



ANCIENT DNA

The history of Coast Salish “wooly dogs” revealed by ancient genomics and Indigenous Knowledge

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Ancestral Coast Salish societies in the Pacific Northwest kept long-haired “wooly dogs” that were bred and cared for over millennia. However, the dog wool-weaving tradition declined during the 19th century, and the population was lost. In this study, we analyzed genomic and isotopic data from a preserved woolly dog pelt from “Mutton,” collected in 1859. Mutton is the only known example of an Indigenous North American dog with dominant precolonial ancestry postdating the onset of settler colonialism. We identified candidate genetic variants potentially linked with their distinct woolly phenotype. We integrated these data with interviews from Coast Salish Elders, Knowledge Keepers, and weavers about shared traditional knowledge and memories surrounding woolly dogs, their importance within Coast Salish societies, and how colonial policies led directly to their disappearance.

Dogs were introduced to the Americas from Eurasia via northwestern North America ~15,000 years ago and have been ubiquitous in Indigenous societies of the Pacific Northwest (PNW) for millennia (1–4). Coast Salish peoples in the Salish Sea region (Fig. 1A) kept multiple different types of dogs: hunting dogs, village dogs, and “wooly dogs” with a thick woolen undercoat that was shorn for weaving (4, 5). Dog-wool blankets, often blended with mountain goat wool, waterfowl down, and plant fibers such as fireweed and cattail fluff, were prestigious cultural belongings (6–8). Woolly dogs, known as “sqwemá:y,” “ske’-ha,” “sq’áméy,” “sq’wba’y,” and “q’əbəl” in some Coast Salish languages (9), were emblems of some communities, as depicted in a 19th-century Skokomish/Twana basket (Fig. 1B) (10).

The first comprehensive book on Salish weaving (11) scrutinized most Coast Salish woven blankets in museums around the world, questioning if any contained primarily dog wool and disputing the fiber’s spinnability. More-recent proteomic analysis of 19th-century blankets confirmed the use of dog wool in Coast Salish weaving (12). In addition, zooarchaeological remains thought to be from woolly dogs have been found in dozens of archaeological sites in Coast Salish territories beginning ~5,000 years before present (B.P.) (2, 4) (Fig. 1A). The last Coast Salish woolly dogs likely lived in the late 19th and early 20th centuries (5, 13). Later photographs and records referring to woolly dogs extend into the 20th century, but these examples likely reflect mixed ancestry or non-Indigenous breeds (9).

The decline in dog-wool weaving has previously been attributed to the proliferation of

machine-made blankets by British and American trading companies in the early 19th century (11, 13). However, this explanation ignores the cultural importance of woolly dogs, as reflected through their enduring use by weavers, particularly for high-status items such as regalia (7, 14). Given their role in Coast Salish societies, it is unlikely that the entire dog-wool tradition would have been abandoned simply because of the ready availability of imported textiles. Furthermore, this explanation ignores weavers’ efforts to maintain culturally relevant practices in the face of settler colonialism. The use of blankets and robes served not only a functional purpose but also a spiritually protective role in Coast Salish cultures. Wearing a ceremonial blanket was spiritually transformative because it intertwined the creator of the blanket, the wearer, and the community (13–15).

The only known pelt of an extinct Coast Salish woolly dog is of “Mutton,” a dog cared for by naturalist and ethnographer George Gibbs during the Northwest Boundary Survey (1857–1862). According to Gibbs’s field journal and Smithsonian ledgers [National Museum of Natural History (USNM) A4401 to A4425], Mutton became ill and died in late 1859 (9, 15). His pelt and lower leg bones are housed at the Smithsonian Institution (USNM 4762) (figs. S2 and S4).

