

ESTUDIOS DE ANTROPOLOGÍA BIOLÓGICA

VOLUMEN XIV

*

Editoras

Josefina Mansilla Lory
Abigail Meza Peñaloza



Instituto Nacional
de Antropología
e Historia



Consejo Nacional
para la
Cultura y las Artes



UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
INSTITUTO DE INVESTIGACIONES ANTROPOLÓGICAS
INSTITUTO NACIONAL DE ANTROPOLOGÍA E HISTORIA
ASOCIACIÓN MEXICANA DE ANTROPOLOGÍA BIOLÓGICA
MÉXICO 2009

Comité editorial

Xabier Lizarraga Cruchaga
José Antonio Pompa y Padilla
Carlos Serrano Sánchez
Luis Alberto Vargas Guadarrama

Todos los artículos fueron dictaminados

Primera edición: 2009

© 2009, Instituto de Investigaciones Antropológicas
Universidad Nacional Autónoma de México
Ciudad Universitaria, 04510, México, D.F.

© 2009, Instituto Nacional de Antropología e Historia
Córdoba 45, Col. Roma, 06700, México, D.F.
sub_fomento.cncpbs@inah.gob.mx

© 2009, Asociación Mexicana de Antropología Biológica

ISSN 1405-5066

Prohibida la reproducción total o parcial por cualquier medio sin la autorización
escrita del titular de los derechos patrimoniales

D.R. Derechos reservados conforme a la ley
Impreso y hecho en México
Printed in Mexico

SETTLEMENT OF THE ALEUTIAN ISLANDS AND ITS GENETIC SEQUELAE

Michael H. Crawford

Laboratory of Biological Anthropology, University of Kansas

RESUMEN

El trabajo se enfoca en la última migración de siberianos hacia el continente americano –la dispersión de aleutianos y esquimales. Se examinan: 1) los datos moleculares y arqueológicos de los asentamientos en las Islas Aleutianas; 2) la relación filogenética de los aleutianos y los esquimales hablantes de yupik e inupik; 3) la distribución a lo largo del archipiélago de genes (estructura genética) resultado de los patrones de asentamiento de las islas a lo largo del Holoceno.

PALABRAS CLAVE: origen del hombre americano, aleutianos prehistóricos, haplogrupos de ADN mitocondrial.

ABSTRACT

This chapter focuses on the last migration from Siberia into the Americas –the dispersal of the Aleuts and Eskimos. We will examine: 1) the molecular and archaeological evidence for the settlement of the Aleutian Islands; 2) the phylogenetic relationship of the Aleuts to the Yupik- and Inupik-speaking Eskimos; 3) the distribution of genes along the archipelago (i.e. the genetic structure) resulting from the patterns of settlement of the islands throughout the Holocene.

KEY WORDS: Native Americans origins, prehistoric Aleuts, mtDNA haplogroups.

INTRODUCTION

Since European contact in the 15th century, there has been fascination and controversy surrounding the origins of Native Americans and their settlement of the so-called “New World.” Initial explanations about Native Americans and their origins included: 1) They are one of the lost tribes of Israel; 2) There was Egyptian contact, as evidenced by the pyramids of Mexico; 3) The Native Americans are remnants of the inundated continent of Atlantis (Crawford 1998). Yet, some 18th century naturalists, such as George Louis Leclerc (Comte de Buffon) noted morphological, cultural and linguistic similarities between American Indians and populations of Siberia and correctly placed the ancestors of Native Americans in Asia (Buffon 1749). Similarly, Johann Blumenbach concluded that the American Indians originated in Northeastern Siberia and that several migrations occurred –as evidenced by the greater morphological resemblance between the Eskimos and Asian Mongoloids than between Indians and Siberians (Blumenbach 1775).

In the mid-20th century, typologically-oriented researchers such as Joseph Birdsell, explained the observed variation in populations of the Americas as resulting from multiple migrations of Asians and “proto-Europeans,” represented by the contemporary Ainu of the northern Island of Japan and Asian components emanating from the so-called “Amur region” of Siberia (Birdsell 1951). However, Omoto (1972) on the bases of standard genetic markers demonstrated that the Ainu did not show close affinity to European populations but were an Asian isolate. In the 1980s, the banner of multiple migrations into the Americas was picked up by Greenberg, Turner and Zegura (1986), who on the basis of linguistic data, dental and genetic evidence concluded that the observed variation in the Americas was a result of three contemporaneous migrations occurring in the Holocene. These three migrations resulted in the distribution of Amerinds, NaDene-speakers, and Aleut/Eskimos from the Bering land mass to Terra del Fuego. This controversy was further fueled by the developments in molecular genetics in the 1980s and 1990s with the availability of genomic markers: microsatellites, mitochondrial DNA (mt-DNA), and the non recombining regions of the Y-chromosome (NRY). The initial conclusions, based on DNA fingerprints, was that Native Americans and Siberians shared common ancestry (McComb *et al.* 1995). The first mtDNA

comparison of Siberian and New World populations revealed that American Indians possessed a subset of mtDNA haplogroups (A, B, C, D) that are present in Siberian populations (Torroni *et al.* 1993). Based on mtDNA, Schurr argued that was a minimum of two migrations out-of-Asia (Schurr 2004). Other interpretations of the same data, argued for a single migration into the Americas, followed by differentiation of coastal versus inland colonizers (Merriwether *et al.* 1996). Invariably, the various theories of the settlement of the Americas concluded that the Eskimos and Aleuts formed a single migratory branch, crossed Beringia and doubled back in a westerly expansion towards Siberia (Laughlin *et al.* 1979). In addition a number of Russian archaeologists have suggested that some founding populations island-hopped from Kamchatka in an easterly direction (Black 1983). The idea about the presence of a European contribution to the settlement of the Americas persists to the present in the form of an archeologist, Dennis Stanford. He argues, on the basis of the presence of mt-DNA X haplogroup in prehistoric North America and the similarities between Clovis culture and the European Solutrean tradition, that Europeans had contributed to the settlement of the Americas. Unfortunately, the X haplogroup seen in Native Americans is different from the European form plus there is a 10 000 year temporal disparity between the Solutrean and Clovis cultures (Crawford 2007c).

