DOG DOMESTICATION

Origins and diversity of Greenland's *Qimmit* revealed with genomes of ancient and modern sled dogs

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The *Qimmeq* (Greenland sled dog) has worked continuously with the Inuit in Greenland for more than 800 years. However, they now face drastic population declines caused by climate change, urbanization, and competition from snowmobiles. This study sequenced 92 modern and ancient genomes to investigate how centuries of isolation shaped the regional *Qimmeq* populations and the impact of European contact. We found distinct regional populations and evidence for two migrations of dogs into Greenland with the Inuit from Canada. Furthermore, we found that there is minimal European ancestry in present day *Qimmit* and limited recent inbreeding despite low heterozygosity. These insights are critical for conservation efforts aimed at preserving the *Qimmit* amid environmental changes and cultural transitions.

Across the circumpolar Arctic, the ubiquitous presence of sled dogs, which have worked alongside humans for more than 9500 years, is a testament to the technological importance and cultural value of these dogs throughout the region (*1*, *2*). Descended from a common ancestor and adapted to the demanding environment are the Arctic breeds we know today as the Siberian husky, Alaskan malamute, Samoyed, Canadian Inuit dog, and *Qimmeq* (also known as the Greenland sled dog) (*1*). Unique among these Arctic breeds is the *Qimmeq* (plural *Qimmit*). Unlike the other Arctic breeds, these dogs have continuously worked as sled dogs in the same region, with the same people, for nearly a millennium. Where other indigenous dog breeds have been replaced, heavily admixed with other dogs, or have been transitioned from working dogs to companion animals, the *Qimmit* have remained in their traditional role as sled dogs in *Kalaallit Nunaat* (Greenland). However, they are now faced with new pressures from climate change, urbanization, and globalization (*3*). These factors have already begun to have an impact as the number of *Qimmit* in Greenland dropped from ~25,000 in 2002 to ~13,000 in 2020 (*3*, *4*). To reduce the introduction of pathogens and foreign dogs, restrictions have been placed on the movement of dogs in and out of the sledding district (Fig. 1A). In the face of diminishing sea ice and snow necessary for sledding, canine epidemics, and competition with snowmobiles, the human management of the dogs must adapt to maintain a healthy population that can persist for millennia to come (*3*, *4*). To characterize the past and present *Qimmit*, this study generated genomic data from dogs across Greenland to assess their regional differentiation and diversity.

The first introduction of dogs to the Americas occurred in the late Pleistocene, followed by the introduction of cultures associated with Palaeo-Inuit cultural complex around 5500 years before present (BP) (*2*, *5*–*9*). Recent genetic evidence suggests that these populations have been replaced by the dogs accompanying the ancestors of the Yup'ik, Iñupiat, and Inuit from Siberia to Alaska around 1800 BP (*2*, *5*, *6*). Inuit lifeways evolved in northern Alaska and spread across the coast of the North American Arctic around 1000 BP (*7*, *10*–*14*). The inclusion of dogs well adapted to the Arctic in the Inuit toolkit was likely a critical factor in their expansion (*2*). By 800 BP, the Inuit had reached the Thule district in northwest Greenland, spreading south around the coasts of the island during the late 13th century CE (*11*, *13*, *15*). Despite the tightly intertwined histories of the *Qimmeq* and Inuit, little is known about the relationships among the regional populations of dogs in Greenland after their settlement; of particular interest are the now-extinct communities in northeast Greenland.

The ongoing decrease of the *Qimmeq* population in Greenland underlines the importance of capturing the breadth of diversity present in the population(s) today to inform conservation strategies for these unique dogs. To characterize the population history of this last remaining indigenous sled dog population, we generated nuclear genomes to a mean depth of coverage per individual ranging from 0.1x to 30.6x for 92 dogs from across Greenland, dating from 800 BP to the modern day (Fig. 1A). We observed high levels of genetic drift, resulting in a very structured population of dogs that was maintained for centuries, with recent changes in regional diversity after the Danish-Norwegian colonization in 1721 CE.

Origin of *Qimmit*

We assessed the shared ancestry between the *Qimmit* and other dog breeds and populations using whole-genome data from 1998 canids (data S2), including 92 *Qimmeq* genomes newly generated for this study and representing three eras: (i) pre-European contact (hereafter "precontact") dogs ($n = 8$) dating between the Inuit arrival in Greenland until the Danish-Norwegian colonization between 1721 and 1884 CE; (ii) postcontact dogs ($n = 21$) from the period after recolonization until 1998 CE; and (iii) present-day *Qimmeq* genomes ($n = 63$) sampled after 1998 CE (Fig. 1A).

