

This is an Open Access document downloaded from ORCA, Cardiff University's institutional repository: <https://orca.cardiff.ac.uk/id/eprint/165764/>

This is the author's version of a work that was submitted to / accepted for publication.

Citation for final published version:

Lin, Audrey T., Hammond-Kaarremaa, Liz, Liu, Hsiao-Lei, Stantis, Chris, McKechnie, Iain, Pavel, Michael, Pavel, Susan sa'hLa mitSa, Wyss, Senaqwila Senakw, Sparrow, Debra qwasen, Carr, Karen, Aninta, Sabhrina Gita, Perri, Angela, Hartt, Jonathan, Bergström, Anders, Carmagnini, Alberto, Charlton, Sophy, Dalén, Love, Feuerborn, Tatiana R., France, Christine A. M., Gopalakrishnan, Shyam, Grimes, Vaughan, Harris, Alex, Kavich, Gwénaëlle, Sacks, Benjamin N., Sinding, Mikkel-Holger S., Skoglund, Pontus, Stanton, David W.G., Ostrander, Elaine A., Larson, Greger, Armstrong, Chelsey G., Frantz, Laurent A. F., Hawkins, Melissa T. R. and Kistler, Logan 2023. The history of Coast Salish “woolly dogs” revealed by ancient genomics and Indigenous Knowledge. *Science* 382 (6676) , pp. 1303-1308.
10.1126/science.adi6549

Publishers page: <http://dx.doi.org/10.1126/science.adi6549>

Please note:

Changes made as a result of publishing processes such as copy-editing, formatting and page numbers may not be reflected in this version. For the definitive version of this publication, please refer to the published source. You are advised to consult the publisher's version if you wish to cite this paper.

This version is being made available in accordance with publisher policies. See <http://orca.cf.ac.uk/policies.html> for usage policies. Copyright and moral rights for publications made available in ORCA are retained by the copyright holders.



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

3 **Authors**

4 Audrey T. Lin^{1*}, Liz Hammond-Kaarremaa^{1,2*}, Hsiao-Lei Liu¹, Chris Stantis^{1,3}, Iain
5 McKechnie⁴, Michael Pavel⁵, Susan sa'hLa mitSa Pavel^{5,6}, Senaqwila Seṅákw Wyss⁷, Debra
6 qwasen Sparrow⁸, Karen Carr⁹, Sabhrina Gita Aninta¹⁰, Angela Perri^{11,12}, Jonathan Hartt¹³,
7 Anders Bergström^{14,15}, Alberto Carmagnini¹⁶, Sophy Charlton^{17,18}, Love Dalén^{19,20}, Tatiana R.
8 Feuerborn^{21,22}, Christine A.M. France²³, Shyam Gopalakrishnan²¹, Vaughan Grimes²⁴, Alex
9 Harris²², Gwénaëlle Kavich²³, Benjamin N. Sacks^{25,26}, Mikkel-Holger S. Sinding²⁷, Pontus
10 Skoglund¹⁴, David W.G. Stanton^{16,28}, Elaine A. Ostrander²², Greger Larson¹⁷, Chelsey G.
11 Armstrong¹³, Laurent A.F. Frantz^{10,16}, Melissa T.R. Hawkins²⁹, Logan Kistler^{1*}

12 **Affiliations**

- 13 1. Department of Anthropology, National Museum of Natural History, Smithsonian Institution,
14 Washington DC, USA
- 15 2. Vancouver Island University, Nanaimo, BC, Canada
- 16 3. Department of Geology and Geophysics, University of Utah, Salt Lake City, UT, USA
- 17 4. Department of Anthropology, University of Victoria, Victoria, BC, Canada
- 18 5. Twana/Skokomish Indian Tribe. Skokomish Nation, WA, USA
- 19 6. Coast Salish Wool Weaving Center, Skokomish Nation, WA, USA
- 20 7. Sk̓wx̓wú7mesh ʔxwumixw (Squamish Nation), North Vancouver, BC, Canada
- 21 8. Musqueam First Nation, Vancouver, BC, Canada
- 22 9. Karen Carr Studio, Silver City, NM, USA
- 23 10. School of Biological and Behavioural Sciences, Queen Mary University of London, London,
24 UK
- 25 11. Department of Anthropology, Texas A&M University, College Station, TX, USA
- 26 12. Chronicle Heritage, AZ, USA
- 27 13. Indigenous Studies, Simon Fraser University, Burnaby, BC, Canada
- 28 14. Ancient Genomics Laboratory, The Francis Crick Institute, London, UK
- 29 15. School of Biological Sciences, University of East Anglia, Norwich, UK
- 30 16. Palaeogenomics Group, Department of Veterinary Sciences, Ludwig Maximilian University
31 Munich, Munich, Germany
- 32 17. PalaeoBARN, School of Archaeology, University of Oxford, Oxford, UK
- 33 18. BioArCh, Department of Archaeology, University of York, York, UK

- 34 19. Centre for Palaeogenetics, Stockholm, Sweden
- 35 20. Department of Zoology, Stockholm University, Stockholm, Sweden
- 36 21. Center for Evolutionary Hologenomics, The Globe Institute, University of Copenhagen,
37 Copenhagen, Denmark
- 38 22. National Genome Research Institutes, National Institutes of Health, Bethesda, MD, USA
- 39 23. Museum Conservation Institute, Smithsonian Institution, Suitland, MD, USA
- 40 24. Memorial University of Newfoundland, St. Johns, NL, Canada
- 41 25. Mammalian Ecology and Conservation Unit, Veterinary Genetics Laboratory, School of
42 Veterinary Medicine, University of California Davis, Davis, CA, USA
- 43 26. Department of Population Health and Reproduction, School of Veterinary Medicine,
44 University of California-Davis, Davis, CA, USA
- 45 27. Department of Biology, University of Copenhagen, Copenhagen, Denmark
- 46 28. Cardiff School of Biosciences, Cardiff University, Cardiff, UK
- 47 29. Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian
48 Institution, Washington DC, USA
- 49 * Corresponding author

50

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

61

62 **1 sentence summary:** A 19th century dog genome and Traditional Knowledge illuminate the
63 life, history, and decline of Coast Salish woolly dogs

64

65 **Main Text:** Dogs were introduced to the Americas from Eurasia via northwestern North
66 America ~15,000 years ago, and have been ubiquitous in Indigenous societies of the Pacific
67 Northwest (PNW) for millennia (1–4). Coast Salish peoples in the Salish Sea region (**Fig. 1A**)
68 kept multiple different types of dogs: hunting dogs, village dogs, and “woolly dogs” with a thick
69 woolen undercoat that was shorn for weaving (4, 5). Dog wool blankets, often blended with
70 mountain goat wool, waterfowl down, and plant fibers like fireweed and cattail fluff, were

71 prestigious cultural belongings (6–8). Woolly dogs, known as sqwemá:y, ske'-ha, sqʷəméy',
72 sqʷbaý, and QebeO in some Coast Salish languages (9), were emblems of some communities, as
73 depicted in a 19th century Skokomish/Twana basket (**Fig. 1B** (10)).

74

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

84

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

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

101 Here, we combine genomic analysis, ethnographic research, stable isotope and zooarchaeological
102 analysis, and archival records to investigate this iconic dog's history, including ancestry, the
103 genetic underpinnings of woolliness, and their ultimate decline. We sequenced Mutton's nuclear
104 genome to a mean 3.4x depth of coverage and, for comparison, a non-woolly village dog (**Figs.**
105 **S3, S5**) from the nearby Semiahmoo Bay region to low coverage (0.05x; “SB dog” hereafter,
106 USNM 3512; collected 1858). For additional genomic context, we increased the coverage of an
107 ancient dog from Port au Choix, Newfoundland (AL3194; 4,020 cal BP) (3), from 1.9x to 11.9x,
108 and sequenced the genome of an ancient dog from Teshekpuk Lake, Alaska (ALAS_015; 3,763
109 BP; 1.23x), three modern coyotes, and 59 modern dogs representing 21 breeds (**DataS1**). We
110 also undertook $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope analysis of Mutton and the SB dog to test for
111 substantial differences in their dietary life histories. Finally, we interviewed seven Coast Salish
112 Elders, Knowledge Keepers, and wool weavers about family histories and traditional knowledge
113 surrounding woolly dogs to provide a cultural framework for interpreting the genomic analyses

114 (9). The interviewees span several Coast Salish communities, including Stó:lō, Squamish,
115 Snuneymuxw, and Musqueam Nations in British Columbia (BC) and Suquamish, and
116 Skokomish/Twana in Washington.

117

118 *Woolly dog origins*

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

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

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

145 To place a timeframe on the divergence of Mutton’s maternal lineage, we performed a molecular
146 clock analysis on the mitochondrial phylogeny (**DataS1**). The results suggest a mitochondrial
147 common ancestor estimated between 4,776 and 1,853 years BP for the subclade containing
148 Mutton, PRD10, and the two Alaskan dogs (95% highest posterior density; **Figs. 2A, S16**).

149 Although we are limited by the analysis of a single individual, this timing is generally consistent
150 with the increasing occurrence of small sized ‘woolly’ dog zooarchaeological remains in the
151 regions surrounding the Salish Sea (2).

152 To assess Mutton’s nuclear ancestry, we analyzed 217 globally distributed ancient and modern
153 dogs. Outgroup- f_3 statistics reveal that Mutton carries substantially greater shared genetic drift

154 with PCDs than with any other dogs, specifically, archaeological remains of a dog from Port au
155 Choix, Newfoundland (4,020 cal BP), and from Weyanoke Old Town, Virginia (~1,000 BP)
156 (Figs. 2B, S17). Since Mutton lived after European colonization and waves of pre-colonial dog
157 introductions (3, 21), we tested for gene flow from introduced lineages using D-statistics. We
158 found that European breeds yielded strongly positive D-statistics, indicating that Mutton’s non-
159 PCD ancestry most likely stemmed from introduced European dogs (Fig. 2C).

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

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

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

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

190 Woolly dogs were treated as beloved extended family members. According to Debra qwasen
191 Sparrow, a Musqueam Master weaver, her grandfather [Ed Sparrow, (1898-1998)] told her
192 “every village had [woolly dogs], that they were like gold because they were mixed with the
193 mountain goat and then rove and spun” (9). Dogs also comprised a form of wealth and status for

194 Coast Salish women, who carefully managed the dogs to maintain their woolly coats, isolating
195 them on islands or in pens to strictly manage their breeding (9, 17, 23). Often island names
196 reflect their connection with dogs, such as *sqwiqwm'i* (“Little Dog”) village on Cameron Island
197 in Nanaimo, Snuneymuxw territory, British Columbia. The prevention of interbreeding wool
198 dogs with hunting or village dogs was critical for maintaining their unique hair characteristics:
199 soft guard hairs with an unusually long crimped undercoat (**Fig. S2**), which was highly spinnable
200 and made warm blanket yarn. These management practices likely contributed to Mutton's PCD
201 ancestry long after the onset of settler colonialism.

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

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

225 Candidate selection genes in Mutton include *KANK2*, a steroid signaling regulator responsible
226 for hereditary diseases of the hair shaft in humans (32). A unique non-synonymous mutation in
227 Mutton lies in the adjacent amino acid to the *KANK2* mutation causing a “woolly” hair
228 phenotype in humans (32). *KRT77* is a member of the keratin gene family responsible for the
229 structural integrity of cells in the epithelium and hair follicles. Mutations in keratin genes are
230 linked to curly hair phenotype in other dogs, rats, and mice (31), woolly hair and hereditary hair
231 loss in humans (26, 30), and multiple *KRT* genes underwent selection in woolly mammoths (25).
232 *CERS3*, *PRDM5*, *HAPLN1* are associated with maintaining the integrity of the skin or connective
233 tissue in humans (27, 28). *GPNMB* is involved in multiple cellular functions in the epidermis,
234 potentially mediating pigmentation (29). We also manually evaluated 15 specific variants from

235 previous literature linked with hair characteristics in living dog breeds (**DataS4**). Apart from a
236 widespread *FGF5* mutation conferring long hair (33, 34), Mutton showed the ancestral allele in
237 all cases with data present (**DataS4**), illustrating the independent origins of woolly dogs' unique
238 phenotype.

239

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

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

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

263 Through these compounding waves of colonialism, the transmission of important knowledge
264 relating to the husbandry of the woolly dog, processing the hair, spinning, and weaving was
265 interrupted. Stó:lō Elder Rena Point Bolton, 95 years old in 2022, recalls how Th'etsimiya, her
266 great-grandmother, had kept woolly dogs, but was forced to give them up: "*They were told they
267 couldn't do their cultural things. There was the police, the Indian Agent and the priests. The
268 dogs were not allowed. She had to get rid of the dogs.*" (9). The dogs represented high status and
269 traditional practices that threatened British and later Canadian dominion, and as such were
270 removed via policies of assimilation (40–42). The weaving traditions were not completely lost,
271 as many cultural teachings and types of expertise were carried on in secret. Bolton said: "*Our
272 people were not allowed to spin on shxwqáqelets [traditional spindle whorls]. They could spin
273 on a European one but not on the shxwqáqelets. They couldn't use their looms, and they would
274 take them out and burn them or they would give them to museums or collectors...The generation*

275 *that was there when the Europeans came and colonized us, that's where it ended, and there*
276 *[were] just a few people who went underground. And my grandmother and my mother were two*
277 *of them.” (9).*

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

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

295

296 **References and Notes**

- 297 1. D. Fedje, Q. Mackie, D. McLaren, B. Wigen, J. Southon, Karst caves in Haida Gwaii:
298 Archaeology and paleontology at the Pleistocene-Holocene transition. *Quat. Sci. Rev.* **272**,
299 107221 (2021).
- 300 2. I. McKechnie, M. L. Moss, S. J. Crockford, Domestic dogs and wild canids on the
301 Northwest Coast of North America: Animal husbandry in a region without agriculture?
302 *Journal of Anthropological Archaeology.* **60**, 101209 (2020).
- 303 3. M. Ní Leathlobhair, A. R. Perri, E. K. Irving-Pease, K. E. Witt, A. Linderholm, J. Haile, O.
304 Lebrasseur, C. Ameen, J. Blick, A. R. Boyko, S. Brace, Y. N. Cortes, S. J. Crockford, A.
305 Devault, E. A. Dimopoulos, M. Eldridge, J. Enk, S. Gopalakrishnan, K. Gori, V. Grimes, E.
306 Guiry, A. J. Hansen, A. Hulme-Beaman, J. Johnson, A. Kitchen, A. K. Kasparov, Y.-M.
307 Kwon, P. A. Nikolskiy, C. P. Lope, A. Manin, T. Martin, M. Meyer, K. N. Myers, M.
308 Omura, J.-M. Rouillard, E. Y. Pavlova, P. Sciulli, M.-H. S. Sinding, A. Strakova, V. V.
309 Ivanova, C. Widga, E. Willerslev, V. V. Pitulko, I. Barnes, M. T. P. Gilbert, K. M. Dobney,
310 R. S. Malhi, E. P. Murchison, G. Larson, L. A. F. Frantz, The evolutionary history of dogs
311 in the Americas. *Science.* **361**, 81–85 (2018).
- 312 4. S. J. Crockford, *Osteometry of Makah and Coast Salish Dogs* (Archaeology Press, Simon
313 Fraser University, 1997).

- 314 5. R. Schulting, The Hair of the Dog: The Identification of a Coast Salish Dog-Hair Blanket
315 from Yale, British Columbia. *Canadian Journal of Archaeology / Journal Canadien*
316 *d'Archéologie*. **18**, 57–76 (1994).
- 317 6. W. H. Dall, G. Gibbs, *Tribes of the Extreme Northwest, and Tribes of Western Washington*
318 *and Northwestern Oregon: Volume I* (Cosimo Classics, 1877).
- 319 7. W. Suttles, "Productivity and its Constraints: A Coast Salish Case" in *Indian Art Traditions*
320 *of the Northwest Coast*, R. L. Carlson, Ed. (Archaeology Press, Simon Fraser University,
321 Burnaby, B.C., 1982), p. 70.
- 322 8. H. G. Barnett, *The Coast Salish of British Columbia* (University of Oregon, Eugene, OR,
323 1955), vol. 4 of *Monographs : Studies in anthropology*.
- 324 9. see Supplementary Materials.
- 325 10. Burke museum basketry exhibition. *Burke Museum*, (available at
326 <https://www.burkemuseum.org/static/baskets/idgame/dreport.html>).
- 327 11. P. Gustafson, *Salish Weaving* (Douglas & McIntyre, Seattle, WA, 1980).
- 328 12. C. Solazzo, S. Heald, M. W. Ballard, D. A. Ashford, P. T. DePriest, R. J. Koestler, M. J.
329 Collins, Proteomics and Coast Salish blankets: a tale of shaggy dogs? *Antiquity*. **85**, 1418–
330 1432 (2011).
- 331 13. R. L. Barsh, J. M. Jones, W. Suttles, "History, ethnography, and archaeology of the Coast
332 Salish woolly-dog" in *Proceedings of the 9th Conference of the International Council of*
333 *Archaeozoology, Durham, August 2002*, L. M. Snyder, E. A. Moore, Eds. (Oxbow Books,
334 Park End Place, Oxford, OX1 1HN, 2006), pp. 2–11.
- 335 14. L. H. Tepper, J. George, W. Joseph, *Salish blankets* (University of Nebraska Press, Lincoln,
336 NE, 2017).
- 337 15. G. Gibbs, Journal, Northwest Boundary Survey, 1857-1862 (1859), ,
338 doi:10.5962/bhl.title.97030.
- 339 16. K. T. Carlson, "Expressions of Cultural Identity" in *A Stó:Lō-Coast Salish Historical Atlas*,
340 K. Carlson, A. J. McHalsie, Eds. (Douglas & McIntyre, Sto:lo Nation, Seattle,
341 WA;Chilliwack, B.C;Vancouver, 2001), p. 25.
- 342 17. J. K. Lord, *The naturalist in Vancouver Island and British Columbia* (R. Bentley, London,
343 1866).
- 344 18. F. W. Howay, The Dog's Hair Blankets of the Coast Salish. *The Washington Historical*
345 *Quarterly*. **9**, 83–92 (1918).
- 346 19. A. Bergström, L. Frantz, R. Schmidt, E. Ersmark, O. Lebrasseur, L. Girdland-Flink, A. T.
347 Lin, J. Storå, K.-G. Sjögren, D. Anthony, E. Antipina, S. Amiri, G. Bar-Oz, V. I. Bazaliiskii,
348 J. Bulatović, D. Brown, A. Carmagnini, T. Davy, S. Fedorov, I. Fiore, D. Fulton, M.