BACKGROUND

The map in figure 1 shows the 1 500 km expanse of islands stretching from the Alaska Peninsula to the Kamchatka Peninsula in Siberia. This chain of approximately 200 islands was carved out by volcanic activity and is located in a harsh, treeless landscape that includes high wind and frequent fog. Currently, only 11 islands (including the Pribilofs) are inhabited by Aleuts. At first Contact with Russian explorers Bering and Chirikof in 1741, the Aleut population (who called themselves Unangin) has been estimated from 9 000 to 40 000 persons, inhabiting the larger islands (Liapunova 1996, Frolich 2002). After Contact with Russian merchants, explorers and military, the population at its nadir was reduced to fewer than 2 000 individuals. Depopulation was due to an assortment of diseases (smallpox, tuberculosis, measles and influenza), warfare, and forcible relocation in

1825-1828 to the Commander Islands (Medni and Bering) and Pribilof Islands (St. George and St. Paul).

Various theories have been proposed about the origins of the Aleuts, with Laughlin *et al.* 1979, hypothesizing that the Aleuts originated in Siberia and migrated along the southern coastline of the Beringian landmass. This initial migration was followed by a bifurcation of the ancestral population into the Eskimos and Aleuts. The Eskimos moved northwardly along the northern slope of Alaska, while the Aleuts Island hopped in a westerly direction towards Siberia (see figure 2). The Siberian founding group that crossed Beringia inland, expanded into Alaska and eventually became the Amerindians of North and South America. The earliest archaeological evidence for human occupation of the Aleutian Islands dates back to 9 000 years BP in Anagula (proximal to Umnak Island) and Hog Island (off the coast of Unalaska). The archaeological evidence suggests that the Aleuts reached the central Aleutians (Andreanofs) approximately 6 000 years ago (O'Leary 2001) and the far Western Aleutian Islands (Near Islands) 3 500 years ago (West *et al.* 1999). The Aleut westerly expansion from Alaska reached Attu Island, but apparently failed to colonize the Commander

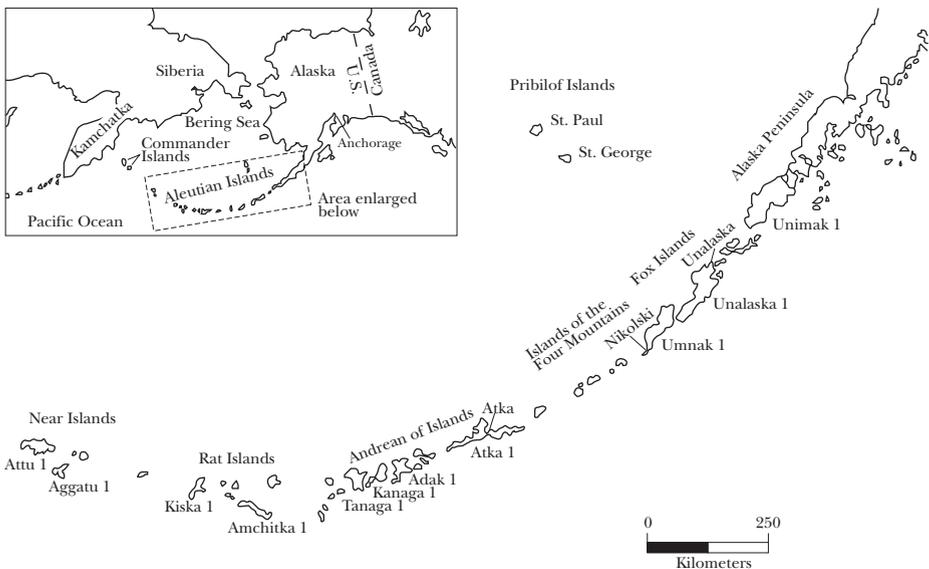


Figure 1. Map of the Aleutian and Pribilof Islands showing the geographic expanse of the Aleutian Archipelago.