A neighbor-joining phylogenetic tree was constructed using identity-by-state (IBS) of pseudohaploid genotypes, including only transversions, from precontact and postcontact *Qimmit* >0.9x coverage ($n = 23$) and present-day *Qimmit* >3x coverage ($n = 60$), together with a black-backed jackal (*Canis mesomelas*) outgroup and a geographically balanced selection of wolves ($n = 28$) and dogs from East and Southeast Asia ($n = 82$), modern Europe ($n = 106$), ancient Europe ($n = 11$), West and South Asia and Africa ($n = 51$), and non-*Qimmit* Arctic dogs ($n = 39$) (Fig. 1B and fig. S1). The shared origin of the Arctic dog populations is apparent in the tree, with *Qimmit* and a 3700-year-old dog from Alaska (Teshekpuk1) forming a monophyletic clade within a broader

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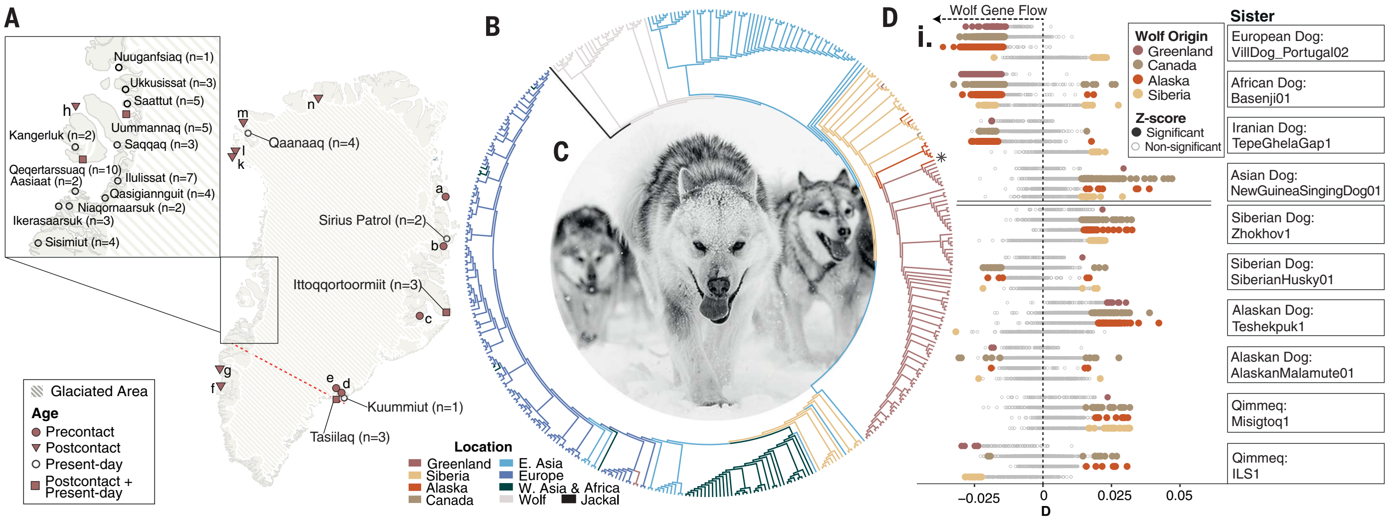

Fig. 1. Relationship of Greenland dogs to global dogs. (**A**) *Qimmeq* genomes sequenced to ≥0.1x coverage. Precontact ($n = 8$) ages were estimated from the archaeological context: (a) Stormbugt ($n = 1$), (b) Dødemandsbugten ($n = 1$), (c) Hekla Havn ($n = 3$), (d) Misigtoq ($n = 1$), (e) Sukersit ($n = 1$), and (j) Inugsuk ($n = 1$). Postcontact dogs ($n = 21$) from ethnographic collections or without stratigraphic contexts, collection/accession date as *terminus ad quem*: Ittoqqortoormiit ($n = 1$), Tasiilaq ($n = 3$), (f) Nuuk ($n = 1$), (g) Maniitsoq ($n = 1$), Qeqertarsuaq ($n = 1$), (h) Qeqertarssuatsiaq ($n = 1$), Uummannaq ($n = 2$), (i) Nugarsuk ($n = 1$), (k) Appat ($n = 1$), (l) North Star Bay ($n = 1$), (m) Siorapaluk ($n = 4$), (n) Monumentet ($n = 1$), and unknown locations on the east ($n = 1$) and west ($n = 2$) coasts. Towns with present-day genomes ($n = 63$) from buccal swabs are labeled with number of genomes. The red line demarcates the Sledding District with only *Qimmit*. (**B**) Neighbor-joining tree constructed from IBS distances with 1000 bootstrap replicates using pseudohaploid genomes from 401 dogs and wolves, with a black-backed jackal (BBJ) outgroup. Teshekpuk1 is marked with an asterisk. (**C**) Photo of *Qimmit* [photo by Carsten Egevang]. (**D**) Admixtools D-statistics wolf introgression into *Qimmit* relative to other dogs (sisters) and a BBJ outgroup: D(BBJ, wolf; *Qimmeq*, sister). *Z*-scores of −3 to 3 were considered nonsignificant, indicated in gray. (i) Non-Arctic dogs as sister. (ii) Arctic dogs as sister.

clade that includes Siberian and Alaskan dogs, as well as an ~4000-year-old dog from Port au Choix, Canada (figs. S1 to S6). The close relationship between the *Qimmit* and Teshekpuk1, despite intervening millennia and a distance of >2000 km, lends support to the hypothesis that the Inuit settled the North American Arctic rapidly (*13*). Three dogs from Greenland (Nuuk2, Maniitsoq1, and QTQ11) are observed outside of the *Qimmit* clade and principal component analysis (PCA) cluster, indicating mixed ancestry (Fig. 1B and figs. S1 to S3).

