

1 **Title: The History of Coast Salish ‘Woolly Dogs’ Revealed by Ancient Genomics and**  
2 **Indigenous Knowledge**

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52

53 **Abstract:** Ancestral Coast Salish societies in the Pacific Northwest kept long-haired “woolly”  
54 dogs that were bred and cared for over millennia. However, the dog wool-weaving tradition  
55 declined during the 19<sup>th</sup> century, and the population was lost. Here, we analyze genomic and  
56 isotopic data from a preserved woolly dog pelt, “Mutton”, collected in 1859. Mutton is the only  
57 known example of an Indigenous North American dog with dominant pre-colonial ancestry  
58 postdating the onset of settler colonialism. We identify candidate genetic variants potentially  
59 linked with their unique woolly phenotype. We integrate these data with interviews from Coast  
60 Salish Elders, Knowledge Keepers, and weavers about shared traditional knowledge and  
61 memories surrounding woolly dogs, their importance within Coast Salish societies, and how  
62 colonial policies led directly to their disappearance.

63

64 **1 sentence summary:** A 19th century dog genome and Traditional Knowledge illuminate the  
65 life, history, and decline of Coast Salish woolly dogs

66

67 **Main Text:** Dogs were introduced to the Americas from Eurasia via northwestern North  
68 America ~15,000 years ago, and have been ubiquitous in Indigenous societies of the Pacific  
69 Northwest (PNW) for millennia (1–4). Coast Salish peoples in the Salish Sea region (**Fig. 1A**)

70 kept multiple different types of dogs: hunting dogs, village dogs, and “woolly dogs” with a thick  
71 woolen undercoat that was shorn for weaving (4, 5). Dog wool blankets, often blended with  
72 mountain goat wool, waterfowl down, and plant fibers like fireweed and cattail fluff, were  
73 prestigious cultural belongings (6–8). Woolly dogs, known as sqwemá:y, ske'-ha, sqʷəméy',  
74 sqʷbaý, and QebeO in some Coast Salish languages (9), were emblems of some communities,  
75 as depicted in a 19<sup>th</sup> century Skokomish/Twana basket (**Fig. 1B** (10)).

76  
77 The first comprehensive book on Salish weaving (11) scrutinized most Coast Salish woven  
78 blankets in museums around the world, questioning if any contained primarily dog wool, and  
79 disputing the fiber's spinnability. More recent proteomic analysis of 19<sup>th</sup> century blankets  
80 confirmed the use of dog wool in Coast Salish weaving (12). In addition, zooarchaeological  
81 remains thought to be from woolly dogs have been found in dozens of archaeological sites in  
82 Coast Salish territories beginning ~5,000 years before present (BP) (2, 4) (**Fig. 1A**). The last  
83 Coast Salish woolly dogs likely lived in the late 19<sup>th</sup>/early 20<sup>th</sup> centuries (5, 13). Later  
84 photographs and records referring to woolly dogs extend into the 20<sup>th</sup> century, but these  
85 examples likely reflect mixed ancestry or non-Indigenous breeds (9).

86  
87 The decline in dog wool weaving has previously been attributed to the proliferation of machine-  
88 made blankets by British and American trading companies in the early 19<sup>th</sup> century (11, 13).  
89 However, this explanation ignores the cultural importance of woolly dogs, as reflected through  
90 their enduring use by weavers, particularly for high status items like regalia (7, 14). Given their  
91 role in Coast Salish societies, it is unlikely that the entire dog wool tradition would have been  
92 abandoned simply because of the ready availability of imported textiles. Further, this explanation  
93 ignores weavers' efforts to maintain culturally relevant practices in the face of settler colonialism.  
94 The use of blankets and robes served not only a functional purpose, but also a spiritually  
95 protective role in Coast Salish cultures. Wearing a ceremonial blanket was spiritually  
96 transformative since it intertwined the creator of the blanket, the wearer, and the community (13–  
97 15).

98 The only known pelt of an extinct Coast Salish woolly dog is of “Mutton”, a dog cared for by  
99 naturalist and ethnographer George Gibbs during the Northwest Boundary Survey (1857-1862).  
100 According to Gibbs's field journal and Smithsonian ledgers (USNM A4401-A4425), Mutton  
101 became ill and died in late 1859 (9, 15). His pelt and lower leg bones are housed at the  
102 Smithsonian Institution (USNM 4762) (**Figs. S2, S4**).