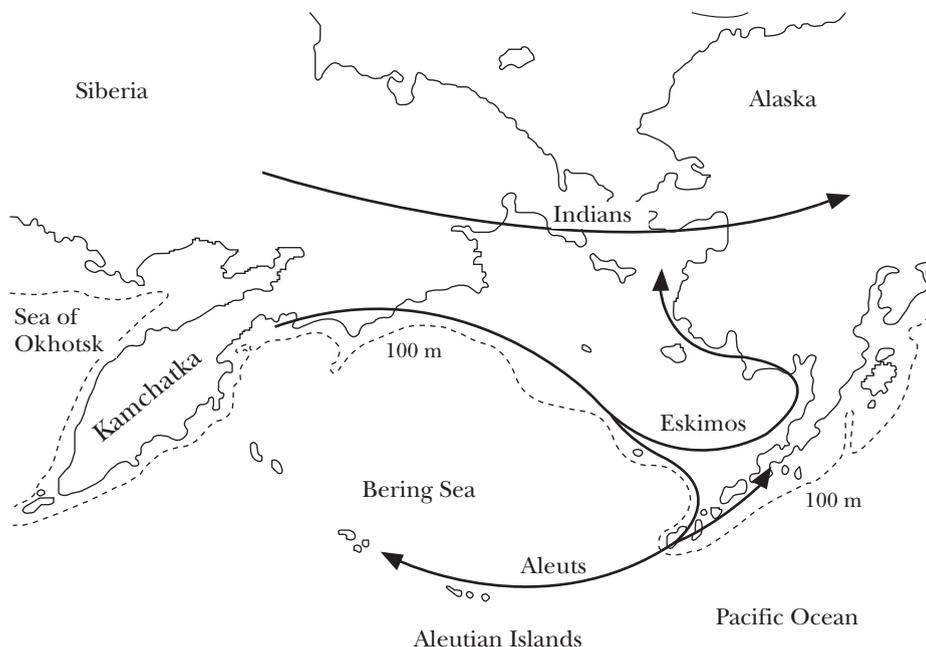


Figure 2. Diagrammatic representation of W. Laughlin's reconstruction of the expansion of the Aleuts, Eskimos and Amerindians out of Siberia (Laughlin *et al.* 1979: 92).

Islands. Aleuts from central and western Aleutian Islands were forcibly relocated by Russians to the Commander Islands (Atka families to Bering Island, Attu families to Medni) between 1825 and 1828 to harvest seal fur and supply the early explorers.

METHODS

A collaborative research program was developed with Dennis O'Rourke (University of Utah) and Dixie West (University of Kansas) to answer a series of questions concerning the anthropological genetics of the Aleuts: Where in Siberia did the Aleuts originate? Were the prehistoric Aleuts members of a single, continuous population that differentiated regionally? What were the evolutionary connections among the Aleuts, Eskimos and NaDene-speakers? Do the contemporary Aleuts reflect the ancient genetic structure or have more recent demographic events obscured prehistoric

patterns? (Crawford 2007a, b). The University of Kansas group focused on DNA variation in contemporary populations of the Aleutian Islands, while the University of Utah researchers attempted to reconstruct peopling of the archipelago based on ancient DNA extracted from skeletal remains.

From 1999 to 2007, field expeditions from the University of Kansas and the Institute of Medical Genetics, Russian Academy of Sciences, Moscow, collected DNA samples from the inhabited Aleutian Islands plus comparative data from indigenous populations of Kamchatka, Russia (Crawford 2007b). This research was approved by the University of Kansas Advisory Committee on Human Experimentation, the Aleut Corporation, Aleutian/Pribilof Island Association and the Tribal Councils from each community. Informed consent was administered to each person who volunteered to participate in this study. The eleven Aleutian Islands that were sampled included: Akutan, Atka, Bering, False Pass, King Cove, Nelson Lagoon, Nikolski, Sand Point, St. George, St. Paul, and Unalaska. In addition, DNA samples were collected from Aleuts relocated to Anchorage, plus Koryak, Itel'men, and Even populations in Kamchatka. Other haplogroup frequency and comparative sequence data on Chukchi, Siberian Eskimo, Alaskan Yupik, and Athapaskans were obtained from the literature.

DNA was extracted from buccal swabs, mouth rinses or blood either in the field using Chelex methods of extraction or in the Laboratory of Biological Anthropology, University of Kansas, using phenol-chloroform method. Standard restriction fragment length polymorphisms (RFLPs) were used to identify mtDNA haplogroups, first through PCR amplification of short segments that contained the restriction sites and then cuts by restriction enzymes. The primer pairs and amplification conditions are described in Rubicz *et al.* 2003. Approximately 400 bp (np 16000-16400) of HVS-I region were directly sequenced using Big Dye Terminator Kits and the Core Facility at the University of Kansas Museum of Natural History. Analytical methods applied to the mt-DNA genotypic frequencies and sequences are described by Rubicz *et al.* (2007).

RESULTS

Aleuts exhibit unique frequencies of only two (A and D) of the five Siberian founding mt-DNA haplogroups (A, B, C, D, and X). Figure 3 plots

the distribution of the A and D haplogroups in the Aleut populations of the archipelago. While the earlier reports, based primarily on samples from central islands, suggested that mtDNA haplogroup A is present in 29% of the Aleuts, and D occurs in 71% of the samples, additional data on the eastern islands indicates greater complexity exists (Rubicz *et al.* 2003, Zlojutro *et al.* 2006). Figure 3 is suggestive of a clinal distribution from the Alaska Peninsula with A being higher in the eastern Aleutian Islands and diminishing in frequencies throughout the central and western islands and the D haplogroup highest among western Aleut communities and reaching fixation on Bering Island. This clinal distribution may be indicative of gene flow from Eskimo groups (who contrast from the Aleuts by exhibiting high frequencies of haplogroup A and low frequencies of D) along the ethnic boundaries on the Alaska Peninsula.

