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ARTICLE

Evidence for the persistence of ancient Beothuk and Maritime Archaic mitochondrial DNA genome lineages among modern Native American peoples

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Abstract: The Beothuk were a Native American people who formerly occupied the island of Newfoundland, and who are generally accepted to have become culturally extinct in 1829. The Beothuk succeeded the Maritime Archaic people on the island after a hiatus of ca. 1.4 ka, and were themselves succeeded by the extant Mi'kmaq within historic times. Genetic continuity between ancient and modern Native Americans remains of interest. Complete aDNA mitogenomes from ancient Beothuk and Maritime Archaic were compared with the most closely related modern mitogenomes as obtained by BLAST search of GenBank. Beothuk mitogenomes in five clades are in one case identical to and otherwise differ by minima of three to eight SNPs from the most closely related modern mitogenomes. Maritime Archaic mitogenomes in 12 clades are in one case identical to and otherwise differ by minima of one to nine SNPs from the most similar modern mitogenomes. The single available modern Mi'kmaq mitogenome differs from the most similar Beothuk and Maritime Archaic mitogenomes by 12 and 22 SNPs, respectively. Phylogenetic analysis and sequence similarities imply lineage extinction of most ancient clades, as well as continuity of two Beothuk and at least one Maritime Archaic lineages in modern Native Americans and their descendants.

Key words: Native Americans, Beothuk, Maritime Archaic, haplogroups A, B, C, D, and X, ancient DNA.

Résumé : Les Béothuks étaient les membres d'un peuple indigène qui occupait antérieurement l'île de Terre-Neuve et dont on rapporte généralement qu'il se serait éteint en tant qu'entité culturelle distincte en 1829. Les Béothuks auraient succédé aux peuples Maritimes Archaïques sur l'île après un hiatus d'environ 1400 ans, et auraient eux-mêmes été suivis des Micmacs plus récemment. La continuité génétique entre les peuples autochtones plus anciens et modernes demeure d'intérêt. Dans ce travail, l'auteur compare les mitogénomes de l'ADN ancien (aDNA) provenant d'individus des peuples Béothuks et Maritimes Archaïques avec ceux des plus proches mitogénomes contemporains identifiés en interrogeant GenBank à l'aide de l'outil BLAST. Les mitogénomes des Béothuks forment cinq clades qui sont soit identiques ou diffèrent par au minima trois à huit SNP des mitogénomes contemporains les plus apparentés. Les mitogénomes des Maritimes Archaïques forment 12 clades qui sont soit identiques ou diffèrent par au un à neuf SNP de leurs pendants modernes. Le seul mitogénome Micmac moderne diffère des mitogénomes Béothuks et Maritimes Archaïques les plus proches par 12 et 22 SNP, respectivement. Des analyses phylogénétiques et de similarité des séquences suggèrent une extinction des clades les plus anciens et une continuité de deux lignages Béothuks et d'un lignage Maritimes Archaïques au sein des Amérindiens modernes et de leurs descendants. [Traduit par la Rédaction]

Mots-clés : Amérindiens, Béothuks, peuples Maritimes Archaïques, haplogroupes A, B, C, D et X, ADN ancien.

Introduction

The Beothuk were members of the "Red Ochre" culture (Marshall 1996) that inhabited the island of Newfoundland on the extreme Atlantic coast of North America ca. 2.1–0.2 ka BP, at the end contemporaneously with an extant Algonquian people, the Mi'kmaq, prior to and during early European colonization of the interior <1800 CE. The Beothuk are generally accepted to have become culturally extinct with the deaths of the last known members, Shanawdithit (1801?–1829), her uncle Nonosabasut (?–1819), and his wife Demasduit (?–1820) (Marshall 1996). The Beothuk succeeded the immediately previous inhabitants of the island and (or) the adjacent coast of Labrador, the Maritime Archaic ca. 8.0–3.4 ka BP, after an interval of ca. 1.4 ka (Renouf and Bell 2011). Other peoples in this area at this time include the

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Dorset Paleo-Eskimo, who overlap temporally with both the Maritime Archaic and Beothuk ca. 2.1–1.1 ka BP (Renouf 2011). An outstanding question is the possible survival of Beothuk genetic lineages in the modern Mi'kmaq and (or) other modern persons of Native American descent (Aylward and Joe 2018).