- 349 Germonpré, J. Haile, E. K. Irving-Pease, A. Jamieson, L. Janssens, I. Kirillova, L. K.
350 Horwitz, J. Kuzmanovic-Cvetković, Y. Kuzmin, R. J. Losey, D. L. Dizdar, M. Mashkour,
351 M. Novak, V. Onar, D. Orton, M. Pasarić, M. Radivojević, D. Rajković, B. Roberts, H.
352 Ryan, M. Sablin, F. Shidlovskiy, I. Stojanović, A. Tagliacozzo, K. Trantalidou, I. Ullén, A.
353 Villaluenga, P. Wapnish, K. Dobney, A. Götherström, A. Linderholm, L. Dalén, R. Pinhasi,
354 G. Larson, P. Skoglund, Origins and genetic legacy of prehistoric dogs. *Science*. **370**, 557–
355 564 (2020).
- 356 20. S. Castroviejo-Fisher, P. Skoglund, R. Valadez, C. Vilà, J. A. Leonard, Vanishing native
357 American dog lineages. *BMC Evol. Biol.* **11**, 73 (2011).
- 358 21. C. Ameen, T. R. Feuerborn, S. K. Brown, A. Linderholm, A. Hulme-Beaman, O.
359 Lebrasseur, M.-H. S. Sinding, Z. T. Lounsbury, A. T. Lin, M. Appelt, L. Bachmann, M.
360 Betts, K. Britton, J. Darwent, R. Dietz, M. Fredholm, S. Gopalakrishnan, O. I. Goriunova,
361 B. Grønnow, J. Haile, J. H. Hallsson, R. Harrison, M. P. Heide-Jørgensen, R. Knecht, R. J.
362 Losey, E. Masson-MacLean, T. H. McGovern, E. McManus-Fry, M. Meldgaard, Å.
363 Midtdal, M. L. Moss, I. G. Nikitin, T. Nomokonova, A. H. Pálisdóttir, A. Perri, A. N. Popov,
364 L. Rankin, J. D. Reuther, M. Sablin, A. L. Schmidt, S. Shirar, K. Smiarowski, C. Sonne, M.
365 C. Stiner, M. Vasyukov, C. F. West, G. B. Ween, S. E. Wennerberg, Ø. Wiig, J. Woollett, L.
366 Dalén, A. J. Hansen, M. T. P. Gilbert, B. N. Sacks, L. Frantz, G. Larson, K. Dobney, C. M.
367 Darwent, A. Evin, Specialized sledge dogs accompanied Inuit dispersal across the North
368 American Arctic. *Proc. Biol. Sci.* **286**, 20191929 (2019).
- 369 22. D. Hillis, I. McKechnie, E. Guiry, D. E. St Claire, C. T. Darimont, Ancient dog diets on the
370 Pacific Northwest Coast: zooarchaeological and stable isotope modelling evidence from
371 Tseshaht territory and beyond. *Sci. Rep.* **10**, 15630 (2020).
- 372 23. M. Eells, G. P. Castile, The Indians of Puget Sound: The Notebooks of Myron Eells. (*No*
373 *Title*) (1985) (available at <https://cir.nii.ac.jp/crid/1130282269923522048>).
- 374 24. K. G. Daly, V. Mattiangeli, A. J. Hare, H. Davoudi, H. Fathi, S. B. Doost, S. Amiri, R.
375 Khazaeli, D. Decruyenaere, J. Nokandeh, T. Richter, H. Darabi, P. Mortensen, A. Pantos, L.
376 Yeomans, P. Bangsgaard, M. Mashkour, M. A. Zeder, D. G. Bradley, Herded and hunted
377 goat genomes from the dawn of domestication in the Zagros Mountains. *Proc. Natl. Acad.*
378 *Sci. U. S. A.* **118**, e2100901118 (2021).
- 379 25. D. Díez-Del-Molino, M. Dehasque, J. C. Chacón-Duque, P. Pečnerová, A. Tikhonov, A.
380 Protopopov, V. Plotnikov, F. Kanellidou, P. Nikolskiy, P. Mortensen, G. K. Danilov, S.
381 Vartanyan, M. T. P. Gilbert, A. M. Lister, P. D. Heintzman, T. van der Valk, L. Dalén,
382 Genomics of adaptive evolution in the woolly mammoth. *Curr. Biol.* (2023),
383 doi:10.1016/j.cub.2023.03.084.
- 384 26. Y. Shimomura, M. Wajid, L. Petukhova, M. Kurban, A. M. Christiano, Autosomal-
385 dominant woolly hair resulting from disruption of keratin 74 (KRT74), a potential
386 determinant of human hair texture. *Am. J. Hum. Genet.* **86**, 632–638 (2010).
- 387 27. F. P. W. Radner, S. Marrakchi, P. Kirchmeier, G.-J. Kim, F. Ribierre, B. Kamoun, L. Abid,
388 M. Leipoldt, H. Turki, W. Schempp, R. Heilig, M. Lathrop, J. Fischer, Mutations in CERS3

- 389 cause autosomal recessive congenital ichthyosis in humans. *PLoS Genet.* **9**, e1003536
390 (2013).
- 391 28. E. M. M. Burkitt Wright, H. L. Spencer, S. B. Daly, F. D. C. Manson, L. A. H. Zeef, J.
392 Urquhart, N. Zoppi, R. Bonshek, I. Tosounidis, M. Mohan, C. Madden, A. Dodds, K. E.
393 Chandler, S. Banka, L. Au, J. Clayton-Smith, N. Khan, L. G. Biesecker, M. Wilson, M.
394 Rohrbach, M. Colombi, C. Giunta, G. C. M. Black, Mutations in PRDM5 in brittle cornea
395 syndrome identify a pathway regulating extracellular matrix development and maintenance.
396 *Am. J. Hum. Genet.* **89**, 346 (2011).
- 397 29. K. B. Biswas, A. Takahashi, Y. Mizutani, S. Takayama, A. Ishitsuka, L. Yang, F. Yang, A.
398 Iddamalgoda, I. Katayama, S. Inoue, GPNMB is expressed in human epidermal
399 keratinocytes but disappears in the vitiligo lesional skin. *Sci. Rep.* **10**, 4930 (2020).
- 400 30. N. Wasif, S. K. U.-H. Naqvi, S. Basit, N. Ali, M. Ansar, W. Ahmad, Novel mutations in the
401 keratin-74 (KRT74) gene underlie autosomal dominant woolly hair/hypotrichosis in
402 Pakistani families. *Hum. Genet.* **129**, 419–424 (2011).
- 403 31. S. Harel, A. M. Christiano, Keratin 71 mutations: from water dogs to woolly hair. *J. Invest.*
404 *Dermatol.* **132** (2012), pp. 2315–2317.
- 405 32. Y. Ramot, V. Molho-Pessach, T. Meir, R. Alper-Pinus, I. Siam, S. Tams, S. Babay, A.
406 Zlotogorski, Mutation in KANK2, encoding a sequestering protein for steroid receptor
407 coactivators, causes keratoderma and woolly hair. *J. Med. Genet.* **51**, 388–394 (2014).
- 408 33. C. Dierks, S. Mömke, U. Philipp, O. Distl, Allelic heterogeneity of FGF5 mutations causes
409 the long-hair phenotype in dogs. *Anim. Genet.* **44**, 425–431 (2013).
- 410 34. E. Cadieu, M. W. Neff, P. Quignon, K. Walsh, K. Chase, H. G. Parker, B. M. Vonholdt, A.
411 Rhue, A. Boyko, A. Byers, A. Wong, D. S. Mosher, A. G. Elkahlon, T. C. Spady, C.
412 André, K. G. Lark, M. Cargill, C. D. Bustamante, R. K. Wayne, E. A. Ostrander, Coat
413 variation in the domestic dog is governed by variants in three genes. *Science.* **326**, 150–153
414 (2009).
- 415 35. J. R. Gibson, *Farming the Frontier: The Agricultural Opening of the Oregon Country,*
416 *1786-1846* (University of British Columbia Press, Vancouver, 1985).
- 417 36. K. Carlson, "The Numbers Game" in *A Stó:Lō-Coast Salish Historical Atlas*, K. Carlson, A.
418 J. McHalsie, Eds. (Douglas & McIntyre, Sto:lo Nation, Seattle, WA;Chilliwack,
419 B.C;Vancouver, 2001), pp. 76–83.
- 420 37. K. T. Carlson, "The Fraser River Gold Rush, 1858" in *A Stó:Lō-Coast Salish Historical*
421 *Atlas*, K. Carlson, A. J. McHalsie, Eds. (Douglas & McIntyre, Sto:lo Nation, Seattle,
422 WA;Chilliwack, B.C;Vancouver, 2001), pp. 92–93.
- 423 38. R. Boyd, Smallpox in the Pacific Northwest: the first epidemics. *BC Studies: The British*
424 *Columbian Quarterly*, 5–40 (1994).

- 425 39. B. Lawrence, *Indians and others : mixed-blood urban Native peoples and indigenous*
426 *nationhood* (University of Nebraska Press, Lincoln, NE, 2004).
- 427 40. Hanson, E., Gamez, D., & Manuel, A, The Residential School System. *Indigenous*
428 *Foundations* (2020), (available at
429 https://indigenousfoundations.arts.ubc.ca/the_residential_school_system/).
- 430 41. R. Fisher, *Contact and Conflict: Indian-European Relations in British Columbia, 1774-1890*
431 *(2nd edition)* (UBC Press, 1992).
- 432 42. H. Bohaker, Makúk: A new history of aboriginal-white relations. *West. Hist. Q.* **40**, 509–509
433 (2009).
- 434 43. C. G. Armstrong, J. Earnshaw, A. C. McAlvay, Coupled archaeological and ecological
435 analyses reveal ancient cultivation and land use in Nuchatlaht (Nuu-chah-nulth) territories,
436 Pacific Northwest. *J. Archaeol. Sci.* **143**, 105611 (2022).
- 437 44. D. Lepofsky, G. Toniello, J. Earnshaw, C. Roberts, L. Wilson, K. Rowell, K. Holmes,
438 Ancient anthropogenic clam gardens of the northwest coast expand clam habitat.
439 *Ecosystems.* **24**, 248–260 (2021).
- 440 45. N. Turner, *Ancient pathways, ancestral knowledge: ethnobotany and ecological wisdom of*
441 *indigenous peoples of northwestern North America* (McGill-Queen’s Press-MQUP, 2014),
442 vol. 74.
- 443 46. J. T. Forrest, P. Kane, J. R. Harper, Paul Kane’s frontier: Including wanderings of an artist
444 among the Indians of north America. *West. Hist. Q.* **3**, 79 (1972).
- 445 47. J. G. Swan, *The Indians of Cape Flattery: At the Entrance to the Strait of Fuca, Washington*
446 *Territory* (Smithsonian Institution, 1868).
- 447 48. C. H. Smith, *The Natural History of Dogs: Canidae Or Genus Canis of Authors : Including*
448 *Also the Genera Hyaena and Proteles* (W.H. Lizars, 1839).
- 449 49. C. Stantis, stantis/Coast-Salish-wool-dogs-isotopes: v0.2-alpha (v0.2-alpha). *Zenodo* (2023),
450 , doi:10.5281/zenodo.7760698.
- 451 50. A. R. Perri, K. J. Mitchell, A. Mouton, S. Álvarez-Carretero, A. Hulme-Beaman, J. Haile, A.
452 Jamieson, J. Meachen, A. T. Lin, B. W. Schubert, C. Ameen, E. E. Antipina, P. Bover, S.
453 Brace, A. Carmagnini, C. Carøe, J. A. Samaniego Castruita, J. C. Chatters, K. Dobney, M.
454 Dos Reis, A. Evin, P. Gaubert, S. Gopalakrishnan, G. Gower, H. Heiniger, K. M. Helgen, J.
455 Kapp, P. A. Kosintsev, A. Linderholm, A. T. Ozga, S. Presslee, A. T. Salis, N. F. Saremi, C.
456 Shew, K. Skerry, D. E. Taranenko, M. Thompson, M. V. Sablin, Y. V. Kuzmin, M. J.
457 Collins, M.-H. S. Sinding, M. T. P. Gilbert, A. C. Stone, B. Shapiro, B. Van Valkenburgh,
458 R. K. Wayne, G. Larson, A. Cooper, L. A. F. Frantz, Dire wolves were the last of an ancient
459 New World canid lineage. *Nature.* **591**, 87–91 (2021).

- 460 51. B. D. Galloway, *Dictionary of Upriver Halkomelem* (University of California Press,
461 Berkeley and Los Angeles, California, 2009), vol. 1 of *University of California Publications*
462 *in Linguistics*.
- 463 52. T. T. Waterman, *Notes on the ethnology of the Indians of Puget Sound. Indian notes and*
464 *monographs* (Museum of the American Indian, Heye Foundation, New York, 1973),
465 *Miscellaneous*.
- 466 53. G. Keddie, Prehistoric dogs of BC: Wolves in Sheep Clothing. *The Midden*. **25** (1993).
- 467 54. B. D. Galloway, *Phonology, morphology, and classified word list for the Samish dialect of*
468 *Straits Salish* (University of Ottawa Press, Ottawa, ON, Canada, 1990).
- 469 55. D. Drachman, *T. Skokomish Indian, Ed* (Skokomish Indian Tribe, 2020).
- 470 56. P. Kane, *Wanderings of an artist among the Indians of North America: from Canada to*
471 *Vancouver's Island and Oregon through the Hudson's Bay Company's territory and back*
472 *again* (Longman, Brown, Green, Longmans and Roberts, London, 1859), vol. 35931.
- 473 57. J. D. Leechman, Portraits. Adams, Mrs. Mary and her dog, Jumbo. March 1920. Small
474 fishing canoe made by Jack Adams, of Port Madison Reservation (1920), (available at
475 <https://cdm16118.contentdm.oclc.org/digital/collection/p16118coll33/id/79/rec/7>).
- 476 58. T. T. Waterman, G. Coffin, *Types of canoes on Puget Sound* (Museum of the American
477 Indian, Heye Foundation, New York, 1920).
- 478 59. D. Leechman, Fleece-Bearing Dogs. *Nature Magazine*. **14**, 177 (1929).
- 479 60. D. Jenness, Woolly dog 02 (1935), , doi:10.58066/5apq-1n64.
- 480 61. D. Jenness, Woolly dog 01 (1935), , doi:10.58066/tj37-2m64.
- 481 62. G. M. Allen, *Dogs of the American Aborigines* (Museum of Comparative Zoology,
482 Cambridge, MA, 1920), vol. 4.
- 483 63. D. Jenness, W.A. Newcombe - correspondence, SERIES A (1936).
- 484 64. C. B. R. Kennerly, Natural History - Northwest Boundary Survey Zoology. Box 1. Folder 6
485 (1857-1858), (available at https://siarchives.si.edu/collections/fbr_item_modsi1045).
- 486 65. M. Baker, *Survey of the Northwestern Boundary of the United States, 1857-1861*
487 (Government Printing Office, Washington, 1900).
- 488 66. B. G. Miller, *Be of Good Mind: Essays on the Coast Salish* (UBC Press, 2011).
- 489 67. S. F. Baird, Record Unit 7002. Box 26 (1833-1889), (available at
490 https://siarchives.si.edu/collections/siris_arc_217202).
- 491 68. S. F. Baird, General Directions for Collecting and Preserving Objects of Natural History
492 (1848).

- 493 69. J. A. Tuck, An Archaic Cemetery at Port Au Choix, Newfoundland. *Am. Antiq.* **36**, 343–358
494 (1971).
- 495 70. J. A. Tuck, An Archaic Indian Cemetery in Newfoundland. *Sci. Am.* **222**, 112–122 (1970).
- 496 71. M. A. P. Renouf, Palaeoeskimo seal hunters at Port au Choix, northwestern Newfoundland.
497 *Newfoundland Studies.* **9**, 185–212 (1993).
- 498 72. E. J. Guiry, V. Grimes, Domestic dog (*Canis familiaris*) diets among coastal Late Archaic
499 groups of northeastern North America: A case study for the canine surrogacy approach.
500 *Journal of Anthropological Archaeology.* **32**, 732–745 (2013).
- 501 73. J. A. Tuck, *Ancient People of Port Au Choix: The Excavation of an Archaic Indian*
502 *Cemetery in Newfoundland* (Institute of Social and Economic Research, Memorial
503 University of Newfoundland, 1976).
- 504 74. D. W. G. Stanton, F. Alberti, V. Plotnikov, S. Androsov, S. Grigoriev, S. Fedorov, P.
505 Kosintsev, D. Nagel, S. Vartanyan, I. Barnes, R. Barnett, E. Ersmark, D. Döppes, M.
506 Germonpré, M. Hofreiter, W. Rosendahl, P. Skoglund, L. Dalén, Early Pleistocene origin
507 and extensive intra-species diversity of the extinct cave lion. *Sci. Rep.* **10**, 12621 (2020).
- 508 75. A. Bergström, D. W. G. Stanton, U. H. Taron, L. Frantz, M.-H. S. Sinding, E. Ersmark, S.
509 Pfrengle, M. Cassatt-Johnstone, O. Lebrasseur, L. Girdland-Flink, D. M. Fernandes, M.
510 Ollivier, L. Speidel, S. Gopalakrishnan, M. V. Westbury, J. Ramos-Madriral, T. R.
511 Feuerborn, E. Reiter, J. Gretzinger, S. C. Münzel, P. Swali, N. J. Conard, C. Carøe, J. Haile,
512 A. Linderholm, S. Androsov, I. Barnes, C. Baumann, N. Benecke, H. Bocherens, S. Brace,
513 R. F. Carden, D. G. Drucker, S. Fedorov, M. Gasparik, M. Germonpré, S. Grigoriev, P.
514 Groves, S. T. Hertwig, V. V. Ivanova, L. Janssens, R. P. Jennings, A. K. Kasparov, I. V.
515 Kirillova, I. Kurmaniyazov, Y. V. Kuzmin, P. A. Kosintsev, M. Lázničková-Galetová, C.
516 Leduc, P. Nikolskiy, M. Nussbaumer, C. O’Drisceoil, L. Orlando, A. Outram, E. Y.
517 Pavlova, A. R. Perri, M. Pilot, V. V. Pitulko, V. V. Plotnikov, A. V. Protopopov, A.
518 Rehazek, M. Sablin, A. Seguin-Orlando, J. Storå, C. Verjux, V. F. Zaibert, G. Zazula, P.
519 Crombé, A. J. Hansen, E. Willerslev, J. A. Leonard, A. Götherström, R. Pinhasi, V. J.
520 Schuenemann, M. Hofreiter, M. T. P. Gilbert, B. Shapiro, G. Larson, J. Krause, L. Dalén, P.
521 Skoglund, Grey wolf genomic history reveals a dual ancestry of dogs. *Nature.* **607**, 313–320
522 (2022).
- 523 76. T. L. Fulton, B. Shapiro, Setting up an ancient DNA laboratory. *Methods Mol. Biol.* **1963**,
524 1–13 (2019).
- 525 77. H. Schroeder, P. de Barros Damgaard, M. E. Allentoft, Pretreatment: Improving endogenous
526 ancient DNA yields using a simple enzymatic predigestion step. *Methods Mol. Biol.* **1963**,
527 21–24 (2019).
- 528 78. J. Dabney, M. Knapp, I. Glocke, M.-T. Gansauge, A. Weihmann, B. Nickel, C. Valdiosera,
529 N. García, S. Pääbo, J.-L. Arsuaga, M. Meyer, Complete mitochondrial genome sequence of
530 a Middle Pleistocene cave bear reconstructed from ultrashort DNA fragments. *Proc. Natl.*
531 *Acad. Sci. U. S. A.* **110**, 15758–15763 (2013).

- 532 79. J. D. Kapp, R. E. Green, B. Shapiro, A Fast and Efficient Single-stranded Genomic Library
533 Preparation Method Optimized for Ancient DNA. *J. Hered.* **112**, 241–249 (2021).
- 534 80. M. Kircher, S. Sawyer, M. Meyer, Double indexing overcomes inaccuracies in multiplex
535 sequencing on the Illumina platform. *Nucleic Acids Res.* **40**, e3 (2012).
- 536 81. E. Ersmark, L. Orlando, E. Sandoval-Castellanos, I. Barnes, R. Barnett, A. Stuart, A. Lister,
537 L. Dalén, Population demography and genetic diversity in the Pleistocene cave lion. *Open*
538 *Quat.* **1**, 4 (2015).
- 539 82. S. S. T. Mak, S. Gopalakrishnan, C. Carøe, C. Geng, S. Liu, M.-H. S. Sinding, L. F. K.
540 Kuderna, W. Zhang, S. Fu, F. G. Vieira, M. Germonpré, H. Bocherens, S. Fedorov, B.
541 Petersen, T. Sicheritz-Pontén, T. Marques-Bonet, G. Zhang, H. Jiang, M. T. P. Gilbert,
542 Comparative performance of the BGISEQ-500 vs Illumina HiSeq2500 sequencing platforms
543 for palaeogenomic sequencing. *Gigascience.* **6**, 1–13 (2017).
- 544 83. M. Meyer, M. Kircher, Illumina sequencing library preparation for highly multiplexed target
545 capture and sequencing. *Cold Spring Harb. Protoc.* **2010** (2010), doi:10.1101/pdb.prot5448.
- 546 84. E. V. Dutrow, J. A. Serpell, E. A. Ostrander, Domestic dog lineages reveal genetic drivers of
547 behavioral diversification. *Cell.* **185**, 4737–4755.e18 (2022).
- 548 85. M. Schubert, S. Lindgreen, L. Orlando, AdapterRemoval v2: rapid adapter trimming,
549 identification, and read merging. *BMC Res. Notes.* **9**, 88 (2016).
- 550 86. H. Li, R. Durbin, Fast and accurate short read alignment with Burrows–Wheeler transform.
551 *Bioinformatics.* **25**, 1754–1760 (2009).
- 552 87. M. A. DePristo, E. Banks, R. Poplin, K. V. Garimella, J. R. Maguire, C. Hartl, A. A.
553 Philippakis, G. del Angel, M. A. Rivas, M. Hanna, A. McKenna, T. J. Fennell, A. M.
554 Kernytsky, A. Y. Sivachenko, K. Cibulskis, S. B. Gabriel, D. Altshuler, M. J. Daly, A
555 framework for variation discovery and genotyping using next-generation DNA sequencing
556 data. *Nat. Genet.* **43**, 491–498 (2011).
- 557 88. H. Jónsson, A. Ginolhac, M. Schubert, P. L. F. Johnson, L. Orlando, mapDamage2.0: fast
558 approximate Bayesian estimates of ancient DNA damage parameters. *Bioinformatics.* **29**,
559 1682–1684 (2013).
- 560 89. N. Dussex, D. W. G. Stanton, H. Sigeman, P. G. P. Ericson, J. Gill, D. C. Fisher, A. V.
561 Protopopov, V. L. Herridge, V. Plotnikov, B. Hansson, L. Dalén, Biomolecular analyses
562 reveal the age, sex and species identity of a near-intact Pleistocene bird carcass. *Commun.*
563 *Biol.* **3**, 84 (2020).
- 564 90. E. Palkopoulou, S. Mallick, P. Skoglund, J. Enk, N. Rohland, H. Li, A. Omrak, S.
565 Vartanyan, H. Poinar, A. Götherström, D. Reich, L. Dalén, Complete genomes reveal
566 signatures of demographic and genetic declines in the woolly mammoth. *Curr. Biol.* **25**,
567 1395–1400 (2015).