103 Here, we combine genomic analysis, ethnographic research, stable isotope and zooarchaeological  
104 analysis, and archival records to investigate this iconic dog's history, including ancestry, the  
105 genetic underpinnings of woolliness, and their ultimate decline. We sequenced Mutton's nuclear  
106 genome to a mean 3.4x depth of coverage and, for comparison, a non-woolly village dog (**Figs.**  
107 **S3, S5**) from the nearby Semiahmoo Bay region to low coverage (0.05x; “SB dog” hereafter,  
108 USNM 3512; collected 1858). For additional genomic context, we increased the coverage of an  
109 ancient dog from Port au Choix, Newfoundland (AL3194; 4,020 cal BP) (3), from 1.9x to 11.9x,  
110 and sequenced the genome of an ancient dog from Teshekpuk Lake, Alaska (ALAS\_015; 3,763  
111 BP; 1.23x), three modern coyotes, and 59 modern dogs representing 21 breeds (**DataS1**). We  
112 also undertook  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  stable isotope analysis of Mutton and the SB dog to test for

113 substantial differences in their dietary life histories. Finally, we interviewed seven Coast Salish  
114 Elders, Knowledge Keepers, and wool weavers about family histories and traditional knowledge  
115 surrounding woolly dogs to provide a cultural framework for interpreting the genomic analyses  
116 (9). The interviewees span several Coast Salish communities, including Stó:lō, Squamish,  
117 Snuneymuxw, and Musqueam Nations in British Columbia (BC) and Suquamish, and  
118 Skokomish/Twana in Washington.

119

## 120 *Woolly dog origins*

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

129 Early colonial explorers and scholars speculated that woolly dogs originated in Japan (17) or  
130 were recently introduced to the Coast Salish by Dene from their homelands in northern boreal  
131 Canada (18). However, zooarchaeological remains of morphologically distinct dogs in Coast  
132 Salish territories suggest woolly dog husbandry was present for ~5,000 years before European  
133 colonization (2, 4). Furthermore, longstanding oral histories and traditional knowledge hold that  
134 woolly dogs have been part of Coast Salish society for millennia (9).

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

147 To place a timeframe on the divergence of Mutton’s maternal lineage, we performed a molecular  
148 clock analysis on the mitochondrial phylogeny (**DataS1**). The results suggest a mitochondrial  
149 common ancestor estimated between 4,776 and 1,853 years BP for the subclade containing  
150 Mutton, PRD10, and the two Alaskan dogs (95% highest posterior density; **Figs. 2A, S16**).  
151 Although we are limited by the analysis of a single individual, this timing is generally consistent

152 with the increasing occurrence of small sized ‘woolly’ dog zooarchaeological remains in the  
153 regions surrounding the Salish Sea (2).

154 To assess Mutton’s nuclear ancestry, we analyzed 217 globally distributed ancient and modern  
155 dogs. Outgroup- $f_3$  statistics reveal that Mutton carries substantially greater shared genetic drift  
156 with PCDs than with any other dogs, specifically, archaeological remains of a dog from Port au  
157 Choix, Newfoundland (4,020 cal BP), and from Weyanoke Old Town, Virginia (~1,000 BP)  
158 (**Figs. 2B, S17**). Since Mutton lived after European colonization and waves of pre-colonial dog  
159 introductions (3, 21), we tested for gene flow from introduced lineages using D-statistics. We  
160 found that European breeds yielded strongly positive D-statistics, indicating that Mutton’s non-  
161 PCD ancestry most likely stemmed from introduced European dogs (**Fig. 2C**).

162 To refine these results, we used  $f_4$ -ratio tests with six modern European breeds (Chinese Crested  
163 dog, English Cocker Spaniel, Dalmatian, German Shepherd, Lagotto Romagnolo, and  
164 Portuguese Water Dog), estimating that Mutton had 84% PCD and 16% European ancestry  
165 (11.9%–19.9% 2 SE range; **Fig. 2D**). The  $f_4$ -ratio test may slightly over-estimate Mutton’s  
166 European ancestry if the true contributor of this ancestry was equally related (an outgroup) to the  
167 two European breeds in the tests. However, estimates across all permutations are broadly  
168 consistent (**Figs. 2D, S18**), suggesting European ancestry roughly on the order of one great-  
169 grandparent in Mutton’s background. In contrast, outgroup- $f_3$  statistics indicate that the  
170 contemporaneous SB dog appears highly admixed, showing greatest similarity to ancient dogs  
171 from Siberia and Alaska (**Fig. S17**). The distribution of PCD vs. European ancestry tracts in  
172 Mutton can provide some additional insight into the timing of admixture. Although this method  
173 is imprecise due to recent admixture and the scarcity of PCD source population data, we estimate  
174 that Mutton’s European admixture occurred  $10.8 \pm 4.9$  generations before (1 SE). Assuming a  
175 three-year generation time, this analysis suggests admixture ~32 years before Mutton’s birth,  
176 consistent with post-colonial admixture (9).