The deep temporal coexistence among wolves and dogs along the Inuit migration route provided many opportunities for wolf-dog hybridization (*16*). Oral traditions of Thule Inuit, continuing to the present day, emphasize the deliberate hybridization of the *Qimmeq* with wolves to strengthen and reinvigorate the dog populations reinforced by phenotypic similarities (Fig. 1C) (*17*–*20*). Interbreeding was ostensibly accomplished by tethering a female dog in estrus outside of camp to attract a wolf mate (*18*, *19*, *21*). To test for an excess of allele sharing between *Qimmit* and wolves compared with other dog groups, D-statistics were calculated. Our results demonstrate a greater allele sharing between wolves and Arctic dogs relative to European and African dogs (Fig. 1D and fig. S7). However, compared with the 9500-year-old Zhokhov dog and Teshekpuk1, the precontact *Qimmit* have no apparent excess of sharing with wolves (Fig. 1D, ii), reflecting ancient introgression from wolves into the Arctic dog lineage before spreading into North America, as previously proposed (*1*, *22*, *23*). However, the positive signals can be seen in Zhokhov1, Teshekpuk1, and precontact *Qimmit* relative to present-day and some postcontact *Qimmit,* likely reflecting the loss of wolf alleles through drift and more recent European dog introgression (fig. S8). No signal was detected for recent hybridization between the *Qimmeq* and wolves in the current dataset. *Qimmeq*-wolf hybrids have been reported to form strong bonds with a single owner and often display aggression toward humans outside of their "family," killing dogs from outside their team (*20*). This highly territorial behavior makes it difficult to integrate them with new owners and unfamiliar animals, likely leading to challenges in maintaining hybrids on teams and breeding beyond the F_1 generation, similar to other working dog populations (*18*, *24*). Furthermore, the current range of wolves in Greenland is restricted to the northern regions (*25*), reducing the overlap of wolves and *Qimmit.* Together, these factors have limited the impact of wolves on the ancestry of *Qimmit.* One caveat, however, is that oral traditions and the historical record indicate that hybridization has occurred, so hybrids either did not have a pervasive impact on *Qimmeq* ancestry or, because of their rarity, were unsampled in this study.

Regional Greenland dog differentiation

Next, population structure in *Qimmit* was examined using whole-genome sequencing data. PCA demonstrated differentiation in regional populations reflecting geographic isolation after the arrival of the *Qimmit* to Greenland and the subsequent divergence of the *Qimmit* populations (Fig. 2A and figs. S2 and S3). Studies of humans showed clear population structure in their Inuit ancestry, with genetic differentiation between the *Tunu* (east), *Kitaa* (west), and *Avanersuaq* (north) (*26*), reflecting the three distinct dialects of Greenlandic: *Kalaallisut, Tunumiit oraasiat,* and *Inuktun*, respectively (*27*, *28*). These patterns are also evident in the results of our phylogenetic analysis, wherein *Qimmit* largely conform to clades corresponding to the regional differentiation seen in the human populations (fig. S1). We identified an additional precontact northeast population that is unrepresented in human whole-genome datasets (fig. S1). The genetic drift of *Tunu* and *Avanersuaq* populations of *Qimmit* is clear, with the most recent individuals of the regional populations positioned at the extremes of PC2 and the oldest *Qimmit* of *Tunu* and *Kitaa* clustering together. The mirrored population structure observed in the *Qimmit* and the *Kalaallit*, Inuit of Greenland, thus highlights the shared human-dog movements and geographical isolation.

To characterize the divergence and genetic differentiation within Greenland, genome-wide fixation index (F_{ST}) between populations, pairwise IBS, and identity-by-descent (IBD) distances between individuals were calculated. This study sequenced *Qimmit* genomes predating the