- 568 91. H. Li, Aligning sequence reads, clone sequences and assembly contigs with BWA-MEM.
569 *arXiv [q-bio.GN]* (2013), (available at <http://arxiv.org/abs/1303.3997>).
- 570 92. A. McKenna, M. Hanna, E. Banks, A. Sivachenko, K. Cibulskis, A. Kernytzky, K.
571 Garimella, D. Altshuler, S. Gabriel, M. Daly, M. A. DePristo, The Genome Analysis
572 Toolkit: a MapReduce framework for analyzing next-generation DNA sequencing data.
573 *Genome Res.* **20**, 1297–1303 (2010).
- 574 93. R. Poplin, V. Ruano-Rubio, M. A. DePristo, T. J. Fennell, M. O. Carneiro, G. A. Van der
575 Auwera, D. E. Kling, L. D. Gauthier, A. Levy-Moonshine, D. Roazen, K. Shakir, J.
576 Thibault, S. Chandran, C. Whelan, M. Lek, S. Gabriel, M. J. Daly, B. Neale, D. G.
577 MacArthur, E. Banks, Scaling accurate genetic variant discovery to tens of thousands of
578 samples. *bioRxiv* (2017), , doi:10.1101/201178.
- 579 94. T. S. Korneliussen, A. Albrechtsen, R. Nielsen, ANGSD: Analysis of Next Generation
580 Sequencing Data. *BMC Bioinformatics.* **15**, 356 (2014).
- 581 95. L. Orlando, A. Ginolhac, G. Zhang, D. Froese, A. Albrechtsen, M. Stiller, M. Schubert, E.
582 Cappellini, B. Petersen, I. Moltke, P. L. F. Johnson, M. Fumagalli, J. T. Vilstrup, M.
583 Raghavan, T. Korneliussen, A.-S. Malaspinas, J. Vogt, D. Szklarczyk, C. D. Kelstrup, J.
584 Vinther, A. Dolocan, J. Stenderup, A. M. V. Velazquez, J. Cahill, M. Rasmussen, X. Wang,
585 J. Min, G. D. Zazula, A. Seguin-Orlando, C. Mortensen, K. Magnussen, J. F. Thompson, J.
586 Weinstock, K. Gregersen, K. H. Røed, V. Eisenmann, C. J. Rubin, D. C. Miller, D. F.
587 Antczak, M. F. Bertelsen, S. Brunak, K. A. S. Al-Rasheid, O. Ryder, L. Andersson, J.
588 Mundy, A. Krogh, M. T. P. Gilbert, K. Kjær, T. Sicheritz-Ponten, L. J. Jensen, J. V. Olsen,
589 M. Hofreiter, R. Nielsen, B. Shapiro, J. Wang, E. Willerslev, Recalibrating Equus evolution
590 using the genome sequence of an early Middle Pleistocene horse. *Nature.* **499**, 74–78
591 (2013).
- 592 96. A. R. Quinlan, I. M. Hall, BEDTools: a flexible suite of utilities for comparing genomic
593 features. *Bioinformatics.* **26**, 841–842 (2010).
- 594 97. S. Purcell, B. Neale, K. Todd-Brown, L. Thomas, M. A. R. Ferreira, D. Bender, J. Maller, P.
595 Sklar, P. I. W. de Bakker, M. J. Daly, P. C. Sham, PLINK: a tool set for whole-genome
596 association and population-based linkage analyses. *Am. J. Hum. Genet.* **81**, 559–575 (2007).
- 597 98. R. Bouckaert, T. G. Vaughan, J. Barido-Sottani, S. Duchêne, M. Fourment, A.
598 Gavryushkina, J. Heled, G. Jones, D. Kühnert, N. De Maio, M. Matschiner, F. K. Mendes,
599 N. F. Müller, H. A. Ogilvie, L. du Plessis, A. Poppinga, A. Rambaut, D. Rasmussen, I.
600 Siveroni, M. A. Suchard, C.-H. Wu, D. Xie, C. Zhang, T. Stadler, A. J. Drummond, BEAST
601 2.5: An advanced software platform for Bayesian evolutionary analysis. *PLoS Comput. Biol.*
602 **15**, e1006650 (2019).
- 603 99. M. Molak, M. A. Suchard, S. Y. W. Ho, D. W. Beilman, B. Shapiro, Empirical calibrated
604 radiocarbon sampler: a tool for incorporating radiocarbon-date and calibration error into B
605 ayesian phylogenetic analyses of ancient DNA. *Mol. Ecol. Resour.* **15**, 81–86 (2015).

- 606 100. A. Rambaut, A. J. Drummond, D. Xie, G. Baele, M. A. Suchard, Posterior
607 Summarization in Bayesian Phylogenetics Using Tracer 1.7. *Syst. Biol.* **67**, 901–904 (2018).
- 608 101. A. J. Drummond, A. Rambaut, BEAST: Bayesian evolutionary analysis by sampling
609 trees. *BMC Evol. Biol.* **7**, 214 (2007).
- 610 102. N. Patterson, P. Moorjani, Y. Luo, S. Mallick, N. Rohland, Y. Zhan, T. Genschoreck, T.
611 Webster, D. Reich, Ancient admixture in human history. *Genetics.* **192**, 1065–1093 (2012).
- 612 103. T. R. Feuerborn, A. Carmagnini, R. J. Losey, T. Nomokonova, A. Askeyev, I. Askeyev,
613 O. Askeyev, E. E. Antipina, M. Appelt, O. P. Bachura, F. Beglane, D. G. Bradley, K. G.
614 Daly, S. Gopalakrishnan, K. Murphy Gregersen, C. Guo, A. V. Gusev, C. Jones, P. A.
615 Kosintsev, Y. V. Kuzmin, V. Mattiangeli, A. R. Perri, A. V. Plekhanov, J. Ramos-Madriral,
616 A. L. Schmidt, D. Shaymuratova, O. Smith, L. V. Yavorskaya, G. Zhang, E. Willerslev, M.
617 Meldgaard, M. T. P. Gilbert, G. Larson, L. Dalén, A. J. Hansen, M.-H. S. Sinding, L. Frantz,
618 Modern Siberian dog ancestry was shaped by several thousand years of Eurasian-wide trade
619 and human dispersal. *Proc. Natl. Acad. Sci. U. S. A.* **118** (2021),
620 doi:10.1073/pnas.2100338118.
- 621 104. V. M. Narasimhan, N. Patterson, P. Moorjani, N. Rohland, R. Bernardos, S. Mallick, I.
622 Lazaridis, N. Nakatsuka, I. Olalde, M. Lipson, A. M. Kim, L. M. Olivieri, A. Coppa, M.
623 Vidale, J. Mallory, V. Moiseyev, E. Kitov, J. Monge, N. Adamski, N. Alex, N.
624 Broomandkhoshbacht, F. Candilio, K. Callan, O. Cheronet, B. J. Culleton, M. Ferry, D.
625 Fernandes, S. Freilich, B. Gamarra, D. Gaudio, M. Hajdinjak, É. Harney, T. K. Harper, D.
626 Keating, A. M. Lawson, M. Mah, K. Mandl, M. Michel, M. Novak, J. Oppenheimer, N. Rai,
627 K. Sirak, V. Slon, K. Stewardson, F. Zalzal, Z. Zhang, G. Akhatov, A. N. Bagashev, A.
628 Bagnera, B. Baitanayev, J. Bendezu-Sarmiento, A. A. Bissembaev, G. L. Bonora, T. T.
629 Charynov, T. Chikisheva, P. K. Dashkovskiy, A. Derevianko, M. Dobeš, K. Douka, N.
630 Dubova, M. N. Duisengali, D. Enshin, A. Epimakhov, A. V. Fribus, D. Fuller, A.
631 Goryachev, A. Gromov, S. P. Grushin, B. Hanks, M. Judd, E. Kazizov, A. Khokhlov, A. P.
632 Krygin, E. Kupriyanova, P. Kuznetsov, D. Luiselli, F. Maksudov, A. M. Mamedov, T. B.
633 Mamirov, C. Meiklejohn, D. C. Merrett, R. Micheli, O. Mochalov, S. Mustafokulov, A.
634 Nayak, D. Pettener, R. Potts, D. Razhev, M. Rykun, S. Sarno, T. M. Savenkova, K.
635 Sikhymbaeva, S. M. Slepchenko, O. A. Soltobaev, N. Stepanova, S. Svyatko, K. Tabaldiev,
636 M. Teschler-Nicola, A. A. Tishkin, V. V. Tkachev, S. Vasilyev, P. Velemínský, D. Voyakin,
637 A. Yermolayeva, M. Zahir, V. S. Zubkov, A. Zubova, V. S. Shinde, C. Lalueza-Fox, M.
638 Meyer, D. Anthony, N. Boivin, K. Thangaraj, D. J. Kennett, M. Frachetti, R. Pinhasi, D.
639 Reich, The formation of human populations in South and Central Asia. *Science.* **365**,
640 eaat7487 (2019).
- 641 105. S. Marciniak, M. R. Mughal, L. R. Godfrey, R. J. Bankoff, H. Randrianatoandro, B. E.
642 Crowley, C. M. Bergey, K. M. Muldoon, J. Randrianasy, B. M. Raharivololona, S. C.
643 Schuster, R. S. Malhi, A. D. Yoder, E. E. Louis Jr, L. Kistler, G. H. Perry, Evolutionary and
644 phylogenetic insights from a nuclear genome sequence of the extinct, giant, “subfossil”
645 koala lemur *Megaladapis edwardsi*. *Proc. Natl. Acad. Sci. U. S. A.* **118**, e2022117118
646 (2021).

- 647 106. G. H. Perry, D. Reeves, P. Melsted, A. Ratan, W. Miller, K. Michelini, E. E. Louis Jr, J.
648 K. Pritchard, C. E. Mason, Y. Gilad, A genome sequence resource for the aye-aye
649 (*Daubentonia madagascariensis*), a nocturnal lemur from Madagascar. *Genome Biol. Evol.*
650 **4**, 126–135 (2012).
- 651 107. The International HapMap Consortium, A second generation human haplotype map of
652 over 3.1 million SNPs. *Nature*. **449**, 851–861 (2007).
- 653 108. J. Reimand, M. Kull, H. Peterson, J. Hansen, J. Vilo, g:Profiler—a web-based toolset for
654 functional profiling of gene lists from large-scale experiments. *Nucleic Acids Res.* **35**,
655 W193–W200 (2007).
- 656 109. S. Grote, GOfuncR: Gene ontology enrichment using FUNC. R package version 1.20.0
657 (2023), , doi:10.18129/B9.bioc.GOfuncR.
- 658 110. D. W. Huang, B. T. Sherman, R. A. Lempicki, Systematic and integrative analysis of
659 large gene lists using DAVID bioinformatics resources. *Nat. Protoc.* **4**, 44–57 (2009).
- 660 111. B. T. Sherman, M. Hao, J. Qiu, X. Jiao, M. W. Baseler, H. C. Lane, T. Imamichi, W.
661 Chang, DAVID: a web server for functional enrichment analysis and functional annotation
662 of gene lists (2021 update). *Nucleic Acids Res.* **50**, W216–W221 (2022).
- 663 112. Y. Shimomura, M. Wajid, Y. Ishii, L. Shapiro, L. Petukhova, D. Gordon, A. M.
664 Christiano, Disruption of P2RY5, an orphan G protein–coupled receptor, underlies
665 autosomal recessive woolly hair. *Nat. Genet.* **40**, 335–339 (2008).
- 666 113. G. M. Khan, N. Hassan, N. Khan, M. Humayun, K. Khan, S. Khaliq, F. U. Rehman, S.
667 Ahmed, K. Shah, S. A. Khan, N. Muhammad, A. Wali, S. Khan, S. Basit, M. Ayub, Biallelic
668 mutations in the *LPAR 6* gene causing autosomal recessive wooly hair/hypotrichosis
669 phenotype in five Pakistani families. *Int. J. Dermatol.* **58**, 946–952 (2019).
- 670 114. M.-T. Romano, A. Tafazzoli, M. Mattern, S. Sivalingam, S. Wolf, A. Rupp, H. Thiele, J.
671 Altmüller, P. Nürnberg, J. Ellwanger, R. Gambon, A. Baumer, N. Kohlschmidt, D. Metze,
672 S. Holdenrieder, R. Paus, D. Lütjohann, J. Frank, M. Geyer, M. Bertolini, P. Kokordelis, R.
673 C. Betz, Bi-allelic mutations in LSS, encoding lanosterol synthase, cause autosomal-
674 recessive hypotrichosis simplex. *Am. J. Hum. Genet.* **103**, 777–785 (2018).
- 675 115. K. Shah, S. Basit, G. Ali, K. Ramzan, M. Ansar, W. Ahmad, A novel homozygous
676 frameshift variant in the C3orf52 gene underlying isolated hair loss in a consanguineous
677 family. *Eur. J. Dermatol.* **31**, 409–411 (2021).
- 678 116. M. Tariq, A. Azhar, S. M. Baig, N. Dahl, J. Klar, A novel mutation in the Lipase H gene
679 underlies autosomal recessive hypotrichosis and woolly hair. *Sci. Rep.* **2**, 730 (2012).
- 680 117. G. Törnqvist, A. Sandberg, A.-C. Häggglund, L. Carlsson, Cyclic expression of *lhx2*
681 regulates hair formation. *PLoS Genet.* **6**, e1000904 (2010).

- 682 118. S. Harshuk-Shabso, H. Dressler, C. Niehrs, E. Aamar, D. Enshell-Seijffers, Fgf and Wnt
683 signaling interaction in the mesenchymal niche regulates the murine hair cycle clock. *Nat.*
684 *Commun.* **11**, 5114 (2020).
- 685 119. X. Lim, S. H. Tan, K. L. Yu, S. B. H. Lim, R. Nusse, Axin2 marks quiescent hair follicle
686 bulge stem cells that are maintained by autocrine Wnt/ β -catenin signaling. *Proc. Natl. Acad.*
687 *Sci. U. S. A.* **113**, E1498-505 (2016).
- 688 120. D. J. Tobin, A. Gunin, M. Magerl, B. Handijski, R. Paus, Plasticity and cytokinetic
689 dynamics of the hair follicle mesenchyme: implications for hair growth control. *J. Invest.*
690 *Dermatol.* **120**, 895–904 (2003).
- 691 121. E. Hoover, M. Alhaji, J. L. Flores, *Physiology, Hair* (StatPearls Publishing, 2022).
- 692 122. L. Alonso, E. Fuchs, The hair cycle. *J. Cell Sci.* **119**, 391–393 (2006).
- 693 123. C. J. Peter, A. Saito, Y. Hasegawa, Y. Tanaka, M. Nagpal, G. Perez, E. Alway, S.
694 Espeso-Gil, T. Fayyad, C. Ratner, A. Dincer, A. Gupta, L. Devi, J. G. Pappas, F. M.
695 Lalonde, J. A. Butman, J. C. Han, S. Akbarian, A. Kamiya, In vivo epigenetic editing of
696 Sema6a promoter reverses transcallosal dysconnectivity caused by C11orf46/Arl14ep risk
697 gene. *Nat. Commun.* **10**, 4112 (2019).
- 698 124. M. Okada, I. M. Cheeseman, T. Hori, K. Okawa, I. X. McLeod, J. R. Yates 3rd, A. Desai,
699 T. Fukagawa, The CENP-H-I complex is required for the efficient incorporation of newly
700 synthesized CENP-A into centromeres. *Nat. Cell Biol.* **8**, 446–457 (2006).
- 701 125. M. Lokaj, S. K. Kösling, C. Koerner, S. M. Lange, S. E. C. van Beersum, J. van
702 Reeuwijk, R. Roepman, N. Horn, M. Ueffing, K. Boldt, A. Wittinghofer, The interaction of
703 CCDC104/BARTL1 with Arl3 and implications for ciliary function. *Structure.* **23**, 2122–
704 2132 (2015).
- 705 126. Y.-J. Lee, S.-R. Ho, J. D. Graves, Y. Xiao, S. Huang, W.-C. Lin, CGRRF1, a growth
706 suppressor, regulates EGFR ubiquitination in breast cancer. *Breast Cancer Res.* **21**, 134
707 (2019).
- 708 127. Z. Liu, Y. Xiang, G. Sun, The KCTD family of proteins: structure, function, disease
709 relevance. *Cell Biosci.* **3**, 45 (2013).
- 710 128. S. Chauhan, X. Zheng, Y. Y. Tan, B.-H. Tay, S. Lim, B. Venkatesh, P. Kaldis, Evolution
711 of the Cdk-activator Speedy/RINGO in vertebrates. *Cell. Mol. Life Sci.* **69**, 3835–3850
712 (2012).
- 713 129. A. Ghelli Luserna di Rorà, C. Cerchione, G. Martinelli, G. Simonetti, A WEE1 family
714 business: regulation of mitosis, cancer progression, and therapeutic target. *J. Hematol.*
715 *Oncol.* **13**, 126 (2020).
- 716 130. R. P. Mecham, Overview of extracellular matrix. *Curr. Protoc. Cell Biol.* **Chapter 10**
717 (2012), doi:10.1002/0471143030.cb1001s57.

- 718 131. G. Donati, V. Proserpio, B. M. Lichtenberger, K. Natsuga, R. Sinclair, H. Fujiwara, F. M.
719 Watt, Epidermal Wnt/ β -catenin signaling regulates adipocyte differentiation via secretion of
720 adipogenic factors. *Proc. Natl. Acad. Sci. U. S. A.* **111**, E1501–E1509 (2014).
- 721 132. S. Tsukada, M. Iwai, J. Nishiu, M. Itoh, H. Tomoike, M. Horiuchi, Y. Nakamura, T.
722 Tanaka, Inhibition of experimental intimal thickening in mice lacking a novel G-protein-
723 coupled receptor. *Circulation.* **107**, 313–319 (2003).
- 724 133. L. Guo, H. Zhang, Y. Hou, T. Wei, J. Liu, Plasmalemma vesicle-associated protein: A
725 crucial component of vascular homeostasis. *Exp. Ther. Med.* **12**, 1639–1644 (2016).
- 726 134. Y. Xu, J. Rong, Z. Zhang, The emerging role of angiotensinogen in cardiovascular
727 diseases. *J. Cell. Physiol.* **236**, 68–78 (2021).
- 728 135. M. A. Kaetzel, H. C. Chan, W. P. Dubinsky, J. R. Dedman, D. J. Nelson, A role for
729 annexin IV in epithelial cell function. Inhibition of calcium-activated chloride conductance.
730 *J. Biol. Chem.* **269**, 5297–5302 (1994).
- 731 136. S. Kreft, A. R. Klatt, J. Straßburger, E. Pöschl, R. J. Flower, S. Eming, C.
732 Reutelingsperger, A. Brisson, B. Brachvogel, Skin wound repair is not altered in the absence
733 of endogenous AnxA1 or AnxA5, but pharmacological concentrations of AnxA4 and
734 AnxA5 inhibit wound hemostasis. *Cells Tissues Organs.* **201**, 287–298 (2016).
- 735 137. M. Cieslak, M. Reissmann, M. Hofreiter, A. Ludwig, Colours of domestication. *Biol.*
736 *Rev. Camb. Philos. Soc.* **86**, 885–899 (2011).
- 737 138. S. M. Schmutz, T. G. Berryere, N. M. Ellinwood, J. A. Kerns, G. S. Barsh, MC1R studies
738 in dogs with melanistic mask or brindle patterns. *J. Hered.* **94**, 69–73 (2003).
- 739 139. N. Dürig, A. Letko, V. Lepori, S. Hadji Rasouliha, R. Loechel, A. Kehl, M. K. Hytönen,
740 H. Lohi, N. Mauri, J. Dietrich, M. Wiedmer, M. Drögemüller, V. Jagannathan, S. M.
741 Schmutz, T. Leeb, Two MC1R loss-of-function alleles in cream-coloured Australian Cattle
742 Dogs and white Huskies. *Anim. Genet.* **49**, 284–290 (2018).
- 743 140. B. Hédan, E. Cadieu, N. Botherel, C. Dufaure de Citres, A. Letko, M. Rimbault, C.
744 Drögemüller, V. Jagannathan, T. Derrien, S. Schmutz, T. Leeb, C. André, Identification of a
745 missense variant in MFSD12 involved in dilution of phaeomelanin leading to white or
746 cream coat color in dogs. *Genes (Basel).* **10**, 386 (2019).
- 747 141. C. Drögemüller, U. Philipp, B. Haase, A.-R. Günzel-Apel, T. Leeb, A noncoding
748 melanophilin gene (MLPH) SNP at the splice donor of exon 1 represents a candidate causal
749 mutation for coat color dilution in dogs. *J. Hered.* **98**, 468–473 (2007).
- 750 142. A. Bauer, A. Kehl, V. Jagannathan, T. Leeb, A novel MLPH variant in dogs with coat
751 colour dilution. *Anim. Genet.* **49**, 94–97 (2018).
- 752 143. S. L. Van Buren, K. M. Minor, R. A. Grahn, J. R. Mickelson, J. C. Grahn, J. Malvick, J.
753 R. Colangelo, E. Mueller, P. Kuehnlein, A. Kehl, A third MLPH variant causing coat color
754 dilution in dogs. *Genes (Basel).* **11**, 639 (2020).

