central Asian origin. Admixture estimates (using Admix 3.1) based on nine autosomal STRs revealed that approximately 40% of
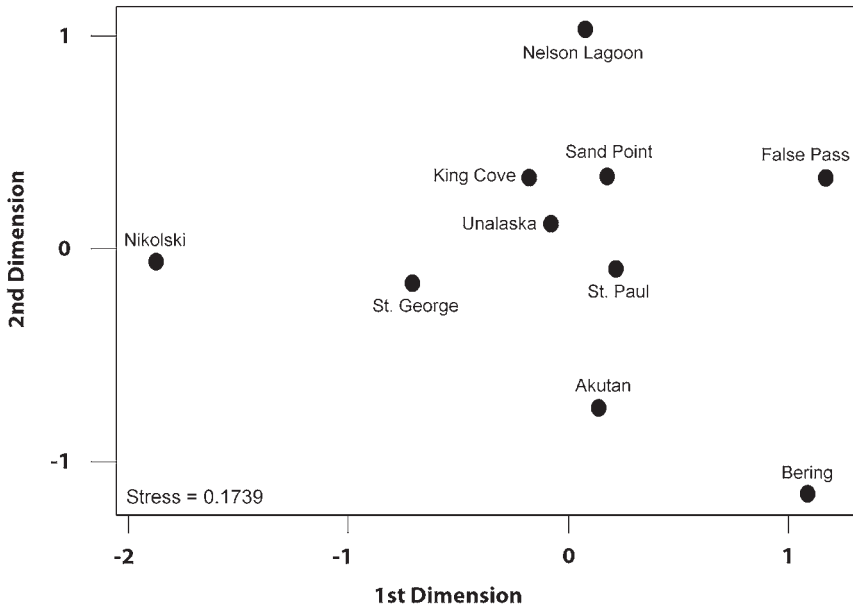
Figure 5. Multidimensional scaling plot of the genetic relationships of 10 Aleut populations (based on intermatch-mismatch distances). The statistic "stress" measures the goodness-of-fit of the distances in the projected space to the monotone function of the original distances.

the genes in the Bering gene pool were of Russian origin and 60% were Aleut [see Rubicz et al. 2010 (this issue)].

Geography and Genetics.   Because the Aleuts are distributed as island populations along an east-west axis of almost 1,500 km, from the Alaska Peninsula to Kamchatka, it is expected that geographic isolation contributes to genetic affinities. To test this relationship between geography and genetics, we constructed matrices using geographic distances and genetic distances based on mtDNA sequences from residents of 11 Aleutian islands. Mantel tests were used to measure the correlation between geographic and genetic distance matrices (Mantel 1967). The relationship between geography and genetics was highly significant, with $r = 0.72$ and $P < 0.000$ (Crawford 2007). The significance of this relationship between genetics and geography is astounding when the history of the Aleutian Islands is considered. In addition to the depopulation of the archipelago following Russian contact, the Russian-American Company relocated Aleuts from Attu, Atka, and Unalaska to create new aggregates, such as St. Paul, St. George, Bering Island, and Medni [see Rubicz et al. 2010 (this issue)]. Aleuts from Attu were also relocated during World War II to Japan, and Aleuts from Atka and other western groups were moved to camps in Alaska. Genetic admixture with Russians was
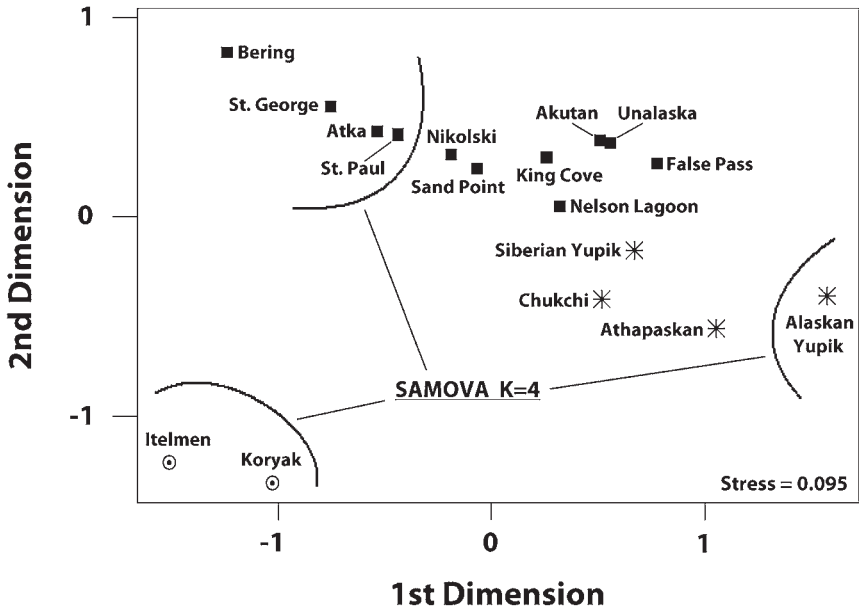
Figure 6. Combined plot of multidimensional scaling and SAMOVA indicating genetic boundaries in the circumpolar region. Asterisks denote populations that are ethnically not Aleut.