177 To test for dietary differences between Mutton and the SB dog, we performed stable isotope  
178 analysis of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  on bone collagen and hair keratin. The SB dog has high  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$   
179 values similar to archaeological dogs from the PNW (22), indicating a traditional marine-based  
180 diet (**Figs. S13-S14**). Mutton’s isotope values reveal a more terrestrial and C3-rich diet, likely  
181 reflecting Mutton’s life and travels with Gibbs from an early age (**Figs. S14-B,C, S15, (9)**).

182 The persistence of a high proportion of post-colonial PCD ancestry may reflect concerted efforts  
183 by Coast Salish peoples to maintain the breed against the pressure of gene flow from non-native  
184 dogs. Mutton lived near the end of traditional woolly dog husbandry (5, 9, 13). Although he had  
185 mixed ancestry, Mutton’s background is dominated by PCD ancestors, compared to the  
186 contemporaneous SB dog. This may indicate careful reproductive management to maintain  
187 woolly dogs’ unique genetic makeup and phenotype until their decline. Mutton’s fraction of  
188 European ancestry also highlights the turbulent cultural moment when Mutton lived and  
189 illustrates how interbreeding with settler-introduced dogs could have threatened the survival of  
190 woolly dogs.

191 *The influence of people on the woolly dog genome*

192 Woolly dogs were treated as beloved extended family members. According to Debra qwasen  
193 Sparrow, a Musqueam Master weaver, her grandfather [Ed Sparrow, (1898-1998)] told her  
194 “every village had [woolly dogs], that they were like gold because they were mixed with the  
195 mountain goat and then rove and spun” (9). Dogs also comprised a form of wealth and status for  
196 Coast Salish women, who carefully managed the dogs to maintain their woolly coats, isolating  
197 them on islands or in pens to strictly manage their breeding (9, 17, 23). Often island names  
198 reflect their connection with dogs, such as *sqwiqwmi* (“Little Dog”) village on Cameron Island  
199 in Nanaimo, Snuneymuxw territory, British Columbia. The prevention of interbreeding wool  
200 dogs with hunting or village dogs was critical for maintaining their unique hair characteristics:  
201 soft guard hairs with an unusually long crimped undercoat (**Fig. S2**), which was highly spinnable  
202 and made warm blanket yarn. These management practices likely contributed to Mutton's PCD  
203 ancestry long after the onset of settler colonialism.

204 Long-term husbandry for woolly hair likely limited woolly dogs' effective population size,  
205 which would be reflected in nucleotide diversity and thus in Mutton's heterozygosity. We found  
206 that Mutton's heterozygosity is in the lowest range of living breeds (n=51) and village dogs  
207 (n=42) downsampled to the same coverage (**Fig. 3A**). Additionally, runs of homozygosity  
208 (ROH) better reflect recent demography than global heterozygosity. Using an ROH method  
209 optimized for low coverage (9, 24), we estimate that 15.7% of Mutton's genome is in ROH of  
210 2.5Mbp or greater, again in the range of modern breeds. The ancient Port au Choix dog also has  
211 low genomic heterozygosity and 11.3% ROH, so Mutton's low heterozygosity may partly reflect  
212 shared demographic history from a small PCD founding population (**Fig. 3A**). Because of recent  
213 European admixture, Mutton's genome is inevitably more heterozygous than his recent woolly  
214 dog ancestors.

215 To search for evidence of genetic mechanisms for woolliness, we used maximum likelihood-  
216 based estimation of the enrichment of non-synonymous mutations (dN/dS) observed within  
217 Mutton's coding regions (9). We evaluated 11,112 genes with sufficient sequence coverage for  
218 all dogs and outgroups (**DataS1**), and restricted selection candidate identification to genes with  
219 elevated dN/dS in Mutton but lacking any non-synonymous mutations in three other dogs,  
220 including one PCD (**Fig. 3B**). Although power to detect selection is fundamentally limited with  
221 only a single genome, we identified a candidate set of genes with high lineage-specific dN/dS  
222 values. We identified 125 genes as candidates for positive selection in woolly dogs (**DataS2**).  
223 Among these, 28 have plausible links to hair growth and follicle regeneration based on a model  
224 of the hair growth cycle (**Fig. S12**), and are associated with cell replication, proliferation, the  
225 formation of extracellular matrix components, vascularization, and related processes (25–31)  
226 (**Fig. 3C, DataS3**).