- 755 144. G. Renaud, K. Hanghøj, T. S. Korneliussen, E. Willerslev, L. Orlando, Joint Estimates of
756 Heterozygosity and Runs of Homozygosity for Modern and Ancient Samples. *Genetics*. **212**,
757 587–614 (2019).
- 758 145. C. Pacheco, A. V. Stronen, B. Jędrzejewska, K. Plis, I. M. Okhlopkov, N. V. Mamaev, S.
759 V. Drovetski, R. Godinho, Demography and evolutionary history of grey wolf populations
760 around the Bering Strait. *Mol. Ecol.* **31**, 4851–4865 (2022).
- 761 146. M. A. Katzenberg, N. C. Lovell, Stable isotope variation in pathological bone. *Int. J.*
762 *Osteoarchaeol.* **9**, 316–324 (1999).
- 763 147. R. Longin, New method of collagen extraction for radiocarbon dating. *Nature*. **230**, 241–
764 242 (1971).
- 765 148. T. A. Brown, D. E. Nelson, J. S. Vogel, J. R. Southon, Improved Collagen Extraction by
766 Modified Longin Method. *Radiocarbon*. **30**, 171–177 (1988).
- 767 149. J. Harris, S. Anderson, "Introduction" in *Letters from the 49th Parallel, 1857-1873:*
768 *Selected Correspondence of Joseph Harris and Samuel Anderson* (Champlain Society,
769 Toronto, 2013), pp. xiii–cviii.
- 770 150. Pesticides. *National Museum of the American Indian*, (available at
771 <https://americanindian.si.edu/explore/collections/conservation/pesticides>).
- 772 151. S. H. Ambrose, Preparation and characterization of bone and tooth collagen for isotopic
773 analysis. *J. Archaeol. Sci.* **17**, 431–451 (1990).
- 774 152. S. H. Ambrose, L. Norr, On Stable Isotopic Data and Prehistoric Subsistence in the
775 Soconusco Region. *Curr. Anthropol.* **33**, 401–404 (1992).
- 776 153. T. C. O’Connell, R. E. M. Hedges, M. A. Healey, A. H. R. W. Simpson, Isotopic
777 Comparison of Hair, Nail and Bone: Modern Analyses. *J. Archaeol. Sci.* **28**, 1247–1255
778 (2001).
- 779 154. E. McManus-Fry, R. Knecht, K. Dobney, M. P. Richards, K. Britton, Dog-human dietary
780 relationships in Yup’ik western Alaska: The stable isotope and zooarchaeological evidence
781 from pre-contact Nunalleq. *Journal of Archaeological Science: Reports*. **17**, 964–972
782 (2018).
- 783 155. E. Guiry, T. C. A. Royle, R. G. Matson, H. Ward, T. Weir, N. Waber, T. J. Brown, B. P.
784 V. Hunt, M. H. H. Price, B. P. Finney, M. Kaeriyama, Y. Qin, D. Y. Yang, P. Szpak,
785 Differentiating salmonid migratory ecotypes through stable isotope analysis of collagen:
786 Archaeological and ecological applications. *PLoS One*. **15**, e0232180 (2020).
- 787 156. Z. Sharp, Principles of Stable Isotope Geochemistry, 2nd edition (2017) (available at
788 https://digitalrepository.unm.edu/unm_oer/1/?fref=gc&dti=175833885799280).

- 789 157. W. F. Keegan, M. J. DeNiro, Stable Carbon- and Nitrogen-Isotope Ratios of Bone
790 Collagen Used to Study Coral-Reef and Terrestrial Components of Prehistoric Bahamian
791 Diet. *Am. Antiq.* **53**, 320–336 (1988).
- 792 158. M. Minagawa, E. Wada, Stepwise enrichment of ^{15}N along food chains: Further
793 evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim. Cosmochim. Acta.* **48**,
794 1135–1140 (1984).
- 795 159. M. J. DeNiro, S. Epstein, Influence of diet on the distribution of carbon isotopes in
796 animals. *Geochim. Cosmochim. Acta.* **42**, 495–506 (1978).
- 797 160. J. Hoefs, *Stable Isotope Geochemistry* (Springer International Publishing).
- 798 161. K. Smith, M. J. Rennie, New approaches and recent results concerning human-tissue
799 collagen synthesis. *Curr. Opin. Clin. Nutr. Metab. Care.* **10**, 582–590 (2007).
- 800 162. C. I. Jackson, *Letters from the 49th Parallel, 1857-1873: Selected Correspondence of*
801 *Joseph Harris and Samuel Anderson* (Champlain Society, Toronto, 2000), vol. 63.

802

803 **Acknowledgements:** We wish to express our deep gratitude to the Honorable Steven Point,
804 Grand Chief and Dr. Gwen Point of the Stó:lō Nation for giving us permission and
805 encouragement for this research. Thanks to Candace Wellman for her role in re-discovering
806 Mutton, assistance with history of the area, and photographs. We raise our hands in thanks to all
807 people within the Coast Salish communities who have graciously shared their time and
808 knowledge to realize this project, specifically: Xweliqwiya Rena Point Bolton (Stó:lō Nation);
809 Danielle Morsette (Suquamish/Shxwhá:y Village); Eliot Kwulasultun White (Snuneymuxw First
810 Nation); Sulqwan Philomena Williams (Cowichan); Violet Snu'Meethia Elliott (Snuneymuxw);
811 Tracy Sesemiya Williams Skw̓xwú7mesh Úxwumixw (Squamish Nation); Andrea Fritz, Norris
812 family (Lyacksun); Tillie Jones (Tulalip); Tami Hohn (Puyallup); qwatələmu Nancy Bob
813 (Lummi). Interviews were carried out under Institutional Review Board and Research Ethics
814 Board approvals from the Smithsonian Institution (Human Subjects Protocol #HS220007) and
815 Vancouver Island University (#101410), with informed consent including explicit opt-in
816 permissions to reprint quotations with personal attribution. Computations performed for this
817 paper were conducted on the Smithsonian High Performance Cluster, Smithsonian Institution:
818 <https://doi.org/10.25572/SIHPC>, and the Leibniz Supercomputing Centre (LRZ). Portions of the
819 laboratory work were conducted in and with the support of the Laboratories for Analytical
820 Biology (L.A.B.) facilities of the National Museum of Natural History. Thanks to Tom Gilbert
821 for funding the processing/sequencing of AL3194, John Ososky for specimen handling
822 assistance, and Ludovic Orlando and Sierra Harding for providing helpful comments on the
823 manuscript.

824

825

826 **Supplementary Materials**

827 Materials and Methods

828 Figs. S1 to S19

829 Tables 1 and 2

830 References (50-162)

831

832 **Funding:** Research was supported by SI funds to LK. ATL, H-LL, and CS were supported by
833 Smithsonian postdoctoral fellowships. Funding for stable isotope analysis provided by
834 Smithsonian Museum Conservation Institute federal and trust funds. PS was supported by
835 EMBO, the Vallee Foundation, the European Research Council (grant no. 852558), the
836 Wellcome Trust (217223/Z/19/Z), and Francis Crick Institute core funding (FC001595) from
837 Cancer Research UK, the Medical Research Council, and the Wellcome Trust. VG was
838 supported by an SSHRC-IG.

839

840 **Author contributions:** Conceptualization: ATL, LH-K, LK; Methodology: ATL, LK, H-LL,
841 LH-K, SGA, CS, CAMF, KC; Investigation: ATL, LK, CS, SGA, H-LL, MTRH, LH-K, JH, IM,
842 GK, TRF, M-HSS, SG, LF, AB, AC, AH; Formal analysis: ATL, LK, CS, CAMF, SGA, DWGS,
843 AH; Visualization: ATL, LK, CS, KC, MH, GK, IM; Resources: LK, MTRH, VG, BNS, IM,
844 EAO; Funding acquisition: LK, PS, LD; Supervision: LK, LH-K; Writing – original draft: ATL,
845 LK, LH-K; Writing – review & editing: all authors.

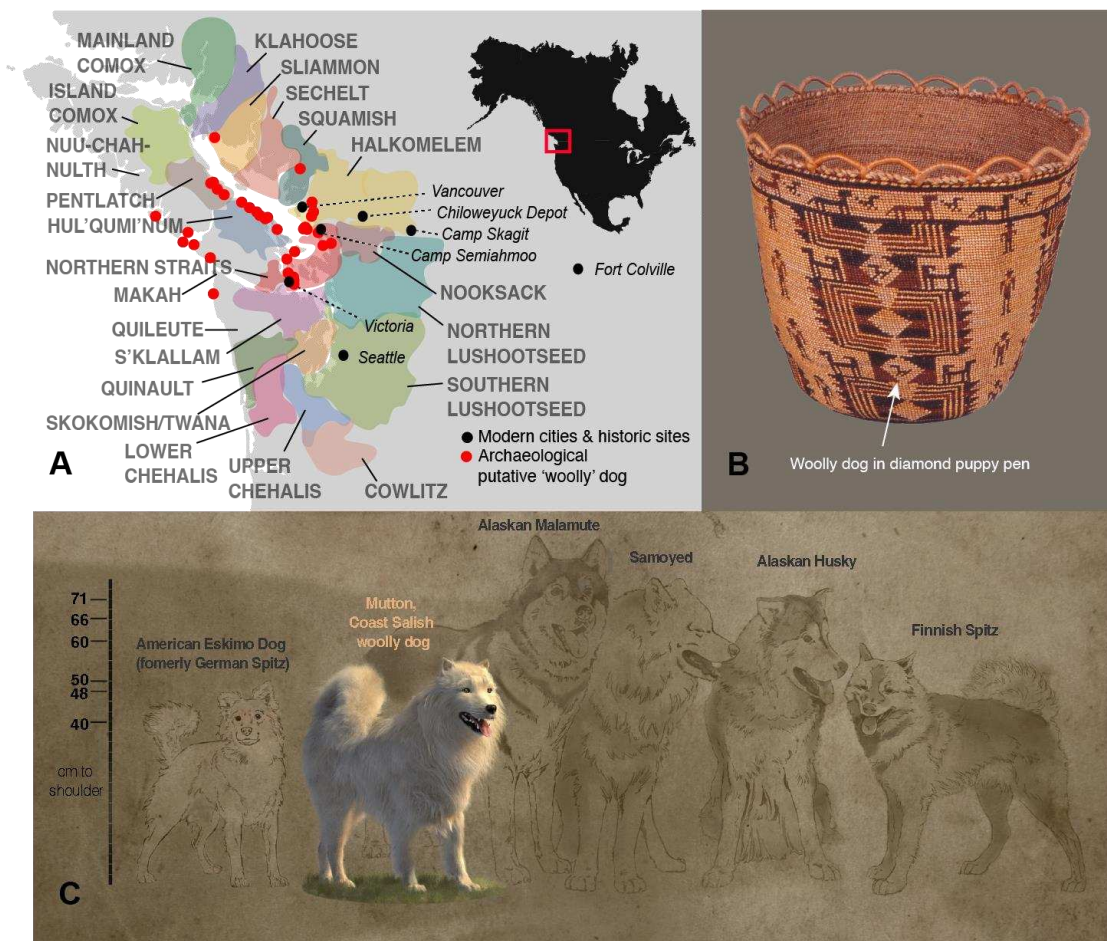
846

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

848

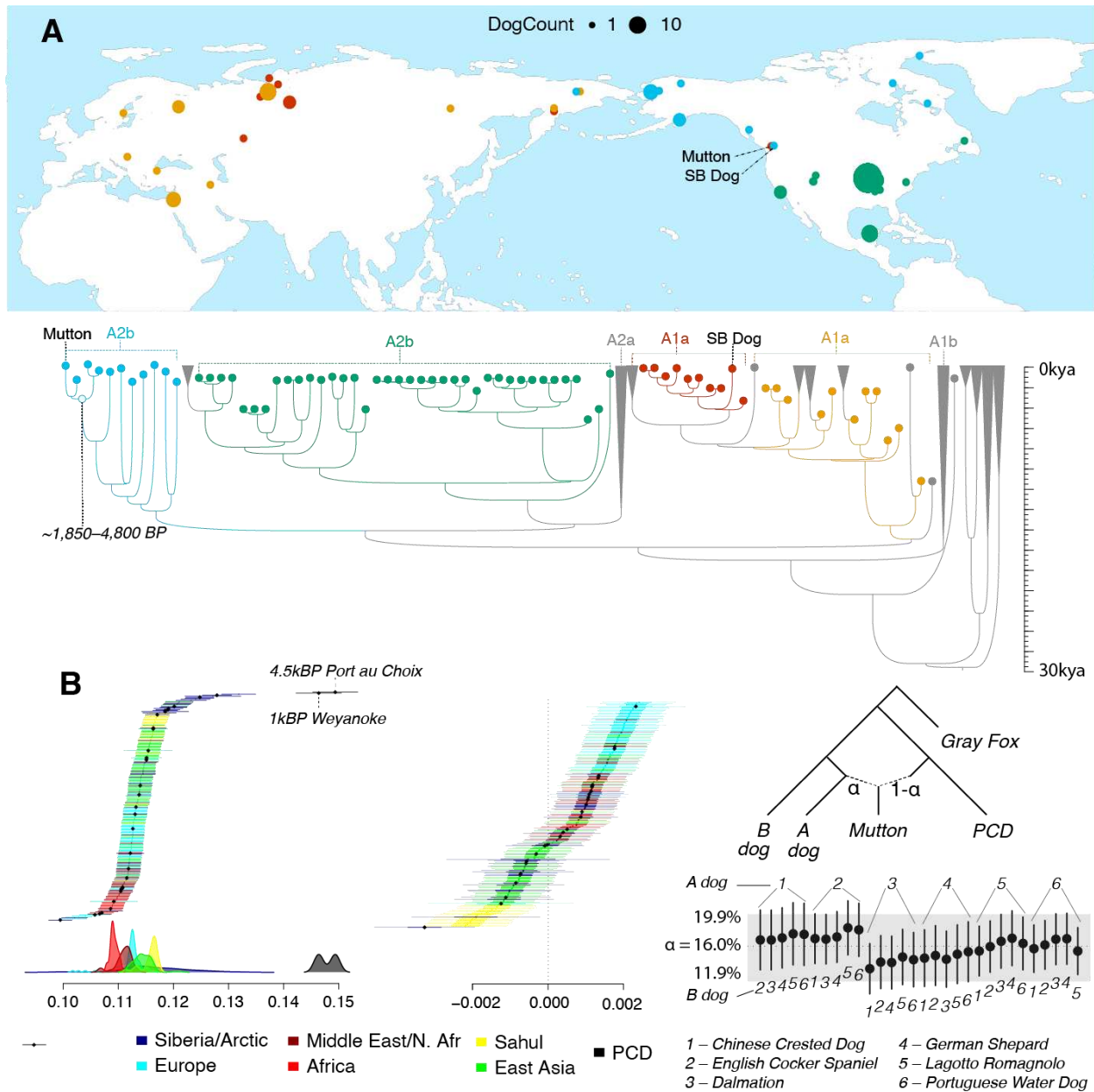
849 **Data availability:** Genomic sequencing data for Mutton, SB dog, the Port au Choix dog
850 (AL3194), and ALAS_015 are available for non-commercial use via NCBI SRA Project
851 Accession PRJNA1005336 and BioSample Accessions SAMN36985984-SAMN36985987. The
852 SRA Project Accession for the modern coyote from Wyoming is PRJNA734649. Stable isotope
853 data are available (49). All other public genomic data sources are provided in **DataS1**.

854



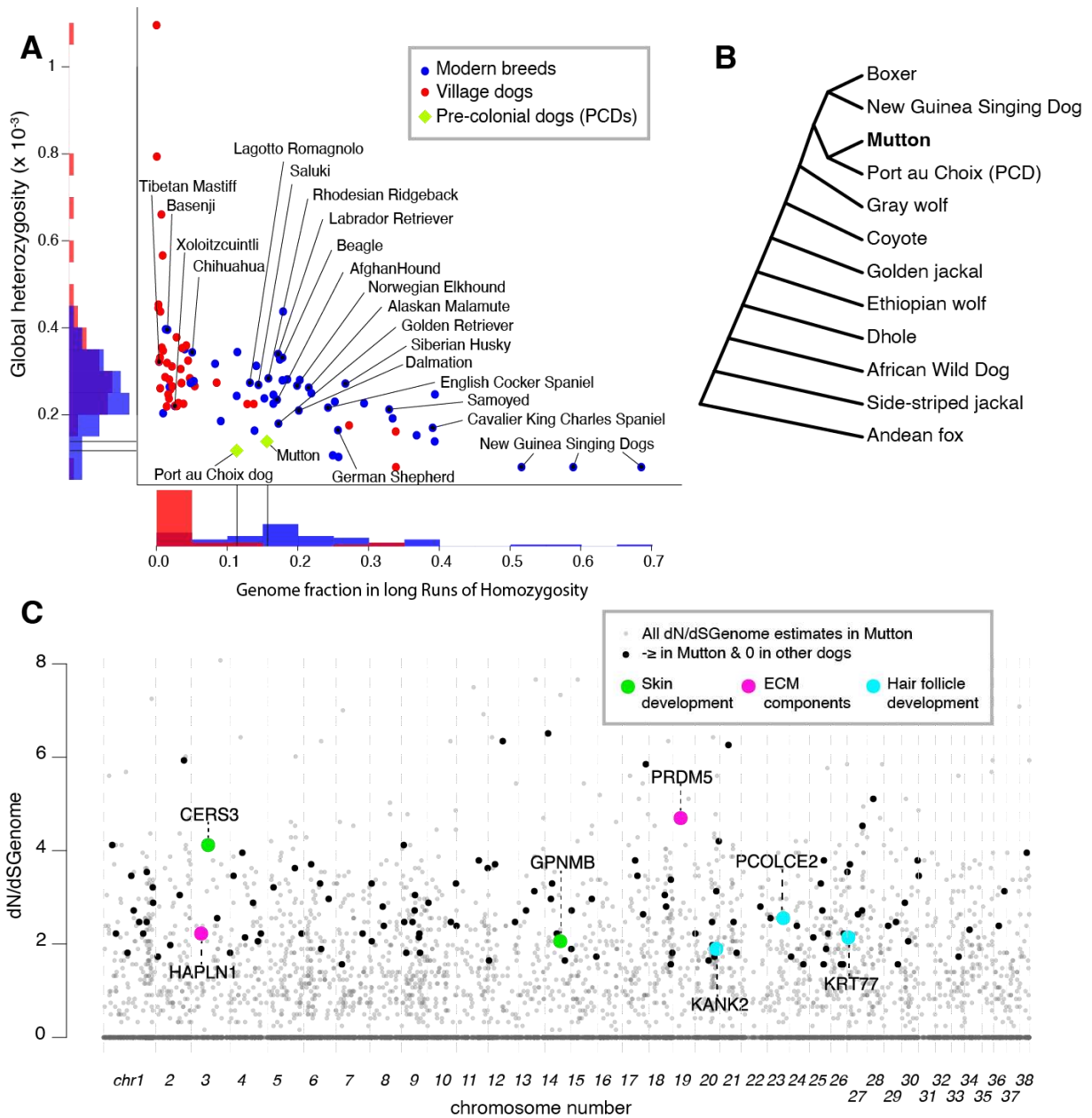
856

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



869

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



881

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

893 including one PCD (9). Several genes with high dN/dS_{genome} in Mutton (shown in gray) are
894 excluded as selection candidates because they carry at least one non-synonymous mutation in
895 other dogs. This approach is designed to conservatively highlight genes where selection is more
896 likely specific to Mutton's lineage rather than during dog domestication or in the common
897 ancestors of PCDs. Candidate genes discussed in text are indicated.

Supplementary Materials for

The History of Coast Salish ‘Woolly Dogs’ Revealed by Ancient Genomics and

Indigenous Knowledge

Audrey T. Lin^{1*}, Liz Hammond-Kaarremaa^{1,2*}, Hsiao-Lei Liu¹, Chris Stantis^{1,3}, Iain McKechnie⁴, Michael Pavel⁵, Susan sa'hLa mitSa Pavel^{5,6}, Senaqwila Senákw Wyss⁷, Debra qwasen Sparrow⁸, Karen Carr⁹, Sabhrina Gita Aninta¹⁰, Angela Perri^{11,12}, Jonathan Hartt¹³, Anders Bergström^{14,15}, Alberto Carmagnini¹⁶, Sophy Charlton^{17,18}, Love Dalén^{19,20}, Tatiana R. Feuerborn^{21,22}, Christine A.M. France²³, Shyam Gopalakrishnan²¹, Vaughan Grimes²⁴, Alex Harris²², Gwénaëlle Kavich²³, Benjamin N. Sacks^{25,26}, Mikkel-Holger S. Sinding²⁷, Pontus Skoglund¹⁴, David W.G. Stanton^{16,28}, Elaine A. Ostrander²², Greger Larson¹⁷, Chelsey G. Armstrong¹³, Laurent A.F. Frantz^{10,16}, Melissa T.R. Hawkins²⁹, Logan Kistler^{1*}

*Corresponding author. Email: linat@si.edu (A.T.L.);

liz.hammond-kaarremaa@viu.ca (L.H.-K.); kistlerl@si.edu (L.K.)

The PDF file includes:

Materials and Methods

Figs. S1 to S19

Tables 1 and 2

References

Other Supplementary Materials for this manuscript include the following:

DataS1 to S5

930 **I. Materials**

931

932 Archaeological/historic samples and context

933

934 *Wool dogs in some Coast Salish languages*

935 Halq'emelem: sqwemá:y (51)

936 Hul'q'umi'num': sqwumey'

937 Lushootseed: sqí aʔ or ske'-ha (52)

938 Lower Cowlitz: kimia (53)

939 Samish: sqʷəméy̓ (54)

940 SENĆOTEN (Saanich): sqʷəméy̓ (54)

941 Tuwaduq: QebeO or qaQebeO (55)

942 Twana: Sqwbaý (13)

943

944 *Documentary evidence of purported woolly dogs*

945 The most famous contemporary depiction of the Coast Salish weaving complex is a painting by
946 Paul Kane, “A Woman Weaving a Blanket” 912.1.93, **Fig. S1**), painted two years after Kane
947 visited the PNW and did a few sketches while visiting Southern Vancouver Island in 1847. His
948 original sketch of the dog is more detailed than the dog featured in the painting. Kane had
949 observed, “They have a peculiar breed of small dogs with long hair of a brownish black and a
950 clear white” (56).