In this study, we combined genomic analysis, ethnographic research, stable isotope and zooarchaeological analysis, and archival records to investigate this iconic dog’s history, including ancestry, the genetic underpinnings of wooliness, and their ultimate decline. We sequenced Mutton’s nuclear genome to a mean 3.4× depth of coverage and, for comparison, a nonwoolly village dog (figs. S3 and S5) from

the nearby Semiahmoo Bay region to low coverage (0.05×; “SB dog” hereafter, USNM 3763, collected 1858). For additional genomic context, we increased the coverage of an ancient dog from Port au Choix, Newfoundland [AL3194; 4020 calibrated years B.P. (cal B.P.)] (3), from 1.9× to 11.9×, and sequenced the genome of an ancient dog from Teshekpuk Lake, Alaska (ALAS_015; 3763 BP; 1.23×); three modern coyotes; and 59 modern dogs representing 21 breeds (data S1). We also undertook $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable-isotope analysis of Mutton and the SB dog to test for substantial differences in their dietary life histories. Lastly, we interviewed seven Coast Salish Elders, Knowledge Keepers, and wool weavers about family histories and traditional knowledge surrounding woolly dogs to provide a cultural framework for interpreting the genomic analyses (9). The interviewees span several Coast Salish communities, including Stó:lō, Squamish, Snuneymuxw, and Musqueam Nations in British Columbia (BC) and Suquamish and Skokomish/Twana in Washington.

Woolly dog origins

Throughout northwestern North America there are numerous oral histories and origin stories

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involving the woolly dog. Skokomish/Twana Elder Michael Pavel reports that in a former time, when all beings including woolly dogs were recognized as relatives, all were “people” and were as family. High-status Qw’ó:ntl’an women are an example of those who trace their lineages from the woolly dog at a time when all beings were one family (16). According to Pavel: “And out of [the origin story], [woolly dogs] were given the gift of the wool, and they were able to teach the women how to gather the wool, how to process the wool, how to spin the wool, and how to weave with the wool” (9).

Early colonial explorers and scholars speculated that woolly dogs originated in Japan (17) or were recently introduced to the Coast Salish by the Dene people from their homelands in northern boreal Canada (18). However, zooarchaeological remains of morphologically distinct dogs in Coast Salish territories suggest that woolly dog husbandry was present for ~5000 years before European colonization (2, 4). Furthermore, longstanding oral histories and traditional knowledge hold that woolly dogs have been part of Coast Salish society for millennia (9).

To test whether Mutton has precolonial or settler dog ancestry, we first compared his mitochondrial genome with 207 ancient and modern dogs from a global sampling. Mutton carries the A2b mitochondrial DNA (mtDNA) haplotype, which emerged after dogs initially arrived from Eurasia (3). Most of this mtDNA lineage of so-called precolonial dogs (PCDs) disappeared after European colonization (3, 19, 20). Mutton’s nearest mtDNA neighbor is an ancient dog (PRD10, ~1,500 B.P.) from Prince Rupert Harbour, BC (Fig. 2A and fig. S16). PRD10 is the only archaeological dog from the PNW in the mtDNA dataset, and this similarity reflects the deep roots of Mutton’s maternal ancestry in the region. A pair of modern and ancient (~620 B.P.) dogs from Alaska form a sister clade of the Mutton-PRD10 grouping, further underscoring the long-term maternal population structure in northwestern North America. By contrast, the SB dog carries an A1a haplotype, which is similar to that of most modern European dogs and is the most common present-day haplotype worldwide (found in 64 out of 207 dogs in our analysis) (21).

To place a timeframe on the divergence of Mutton’s maternal lineage, we performed a molecular-clock analysis on the mitochondrial phylogeny (data S1). The results suggest a mitochondrial common ancestor estimated between 4776 and 1853 years B.P. for the subclade containing Mutton, PRD10, and the two Alaskan dogs (95% highest posterior density; Fig. 2A and fig. S16). Although we are limited by the analysis of a single individual, this timing is generally consistent with the increasing occurrence of small-sized woolly dog zooarchaeological remains in the regions surrounding the Salish Sea (2).