227 Candidate selection genes in Mutton include *KANK2*, a steroid signaling regulator responsible  
228 for hereditary diseases of the hair shaft in humans (32). A unique non-synonymous mutation in  
229 Mutton lies in the adjacent amino acid to the *KANK2* mutation causing a “woolly” hair  
230 phenotype in humans (32). *KRT77* is a member of the keratin gene family responsible for the  
231 structural integrity of cells in the epithelium and hair follicles. Mutations in keratin genes are  
232 linked to curly hair phenotype in other dogs, rats, and mice (31), woolly hair and hereditary hair

233 loss in humans (26, 30), and multiple *KRT* genes underwent selection in woolly mammoths (25).  
234 *CERS3*, *PRDM5*, *HAPLN1* are associated with maintaining the integrity of the skin or connective  
235 tissue in humans (27, 28). *GPNMB* is involved in multiple cellular functions in the epidermis,  
236 potentially mediating pigmentation (29). We also manually evaluated 15 specific variants from  
237 previous literature linked with hair characteristics in living dog breeds (**DataS4**). Apart from a  
238 widespread *FGF5* mutation conferring long hair (33, 34), Mutton showed the ancestral allele in  
239 all cases with data present (**DataS4**), illustrating the independent origins of woolly dogs' unique  
240 phenotype.

241

#### 242 *The impact of colonialism on the iconic breed's disappearance*

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

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

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

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

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

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

297

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828 **Supplementary Materials**

829 Materials and Methods

830 Figs. S1 to S19

831 Tables 1 and 2

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846 EAO; Funding acquisition: LK, PS, LD; Supervision: LK, LH-K; Writing – original draft: ATL,  
847 LK, LH-K; Writing – review & editing: all authors.

848

849 **Competing interests:** All authors declare there are no competing interests.

850

851 **Data availability:** Genomic sequencing data for Mutton, SB dog, the Port au Choix dog  
852 (AL3194), and ALAS\_015 are available for non-commercial use via NCBI SRA Project  
853 Accession PRJNA1005336 and BioSample Accessions SAMN36985984-SAMN36985987. The  
854 SRA Project Accession for the modern coyote from Wyoming is PRJNA734649. Stable isotope  
855 data are available (49). All other public genomic data sources are provided in **DataS1**.

856

857 **FIGURE CAPTIONS**

858 **Figure 1. Domestic dogs in the culture and society of Indigenous Coast Salish peoples. 1A.**  
859 Coast Salish ancestral lands include the inner coastal waterways of Salish Sea in southwest  
860 British Columbia and Washington State. Archaeological woolly dog data are from (2).  
861 Distribution of the Coast Salish languages in the 19th century as indicated by colored areas. The  
862 map is modified from  
863 [https://commons.wikimedia.org/wiki/File:Coast\\_Salish\\_language\\_map.svg](https://commons.wikimedia.org/wiki/File:Coast_Salish_language_map.svg) and licensed under  
864 CC BY-SA 4.0. **1B.** Woven Skokomish/Twana basket with woolly dog iconography, depicted  
865 with upturned tails. Woolly dog puppies are inside pens represented by diamond shapes (10)  
866 (courtesy of Burke Museum, Catalog number #1-507). **1C.** Forensic reconstruction of a woolly  
867 dog based on Mutton's pelt measurements and archaeological remains (9). Sketches of Arctic  
868 and spitz dog breeds are shown for scale and comparison of appearance, and do not imply a  
869 genetic relationship.

870

871 **Figure 2. Genetic ancestry of woolly dogs. 2A.** mtDNA tree of 207 dogs with A2b (Mutton)  
872 and A1a (SB Dog) haplotypes expanded. Map points correspond to colored tree tips for the most  
873 similar archaeological and historic dog mtDNAs, highlighting the subclades of interest and the  
874 broader haplotypes. Samples used are listed in **DataS1**. **2B.** Outgroup- $f_3$  statistics ( $f_3(\text{GrayFox};$   
875 Mutton, B) or estimation of shared drift between Mutton and 229 other dogs reveals that Mutton  
876 has highest similarity to PCDs. Black point estimates indicate ancient genomes. **2C.** D-statistics  
877 (((PCD, Mutton), Test Dog), Gray Fox) consistent with gene flow into Mutton's background,  
878 with European breeds appearing the most likely contributors to Mutton's non-PCD ancestry. **2D.**  
879  $f_4$ -ratio tests ( $f_4(\text{A, Out; Mutton, AL3194-PortauChoix})$ ;  $f_4(\text{A, Out; B, AL3194-PortauChoix})$ ) to  
880 estimate the proportion of European settler dog ancestry in Mutton's background using six  
881 modern European breeds as proxies for Mutton's European ancestry component.