951

952 There are several well-known 20th century photographs referring to purported woolly dogs. A
953 photograph dated 1912, taken by anthropologist John Douglas Leechman (1890-1980), in the
954 Suquamish Museum Archives, also in the Seattle Public Library, and in a 1929 book, features
955 Virginia Adams and her white spitz dog “Jumbo”, often attributed to be one of the last woolly
956 dogs (57, 58). However, Leechman wrote in a 1929 report that Mrs. Adams said, “Jumbo is like
957 them [wool dogs], but is a white man’s dog” (59).

958

959 Two photographs in the Ian McTaggart-Cowan Fond Collection at the University of Victoria
960 attributed to anthropologist Diamond Jenness (1886-1969), show a dog with floppy ears (60) in
961 one and another photo in which the ears are obscured (61). Jenness and William Henry Arnold
962 “Billy” Newcombe (1884-1960) corresponded with zoologist Glover Allen (1879-1942), the
963 author of the 1920 book *Dogs of the American Aborigines* (62) about these photographs. In a
964 letter dated Dec 28, 1935, Jenness quotes Glover Allen’s suggestion that erect ears are “a rather
965 characteristic trait of the Indian dogs so far as I have seen them” (63). This statement leaves open
966 the question if one or both Jenness photographs indeed are of wool dogs (63).

967

968 *Introduction to Mutton & the Semiahmoo Bay (SB) Dog:*

969 In the early 2000s, specimens of Mutton and the Semiahmoo Bay (SB) Dog were independently
970 rediscovered by historian Candace Wellman and Russel Barsh. As Barsh described (13), both
971 were researching specimens collected for the U.S. National Museum (the precursor to the
972 Smithsonian Institution) in the 1850s by American naturalist C.B.R. Kennerly and American
973 ethnologist George Gibbs. Gibbs and Kennerly were both part of the Northwest Boundary
974 Survey for the United States government.

975

976 *USNM 4762, “Mutton” – Chiloweyuck Depot*

977 All original tags read: “Indian Dog ‘Mutton’ Chiloweyuck Depot G. Gibbs” and the original
978 packing slip is written: “Mr G[ibb]’s dog ‘Mutton’ Chiloweyuck Indians.”

979
980 It is unclear which exact community and location Mutton was originally from. Between 1857-
981 1859, Kennerly spent time collecting natural history specimens in southwest British Columbia.
982 “Chiloweyuck Depot” was a forward camp (64, 65). Today, the town of Chilliwack is on the
983 Fraser River, about 75 km east of Vancouver, British Columbia, and is inhabited by the Stó:lō
984 Nation, a political amalgamation of eleven distinct but closely connected communities whose
985 collective territories extend westward along the Fraser River from the southern point of the
986 Fraser Canyon (Hope) and along the Fraser Valley as far as Langley, and including Chilliwack
987 (16, 66). Gibbs also spent time there with Kennerly, and Mutton may have come from a nearby
988 Coast Salish community, such as the Stó:lō (16, 66).

989
990 On August 19, 1859, Kennerly wrote to Spencer Baird, the first curator of the Smithsonian
991 Institution:

992 “We got another splendid goat skin which was sent to Camp Skagit where Mr. Gibbs
993 happened to be & he took charge of it; but most unfortunately his famous Indian dog
994 “Mutton” got at it and ate the head off. He sent it to me yesterday & when I opened the
995 bag & saw the injury I could almost have cried. Mutton was sheared a short time ago, &
996 as soon as his hair grows out we will make a specimen of him.” (67).

997
998 Mutton has a long, very dense double coat with a dense undercoat and long, fine guard hairs. His
999 coat is not pure white but has slightly yellow undertones. His rear and his tail are discolored a
1000 copperish red. According to Baird’s directions (circa 1848) for collecting Natural History
1001 specimens and objects, mammals “larger than a rat” should be skinned, and the interior of the
1002 animal specimens treated with arsenic powder or arsenic mixed with water and alcohol. If
1003 arsenic is not available, the skin should be salted down in casks. The skins should be completely
1004 dry before being packed away (68).

1005
1006 Mutton has small ears in the shape of equilateral triangles, and a very short, pointed muzzle with
1007 a small black nose. His lips and paws are black in color. His limbs are relatively large for his
1008 size, and his feet are large and wide, especially when compared to the SB Dog. Although woolly
1009 dogs had been reported to have perky upright ears and curled, spitz-like tails (13), it is
1010 impossible to tell if Mutton had these features, given the dry and stiff preservation condition (**fig.**
1011 **S2**). During specimen preparation, his skin was nailed flat to dry – iron nails were left embedded
1012 around the jaws and the upper right portion of his neck (**fig. S4**). Mutton was not left to dry
1013 completely before being folded and packed away – consequently, his head is permanently folded
1014 over onto his back (**fig. S4**). The carpals, phalanges, and paws had been left intact. The paws and
1015 toenails look healthy with no visible pathologies, and Mutton does not have double dew claws.

1016
1017 Dimensions of pelt:

1018 70-72 cm from nape of neck to base of tail

1019 Hind leg 19 cm from back edge of back pad to top of leg

1020 Tail length to bone tip 16-17 cm

1021 Hair beyond tip of bone 13 cm

1022

1023 Measurements of hair:
1024 Tail guard hairs 13 cm
1025 Center of back guard hair 10 cm
1026 Center of back under coat ~4 cm
1027 Flank guard hair ~8 cm
1028 Flank undercoat ~3.5 cm

1029
1030 Measurements from X-rays of Mutton’s carpals and phalanges (**fig. S4**) suggest that he may have
1031 been larger than archaeological woolly dogs (**fig. S7**). It is unknown whether Mutton’s size is
1032 typical for woolly dogs, if his admixed ancestry affected his size, or if zooarchaeological
1033 analyses have not yet captured the breadth of size variability in woolly dogs.

1034
1035 *USNM 3512, “Semiahmoo Bay village dog” (SB Dog) – Washington Territory*
1036 Tag says ““Indian dog” collected by A. Campbell and C. Kennerly’.

1037
1038 Between 1858 and 1859, Kennerly shipped two dog pelts and a skull to the U.S. National
1039 Museum. On March 5, 1858, he wrote to Spencer Baird from Semiahmoo Bay (located today
1040 near Blaine and the Lummi Indian Reservation in Washington State, USA):

1041 “... I had two nice skeletons of the otters, & packed them in a box with weights on the
1042 top, & intended to clean them in the morning when to my horror & chagrin the
1043 abominable Indian Dogs during the night got out the bones & gnawed them to pieces. In
1044 pay for this a beautiful skin of a large woolly Dog now hangs outside in a state of
1045 preparation for the Smithsonian Museum & as a warning to all others that may come
1046 around here without their owners with them.” (67).

1047
1048 Barsh explains that Kennerly likely mistook a “village dog” for a woolly dog in his letter to
1049 Baird (13). This skin was originally assigned field number 106 and is now cataloged USNM#
1050 3512. Barsh describes the SB Dog as a medium-sized dog with a relatively long, uniformly
1051 tawny coat, and the undercoat does not match the woolly dog material in the Smithsonian’s 19th
1052 century Coast Salish weavings in color or texture (13). The SB dog is larger in size than Mutton,
1053 and superficially resembles an Irish setter, with a long and silky tawny/ochre/reddish coat, a
1054 relatively long muzzle, and long, slender limbs (**fig. S3**). The dog’s feet are smaller and more
1055 delicate than Mutton’s. The carpals, phalanges, and paws had been left intact (**fig. S3**). The paws
1056 and toenails look healthy with no visible pathologies, and the dog does not have double dew
1057 claws.

1058
1059 Dimensions of pelt:
1060 155 cm long
1061 47 cm wide

1062
1063 *AL3194 - Port au Choix, Newfoundland*

1064 The Port au Choix archaeological site is located on the Port au Choix peninsula, projecting into
1065 the confluence of the Gulf of St. Lawrence and the Strait of Belle Isle, on Newfoundland’s
1066 northwest coast. The area includes several well-preserved sites, including a Maritime Archaic
1067 burial ground (Port au Choix-3) with over 100 preserved burials (Port au Choix-3, Locus II),
1068 which was excavated from 1967-1969 by Memorial University of Newfoundland (69, 70). The

1069 Maritime Archaic are Indigenous groups in the Atlantic Provinces, dating from approximately
1070 9,000-3,500 years ago, and the burial ground at Port au Choix is thought to date to approximately
1071 4,400-3,300 years ago (71). The remains of four Large or “Common Indian” size dogs were
1072 recovered from the Port au Choix-3 burial ground (reviewed in (72)). AL3194 is an older male,
1073 likely weighing between 45-55 pounds, and killed by a blow to the head. The dog was also
1074 buried with another dog in a multi-human burial (73). The direct radiocarbon dating of the dog is
1075 4,300-3,750 calibrated BP (UCIAMS159456). These dogs at Port au Choix were likely used as
1076 companions, hunting aids, or travois dogs (72, 73).

1077
1078 *ALAS_015 – Teshekpuk Lake, Alaska (Collection ID: 28769)*

1079 This sample (p2 premolar from the lower carnassial) (**fig. S6**) was provided by the University of
1080 Alaska Museum of the North, and sent to the Swedish Museum of Natural History, Stockholm
1081 for DNA extraction. Approximately 100 mg of bone powder was collected from the cementum
1082 layer, following previously described methods for permafrost bone and tooth samples (74). The
1083 sample was not directly radiocarbon dated, but mtDNA tip-dating suggests an age interval of 0-
1084 9,452 years BP (point estimate 3,763 years BP) (75).

1085
1086

1087 **II. Methods: X-Ray**

1088

1089 After taking tissue samples for DNA isolation, we x-rayed both Mutton and the SB dog pelts to
1090 get measurements of the bones in the hind feet and forepaws (**figs. S4-S5**). Because of the
1091 stiffness of Mutton’s pelt and the thickness of his hair, it was impossible to get measurements
1092 without using x-ray. The measurement for metatarsal IV of Mutton compared to archaeological
1093 “woolly” dogs are in **fig. S7**. We used a PXS5-927EA Microfocus X-Ray Source with a MARS-
1094 1717V Digital X-Ray Detector. The X-Ray detector has an imaging area of 3072 x 3072 pixels,
1095 with a pixel Size of 139 microns. The spatial resolution is 3.9l pm – 22l pm (Microfocus).

1096

1097 **III. Methods: Portable X-ray fluorescence spectroscopy (p-XRF)**

1098

1099 To determine what preservatives were present in the pelts of both Mutton and the SB dog, we
1100 performed p-XRF analysis. The instrument used was a Bruker Tracer III-SD (handheld p-XRF
1101 spectrometer) with a rhodium tube, no filter, no vacuum/helium flush, with an excitation voltage
1102 of 30 kV, a current of 30 μ A, and a 60s acquisition time. When taking the measurements, the
1103 spectrometer was held on a tripod within a couple of millimeters away from the sample surface.

1104

1105 The SB dog and Mutton’s pelt XRF analysis highlighted the presence of elements (mainly
1106 arsenic, but also chlorine, mercury, antimony, lead, etc.) consistent with previous preservation
1107 treatments such as but not limited to mercuric chloride, vermilion, arsenic soap, and orpiment.
1108 Amounts vary from one location to another possibly due to multiple applications and the way
1109 they were applied. The red stains noticeable on Mutton’s pelt contains high levels of mercury
1110 (**fig. S8**). Overlay of XRF spectra (**fig. S8**) of the two pelts on the fur side show a lot of
1111 similarities apart from the additional presence of antimony on Mutton’s pelt. Higher levels of
1112 sulfur on Mutton’s pelt could be due to the thicker fur and/or additional preservation treatments.
1113 Results are summarized in **Tables 1** and **2** below and as well as XRF spectra (**fig. S8**).

1114

1115
1116
1117
1118
1119
1120
1121
1122
1123
1124
1125
1126
1127
1128
1129
1130
1131
1132
1133
1134
1135
1136
1137
1138
1139
1140
1141
1142
1143
1144
1145
1146
1147
1148
1149
1150
1151
1152
1153
1154
1155
1156
1157
1158
1159
1160

IV. Methods: Genomic analyses

Sampling – NMNH

Destructive sampling permissions was obtained from the Division of Mammals, NMNH. To extract DNA from Mutton and the SB dog, samples were collected. Nitrile gloves were worn and sterile techniques were used including bleaching work surfaces and all tools prior to use. Two or three samples were taken from each specimen from different parts of the pelts:

Mutton:

1. Skin clip between hind limbs ~1 cm long in four pieces
2. Cartilage and adherent muscle from inside of right ear pinna, about 10 pieces largest ~5 mm x 8 mm
3. Skin from front right paw near metal tag w/pink string, ~1 cm in two pieces

SB Dog:

1. Skin surrounding lips and nose, ~10 pieces each about 2 mm x 4-5 mm
2. Front right paw had metacarpals exposed, sampled tissue between bones and also some skin clips ~8 pieces of tissue 1mm x 5 mm, skin 3 mm x 8 mm.

Approximately 50-100 mg of skin or tissue was collected for each subsample. Individual subsamples were placed in a 15 mL falcon tube, sealed, and transferred to the NMNH Ancient DNA laboratory.

DNA Extraction, Library Prep, Sequencing – NMNH – Mutton, SB Dog

All ancient DNA lab work on the Mutton and the SB Dog samples was undertaken in the ancient DNA facility at the Smithsonian National Museum of Natural History under accepted protocols for ancient DNA stringency (76). DNA was isolated from Mutton and SB Dog tissues using a standard protocol for degraded DNA from soft tissues. Briefly, tissue was agitated overnight at 55°C in a buffer containing CaCl₂, SDS, DTT, EDTA, and Proteinase K, according to (77). The following day, an additional equal volume of proteinase K was added to complete tissue digestion. Following (78), 13 volumes of Qiagen buffer PB was added to the lysate, the mixture was passed through Qiagen MinElute columns, washed twice with Qiagen buffer PE, and eluted in 70 µL of TE buffer with tween in two rounds of elution with 15 minutes incubation at 37°C between adding buffer and centrifuging to elute.

Considering the potential damage during previous preservation treatment, the libraries were built by single-stranded library preparation (79) with dual indexing (80). This construction not only targets double-stranded DNA, but also builds libraries from single-stranded DNA templates, which would potentially retain higher complexity compared to conventional double-strand DNA-based library construction. The concentration of adapters, reagents, and PCR cycles were decided based on double strand DNA input (7x PCR cycles for Mutton and 14x PCR cycles for the SB Dog). Libraries were sent to Admera Health and sequencing was performed using paired 150bp reads on an Illumina HiSeq X10 system. A table with a breakdown of the tissues and extracts that delivered the sequencing data can be found in **DataS1**.

1161 *DNA Extraction, Library Prep, Sequencing – CPH/London/Oxford – MU_NP50A_1; AL3194*
1162 *(Port au Choix dog)*

1163 A ~2x coverage sequence of the ancient domestic dog AL3194 was originally published (3) but
1164 has been re-sequenced at a higher coverage for this publication. DNA was extracted and
1165 processed from a pars petrosa in the ancient DNA laboratories at the Globe Institute, University
1166 of Copenhagen. Initially the bone was decontaminated for 10 min in a 7% hypochlorite solution.
1167 It was next digested in an EDTA, urea and proteinase K buffer as in (81), the digest was purified
1168 using phenol-chloroform (82). The original libraries that were previously published (3) were re-
1169 indexed as previously described (3). In short, Illumina libraries were built according to (83) and
1170 a six base-pair barcode joined to the adapter, creating an “internal adapter” resulting in double-
1171 barcoded libraries. The single-end, 80-bp libraries were then sequenced on an Illumina HiSeq
1172 2500 at the Danish National High-Throughput Sequencing Centre (Copenhagen) and on an
1173 Illumina NextSeq 500 at the Natural History Museum (London), respectively.

1174

1175 *DNA Extraction, Library Prep, Sequencing – SMNH – ALAS_015*

1176 ALAS_015 is a domestic dog excavated from Teshekpuk Lake, Alaska. The sample was
1177 processed and sequenced alongside multiple samples for a previous publication (75) at the
1178 Swedish Museum of Natural History in Stockholm, Sweden, using previously described methods
1179 for permafrost bone and tooth samples (74). In brief, this involved DNA extraction using the
1180 methodology previously described (74) and double-stranded Illumina library preparation as
1181 described (83) with dual unique indexes and the inclusion of USER enzyme. Between eight and
1182 ten separate PCR reactions with unique indexes were carried out for each sample to maximize
1183 library complexity. The libraries were across three Illumina NovaSeq 6000 lanes with an S4 100-
1184 bp paired-end set-up at SciLifeLab in Stockholm.

1185

1186 *Sampling, DNA Extraction, Library Prep, Sequencing – UC Davis – coys19 (modern coyote)*

1187 Coys19 (S19-1195) is a modern coyote (*Canis latrans*) from Goshen County, Wyoming. Frozen
1188 muscle tissue was sampled and DNA was extracted using the DNeasy 96 kit according to
1189 manufacturer’s instructions. The library was constructed and sequenced using a partial lane of an
1190 Illumina paired-end 150 base-pair Novaseq 6000 S4 through the DNA Technology Core,
1191 University of California, Davis Genome Center.

1192

1193 *DNA Extraction, Library Prep, Sequencing – NIH*

1194 WGS data was generated from samples collected with owners signed consent in accordance with
1195 standard protocols approved by the NHGRI IACUC committee, protocol #GFS-05-1. Saliva
1196 samples were owner collected and purified using the Performagene® (PG-100) saliva collection
1197 kit (DNA Genotek). Blood samples were collected by licensed veterinarians or veterinary
1198 technicians and genomic DNA was extracted by phenol-chloroform extraction. Purified DNA
1199 was resuspended in 10 mM Tris, 0.01 mM EDTA, pH 8.0 and stored at -80°C (84). Libraries
1200 were constructed using Illumina® DNA PCR-Free Prep Kit with 150 bp paired-end inserts.
1201 Libraries were sequenced at the NIH Intramural Sequencing Center (NISC) using the Illumina
1202 NovaSeq 6000 platform to a target coverage of 20X.

1203

1204 *Genome sequence data processing – NMNH*

1205 All sequence read data resulting from paired-end sequencing had adapter fragments removed,
1206 reads trimmed downstream of the first base with quality score <20, and forward and reverse

1207 reads merged with AdapterRemoval2 (85). We aligned the resulting merged and adaptor-
1208 trimmed sequences to the dog canFam3.1 genome using BWA *aln* with seed disabled (86).
1209 Duplicates were removed using samtools rmdup and reads were then filtered using samtools with
1210 a length of at least 30 base pairs and a mapping quality of at least 20. Reads were re-aligned
1211 around short indels using GATK version 3.8.0 (87). Post-mortem damage was quantified using
1212 mapDamage 2.0 (88), yielding very low deamination as expected with 19th century specimens
1213 (figs. S9-S10).

1214

1215 *Genome sequence data processing – CPH*

1216 All data generated data from the Port au Choix dog constituted single-end sequencing. The raw
1217 fastq files for the previously published sequences from the sample (NCBI: ERR2061050) and the
1218 newly generated sequences from the sample were trimmed of adapters with AdapterRemoval2
1219 (85). Subsequently the data was aligned to the canFam3.1 genome with using BWA *aln* but with
1220 seed disabled. PCR duplicates were then removed using MarkDuplicates by picard
1221 (<http://broadinstitute.github.io/picard>).

1222

1223 *Genome sequence data processing – SMNH*

1224 The genome processing was performed according to methods previously described (89). The
1225 adapters were trimmed and paired-end reads merged using SeqPrep v1.131 with default settings
1226 and a minor modification in the source code, allowing for the best quality scores of bases in the
1227 merged region (90). Sequencing reads were merged and mapped against the reference mtDNA
1228 genome for the domestic dog (canFam3.1) using BWA (86) *aln* with default settings and
1229 deactivated seeding (-l 16,500), allowing more substitutions (-n 0.01) and allowing up to two
1230 gaps (-o 2). BWA samse was used to generate alignments in SAM format. Resulting reads were
1231 processed in Samtools v1.933, converted to BAM format, sorted, and indexed. Duplicates were
1232 removed from the alignments using a custom python script to avoid inflation of length
1233 distribution for loci with deep coverage (86). Picard v1.141
1234 (<http://broadinstitute.github.io/picard>) was used to assign read group information including
1235 library, lane, and sample identity to each bam file. Reads were then re-aligned around indels
1236 using GATK v3.4.0 34 (87) and reads with mapping quality 30 were kept.

1237

1238 *Genome sequence data processing – NIH*

1239 Raw FASTQs were aligned to CanFam 3.1 using BWA mem (91) and sorted with Samtools.
1240 Base quality score recalibration and duplicate marking were applied to each sample (87, 92), and
1241 Haplotypcaller was used for variant discovery (93). Variant calling was performed using
1242 GATK4 best practices (92).

