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Genetic Diversity and Relationships of Tlingit Moieties

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Abstract

The Tlingit from Southeast Alaska belong to the Northwest Coast cultural tradition, which is defined by regionally shared sociocultural practices. A distinctive feature of Tlingit social organization is the matrilineal exogamous marriage system among clans from two opposite moieties: the Raven/Crow and Eagle/Wolf. Clan and moiety membership are determined by matrilineal descent, and previous genetic studies of Northwest Coast populations have shown that there is a relationship between clan membership and genetic variation of matrilines and patrilines. To further understand this association, mitochondrial DNA (mtDNA) sequences from the Tlingit (n=154) are examined. By comparing mtDNA with moiety membership information, we explore the impact of marriage traditions among the Tlingit with their observable genetic variation. At the genetic level, the results support cultural persistence of Tlingit maternal moiety identity despite the negative impacts of European colonization. Our study additionally illustrates the relevance of data derived from Tlingit oral traditions to test hypotheses about population history on the Northwest Coast.

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To understand demographic processes and migrations histories of Northwest Coast societies (Fig. 1) it is essential to contextualize the genetic distribution and cultural characteristics of ancient and modern populations in the region today (Lindo et al. 2017). In addition to archaeological and genetic data, oral traditions are valuable sources of information generated by firsthand observers that should be considered in the scientific study in the Americas (Echo-Hawk 2000). For the Tlingit, oral traditions are intangible properties, a fundamental part of their ideological system whose narrative contains information about clan origins, interrelationships, migrations, and first settlements (Worl 1998). Here, we seek to explore Tlingit clan and moiety systems by integrating genetic data with oral history and the ethnographic record. We examined Tlingit mitochondrial DNA (mtDNA) sequences in terms of clan membership information to elucidate marriage traditions from a biocultural perspective.

Background

The Tlingit share a number of features with other Norwest Coast Cultures which includes a subsistence system heavily reliant on marine resources, distinctive woodworking technology used for the production of ceremonial and utilitarian items, formline art, hierarchical social organization, and spiritual beliefs based on animism (Holm 1965; Suttles 1990; Suttles and Jonaitis 1990; Matson and Coupland 1995; Ames and Maschner 1999; Moss 2011). However, most anthropological research on the Tlingit has focused on investigating their origins and social-political evolution using ethnohistorical, anthropological, and archaeological information (Swanton 1908, 1909, 1911; Krause 1956; de Laguna 1960, 1990; Olson 1967; Emmons and de Laguna 1991; Goldsmith and Haas 1998; Worl 1998; Hope and Thornton 2000). Early archaeological sites in this region include On Your Knees Cave (OYKC) in Prince of Wales

Island (Kemp et al. 2007; Dixon et al. 2014), Ground Hog Bay 2 in the Chilkat Peninsula (Ackerman 1968), and Hidden Falls in Baranof Island (Davis 1989; Ackerman 2007), with dates ranging from 10,500 to 7,500 years before present (YBP), and are defined by microblade assemblages. The form and function of these tools, suggest an increasing reliance on marine resources through time (Matson and Coupland 1995). By the Late Holocene, complex socio-political groups, similar to those reported from ethnohistorical sources, inhabited the northern Northwest Coast. In southeast Alaska, house-depression villages and fortified sites from the Late Holocene resemble Tlingit settlements observed at the time of European contact (Ames and Maschner 1999). Artifact types associated with the ethnographic Tlingit date to as early as 1600 YBP (Moss et al.1989; Moss 2004, 2011).

Moiety and Clan System

The Tlingit follow an exogamous matrilineal system in which clan membership and social status are directly transmitted from mother to children through the concept of *haa tláa yinaanáx* (our mother's side) (Emmons and de Laguna 1991). Clans belong to either of two moieties or "opposite side" (*guneit kanaayi*) descent groups (Swanton 1908:424; Worl 1998:36; Tooker 1971): Raven/Crow (*Yeil naa* or *Tléix' Laayaneidí*) or Eagle/Wolf (*Cha'aak'/Gooch naa* or *Tléix' Shangukeidí*). Moiety members had reciprocal ceremonial duties during important events in the life cycle, but the most important function was marriage regulation. Each moiety is further subdivided into clans, the number of which ranges from 60 to over 70, which, in turn, are divided into lineages or houses (*hit*) (Emmons and de Laguna 1991; de Laguna 1990; Goldsmith and Haas 1998; Hope and Thornton 2000; Hope et al. 2003).

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Members of a clan only married individuals from an opposing moiety (Olson 1967). Political organization centered on clan membership, and clan identity was integral to Tlingit society. The clans possessed territories, rights to resources, and trade routes (de Laguna 1990). Oral accounts and ethnographic literature indicate that communities were initially inhabited by a single clan (de Laguna 1990:213; Worl 1998:43), expanded and diversified to occupy multiple settlements. Thus, clans were not geographically restricted (Emmons and de Laguna 1991). Contemporary clans are products of complex fission and fusions of more ancient clans, making clan histories deeply connected. Oral histories indicate that new clans existed independently, both ceremonially and politically from a parent clan (Worl 1998:123). Russian Orthodox and Protestant missionization, along with the imposition of Russian and American legal practices regarding marriage in the second half of the 19th century, affected not only the role marriage played in society but also altered traditional gender/status roles of women as well rules of inheritance and wealth in Tlingit society (Dauenhauer and Dauenhauer 1994; Kan 1996).

The Tlingit were also distributed in seventeen tribally distinct groups or *kwáans* (Goldschmidt and Haas 1998; de Laguna 1990; Emmons and de Laguna 1991; Hope and Thornton 2000; Hope et al. 2003) (Fig. 2). The *k̲wáan* is interpreted as a geographic unit rather than a meaningful social or political category. Each *k̲wáan* consisted of one or more matrilineal clans that shared one or multiple winter villages. A *k̲wáan* remained an independent body which did not recognize tribal authority or a central governing figure (Emmons and de Laguna 1991:22).

Oral History and Moiety Origins

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Most Tlingit clans trace their origins to the Tsimshian coast, around the mouth of the Skeena River (Swanton 1908, 1909; Olson 1967; de Laguna 1960, 1990; Emmons and de Laguna 1991; Worl 1998), and migrated from present-day Tsimshian territory along a northward route. Migration histories depict movements from the interior to the coast through the Nass, Stikine, and Taku Rivers (de Laguna 1990:205-206). Swanton (1908) and Emmons and de Laguna (1991) hypothesize that the two Tlingit moieties originated from the interaction and intermarriage of two separate Tlingit populations, with oral histories supporting a model where the Raven and Eagle/Wolf moiety clans reached southeast Alaska following different routes, and at different times. The oral accounts also reveal that when later groups arrived in Southeast Alaska, they found an existing population belonging to the Raven moiety (Swanton 1908:407). In this scenario, the first clans that belong to the Raven moiety moved from the Tsimshian Peninsula northwards to the Skeena, Nass, Stikine, and Taku rivers, and later Eagle moiety clans originated from the interior (de Laguna 1990:206). Likewise, Worl (1998, 2005) supports the idea that an ancestral population of the Raven moiety initially moved into the Tlingit territory. Worl's (2005) analysis of the oral traditions also reveals that Eagle/Wolf moiety clans track their migrations from the interior to the coast, and then north, while the Ravens trace theirs from the Nass and Skeena Rivers area. The ethnographic information supports the above scenario. These arguments, derived from anthropological studies and oral history, can be used to explore biocultural information in order to illuminate the migration history of the Tlingit.

Previous Genetic Research

The integration of genetic analyses in anthropology is useful for testing hypotheses about population histories. When combined with evidence from culture history and language, genetic

tools are useful for reconstructing the past (Szathmáry 2017). The Northwest Coast populations were among the first cultural groups to attract the attention of researchers who sought to use genetic evidence to evaluate population histories and relationships (Schurr et al. 1990; Ward et al. 1991; Shields et al. 1993; Szathmáry 1993; Torroni et al. 1993; Ward et al.1993; Lorenz and Smith 1996). Regionally, the Northwest Coast cultures share similarities in their mtDNA haplogroup distributions. Coastal populations such as the Tlingit, Haida, and Tsimshian tend to exhibit high frequencies of haplogroup A, and moderate to low frequencies of haplogroups B, C, and D (Shields et al. 1993; Torroni et al. 1993; Ward et al. 1993; Lorenz and Smith 1996, 1997). This genetic pattern seems to have been already well established around the time the Northwest Coast tradition emerged (e.g. before 3000 YBP), and haplotypes observed in the region have shown continuity throughout time (Raff et al. 2011; Cui et al. 2013; Lindo et al. 2017).

Schurr and colleagues (2012) studied the genetic diversity of modern Tlingit and Haida populations, performing statistical and phylogenetic analyses on mtDNA and Y-chromosomal data in order to investigate the influence of migration and cultural practices (marriage) as well as the relationship between linguistic groups. A majority of Tlingit and Haida individuals belonged to subhaplogroup A2 with a lower frequency belonging to either haplogroup C or D (Schurr et al. 2012). Both populations exhibited less haplotype variation compared to Artic and central Northwest Coast populations (Schurr et al. 2012). Genetic distances (F_{ST}) of Northwest Coast populations were high, indicating considerable population differentiation in the region. Finally, Schurr and colleagues (2012) found a high correspondence between mitochondrial haplotypes and maternal moiety affiliation. The researchers found a strong association between geographic range, clan identity, and genetic composition among Tlingit individuals, and were able to differentiate haplotypes that were exclusive of each moiety.

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Research Objectives

Mitochondrial DNA collected from Tlingit volunteers was used to address the relationships between maternal genetic composition and marriage traditions in Tlingit cultural history. The general objective is to expand the knowledge about the genetic patterns of the northern Northwest Coast groups by integrating genetic data of modern Tlingit populations in the context of oral history, ethnographic accounts, and marriage traditions. Thus, this study aims to test the hypothesis that clan social customs have had a profound impact on the modern genetic composition of the two moieties: Eagle/Wolf and Raven/Crow. A main assumption is that sociocultural signatures of marriage customs are traceable through mtDNA haplotype patterning and moiety membership. If this holds true, the clans found in the Eagle/Wolf moiety should have distinctive matrilineal lineages from those observed in Raven moiety clans. According to the reviewed ethnographic studies and oral histories, both groups represent two different populations that could, in turn, reflect two separate population movements into the historical Tlingit territory of Southeast Alaska. Swanton (1908), Emmons and de Laguna (1991) and Worl (1998, 2005) support the idea that clans found in the Raven moiety are descendants of the first Tlingit group that reached southeast Alaska. In this scenario, the two Tlingit moieties are descendants of two distinct ancestral populations.

Materials and Methods

Sample Collection

Saliva samples from a total of 236 volunteers were obtained during Celebration 2008, a biannual cultural festival organized by the Sealaska Heritage Institute to commemorate the local traditions of Tlingit, Haida, and Tsimshian cultures (Supplemental Tables 1 and 2). This included 154

study participants/volunteers who self-identified as Tlingit. With the help of the local community, we also collected genealogical and clan information from the participants. Samples and genealogical data were collected with approval of Washington State University IRB (IRB No. 10379) and Sealaska Heritage Institute. Data on genealogical relatives was not collected, therefore related individuals were not removed from this study. Additionally, precise geographical information regarding *kwáan* membership was not obtained.

Mitochondrial DNA Extraction and Analysis

DNA was extracted from saliva samples with the NORGEN Biotek Corp. Saliva DNA Isolation Kit. Mitochondrial DNA variation was analyzed by screening the samples obtained in this study for markers that define mtDNA haplogroups A, B, C, and D (Forster et al. 1996; Schurr et al. 1990). The polymorphisms that define the haplogroups are: A) *Hae*III site gain at nucleotide position (np) 663; B) A 9 bp deletion in region V of the mtDNA genome, between Cytochrome oxidase II and tRNA-LYS genes; C) *Alu*I site gain at np 13,262; D) *Alu*I site loss at np 5176. Nucleotide positions (nps) 16001– 16556 of the mtDNA genome were sequenced in two or three overlapping fragments following Kemp and colleagues (2010). Sequencing was conducted by the College of Agricultural and Environmental Sciences Genomics Facility at the University of California, Davis. Sequences were aligned to the Cambridge Reference Sequence (Anderson et al. 1981; Andrews et al. 1999) in Sequencher (v. 4.5).

Comparative Analyses

In order to contextualize the mtDNA variation identified, the Tlingit dataset produced for this study (n=154) was compared to previously reported northern North American indigenous

mtDNA hypervariable segment I (HVSI) sequences, as well as two Artic populations. The datasets include: the Tlingit from Yakutat Bay and Hoonah in Alaska (Schurr et al. 2012 n=54), Haida (Schurr et al. 2012 n=20; Ward et al. 1993 n=41; this study n=14), Alaskan Athapaskan (Shields et al. 1993 n=18; this study n=1), Aleut (Rubicz et al. 2003 n=163), Bella Coola (Ward et al. 1993 n=40), Nuu-Chah-Nulth (Ward et al. 1991 n=63), Tsimshian (Achilli et al.2013 n=1; Cui et al. 2013 n=2; this study n=5), Canadian (n=96) and Greenland Inuit (n=261) (Helgason et al. 2006) (Supplemental Table 3 and Fig. 3).