Duggan et al. (2017) recovered mitogenome sequences from aDNA of individuals representative of the Maritime Archaic, Dorset, and Beothuk peoples, on the island of Newfoundland and adjacent southern shore of Labrador, dating from ca. 7700 BCE – 1820 CE. Inter alia, they concluded that there is a genetic as well as temporal discontinuity between the Maritime Archaic and the Beothuk, and that the former are not the ancestors of the latter. Here, Beothuk and Maritime Archaic mitogenomes are compared with the most closely related sequences of modern persons in the GenBank database. These comparisons bear on the utility of mtDNA sequence data for the association of living persons to extant or extinct Native American peoples.

Materials and methods

aDNA samples

Duggan et al. (2017) provide complete or near complete 16 579 bp mtDNA genome sequence alignments (including indels) from aDNA of 74 individuals from the island of Newfoundland and southern coastal Labrador, including 18 Beothuk (including Nonosabasut and Demasduit), 54 Maritime Archaic, and two Paleo-Eskimo. The Maritime Archaic and Beothuk cultures are disjunct by about 1.4 ka (Renouf 2011; Duggan et al. 2017). These sequences and those described next were aligned with the 16 569 bp revised Cambridge Reference Sequence (rCRS) by tacit removal of 10 indels.

GenBank searches and phylogenetic analysis

Neighbor Joining (NJ) and Maximum Likelihood (ML) analyses of unweighted pairwise sequence differences were done with MEGA X (Kumar et al. 2018), without the rCRS sequence. From an initial NJ analysis of the eight distinct Beothuk and 31 distinct Maritime Archaic aDNA mitogenomes, BLAST searches in GenBank were made with the most basal aDNA sequence in each of the identified clusters. These searches identified 27 archived sequences with the greatest phenetic similarity to one or another of the aDNA sequences. Included is a search with a mitogenome (GenBank HQ287872) from an individual of self-identified "French" ancestry from the Port au Port Peninsula of western Newfoundland, who is inferred to have Mi'kmaq matrilineal ancestry (Pope et al. 2011), as well as the aDNA mitogenomes of "Kennewick Man" (Rasmussen et al. 2015) and a Saqqaq Paleo-Eskimo (Gilbert et al. 2008). The initial NJ analysis identified several Ojibwe sequences in haplogroup X4 from Perego et al. (2009): all 10 X4 sequences in that study were then included. ML analysis was then performed for the combined contig of 105 mitogenomes (GTR model, pairwise exclusion of gaps and missing bases, NNI branch swapping), and 3000 bootstrap replications under the same conditions.

Results

Phylogenetic relationships of mitogenomic clades

Figure 1 shows the ML analysis of these mitogenomes. Midpoint rooting separates mitogenomes assignable to haplogroups A, B, and X in super-group N from those in haplogroups C and D in super-group M. The eight distinct Beothuk sequences occur in five clades (B1–B5), within all haplogroups except B. The 33 distinct Maritime Archaic sequences occur in 12 clades (MA1–MA12) in all five haplogroups. Haplogroup assignments agree with those of Duggan et al. (2017). Other ethnic and (or) geographic provenance indicated in the GenBank accessions are given where available.