prevalent in the western and central Aleutian Islands after Russian contact in the 18th century, followed later by admixture with English and Scandinavian fishermen who settled in the eastern islands. Despite these demographic changes, the mtDNA sequences have "preserved" the genetic structure of precontact Aleutian populations. However, a comparison of matrices based on Y-chromosome haplotype distances and geographic distances between the islands yields a nonsignificant correlation of $r = 0.379$ ($P = 0.130$). Although the correlation between

Table 3. Chronology Measured by the Presence of Specific Mutations in Either Haplogroup A or D

Mutation	Cluster	N	Age
161115T	A	56	25,225 ± 13,666
162126G	A7 (Aleut)	34	6,529 ± 3,511
	D1	28	36,643 ± 11,050
	D2	142	5,400 ± 2,550

The p statistic was estimated using Network, version 4.0, calibrated to a rate of 20,180 years per mutation (Zlojutro et al. 2006).
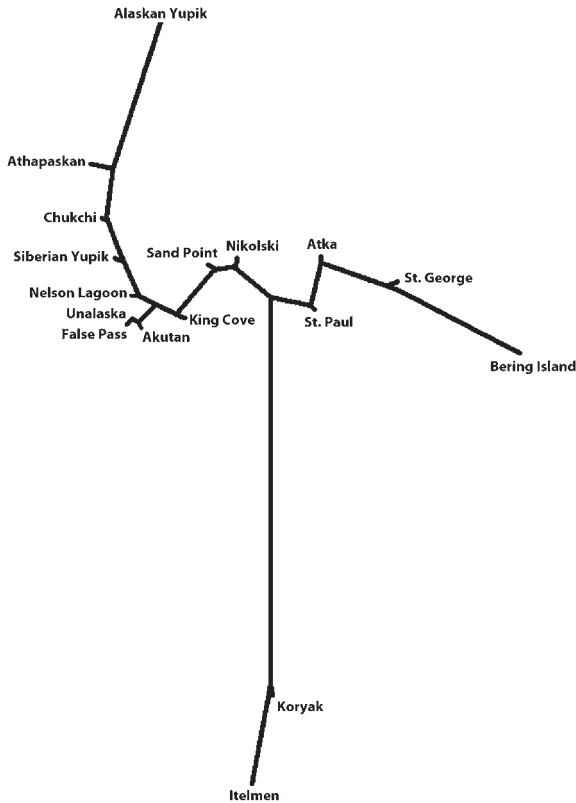
Figure 7. Neighbor-joining tree based on the D_A distance matrix of HVS-I data from the circumpolar region showing the genetic relationships of the Aleuts to surrounding populations.

geography and Y-chromosome STR genetic distances is high, it is not statistically significant. Mantel tests for mtDNA and Y-chromosome STR distances yielded a correlation of 0.26 that is not statistically significant ($P = 0.164$). These results indicate extreme asymmetry between the relationship between genetics and geography for mtDNA sequences and that for Y-chromosome STRs.