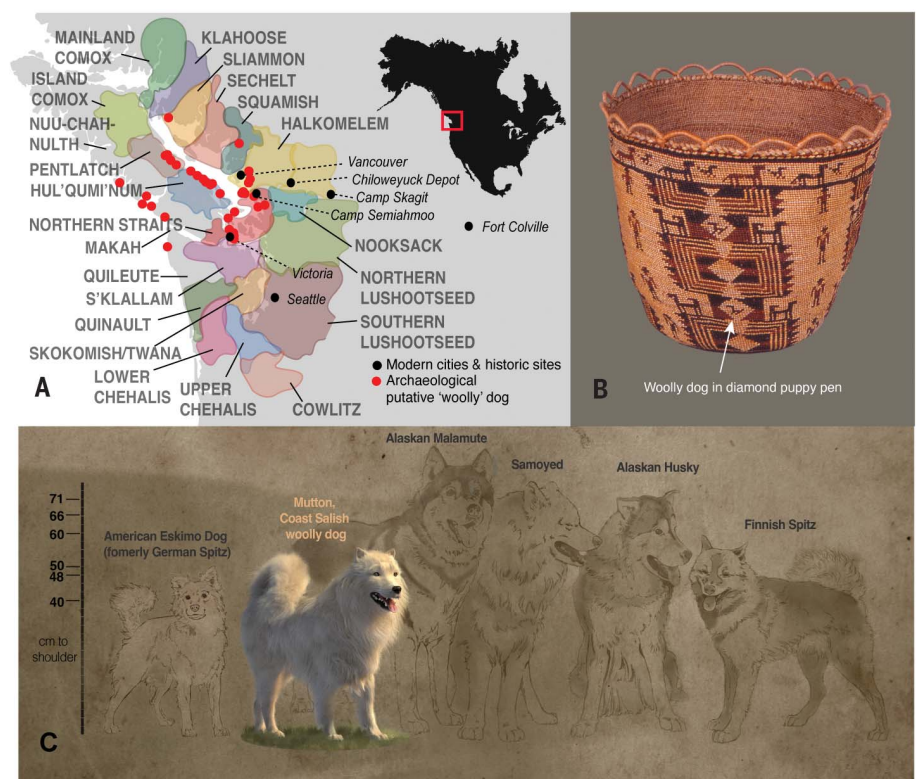


Fig. 1. Domestic dogs in the culture and society of Indigenous Coast Salish peoples. (A) Coast Salish ancestral lands include the inner coastal waterways of the Salish Sea in southwest British Columbia and Washington State. Archaeological woolly dog data are from (2). Distribution of the Coast Salish languages in the 19th century are as indicated by colored areas. [The map is modified from https://commons.wikimedia.org/wiki/File:Coast_Salish_language_map.svg and licensed under CC BY-SA 4.0.] (B) Woven Skokomish/Twana basket with woolly dog iconography, depicted with upturned tails. Woolly dog puppies are inside pens represented by diamond shapes (10) [courtesy of Burke Museum, catalog no. 1-507]. (C) Forensic reconstruction of a woolly dog based on Mutton’s pelt measurements and archaeological remains (9). Sketches of Arctic and spitz dog breeds are shown for scale and comparison of appearance and do not imply a genetic relationship.