1243

1244 *Error estimation in ancient genomes*

1245 For the 40 ancient nuclear genomes analyzed here (DataS1), we used ANGSD (94) to estimate
1246 sequence error rates in aligned reads following the method described in (95). As expected,
1247 deamination drove higher observed mismatch rates in C->T and G->A mismatch types, which
1248 are mitigated as described below. We observed very low error rates across other mismatch types:
1249 mean error = $3.95 \cdot 10^{-4}$, range $1.32 \cdot 10^{-4}$ to $1.15 \cdot 10^{-3}$. The highest error rates by mismatch type
1250 were observed in C->A and the complementary G->T (mean $6.4 \cdot 10^{-4}$, range $1.4 \cdot 10^{-4}$ to $2.0 \cdot 10^{-3}$
1251 in both types). Overall, we observe low error rates in ancient genomes, and no outliers with

1252 problematic levels of sequencing error. Overall and per-mismatch error rates are given for all
1253 samples in **DataS1**.

1254

1255 *Damage mitigation and variant calling in ancient specimens*

1256 Because we used ancient dog datasets from a wide variety of studies with variable DNA
1257 preparation and data handling strategies, we adopted a conservative approach to variant calling in
1258 light of cytosine deamination in ancient DNA. We first used mapDamage (88) to independently
1259 model C->T and G->A misincorporation in both forward and reverse positions, accounting for
1260 all permutations of single- and double-stranded library preparation and adapter configurations.
1261 We then used the delta-S and lambda values inferred in all four contexts to rescale base quality
1262 scores using the phred scale to enforce observed uncertainty in possibly deaminated bases
1263 according to their position, and discarded reads with length <30bp. For heterozygosity and ROH
1264 estimation in Mutton and the Port au Choix dog (see below), we used a version of the bam
1265 alignment files without base rescaling, as ROHan includes its own integrated strategy for error
1266 mitigation and these analyses were based on transversions only. We then used samtools *mpileup*
1267 (<http://www.htslib.org/doc/samtools-mpileup.html>) to summarize all positional read support with
1268 base quality recalibration disabled, and with a minimum base quality of 20 after rescaling for
1269 damage. We finally created a genome-wide pseudohaploid fasta file—we selected a base at
1270 random for each position from an allele supported by ≥ 2 non-redundant reads, and with
1271 maximum coverage at the individual's .999 quantile, which was sufficient to avoid spiking
1272 coverage artifacts. Pseudohaploid base calls were extracted from these ancient dogs to match the
1273 modern reference panel using bedtools (96) and merged with modern reference panel using
1274 PLINK (97). SNP-based analyses (d-, outgroup-f3 and f4-ratio statistics) were restricted to 14.45
1275 million sites with minor allele frequency ≥ 0.01 and genotype missingness ≤ 0.5 .

1276

1277 *Bayesian molecular clock mitochondrial genome phylogeny*

1278 Bayesian phylogenetic analyses were computed using BEAST v2.6.3 (98). We used tip dating,
1279 the strict molecular clock and a lognormal distribution with a mean in real space of $1.0 \cdot 10^{-8}$, an
1280 upper bound of $1.0 \cdot 10^{-6}$ substitutions/site/year, and a lower bound of $1.0 \cdot 10^{-10}$
1281 substitutions/site/year (these bounds are part of a separate uniform prior and are not part of the
1282 lognormal distribution itself). HKY+ Γ substitution model was used with four rate categories for
1283 gamma-distributed rates across sites. An exponential prior for kappa and a lognormal prior was
1284 selected for the gamma shape prior, with default parameters. These priors were previously used
1285 in the BEAST v2 analyses on ancient and modern dog mitochondrial genomes (99). Mean date
1286 estimates for all the mtDNA sequences for the analysis were used because accounting for age
1287 uncertainty has negligible or minimal impacts on the resulting estimates in AL3194 (99).
1288 Constant coalescent population model was selected as the tree prior. Default settings were used
1289 for all other parameters. Posterior distributions of parameters were estimated by Markov chain
1290 Monte Carlo (MCMC) sampling. Samples were drawn every 10,000 steps over a total of at least
1291 1 billion steps. The first 15% of samples were discarded as burn-in. Sampling was considered
1292 sufficient when the effective sample size of each parameter exceeded 100. When required,
1293 additional MCMC analyses were run to achieve sufficient sampling. The trace files were
1294 assessed using Tracer (100) and samples from two independent runs were merged using
1295 LogCombiner (101).

1296

1297 *Ancestry analyses: outgroup-f3 statistics*

1298 To reinforce the PCD ancestry of Mutton and to explore whether Mutton has any European
1299 ancestry, we calculated outgroup- f_3 statistics using AdmixTools v7.0.2 (102). Outgroup- f_3
1300 statistics were calculated for Mutton, SB Dog, Port au Choix dog (AL3194) and Weyanoke dog
1301 (AL3223), comparing each respective dog to 229 other ancient and modern dogs, and GrayFox
1302 as the outgroup population (fig. S17). f_3 (GrayFox; Mutton, B) reveals that Mutton has the
1303 highest f_3 value and genetic similarity with other PCD dogs, specifically the 4,020 year old dog
1304 from Port au Choix, Newfoundland and the 1,000 year old dog from Weyanoke Old Town,
1305 Virginia, relative to the outgroup Gray Fox. The f_3 -(AL3194 PortauChoix, B, GrayFox) and f_3 -
1306 (AL3223 Weyanoke, B, GrayFox) analyses also reinforce the greatest similarity to the PCD
1307 dogs, followed by two ancient Arctic dogs from Alaska (ALAS_015) and Zhokov Island in the
1308 East Siberian Sea (CGG6) (fig. S17). As for the SB Dog, the outgroup- f_3 statistics have greater
1309 error bars because of lower coverage, but the dog shows greatest similarity to ancient dogs from
1310 Northwest and Arctic Siberia (TRF.05.17 and TRF.05.16) and Alaska (ALAS_015) (fig. S17).

1311

1312 *Ancestry analyses: D-statistics*

1313 We calculated D-statistics using AdmixTools v7.0.2 (102). D-statistics provide evidence for
1314 admixture and gene flow. The syntax is: (W, X, Y, Z), where W is GrayFox, X is a modern dog
1315 breed, Y is Port au Choix (AL3194) or Weyanoke dog (AL3223), and Z is Mutton. If the Z-score
1316 is positive, then the gene flow occurred between X and Z, assuming W is a true outgroup. If the
1317 Z-score is negative, then the gene flow occurred between X and Y. The results suggest evidence
1318 of recent European admixture in Mutton (Z-score > 3), with highest Z-scores coming from
1319 admixture sources of boxers, Portuguese water dogs, English Cocker Spaniels, and Lagotto
1320 Romagnolo breeds. Moreover, there is a positive correlation between D-statistic values and the
1321 Z-scores, of both Port au Choix dog and Weyanoke dog, relative to Mutton.

1322

1323 *Ancestry analyses: f_4 -ratio tests*

1324 To model the Mutton's ancestry, we used f_4 -ratio analysis with the following syntax: f_4 (A, Out;
1325 Mutton, AL3194 PortauChoix): f_4 (A, Out; B, AL3194 PortauChoix) where modern dog breeds
1326 are in the A and B placement, and AL3194 (Port au Choix dog) serves as a proxy for all ancient
1327 PCD dogs. We used modern dogs for the donor placements because ancient European dogs have
1328 too much admixture signal from ancient Arctic dogs, where it cannot be distinguished whether
1329 PCD dogs have Arctic ancestry or recent Arctic admixture (19, 103). Moreover, the modern dogs
1330 are a better proxy for what European settlers would have brought than ancient, multi-kya dogs.
1331 Six modern dog breeds selected are: Chinese Crested dog, English Cocker Spaniel, Dalmatian,
1332 German Shepherd, Lagotto Romagnolo, and Portuguese Water Dog (fig. S18). These dogs were
1333 chosen because when performing D-statistics, these modern dog breeds had the highest Z-score >
1334 3 when in the admixture source placement X (GrayFox, X, AL3194 PortauChoix, Mutton),
1335 indicating gene flow between X and Mutton (DataS1).

1336

1337 *Ancestry analyses: DATES*

1338 To estimate the timing of European admixture into Mutton's predominately PCD ancestry, we
1339 used DATES (104) to analyze the distribution of chromosomal ancestry blocks. We used
1340 assumed 1Mbp = 1cM and used default settings with jackknife estimation of standard error by
1341 reiteratively leaving out one chromosome. The PCD population was represented by the Port au
1342 Choix dog—the only high-coverage PCD genome currently available—and the European source
1343 population was represented by 27 individuals across the same six breeds used above in f_4 -ratio

1344 tests. In our case, the precision of this method is limited due to the scarcity of high-quality PCD
1345 source population data, and the likely recency of admixture. However, our estimate of admixture
1346 10.8 generations in the past \pm one standard error of 4.9 generations is broadly consistent with
1347 post-colonial admixture from one or more European dogs in Mutton's background.

1348
1349 *dN/dS selection analyses*

1350 An elevated ratio of non-synonymous (dN) to synonymous (dS) substitutions in coding regions
1351 can indicate selection on a basis of a single individual, and so offers insight into woolly dog
1352 selection pressures based on Mutton. Working within a single target genome with variable
1353 coverage among genes, we are very limited in our ability to identify selection via statistical
1354 dN/dS outliers. That is, we cannot rule out elevated dN/dS specific to Mutton's lineage in genes
1355 by chance through functionally neutral mutation and drift. Nonetheless, this strategy provides a
1356 starting point for interrogating plausible interaction between genetic loci and woolly dogs'
1357 unique phenotype, and yielded compelling links to several wool-, skin-, and hair-related loci
1358 from previous literature (see below).

1359
1360 The branching order used in dN/dS analysis to identify genes under selection in Mutton
1361 compared to other canids was used according to (50). We separately estimated dN/dS in Mutton
1362 and three other dogs—a boxer to represent European dogs, a New Guinea singing dog
1363 representing the Sahul lineage (19), and the Port au Choix dog (AL3194) representing PCDs. In
1364 each gene alignment, we hard-masked all sites there were missing in at least one genome so that
1365 results would not be biased by variable genomic coverage. We analyzed 11,112 genes for high
1366 dN/dS ratios, restricting analyses to genes with at least 100 codons called in all individuals.
1367 Following previous studies (105, 106), we accommodated high gene-level stochasticity in dS by
1368 first calculating a single genome-wide dS_{genome} value for each lineage, and then estimating
1369 $dN_{\text{gene}}/dS_{\text{genome}}$ at all loci independently. Following previous studies (105, 106), we restricted
1370 analysis to loci where local $dS \leq$ the mean plus 2 standard deviations of genome-wide dS, and
1371 considered genes with $dN/dS_{\text{genome}} > 1.5$ to be the strongest positive selection candidates.
1372 However, we further restricted our identification of selection candidates in Mutton to genes
1373 where $dN/dS_{\text{genome}} = 0$ in the other three dog lineages. This helps us assume that inferred
1374 selection most likely reflects woolly dogs' background, compared with selection on PCDs or
1375 even selection associated with dog domestication. This approach yielded 125 candidates for
1376 selection, as detailed further in the main text.

1377
1378 Following the methodology described in (107), we also calculated gene-level ratios of
1379 nonsynonymous to synonymous polymorphisms (pN/pS) in a sample of 95 modern dog genomes
1380 (**DataS1**). The goal of this analysis is to test whether our dN/dS_{genome} approach with a
1381 standardized denominator may enrich for genes that tend to tolerate polymorphism, leading to a
1382 biased set of selection candidates or likely false positives. After (107), we first examined the
1383 effects of all possible single mutations in the alignment on amino acid identity to quantify the
1384 number of potential synonymous and non-synonymous mutations under a uniform mutation
1385 model. Polymorphic sites between all pairs of samples were then assessed as synonymous or
1386 non-synonymous, so single values of observed/potential polymorphisms could be computed for
1387 both synonymous (pS) and non-synonymous (pN) mutations. The ratio of these values, pN/pS,
1388 can be treated as a proxy for tolerance of amino acid substitutions at the gene level. Comparison
1389 of pN/pS values between the 125 selection candidates and all other genes revealed no significant

1390 difference (Wilcoxon $p = 0.134$; Students t-test $p = 0.174$). On this basis, we observe no biasing
1391 effect on tolerance of polymorphism in selection candidates introduced by the dN/dS_{genome}
1392 approach.

1393
1394

1395 *Gene Ontology*

1396 We used the GO database within g:Profiler (108) to identify any functional category enrichment
1397 among the set of 125 genes within the woolly dog lineage dN/dS_{genome} values >1.5 , *Canis lupus*
1398 *familiaris* as the query organism, and all known genes for the statistical domain scope. We found
1399 significant enrichment following the g:SCS algorithm (108) of multiple test corrections, which is
1400 calculated based on a P-value of 0.05. This algorithm operates under the assumption that genes
1401 associated to a given GO term are implicitly associated to all the general parents of this term,
1402 since GO consists of hierarchically related general and specific terms. Genes were significantly
1403 enriched in 5 GO: Molecular Function categories (calcium-dependent phospholipid binding,
1404 molecular function, transferase activity, catalytic activity, ion binding); 3 GO: Biological Process
1405 categories (regulation of cellular processes, multicellular organismal process,
1406 biological_process); 3 GO: Cellular Component categories (cellular_component, cellular
1407 anatomical entity, membrane); and 2 KEGG categories (KEGG root term, Metabolic pathways);
1408 and 1 Human Phenotype Ontology category (Autosomal recessive inheritance) (**fig. S11**). Many
1409 individual genes were found within multiple GO functional categories (**DataS2**).

1410

1411 We used the hypergeometric test in analyzing gene enrichment in GO categories using GOfuncR
1412 (109). The hypergeometric test compares positively selected genes in Mutton's lineage compared
1413 to "background" genes that are conserved in all canids. GO annotations and gene coordinates
1414 were used using the *Homo sapiens* annotation package. Correction for multiple testing and test
1415 interdependency was computer using family-wise error rates (FWER), which are based on
1416 random permutations (1000 random datasets) of the gene-associated variables. The results for
1417 from both tests are in **DataS2**, "res_Hypergeometric" tab. Categories involving cell signaling
1418 and cell metabolism are generally enriched (overrepresented raw $p < 0.01$). No GO category
1419 containing the terms "hair cycle" or "skin" are overrepresented (raw $p > 0.01$).

1420

1421 *Annotation of candidate genes under selection*

1422 To home in more specifically on the gene candidates that may contribute to the woolly dog
1423 phenotype, we used DAVID for initial functional annotation, and additionally manually
1424 annotated the candidate genes through a literature search. The provided gene list comprising 125
1425 genes is in **DataS3** (110, 111), "Annotations" and "geneList" tabs.

1426 Within these 125 genes, through manual curation we identified 28 genes as candidates involved
1427 in the hair growth cycle of woolly dogs (**fig. S12**). We determined that manual curation was
1428 necessary due to the limitations of GO category databases in adequately identifying up-to-date
1429 gene associations published in the literature. Our assessment is reflected through querying
1430 several genes on Gene Ontology Resource (<http://geneontology.org/>) which in the main
1431 manuscript we have identified as related to woolly hair and skin – *KANK2*, *PCOLCE2*, *KRT77*,
1432 *GPNMB*, *CERS3*, and *ANXA4*. The results are listed in **DataS2**, "AmiGO2" tab.

1433 Key words related to hair and skin do not appear in any of the GO descriptions for *KANK2*,
1434 *PCOLCE2*, *GPNMB*, and *ANXA4*. Key words for skin do appear in the GO descriptions for
1435 *KRT77* (“structural constituent of skin epidermis” and “keratinization”) and *CERS3*
1436 (“cornification” and “keratinocyte differentiation”) however all GO terms are dominated by
1437 more non-specific molecular, cellular, and structural processes (e.g. “protein binding”,
1438 “cytoplasm”, “cell adhesion”, “DNA binding”, “calcium ion binding”).

1439 In addition, we have queried Gene Ontology Resource and MGI database
1440 (<http://www.informatics.jax.org>) 15 hair-related genes (keywords “hair cycle” or “woolly hair”)
1441 in found in the literature. The genes queried are: *AHNAK2* (25), *KRT8* (25), *FLG* (25), *PRSS8*
1442 (25), *P2RY5/LPAR5* (112, 113), *LSS* (114), *C3ORF52/BC016579* (115), *LIPH* (116), *LHX2*
1443 (117), *FGF1* (118), *FGF2* (118), *FGF5* (118), *DKK2* (118), *NOCTUM* (118), and *AXIN2* (119).
1444 With the exception of *FLG* with associated GO categories of “cornified envelope”, “epidermis
1445 development”, “epidermal cell differentiation”, “establishment of skin barrier”, among other
1446 terms, and *KRT8*’s association with “keratin filament”, most of the GO terms are dominated by
1447 non-specific molecular, cellular, and structural processes (e.g. “intermediate filament”,
1448 “cytosol”, “protein binding”, “centrosome”) or more specific processes not clearly related to skin
1449 or hair (e.g. “ubiquitin protein ligase binding”, “negative regulation of canonical Wnt signaling
1450 pathway”, “beta-catenin binding”, and “positive regulation of sodium ion transmembrane
1451 transport”). These results are listed in **DataS2**, “LitHairGenes_AmiGO2”.

1452 Finally, additional query results in **DataS3**, “MGI_GO_MP_Databases” tab demonstrate that
1453 panels of hand-picked hair genes from the literature do not flag these categories as enriched. We
1454 queried the 125 genes under positive selection against several GO and mammalian phenotype
1455 lists in the MGI database. These 125 genes under positive selection had each been queried
1456 against the genes within 3 GO terms (SkinDevelopment GO:004358, 340 genes;
1457 HairCycleProcess GO:0022405, 121 genes; HairCycle GO:0042633, 142 genes) and 2 MP
1458 (Mammalian Phenotype) terms (IntegumentPhenotype MP:0010771, 6,991 genotypes; abnormal
1459 coat/ hair morphology MP:0000367, 3,260 genotypes). SkinDevelopment GO:004358 contained
1460 3 genes out of 125, IntegumentPhenotype MP:0010771 contained 10 genes out of 125, and
1461 abnormal coat/ hair morphology MP:0000367 contained 2 genes out of 125. HairCycleProcess
1462 GO:0022405 and HairCycle GO:0042633 contained 0 genes out of the 125 queried. By going by
1463 this assessment, only 14 individual genes are associated with skin development, mammalian
1464 integument (which includes hair), and abnormal coat/hair morphology.

1465 The hair follicle is a dynamic environment that is continuously remodeled (120). Hair is formed
1466 by rapid cell division and differentiation of stem cells that form keratinocytes that migrate,
1467 flatten, and die, forming dead, keratinized cells (121). The final hair product exposed on the
1468 surface of the skin is composed entirely of keratin (dead cells). Hair follicle growth is regulated
1469 in a cyclical manner, with stages of rapid growth and elongation of the hair shaft and periods of
1470 quiescence and regression. In the hair growth cycle, hair follicles undergo anagen, where an
1471 entire hair shaft is grown from tip to root; catagen, where hair stops growing and the hair follicle
1472 undergoes apoptosis-driven regression; telogen, a rest phase where the follicle prepares its stem
1473 cells to receive a signal for the next growth phase; and exogen, where the entire shaft is released.
1474 The events of the hair growth cycle is complex and involves tight regulation of stem cell
1475 quiescence and activation, cell proliferation, differentiation, and apoptosis (122).

1476
1477 Several genes with potential links to the unique woolly hair phenotype include *KANK2*, *KRT77*,
1478 and *GPNMB* which are discussed in the main text. As discussed in the main text, Mutton
1479 contains a mutation in the *KANK2* gene immediately adjacent to a causal variant in humans
1480 linked to a congenital “woolly” hair phenotype (32). This substitution observed in Mutton is
1481 unique among the canids. In pairwise comparisons, the *KANK2* amino acid sequence is 89.5%
1482 conserved between dogs and humans, 99.4% conserved on average between all canids used in
1483 the dN/dS analysis, and 99.85% conserved on average the dogs used for pN/pS analysis.

1484
1485 We also identified twenty genes associated with cell replication and proliferation, or cytoskeletal
1486 components: *ARL14EP* (ADP ribosylation factor like GTPase 14 effector protein) (123), *CDIPT*
1487 (CDP-diacylglycerol--inositol 3-phosphatidyltransferase) (RefSeq, Nov 2013), *CENPQ*
1488 (centromere protein Q) (124), *CFAP36* (cilia and flagella associated protein 36) (125), *CGRRF1*
1489 (cell growth regulator with ring finger domain 1) (126), *DNAAF3* (dynein axonemal assembly
1490 factor 3) (RefSeq, May 2012), *FOSL1* (FOS like 1, AP-1 transcription factor subunit) (RefSeq,
1491 July 2012), *KATNAL1* (katanin catalytic subunit A1 like 1) (Alliance of Genome Resources, Apr
1492 2022), *KCTD21* (potassium channel tetramerization domain containing 21) (127), *KLHL22*
1493 (potassium channel tetramerization domain containing 21) (Alliance of Genome Resources, Apr
1494 2022), *LOC100682940* (putative speedy protein E7) (128), *PNMA2* (PNMA family member 2)
1495 (Alliance of Genome Resources, Apr 2022), *QSOX1* (quiescin sulfhydryl oxidase 1) (RefSeq, Jul
1496 2008), *RANBP10* (RAN binding protein 10) (RefSeq, Feb 2016), *SART1* (spliceosome associated
1497 factor 1 recruiter of U4/U6.U5 tri-snRNP) (RefSeq, July 2008), *TJP3* (tight junction protein 3)
1498 (RefSeq, May2022), *TOB1* (TOB1 transducer of ERBB2, 1) (RefSeq, Aug 2011), *TRIT1* (tRNA
1499 isopentenyltransferase 1) (RefSeq, Aug 2015), *TTC23L* (tetratricopeptide repeat domain 23 like)
1500 (Alliance of Genome Resources, Apr 2022), *WEE1* (WEE1 G2 checkpoint kinase) (129).