Even though the Aleuts experienced massive population reductions and genetic bottlenecks, considerable variation persists at the mtDNA

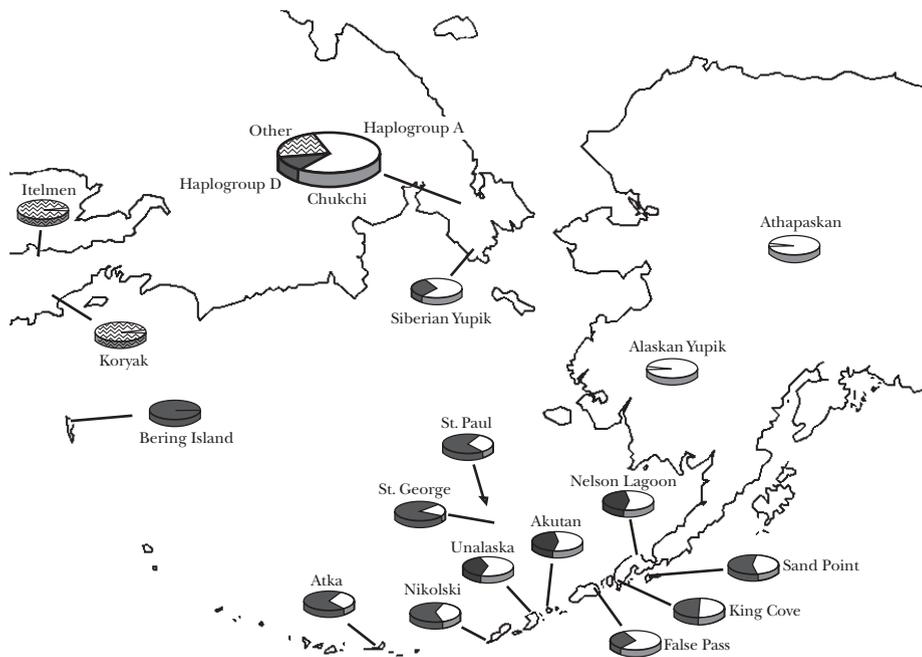


Figure 3. Frequencies of mtDNA haplogroups in the Aleutian Islands, N. E. Siberia and Alaska displayed as pie charts (Crawford 2007a, West *et al.* 2007).

sequence level. Despite known admixture with Russians in the western islands and Scandinavian and British fishermen in the eastern islands, no European mtDNA haplogroups were observed in any Aleuts who claimed native ancestry along the maternal lineage. These data demonstrate that gene flow occurred primarily in one direction from Russian males to the Aleut females.

Table 1 provides a listing of the sample sizes of individuals and the frequencies of the mt-DNA haplogroups in the eleven Aleut Island populations. The sample sizes from some islands are relatively small, e.g. only 10 individuals out of a total of 36 residents of Nikolski claimed Aleut ancestry and were willing to participate in the study. The 35 listed from Bering Island are of Aleut ancestry and claim no Russian admixture. Although larger samples were collected, e.g. $n = 60$ for King Cove, only 33 sequences were from individuals unrelated for the past three generations). Similarly, 60 individuals were sampled at Sand Point, but only 38 sequences were utilized from unrelated individuals.

Based on median network analysis and multi-dimensional scaling, Aleuts are closest to Chukotkan populations (Siberian Eskimos and Chukchi) than to Native American or Kamchatkan populations (Koryaks and

Table 1
Mitochondrial DNA Haplogroup Frequencies in Eleven Aleut
Populations of 267 Unrelated Individuals

Population	Sample Size	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	0.285	0.714
Unalaska	28	0.607	0.393
Total	267		

Itel'men). Aleuts also lack the 16 265 mutation of mtDNA A that is specific to Eskimo populations (Rubicz *et al.* 2003). The two main haplotypes in figure 4 are D1 and D2, with D2 occurring primarily among Aleuts but a few are observed in the Siberian Eskimos and Chukchi. D1 is more diverse than D2 or D3 nodes. None of the D2 (16271C) were found in Amerindian or Athapaskan groups. Median network analysis of HVS-I of A haplogroup individuals (see Rubicz *et al.* 2003) indicated that A7 (subclade of A3-16192T) is an Aleut specific haplotype. A3 occurs at almost 34% frequency in Aleuts. Zlojutro *et al.* (2006) observed that the network of Aleut mt-DNA sequences is composed of three star-like clusters (A3, A7, and D2) that suggest two expansion events: one consisting of A3 lineages approximately 19 900 years BP and the other (A7 and D2 lineages) is Aleut specific and occurred approximately 5 500 years ago.