Multivariate Analysis

Fixation index (F_{ST}) values were calculated for all pairs of populations in Arlequin (v. 3.5.1.3) (Excoffier and Lischer 2010) (Table 1). Pairwise genetic distances between Tlingit and comparative populations were estimated from HVSI data using the Tamura-Nei model of evolution (Tamura and Nei 1993). The calculations were made in Arlequin (v. 3.5.1.3) (Excoffier and Lischer 2010). These inter-population values were then used as a distance matrix input for a Multi-Dimensional Scaling (MDS) plot using STATA 12 (Fig. 4**)**.

Phylogenetic Analysis

To explore the genetic structure of the Tlingit clan system with neighboring populations, two median-joining networks of haplotypes belonging to haplogroups A were built in Network (v.4.6.1.2) using mtDNA first hypervariable region of the mitochondrial genome (HVSI). The first network consisted of HVSI (nps 16041-16383) sequences from Tlingit, (this study n=142; Schurr et al. 2012 n=55), Haida (this study n=13; Schurr et al. 2012 n=19; Ward et al. 1993

n=21), Tsimshian (n=3), and Alaskan Athapaskan (this study n=1; Shields et al. 1993 n=18) populations (Fig. 5).

In order to assess moiety genetic variation, a median-joining network of HVSI haplotypes belonging to haplogroup A2 (Fig. 6). For this network, a subset of Tlingit individuals that reported clan maternal ancestry to at least one generation was used (Raven n=47; Eagle n=35). To minimize the problem of reticulation within the network, data on rate heterogeneity on the HVSI of the human mitochondrial genome obtained by Meyer et al. (1999) were used to modify the weights of mutational positions that showed higher relative mutation rates than average. The weight values for these positions were assigned as described by Kemp and colleagues (2010). In this way, reticulation due to mutational "hotspots" was reduced.

Analysis of Molecular Variance

A hierarchical analysis of molecular variance (AMOVA) was conducted in order to explore the genetic structure among the Tlingit. Sequences were sorted by moiety, excluding those composed of a single individual. The analysis used data from 76 Tlingit (Raven=42; Eagle/Wolf=34) individuals for whom both moiety and clan information were available (Table 2). A second AMOVA was conducted removing two individuals of Tagish descent that belonged to haplogroup B in order to assess the impact of this variation in the final results (Table 3).

Results

Mitochondrial DNA Variation

The majority of Tlingit individuals from this study exhibit haplogroup A2 haplotypes (Supplemental Table 2 and Table 4). The two most common A2 lineages are types 1 (n=44), and

2 (n=41) (Table 4). The former lineage is widespread in the Americas (Shields et al. 1993; Torroni et al. 1993; Ward et al. 1993; Lorenz and Smith 1996; Forster et al. 1996; Helgason et al. 2006; Schurr et al. 2012), while the latter is more restricted to populations of the Northwest Coast, such as Nuu-Chah-Nulth, Bella Coola (Lorenz and Smith 1997; Malhi et al. 2004), Haida, Tlingit (Schurr et al. 2012), as well as populations from California (Johnson and Lorenz 2006), the American Southwest, Mexico (Kemp et al. 2010), and South America (Fuselli et al. 2003). Type 3 with a transition at nucleotide position (np) 16519 relative to type 2, was shared among 6 Tlingit individuals. Type 7 was present in about 10% of Tlingit sequences (n=17). This haplotype has been previously reported in 19 Tlingit individuals (Schurr et al. 2012).

Twelve percent of Tlingit individuals (n=19) belonged to type 4, a common A2 lineage in the Americas. This mtDNA HVSI haplotype is the same exhibited by the 550 year old remains of the individual found in Canada known as *Kwäday Dän Ts'ìnchi* (Long-ago dead person) (Monsalve et al. 2002). This A2 variant has been reported in Haida (Ward et al. 1993), Maya (Torroni et al. 1993), Quiche (Boles et al. 1995), and Brazilian populations (Alves-Silva et al. 2000).

Three Tlingit individuals, including one belonging to the Raven moiety, exhibit type 5. This is an A2 subhaplogroup known as A2a5 (Tamm et al. 2007). It is estimated that this A2a sublineage originated in Alaska between 4000–7000 YBP, followed by western and southern expansions of Athapaskan speakers between 3000-600 YBP (Achilli et al. 2013; Ives 1990; Malhi et al. 2008; Matson 2007; Monroe et al. 2013; Seymour 2009). In addition, four percent of the Tlingit (n=6) exhibit type 10.

One Tlingit individual belongs to haplogroup A2b1 (type 11) (Achilli et al. 2008). The transition at np 16265 defines this A2b subhaplotype (Achilli et al. 2008). A2b1 is frequently

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found in Artic populations such as the Inuit (Volodko et al. 2008; Raff et al. 2015) and has also been previously reported before in one Tlingit individual (Schurr et al. 2012).

Two Tlingit individuals belong to type 12, which is haplogroup B2a. This B2 branch has been reported in one Tsimshian individual (Achilli et al. 2013), is predominantly found in populations of the American Southwest (Kemp et al. 2010; Monroe et al. 2013), and may represent a founding haplotype in the Americas (Achilli et al. 2013). Only two Tlingit individuals belong to haplogroup C, with one participant from the Wolf clan belonging to the basal C lineage, while an individual belonging to the Eagle moiety exhibited the C1 variant.

At a regional level, Tlingit mtDNA diversity is similar to other Northwest Coast populations. Tlingit, Haida, Tsimshian, Tsimshian, Alaskan Athapaskan, and Inuit populations are characterized by high frequencies of haplogroup A (ranging from about 70 percent in Haida to 100 percent in Athapaskan populations). Haplogroup B is also present in moderate frequencies among the Tsimshian. Tlingit, Haida, and Alaskan Athapaskans (Fig. 4 and Supplemental Table 3). The A2 haplotype network (Fig. 5) illustrates the distribution of haplotypes among the Tlingit and their neighbors. Tlingit and Haida populations are characterized by sharing five A2 haplotypes.

Moiety Diversity

Table 5 displays the haplotypes found among Tlingit individuals (this study) relative to their clan membership**.** There are seven haplotypes specific to the Raven moiety, two that are specific to the Eagle, and one haplotype that is shared between them. The majority of clans found in the Eagle moiety belong to the A2 lineage with transitions at nps 16111-16223-16290-16319-16362 and the lineage with the additional transition at np 16189. While most individuals belonging to

the Raven moiety are part of the lineage with the transition at np 16129, it is also the only other shared matriline across moieties. All three individuals of the Eagle moiety that belong to this haplotype are members of the *Teikweidí* clan. The Raven moiety is the most diverse, with eight different A2 lineages. Among the Eagle, members of the *Dakl'aweidí* clan are the most diverse, with three mtDNA haplotypes. There are three haplotypes (8, 9, 10) found only in Raven individuals that are most closely related to a haplotype (1) found in the Eagle moiety. Most of the haplotypes are specific to a moiety as illustrated by the A2 haplotype network of Tlingit individuals organized by moiety (Figure 6).

The AMOVA analyses reveal additional information in regards to mtDNA variation and clan structure. When grouped by moiety, the first AMOVA (Table 2) revealed that within-population variation was high (49.41%), while variation between clans (20.91%), and among moiety is low (29.68%). This is likely due to the two mtDNA sequences from two members of the *Dakl'aweidí* Eagle clan who belong to the B2a lineage. These Tlingit individuals reported having a distant Tagish ancestry, a northern Northwest Coast group of the Yukon. Thus, the presence of this lineage in the Tlingit dataset might be a product of gene flow between Tagish and Tlingit populations. In order to assess the impact of this lineage, a second AMOVA was performed, excluding these individuals (Table 3). The variation among groups component rose, although the within populations variation remained moderate. These results suggest that Eagle and Raven clans are genetically distinct, although there is also considerable variation within each clan.

Discussion

Mitochondrial DNA Variation and Moiety Membership

The analysis of mtDNA variation in Tlingit individuals provide biological data that, in conjunction with oral traditions, ethnographic, and archaeological data, can be integrated into the reconstruction of population histories of the Northwest Coast peoples. The material derived from this study contributes to an increasing mtDNA dataset in the Americas and provides new information about the population history of the Northwest Coast peoples. Overall, the data indicates that the Tlingit individuals analyzed in this study exhibit a strong correspondence between moiety membership and mtDNA lineages, which is a product of the dual marriage system. On a regional level, Tlingit populations are marked by a high frequency of haplogroup A2, which is one of the most common founding lineages in the Americas (Achilli et al. 2008; Just et al. 2008; Perego et al. 2009).

A closer examination of the A2 lineages present among the Tlingit offers significant details about the genetic composition of this group. The distribution of mtDNA lineages among clans from the Raven and Eagle moieties supports the idea that both groups are distinguishable on a genetic level, even after the detrimental effects European contact and the United States government had on Tlingit cultural practices. Overall, it is possible to separate members from the Eagle and Raven moieties based on their haplotypes. Moieties only share the type 2 haplotype. Moreover, all three individuals of the Eagle moiety that belong to this haplotype are members of the *Teikweidí* clan. However, each moiety also has exclusive lineages. Members of clans found in the Eagle moiety belong to three A2 and one B2 lineages. On the other hand, members of the Raven moiety belong to eight different A2 lineages. Most of the clans in the Eagle moiety are part of the basal A2 haplogroup and the *Kwäday Dän Ts'ìnchi* lineage, while the majority of clans in the Raven moiety exhibit the transition at np 16129. However, intramoiety variation for each moiety is high. The Raven moiety is considerably more diverse than the Eagle. Members of

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the *L'uknax.ádi* Raven clan belong to four different haplotypes, which make this clan the most diverse. This diversity could support the argument that clans in the Raven moiety represent the ancestral Tlingit population, although the current evidence cannot exclude the possibility that Eagle lineages were also part of the ancestral maternal gene pool. Assuming that the basal A2 lineage represents the genetic composition of Tlingit ancestors, then clans in the Eagle moiety can trace back directly to the same ancestral population as the clans found in the Raven moiety. The fact that there are individuals belonging to the Raven moiety that are more closely related to the basal A2 (e.g. types 9 and 11) which is characteristic of the Eagle moiety could alternatively be explained as a product of events where some clans belonging to the Raven moiety decided to integrate into the Eagle moiety.

Schurr and colleagues (2012) reported Raven moiety clans that belonged to the basal A2 haplotype. This would suggest that the founder A2 lineage was present in both moieties, and then particular haplotypes within each moiety arose over time. However, the type 2 A2 lineage is shared with clans from both Eagle and Raven moieties, marking it as possible early ancestral lineage. If this is the case, individuals belonging to clans found in the Raven moiety are most likely direct descendants of the original Tlingit inhabitants, which is consistent with oral histories and ethnographic evidence (de Laguna 1960, 1990; Emmons and de Laguna 1991; Swanton 1908; Worl 1998, 2005).

This study supports the idea that Tlingit moieties are distinguishable biocultural units. AMOVA results indicate higher variation among the Tlingit population but with lower subgroups diversity, meaning that moieties are genetically structured. Finally, the only individual from this study that belonged to the Neix.ádi clan exhibited the basal A2 haplogroup. Consequently, the sample size is not significant to offer a definite answer about the hypothetical

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separate origins of this clan. However, the fact that the individual belongs to the basal A2 haplogroup, common among both Eagle and Raven clans, does not suggest that Neix.ádi is external to the moiety system. Future studies focusing on sampling members of this clan could offer some insights into this particular issue.

An interesting finding was the presence of haplogroup B2a. Achilli and colleagues (2013) reported a Tsimshian individual belonging to one of these lineages. The presence of this subhaplogroup in Tlingit, Haida, and Tsimshian and its estimated age of 8,000 – 10,000 YBP (Achilli et al. 2013) supports the idea that B2a is a founding lineage in the Americas, or an earlier haplotype originating along the Northwest Coast.

With regards to temporal continuity, it was not possible to detect a direct matrilineal link between *Shuká Kaa*, the male individual found in On Your Knees Cave (Kemp et al. 2007), and modern Northwest Coast populations, since no individuals in this study exhibited haplotypes belonging to subhaplogroup D4h3a. One possibility for the absence of this lineage in contemporary Tlingit populations is that D4h3a decreased in frequency over time due to genetic drift, despite continuity of nuclear DNA in the region (Lindo et al. 2017). This would make the lineage rare in certain areas, where certain founding lineages might have been replaced others (Schurr et al. 2012:430). In contrast, direct maternal ancestry can be traced between Kwäday Dän Ts'ìnchi from Canada, and the Tlingit, and Haida. The A2 lineage with the transition at np 16189 is common in other Northwest Coast populations (Ward et al. 1993). The presence of this variant indicates regional continuity of this lineage for at least 550 years.

Finally, an issue that was not possible to address due to the lack of geographic information was the comparison of different Tlingit tribes or kwaan (geographic units). Future research should focus on integrating this variable and compare this with previously reported

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Tlingit sequences in order to gain a full understanding of moiety history in terms of genetic composition.