1501
1502 The extracellular matrix (ECM) is a large network of proteins and other molecules that
1503 encompasses and gives structure to cells and tissues, allowing for cell communication, growth,
1504 movement, proliferation, adhesion, differentiation, and apoptosis. The ECM also provides an
1505 important role in tissue damage repair (130). During anagen development, the ECM increases
1506 rapidly and decreases when the transition to full anagen is complete (120). We identified three
1507 genes linked to the formation of extracellular matrix (ECM) components: *PRDM5* (PR/SET
1508 domain 5) and *HAPLN1* (hyaluronan and proteoglycan link protein 1) which both encode for
1509 genes involved in ECM development and maintenance (28), and *PCOLCE2* (procollagen C-
1510 endopeptidase enhancer 2) which enables collagen and heparin binding activity, and is
1511 downregulated in growing hair follicles (131).

1512
1513 The development of the hair follicle requires the presence of blood vessels that nourish the
1514 growing follicle, supporting the delivery of nutrients and the removal of waste (121). We
1515 identified three genes associated with the vascular system and the mediation of blood pressure,
1516 including *GPR180* (G-protein coupled receptor 180) (132), *PLVAP* (plasmalemma vesicle
1517 associated protein) (133), and *AGT* (angiotensinogen) (134).

1518
1519 Finally, we identified three genes associated with the skin or epidermis: *GPNMB* (described in
1520 the main text), *ANXA4* (annexin 4) (135, 136), and *CERS3* (ceramide synthase 3), which is

1521 responsible for creating a protective barrier from the environment in the epidermis. *CERS3*
1522 mutations cause autosomal recessive congenital ichthyosis in humans (27).

1523

1524 *Variants associated with coat color*

1525 We checked Mutton's genotype of 15 different variants associated with coat color and texture
1526 variation in dogs, summarized in **Data S4**. Although these sites are covered by a small number of
1527 reads (up to 7) manual examination of curated read alignments at these sites provides evidence of
1528 at least one allele in most cases.

1529

1530 FGF5 genotypes

1531 There are 5 known polymorphisms in the *FGF5* gene (fibroblast growth factor 5) that are linked
1532 to the long hair phenotype in dogs (33). The c.284G>T mutation (p.Cys95Phe) is found in most
1533 long-haired dogs, although it does not account for long hair in all dogs. Long hair in certain dogs
1534 appears to be expressed in a heterogeneous fashion, with multiple alleles present, even within the
1535 single *FGF5* gene. For example, the g.8193T>A and c.559_560dupGG mutations have been
1536 identified in Afghan hounds (33). We investigated whether Mutton's long hair phenotype can be
1537 attributed to any of the *FGF5* genotypes conferring long hair. We found that Mutton has only the
1538 c.284G>T genotype, with 3 reads covering the position chr32:4509366. Disregarding sequence
1539 error and reference bias, 3 consistent reads confer 87.5% chance of a homozygote. All long-hair-
1540 associated mutations in dogs follow a recessive mode of inheritance (33), so it is reasonable to
1541 conclude that Mutton is homozygous for the c.284G>T mutation. However, for other mutations
1542 in *FGF5*, Mutton is the wild type (**DataS4**). If there are any other polymorphic alleles
1543 responsible for Mutton's long hair, they lie elsewhere.

1544

1545 MC1R genotypes

1546 There are multiple polymorphisms in the *MC1R* (melanocortin 1 receptor) gene, a G-protein-
1547 coupled receptor primarily located on the surface of melanocytes. When *MC1R* signaling is
1548 induced, melanocytes produce brown-black eumelanin. Mutations in *MC1R* are linked to coat
1549 color variation in domestic and wild animals including brindling, spotting, and a melanistic mask
1550 or grizzle in dogs (reviewed in (137)). The c.916C>T mutation (p.Arg306ter) is associated with a
1551 light coat color in Australian Cattle dogs and Siberian huskies. Mutton has the wild type
1552 genotype (c.916C) with 3 reads covering the position of chr5:63694334, therefore most likely a
1553 homozygote, disregarding sequence error and reference bias. Mutton is also wild type for
1554 the 63695679C>G mutation which is associated with a light coat color in Australian cattle dogs
1555 (138), with 2 reads covering the position of chr5:63695679. A c.816_817delICT mutation in
1556 chr5:63694432 confers a light coat color in Alaskan and Siberian huskies (138), and there was no
1557 coverage in that position in Mutton. Dark spots (e.g. "grizzle" or "domino" patterns in Salukis
1558 and Afghan hounds) are linked to a c.233G>T (p.Gly78Val) mutation (34, 138), and Mutton
1559 appears to be wild type at the position of chr5: 63695017 with 1 read. c.790G>A (p.Val264Met)
1560 is linked to a "black mask" coloring in Leonbergers and Malinois (138, 139), and Mutton
1561 appears to be homozygous wild type for that allele, with 3 reads spanning the position chr5:
1562 63694460.

1563

1564 KRT71 genotype

1565 Curly or wire hair coats in the Airedale Terrier, Bichon Frise, Kuvasz, Portuguese Water dog,
1566 Poodle, Welsh Terrier, and Wire Fox Terrier breeds are associated with a c.451 C>T

1567 (p.Arg151Trp) mutation in the *KRT71* (keratin 71) gene (34). Mutton carries the wild type allele
1568 in 2 recovered reads spanning the position at chr27: 2539354.

1569

1570 MFSD12 genotypes

1571 A light coat color is also associated with a c.166 C>T mutation in the *MFSD12* (major facilitator
1572 superfamily domain containing 12) gene in Shepherds, Poodles, Cotons de Tulear, Bichon Frise
1573 dog breeds (140). Unfortunately, we could not genotype Mutton for this variant, as there was no
1574 coverage at that position.

1575

1576 MLPH genotypes

1577 Light or diluted coat color is associated with three recessively inherited variants in the *MLPH*
1578 (melanophilin) gene. A c.-22G > A mutation is found in beagles and Doberman pinschers (141),
1579 and Mutton is wild type at this allele, with 3 reads spanning chr25:48121642. The c.705G > C
1580 mutation is found in chow chows (142) and Mutton is wild type at this allele with 7 reads
1581 spanning chr25:48150787. Finally, a c.669C > T mutation is found in many dog breeds (143) and
1582 Mutton is wild type at this allele with 3 reads spanning chr25:48150751.

1583

1584 *Heterozygosity analysis*

1585 We used ROHan (144) to estimate autosomal genomic heterozygosity in Mutton, the Port au
1586 Choix dog, and 89 comparative breeds and village dogs, providing a mappability mask generated
1587 with SNPable (<https://lh3lh3.users.sourceforge.net/snpable.shtml>), and using a --rohmu value of
1588 $4 \cdot 10^{-5}$. In estimating genome-wide heterozygosity, ROHan used the Watterson's theta formula
1589 where segregating sites is four times the mutation rate multiplied by the effective population size
1590 (144). By assuming that the effective population size (N_e) of contemporary grey wolf
1591 populations is $\sim 1,000$ (145), an inbred population will have one order of magnitude lower level
1592 of segregating sites and mutation rate of $1 \cdot 10^{-8}$. Rather than using the damage-rescaled read
1593 alignments described above, we used bam2prof in the ROHan package to accommodate the low
1594 level of deamination in Mutton's genome, and we restricted the analysis to transversions only in
1595 all samples to accommodate the higher deamination in the Port au Choix dog at low coverage.
1596 Because of Mutton's relatively low coverage (estimated at 3.44x in ROHan), we tested for
1597 possible depression of heterozygosity estimates by randomly downsampling all other dogs to the
1598 same level ten times independently and repeating the analysis. Downsampled runs were highly
1599 consistent between replicates for each dog (average standard deviation of replicates $1.4 \cdot 10^{-6}$) and
1600 drove a mean 11.2% decrease in heterozygosity estimates. We show the downsampled estimates
1601 in **Fig. 3C**, and full results are provided in **DataS1 – ROHanDataset**.

1602

1603 Although ROHan is validated for 5-8x coverage for accurately inferring ROH in samples with
1604 variable deamination (144), it can be used to estimate global heterozygosity in samples with
1605 lower coverage, especially with low deamination and/or when analyzing transversions only.
1606 ROHan was tested on three levels of post-mortem deamination: 1) high in the "ATP2" sample, 2)
1607 medium in "LaBrana", and 3) low in "Ust-'Ishim" (144). These samples have their highest
1608 deamination rate at least 0.3, 0.15, and 0.06 respectively. Mutton's low damage rate assessed by
1609 ROHan (0.05) is akin to a low damage sample tested in ROHan, Ust-'Ishim, with deamination
1610 rate 0.06 (144). The estimates of genome-wide heterozygosity using Watterson's theta under a
1611 lower coverage (3x) are only slightly lower than the true simulated Watterson's theta estimate
1612 (144). Because we use transversions only and compare between samples downsampled to a

1613 standardized coverage level, this approach provides a robust estimate of the relative global
1614 heterozygosity among samples.

1615

1616 *Runs of Homozygosity (ROH)*

1617 Because ROHan has not been validated for accurate ROH inference at Mutton's coverage level
1618 (144) we adapted a low-coverage method for conservative inference of long ROH in ancient
1619 genomes (24). Briefly, we used the *.hEst.gz output from the downsampled ROHan runs
1620 described above as an estimate of heterozygosity in 500kbp non-overlapping windows to
1621 standardize across variable coverage levels, using transversions only. Windows with
1622 heterozygosity below $4 \cdot 10^{-5}$ and at least 50,000 valid sites were considered candidates for runs of
1623 homozygosity. We inferred long runs of homozygosity (at least 2.5Mbp) where at least five
1624 consecutive windows met these criteria. The total genomic fraction in long ROH reported in **Fig.**
1625 **3A** and **DataS1** was computed as the number of total windows in long ROH on this basis divided
1626 by the total number of windows with the minimum number of valid sites analyzed. This
1627 approach, which has been previously validated for ancient goats (24) focuses on providing a
1628 conservative and standardized estimate of long ROH for comparison between individuals.

1629

1630 **VII. Methods: Stable isotope analysis**

1631 Destructive sampling permissions was obtained from the Division of Mammals, NMNH. For
1632 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from bone collagen, samples of ~150 mg were taken from cortical bone, excluding
1633 bones with pathological changes on the principle that changes in the metabolic pathways of the
1634 tissue as a result of disease may affect the isotopic values (146). As both dogs had been
1635 processed into pelts by the explorers, few bones remained for sampling. Sample options for
1636 cortical bone were limited, however bones in the paws had been left attached to the pelts and
1637 were therefore utilized for stable isotope analysis. For both Mutton and the SB dog, a second
1638 metacarpal were sampled with a rotary saw. The bone samples were abraded with a Dremel
1639 attachment to remove soft tissue, and then prepared following a modified Longin method (147,
1640 148). Samples were demineralized in 0.6 M HCl at 4°C for 24 h increments until reaction ceased,
1641 rinsed five times in ultra-pure 18.2MΩ H₂O, then reacted in 0.03 M HCl at 95°C for 18 h to
1642 separate soluble and insoluble phases of collagen. The resulting supernatant was lyophilized to
1643 isolate purified collagen extract.

1644

1645 For $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from hair keratin, hair was cut as close to the skin as possible. Both dogs
1646 appeared to be double-coated, and since these two types of hairs grow at different rates, the
1647 undercoat hairs were discarded. The topcoat hairs were cut into incremental 1 cm sections to
1648 create a time sequence. In the 19th century, collectors would treat animals with arsenic before
1649 shipping (149), and the Smithsonian Institution would use arsenic trioxide (As₂O₃) or arsenous
1650 acid and mercury as mercuric chloride (HgCl₂) as pesticide controls (150). To remove these
1651 applied treatments, the hairs were soaked in a chloroform/methanol solution for 4 hr. Hair was
1652 then rinsed five times in ultra-pure 18.2MΩ H₂O and oven-dried at 40°C overnight.
1653 All samples were analyzed on a Thermo Delta V Advantage mass spectrometer at the
1654 Smithsonian Museum Conservation Institute Stable Isotope Mass Spectrometry Laboratory.
1655 Collagen and keratin were weighed into tin capsules, combusted in an Elementar Isotope Cube,
1656 and the resulting N₂ and CO₂ gases measured for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. Data is presented in the
1657 standard delta notation where $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] * 1000$; where X is the heavy isotope of
1658 interest (¹⁵N or ¹³C), R is the isotope ratio (¹⁵N/¹⁴N or ¹³C/¹²C), the standard is atmospheric air

1659 (N) or V-PDB (C), and units are permil (‰). All runs include a set of reference materials for
1660 every 10-12 samples. Reference materials include Costech Acetanilide (calibrated to USGS40
1661 [L-glutamic acid] and USGS41 [L-glutamic acid]) and USGS66 (glycine). Reproducibility of
1662 reference materials and in-house keratin and collagen standards is $\leq 0.2\%$ (1σ) for both $\delta^{13}\text{C}$ and
1663 $\delta^{15}\text{N}$; error associated with all sample data points are reported as $\pm 0.2\%$.
1664 Although diagenetic alteration is expected to be minimal as these dogs were kept in controlled
1665 museum environments, previously determined criteria for well-preserved collagen were
1666 nonetheless required for statistical analysis. For bone, a C:N ratio of 2.8–3.6, %C values between
1667 15–47% by weight and %N values between 5–17% by weight (151, 152). For hair keratin, C:N
1668 ratios should be between 3.0–3.8 (153).

1670 Results

1671 All samples fell within the quality markers of good preservation as listed above; all samples were
1672 included in subsequent analyses. To accommodate the known offset between hair keratin and
1673 bone collagen stable isotope values, values of 1.41 ‰ and 0.86 ‰ were added to the hair keratin
1674 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively (153). While these values have been derived from humans
1675 which may have slightly different metabolic routing compared to dogs, these conversions have
1676 been used in previous zooarchaeological analyses of dog isotope values (154) and show good
1677 agreement in fur and bone from the same dogs when this correction was applied. **DataS5**
1678 contains the bone collagen and converted hair keratin $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (**fig. S14**). The
1679 original values can be accessed online (49). The SB dog displays relatively restricted nitrogen
1680 and carbon stable isotopes values across all hair and bone samples, averaging $16.3\% \pm 0.5$ (mean
1681 \pm SD) $\delta^{15}\text{N}$ and $-13.9\% \pm 0.5$ $\delta^{13}\text{C}$. The hair and bone samples from Mutton have lower $\delta^{15}\text{N}$
1682 values than the SB dog, as well as lower $\delta^{13}\text{C}$ values, at an average of $10.6\% \pm 0.5$ $\delta^{15}\text{N}$ and -
1683 $17.0\% \pm 1.4$ $\delta^{13}\text{C}$, respectively. The $\delta^{13}\text{C}$ values obtained from Mutton's hair and bone samples
1684 also have greater variability, ranging from -18.7 to -15.3‰ compared to SB Dog's -14.5 to -
1685 13.2‰. Though sample sizes are small, one-way MANOVA shows significant differences
1686 between SB Dog and Mutton's stable isotope values, Pillais' Trace = 0.98, $F(2, 10) = 207.59$, p
1687 < 0.001 (**fig. S13**).

1688
1689 Several $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data from archaeological dogs within the Pacific Northwest have
1690 previously been published (mid-Holocene), along with late-Holocene deer from the broad region,
1691 which are included here as a herbivore reference (**fig. S14A**) (22). While the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
1692 values of the SB Dog align with other archaeological dogs from the broad coastal region,
1693 Mutton's bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are notably distinct from coastal dogs, displaying a
1694 lower $\delta^{15}\text{N}$ value and a lower $\delta^{13}\text{C}$. As Mutton lived alongside George Gibbs during the
1695 boundary survey of the Canadian-US Border (49th parallel), he and Mutton spent the bulk of their
1696 time away from the coast in the elevated mountainous terrain of the Cascade mountains and the
1697 Columbia Plateau. This appears to have influenced Mutton's isotopic signature both for bone
1698 collagen and hair, as these are consistent with a diet largely lacking in marine foods. However,
1699 Mutton's $\delta^{15}\text{N}$ value collagen appears to be more than a trophic level higher than the terrestrial
1700 deer and are plausibly in alignment with existing isotope data from anadromous sockeye and
1701 potamodromous kokanee salmon (*Oncorhynchus nerka*) in the Similkameen and Columbia River
1702 systems (155). Active or recent harvest of these fish is periodically described in Gibbs' journal
1703 by Interior Salish peoples. As he was simultaneously engaged in collecting efforts for the
1704 Smithsonian, Gibbs additionally describes regular skinning and specimen preparation activities

1705 for a wide range of birds and mammals that would have been actively observed by Mutton and
1706 may have been fed entrails.

1707
1708 The SB Dog remained in its original community where its high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values indicate a
1709 human-provided diet heavy in marine protein (156–158). Incremental hair samples provide a
1710 relative time sequence of diet shortly before death and show a consistent diet that is very similar
1711 to the bone collagen, the latter capturing a lifetime average of isotope values (**fig. S14B**). This
1712 pattern suggests the SB Dog received a consistent diet its entire life, which was likely near the
1713 coast given the high level of marine input. It also suggests little to no seasonal shift in diet.

1714
1715 Mutton's $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values indicate a more complicated dietary history reflecting significant
1716 travels while in Gibbs' care and a change from the native diet. Generally, Muttons' $\delta^{13}\text{C}$ and
1717 $\delta^{15}\text{N}$ values are lower than the SB Dog. The sequential hair $\delta^{13}\text{C}$ values show a clear shift to
1718 more negative values later in life, reflecting C3 plant input or animal protein that consumed more
1719 C3 plants (**fig. S14C**) (159, 160). This is likely due to Gibbs movement inland (**fig. S15**) and
1720 reliance on more terrestrial grain sources for direct consumption or foddering animals which
1721 were fed to Mutton (i.e. pigs, cows, etc.). Historic records of Gibbs' voyage do record a reduced
1722 availability of corn and sugarcane (C4), and increased reliance on hunted game such as grouse
1723 (more C3-reliant) as their journey progressed (149). The sequential hair $\delta^{15}\text{N}$ values show
1724 consistency and similarity to bone collagen values. Without the appropriate baselines and
1725 potential dietary source values to conduct a robust isotopic dietary model, we can say only
1726 generally that $\delta^{15}\text{N}$ pattern suggests two potential scenarios for Mutton: 1) a more omnivorous
1727 lower protein diet throughout life, or 2) a rapid bone turnover rate during adolescence that
1728 captures a significant portion of Mutton's time with Gibbs and the concurrent diet changes as
1729 they travelled inland and relied on more terrestrial sources. The first possibility suggests that the
1730 SB Dog and Mutton, a woolly dog, would have been fed different diets as part of their native
1731 community. The second possibility of rapid bone turnover is perhaps better supported. Mutton's
1732 bone collagen values match with the lower range of hair values observed in proximal hair
1733 sections which grew just before death, suggesting the bone collagen also reflects relatively recent
1734 dietary input. Considering Mutton's young age at death, this scenario is plausible given that bone
1735 turnover is more rapid in young mammals of most species.

1736 1737 **VIII. Methods: Forensic reconstruction of Mutton**

1738 Because Mutton's cranium is not available for study, an archaeological cranial specimen of a
1739 male woolly dog was used (**fig. S19A**). The crania, estimated to be ~1,000 years old, was
1740 originally excavated from the Little Qualicum River archaeological site on the east coast of
1741 Vancouver Island, Qualicum First Nation territory (4, 162). The 3D scan was made at the
1742 University of Victoria Library, used with permission from Iain McKechnie, and is hosted on
1743 Sketchfab
1744 (<https://sketchfab.com/3d-models/coast-salish-wool-dog-skull-aa9f839bfdb84347b5da41c8b76e0263>). The scan was then simplified and all but the surface
1745 geometry was removed, leaving a clean shell (**fig. S19B**). 3D models from scans of canine teeth
1746 were downloaded from a collection loaded on Sketchfab by Ludwig-Maximilians University
1747 Munich, (**fig. S19C**). The teeth were simplified and sized to fit the skull then mirrored to fit the
1748 other side. Because of the wear on the teeth, we believe the dog that the teeth came from was
1749 probably quite a bit older than Mutton. The canine teeth were based generally on those of an
1750

1751 Eskimo dog. We then downloaded a dog skull and jaw posted on Sketchfab by Nature Labs,
1752 Rhode Island School of Design. The jaw was separated and modified slightly to fit the skull, (**fig.**
1753 **S19D**). Comparing the archaeological woolly dog skull with an American Eskimo Dog skull and
1754 a Pomeranian skull, we decided that Mutton didn't have the toy features of a proportionally
1755 shorter maxilla, domed cranium and larger orbits, but had the Mesocephalic skull of a standard
1756 American Eskimo Dog or spitz-type dog.