To further investigate the relationship between geography and genetics, we applied the spatial autocorrelation method of Bertorelle and Barbujani (1995) using comparisons of mtDNA sequences. The *y* axis is a product-moment coefficient analogous to Moran's *I*, and the *x* axis is the lag distance in kilometers. The highest correlation between populations is in the 500-km distance, followed by lower correlations in the 1,000-km lag and negative correlations at the greater distances (see Figure 10). The relationship between geography and genetics appears
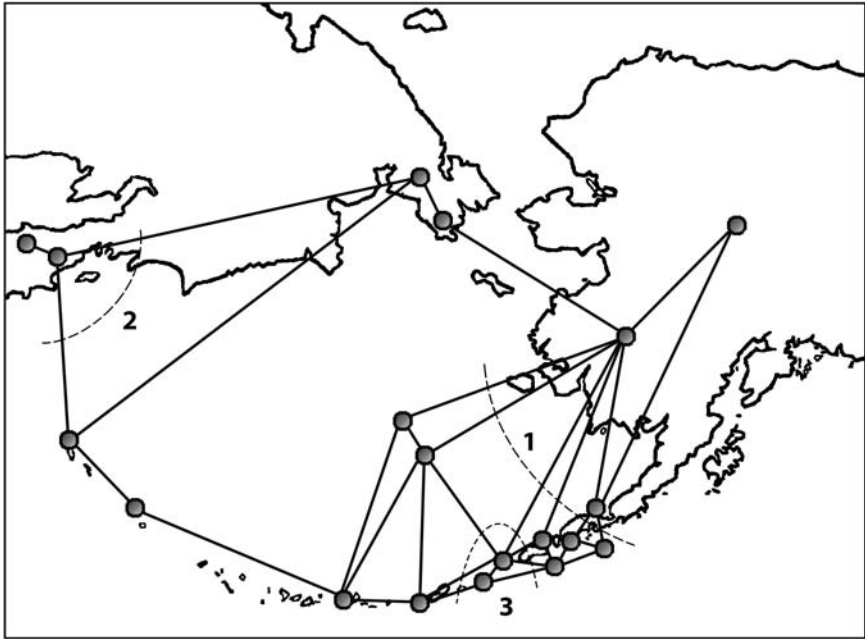
Figure 8. Triangulation plot using the Monmonier algorithm for identifying genetic discontinuity. Numbers in the plot denote the location of regions of discontinuity, based on the proportion of the total genetic variance resulting from differences between groups.

to be linear and highly statistically significant, indicating the possible action of kin migration.

Figure 11 presents a genetic distance landscape generated through interpolation connecting populations from Kamchatka to the Aleutian Islands to the Alaskan mainland. The x and y axes correspond to geographic locations, and the z axis reflects residual genetic distances generated by linear regression of pairwise genetic distances of nearest populations on geographic distances (Miller et al. 2006). The open squares in the figure represent the Aleutian populations, Kamchatkan native groups (Itel'men and Koryaks), Chukotkan populations (Chukchi and Siberian Yupik Eskimos), and Alaskan Natives (Athapaskans and Yupik). This surface plot supports the results of the SAMOVA and Monmonier's triangulation analysis. Ridges and peaks along the z axis represent the highest pairwise residual genetic distances, whereas the smaller genetic distances are displayed as depressions in the interpolated surface. Major genetic discontinuities are observed between Kamchatkan populations and Bering Island, as well as between the Alaskan Yupiks and Athapaskans from the Aleutian Islands. The shorter genetic distances, displayed as peaks below the landscape surface, indicate greater genetic similarities between populations.
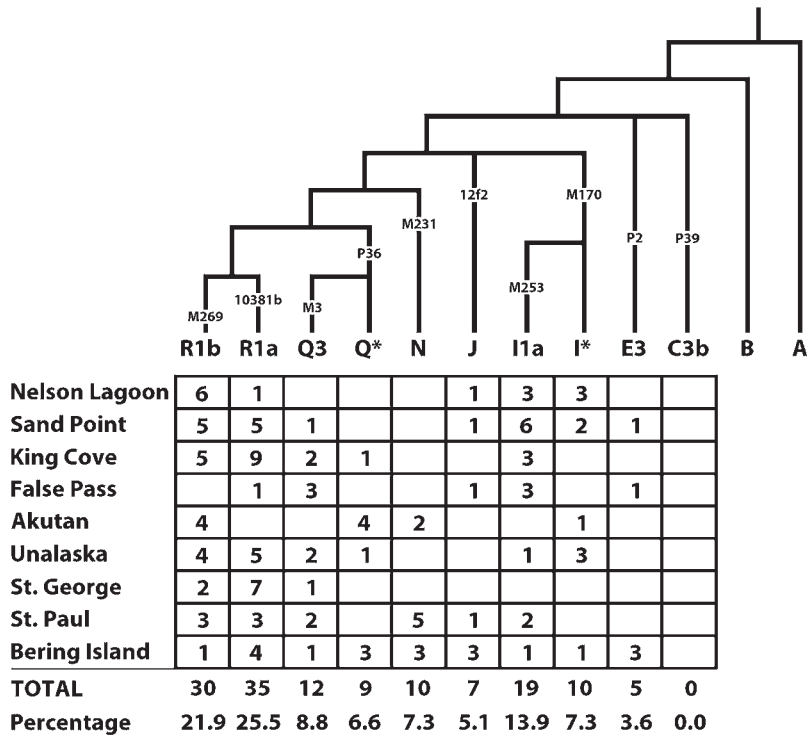
	R1b	R1a	Q3	Q*	N	J	I1a	I*	E3	C3b	B	A
Nelson Lagoon	6	1				1	3	3				
Sand Point	5	5	1			1	6	2	1			
King Cove	5	9	2	1			3					
False Pass		1	3			1	3		1			
Akutan	4			4	2			1				
Unalaska	4	5	2	1			1	3				
St. George	2	7	1									
St. Paul	3	3	2		5	1	2					
Bering Island	1	4	1	3	3	3	1	1	3			
TOTAL	30	35	12	9	10	7	19	10	5	0		
Percentage	21.9	25.5	8.8	6.6	7.3	5.1	13.9	7.3	3.6	0.0		