882

883 **Figure 3. Genomic outcomes of management and selection. 3A.** Global heterozygosity and  
884 long runs of homozygosity over transversions in Mutton compared to modern dogs and the  
885 ancient Port au Choix dog. All dogs have been downsampled to Mutton's coverage level for  
886 analysis. **3B.** Tree schematic used in dN/dS analysis to identify genes under selection in Mutton  
887 compared to other canids. Branching order after (50). dN/dS estimates were done separately  
888 including one of the four dogs plus all other canids. Genes with elevated  $dN/dS_{\text{Genome}}$  values in  
889 multiple dogs could reflect more ancient shared selection before the separation of the woolly dog  
890 lineage. Therefore, likely candidates for selection in woolly dogs were conservatively assessed  
891 where  $dN/dS_{\text{Genome}} > 1.5$  in Mutton (9), but  $dN = 0$  in the other three dogs, including one PCD. **3C.**  
892 Genes with an excess of non-synonymous mutations in Mutton. Black points are the 125  
893 selection candidates on the basis of  $dN/dS_{\text{genome}} \geq 1.5$  in Mutton but  $dN=0$  in three other dogs  
894 including one PCD (9). Several genes with high  $dN/dS_{\text{genome}}$  in Mutton (shown in gray) are  
895 excluded as selection candidates because they carry at least one non-synonymous mutation in  
896 other dogs. This approach is designed to conservatively highlight genes where selection is more



897 likely specific to Mutton's lineage rather than during dog domestication or in the common  
898 ancestors of PCDs. Candidate genes discussed in text are indicated.

Uncorrected Proof

899 **Table 1: XRF analysis results of pelt of SB Dog (USNM 3512).**

Spectrum Name and Description	Elements Detected	Materials Inferred
6575.10.16_3512_40kv_30uA_01_skin	Major: As Minor: Cl, Ca, Fe, K Trace: S, Ba, Si, P, Sr, Hg, Pb, Mn	Most of the elements detected may be associated to previous preservation treatment. Traces of elements such as Ca, Cl, Fe, K, S, and P may be associated with the skin.
6575.10.16_3512_40kv_30uA_02_skin	Major: As, K, Cl Minor: Ca, Fe Trace: S, Ba, Si, P, Sr, Hg, Pb	Less arsenic and calcium, and more potassium than location 01.
6575.10.16_3512_40kv_30uA_03_bone_backleft	Major: Ca Minor: K, Fe, As Trace: S, Ba, Hg, Sr, P	High amounts of calcium (Ca) consistent with presence of bone.
6575.10.16_3512_40kv_30uA_04_paw_p.r._front	Major: As Minor: Cl, Ca, Fe, K Trace: S, Ba, Si, P, Sr, Hg, Pb, Mn	Similar to location 01 (skin) but less calcium (Ca), and arsenic (As).
6575.10.16_3512_40kv_30uA_05_tag	Major: Cu Minor: - Trace: As, Hg, Cl, Ca, Ba, Pb	High amounts of copper (Cu) associated to the tag. Other trace elements most likely due to previous preservation treatments.
6575.10.16_3512_40kv_30uA_06_papertag	Major: Cu, Zn Minor: - Trace: As, Hg, Cl, Ca, Ba, K	Copper (Cu) and zinc (Zn) detected on paper tag, most likely from the small brass ring. Other trace elements most likely due to contamination from previous preservation treatments.
6575.10.16_3512_40kv_30uA_07_fur_head	Major: As, S, Cl Minor: Ca, Fe, K, Zn Trace: Ba, P, Hg, Pb, Mn	High presence of sulfur (from the fur) and other similar elements detected from previous preservation treatments.