Conclusions

The results obtained in this study are consistent with Tlingit clan history derived from oral histories and the ethnographic and archaeological record. On a regional scale, the Tlingit mtDNA sequences look similar to other Northwest Coast populations, sharing a significant number of lineages with their surrounding neighbors. At the same time, their internal structure has been culturally shaped in terms of marriage traditions. The effects of these practices have produced long-lasting genetic signatures that are recognizable even after the impact of the European and United States colonization and the change of marriage practices associated to missionization, boarding schools, and the outlaw of cultural practices. Members of the different Tlingit clans are distinguishable from each other on the dual moiety level. The unity within Eagle and Raven moieties is not only sociocultural, but also biological.

The antiquity of Raven and Eagle moieties cannot be addressed by the current genetic information. Archaeological and historical data remains inconclusive in terms of the Tlingit first populations, as we have a rough estimation for the origins of the moiety system within the past 3000 years. Thus, defining specific chronologies for the origins of clans that belong to the Raven and Eagle moieties was beyond the scope of this paper. However, it has been shown the importance of oral histories to establish relative time boundaries, and more importantly, to develop models about sociocultural change. It can be argued that the biological elements of clan membership correspond to what is known in the ethnohistorical and oral record. The observed

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haplotype patterns are strong indicators of the genetic integrity of the matrilineal clan system. In sum, this study supports the idea that Tlingit moieties are distinguishable biocultural units.

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Literature Cited

Achilli, A., U. A. Perego, C. M. Bravi et al. 2008. The phylogeny of the four Pan-American mtDNA haplogroups: Implications for evolutionary and disease studies. *PLoS One* 3:1–8.

Achilli, A., U. A. Perego, H. Lancioni et al. 2013. Reconciling migration models to the Americas with the variation of North American native mitogenomes. *Proc. Natl. Acad. Sci. U. S. A.* 110:14,308–14,313.

Ackerman, R. E. 1968. *The Archaeology of the Glacier Bay Region, Southeastern Alaska: Final Report of the Archeological Survey of the Glacier Bay National Monument.* Reports of Investigations. No. 44. Pullman, WA: Washington State University, Laboratory of Anthropology.

Ackerman, R. E. 2007. The microblade complexes of Alaska and the Yukon: Early interior and coastal adaptations. In *Origin and Spread of Microblade Technology in Northern Asia and North America*, Y. V. Kuzmin, S. G. Keates, and C. Shen, eds. Burnaby, BC: Archaeology Press, Simon Fraser University, 147–170.

Alves-Silva, J., M. da Silva Santos, P. E. Guimarães et al. 2000. The ancestry of Brazilian mtDNA lineages. *Am. J. Hum. Genet.* 67:444–461.

Ames, K. M., and H. D. G. Maschner. 1999. *Peoples of the Northwest Coast: Their Archaeology and Prehistory*. New York: Thames and Hudson.

Anderson, S., A. T. Bankier, B. G. Barrell et al. 1981. Sequence and organization of the human mitochondrial genome. *Nature* 290:457–465.

Andrews, R. M., I. Kubacka, P. F. Chinnery et al. 1999. Reanalysis and revision of the Cambridge reference sequence for human mitochondrial DNA. *Nat. Genet.* 23:147.

Pre-print version. Visit http://digitalcommons.wayne.edu/humbiol/ after publication to acquire the final version.

Boles, T. C., C. C. Snow, and E. Stover. 1995. Forensic DNA testing on skeletal remains from mass graves: A pilot project in Guatemala. *J. Forensic. Sci.* 40:349–355.

Cui, Y., J. Lindo, C. E. Hughes et al. 2013. Ancient DNA analysis of mid-Holocene individuals from the Northwest coast of North America reveals different evolutionary paths for mitogenomes. *PLoS One* 8:1–8.

Davis, S. D., ed. 1989. *The Hidden Falls Site, Baranof Island, Alaska*, Aurora Monograph Series, volume V. Fairbanks, AK: Alaska Anthropological Association.

de Laguna, F. 1960. The story of a Tlingit community: A problem in the relationship between archaeological, ethnological, and historical methods. *Bureau Am. Ethnol. Bull.* 172:1–254.

de Laguna, F. 1990. Tlingit. In *Handbook of North American Indians, Vol. 7: Northwest Coast*, W. Suttles, ed. Washington, D.C.: Smithsonian Institution Press, 203–228.

Dauenhauer, N. M., and R. Dauenhauer. 1994. *Haa Kusteeyi: Our Culture*. Seattle, WA: University of Washington Press.

Dixon, E. J., T. H. Heaton, C. M. Lee et al. 2014. Evidence of maritime adaptation and coastal migration from Southeast Alaska. In *Kennewick Man: The Scientific Investigation of an Ancient American Skeleton*, D. W. Owsley and R. L. Jantz, eds. College Station, TX: Texas A&M University Press, 537–548.

Echo-Hawk, R. C. 2000. Ancient history in the New World: Integrating oral traditions and the archaeological record in deep time. *Am. Antiq.* 65:267–290.

Emmons, G. T., and F. de Laguna. 1991. The Tlingit Indians. *Anthropological Papers of the American Museum of Natural History*, no. 70. Seattle, WA: University of Washington Press; New York: American Museum of Natural History.

Pre-print version. Visit http://digitalcommons.wayne.edu/humbiol/ after publication to acquire the final version.

Excoffier, L., and H. E. L. Lischer. 2010. Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Mol. Ecol. Resour.* 10:564–567.

Forster, P., R. Harding, A. Torroni et al. 1996. Origin and evolution of Native American mtDNA variation: A reappraisal. *Am. J. Hum. Genet.* 59:935–945.

Fuselli, S., E. Tarazona-Santos, I. Dupanloup et al. 2003. Mitochondrial DNA diversity in South America and the genetic history of Andean Highlanders. *Mol. Biol. Evol.* 20:1,682–1,691.

Goldschmidt, W. R., and T. H. Hass. 1998. *Haa Aaní, Our Land: Tlingit and Haida Land Rights and Use*. Seattle, WA: University of Washington Press.

Helgason, A., G. Pálsson, H. S. Pedersen et al. 2006. mtDNA variation in Inuit populations of Greenland and Canada: Migration history and population structure. *Am. J. Phys. Anthropol.* 130:123–134.

Holm, B. 1965. *Northwest Coast Indian Art: An Analysis of Form*. Seattle, WA: University of Washington Press.

Hope, A., and T. F. Thornton, eds. 2000. *Will the Time Ever Come? A Tlingit Sourcebook.* Fairbanks, AK: Alaska Native Knowledge Network, Center for Cross-Cultural Studies, University of Alaska Fairbanks.

Hope III, A., P. Metcalfe, S. Kraft et al. 2003. *Traditional Tlingit Country,* circa late nineteenth century, 4th ed. revised. Juneau, AK: Tlingit Readers, Inc. http://www.ankn.uaf.edu/ANCR/Southeast/TlingitMap/TlingitMap.pdf.

Ives, J. W. 1990. *A Theory of Northern Athapaskan Prehistory: Investigations in American Archaeology*. New York: Westview Press.

Pre-print version. Visit http://digitalcommons.wayne.edu/humbiol/ after publication to acquire the final version.

Johnson, J. R., and J. G. Lorenz. 2006. Genetics, linguistics, and prehistoric migrations: An analysis of California Indian mitochondrial DNA lineages. *J. Calif. Gt. Basin Anthropol.* 26:33–64.

Just, R. S., T. M. Diegoli, J. L. Saunier et al. 2008. Complete mitochondrial genome sequences for 265 African American and U.S. "Hispanic" individuals. *Forensic Sci. Int. Genet.* 2:E45–E48.

Kan, S. 1996. Clan mothers and godmothers: Tlingit women and Russian Orthodox Christianity, 1840–1940. *Ethnohistory* 43:613–641.

Kemp, B. M, A. González-Oliver, R. S. Malhi et al. 2010. Evaluating the farming/language dispersal hypothesis with genetic variation exhibited by populations in the Southwest and Mesoamerica. *Proc. Natl. Acad. Sci. U. S. A.* 107:6,759–6,764.

Kemp, B. M, R. S. Malhi, J. McDonough et al. 2007. Genetic analysis of early holocene skeletal remains from Alaska and its implications for the settlement of the Americas. *Am. J. Phys. Anthropol.* 132:605–621.

Krause, A. 1956. *The Tlingit Indians: Results of a Trip to the Northwest Coast of America and the Bering Straits*. E. Gunther, trans. Seattle, WA: University of Washington Press.

Lindo, J., A. Achilli, U. A. Perego et al. 2017. Ancient individuals from the North American Northwest Coast reveal 10,000 years of regional genetic continuity. *Proc. Natl. Acad. Sci. U. S. A.* 114:4,093–4,098.

Lorenz, J. G, and D. G. Smith. 1996. Distribution of four founding mtDNA haplogroups among Native North Americans. *Am. J. Phys. Anthropol.* 101:307–323.

Lorenz, J. G., and D. G. Smith. 1997. Distribution of sequence variation in the mtDNA control region of Native North Americans. *Hum. Biol.* 69:749–776.

Pre-print version. Visit http://digitalcommons.wayne.edu/humbiol/ after publication to acquire the final version.

Malhi, R. S, K. E. Breece, B. A. Shook et al. 2004. Patterns of mtDNA diversity in northwestern North America. *Hum. Biol.* 76:33–54.

Malhi, R. S., A. González-Oliver, K. B. Schroeder et al. 2008. Distribution of Y chromosomes among Native North Americans: A study of Athapaskan population history. *Am. J. Phys. Anthropol.* 137:412–424.

Matson, R. G. 2007. *Athapaskan Migrations: The Archaeology of Eagle Lake, British Columbia*. Tucson, AZ: University of Arizona Press.

Matson, R. G., and G. Coupland. 1995. *The Prehistory of the Northwest Coast*. San Diego, CA: Academic Press.

Meyer, S., G. Weiss, and A. von Haeseler. 1999. Pattern of nucleotide substitution and rate heterogeneity in the hypervariable regions I and II of human mtDNA. *Genetics* 152:1,103–1,110.

Monroe, C., B. M. Kemp, and D. G. Smith. 2013. Exploring prehistory in the North American southwest with mitochondrial DNA diversity exhibited by Yumans and Athapaskans. *Am. J. Phys. Anthropol.* 150:618–631.

Monsalve, M. V., A. C. Stone, C. M. Lewis et al. 2002. Brief communication: Molecular analysis of the Kwäday Dän Ts'finchi ancient remains found in a glacier in Canada. *Am. J. Phys. Anthropol.* 119:288–291.

Moss, M. L. 2004. *Archaeological Investigations of Cape Addington Rockshelter: Human Occupation of the Rugged Seacoast on the Outer Prince of Wales Archipelago, Alaska.* University of Oregon Anthropological Paper no. 63. Eugene: OR: University of Oregon.

Moss, M. L. 2011. *Northwest Coast: Archaeology as Deep History*. Washington, D.C.: The SAA Press.

Pre-print version. Visit http://digitalcommons.wayne.edu/humbiol/ after publication to acquire the final version.

Moss, M. L., J. M. Erlandson, and R. Stuckenrath. 1989. The antiquity of Tlingit settlement on Admiralty Island, Southeast Alaska. *Am. Antiq.* 54:534–543.

Olson, R. L. 1967. *Social Structure and Social Life of the Tlingit in Alaska.* Anthropological Records Volume 26. Berkeley, CA: University of California Press.

Perego, U. A., A. Achilli, N. Angerhofer et al. 2009. Distinctive Paleo-Indian migration routes from Beringia marked by two rare mtDNA haplogroups. *Curr. Biol.* 19:1–8.

Raff, J. A., D. A. Bolnick, J. Tackney et al. 2011. Ancient DNA perspectives on American colonization and population history. *Am. J. Phys. Anthropol.* 146:503–514.

Raff, J. A., M. Rzhetskaya, J. Tackney et al. 2015. Mitochondrial diversity of Iñupiat people from the Alaskan North Slope provides evidence for the origins of the Paleo- and Neo-Eskimo peoples. *Am. J. Phys. Anthropol.* 157:603–614.

Rubicz, R., T. G. Schurr, P. L. Babb et al. 2003. Mitochondrial DNA variation and the origins of the Aleuts. *Hum. Biol.* 75:809–835.

Schurr, T. G., S. W. Ballinger, Y. Y. Gan et al. 1990. Amerindian mitochondrial DNAs have rare Asian mutations at high frequencies, suggesting they derived from four primary maternal lineages. *Am. J. Hum. Genet.* 46:613–623.

Schurr, T. G., M. C. Dulik, A. C. Owings et al. 2012. Clan, language, and migration history has shaped genetic diversity in Haida and Tlingit populations from Southeast Alaska. *Am. J. Phys. Anthropol.* 148:422–435.

Seymour, D. J. 2009. Comments on genetic data relating to Athapaskan migrations: Implications of the Malhi et al. study for the Southwestern Apache and Navajo. *Am. J. Phys. Anthropol.* 139:281–283.

Pre-print version. Visit http://digitalcommons.wayne.edu/humbiol/ after publication to acquire the final version.

Shields, G. F., A. M. Schmiechen, B. L. Frazier et al. 1993. mtDNA sequences suggest a recent evolutionary divergence for Beringian and northern North American populations. *Am. J. Hum. Genet.* 53:549–562.

Suttles, W. 1990. Introduction. In *Handbook of North American Indians, Vol. 7: Northwest Coast*, W. Suttles, ed. Washington, D.C.: Smithsonian Institution Press, 1–15.