Figure 9. Y-chromosome haplotypes based on SNPs for the Aleutian Islands (Zlojutro et al. 2009).

Discussion

Peopling of the Americas: Broader Perspectives. The molecular and genetic evidence from Siberian and Native American populations has been interpreted to support a variety of different peopling models for the Americas: four migrations based on *GM* data (Schanfield 1992); a three-wave model based on linguistic, dental, and genetic data (Greenberg et al. 1986); and a two- or one-migration model based on mtDNA (Merriwether et al. 1995; Schurr 2004). Y-chromosome haplotypes were initially interpreted to suggest more than one paternal migration from the "general region of Lake Baikal to the Americas" based on the presence of haplogroups Q3 and R (Karafet et al. 1997, 1999). Later analyses (Zegura et al. 2004) based on SNPs and microsatellite haplotypes appear more consistent with a single Y-chromosome entry into the Americas.

Schroeder et al. (2007) reported on the presence of a ubiquitous private allele (a 9-trinucleotide repeat) at the *D9S1120* microsatellite locus in populations of the Americas and in two western Siberian groups. This repeat allele is absent in all the Siberian populations tested to date, with the exception of the Chukchi
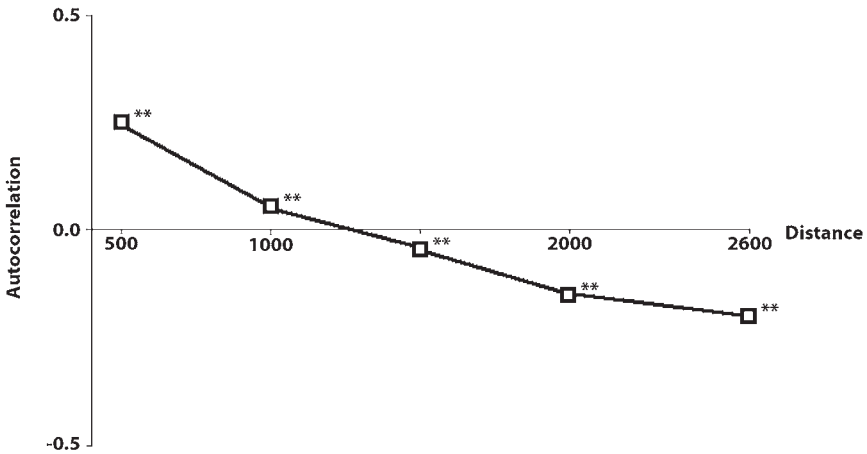
Figure 10. Spatial autocorrelation plot of the populations of the Aleutian Islands using mtDNA sequences and the methods of Bertorelle and Barbujani (1995). Double asterisks denote the highly significant relationship between geography (lag distances in kilometers) and genetics (product-moment coefficient analogous to Moran's *I*) ($P < 0.000$).

of Chukotka and the Koryaks of Kamchatka. The *D9S1120* repeat allele occurs in all Native American populations (both North and South America) and varies in frequency from as high as 97% among the Surui to 10% among the Seri. The 9-repeat allele appears to be absent in the remainder of the world—Africa, Europe, and Asia. The incidence of this allele among the Chukchi is not surprising because, on the basis of mtDNA sequences, the Aleuts share mtDNA lineages with the Chukchi and Siberian Eskimos. However, the Koryaks of Kamchatka display a distinctive profile of mtDNA haplogroups and have been effectively eliminated as potential ancestors of the Aleuts.