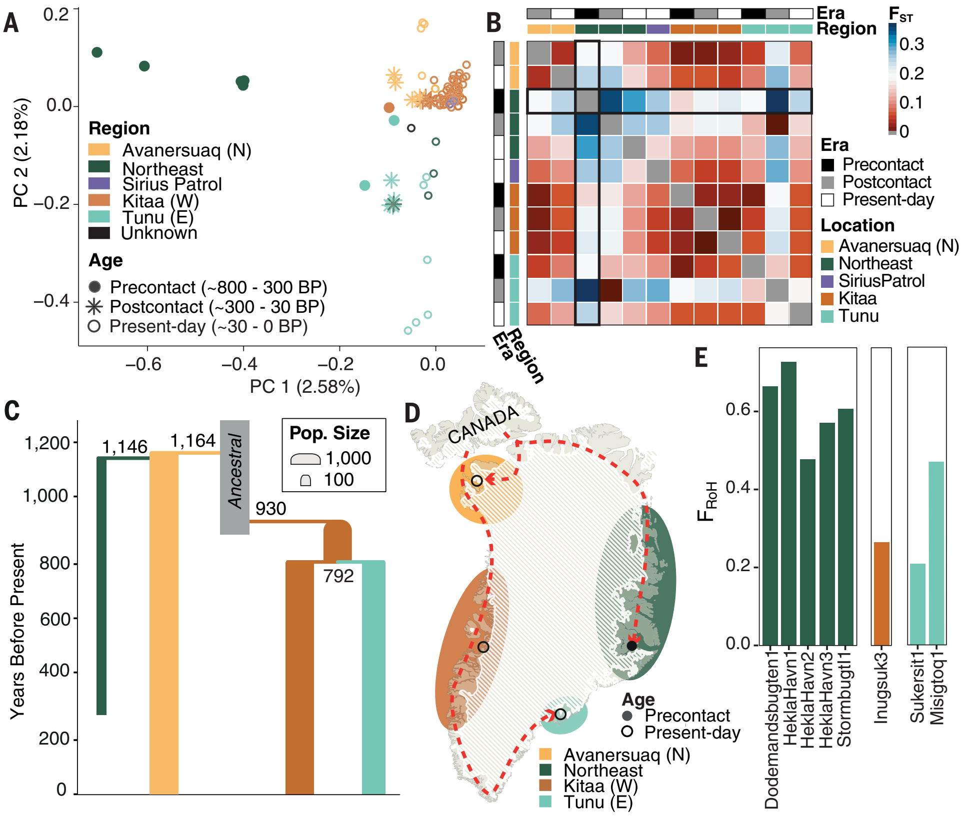

Fig. 2. Population structure of Greenland dogs. (**A**) PCA of pseudohaploidized genomes of *Qimmit*. Nonmodern genomes 0.1x to 4x are projected onto the PCA generated with smartPCA. Genomes' geographical and temporal origin are indicated with color and shape, respectively. (**B**) F_{ST} calculations with Plink2 for the dog populations of Greenland divided by temporal (marked with grayscale) and geographical origin (colored with the same palette as the PCA) with the extinct precontact northeast population highlighted with a black outline. (**C**) Highest-likelihood Fastsimcoal28 model for the divergence of the *Qimmeq* populations. Times are based on a 3-year generation time. (**D**) Locations of genomes used for the model are marked. The red line indicates the migration route for the arrival of dogs to the northeast from Canada supported by the model results. (**E**) F_{RoH} results for the eight precontact *Qimmit* shown for the archaeological sites in each region with greater than 0.9x mean coverage of the nuclear genome as calculated by Plink1.9.

disappearance of Inuit from the northeast. Their disappearance followed the only known contact in northeast Greenland between the Inuit and Europeans occurring in 1823 CE (*29*), thus generating the whole-genome insight into the relationship of these dogs and, by proxy, humans to the rest of Greenland. The absence of oral history, traditions, human genetics, and linguistics has resulted in archaeological evidence providing the only insight into the origin of the population (*30*–*32*). Our results show that precontact northeast *Qimmit* were a homogeneous population that shared the highest IBS and IBD with contemporaneous individuals from the northeast (fig. S6). When dogs outside of the region are considered, they have the lowest F_{ST} with precontact *Qimmit* of *Kitaa* ($F_{ST} = 0.184$), precontact *Qimmit* of *Tunu* ($F_{ST} = 0.195$), and postcontact *Avanersuaq Qimmit* ($F_{ST} = 0.202$), suggesting a high level of differentiation through discontinued gene flow between the populations and drift over time (Fig. 2B). After the disappearance of the Inuit in the northeast, a permanent settlement, Ittoqqortoormiit, was established in 1925 CE, populated by Inuit and *Qimmit* from Tasiilaq, a settlement in *Tunu* (*28*). The discontinuity of precontact northeast *Qimmit* and the later postcontact and present-day *Qimmit* is apparent, as well as the connection to the *Tunu Qimmit* (Fig. 2, A and B, and figs. S4 to S6). Furthermore, a second population of *Qimmit* currently resides in Daneborg in northeast Greenland, managed by the Danish SIRIUS Patrol established in 1950 CE. The SIRIUS Patrol dogs (SPDs) were brought from settlements in *Kitaa* (*33*), and the relationship between SPDs and *Kitaa* *Qimmit* can be seen through the PCA, F_{ST}, neighbor-joining tree, and outgroup F3 (Fig. 2, A and B, and figs. S1 to S5).