Suttles, W., and A. Jonaitis. 1990. History of research in ethnology. In *Handbook of North American Indians, Vol. 7: Northwest Coast*, W. Suttles, ed. Washington, D.C.: Smithsonian Institution Press, 73–87.

Swanton, J. R. 1908. *Social Condition, Beliefs, and Linguistic Relationship of the Tlingit Indians*. *Twenty-sixth Annual Report of the Bureau of American Ethnolog*y. Washington, D.C.: Smithsonian Institution.

Swanton, J. R. 1909. *Tlingit Myths and Texts.* Smithsonian Institution, Bureau of American Ethnology Bulletin 39. Washington, D.C.: United States Government Printing Office.

Swanton, J. R. 1911. Tlingit. In *Handbook of American Indian Languages*, vol. 1, F. Boas ed. Smithsonian Institution, Bureau of American Ethnology Bulletin 40. Washington, D.C.: United States Government Printing Office, 159–204.

Szathmáry, E. J. E. 1993. Genetics of aboriginal North Americans. *Evol. Anthropol*. 1:202–220.

Szathmáry, E. J. E. 2018. Exceeding Hrdlička's aims: 100 years of genetics in anthropology. *Am. J. Phys. Anthropol.* 165:754–776.

Tamm, E., T. Kivisild, M. Reidla et al. 2007. Beringian standstill and spread of Native American founders. *PLoS One* 2:1–6.

Pre-print version. Visit http://digitalcommons.wayne.edu/humbiol/ after publication to acquire the final version.

Tamura, K., and M. Nei. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Mol. Biol. Evol.* 10:512–526.

Tooker, E. 1971. Clans and moieties in North America. *Curr. Anthropol.* 12:357–376.

Torroni, A., T. G. Schurr, M. F. Cabell et al. 1993. Asian affinities and continental radiation of the four founding Native American mtDNAs. *Am. J. Hum. Genet.* 53:563–590.

Volodko, N. V., E. B. Starikovskaya, I. O. Mazunin et al. 2008. Mitochondrial genome diversity in Arctic Siberians, with particular reference to the evolutionary history of Beringia and Pleistocenic peopling of the Americas. *Am. J. Hum. Genet.* 82:1,084–1,100.

Ward, R. H., B. L. Frazier, K. Dew-Jager et al. 1991. Extensive mitochondrial diversity within a single Amerindian tribe. *Proc. Natl. Acad. Sci. U. S. A.* 88:8,720–8,724.

Ward, R. H., A. Redd, D. Valencia et al. 1993. Genetic and linguistic differentiation in the Americas. *Proc. Natl. Acad. Sci. U. S. A.* 90:10,663–10,667.

Worl, R. 1998. Tlingit at.oow: Tangible and intangible property. PhD diss., Harvard University.

Worl, R. K. 2005. *The Native American Graves Protection & Repatriation Act: Integrating Science & Stories: Tlingit Ancient History*. 2019 reprint of paper presented to the Society for Applied Anthropology. Juneau, AK: Sealaska Heritage Institute.

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Table 1. Pairwise Fst Values for HVSI Sequences in Northern American Populations

ALE= Aleut; ATH= Alaskan Athapaskan; BEL= Bela Coola; CAI= Canadian Inuit; GRI= Greenland Inuit; HAI=Haida; NUU= Nuu-chah-nulth; TLI=Tlingit; TSI=Tsimshian. P-values are shown in the upper matrix.

	TLI	HAI	TSI	ATH	ALE	BEL	NUU	CAI	GRI
TLI	*	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
HAI	0.10699	*	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
TSI	0.31127	0.27033	*	<0.01	<0.01	0.024	<0.01	<0.01	<0.01
ATH	0.19630	0.16453	0.29761	*	<0.01	<0.01	<0.01	<0.01	<0.01
ALE	0.38171	0.37506	0.38487	0.35695	*	<0.01	<0.01	<0.01	<0.01
BEL	0.16358	0.11224	0.12059	0.18629	0.22528	*	<0.01	<0.01	<0.01
NUU	0.31781	0.21980	0.15670	0.23782	0.23964	0.07170	*	<0.01	<0.01
CAI	0.23223	0.19907	0.40007	0.24334	0.43067	0.27101	0.32611	*	<0.01
GRI	0.24367	0.22260	0.46314	0.14858	0.48989	0.35247	0.42941	0.06392	*

Table 2. Results of Tlingit AMOVA

	% Variation	P-value
Among group	29.68	<0.01
Among populations within groups	20.91	<0.01
Within populations	49.41	<0.01

Table 3. Results of Tlingit AMOVA without Tlingit/Tagish Haplogroup B Sequences

	% Variation	P-value
Among group	38.49	<0.01
Among populations within groups	26.99	<0.01
Within populations	34.52	<0.01

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Table 4. MtDNA HVSI Haplotypes Exhibited by Tlingit Participants

Hap #	HVSI	Haplogroup
1	16111T-16223T-16290T-16319A-16362C	A
2	16111T-16129A-16223T-16290T-16319A-16362C	A
3	16111T-16129A-16223T-16290T-16319A-16362C-16519C	A
4	16111T-16189C-16223T-16290T-16319A-16362C	A
5	16111-16189-16192-16212-16223-16233-16290-16319-16331	A
6	16111T-16129A-16145A-16223T-16290T-16319A-16362C	A
7	16111T-16129A-16218T-16223T-16290T-16319A-16362C	A
8	16111T-16129A-16223T-16290T-163111C-16319A-16362C	A
9	16111T-16218T-16223T-16235G-16290T-16319A-16362C	A
10	16111T-16223T-16235G-16290T-16319A-16362C	A
11	16111T-16223T-16265G-16290T-16319A-16362C	A
12	16183C-16189C-16217C-16278T-16399G-16483A-16519C	B

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Table 5. MtDNA HVSI Haplotypes Organized by Moiety and Clan of Participants

Moiety	Clan	Haplotype #
Eagle	Chookaneidí	1
Eagle	Dakl'aweidí	1, 4, 12(Hap B)
Eagle	Kaagwaantaan	1, 4
Eagle	Kluckwan	1
Eagle	Neix.adi	1
Eagle	Shangukeidí	1
Eagle	Teikweidí	2
Eagle	Tsaagweidi	1, 4
Eagle	Wooshkeetan	1
Eagle	Yanyeidí	1, 4
Raven	Deisheetaan	2, 3, 7
Raven	Gaanax.ádi	2
Raven	Gaanaxteidí	3, 9, 10
Raven	Ishkaahittaan	3
Raven	Kaach.ádi	2
Raven	Kiks.ádi	2, 8, 10
Raven	Kookhíttaan	2
Raven	L'eineidí	2, 6
Raven	L'uknax.ádi	3, 8, 10, 11
Raven	Sukteeneidí	2
Raven	Taakw.aaneidí	3

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Raven	T'akdeintaan	8

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Supplementary Table S1. Ethnicity, Moiety, and Clan Information of Participants

Sequences from individuals with * were not reported due to sampling error.

Sample ID	Sex	Ethnicity	Moiety	Clan
AK001	F	Unknown		
AK002	F	Tlingit		
AK003	F	Tlingit	Eagle	Chookaneidí
AK004	F	Tlingit	Raven	Kiks.ádi
AK005	F	Tlingit	Raven	
AK006	F	Tlingit	Raven	L'eineidí
AK007	M	Tlingit	Eagle	Kaagwaantaan
AK008	M	Tlingit	Raven	Gaanaxteidí
AK009	F	Tlingit/Nez Perce	Raven	
AK010	F	Haida		
AK011	F	Tlingit	Eagle	Dakl'aweidí
AK012*	M	Unknown		
AK013	M	Tlingit	Raven	L'eineidí
AK014	M	Tlingit	Raven	
AK015	F	Tlingit/Caucasian		
AK016	F	Haida	Raven	
AK017	F	Unknown		
AK018	M	Tlingit	Eagle	Kaagwaantaan
AK019	F	Tlingit	Raven	T'akdeintaan
AK020	F	Cherokee		

AK021	F	Tsimshian		
AK022	F	Tlingit	Eagle	
AK023	M	Tlingit	Eagle	Kaagwaantaan
AK024	F	Tlingit	Raven	Gaanaxteidí
AK025	F	Tlingit	Wolf	
AK026	M	Tlingit	Raven	
AK027*	F	Tlingit	Wolf	
AK028	F	Tlingit	Eagle	
AK029	M	Tlingit	Raven	Deisheetaan
AK030	M	Tlingit	Raven	Deisheetaan
AK031	F	Tlingit	Raven	
AK032	F	Sioux		
AK033	F	Tlingit	Eagle	
AK034	F	Tlingit	Eagle	
AK035	F	Tsimshian		
AK036*	M	Tlingit		
AK037*	F	Tlingit	Eagle	Shangukeidí
AK038	F	Tlingit	Raven	T'akdeintaan
AK039	M	Tlingit	Raven	Gaanax.ádi
AK040	F	Tlingit	Raven	Gaanaxteidí
AK041	F	Tlingit	Eagle/Wolf	
AK042	M	Tlingit	Eagle	Dakl'aweidí
AK043	F	Chinookan		

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AK044	F	Chinookan		
AK045	F	Tlingit	Raven	
AK046	M	Tlingit	Eagle	Dakl'aweidí
AK047	F	Tlingit	Raven	L'eineidí
AK048	M	Nisga'a		
AK049	F	Tlingit		
AK050	M	Tlingit	Raven	
AK051	M	Tsimshian/Cherokee		
AK052	F	Tsimshian/Cherokee		
AK053	F	Cherokee		
AK054	M	Tlingit	Raven	
AK055	F	Tlingit	Raven	Ishkaahittaan
AK056	M	Tlingit		
AK057	F	Tlingit	Raven	Kookhíttaan
AK058	F	Tlingit	Eagle	
AK059	F	Kwakiutl		
AK060	M	Tlingit	Eagle	
AK061	M	Tlingit	Raven	Kiks.ádi
AK062	F	Tlingit	Eagle	Dakl'aweidí
AK063	F	Tlingit	Crow	
AK064	M	Haida		
AK065	F	Tlingit	Wolf	Kaagwaantaan
AK066	F	Tlingit	Eagle	

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AK067	M	Unknown		
AK068	F	Tlingit	Eagle	
AK069	F	Tlingit	Eagle	Dakl'aweidí
AK070	M	Unknown		
AK071	F	Tlingit	Eagle	Dakl'aweidí
AK072	N/A	Tlingit	Raven	
AK073	F	Tlingit	Eagle	Dakl'aweidí
AK074	F	Tlingit	Raven	Deisheetaan
AK075	M	Athapaskan		
AK076*	F	Tlingit	Raven	
AK077	M	Tlingit		
AK078	F	Tlingit	Eagle	Kluckwan
AK079	M	Haida/European		
AK080	M	Haida/Tsimshian/European		
AK081	M	Haida		
AK082*	F	Tlingit		
AK083	M	Tlingit	Eagle	
AK084	M	Tlingit	Eagle	Yanyeidí
AK085	F	Tlingit	Eagle	
AK086	F	Tlingit	Raven	Kookhíttaan
AK087	F	Tlingit		
AK088	F	Tlingit	Raven	L'eineidí
AK089	F	Tlingit		

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AK090	F	Tlingit	Raven	Deisheetaan
AK091	M	Tlingit	Raven	L'eineidí
AK092	F	Tlingit	Raven	
AK093	F	Tlingit	Raven	Kiks.ádi
AK094	F	European		
AK095	F	Tlingit		
AK096	F	European		
AK097	F	Tlingit		
AK098	F	Haida		
AK099	F	Haida	Raven	
AK100	F	Tlingit	Eagle	Dakl'aweidí
AK101	F	Haida		
AK102	F	Tlingit		
AK103	F	Tlingit	Raven	
AK104	F	Tlingit	Raven	Kiks.ádi
AK105	F	Tlingit	Raven	Deisheetaan
AK106	M	Tlingit	Eagle	
AK107	M	Tlingit	Eagle	Wooshkeetan
AK108	F	Tlingit	Ravev	Kaach.ádi
AK109	F	Tlingit	Raven	L'eineidí
AK110	F	Tlingit	Raven	T'akdeintaan
AK111	F	Tlingit	Raven	L'uknax.ádi
AK112	F	Kootenai/Salish/Cree		

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AK113	F	Tsimshian	Eagle	
AK114	F	European		
AK115	F	Tlingit	Eagle	Kaagwaantaan
AK116	M	Haida	Eagle	
AK117	M	Tlingit	Raven	L'uknax.ádi
AK118	F	Tlingit	Raven	
AK119	F	European		
AK120	F	Cree		
AK121	F	Tsimshian	Eagle	
AK122	F	Tlingit	Eagle	
AK123	F	Haida		
AK124	F	Tlingit	Eagle	Kaagwaantaan
AK125	M	Tlingit	Wolf	Kaagwaantaan
AK126	M	Caucasian		
AK127	F	Unknown		
AK128	M	Unknown		
AK129	F	Tlingit	Eagle	Tsaagweidi
AK130	F	Tlingit	Raven	Gaanaxteidí
AK131	F	Tlingit	Eagle	Dakl'aweidí
AK132	M	Tlingit	Raven	L'uknax.ádi
AK133	F	Tlingit	Eagle	
AK134	F	Tlingit	Eagle	
AK135	F	Tashon		