Diversity and relationships of ancient versus modern mitogenomes

The BLAST search of GenBank identified mitogenomes from modern persons that differed from the most similar Beothuk clades by minima of zero to eight SNPs (Table 1). The sequence of Demasduit differs from those of four other Beothuk (clade B1, haplogroup C) and one modern individual by one SNP each. The individual with sequence KX379141 has traced a maternal genealogy back five generations, and found no Native American ancestor (pers. comm. to the author). The sequence of Nonosabasut is identical to that of three other Beothuk (clade B5, haplogroup X) and one Ojibwe. In the remaining three clades, the monophyletic sequences of BTK76 (clade B2, haplogroup C) and BTK54 (clade B3, haplogroup D) differ by eight and five SNPs from the most closely related non-Beothuk sequences. Clade B4 (haplogroup A) comprises eight identical or near-identical Beothuk sequences in haplogroup A, including that of the individual of greatest ^{14}C-calibrated antiquity (BTK73: ca. 700 CE), and differs by three SNPs from the most similar non-Beothuk sequence, from an Ojibwe individual.

A similar search with the Maritime Archaic sequences in 12 clades identified one (BTK178) identical to a modern sequence, and otherwise minimum differences of one to nine SNPs (Table 1). The mitogenome of the most ancient Maritime Archaic individual from L'Anse Amour ca. 7700 BCE differs from that of the most similar Maritime Archaic (clade MA1) and several modern sequences by four SNPs, and is otherwise phylogenetically more closely related to the Demasduit-inclusive clade B1 than any Maritime Archaic clade.

The clade inclusive of the single known modern Mi'kmaq mitogenome HQ287872 in haplogroup A (Pope et al. 2011) differs from the most closely related Beothuk and Maritime Archaic sequences by 22 and 12 SNPs, respectively, and from the two most closely related modern sequences

Fig. 1. Phylogenetic relationships inferred by Maximum Likelihood analysis among 105 mitogenomes, including 72 aDNA genomes from 18 Beothuk and 54 Maritime Archaic individuals (all Duggan et al. 2017), two other aDNA genomes (Gilbert et al. 2008; Rasmussen et al. 2015), and 31 genomes from modern individuals with Native American maternal ancestry drawn from GenBank. The modern mitogenomes shown are those with closest phenetic similarity to the basal-most sequences in the Beothuk and Maritime Archaic clades. The Beothuk occur in five clades (red: B1–B5) assignable to haplogroups C and D within super-group M, and haplogroups A and X in super-group N. The Maritime Archaic occur in 12 clades (green: MA1–MA12), assignable to the same four haplogroups as well as haplogroup B in super-group N. The 10 Ojibwe mitogenomes in haplogroup X (Perego et al. 2009) are marked Oj and indicated in blue.