The divergences of precontact dog populations in Greenland were estimated with demographic modeling using Fastsimcoal2 on imputed genotypes from precontact northeast *Qimmeq* with GLIMPSE1 and present-day *Qimmit* genotypes called with GATK (*34*–*38*). We tested four topologies (fig. S9) to model the time of divergence of the regional *Qimmit* populations, and 150 replicates were generated using the same parameters for each model. Model4, testing the most recent divergence of the precontact northeast *Qimmit* from *Tunu*, yielded the worst fit, thus refuting a southern origin of the northeast *Qimmit* (figs. S9 and S10). These results corroborate archaeological evidence showing typological similarities between northeast *Qimmit* and *Avanersuaq Qimmit* (*30*). Model 2 showed the best delta likelihood and Akaike information criterion (figs. S9 and S10) and supports a two-wave process for the settlement of Greenland. Using a 3-year generation time, the replicate with the best fit for Model2 estimates the divergence of *Avanersuaq* from the ancestral population ~1164 years ago (~388 generations), followed quickly by the divergence of the northeast *Qimmit* from the *Avanersuaq Qimmit* ~1146 years ago (~382 generations), assuming a generation time of 3 years (Fig. 2C and fig. S10, D to K). A later divergence from the ancestral population ~930 years ago (310 generations) gave rise to the most common ancestor of *Kitaa* and *Tunu Qimmit*. These populations then diverged ~792 years ago (~264 generations). Although three models received similar support, the one with the highest likelihood agreed with archaeological evidence indicating a three-phase model for the peopling of Greenland by the Inuit (*39*). The dogs of the northeast and *Avanersuaq* may descend from the "explorative" phase, whereas the *Kitaa* and *Tunu Qimmit* descend from the later "pioneer" or "settling" phases in the 14th century CE (*39*). Furthermore, these results corroborate the designation of the *Qimmit* as one of the oldest dog breeds (*40*); in fact, each regional population of *Qimmit* predates the establishment of most European breeds during the Victorian Era. These results shed light on the movement and timing of the arrival of the Inuit to Greenland: Either the divergence of *Qimmit* populations predated the arrival of the Inuit or their arrival occurred more than a century earlier than was previously thought (Fig. 2D).

To examine the consequence of the long-term isolation of the dog populations of Greenland, autozygosity was calculated through F_{RoH}, indicating the fraction of the genome found within runs of homozygosity (RoHs) using PLINK1.9 on the present-day and imputed precontact and postcontact *Qimmit* (see the supplementary materials) (*41*, *42*). We found that the precontact *Qimmeq* of *Kitaa* and *Tunu* had lower levels of autozygosity ($F_{RoH} = 20.8$ to 47%) compared with the northeast *Qimmit* ($F_{RoH} = 47.7$ to 72.7%) (Fig. 2E). HeklaHavn1 showed the highest level of autozygosity ($F_{RoH} = 66.5\%$) compared with all precontact dogs. All three dogs at the site originate from unknown stratigraphic contexts excavated from house ruins in 1891 CE. Elevated DNA degradation patterns in HeklaHavn2 suggest that the specimen may be older than the other two dogs from the site (fig. S11). The higher levels of autozygosity in the precontact northeast support the argument for a small population size there and the cessation of immigration into the region after the 15th century CE, as indicated by the archaeological record (*30*).

Impacts of contact with Europeans and colonization on the *Qimmit*

To determine the genetic impact of European contact on the *Qimmit*, changes in diversity and European dog introgression were evaluated. After 985 CE, it is known that Norse settlements were established in southwestern Greenland, but the degree of interaction between the Norse and their Inuit contemporaries remains unclear (*43*, *44*). These settlements were located south of the current boundary of the sledding district. The demise of the Norse settlements in Greenland in the 15th century CE led to the cessation of sustained contact between Europe and Greenland until Danish-Norwegian colonies, missions, and trade stations were established in *Kitaa* from 1721 CE and in *Tunu* in 1884 CE. However, between 1600 and 1800 CE, European vessels visited Greenland on an annual basis. An excess of allele sharing between each *Qimmeq* and 72 modern European breeds was tested using D-statistics, and significant results are indicated by a *Z* score under −3. The admixture fraction was computed with ADMIXTOOLS f4 ratio (*45*). Our results show that dogs from before Danish-Norwegian colonization in Greenland (1721 CE in *Kitaa* and 1884 CE in *Tunu*) did not have an excess of allele sharing with European dogs (Fig. 3A). This suggests, as is the case with humans, that there is no genetic evidence for gene flow between the Inuit and Norse populations of Greenland (*26*, *46*). However, by the turn of the 20th century, admixed dogs were present on the west coast, corroborating the neighbor-joining tree and PCA results (Fig. 1B and figs. S1 to S3 and S12). Two of the three admixed dogs originated from towns outside of the dog sledding district. One of the dogs, Maniitsoq1 (f4 ratio = 0.45), is thought to have been the last "Labrador dog" of Greenland, a distinct population with sleek black fur valued for fur clothing that died in 1958 CE (Fig. 3A). The origin of Greenland's Labrador dogs is unknown, including whether they descended from the dogs introduced after the colonization or from earlier contact with the dogs of European whalers (*18*). A second postcontact dog, Nuuk2, which is dated to 1882 CE, had a high level of European ancestry (f4 ratio = 0.71). Nuuk2 may have also been a Labrador dog in light of the high level of European ancestry and the dark color of its fur (Fig. 3B). The connection between the label "Labrador" for these dogs to either Labrador retriever–related dog breeds or Canada's Labrador region is unclear. Our IBD analyses did not identify extensive sharing between the mixed dogs and other breeds, including breeds in the retriever group, suggesting that the dark-coated "Labrador" dogs in Greenland were a heterogeneous population with no connection to retriever breeds (Fig. 3C and figs. S1 and S13).