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AK136	F	Tlingit	Eagle	Teikweidí
AK137	M	Tlingit	Eagle	
AK138	F	Tlingit	Eagle	
AK139	M	Tlingit	Eagle	
AK140	F	Tlingit	Raven	L'uknax.ádi
AK141	M	Tlingit	Raven	Taakw.aaneidí
AK142	F	Tlingit		
AK143	F	Tlingit	Wolf	
AK144	F	Tutchone	Wolf	
AK145	F	Tutchone	Wolf	
AK146	M	Tlingit	Wolf	Kaagwaantaan
AK147	F	Tlingit	Eagle	Kaagwaantaan
AK148	F	Tlingit		
AK149	M	Inupiat		
AK150	M	Makah		
AK151	F	Tlingit	Raven	L'uknax.ádi
AK152	M	Tlingit	Eagle	Dakl'aweidí
AK153	F	Tlingit/Haida	Eagle	
AK154	F	Tsimshian		
AK155	F	Tlingit		Kiks.ádi
AK156	M	Haida		
AK157	M	Tlingit	Raven	
AK158	M	Tlingit	Eagle	

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AK159	F	Tlingit	Eagle	
AK160	M	Tlingit	Raven	Gaanax.ádi
AK161	M	Tlingit	Crow	
AK162	F	Tlingit	Eagle	
AK163*	F	Unknown		
AK164	F	Tlingit	Raven	
AK165	F	Tlingit	Raven	L'eineidí
AK166	M	Tlingit	Eagle	
AK167	F	Tlingit	Eagle	Kaagwaantaan
AK168	F	Tlingit	Crow	
AK169	M	Unknown		
AK170	M	Tlingit	Eagle	Wooshkeetan
AK171	F	Haida		
AK172	F	Haida/Tlingit		
AK173	M	Tsimshian	Raven	
AK174	M	Tlingit	Raven	Sukteeneidí
AK175	F	Tlingit	Eagle	Dakl'aweidí
AK176	F	Unknown		
AK177	F	Tlingit	Raven	L'eineidí
AK178	F	Tlingit	Eagle	Dakl'aweidí
AK179	F	Tlingit		
AK180	M	Tlingit	Eagle	Shangukeidí
AK181	M	Unknown		

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AK182	M	Tlingit	Eagle	Kaagwaantaan
AK183*	F	Eyak		
AK184	F	Tlingit	Eagle	
AK185	F	Tlingit	Eagle	Kaagwaantaan
AK186	F	Tlingit	Raven	L'uknax.ádi
AK187	M	Tlingit	Raven	L'uknax.ádi
AK188	M	Tlingit	Eagle	Tsaagweidi
AK189	M	European		
AK190	F	Tlingit	Eagle	Kaagwaantaan
AK191	M	Tlingit	Eagle	Wooshkeetan
AK192	F	Tlingit	Raven	
AK193	M	Tlingit	Rave	
AK194	M	Choctaw		
AK195	F	Tlingit	Eagle	Shangukeidí
AK196	M	Tlingit		
AK197	M	Unknown		
AK198	F	Tlingit		
AK199	F	European		
AK200	F	Tlingit		
AK201	F	Tlingit		
AK202	F	Sioux		
AK203	M	Tlingit		
AK204	F	European		

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AK205	M	Tlingit	Raven	L'eineidí
AK206	M	Tlingit	Raven	L'uknax.ádi
AK207	F	Haida		
AK208	M	Tlingit	Eagle	Teikweidí
AK209	M	Tlingit	Eagle	Teikweidí
AK210	F	Tlingit	Raven	Deisheetaan
AK211	F	Tlingit	Eagle	Dakl'aweidí
AK212	F	Unknown		
AK213	F	Ojibway		
AK214	F	Tlingit	Raven	
AK215	M	Tlingit	Eagle	Neix.adi
AK216	M	Inupiaq		
AK217	F	Inupiaq		
AK218	F	NE Asian		
AK219	M	Tlingit	Eagle	Kaagwaantaan
AK220	F	Unknown		
AK221	F	Tlingit	Eagle	Wooshkeetan
AK222	F	Haida		
AK223	M	Tlingit	Raven	
AK224	M	Tlingit	Raven	Gaanax.ádi
AK225	M	Tlingit	Raven	L'uknax.ádi
AK226	M	Navajo		
AK227	F	Tlingit	Eagle	

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AK228	F	Unknown		
AK229	F	European/Mexican		
AK230	F	Tlingit		
AK231	M	Tlingit		
AK232	F	Tlingit		
AK233	F	Unknown		
AK234	M	Tlingit	Eagle	Shangukeidí
AK235	N/A	Haida		
AK236	F	Tlingit	Raven	L'eineidí

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Supplementary Table S2. Nucleotide Positions Sequenced from Participants

HVSI mutations and haplogroups are defined by comparing the polymorphism to the CRS (Anderson et al. 1981; Andrews et al. 1999).

Sample	Coverage	Mutations	HAP
AK001	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK002	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK003	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK004	16018-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK005	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK006	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK007	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK008	16001-16566	16111T-16218T-16223T-16235G-16290T-16319A-16362C	A2
AK009	16001-16537	16160G-16183C-16189C-16217C-16519C	B2
AK010	16001-16531	16111T-16189C-16223T-16290T-16319A-16362C	A2

AK011	16001-16539	16111T-16189C-16223T-16290T-16319A-16362C	A2
AK013	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK014	16001-16566	16111T-16129A-16223T-16290T-163111C-16319A-16362C	A2
AK015	16001-16566	16192T-16240G-16270T	U5
AK016	16001-16538	16111T-16183C-16189C-16217C-16399G-16483A-16519C	B2a
AK017	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK018	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK019	16001-16566	16111T-16129A-16223T-16290T-163111C-16319A-16362C	A2
AK020	16001-16566	16519C	H
AK021	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK022	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK023	16001-16566	16111T-16223T-16290T-16319A-16362C	A2

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AK024	16001-16566	16111T-16223T-16235G-16290T-16319A-16362C	A2
AK025	16001-16566	16037G-16129A-16223T-16298C-16327T-16519C	C
AK026	16001-16566	16111T-16129A-16223T-16290T-163111C-16319A-16362C	A2
AK028	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK029	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK030	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK031	16001-16566	16111T-16129A-16223T-16290T-163111C-16319A-16362C	A2
AK032	16001-16534	16183C-16189C-16223T-16278T-16291T-16319A-16357C-16519C	X
AK033	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK034	16001-16514	16111T-16223T-16290T-16319A-16362C	A2
AK035	16001-16531	16111T-16223T-16290T-16319A-16362C	A2
AK038	16001-16566	16111T-16129A-16223T-16290T-163111C-16319A-16362C	A2

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AK039	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK040	16001-16566	16111T-16223T-16235G-16290T-16319A-16362C	A2
AK041	16001-16534	16111T-16189C-16223T-16290T-16319A-16362C	A2
AK042	16001-16534	16111T-16189C-16223T-16290T-16319A-16362C	A2
AK043	16001-16566	16051G-16223T-16298C-16325C-16327T-16355T	C1d
AK044	16001-16566	16051G-16223T-16298C-16325C-16327T-16355T	C1d
AK045	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK046	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK047	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK048	16001-16566	16111T-16192T-16223T-16243C-16290T-16319A-16362C	A2
AK049	16001-16531	16111T-16189C-16223T-16290T-16319A-16362C	A2
AK050	16001-16566	16111T-16189C-16192T-16212G-16223T-16233G-16290T-16319A-16331G	A2a5

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AK051	16001-16566	16069T-16126C	J
AK052	16001-16519	16069T-16126C	J
AK053	16001-16525	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK054	16001-16526	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK055	16001-16532	16111T-16129A-16223T-16290T-16319A-16362C-16519C	A2
AK056	16037-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK057	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK058	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK059	16001-16566	16111T-16223T-16235G-16290T-16319A-16362C	A2
AK060	16001-16562	16111T-16223T-16290T-16319A-16362C	A2
AK061	16001-16566	16111T-16129A-16223T-16290T-163111C-16319A-16362C	A2
AK062	16037-16490	16111T-16189C-16223T-16290T-16319A-16362C	A2

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AK063	16001-16566	16111T-16223T-16242T-16290T-16319A-16362C	A2
AK064	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK065	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK066	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK067	16001-16530	16111T-16223T-16290T-16319A-16362C	A2
AK068	16001-16528	16111T-16189C-16223T-16290T-16319A-16362C	A2
AK069	16016-16500	16111T-16189C-16223T-16233G-16290T-16319A-16331G	A2
AK070	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK071	16001-16534	16183C-16189C-16217C-16278T-16399G-16483A-16519C	B2a
AK072	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK073	16001-16534	16183C-16189C-16217C-16278T-16399G-16483A-16519C	B2a
AK074	16001-16566	16111T-16129A-16218T-16223T-16290T-16319A-16362C	A2

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AK075	16001-16566	16111T-16192T-16223T-16227G-16234T-16290T-16319A-16362C	A2
AK077	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK078	16001-16528	16111T-16223T-16290T-16319A-16362C	A2
AK079	16015-16566	16162G-16209C-16519C	H
AK080	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK081	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK083	16001-16566	16111T-16189C-16223T-16290T-16319A-16362C	A2
AK084	16001-16526	16111T-16189C-16223T-16290T-16319A-16362C	A2
AK085	16001-16512	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK086	16001-16534	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK087	16040-16566	16111T-16189C-16223T-16290T-16319A-16362C	A2
AK088	16001-16542	16111T-16129A-16223T-16290T-16319A-16362C	A2

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AK089	16001-16542	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK090	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK091	16001-16566	16111T-16129A-16145A-16223T-16290T-16319A-16362C	A2
AK092	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK093	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK094	16001-16566	16126C-16198C-16256T-16294T-16296T-16519C	T2
AK095	16001-16543	16111T-16189C-16192T-16212G-16223T-16233G-16290T-16319A-16331G	A2a5
AK096	16001-16456	16051G-16092C-16129C-16183C-16189C-16362C-	U2e
AK097	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK098	16001-16566	16111T-16223T-16290T-16301T-16319A-16355T-16362C-16519C	A2
AK099	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK100	16001-16566	16111T-16223T-16290T-16319A-16362C	A2

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AK101	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK102	16001-16566	16111T-16129A-16223T-16290T-163111C-16319A-16362C	A2
AK103	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK104	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK105	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK106	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK107	16001-16566	16129A-16223T-16391A-16519C	I
AK108	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK109	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK110	16001-16566	16111T-16129A-16223T-16290T-163111C-16319A-16362C	A2
AK111	16001-16566	16111T-16129A-16223T-16290T-163111C-16319A-16362C	A2
AK112	16001-16566	16223T-16298C-16325C-16327T	C1

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AK113	16001-16414	16111T-16182C-16183C-16189C-16217C-16399G	B2
AK114	16008-16396	16223T-16298C-16325C-16327T	C1
AK115	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK116	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK117	16001-16542	16111T-16223T-16265G-16290T-16319A-16362C	A2b1
AK118	16001-16566	16111T-16129A-16223T-16290T-163111C-16319A-16362C	A2
AK119	16001-16495	16129A-16140C-16172C-16189C-16223T-16311C-16391A	I
AK120	16001-16501	16092C-16111T-16183C-16189C-16217C-16483A	B2a
AK121	16001-16531	16111T-16182C-16183C-16189C-16217C-16399G-16483A-16519C	B2a
AK122	16001-16566	16223T-16231C-16263C-16298C-16325C-16327T-16519C	C1
AK123	16001-16566	16111T-16223T-16290T-16319A-16355T-16362C-16519C	A2
AK124	16001-16566	16111T-16223T-16290T-16319A-16362C	A2

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AK125	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK126	16001-16566	16192T-16240G-16270T	U5
AK127	16034-16566	16111T-16223T-16265G-16290T-16319A-16362C	A2b1
AK128	16001-16566	16111T-16223T-16265G-16290T-16319A-16362C	A2b1
AK129	16001-16531	16111T-16189C-16223T-16290T-16319A-16362C	A2
AK130	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C-16519C	A2
AK131	16001-16531	16111T-16189C-16223T-16290T-16319A-16362C	A2
AK132	16001-16566	16111T-16129A-16223T-16290T-163111C-16319A-16362C	A2
AK133	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK134	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK135	16001-16566	16111T-16192T-16223T-16233G-16290T-16319A-16331G	A2
AK136	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2

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AK137	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK138	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK139	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK140	16021-16566	16111T-16129A-16223T-16290T-163111C-16319A-16362C	A2
AK141	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C-16519C	A2
AK142	16001-16566	16111T-16129A-16218T-16223T-16290T-16319A-16362C	A2
AK143	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK144	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK145	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK146	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK147	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK148	16001-16566	16111T-16129A-16223T-16256T-16290T-16319A-16362C	A2