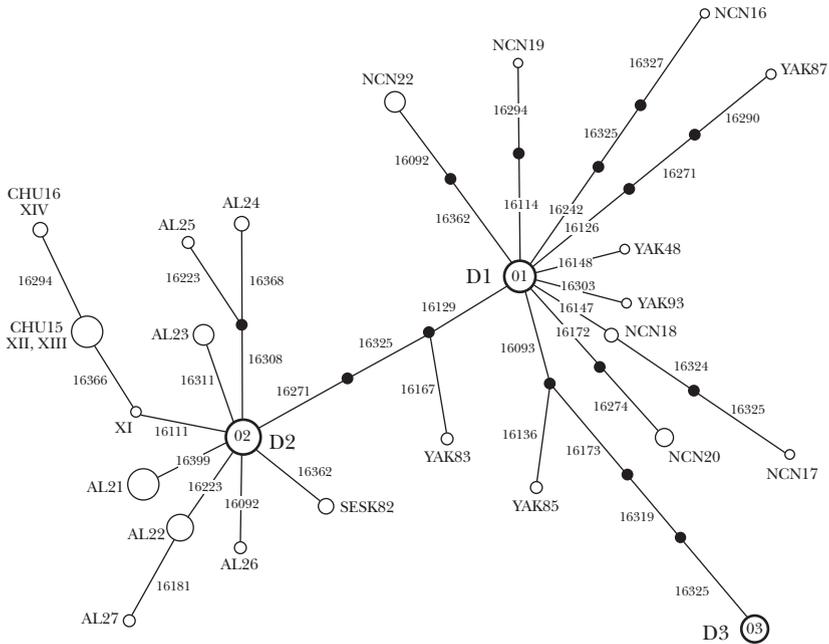


Figure 4. Median Network Analysis of HVS-I sequences of D haplotypes for Bering populations. Population designations are: AL = Aleuts, CHU = Chukotan, KAM = Kamchatkan, GESK = Greenland Eskimo, SESK = Siberian Eskimo, NCN = Nuu-Chah-Nulth, and YAK = Yakima (Rubicz *et al.* 2003).

Chronology

Table 2 provides an estimated age of ancestral and founder nodes in the HVR1 in Aleut populations. The chronology of coalescence is measured by the presence of specific mutations in either the A or D haplogroups. The p statistic was estimated using Network ver. 4.0 calibrated to a rate of 20,180 years per mutation (Zlojutro *et al.* 2006). As seen in table 2, the A2 (16111T) and the D1 mutations found among Aleuts have much greater antiquity and can be traced to Siberia. However, the distinguishing Aleut markers A7 (16212G) and D2 (16271C) have more recent origins of 5000-6000 years BP and apparently correspond to the settlement of the Central and Western Aleutian Islands, following a warming climatic phase.

Table 2
Chronology of Founder Nodes of HVR1 of Aleut populations

Haplotype	Mutation	Cluster	Number	Age
A	16111T	A2	264	29,964 +/- 13,350
A	16212G	A7	33	6,539 +/- 3,551
D	16271C	D2	130	6,035 +/- 2,885

A ubiquitous private allele (a nine trinucleotide repeat-RA) at a microsatellite locus D9S1120 was detected in all populations of the Americas that we tested (Schroeder *et al.* 2007). Figure 5 provides a distribution of the repeat allele in all of the Siberian and Native American populations tested to date. This D9S1120 RA occurs among the Chukchi of Chukotka and the Koryaks of Kamchatka but is absent in all other Siberian groups. All North and South American populations display this allele with frequencies 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, suggesting the occurrence of a mutation in Siberia that was carried into the Americas by a single founding population. However, the presence of this mutation among the Koryaks and Chukchi is intriguing. Although mt-DNA sequences indicate that the Aleuts cluster with the Chukchi, the Koryaks are genetically distinct and are unlikely ancestors of the Aleuts.

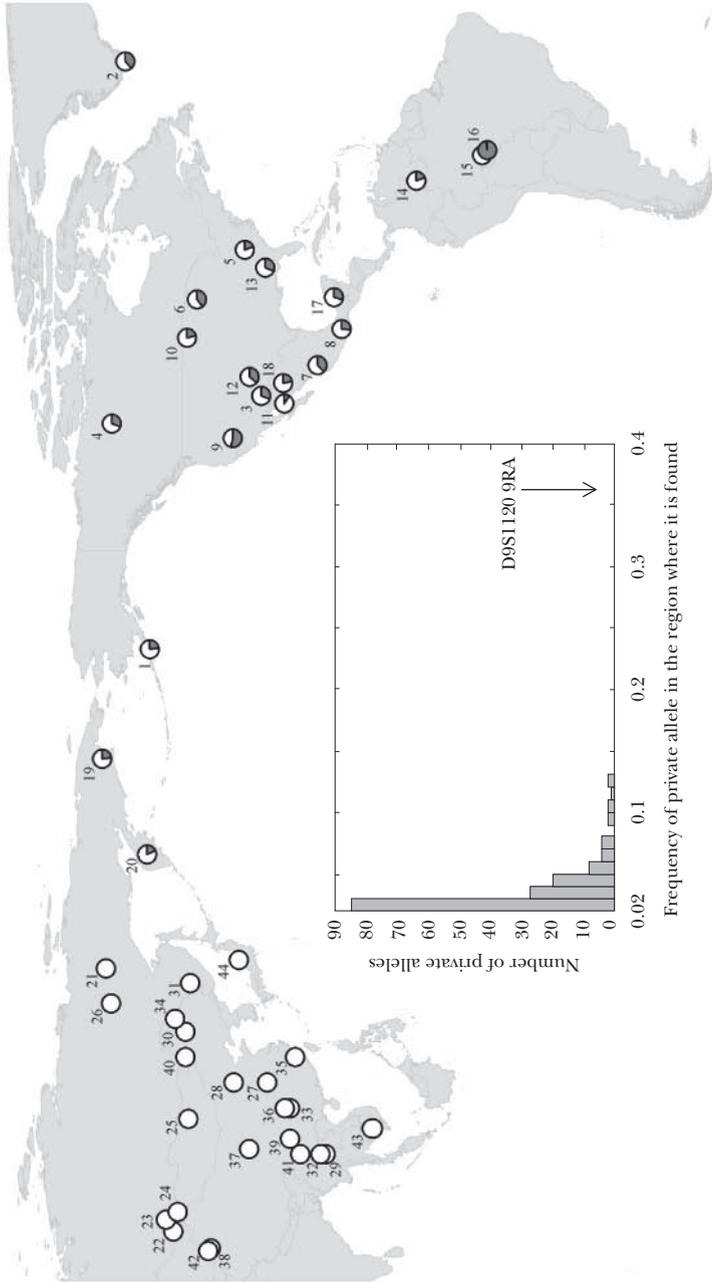


Figure 5. The distribution of the ubiquitous D9S1120.9RA private allele (Schroeder *et al.* 2007).