We found low levels of European ancestry in the present-day *Qimmit*, with a mean f4 admixture ratio of 0.09 across the population and only 53.5% ($n = 38$) showing a signal for European ancestry (Fig. 3A). This differs from the prevalence of European ancestry in the present-day human Greenlandic population, where ~80% of the population were stated to have ~0.25 proportion of their ancestry from Europe (*26*). The low levels of IBD sharing between the highly admixed *Qimmit* and non-Arctic dog breeds suggest that the European introgression was not recent or did not involve purebred dog breeds (Fig. 3C). Although less prevalent in dogs, the distribution of European ancestry in humans and dogs mirrors each other, with the settlements in the north and southeast

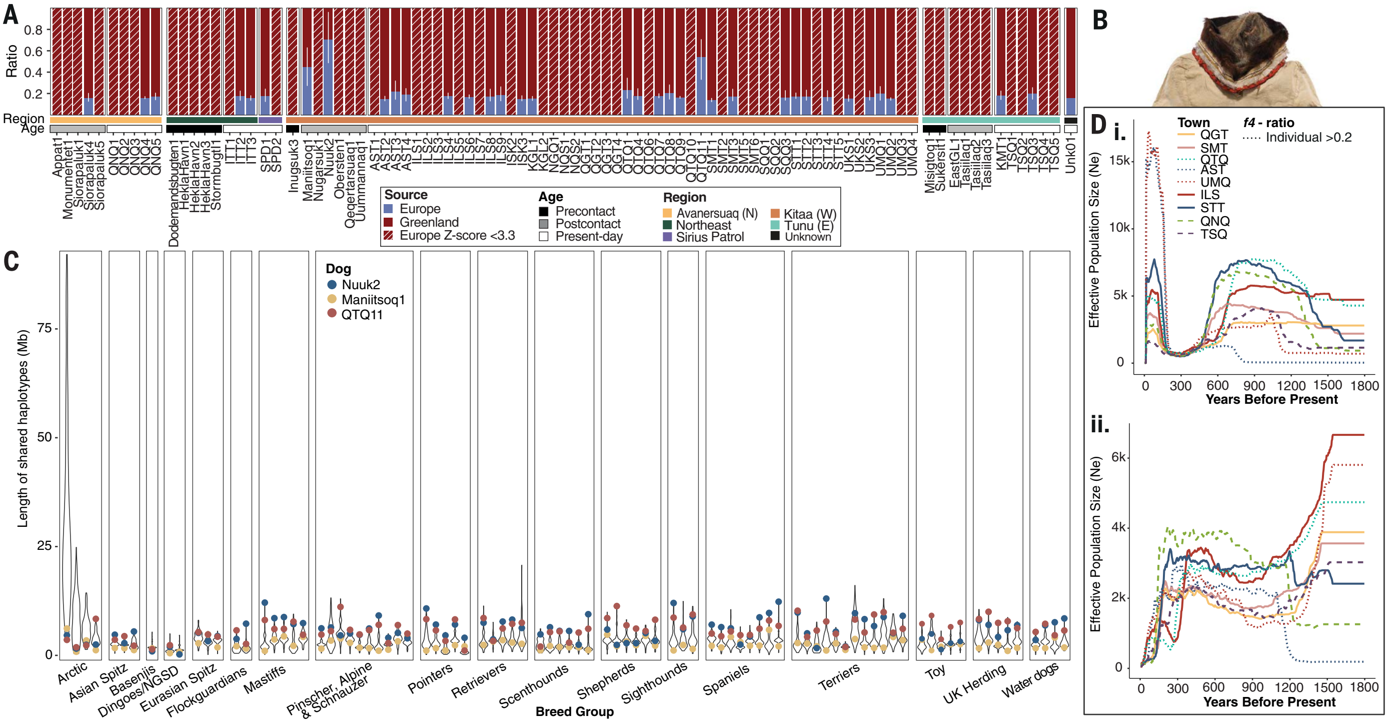

Fig. 3. European dog introgression. (**A**) Admixtools f4 ratio results for the mean across European dogs for introgression into *Qimmit* with BBJ outgroup using the following formula: f4(precontact *Qimmeq*, BBJ; target, basenji)/f4(precontact *Qimmeq*, BBJ; European breed, basenji), after a significant ($Z < -3$) D-statistic test. The minimum and maximum mean f4 ratios for breeds are indicated with SE bars. For all individuals without significant D-statistic tests, a single ancestry origin was modeled, indicated with white hashed bars. (**B**) Photo of Nuuk2 parka with dark fur. [Photo by Roberto Fortuna courtesy of National Museum of Denmark] (**C**) IBD sharing of three mixed dogs with breeds compared with the violin plot of mean sharing between *Qimmeq* and other breeds. (**D**) Effective population size (Ne) for present-day *Qimmit* from towns with ≥4 genomes estimated using GONE. Ne for towns with at least one *Qimmeq* with f4 ratio ≥ 0.2 are indicated with a dotted line. (i) maximum value of recombination rate ($hc = 0.05$). (ii) Maximum value of recombination rate ($hc = 0.01$) corrected for recent migrants.