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AK149	16001-16566	16111T-16223T-16265G-16290T-16319A-16362C	A2b1
AK150	16001-16566	16111T-16290T-16319A-16362C	A2
AK151	16001-16566	16111T-16129A-16223T-16290T-163111C-16319A-16362C	A2
AK152	16001-16531	16111T-16189C-16223T-16290T-16319A-16362C	A2
AK153	16001-16531	16111T-16189C-16223T-16290T-16319A-16362C	A2
AK154	16001-16566	16111T-16223T-16290T-16319A-16362C-16519C	A2
AK155	16001-16566	16111T-16223T-16235G-16290T-16319A-16362C	A2
AK156	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK157	16001-16563	16111T-16223T-16290T-16319A-16355T-16362C-16519C	A2
AK158	16001-16531	16111T-16189C-16223T-16290T-16319A-16362C	A2
AK159	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK160	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2

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AK161	16001-16566	16111T-16223T-16242T-16290T-16319A-16362C	A2
AK162	16001-16513	16111T-16189C-16223T-16290T-16319A-16362C	A2
AK164	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK165	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK166	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK167	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK168	16001-16566	16111T-16223T-16242T-16290T-16319A-16362C	A2
AK169	16001-16533	16111T-16189C-16192T-16223T-16233G-16290T-16319A-16331G	A2
AK170	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK171	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK172	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK173	16001-16566	16220C-16362C-16519C	H

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AK174	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK175	16001-16517	16111T-16189C-16223T-16290T-16319A	A2
AK176	16001-16566	16093C-16519C-16523G	H
AK177	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK178	16001-16462	16111T-16189C-16223T-16290T-16319A-16362C	A2
AK179	16001-16529	16111T-16189C-16223T-16290T-16319A-16362C	A2
AK180	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK181	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK182	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK184	16001-16533	16111T-16189C-16192T-16223T-16233G-16290T-16319A-16331G	A2
AK185	16016-16566	16111T-16223T-16290T-16319A-16362C	A2
AK186	16035-16566	16111T-16223T-16235G-16290T-16319A-16362C	A2

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AK187	16001-16566	16111T-16129A-16223T-16290T-163111C-16319A-16362C	A2
AK188	16001-16528	16111T-16189C-16223T-16290T-16319A-16362C	A2
AK189	16001-16566	16162G-16519C	H
AK190	16001-16528	16111T-16189C-16223T-16290T-16319A-16362C	A2
AK191	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK192	16001-16566	16111T-16129A-16223T-16290T-163111C-16319A-16362C	A2
AK193	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK194	16001-16566	16162G-16519C	H
AK195	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK196	16001-16566	16111T-16129A-16223T-16290T-163111C-16319A-16362C	A2
AK197	16001-16566	16069T-16126C-16519C	J
AK198	16001-16566	16111T-16223T-16290T-16319A-16362C	A2

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AK199	16001-16438	16354T	H
AK200	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK201	16001-16528	16111T-16189C-16223T-16290T-16319A-16362C-16519C	A2
AK202	16001-16566	16519C	H
AK203	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK204	16001-16566	16357C-16519C	H
AK205	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK206	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C-16519C	A2
AK207	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK208	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK209	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK210	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C-16519C	A2

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AK211	16001-16528	16111T-16189C-16223T-16290T-16319A-16362C	A2
AK212	16001-16566	16519C	H
AK213	16001-16566	16192T-16218T-16270T-16320T-	U5
AK214	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C-16519C	A2
AK215	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK216	16001-16566	16111T-16223T-16265G-16290T-16319A-16362C	A2b1
AK217	16001-16566	16111T-16192T-16223T-16290T-16319A-16362C	A2
AK218	16001-16566	16111T-16192T-16220G-16223T-16234T-16290T-16319A-16362C	A2
AK219	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK220	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK221	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK222	16001-16566	16111T-16223T-16290T-16319A-16362C	A2

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AK223	16001-16566	16111T-16223T-16235G-16290T-16319A-16362C	A2
AK224	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2
AK225	16016-16566	16111T-16129A-16223T-16290T-163111C-16319A-16362C	A2
AK226	16001-16515	16183C-16189C-16217C	B2
AK227	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK228	16001-16566	16111T-16223T-16265G-16290T-16319A-16362C	A2b1
AK229	16016-16566	16093C-16111T-16223T-16290T-16319A-16362C	A
AK230	16001-16566	16111T-16223T-16235G-16290T-16319A-16362C	A2
AK231	16001-16504	16111T-16223T-16290T-16319A-16362C	A2
AK232	16001-16566	16111T-16189C-16192T-16212G-16223T-16233G-16290T-16319A-16331G	A2a5
AK233	16001-16566	16192T-16256T-16270T-16399G	U5
AK234	16034-16566	16111T-16223T-16290T-16319A-16362C	A2

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AK235	16001-16566	16111T-16223T-16290T-16319A-16362C	A2
AK236	16001-16566	16111T-16129A-16223T-16290T-16319A-16362C	A2

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Supplementary Table S3. Mitochondrial DNA HVSI Haplogroup Frequencies (Counts and Percentages) Displayed by Populations Included in This Study, Locations, and Sources

Population	n	A	B	C	D	X	Location	Reference
Tlingit	154	150(97.4)	2(1.3)	2(1.3)	0	0	SE Alaska	This study
Tlingit	58	55(94.8)	0	1(1.7)	2(3.5)	0	SE Alaska	Schurr et al. 2012
Haida	14	13(92.9)	1(7.1)	0	0	0	SE Alaska	This study
Haida	20	19(95)	0	1(5)	0	0	SE Alaska	Schurr et al. 2012
Haida	41	36(87.8)	0	3(7.3)	2(4.9)	0	British Columbia	Ward et al. 1993
Tsimshian	5	3(60)	2(40)	0	0	0	SE Alaska	This study
Tsimshian	2	2(100)	0	0	0	0	SE Alaska	Cui et al.2013
Tsimshian	1	0	1(100)	0	0	0	SE Alaska	Achilli et al. 2013
Alaskan Athapaskan	1	1(100)	0	0	0	0	SE Alaska	This study
Alaskan Athapaskan	18	18(100)	0	0	0	0	Central Alaska	Shields et al. 1993
Aleut	163	56(34.4)	0	0	107(65.6)	0	W Alaska	Rubicz et al.2003
Bella Coola	40	25(62.5)	2(5)	3(7.5)	10(25)	0	British Columbia	Ward et al. 1993

Nuu Chah Nulth	63	28(44.5)	2(3.2)	12(19)	14(22.2)	7(11.1)	British Columbia	Ward et al. 1991
Canadian Inuit	96	84(87.5)	0	0	12(12.5)	0	Nunavut	Helgason et al. 2006
Greenland Inuit	291	278(95.5)	0	0	13(4.5)	0	West Greenland	Helgason et al. 2006

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Supplementary Table S4. Samples with HVSI Mutations, Moiety, and Clan Information Used for the Haplogroup A2 Tlingit Network

Sample	HVSI	Moiety	Clan
AK091-A19	16111T-16129A-16145A-16223T-16290T-16319A-16362C	Raven	L'eineidí
AK074-A11	16111T-16129A-16218T-16223T-16290T-16319A-16362C	Raven	Deisheetaan
AK019A5	16111T-16129A-16223T-16290T-163111C-16319A-16362C	Raven	T'akdeintaan
AK038-A5	16111T-16129A-16223T-16290T-163111C-16319A-16362C	Raven	T'akdeintaan
AK061-A5	16111T-16129A-16223T-16290T-163111C-16319A-16362C	Raven	Kiks.ádi
AK110-A5	16111T-16129A-16223T-16290T-163111C-16319A-16362C	Raven	T'akdeintaan
AK111-A5	16111T-16129A-16223T-16290T-163111C-16319A-16362C	Raven	L'uknax.ádi
AK132-A5	16111T-16129A-16223T-16290T-163111C-16319A-16362C	Raven	L'uknax.ádi
AK140-A5	16111T-16129A-16223T-16290T-163111C-16319A-16362C	Raven	L'uknax.ádi
AK151-A5	16111T-16129A-16223T-16290T-163111C-16319A-16362C	Raven	L'uknax.ádi
AK187-A5	16111T-16129A-16223T-16290T-163111C-16319A-16362C	Raven	L'uknax.ádi
AK225-A5	16111T-16129A-16223T-16290T-163111C-16319A-16362C	Raven	L'uknax.ádi
AK004A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	Kiks.ádi
AK006A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	L'eineidí
AK013A4	16111T-16129A-16223T-16290T-16319A-16362C	Raven	L'eineidí
AK029-A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	Deisheetaan
AK030-A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	Deisheetaan
AK039-A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	Gaanax.ádi
AK047-A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	L'eineidí
AK057-A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	Kookhittaan
AK086-A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	Kookhittaan
AK088-A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	L'eineidí

AK090-A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	Deisheetaan
AK093-A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	Kiks.ádi
AK104-A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	Kiks.ádi
AK105-A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	Deisheetaan
AK108-A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	Kaach.ádi
AK109-A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	L'eineidí
AK136-A1	16111T-16129A-16223T-16290T-16319A-16362C	Eagle	Teikweidí
AK160-A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	Gaanax.ádi
AK165-A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	L'eineidí
AK174-A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	Sukteeneidí
AK177-A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	L'eineidí
AK205-A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	L'eineidí
AK208-A1	16111T-16129A-16223T-16290T-16319A-16362C	Eagle	Teikweidí
AK209-A1	16111T-16129A-16223T-16290T-16319A-16362C	Eagle	Teikweidí
AK224-A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	Gaanax.ádi
AK236-A1	16111T-16129A-16223T-16290T-16319A-16362C	Raven	L'eineidí
AK055-A1	16111T-16129A-16223T-16290T-16319A-16362C-16519C	Raven/Crow	Ishkaahittaan
AK130-A1	16111T-16129A-16223T-16290T-16319A-16362C-16519C	Raven	Gaanaxteidí
AK141-A10	16111T-16129A-16223T-16290T-16319A-16362C-16519C	Raven	Taakw.aaneidí
AK206-A1a	16111T-16129A-16223T-16290T-16319A-16362C-16519C	Raven	L'uknax.ádi
AK210-A1a	16111T-16129A-16223T-16290T-16319A-16362C-16519C	Raven	Deisheetaan
AK011A4	16111T-16189C-16223T-16290T-16319A-16362C	Eagle	Dakl'aweidí
AK042-A4	16111T-16189C-16223T-16290T-16319A-16362C	Raven	Dakl'aweidí
AK084-A4	16111T-16189C-16223T-16290T-16319A-16362C	Eagle	Yanyeidí
AK129-A4	16111T-16189C-16223T-16290T-16319A-16362C	Eagle	Tsaagweidi

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AK131-A4	16111T-16189C-16223T-16290T-16319A-16362C	Raven	Dakl'aweidí
AK152-A4	16111T-16189C-16223T-16290T-16319A-16362C	Raven	Dakl'aweidí
AK188-A4	16111T-16189C-16223T-16290T-16319A-16362C	Eagle	Tsaagweidi
AK190-A4	16111T-16189C-16223T-16290T-16319A-16362C	Eagle	Kaagwaantaan
AK211-A4	16111T-16189C-16223T-16290T-16319A-16362C	Eagle	Dakl'aweidí
AK008A3	16111T-16218T-16223T-16235G-16290T-16319A-16362C	Raven	Gaanaxteidí
AK024-A6	16111T-16223T-16235G-16290T-16319A-16362C	Raven	Gaanaxteidí
AK040-A13	16111T-16223T-16235G-16290T-16319A-16362C	Raven	Gaanaxteidí
AK155-A13	16111T-16223T-16235G-16290T-16319A-16362C	Raven	Kiks.ádi
AK186-A13	16111T-16223T-16235G-16290T-16319A-16362C	Raven	L'uknax.ádi
AK117-A8	16111T-16223T-16265G-16290T-16319A-16362C	Raven	L'uknax.ádi
AK003A2	16111T-16223T-16290T-16319A-16362C	Eagle	Chookaneidí
AK007A2	16111T-16223T-16290T-16319A-16362C	Eagle	Kaagwaantaan
AK018A2	16111T-16223T-16290T-16319A-16362C	Raven	Kaagwaantaan
AK023-A2	16111T-16223T-16290T-16319A-16362C	Eagle/Wolf	Kaagwaantaan
AK046-A2	16111T-16223T-16290T-16319A-16362C	Eagle	Dakl'aweidí
AK065-A2	16111T-16223T-16290T-16319A-16362C	Eagle	Kaagwaantaan
AK078-A2	16111T-16223T-16290T-16319A-16362C	Eagle	Kluckwan
AK100-A2	16111T-16223T-16290T-16319A-16362C	Eagle	Dakl'aweidí
AK115-A2	16111T-16223T-16290T-16319A-16362C	Eagle/Wolf	Kaagwaantaan
AK124-A2	16111T-16223T-16290T-16319A-16362C	Eagle	Kaagwaantaan
AK125-A2	16111T-16223T-16290T-16319A-16362C	Eagle/Wolf	Kaagwaantaan
AK146-A2	16111T-16223T-16290T-16319A-16362C	Eagle	Kaagwaantaan
AK147-A2	16111T-16223T-16290T-16319A-16362C	Eagle	Kaagwaantaan
AK167-A2	16111T-16223T-16290T-16319A-16362C	Eagle	Kaagwaantaan

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AK170-A2	16111T-16223T-16290T-16319A-16362C	Eagle	Wooshkeetan
AK180-A2	16111T-16223T-16290T-16319A-16362C	Eagle	Shangukeidí
AK182-A2	16111T-16223T-16290T-16319A-16362C	Eagle/Wolf	Kaagwaantaan
AK185-A2	16111T-16223T-16290T-16319A-16362C	Eagle	Kaagwaantaan
AK191-A2	16111T-16223T-16290T-16319A-16362C	Eagle	Wooshkeetan
AK195-A2	16111T-16223T-16290T-16319A-16362C	Eagle	Shangukeidí
AK215-A2	16111T-16223T-16290T-16319A-16362C	Eagle	Neix.adi
AK219-A2	16111T-16223T-16290T-16319A-16362C	Eagle	Kaagwaantaan
AK221-A2	16111T-16223T-16290T-16319A-16362C	Eagle	Wooshkeetan
AK234-A2	16111T-16223T-16290T-16319A-16362C	Eagle	Shangukeidí

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Figure Captions

Figure 1. Map of the Northwest Coast culture area with approximate boundaries of the territories inhabited by the Northwest Coast populations mentioned in this study (1) Tlingit; (2) Haida; (3) Tsimshian; (4) Bella Coola; (5) Kwakuitl; (6) Nuu-chah-nulth; (7) Coast Salish; (8) Chinook; (9) Oregon Athapaskan. Redrawn from Suttles (1990).