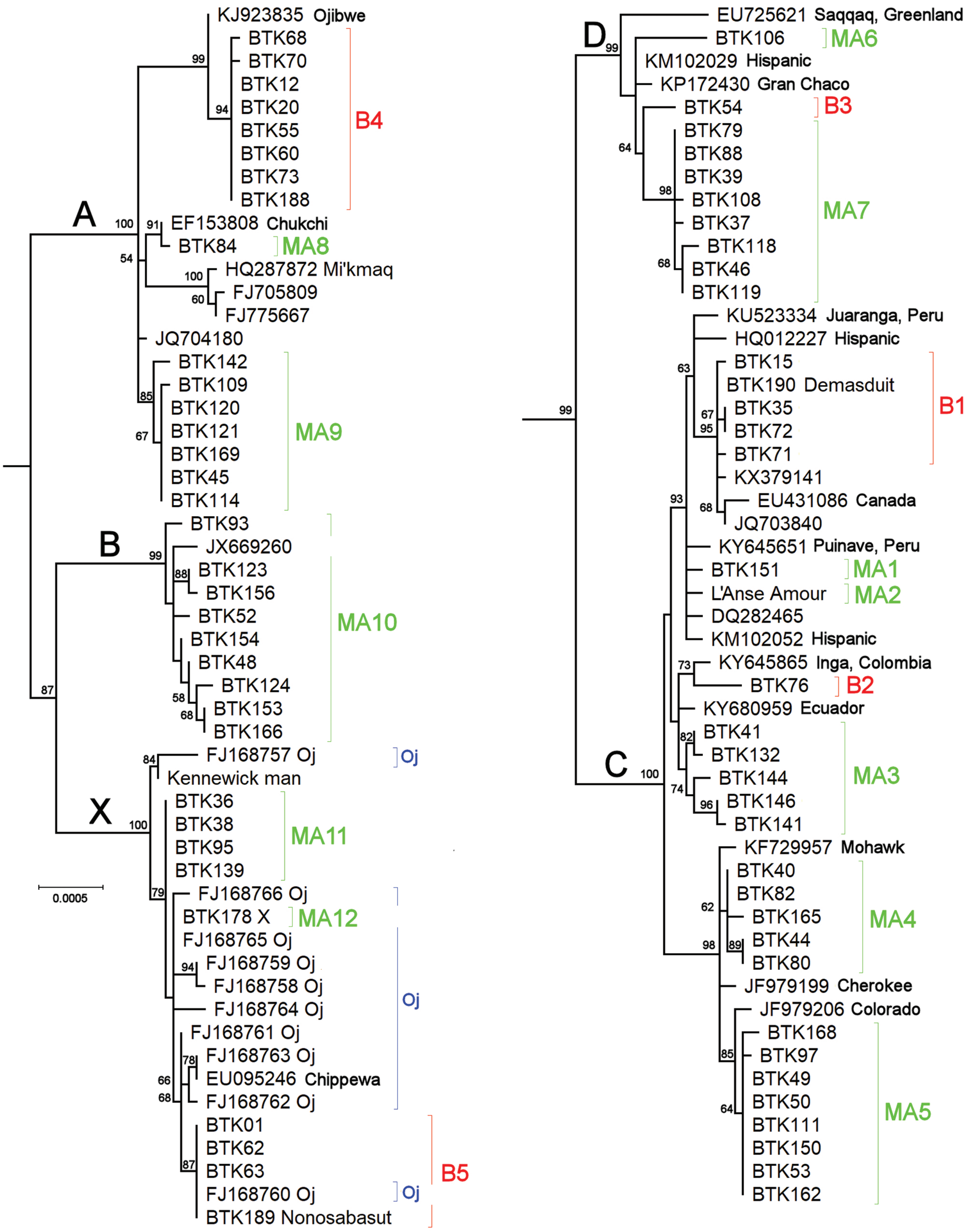

Table 1. Clade structure of ancient with respect to modern mitogenomes.

			Clade			
Clade	aDNA Ref	Modern	*n*	min Δ	max Δ	Type
B1	BTK190	KX379141	2	1	1	Poly
B2	BTK76	KY645865	1	8	—	—
B3	BTK54	KM102029	1	5	—	—
B4	BTK12	KJ923835	3	3	4	Mono
B5	BTK189	FJ168760	1	0	1	Poly
MA1	BTK151	DQ282465	1	4	—	Poly
MA2	L'Anse Amour	KM102052	1	4	—	Poly
MA3	BTK41	KY680959	4	4	8	Mono
MA4	BTK40	KF729957	4	3	7	Mono
MA5	BTK49	JF979206	3	3	4	Mono
MA6	BTK106	KM102029	1	9	—	—
MA7	BTK39	KM102029	5	5	8	Mono
MA8	BTK84	EF153808	1	1	—	—
MA9	BTK120	JQ704180	3	4	5	Mono
MA10	BTK52	JX669260	7	3	6	Para
MA11	BTK36	FJ168761	1	1	2	Mono
MA12	BTK178	FJ168765	1	0	—	—
D1	BTK75	EU725621	2	6	19	Mono