carrying less European ancestry, corresponding to their greater isolation from Europe (*26*). *Kitaa* had the highest prevalence of European ancestry, observed in 30 of the 54 dogs (55.6%), with f4 ratios ranging from 0 to 0.54. The highest f4 ratio fraction for European ancestry was identified in a dog from Qeqertarsuaq (QTQ11), confirming mixed ancestry of the dog with known phenotypic differences. Compared with other Arctic breeds, including Alaskan malamutes and samoyeds, the present-day *Qimmit* has substantially lower levels of European ancestry (Fig. 3C). Illumina CanineHD Whole-Genome BeadChip have revealed that European gene flow into the Siberian husky was differentially dependent on the subset of the population studied, and that European introgression has been most widespread in the racing dogs (*23*). The limited European dog ancestry in the *Qimmit* underlines success of policies in Greenland to preserve the *Qimmeq,* including the advised cessation of dog importations in 1904 CE and legislation restricting the importation of dogs to settlements within the sled dog district (Fig. 1A) in 1998 CE (*47*). However, estimates of the effective population size shows an accelerated decline in the past 150 years consistent with recent reduction in the census population since 1990 CE, after accounting for the recent introgression (Fig. 3D and fig. S14) (*4*).

Although other dog populations across the Americas were being heavily mixed or replaced with European dogs, the number of *Qimmit* was declining, reflecting that maintaining the dogs in isolated populations could have resulted in substantial inbreeding. To investigate this possibility, we evaluated the diversity of the present-day *Qimmit* compared with their precontact and postcontact ancestors. Heterozygosity and RoH were calculated for each individual using imputed genotypes for the precontact and postcontact and GATK called present-day *Qimmit* genotypes using PLINK1.9 according to Meadows *et al.* with modified missingness (–homozyg-window-missing 10) and heterozygosity (–homozyg-window-het 5) tolerated per window (–homozyg-window-snp 100) to compensate for the reduction in sites included when removing transitions (*41*, *42*). A secondary hidden Markov model (HMM)–based method was implemented to identify genomic segments depleted of heterozygous genotype calls (see the supplementary materials). Comparison of PLINK- and HMM-based identification of RoH revealed that both methods had highly concordant F_{RoH} proportions and positions of RoH segments (jaccard mean = 0.69) (fig. S15 and data S6). Across the dataset of modern and ancient genomes, PLINK consistently reported a greater volume and shorter RoHs (figs. S15 to S17). The HMM method identified longer segments, reflecting regions with lower than the median heterozygosity across an individual's genome, as opposed to unbroken stretches of homozygosity, because of the unlimited number of heterozygous sites tolerated (fig. S16). We found that the total length of the genome composed of RoH in present-day *Qimmit* is within the range of modern breed dogs (Fig. 4B and figs. S15 and S16). Distinct from other breeds with pedigree-based breeding strategies, *Qimmit* have a greater number of RoHs than breeds with pedigree-based breeding strategies detected with both methods (Fig. 4B and figs. S15 and S16). *Qimmit* show comparable levels of F_{RoH} and volume of runs to the free-breeding populations of dingoes and New Guinea singing dogs (Fig. 4B and figs. S15 and S16). Parallels can be drawn between the histories of the dingo, New Guinea singing dog, and *Qimmeq* populations, including the substantial bottleneck during the founding of the population and long-term isolation of the populations.

We also observed regionally specific changes in diversity in the *Qimmeq* populations between the precontact era and the present day. In *Tunu*, our results reveal a trend of decreasing heterozygosity and inflating F_{RoH}, reflecting an increased accumulation of RoHs, until the early colonization period (Fig. 4, A and B, and fig. S16). This coincides with declining conditions in *Tunu* in the 19th century, including the loss of ~20% of the human population between 1884 and 1894 CE to famine (*48*). The dog population thus mirrors an extended period of adverse circumstances in *Tunu*. The elevated F_{RoH} of *Tunu* parallels that observed in the northeast, foreshadowing the possible fate of the *Qimmit* of *Tunu*. Fortunately, the heterozygosity of the present-day *Qimmit* of *Tunu* has rebounded since the early 20th century, coinciding with urbanization through the emigration of small, local groups of dogs to larger settlements, increasing the availability of unrelated mates and reducing the RoH without introducing high levels of European ancestry. In *Avanersuaq*, heterozygosity decreased between 1977 CE and the present day, which may reflect the genetic impact of the disease outbreaks in the region; e.g., the 1988 CE distemper epidemic in Qaanaaq resulted in the loss of ~80% of dogs (Fig. 4C) (*49*, *50*). Reflective of the larger settlement density, the *Qimmit* of *Kitaa* has the greatest range of heterozygosity (0.047 to 0.199) and F_{RoH} (0.104 to 0.535) (Fig. 4, A and C). Furthermore, we identified only three pairs of related individuals (second degree or closer). This suggests that the relatedness between teams of dogs is low, reflecting our success in sample selection aimed at sampling unrelated *Qimmit* (Fig. 4C, data S3, and fig. S18). Calculation of the