Figure 2. Map of the historical Tlingit territories with approximate boundaries: (1) Ġalyáx Kwáan – Yakataga/Controller Bay; (2) Laaxaayík Kwáan – Yakutat; (3) Ġunaaxoo Kwáan – Dry Bay; (4) Jilḵaat Kwáan – Chilkat; (5) Jilḵoot Kwáan – Chilkoot; (6) Xuuna Kwáan – Hoonah; (7) Aak'w Kwáan – Juneau; (8) T'aaku Kwáan – Taku; (9) Sheey At'ika Kwáan – Sitka; (10) Xutsnoowú Kwáan – Angoon; (11) S'awdaan Kwáan – Sumdum; (12) Kooyu Kwáan – Kuiu Island; (13) Ḵeex Kwáan – Kake; (14) Shtax'héen Kwáan – Wrangell; (15) Takjik'aan Kwáan and Hinya Kwáan – Prince of Wales and Klawock; (16) Sanyaa Kwáan – Cape Fox; (17) Taant'a Kwáan – Ketchikan. Drawn based on information from Goldschmidt and Haas (1998), de Laguna (1990), Emmons and de Laguna (1991), Hope and Thornton (2000), and Hope et al. (2003).

Figure 3. Haplogroup frequencies for the Tlingit and comparative populations.

Figure 4. MDS plot of pairwise Fst estimates: TLI=Tlingit; HAI=Haida; TSI=Tsimshian; ATH=Alaskan Athapascan; BEL=Bella Coola; NUU=Nuu-chah-nulth; CAI=Canadian Inuit; GRI=Greenland Inuit; ALE=Aleut.

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Figure 5. Reduced median-network of HVSI (from position 16041 to 16383) Haplogroups A2 sequences from Tlingit (this study n=142; Schurr et al. 2012 n =55), Haida (this study n=13; Schurr et al. 2012 n=19; Ward et al. 1993 n=21), Tsimshian (this study n=3; Cui et al. 2013 n=2), and Alaskan Athapaskan (this study n=1; Shields et al. 1993 n=18) populations. The central node exhibits the following mutations relative to the Cambridge Reference Sequence (Anderson et al. 1981; Anderson et al. 1999): 16111T-16223T-16290T-16319A-16362C. Mutational positions in red represent transitions. Black dot represents a median vector.

Figure 6. Reduced median-network of HVSI sequences (from position 16041 to 16519) from Tlingit clans found in the Raven (n=47) and Eagle (n=35) moieties from this study. The right A2 node exhibits the following mutations relative to the Cambridge Reference Sequence (Anderson et al. 1981; Anderson et al. 1999): 16111T-16223T-16290T-16319A-16362C. Mutational positions in red represent transitions.

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Figure 1.

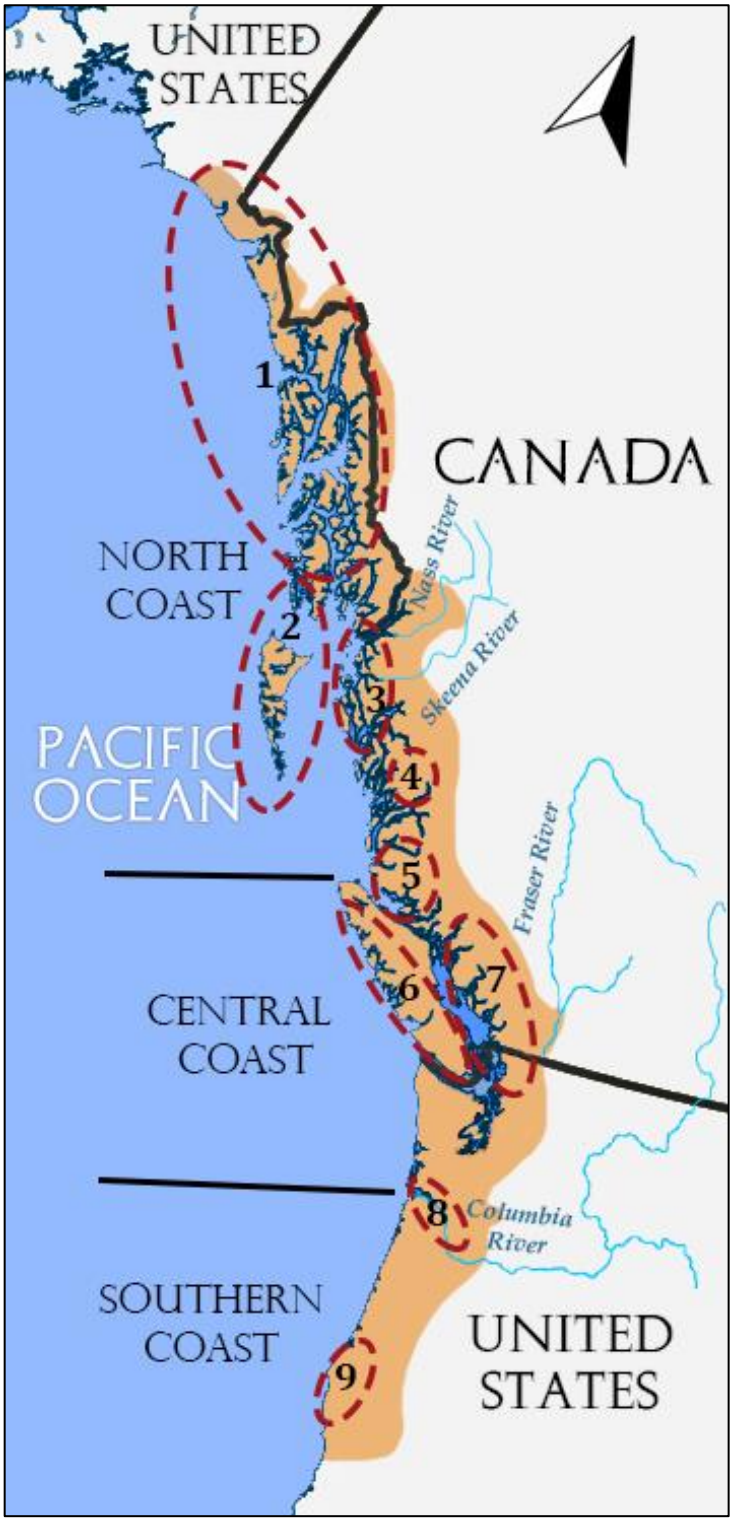

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Figure 2.

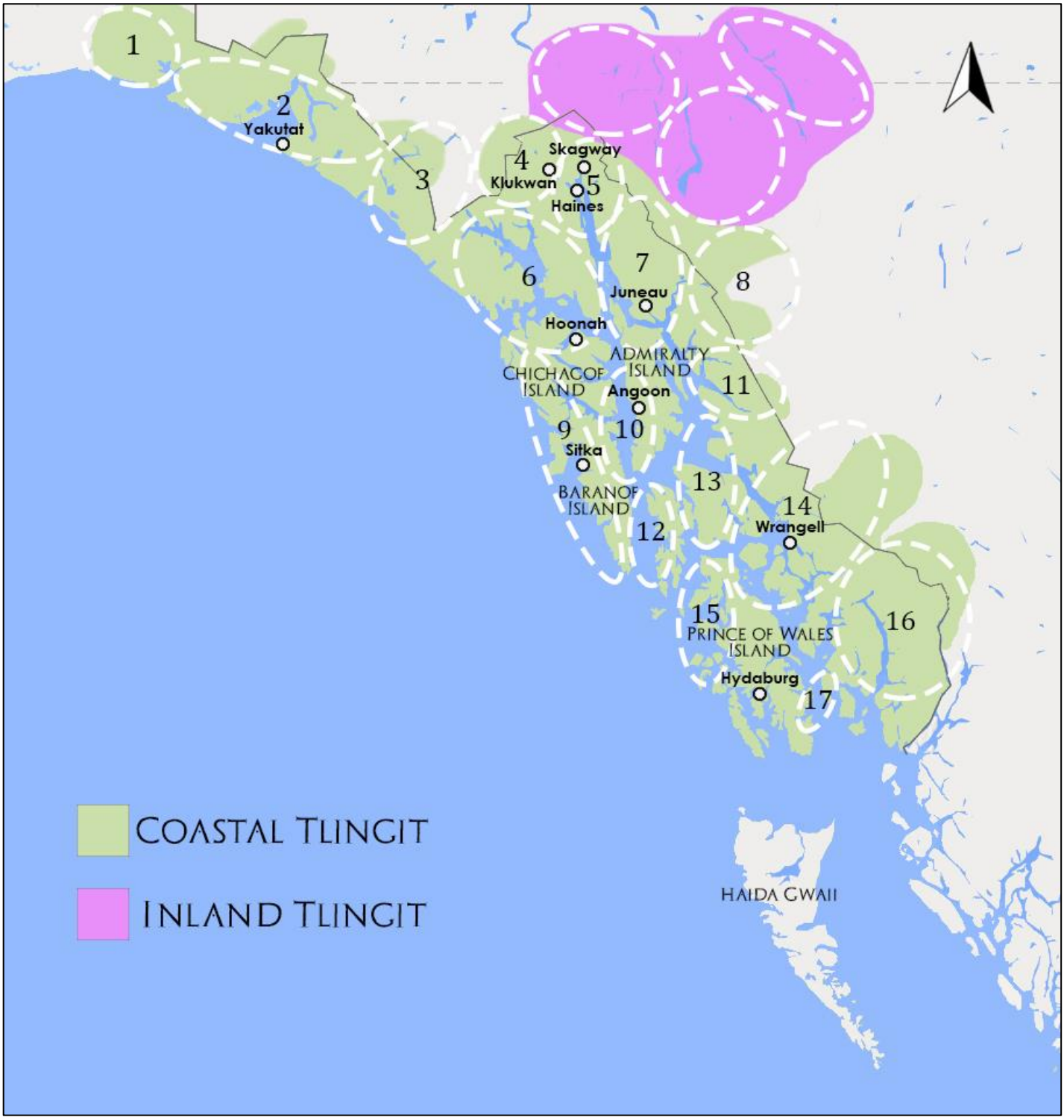

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Figure 3.

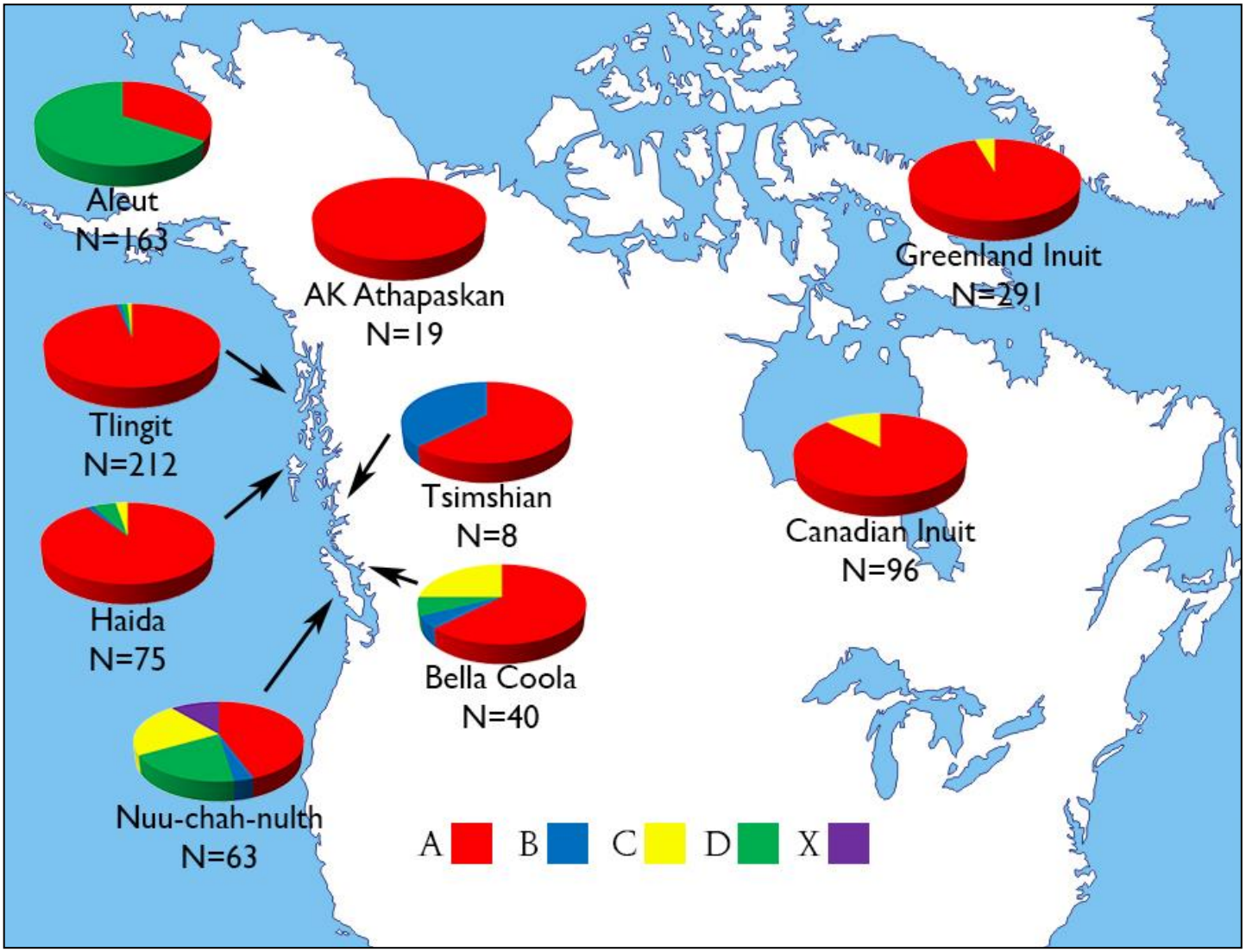

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Figure 4.