The findings by Schroeder et al. (2007) suggest that the Chukchi and Koryaks shared common ancestry with the Siberian populations that peopled the Americas. Thus the presence of the ubiquitous 9-repeat allele in western Siberia and Native Americans appears to contradict the widely accepted interpretation that the Altai populations (who exhibit all five of the founding mtDNA haplogroups—A, B, C, D, and X) shared common ancestry with the founding populations of Native Americans (Schurr 2004). Based on this interpretation, one would expect the Altai populations to exhibit the *D9S1120* 9-repeat allele if they in fact share a common ancestry with the early Native American populations that expanded into the Americas. The presence of this allele in all the populations tested in the Americas and its absence in most of the Siberian groups does lend further support to the single-wave migration theory for the peopling of the Americas. The sequencing of the region surrounding this allele is suggestive of the common ancestry of
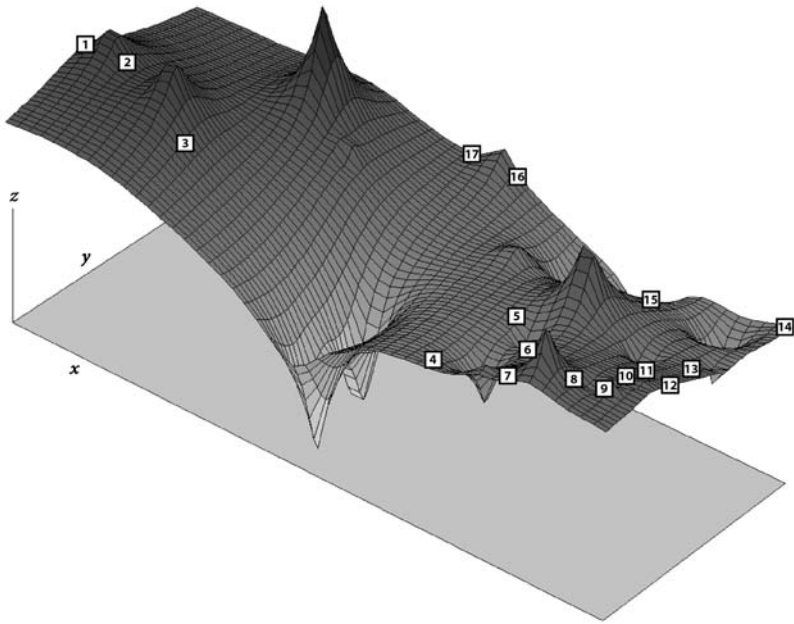
Figure 11. A genetic landscape interpolation method connecting the populations from Alaska to Siberia. The method of Miller et al. (2006) was used to create a genetic surface based on genetic distance residuals, and geographic locations define the other two axes. Populations: (1) Itel'men, (2) Koryak, (3) Bering Island, (4) Atka Island, (5) St. Paul, (6) St. George, (7) Nikolski, (8) Unalaska, (9) Akutan, (10) False Pass, (11) King Cove, (12) Sand Point, (13) Nelson Lagoon, (14) Athapaskan, (15) Alaskan Yupik, (16) Siberian Yupik, (17) Chukchi.

the 9-repeat allele and also suggests that all populations of the Americas and the Chukchi and Koryaks share common ancestry (Schroeder et al. 2009).

Peopling of the Aleutian Archipelago.   More recent osteological analyses have raised some questions concerning the phylogenetic relationship of the Aleuts to other populations of Beringia. Ossenberg (2003), on the basis of discrete cranial traits, found that Aleuts, and particularly the Chaluka sample, clustered with the Na-Dene and with the early Uyak sample from Kodiak Island. However, the westernmost Aleuts from Attu and Agattu tended to cluster with Yupik-speaking Eskimos rather than with other Aleuts. Skeletal remains are highly plastic, though, and the observed similarity between the Na-Dene and Aleuts may be the result of sharing similar environmental conditions.