Genetic diversity

Nucleotide diversity is lowest for the Bering Island Aleuts (0.0007) than in any Arctic population studied to date (Rubicz 2007). Siberian Eskimos have the next lowest nucleotide diversity, followed by West Greenland Eskimos (0.0051) and St. George Aleuts. According to Rubicz (2007), the total Aleut sample exhibits similar nucleotide diversity (0.0110) as found in the aggregated St. Paul community (0.0101).

Genetic structure

Given the geographical expanse of the Aleutian Islands along an east-west axis, from the Alaska Peninsula to Kamchatka, it is not surprising that an intimate relationship exists between geographic and mt-DNA intermatch genetic distributions. While a significant Mantel correlation between geographic and mt-DNA genetic distances matrices has been demonstrated in the indigenous populations of Siberia, $r = 0.55$, $P > 0.001$, it is even more pronounced in the Aleutian Islands (Crawford *et al.* 1997). The relationship between GEO matrix (geographic distance in kilometers between populations) and GEN (genetic distances based on R-matrix analysis) for the Aleutian Islands is $r = 0.72$, $P > 0.000$ (Crawford 2007a). Siberian indigenous populations were reproductively isolated from each other during the Pleistocene by a combination of glacial ice and the inland Mansi Sea, preventing temporary east-west migration. In contrast, the Aleut populations are distributed spatially like beads along a necklace. Mantel tests comparing genetic distances among Aleutian Island populations based on Y-chromosome haplotype distances and geographic distances yield a non-significant correlation ($r = 0.379$, $p > 0.130$ n.s.). Similar Mantel comparisons between mtDNA intermatch distances and Y STRs (Nei's Da) yield a non significant result ($r = 0.26$, $p = 0.164$ n.s.). Mt-DNA and Y STR genetic distance do not correlate because of gene flow primarily from Russian males to Aleut females.

The AMOVA approach has been used for hierarchical analysis of genetic diversity in a set of sampled populations (Excoffier *et al.* 1992). Variances based on mtDNA sequences were partitioned using this AMOVA method of Excoffier *et al.* (1992) on eleven island populations (Crawford 2007a). AMOVA analysis reveals that 86% of the variance is among residents

within island populations, while 14% is among populations (Rubicz *et al.* 2003). AMOVA analysis reveals that most of the genetic variation based on mtDNA sequences occurs within the population.

Dupanloup *et al.* (2002) have developed a method of defining groups of populations that are geographically homogeneous and maximally differentiated from each other by identifying genetic barriers between inferred groups. Two dimensional space is constructed using adjoining convex polygons (i.e. Voronoi) from the geographical location of n populations. An *a priori* partition of n populations into K groups is initially chosen at random and the genetic barriers are identified as edges of the Voronoi polygons. The SAMOVA algorithm finds the maximally differentiated groups that correspond to predefined barriers by maximizing the proportion of total genetic variance due to differences between groups.

Figure 6 provides a combination of a multidimensional plot of Aleut, Kamchatkan, Chukotkan and Central Alaskan populations with a plot of the SAMOVA based genetic barriers (Crawford 2007a). This plot reveals that barriers exist between the Alaskan Yupik Eskimos, Kamchatkan and

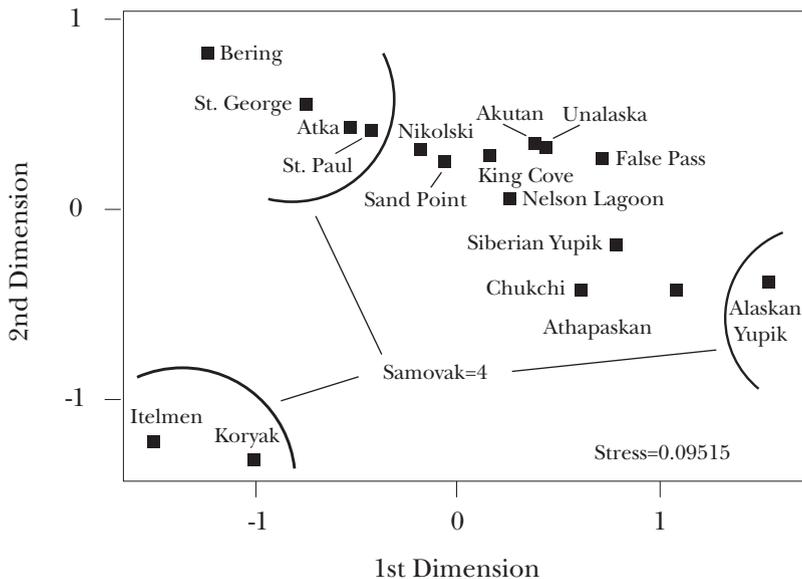


Figure 6. Multidimensional Scaling (MDS) plot based on mt-DNA sequences combined with a SAMOVA plot of the genetic discontinuity among populations of the Aleutian Islands, Kamchatka and Alaska (Crawford 2007a).

Aleut populations. The Chukchi and the Siberian Eskimos cluster with the Aleut groups. The western Aleut populations cluster with the two aggregated communities of the Pribilof Islands and collective are distinct from the other Aleut groups.