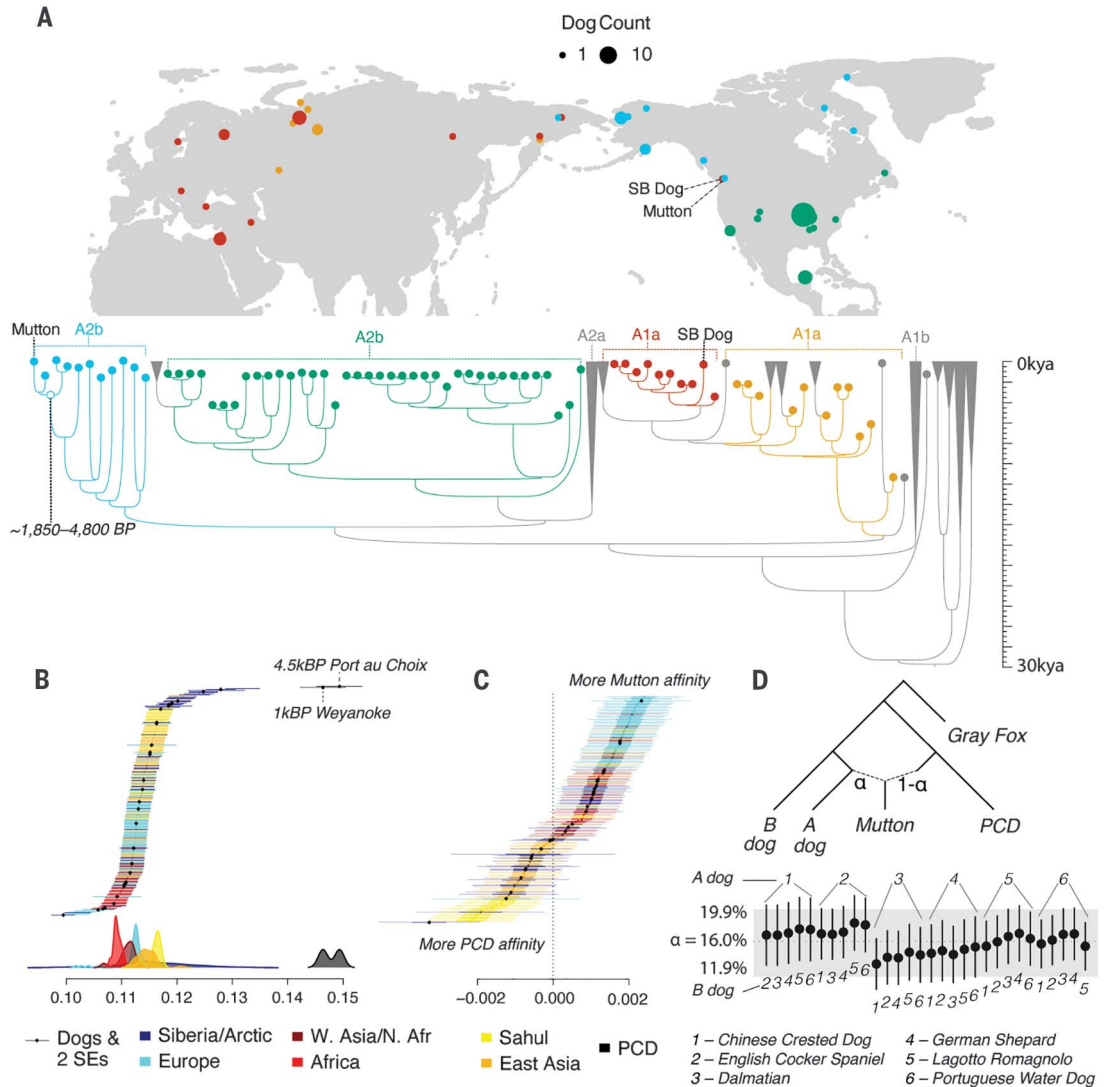
To assess Mutton’s nuclear ancestry, we analyzed 217 globally distributed ancient and modern dogs. Outgroup- f_3 statistics reveal that Mutton carries substantially greater shared genetic drift with PCDs than with any other dogs, specifically, with the archaeological remains of a dog from Port au Choix, Newfoundland (4020 cal B.P.), and from Weyanoke Old Town, Virginia (~1,000 B.P.) (Fig. 2B and fig. S17). Because Mutton lived after European colonization and waves of precolonial dog introductions (3, 21), we tested for gene flow from introduced lineages using D-statistics. We found that European breeds yielded strongly positive D-statistics, indicating that Mutton’s non-PCD ancestry most likely stemmed from introduced European dogs (Fig. 2C).