Note: For each clade identified in Fig. 1, the modern GenBank sequence (Modern) most similar to the basal aDNA sequence within the clade (aDNA Ref) was identified by BLAST search. Clades B2, B3, MA1, MA2, MA6, MA8, and MA12 each comprise single mitogenomes. Otherwise, *n* is the number of distinct sequences in each clade, and min Δ and max Δ are the minimum and maximum phenetic differences between the modern sequence and aDNA sequences in the clade. For clades that include more than one distinct sequence, Mono and Poly identify monophyletic and polyphyletic clades sensu stricto (cf. Wiley and Lieberman 2011) with respect to inclusion of modern sequences. Clade MA10 is monophyletic with respect to MA except for the inclusion of JX669260, and therefore paraphyletic (Para) sensu lato. Note that KM102029 is at the base of a polytomy that includes clades M6, M7, and B3 (Fig. 1). Clades with a single sequence are left undefined.

by one or two SNPs. Neither of these sequences has an assigned ethnic origin.

Clades MA11, MA12, and B5 in haplogroup X4 are interspersed among 10 mitogenomes from modern Ojibwe individuals (GenBank FJ168757–FJ168766: Perego et al. 2009), including the mitogenomes identical with those of Nonosabasut (B5) and Maritime Archaic BTK178 (MA12) described above. Several other GenBank accessions, including two identical to BTK178, are identified as Ojibwe within the multi-ethnic clade bounded by FJ168757. This includes EU095246, identified as Chippewa, an alternative exonym for Ojibwe (see below). Note as well KJ923835, identified as "Ojibwe" and sister to clade B4.

The two mitogenomes from Dorset individuals in Duggan et al. (2017) are most closely related to EU725621 in haplogroup D, another aDNA ca. 2000 BCE from a Saqqaq Paleo-Eskimo from Greenland, from which they differ by 6 and 19 SNPs (Table 1).

Discussion

Genetic relationships of ancient and modern Native American mitogenomes

Modern individuals of Native American descent are shown to have mitogenome sequences most closely related to and identical or nearly so (zero to eight SNPs) to those of the ancient Beothuk and Maritime Archaic individuals identified by Duggan et al. (2017). The two Beothuk individuals of most recent historical provenance, Nonosabasut and Demasduit, have mitogenomes identical or nearly so, respectively, to modern individuals of Ojibwe ancestry, as does one Maritime Archaic individual. The mitogenome of the L'Anse Amour Maritime Archaic individual, separated by almost 10 ka from that of modern individuals, differs from them by as few as four SNPs. The mitogenome of the Beothuk individual of greatest antiquity (ca. 1.3 ka BP) is identical to that of four other Beothuk, in a clade nested among several modern Ojibwe lineages.

Each of the five Beothuk and 12 Maritime Archaic lineages is reciprocally monophyletic with respect to the lineages in the other group, including two Beothuk and five Maritime Archaic singletons. On this evidence, Duggan et al. (2017) concluded that the Maritime Archaic and Beothuk reflect genetically and temporally disjunct tenures of the island, and that their distinct haplotypic spectra reflect coalescent ancestry in a much more ancient population in southwestern North America >15 ka BP.

Sequence similarity, clade structure, and inferences of genetic continuity between ancient and modern Native Americans