Admixture estimates

Based on mtDNA haplogroups, the Aleuts of the Archipelago appear to have experienced no gene flow from European populations. Yet, morphologically, historically here is evidence of considerable admixture of western Aleuts and Russians and eastern Aleuts and Scandinavians and British fishermen. There was one report of the presence of haplogroup C on St. Paul of the Pribilof Islands, not found in Aleut populations, but present in Athapaskan groups (Merriwether *et al.* 1996). Based on those data, it appears that more than 10% of the St. Paul gene pool has Athapaskan genes. However, this community has experienced less than 1% European admixture (Rubicz *et al.* 2003).

Different genetic markers provide vastly different proportions of admixture in the Aleut populations. When nine recombinant autosomal STRs (D3S1358, vWA, FGA, D8S1179, D21S11, D18S51, D13S317, D7S820 and Amelogenin) were used to measure admixture on Bering Island, we estimated that 40% of the gene pool was of Russian origin and 60% was Aleut. In contrast, non-recombining portions of the Y-chromosome (NYR) lineages reveal that only 15% of the Y-chromosomes are of Native origins (lineages Q or Q3), while 85% of the Y-chromosomes are of Russian, Western European or Central Asian origin (Rubicz 2007). Thus, these findings support the culturally based interpretation that most of the marriages were between Russian males and Aleut females (Reedy-Maschner 2008).

DISCUSSION

This study documents how unique historical events have evolutionary sequelae. Despite the demographic upheavals following contact with Russians in the 18th century, depopulation, genetic bottleneck, population relocation and aggregation, the underlying genetic structure of the

populations of the Aleutian Islands is etched in the mt-DNA sequences. Genetic distances calculated from the observed molecular variation are highly correlated to geography –preserving the regional genetic differentiation of the populations of the Aleutian Archipelago following the peopling events. Similar differentiation is observed in Aleut dialects with distinct features observed in western, central and eastern islands. However, because of the direction of gene flow from Russian males to Aleut females, no statistically significant relationship was observed between geographical distances and genetic distances measured by NRY markers. The populations of the Aleutian Archipelago provide a dramatic example of genomic asymmetry between mt-DNA and NRY regions of the genome.

Aleutian Islands offer examples of the action of genetic drift through the decrease of genetic variability. The founder effect can be seen on Bering Island with the fixation of the D haplogroup. The Aleut populations display the presence of two of the five founding haplogroups –A and D. The frequencies of these haplogroups vary from island to island, but approximating a clinal distribution in the incidence of D from the eastern islands to the Commander Islands, where D is fixed at 100%. Derebeneva *et al.* 2002, acknowledge the existence of both A and D in the Aleut parental populations but then state: “It is apparent that haplogroup A mtDNAs were present in the parental Aleut groups residing on the Aleutians ...but then were lost through genetic drift, because of the genocide of the natives at the end of 18th century.” (Derebeneva *et al.* 2002: 420).

The likelihood of fixation due to genetic drift in five generations is remote (Rubicz *et al.* 2003). The loss of A haplogroup due to differential mortality due to genocide is also low. The most likely explanation for the loss of A haplogroup and the fixation of D, is the founder effect. The families brought to Bering Island consisted of individuals disproportionately of D haplogroup.

Acknowledgements

This research was supported in part by grants from the National Science Foundation: OPP-999-0590, and OPP-0327676. I would like to thank the Aleut Corporation, Aleutian/Pribilof Island Association and the Tribal Councils from: Akutan, Atka, Bering, False Pass, King Cove, Nelson Lagoon, Nikolski, St. George, St. Paul, and Unalaska. This research could

not have been possible without research assistants: Rohina Rubicz and Mark Zlojutro, and Aleut researchers Alice Petrivelli and Liza Mack. My thanks to my collaborators, Dixie West and Dennis O'Rourke.

REFERENCES

BIRDSELL, J.

- 1951 The problem of the early peopling of the Americas as viewed from Asia, *Physical Anthropology of the American India*: 1-68, Ed. W. Laughlin, Viking, New York.

BLACK, L.

- 1983 Some problems in the interpretation of Aleut prehistory, *Arctic Anthropology*, 20: 49-78.

BLUMENBACH, J. F.

- 1775 *De Generis Humani Varietate Nativa*, Vandenhoeck et Ruprecht, Göttingen.

BUFFON, C. D. G.

- 1749 *Historie Naturelle*, L'imprimerie royale, Paris.

CRAWFORD, M. H.

- 1998 *The Origins of Native Americans. Evidence from Anthropological Genetics*, Cambridge University Press, Cambridge.
- 2007a Genetic structure of circumpolar populations: A synthesis, *American Journal of Human Biology*, 19: 203-217.
- 2007b The importance of field research in anthropological genetics: Methods, Experiences and results, en M.H. Crawford (ed.), *Anthropological Genetics. Theory, Methods and Applications*, pp. 79-111, University of Cambridge Press, Cambridge.
- 2007c Review of *Handbook of North American Indians. Vol. 3. Environment, Origins, and Population*, D.H. Ubelaker (ed.), Smithsonian Institution, *American Journal of Human Biology*, 19(6): 888-890.

CRAWFORD, M. H., J. T. WILLIAMS, R. DUGGIRALA

- 1997 Genetic structure of the indigenous populations of Siberia, *American Journal of Physical Anthropology*, 104: 177-192.

DERBENEVA, O., R., SUKERNIK, N. V. VOLODKO, S. H. HOSSEINI, M.T. LOTT, D. C. WALLACE

2002 Analysis of mitochondrial DNA diversity in the Aleuts of the Commander Islands and its implications for the genetic history of Beringia, *American Journal of Human Genetics*, 71: 415-421.