To refine these results, we used f_4 -ratio tests with six modern European breeds (Chinese Crested dog, English Cocker Spaniel, Dalmatian, German Shepherd, Lagotto Romagnolo, and Portuguese Water Dog), estimating that Mutton had 84% PCD ancestry and 16% European ancestry (11.9 to 19.9% 2 SE range; Fig. 2D). The f_4 -ratio test may slightly overestimate Mutton’s

European ancestry if the true contributor of this ancestry was equally related (an outgroup) to the two European breeds in the tests. However, estimates across all permutations are broadly consistent (Fig. 2D and fig. S18), suggesting European ancestry roughly on the order of one great-grandparent in Mutton’s background. By contrast, outgroup- f_3 statistics indicate that the contemporaneous SB dog appears highly admixed, showing the greatest similarity to ancient dogs from Siberia and Alaska (fig. S17). The distribution of PCD versus European ancestry tracts in Mutton can provide some additional insight into the timing of admixture. Although this method is imprecise because of recent admixture and the scarcity of PCD source–population data, we estimate that Mutton’s European admixture occurred 10.8 ± 4.9 generations before (1 SE). Assuming a 3-year generation time, this analysis suggests admixture ~32 years before Mutton’s birth, consistent with postcolonial admixture (9).

To test for dietary differences between Mutton and the SB dog, we performed stable isotope analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ on bone collagen and

Fig. 2. Genetic ancestry of woolly dogs. (A) mtDNA tree of 207 dogs with A2b (Mutton) and A1a (SB Dog) haplotypes expanded. The map points correspond to colored tree tips for the most similar archaeological and historic dog mtDNAs, highlighting the subclades of interest and the broader haplotypes. Samples used are listed in data S1. (B) Outgroup- f_3 statistics (f_3 (Gray Fox; Mutton, B)) or estimation of shared drift between Mutton and 229 other dogs revealed that Mutton has the highest similarity to PCDs. Black-point estimates indicate ancient genomes. (C) D-statistics (((PCD, Mutton), Test Dog), Gray Fox) consistent with gene flow into Mutton's background, with European breeds appearing the most likely contributors to Mutton's non-PCD ancestry. (D) f_4 -ratio tests (f_4 (A, Out; Mutton, AL3194-Port au Choix); f_4 (A, Out; B, AL3194-Port au Choix)) to estimate the proportion of European settler-dog ancestry in Mutton's background, performed by using six modern European breeds as proxies for Mutton's European ancestry component.



hair keratin. The SB dog has high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values similar to those of archaeological dogs from the PNW (22), indicating a traditional marine-based diet (figs. S13 and S14). Mutton's isotope values reveal a more terrestrial and complement C_3 component-rich diet, likely reflecting Mutton's life and travels with Gibbs from an early age (fig. S14, B and C, and fig. S15) (9).

The persistence of a high proportion of post-colonial PCD ancestry may reflect concerted efforts by Coast Salish peoples to maintain the breed against the pressure of gene flow from nonnative dogs. Mutton lived near the end of traditional woolly dog husbandry (5, 9, 13). Although he had mixed ancestry, Mutton's background is dominated by PCD ancestors, as compared with that of the contemporaneous SB dog. This finding may indicate careful reproductive management to maintain woolly dogs' distinct genetic makeup and phenotype until their decline. Mutton's fraction of European ancestry also highlights the turbulent cultural moment at the time

Mutton lived and illustrates how interbreeding with settler-introduced dogs could have threatened the survival of woolly dogs.

The influence of people on the woolly dog genome

Woolly dogs were treated as beloved extended family members. According to Debra qwasen Sparrow, a Musqueam Master Weaver, her grandfather [Ed Sparrow (1898–1998)] told her that "every village had [woolly dogs], that they were like gold because they were mixed with the mountain goat and then rove and spun" (9). Dogs also comprised a form of wealth and status for Coast Salish women, who carefully managed the dogs to maintain their woolly coats, isolating them on islands or in pens to strictly manage their breeding (9, 17, 23). Island names often reflect their connection with dogs, such as "sqwiqwmi" ("Little Dog") village on Cameron Island in Nanaimo, Snuneymuxw territory, BC. The prevention of interbreeding wool dogs with hunting or village dogs was critical for