The data and analysis in Duggan et al. (2017) provide a quantitative framework to understand the genetic relationships of two ancient Newfoundland peoples. This framework may be extended to comparison of modern and ancient peoples. Alternative ethnographic hypotheses (cf. Marshall 1996) ask whether incoming Mi'kmaq displaced contemporaneous Beothuk over time with a greater or lesser degree of genetic interchange, or succeeded them after temporal discontinuity with no effective genetic continuity. The Beothuk / Maritime Archaic comparison models the latter. Despite persistent claims, there are no known families and (or) individuals that can trace a reliably documented, unbroken maternal (or other) ancestry to a Beothuk ancestor as far back as 200 years, prior to their cultural extinction in the 1820s. Claims of continuity are especially common in the province of Newfoundland and Labrador, where Beothuk contacts with Europeans or Euro-Americans date back to the early 1500s, and with seasonal Mi'kmaq migrants or residents even earlier (Marshall 1996; Martijn 2003). Given the reasonably comprehensive sample of historic Beothuk and Maritime Archaic lineages now available to establish group priors for comparison, we can now test specific hypotheses of affinity based on the degree of similarity and relatedness. Does identity or near identity of the mitogenome lineages of modern Native American or Native American descendants with ancient sequences suggest continuity with Beothuk or Maritime Archaic maternal lineages? Does the absence of closely related modern relatives to any ancient clade suggest lineage extinction? In this discussion, it must be emphasized that the ancient and modern lineages compared are those that we know about, and that absence of evidence of affinity is not necessarily evidence of absence.

Lineage extinction versus direct and collateral descent

The Maritime Archaic include six monophyletic clades (MA3, MA4, MA5, MA7, MA9, and MA11) with multiple members that are distinct (three to eight SNPs) from the most closely related modern sister mitogenome (Table 1). Allowing for limited sampling, these can be taken as indications of lineage extinction, as do the single mitogenomes in clades MA1, MA2, and MA6 that differ from those of modern individuals by four SNPs each. These account for 19 out of 32 observed Maritime Archaic mitogenome types in 9 of 12 clades. Presence of the modern JX669260 lineage in clade MA10 (with 7 SNP differences) likely reflect persistent polymorphism from the much older coalescent population. This may also explain pairing of the modern EF153808 Chukchi lineage with clade MA8, with only a single SNP difference over a wide geographic distance and a temporal separation of several thousand years. The exception to these patterns of lineage extinction or coalescent ancestry of Maritime Archaic with respect to modern persons is the identity of clade MA12 with three modern Ojibwe sequence. This suggests continuity of at least one extremely ancient Maritime Archaic lineage within a modern Native American group, in contrast to their lack of continuity within the ancient Beothuk.

In the Beothuk, clade B4 is the only monophyletic, multi-member lineage with the lineage extinction pattern seen in most Maritime Archaic clades. Clade B1 is a well-supported (95% bootstrap) but unresolved polytomy including BTK190 Demasduit and multiple modern individuals (Fig. 1). Clade B5 includes BTK189 Nonosabasut and three other Beothuk mitogenomes identical with one Ojibwe sequence, and is the sister to another Ojibwe-specific clade. This suggests continuity of ancient Beothuk lineages within modern Algonquian Native Americans and their descendants, those that include two of the last surviving Beothuk. Detectability of specific Ojibwe connections with ancient Beothuk and Maritime Archaic lineages reflects in part the more extensive sampling of this people (Perego et al. 2009), in contrast to other First Nations with insufficient sampling to establish group priors.

Haplogroup X includes several Ojibwe closely related or identical to ancient individuals in clades MA11, MA12, and B5. The Ojibwe, like the Mi'kmaq and Algonquian people, were in the pre-contact period located near the mouth of the St. Lawrence River, and ca. 1660 moved inland to the Great Lakes region with the assistance of their "allied brothers," the Mi'kmaq (Dickason and Newbigging 2015). The endonym Ojibwe is alternatively anglicized as Chippewa, and includes the Saulteaux. Given possible geographic, cultural, and (or) temporal continuity among the Beothuk, Ojibwe, and (or) the Mi'kmaq, mitogenomic clades with perfect or near-perfect matches between ancient Beothuk (or Maritime Archaic) and modern Algonquian individuals may be the likeliest candidates for what these maternal lineages would look like, if such persist to the present day. Future identification of modern individuals with mitogenomes in clade B5 and possibly B1 might be taken as evidence of genetic persistence of Beothuk matrilines.