DUPANLOUP, I., S. SCHNEIDER, L. EXCOFFIER

2002 A simulated annealing approach to define genetic structure of populations, *Molecular Ecology*, 11: 2571-2581.

EXCOFFIER, L., P. SMOUSE, J. QUATTRO

1992 Analysis of molecular variance inferred from metric distance among DNA haplotypes: Application to human mitochondrial DNA restriction data, *Genetics*, 131: 479-491.

FROLICH, B.

2002 Aleutian settlement distribution on Adak, Kagalaska, Buldir and Attu Islands, Alaska, en B. Frohlich, A. Harper, and R. Gilberg. (eds.), *To the Aleutians and Beyond: The Anthropology of William S. Laughlin*, Publications of the National Museum, Ethnographic Series, vol. 20, The National Museum of Denmark, Copenhagen.

GREENBERG, J. H., C. G. TURNER AND S. L. ZEGURA

1986 The settlement of the Americas: A comparison of the linguistic, dental, and genetic evidence, *Current Anthropology*, 27: 477-947.

LAUGHLIN, W. S., J. JORGENSEN, B. FROHLICH

1979 Aleuts and Eskimos: Survivors of the Bering Land Bridge Coast, en W. S. Laughlin and A. B. Harper (eds.), *The First Americans: Origins, Affinities, and Adaptations*, pp. 91-104, Gustav Fischer, New York.

LIAPUNOVA, R. G.

1996 *Essays on the ethnography of the Aleuts*. Rasmuson Library Historical Translation Series, J. Shelest, translation, vol. 9, University of Alaska Press, Fairbanks.

MCCOMB, J., N. BLAGITKO, A. COMUZZIE, W. R. LEONARD, R. I. SUKERNIK, M. S. SCHANFIELD, M. H. CRAWFORD

1995 VNTR variation in Siberian indigenous populations, *Human Biology*, 67 (2): 217-229.

MERRIWETHER, D. A., W. W. HALL, A. VAHLNE, R. E. FERRELL

- 1996 mtDNA variation indicates Mongolia may have been the source for the founding population for the New World, *American Journal of Human Genetics*, 59: 204-212.

O'LEARY, M.

- 2001 Volcanic ash stratigraphy for Adak Island, central Aleutian archipelago, D. Dumond (ed.), *Archaeology in the Aleutian Zone of Alaska. Some Recent Research*, University of Oregon Anthropological, Papers 58, University of Oregon Press, Eugene, Oregon.

OMOTO, K.

- 1972 Polymorphic and genetic affinities of the Ainu of Hokkaido, *Human Biology of Oceania*, 1: 278-288.

REEDY-MASCHNER, K.

- 2008 Where did all the Aleut men go?: Aleut male attrition and related patterns in Aleutian demography and social organization, en M. H. Crawford, D. H. O'Rourke, and D. L. West (eds.), *The Aleutian Islands: Archaeology, Demography and Genetics*, University of Utah Press, Salt Lake City, Utah.

RUBICZ, R. C.

- 2007 *Evolutionary Consequences of Recently Founded Aleut Communities in the Commander and Pribilof Islands*, Unpublished Ph.D. dissertation, University of Kansas, Lawrence, KS.

RUBICZ, R. C., T. G. SCHURR, P. L. BABB, M. H. CRAWFORD

- 2003 Mitochondrial DNA variation and the origins of the Aleuts, *Human Biology* 75: 809-835.

RUBICZ, R. C., P. E. MELTON, M. H. CRAWFORD

- 2007 Molecular markers in anthropological genetic studies, en M. H. Crawford (ed.), *Anthropological Genetics. Theory, Methods and Applications*, pp. 141-186, Cambridge University Press, Cambridge.

SCHROEDER, K. B., T. G. SCHURR, J. C. LONG, N. A. ROSENBERG, M. H. CRAWFORD, L. A. TARSKALA, L. P. OSIPOVA, S. I. ZHADANOV, D. G. SMITH

- 2007 A private allele ubiquitous in the Americas, *Biology Letters. Population Genetics*, 3: 218-223.

SCHURR, T. G.

2004 The peopling of the New World: Perspectives from molecular anthropology, *Annual Review of Anthropology*, 33: 551-583.

TORRONI, A., R. I. SUKERNIK, T. G. SCHURR, Y. B. STARIKOVSKAYA, M. F. CABELL, M. H. CRAWFORD, A. G. COMUZZIE, D. G. WALLACE

1993 Mitochondrial DNA variation of aboriginal Siberians reveals distinct genetic affinities with native Americans, *American J. Human Genetics*, 53(3): 563-590.

WEST, D., C. LEFEVRE, D. CORBETT, A. B. SAVINETSKY

1999 Radiocarbon dates for the Near Islands, Aleutian Islands, Alaska, *Current Research in the Pleistocene*, 16: 83-85.

WEST, D., M. H. CRAWFORD, A. B. SAVINETSKY

2007 Genetic, prehistory and the colonization of the Aleutian Islands, *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 98: 47-57.

ZLOJUTRO, M., R. C. RUBICZ, E. J. DEVOR, V. A. SPITSYN, S. V. MAKAROV, K. WILSON, M. H. CRAWFORD

2006 Genetic structure of the Aleuts and Circumpolar populations based on mitochondrial DNA sequences: A synthesis, *American Journal of Physical Anthropology*, 129(3): 446-464.