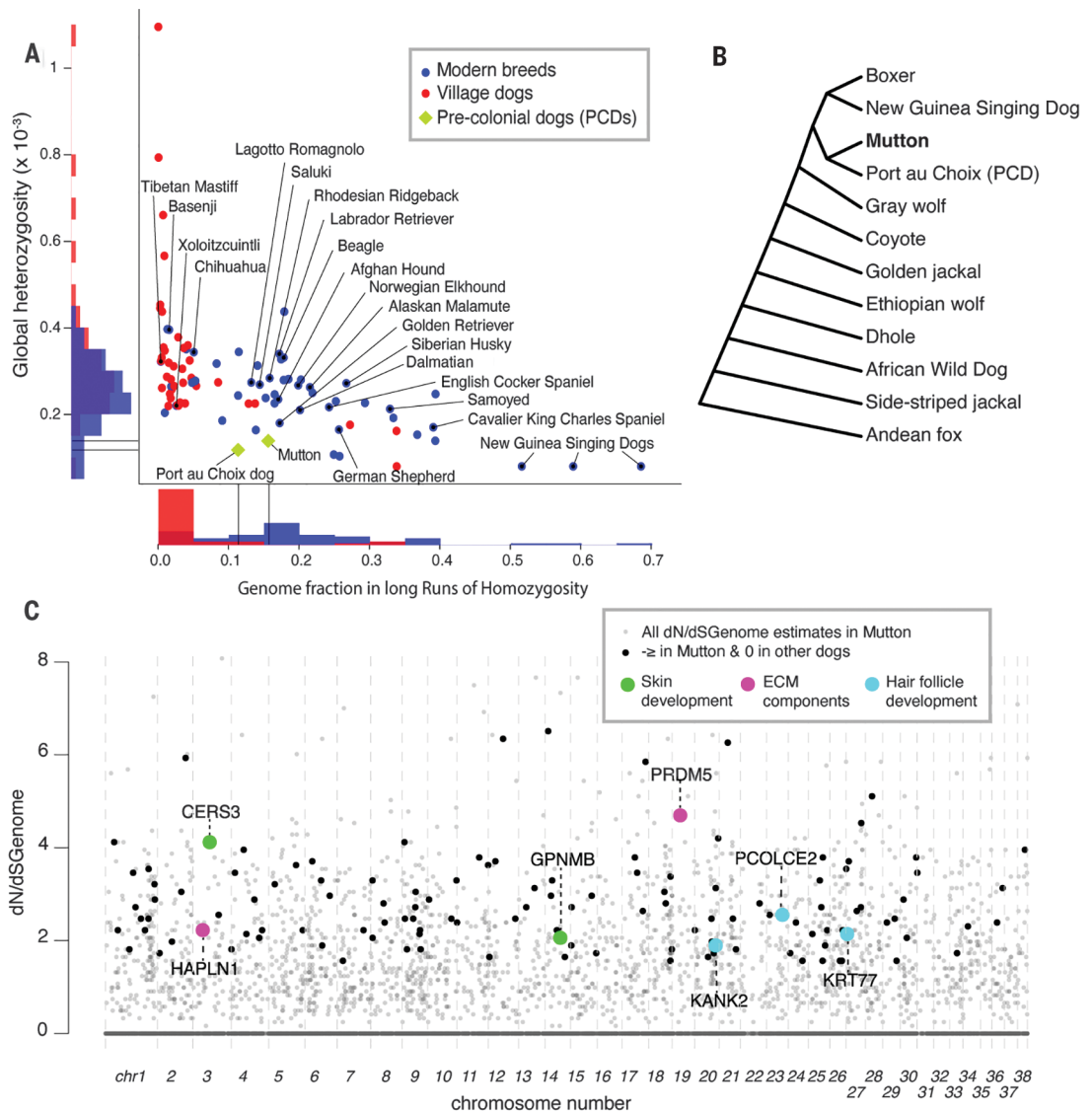
maintaining their distinct hair characteristics: soft guard hairs with an unusually long, crimped undercoat (fig. S2), which was highly spinnable and could be made into warm blanket yarn. These management practices likely contributed to Mutton's PCD ancestry long after the onset of settler colonialism.