Blood groups and protein markers also lead to considerable disagreement on who shared common ancestry with the Aleuts and exhibited the closest genetic affinities with them. Based on standard genetic markers, Harper (1980) found that

the Aleuts were closely related to Eskimos. In contrast, Ousley (1995) grouped the Aleuts with American Indians. Szathmary and Ossenberg (1978) demonstrated that the Aleuts' closest affinities were to Chukchi and Asiatic Eskimos. Rychkov and Sheremetyeva (1972) concluded that the Eskimos were equally related to both Native American and North Asian populations.

In Szathmary's (1979) evaluation of three theories of origins of populations of the circumpolar regions, the only available array of allelic blood group frequencies (based on a maximum of 60 individuals) representing the Aleutian Islands came from the Commander Islands, Medni, and Bering (Rychkov and Sheremetyeva 1972). Twenty-four genes of the ABO, RH, MNSs, Diego, Duffy, Kell, Kidd, and P loci were used to generate a circumpolar phylogeny. Szathmary did note that the Aleuts of the Commander Islands were descendants of "a very heterogeneous founding population that included Aleut, Kodiak Eskimo, Indians from Sitka, Kamchadal from Kamchatka, and other Siberian indigenes, as well as persons of Baltic origins" (Szathmary 1979: 202). However, these data were used to construct a minimum-string tree and a dendrogram (with some cautionary notes) to interpret the phylogeny of circumpolar populations. Given the paucity of information about the genetics of the populations of the Aleutian Islands, it is interesting to note that no researcher studied the molecular genetics of these populations until our field investigations in 1999.

A comparison of mtDNA sequences based on a median network analysis of haplogroups A and D indicates that the Aleuts cluster closest genetically with the Chukchi and Siberian Eskimos of the Chukchi Peninsula—an area that was connected to the Bering landmass (Rubicz et al. 2003). The Alaskan Eskimos failed to cluster with the Aleuts, despite the similarity of their languages and the migration theories by Laughlin that the Aleuts and Eskimos formed a single founding population that bifurcated following the inundation of Beringia in the Holocene. These results raise a question as to whether the Alaskan Eskimos may have expanded from Siberia as a separate migration from the Aleuts.

Using archaeological and cranial studies, Zlojutro et al. (2006) critically examined the theories concerning the peopling of the Aleutian Islands. They attempted to integrate these theories with the available molecular data, which led them to four models: (1) the continuous occupation of the eastern Aleutians by a single Paleo-Arctic population, (2) an early migration of people with predominantly subhaplogroup A3 who experienced outside gene flow over a short time, (3) an early migration of a group with subhaplogroup A3 that experienced a gradual and indigenous change in gene flow, and (4) an initial gene pool of the earliest inhabitants of the eastern islands that contained both the D2 and A7 mtDNA lineages, and subhaplogroup A3 was introduced into the Aleut gene pool by gene flow from Eskimo neighbors.

Zlojutro et al.'s (2006) first model proposes a continuous occupation of the eastern Aleutians by a single population. According to this model, after the recession of the Wisconsin ice mass, the eastern Aleutians were populated 9,000 to 8,000 years ago by a Paleo-Arctic group that used unifacial blade technologies (as seen in

the Anangula phase; Dumond and Knecht 2001) and possessed the major mtDNA subhaplogroups A3 (including the A7 branch) and D2, which are currently exhibited by contemporary Aleuts. The molecular-based estimate of coalescence of subhaplogroup D2 is 6,035 ± 2885 years, which is slightly more recent than the 8,000–9,000 years presence of Aleuts during the Anangula phase (Mason 2001; Rubicz et al. 2003). Approximately 6,000 years ago, maritime technological developments and climatic changes permitted the westward movement along the island chain. This migration was most likely kin structured and resulted in the expansion of subhaplogroups A7 and D2 at a cost to the A3 lineage (see Figure 3). The expansion of subhaplogroup A7 corresponds fairly closely to the time estimate measured through coalescence of mtDNA sequences, 6,529 ± 3,511 years (Zlojutro et al. 2006).