900 Note: Whenever hypothesis is offered for possible material identification, this should be  
901 confirmed with a complementary technique. Other materials are possible. The instrument cannot  
902 detect organic materials and materials containing only elements lighter than aluminum. Also,  
903 elements present in very small quantities may escape detection. The argon (Ar) peak from the air  
904 can be detected when no vacuum pump is used. The rhodium (Rh) peak is due to the instrument  
905 tube (as well as traces of palladium (Pd) and possibly nickel (Ni), copper (Cu), and zinc (Zn)).

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914 **Table 2: XRF analysis results of Mutton from NMNH collection (USNM 4762).**

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Spectrum Name and Description	Elements Detected	Materials Inferred
6575.10.16_4762_40kv_30uA_01_redhair	Major: Hg Minor: As Trace: Fe, Ca, Ba/Ti, K, P, Sb, Pb	Red stain contains high levels of mercury (Hg).
6575.10.16_4762_40kv_30uA_02_whitehair	Major: S Minor: Cl, As, Fe, Sb Trace: Ca, Ba/Ti, K, P, Mn, Hg, Pb	High presence of sulfur (from the fur) and other similar elements detected from previous preservation treatments (such as chlorine, arsenic, and antimony).
6575.10.16_4762_40kv_30uA_03_whitehairfront	Major: S Minor: Cl, As, Fe, K Trace: Ca, Ba/Ti, P, Mn, Hg, Pb	Similar to location 02 but no antimony (Sb) and more potassium (K).
6575.10.16_4762_40kv_30uA_04_redhairfront	Major: Hg Minor: As, K Trace: Fe, Ca, Ba/Ti, P, Pb	Similar to location 01 but slightly more potassium (K).
6575.10.16_4762_40kv_30uA_05_skinfront	Major: K, As, Sb Minor: Cl, S, Fe, P Trace: Ca, Ba/Ti, Mn, Hg, Pb	Highlighting elements used for treating the skin and/or associated with the skin composition. High potassium (K), antimony (Sb), and arsenic (As). Slightly higher content of phosphorus (P).
6575.10.16_4762_40kv_30uA_06_nail	Major: Fe Minor: As, K Trace: S, Cl, Hg, Sb, Ca, Mn, Zn	Iron nail. Notable amount of arsenic (As) and potassium (K).

916 Note: Whenever hypothesis is offered for possible material identification, this should be  
 917 confirmed with a complementary technique. Other materials are possible. The instrument cannot  
 918 detect organic materials and materials containing only elements lighter than aluminum. Also,  
 919 elements present in very small quantities may escape detection. The argon (Ar) peak from the air  
 920 can be detected when no vacuum pump is used. The rhodium (Rh) peak is due to the instrument  
 921 tube (as well as traces of palladium (Pd) and possibly nickel (Ni)). On the spectra, only the  
 922 elements related to the samples have been labelled.

923

924

925 **DataS1. [Supplementary spreadsheet]**

926 IDs and metadata of newly generated genomes (NewGenomesMetadata), Extracts data from  
927 Mutton and SB Dog (ExtractsData), estimated error rates in ancient genomes used  
928 (AncientGenomeError), samples and metadata for mtDNA analyses (mtDNAdataset), samples  
929 and metadata for RoHan analysis (RoHanDataset), samples and metadata for dn/dS analysis  
930 (dNdSDataset), samples and metadata for outgroup- $f_3$  analyses (f3Dataset).

931

932 **DataS2. [Supplementary spreadsheet]**

933 g:Profiler (108) results after querying 125 genes. Separate tabs show results within the categories  
934 in GO: Molecular Function (GO\_MF), GO: Biological Process (GO\_BP), GO: Cellular  
935 Component (GO\_CC), KEGG, and Human Phenotype Ontology (HP), gene list with dn/dS  
936 values in Mutton (mutton\_dndList), hypergeometric test results for gene enrichment  
937 (res\_Hypergeometric), Wilcoxon rank-sum test results for gene enrichment (res\_RankSum),  
938 Gene Ontology Resource query results for several hair/skin genes (AmiGO2).

939

940 **DataS3. [Supplementary spreadsheet]**

941 125 gene list annotated manually (Annotations) by DAVID (110, 111), (geneList), and results of  
942 querying hair and skin categories in MGI Gene Ontology database  
943 (<https://www.informatics.jax.org/>) (MGI\_GO\_MP\_Databases).

944

945 **DataS4. [Supplementary spreadsheet]**

946 Mutton's genotype of variants associated with hair phenotype in dogs.

947

948 **Data S5. [Supplementary spreadsheet]**

949 Bone collagen and hair keratin  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of Mutton, SB Dog, and referenced  
950 comparative dog bone collagen data from previous research in the PNW (22).

951