Long-term husbandry for woolly hair likely limited woolly dogs' effective population size, which would be reflected in nucleotide diversity and thus in Mutton's heterozygosity. We found that Mutton's heterozygosity is in the lowest range of living breeds ($n = 51$) and village dogs ($n = 42$) downsampled to the same coverage (Fig. 3A). Additionally, runs of homozygosity (ROH) better reflect recent demography than global heterozygosity. Using an ROH method optimized for low coverage (9, 24), we estimate that 15.7% of Mutton's genome is in ROH of 2.5 mega-base pairs (Mbp) or greater, again in the range of modern breeds. The ancient Port au Choix dog also has low genomic heterozygosity and 11.3% ROH, so Mutton's low

Fig. 3. Genomic outcomes of management and selection.

(A) Global heterozygosity and long runs of homozygosity over transversions in Mutton compared with modern dogs and the ancient Port au Choix dog. All dogs have been downsampled to Mutton's coverage level for analysis. (B) Tree schematic used in dN/dS analysis to identify genes under selection in Mutton compared with other canids. The branching order is based on (50). dN/dS_{genome} estimates were done separately including one of the four dogs plus all other canids. Genes with elevated dN/dS_{genome} values in multiple dogs could reflect more ancient shared selection before the separation of the woolly dog lineage.

Therefore, likely candidates for selection in woolly dogs were conservatively assessed where dN/dS_{genome} > 1.5 in Mutton (9) but dN = 0 in the other three dogs, including one PCD. (C) Genes with an excess of nonsynonymous mutations in Mutton. Black points are the 125 selection candidates identified on the basis of dN/dS_{genome} ≥ 1.5 in Mutton but dN = 0 in three other dogs, including one PCD (9). Several genes with high dN/dS_{genome} in Mutton (shown in gray) are excluded as selection candidates because they carry at least one nonsynonymous mutation in other dogs. This approach is designed to conservatively highlight genes in which selection is more likely specific to Mutton's lineage rather than during dog domestication or in the common ancestors of PCDs. Candidate genes discussed in text are indicated.



heterozygosity may partly reflect shared demographic history from a small PCD founding population (Fig. 3A). Because of recent European admixture, Mutton's genome is inevitably more heterozygous than that of his recent woolly dog ancestors.

To search for evidence of genetic mechanisms for wooliness, we used maximum likelihood-based estimation of the enrichment of nonsynonymous mutations (dN/dS) (ratio of nonsynonymous to synonymous mutations) observed within Mutton's coding regions (9). We evaluated 11,112 genes with sufficient sequence coverage for all dogs and outgroups (data S1) and restricted selection-candidate identification to genes with elevated dN/dS in Mutton but lacking any nonsynonymous mutations in three other dogs, including one PCD (Fig. 3B). Although power to detect selection is funda-

mentally limited with only a single genome, we identified a candidate set of genes with high lineage-specific dN/dS values. We identified 125 genes as candidates for positive selection in woolly dogs (data S2). Among these, 28 have plausible links to hair growth and follicle regeneration according to a model of the hair-growth cycle (fig. S12) and are associated with cell replication, proliferation, the formation of extracellular matrix components, vascularization, and related processes (25–31) (Fig. 3C and data S3).

Candidate selection genes in Mutton include *KANK2*, a steroid-signaling regulator responsible for hereditary diseases of the hair shaft in humans (32). A distinct nonsynonymous mutation in Mutton lies in the amino acid adjacent to the *KANK2* mutation, causing a “woolly” hair phenotype in humans (32). *KRT77* is a

member of the keratin gene family responsible for the structural integrity of cells in the epithelium and hair follicles. Mutations in keratin genes are linked to curly-hair phenotype in other dogs, rats, and mice (31), and to woolly hair and hereditary hair loss in humans (26, 30); and multiple *KRT* genes underwent selection in woolly mammoths (25). *CERS3*, *PRDM5*, and *HAPLN1* are associated with maintaining the integrity of the skin or connective tissue in humans (27, 28). *GPNMB* is involved in multiple cellular functions in the epidermis, potentially mediating pigmentation (29). We also manually evaluated 15 specific variants from previous literature that are linked with hair characteristics in living dog breeds (data S4). Apart from a widespread *FGF5* mutation conferring long hair (33, 34), Mutton showed the ancestral allele in all cases with data present (data S4),

illustrating the independent origins of woolly dogs' distinct phenotype.