Assignment of individuals to Native American and First Nations groups

One such person of historic interest is Santu Toney (ca. 1835–1920), long described in the anthropological literature as a Beothuk woman (Diamond 2018). Ethnographer Frank Speck in 1910 interviewed Joe Toney, Santu's son, who told Speck that his mother said that her father ("Kop") was an "Osa'yana Indian" from Newfoundland. "*This naturally startled me, because it referred indirectly to the supposedly extinct Beothuk….*" (Speck 1922:56). Osa'yana is a Mi'kmaq word for the Beothuk and (or) the Montagnais (Speck 1922:177). Kop's subsequent history is unknown. Santu married a Mi'kmaq man by whom she had several children, including Joe. Given this parentage, Santu would (of course) not have inherited her father's Y-chromosome, and would have inherited her own mother's Mi'kmaq mtDNA genome. Thus, neither Y- nor mtDNA Beothuk markers would be expected in any of Santu's descendants. The fraction of any paternal Beothuk-specific nucDNA markers would be reduced to 0.25 in her children, and by a further 0.5 in each subsequent generation.

Use of genomic methods to assign modern or ancient individuals to particular ethnic groups, or to distinguish among such groups, requires more accurate knowledge of prior probabilities of assignment than is available for most if not all modern Native American and First Nations groups. In response to the ongoing and potential impact of commercial genetic testing in "Indian Country," Tallbear (2013) has emphasized that indigenous identity involves dynamic interactions of politics, culture, and biology, beyond that of simplistic measures of genetic affinity. Equally important is a nuanced appreciation of ethical considerations for the community, and knowledge of their genealogy, history, and anthropology (Pullman 2018). In this light, it is gratifying to note the repatriation in March 2020 of the remains of Nonosabasut and Demasduit to their home island.

Some implications for commercial genetic testing

Commercial tests of genetic ancestry, based on partial or complete mtDNA genomes along with Y-DNA and (or) nuclear markers, is now routine. Companies claim to assess ancestries of single individuals as proportional contributions from prior probabilities drawn from ethnic or national groups defined a priori, including Native American peoples. Few if any of these tests include reliable priors for individual Native American tribes or Canadian First Nations. A forensic concern that arises from the present data are that "Beothuk ancestry" might be asserted based on an unscrupulous utterance of one of the eight known Beothuk sequences, in the absence of independently authenticated laboratory data. An instance that anticipates this occurred in late 2016, where a commercial company claimed to have provided a client with evidence of "Beothuk DNA", though no original data were ever produced. The company was unaware of the only comparative data and analyses in Kuch et al. (2007) and Pope et al. (2011). After intensive media scrutiny, the claim was withdrawn (CBC website, 27 January 2017 [http://www.cbc.ca/news/canada/newfoundland-labrador/beothuk-dna-ancestry-genetics-1.3953668]).

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Afterword

The MS by A Collier & SM Carr that appears in *Mitochondrial DNA Part A*, 30(1): 68–74 was withdrawn in April 2018, but because of a production error by the journal has now appeared in the print edition. The present analysis includes mitogenomes from Maritime Archaic (Duggan et al. 2017), Ojibwe (Perego et al. 2009), and other individuals not included in the prior MS. The author requests that any reference to this analysis be made to the current MS and not that in *Mitochondrial DNA Part A*.

References

Aylward, C., and Joe, M. 2018. Beothuk and Mi'kmaq: an interview with Chief Misel Joe. *In* Tracing ochre: changing perspectives on the Beothuk. *Edited by* F. Polack. University of Toronto Press, Toronto, Ont. pp. 117–132.

Diamond, B. 2018. Santu Toney: a Transnational Beothuk woman. *In* Tracing ochre: changing perspectives on the Beothuk. *Edited by* F. Polack. University of Toronto Press, Toronto, Ont. pp. 247–268.

Dickason, O.P., and Newbigging, W. 2015. Indigenous Peoples within Canada: a concise history. Oxford University Press, Don Mills, Ontario, Canada. 434 pp.