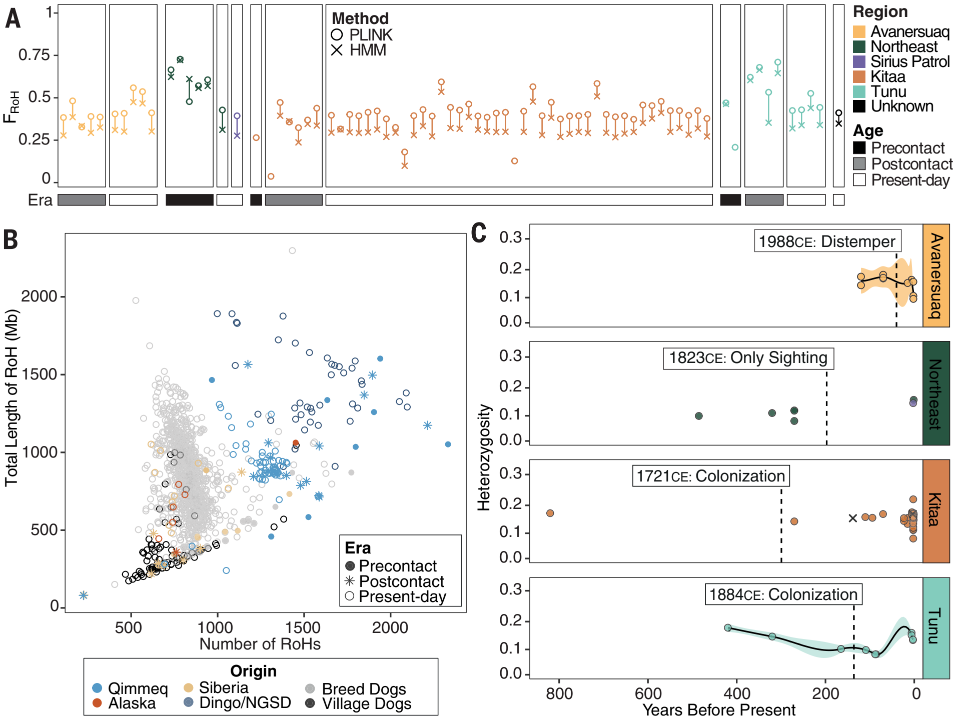

Fig. 4. Diversity. (**A**) Individual F_{RoH} for *Qimmit* of each era and location as calculated with each method. (**B**) Cumulative length of RoH segments and number of RoH segments in the dog genome for breed dogs, village dogs, *Qimmit*, and ancient Alaskan and Siberian dogs. (**C**) Proportion of heterozygous SNPs for each genome split by region of origin. A LOESS regression was applied, and each colored shaded area depicts the confidence interval. Because of the large confidence intervals for *Kitaa* and northeast, the regression was not plotted. Dates of notable events in the regions are indicated with dashed lines.

genetic load through the presence of derived alleles at sites with high levels of conservation (>1.5 phyloP) across 240 mammalian species revealed that proportion of genetic load in the realized, homozygous state was highest in the postcontact *Tunu* and northeast *Qimmit*. The proportion of homozygous genetic load was variable across the present-day *Qimmit*, suggesting the possibility that deleterious alleles may become fixed if the population size shrinks and inbreeding increases (fig. S19). Sinding *et al.* identified several putative genes that have contributed to the adaptation of *Qimmit* to a high-fat diet, potentially pain tolerance and thermoreception, and the management of exercise-induced hypoxia (*1*). Unexpectedly, the heavy artificial and natural selection that *Qimmit* have faced has facilitated shaping a healthy population of dogs despite the small population and high levels of RoH. Survival in the Arctic and performance as a sled dog have been the primary pressures shaping the dogs.

To date, the study of dogs using ancient DNA has focused on broad time frames and geographical scales. The results of this study present the foundation for future work using time-series genomes from regional populations to study the local evolution of animals shaped by humans and environments. In this study, the breadth of the *Qimmeq* population currently residing in Greenland has been captured at a critical moment, when the rapidly disappearing sea ice in Greenland, which is relied upon for dog sledding, and transition away from traditional lifestyles have already contributed to a shrinking number of dogs. The present-day *Qimmit* is composed of three distinct populations resulting from centuries of isolation and two recently founded populations in northeast Greenland. Each of these populations has experienced unique demographic histories with fluctuations in diversity, as seen through the heterozygosity and RoH. Our genetic evidence for the divergence of the northeast *Qimmit* from the other regions of Greenland and Canada sheds light on the history of their Inuit counterparts from the region and underlines the value of studying human migrations through the parallel histories of their dogs. These insights into the *Qimmit* provide a baseline for levels of inbreeding and introgression that can serve as a foundation for informed management aimed at the preservation of these remarkable dogs. Studies such as this demonstrate the relevance of paleogenomic insight into current conversations and decisions centered around conservation and preservation of culturally significant species.

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SUPPLEMENTARY MATERIALS

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Materials and Methods; Supplementary Text; Figs. S1 to S21; Table S1; References (*51–96*); Data S1 to S6

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