The impact of colonialism on the iconic breed's disappearance

Woolly dogs' decline throughout the 19th century is not fully understood. The narrative that the influx of trade blankets into the region led to the abandonment of woolly dog husbandry oversimplifies a complex scenario. By 1857 (a year before Mutton's birth) in Stó:lō territory, where Mutton was most likely acquired, the settler population consisted of only a few dozen permanent settlers at Fort Langley (35, 36). The following year, more than 33,000 miners arrived at present-day BC during the 1858 Fraser River Gold Rush. This large-scale migration set off conflicts between miners, colonial governments, and Indigenous peoples. Indigenous populations declined by an estimated two-thirds between 1830 and 1882 (37). Smallpox epidemics—almost one every generation from the 1700s to 1862 (38)—are estimated to have killed more than 90% of Indigenous people in some villages across BC (38), along with steady depopulation due to other introduced diseases such as mumps, tuberculosis, and influenza (37).

Survival of woolly dogs depended upon the survival of their caretakers. In addition to disease, expanding colonialism increased cultural upheaval, displacement of Indigenous peoples, and a diminished capacity to manage the breed. Policies targeted Indigenous governance and inherent rights, resulting in the deliberate disenfranchisement and criminalization of Indigenous cultural practices (39). Indigenous women, the caretakers of woolly dogs and weaving knowledge, were specifically targeted. Missionization efforts reduced women's roles in society, and legislation such as the Indian Act (1876) explicitly prohibited women from participating in local governance, denied women basic property rights, and restricted their movement (39). In the 20th century, transference of cultural knowledge was further disrupted by mandatory residential schooling designed to remove children from their families and suppress culture (40).

Through these compounding waves of colonialism, the transmission of important knowledge relating to woolly dog husbandry and hair processing, spinning, and weaving was interrupted. Stó:lō Elder Rena Point Bolton, 95 years old in 2022, recalls how Th'etsimiya, her great-grandmother, had kept woolly dogs, but was forced to give them up: "They were told they couldn't do their cultural things. There was the police, the Indian Agent and the priests. The dogs were not allowed. She had to get rid of the dogs" (9). The dogs represented high status and traditional practices that threatened British and later Canadian dominion and as such were removed through policies of assimilation (40–42). The weaving traditions

were not completely lost, because many cultural teachings and types of expertise were carried on in secret. Bolton said: "Our people were not allowed to spin on shxwqáqets [traditional spindle whorls]. They could spin on a European one but not on the shxwqáqets. They couldn't use their looms, and they would take them out and burn them or they would give them to museums or collectors ... The generation that was there when the Europeans came and colonized us, that's where it ended, and there [were] just a few people who went underground. And my grandmother and my mother were two of them" (9).

A growing body of research demonstrates how peoples of the PNW cared for and managed their ancestral lands, cultivating diverse and highly localized plants and marine foods (43–45). Woolly dogs may have also been similarly localized and diverse. We focused on Coast Salish dogs, but non-Salish peoples in the PNW also kept woolly dogs. For example, Nuuchahnulth peoples of western Vancouver Island kept a different wool dog that was reportedly bigger and had coats of different colors, including brown, spotted, black, gray, or white (46–48). These differences could be population-specific, or they could be a result of widespread phenotypic diversity, as noted by explorers in the 18th and 19th centuries (17), reflecting trade among the different Indigenous communities.

Weaving and woolly dogs are intertwined in Coast Salish culture and society, which cannot be separated from the long-time management of their ancestral homelands. Weavers, artists, and Elders continue to promote the renewal of traditional or customary weaving knowledge and practices. Artist Eliot Kwulasultun White-Hill (Snuneymuxw) said (9): "It starts to unravel, in a way, people's understanding of us as a hunter gatherer society ... Our relationship with the woolly dogs, our relationship with the camas patches and the clam beds, the way that we tended the land and tended the forests ... these all show the systems in place that are far more complex than what people take for granted about Coast Salish culture."

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SUPPLEMENTARY MATERIALS

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Materials and Methods

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Data S1 to S5

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