In the second model of Zlojutro et al. (2006), the earliest migrants into the eastern Aleutian Islands had predominantly subhaplogroup A3, a common lineage in Beringia, as reflected by its contemporary presence in Na-Dene, Eskimos, and Aleuts. Approximately 6,500 years ago there was a shift from unifacial to bifacial technology; this shift is attributed to a population intrusion that resulted in the introduction of subhaplogroup D2 (present among the Chukchi) into Beringia. This event produced genetic admixture in the eastern Aleutian Islands and a subsequent expansion into the western regions of the archipelago (made possible by the development of maritime technology), accompanied by the spread of both subhaplogroup D2 and subhaplogroup A7. The Adreanof Islands, further west in the Aleutians, were settled 5,000 years ago, the Near Islands 2,500 years ago, and the Rat Islands 3,500 years ago (Dumond 2001).

The third model of Zlojutro et al. (2006) is similar to the second model in its assumption that the earliest inhabitants of the eastern Aleutian Islands had the A3 mtDNA lineage, but it deviates in its interpretation that the shift from unifacial to bifacial technology was abrupt and a result of intrusion from outside. This model assumes that the shift was a gradual process initiated by indigenous populations. The Arctic Small Tool tradition (ASTt), a complex of traits represented by the Denbigh Flint Complex, appeared in Beringia about 4000 BP and spread throughout Alaska and the Arctic region (Dumond 2001). This rapid expansion generated gene flow into the archipelago, bringing the D2 subhaplogroup. The introduction of this cultural complex (consisting of microblades, burins, and small bifacial points, many without stems or notches) resulted in the population growth and expansion along the archipelago and the spread of the D2 and A7 lineages.

The last model of Zlojutro et al. (2006) assumes that the gene pool of the earliest inhabitants of the eastern islands contained both the D2 and A7 mtDNA lineages. The westerly population expansion, approximately 6000 BP, was fueled by maritime technological innovations and possibly climatic changes. Gene flow, associated with trade, brought the A3 lineage from Eskimo and Aluttiq populations from the Alaska Peninsula and Kodiak Island. This model of gene flow and cultural contact of the Aleuts with their Eskimo neighbors is supported by the clinal distribution of the A and D mtDNA haplogroups in contemporary populations (see Figure 2). The higher incidence of haplogroup A in the eastern Aleutian Islands may reflect

this gene flow. This model may well address the question concerning the mtDNA lineage (A3) shared between the Aleuts and the Athapaskans (Zlojutro et al. 2006). In addition, on the basis of discrete cranial traits, Ossenberg (2003) found that the Chaluka Aleuts clustered with the Eyak of Kodiak Island.

Genetic Structure of the Aleutian Island Populations. Given the distribution of the Aleutian Islands along an east-west axis, from the Alaska Peninsula to Kamchatka, Siberia, it is not surprising that a relationship exists between the geographic and genetic distributions. Although the correlation between geographic distances and genetic distances in indigenous populations of Siberia is high and statistically significant (Crawford et al. 1997), it is more pronounced in the Aleutian Islands. The correlation between geographic and genetic distance matrices (genetic distances r_{ij} computed using allele frequencies of blood groups and protein variants) in Siberia is $r = 0.55$ ($P < 0.001$), whereas the geographic-genetic distance correlation for the Aleutian Islands is $r = 0.72$ ($P < 0.000$) (Crawford 2007). Siberian indigenous populations were reproductively isolated from each other during the Pleistocene by a combination of glacial ice and the inland Mansi Sea, preventing east-west migration. In contrast, the Aleut populations are distributed spatially like beads on a necklace and were populated by fission along family lines and then separated by the sea and harsh environmental conditions.

Inhabitants of the Aleutian Islands whose mothers and grandmothers claim Aleut ethnicity exhibit only the founding haplogroups, that is, either A or D. Thus there appears to be little evidence of Russian, Scandinavian, or English gene flow along the maternal side. In contrast, most of the Y chromosomes are of European origin. Out of a sample of 134 men claiming Aleut ethnicity, only 15% are of Native American origin (Zlojutro 2008). In this issue of *Human Biology*, Katherine Reedy-Maschner poses a rhetorical question: "Where did all the Aleut men go?" The answer is that their genes are still in the Aleut gene pool but amount to only 15%, as measured by the presence of native Y chromosomes.

This research clearly demonstrates that the gene flow into the Aleutian Islands took the form of Russian males with Aleut females in the western and central regions. This direction of gene flow was a stated policy of the Russian colonial administration, which encouraged higher fertility and political control. As a result of this policy, the genetic structure of the Aleuts was preserved on the maternal side but is barely detectable among the paternal lineages.

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