Duggan, A.T., Harris, A.J.T., Marciniak, S., Marshall, I., Kuch, M., Kitchen, A., et al. 2017. Genetic discontinuity between the Maritime Archaic and Beothuk populations in Newfoundland, Canada. Curr. Biol. **27**: 3149–3156. doi:10.1016/j.cub.2017.08.053. PMID:29033326.

Gilbert, M.T., Kivisild, T., Gronnow, B., Andersen, P.K., Metspalu, E., Reidla, M., et al. 2008. Paleo-Eskimo mtDNA genome reveals matrilineal discontinuity in Greenland. Science, **320**: 1787–1789. doi:10.1126/science.1159750. PMID:18511654.

Kuch, M., Gröcke, D.R., Knyf, M.C., Gilbert, M.T., Younghusband, B., Young, T., et al. 2007. A preliminary analysis of the DNA and diet of the extinct Beothuk: a systematic approach to ancient human DNA. Am. J. Phys. Anthopol. **132**: 594–604. doi:10.1002/ajpa.20536. PMID:17205549.

Kumar, S., Stecher, G., Li, M., Knyaz, C., and Tamura, K. 2018. MEGA X: molecular evolutionary genetic analysis across computing platforms. Mol. Biol. Evol. **36**: 1547–1549. doi:10.1093/molbev/msy096. PMID:29722887.

Marshall, I. 1996. A history and ethnography of the Beothuk. McGill-Queen's, Toronto, Ont. 640 pp.

Martijn, C.A. 2003. Early Mi'kmaq presence in southern Newfoundland: an ethnohistorical perspective, c. 1500–1763. Newfoundland Studies, **19**: 44–102.

Perego, U.A., Achilli, A., Angerhofer, N., Accetturo, M., Pala, M., Olivieri, A., et al. 2009. Distinctive Paleo-Indian migration routes from Beringia marked by two rare mtDNA haplogroups. Curr. Biol. **19**: 1–8. doi:10.1016/j.cub.2008.11.058. PMID:19135370.

Pope, A.M., Carr, S.M., Smith, K.N., and Marshall, H.D. 2011. Mitogenomic and microsatellite variation in descendants of the founder population of Newfoundland: high genetic diversity in an historically isolated population. Genome, **54**(2): 110–119. doi:10.1139/G10-102. PMID:21326367.

Pullman, D. 2018. Bioarchaeology, Bioethics, and the Beothuk. *In* Tracing ochre: changing perspectives on the Beothuk. *Edited by* F. Polack. University of Toronto Press, Toronto, Ont. pp. 152–176.

Rasmussen, M., Sikora, M., Albrechtsen, A., Korneliussen, T.S., Moreno-Mayar, J.V., Poznik, G.D., et al. 2015. The ancestry and affiliations of Kennewick Man. Nature, **523**: 455–458. doi:10.1038/nature14625. PMID:26087396.

Renouf, M.A.P. 2011. The cultural landscapes of Port au Choix. Springer. 324 pp.

Renouf, M.A.P., and Bell, T. 2011. Across the tickle: the Gould Site, Port au Choix-3 and the Maritime Archaic Indian mortuary landscape. *In* The cultural landscapes of Port au Choix. *Edited by* M.A.P. Renouf. Springer. pp. 43–63.

Speck, F.G. 1922. Beothuk and Micmac. Part I. Studies of the Beothuk and MicMac of Newfoundland. *In* Indian notes and monographs. *Edited by* F.W. Hodge. Museum of the American Indian, New York. [Reprinted as: Beothuk an [*sic*: and] Micmac – Primary Source edition].

Tallbear, K. 2013. Native American DNA. University of Minnesota Press, St. Paul, Minn. 252 pp.

Wiley, E.O., and Lieberman, B.S. 2011. Phylogenetics: theory and practice of phylogenetic systematics. 2nd ed. Wiley-Blackwell, New York. 406 pp.