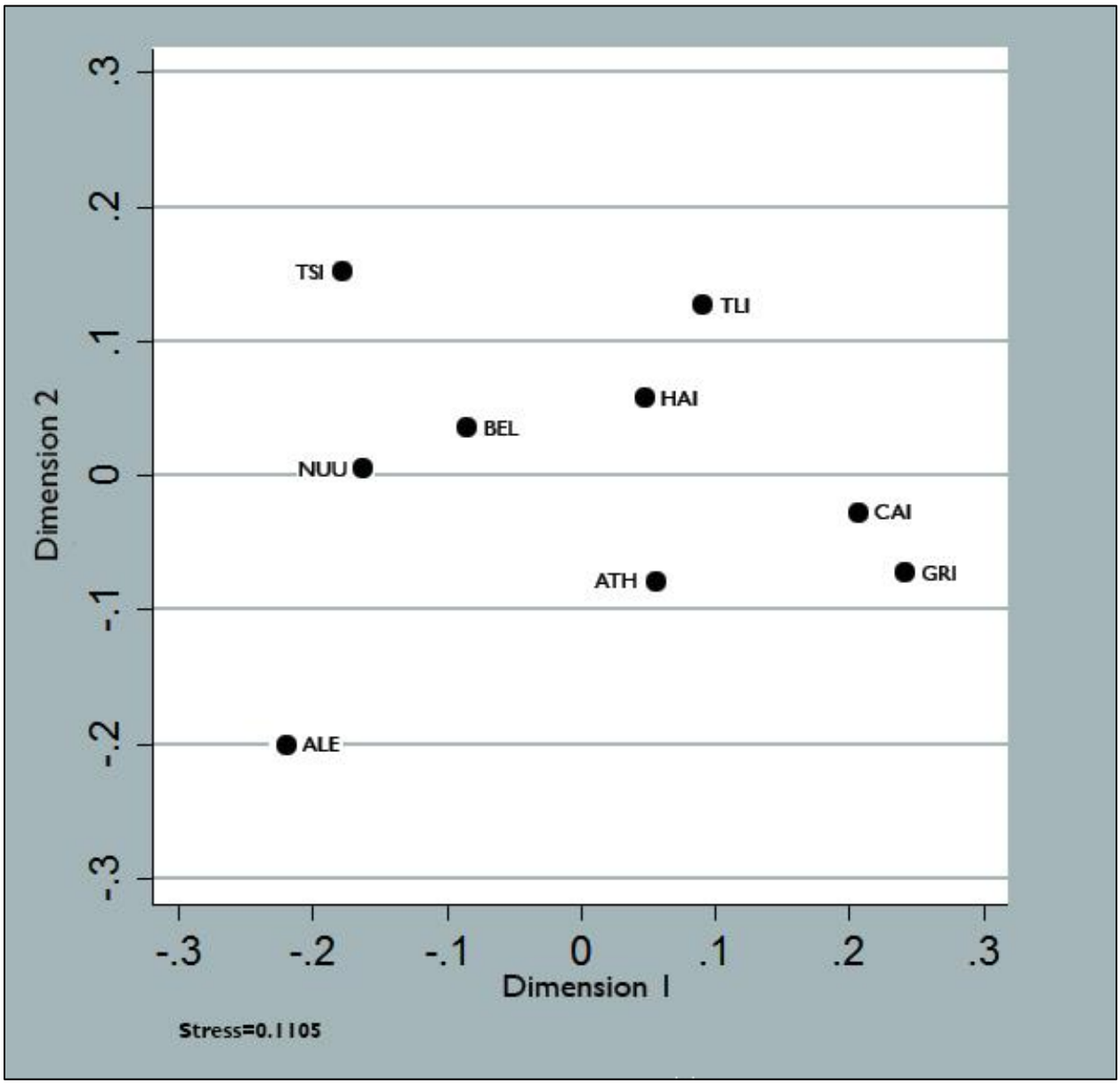

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Figure 5.

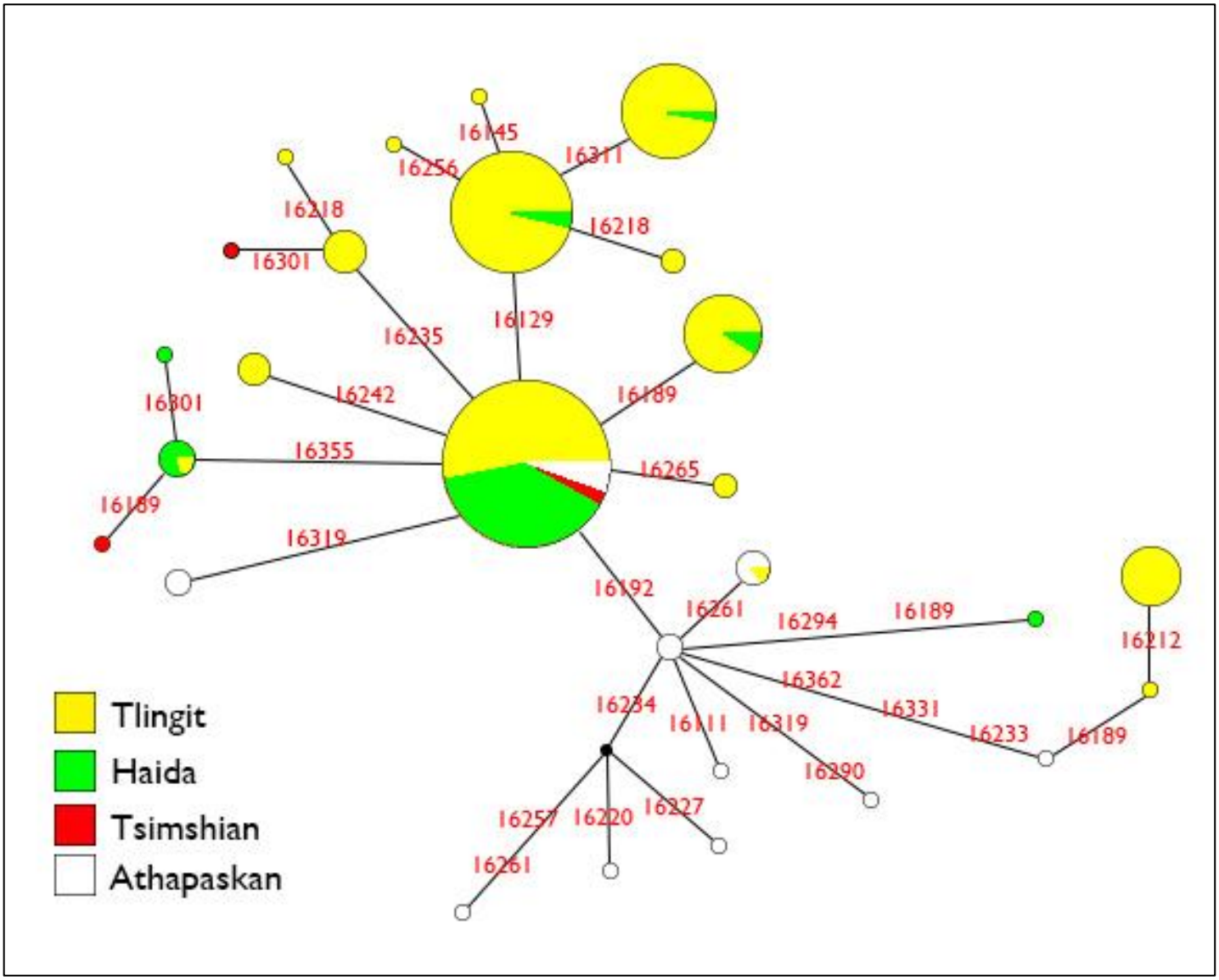

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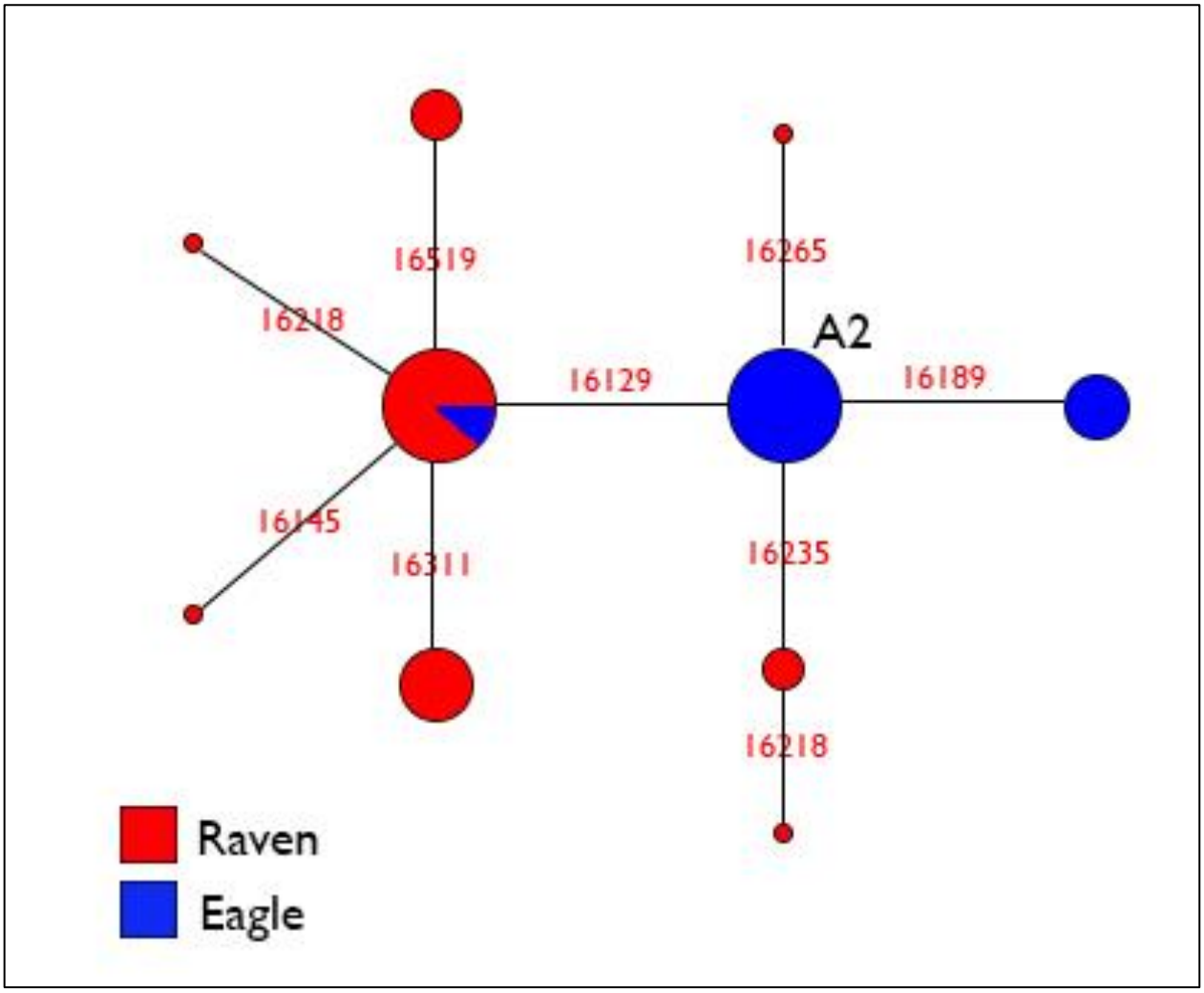
Figure 6.



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