1757
1758 Once the skull, jaw and teeth were assembled, a set of bars representing measurements taken
1759 from Mutton's pelt was used as proportion reference for Mutton's spine, ears, tail, and legs (**fig.**
1760 **S19E**). The pelt is distorted by age and the preservation process, so the measurements were not
1761 exact representations. More weight was given to the measurements for the metatarsals, ears, and
1762 the spine, which likely matched Mutton's proportions in life most closely. A dog without fur was
1763 modeled based on the skull, proportions, historical photographs of woolly dogs and written
1764 descriptions of Mutton **fig. S19E**.

1765
1766 After review and recommended modifications of the initial hairless model, hair was added to the
1767 Mutton reconstruction using Blender 3.5's (<https://www.blender.org/download/releases/3-5/>)
1768 hair curve system and hair particle system. Additional small components were created using
1769 Zbrush 2022 fibermesh system (<https://www.maxon.net/en/zbrush>).

1770 Several haired versions of Mutton were reviewed for color, proportions and an appropriate sense
1771 of cleanliness and grooming. The final version of Mutton was rendered in Blender 3.5 and
1772 displayed alongside several modern spitz-type breeds (American Eskimo Dog, Alaskan
1773 Malamute, Samoyed, Alaskan Husky, Finnish Spitz) besides him for size comparison, (**Fig.**
1774 **1C**).

1775 1776 1777 **IX. Methods: Ethnographic Interviews**

1778 1779 *Pre-interview preparation*

1780 With any project involving Indigenous People it is important to work with community
1781 knowledge holders in a respectful manner and with good heart. Before commencing the project,
1782 for both the ethnographic component and the scientific analysis, it was decided to first consult
1783 with a representative of the Coast Salish Nations who, in the past, had kept and used the dogs for
1784 their wool. The woolly dog specimen at the Smithsonian NMNH known as "Mutton" was
1785 acquired in 1858-59 near modern day Chilliwack, BC. Although Mutton could have come from
1786 elsewhere, it was decided to first discuss the project with the Honorable Steven Point OBC,
1787 Chancellor of University of British Columbia, former Lieutenant Governor of British Columbia
1788 and Grand Chief of the Stó:lō Nation, and his wife Dr. Gwen Point, Chancellor of the University
1789 of the Fraser Valley. The Stó:lō Nation is a political amalgamation of eleven Stó:lō communities
1790 whose collective territories extend westward along the Fraser River from the southern point of
1791 the Fraser Canyon (Hope) and along the Fraser Valley as far as Langley and including
1792 Chilliwack.

1793
1794 With Honorable Steven Point's and Dr. Gwen Point's approval to proceed with our research, an
1795 advisory committee was then formed. Coast Salish communities are numerous and cover a large
1796 geographic area both north and south of the USA/Canada border, with territories extending

1797 approximately 150 miles both east to west and north to south. This was too large of an area, with
1798 too many communities to create an advisory committee with representatives from each
1799 community, so a “community of interest” committee was created consisting of Coast Salish
1800 people, living both north and south of the border, having publicly expressed an interest in the
1801 Coast Salish Woolly dog: Coast Salish weavers, Knowledge Keepers, Elders, and young people.
1802 Interview protocols were approved by the Smithsonian Institution Human Subjects Protocol #
1803 HS220007, and by the Smithsonian Information and Privacy Office as well as the Research
1804 Ethics Board at Vancouver Island University, Nanaimo (#101410), and followed the practice of
1805 free and prior informed consent.

1806
1807 The advisory committee helped create, edit, and then review the recruitment documents, the
1808 interview agenda, and the questions (around three dozen) for the interviews.

1809
1810 *Community interviews and ethnographic documents*

1811 We conducted semi-structured interviews focused on woolly dogs in 2022. Interviewees were
1812 selected for their knowledge of woolly dogs, their memories, and their concerns on how the
1813 history surrounding the dogs has been presented. A total of seven interviews were conducted.
1814 Interview questions revolved around understanding the following subjects: the role and value of
1815 dogs in society, description of woolly dogs, the use of dog wool in blankets, diet and husbandry
1816 of dogs, companionship of dogs, colonial practices/policies that impacted woolly dogs,
1817 processing, spinning and weaving the dog wool, and thoughts on how the knowledge gathered
1818 from this project should be shared.

1819
1820 All interview recordings, transcriptions and typed field notes were given to the participants for
1821 review and approval. The advisory committee also reviewed the summary of the interviews.

1822
1823 *Interviewees:*

1824 Xweliqwiya Rena Point Bolton, Stó:lō, Elder, 95 years old, Interviewed February 7th, 2022
1825 Danielle Morsette, Master weaver, Suquamish and Shxwhá:y, 34 years old, Interviewed
1826 February 4th, 2022
1827 Susan sa'hLa mitSa Pavel, Skokomish, 53 years old, Interviewed February 15th, 2022
1828 Michael Pavel, Skokomish Elder, 63 years old, Interviewed March 4th, 2022
1829 Debra qwasen Sparrow, Master weaver, Musqueam, Interviewed April 15th, 2022
1830 Senaqwila Wyss, Sk̓wx̓wú7mesh Úxwumixw (Squamish Nation), Interviewed April 7th, 2022
1831 Eliot Kwulasultun White-Hill, Snuneymuxw, 26 years old, Interviewed June 20th, 2022

1832
1833 *Emerging themes*

1834 Interviewees’ responses were grouped into themes and key representative quotes for each theme
1835 were selected.

1836
1837 The roles of dogs in society

1838 Different roles of dogs were identified, such as wool dogs, hunting dogs, or village dogs, and the
1839 dogs were treated differently depending on their role.

1840 “You can see that there’s different uses, different breeds, different types of jobs
1841 and roles that the dogs were in in the community.”

1842 (Senaqwila Wyss, Sk̓wx̓wú7mesh Úxwumixw (Squamish Nation))

1843 *“My grandfather [Ed Sparrow born in 1898] told me that every village had wool*
1844 *dogs, that they were like gold because of course, their fibers were mixed with the*
1845 *mountain goat and then rove [made into a roving for spinning] and spun.”*

1846 (Debra qwasen Sparrow, Master weaver, Musqueam)
1847

1848 Description of the woolly dog

1849 Interviewees were able to recall who had told them what the woolly dog looked like. Common
1850 descriptions included a medium to small dog, white in color, with a curled tail. The curved tail is
1851 reflected in the design work on the Skokomish basketry.

1852 *“Uncle did talk about the dog in that way that it was always an upturned tail.”*

1853 (Susan sa’hLa mitSa Pavel, Skokomish)
1854

1855 The use of dog wool in blankets

1856 Some interviewees were able to describe the processing, spinning and use in blankets. In one
1857 case, the interviewee’s grandfather could recall the names of the women who were making the
1858 yarn and the blanket.

1859 *“And out of it [an origin story] they were given the gift of the wool, and they were*
1860 *able to teach the women how to gather the wool, how to process the wool, how to*
1861 *spin the wool, how to weave with the wool, over time.”*

1862 (Michael Pavel, Elder, Skokomish)

1863 *“I [Ed Sparrow born in 1898] watched my grandmother Spahqia, Thelekwutun’s*
1864 *wife Selisya all working on these blankets. They were all talking all the time then.’*
1865 *He said when they were done, after he watched them, he said ‘they baked that clay*
1866 *that I remember them baking the clay and I remember them, beating it to powder*
1867 *on the table and then mixing it all together’.... I said did you see it? He said ‘Yes’,*
1868 *he seen it. In the back shed. And all the old ladies were together, my*
1869 *grandmother’s Spahqia, Selisya, Thelekwutun’s wife, and he named another one*
1870 *in our language, and he said ‘they worked together. They were working on [a] big*
1871 *piece you know, not like yours. You guys have small pieces. Big pieces.’ he said.*
1872 *‘And big balls of wool they’d already worked on.’ I said ‘Oh, what was the wool*
1873 *made out [of] and he said mountain goat, and those dogs that they kept in pens.’*
1874 *he said.*

1875 (Debra qwasen Sparrow, Master weaver, Musqueam)
1876

1877 Diet of woolly dogs

1878 While the main source of food for the dogs was salmon, some communities fed them elk, others
1879 whatever humans ate. A common thread behind the food was that the food was chosen to
1880 enhance the wool of the dog.

1881 *“My teacher, Virginia Adams. She had mentioned that they were only fed like*
1882 *salmon and just really like such a good diet to keep their coats nice and fluffy.”*

1883 (Danielle Morsette, Master weaver, Suquamish and Shxwhá:y Stó:lō)
1884

1885 Woolly dog husbandry

1886 It was clear that the dogs had to be separated from the regular village dogs to avoid
1887 interbreeding. Some communities used islands to keep them apart, others mentioned pens, and
1888 others said the wool dogs were kept inside and the village or hunting dogs were not allowed in. It
1889 is not known if the dogs were always separated or only when the females were in heat.

1890 “We didn't particularly have an island. We had areas that we dedicated to
1891 care for [dogs] and we would have in this case, pens or places to keep
1892 them separate, so they didn't run away and we could keep them
1893 protected.” (Michael Pavel, Elder, Skokomish)
1894

1895 Woolly dog ownership

1896 A couple of interviewees mentioned that only high-status people kept dogs as it took resources to
1897 keep them.

1898 “Because only the wealthy women of status had them and they weren't allowed to
1899 breed them unless you got permission. Th'etsimiya probably had 10–15 dogs,
1900 little dogs.”

1901 (Xweliqwiya Rena Point Bolton, Elder, Stó:lō, 95 years old)
1902

1903 *There's a village site in Snuneymuxw along the river right near the Cedar Bridge,*
1904 *that translates to two wolves, and it's a story of two supernatural wolves who lived*
1905 *there and walked along the far side of the river. It just seems to me like it's very*
1906 *distinct. With my understanding of our art and the representation of beings in our*
1907 *art, it seems to be a distinct difference between the use of the wool dog or a dog*
1908 *and the wolf, and they carry different meanings within their imagery and the*
1909 *symbolism of it. The wolf would be a helper to people, and so when it's used in*
1910 *their art, that's generally what it means to represent is to honor that connection*
1911 *that they have with the wolf which is a different representation than when people*
1912 *represent the wool dog. I think that the wool dog is more of a representation of*
1913 *wealth for our community to show that we come from high-ranking people. That's*
1914 *kind of an interesting distinction to me when I think about it.*

1915 (Eliot White-Hill, Kwulasultun, Artist, Snuneymuxw)
1916

1917 Colonial policies/practices, cultural genocide, and the demise of the woolly dog

1918 Most accounts of the disappearance of the dog attribute it to the simple explanation of an influx
1919 of cheap Hudson Bay Company blankets, but the situation is much more complicated. First,
1920 smallpox and other diseases decimated the human populations. The dogs could not survive
1921 without caretakers and food. Then colonial policies contributed greatly to the interruption of the
1922 culture and the weaving complex.

1923 “They were told they couldn't do their cultural things. There was the police, the
1924 Indian agent and the priests. The dogs were not allowed. She had to get rid of the
1925 dogs. And so the family never ever saw them. [...]

1926 *No, they were not allowed to keep them because that showed signs of authority*
1927 *and high breeding. The women that had dogs were highborn women and as long*
1928 *as the dogs were there, this reminded the people of who were highborn. And so*
1929 *the dogs were, I don't know what they did to them. They were just either told to get*
1930 *rid of them or they took them... After they took the dogs and what could they do?*
1931 *They only had the mutts that were left around. The ones that they kept for the wool*
1932 *were no longer allowed. And they were the ones that had the long under wool.*
1933 *We were not allowed, our people were not allowed to spin like on the*
1934 *shxwqáqelets, what do you call it? Yeah, the spindle, yeah spindle whorl. Yeah,*
1935 *they could spin on a European one but not on the shxwqáqelets. And they couldn't*

1936 *use their looms, and they would take them out and burn them or they would give*
1937 *them to museums or collectors or whatever, depending on how they were made.*
1938 *I guess you know they were nice to look at and they probably just keep them or*
1939 *sell them, but they confiscated everything and if they caught you making baskets*
1940 *or digging roots or, you know, preparing anything like that, then you would get*
1941 *fined. And if you couldn't pay the fine you went to jail.*
1942 *So everything came to a halt, everything. The singing, the dancing, the drumming.*
1943 *We were not allowed to have any of those things. The blankets were not allowed*
1944 *and the feather garments that were made for dancing. They were not allowed;*
1945 *they would collect them all and burn them, or they would sell them or whatever,*
1946 *you know. The generation that was there when the Europeans came and colonized*
1947 *us, that's where it ended and there was just a few people who sort of went*
1948 *underground. And my grandmother and my mother were two of them.”*
1949 (Xweliqwiya Rena Point Bolton, elder, Stó:lō, 95 years old)
1950

1951 *“Second, the people who were maintaining the dogs also confronted the racism*
1952 *and discrimination of the non-natives, particularly Indian agents, and they killed*
1953 *the dogs. They didn't want the dog producing wool when those would maintain*
1954 *traditional practices that would prevent their ‘civilization’”.*
1955 (Michael Pavel, Elder, Skokomish)
1956

1957 *“I don't remember specifically anything about how the Salish wool dog went*
1958 *extinct in Snuneymuxw, and it's always kind of been really interesting to me too,*
1959 *because I know how significant they were to us and I understand their place*
1960 *within our socio-economic practices.*
1961 *A lot of what I see from looking online says ‘Oh well, it became more convenient*
1962 *to use sheep's wool’ so that these dogs just went extinct. Well, that's one way of*
1963 *looking at it, but I don't think that really would have been the case, because these*
1964 *are really cherished dogs to us and that it would have been more convenient or*
1965 *whatever, that doesn't really align with my understanding of our practices and our*
1966 *culture.*
1967 *I think about when if we're preparing cedar boughs for ceremony, it's really*
1968 *critical that you harvest them before sunrise. You could harvest them anytime*
1969 *around the day, but to us, it's imperative that you do this work in a really specific*
1970 *way, and the protocol is followed. So even if it's less convenient, that's where the*
1971 *energy to it comes from for us.*
1972 *And so with using the dog wool or the mountain goat wool, as opposed to sheep's*
1973 *wool that could have been purchased in bulk or whatever, I just think that it*
1974 *doesn't really make sense to me, and I think that there's probably more to what*
1975 *was going on, whether it was all of the impacts of colonization and I also think*
1976 *that in this case specifically, with the wool dogs, the impacts of the smallpox*
1977 *epidemic probably can't be understated. Where in many communities only one in*
1978 *10 people survived, and I can only imagine that it's difficult enough to keep your*
1979 *loved ones alive never mind that the animals that you keep and maintain. That*
1980 *probably had a devastating impact on the wool dog population as well. And then*
1981 *the ongoing erasure and suppression of our culture.”*
1982 (Eliot White-Hill, Kwulasultun, Artist, Snuneymuxw)

1983
1984
1985
1986
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
2019
2020
2021
2022
2023

Thoughts on knowledge dissemination of the research

While many interviewees mentioned a publication, there was agreement that audio and video or a documentary would be useful and sharing with communities through presentations or via Zoom.

“Part of me says an informational book or little videos like sharing the videos that we had and that kind of stuff. Part of me is like I want it to be detailed records, but it's also how do you make it accessible and palatable for people?”

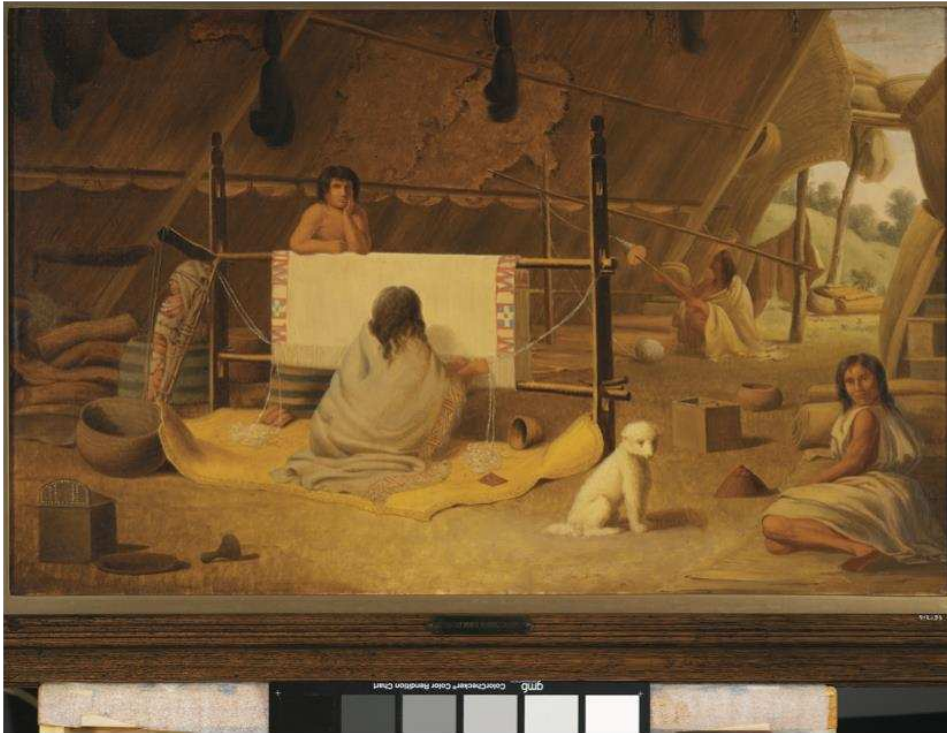
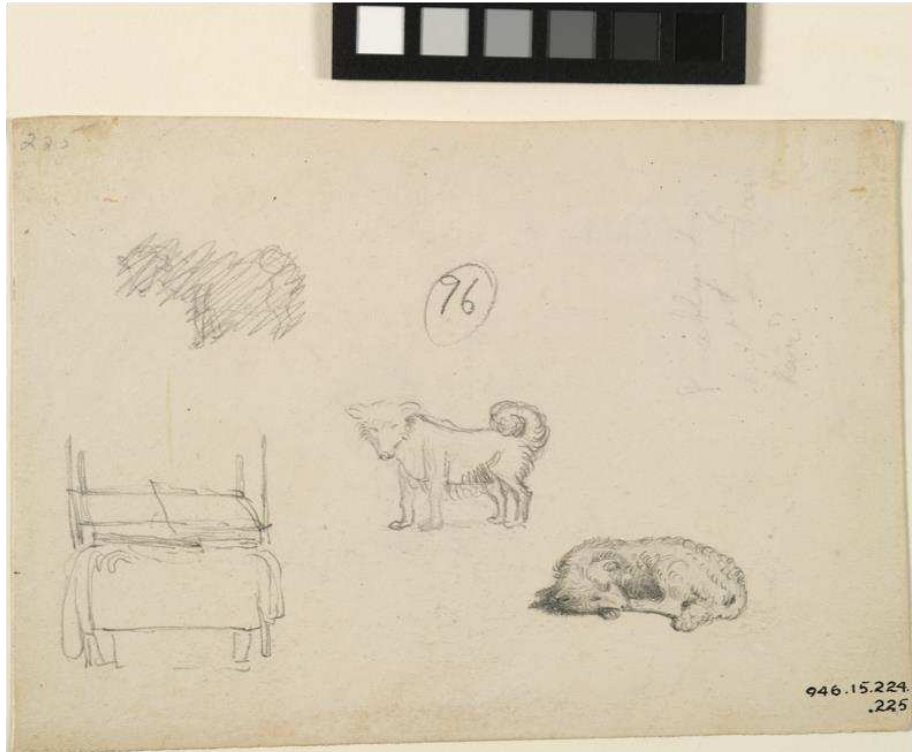
(Senaqwila Wyss, Sk̓w̓wú7mesh Úxwumixw (Squamish Nation))

“Part of the whole narrative around the woolly dog that I find really interesting is that it starts to unravel, in a way, people's understanding of us as a hunter gatherer society, and that our society was so much more complex than what people took, take it for in general. Hunter gatherer is kind of this dominating narrative that just blankets everything and takes away the complexity and the nuances and our relationship with the woolly dogs clearly shows that there is more complexity to this, and that our relationship with the camas patches and the clam beds and the way that we tended the land and tended the forests, these all show the systems that were in place that are far more complex than what people take for granted about Coast Salish culture. And so it's so much about combating this simplistic aspect or the simplistic lens with which our culture is looked at and showing that actually things are much more complex than many may think.”

(Eliot White-Hill, Kwulasultun, Artist, Snuneymuxw)

“Create a publication, so that people can read it, and they can share in that knowledge as well. And maybe it needs to be presented. But it also needs to be given back to the community. And how should that be given back to the community? Well-printed matter, videotapes, audiotapes, or in-person. That's how it should be presented. Let's have a dinner where the people can stand up and provide their own oratory about what all this means, let them express themselves. Let that be an ongoing record. But the thing that's most important out of this is to realize that that wool dog created a gift to produce and to make something to create something to bring something alive. Let's do that. Let's bring that back to life. We want to make sure to realize that the wool dog is still very much a part of our life. And it's generating a conversation, and interaction and outcomes that is the embodiment of goodness.”

(Michael Pavel, Elder, Skokomish)



2024
2025
2026
2027
2028

Fig. S1. Sketches and painting featuring woolly dogs by Paul Kane (1849-1856). *Top panel: "Studies of Wool Dogs and Interior Furnishing" (946.15.225), April-June 1847. Bottom panel: "A Woman Weaving a Blanket" (912.1.93), 1849-1856. Courtesy of ROM (Royal Ontario Museum), Toronto, Canada. ©ROM*



2029
2030
2031

Fig. S2. Mutton Pelt (USNM 4762). *Photograph.*

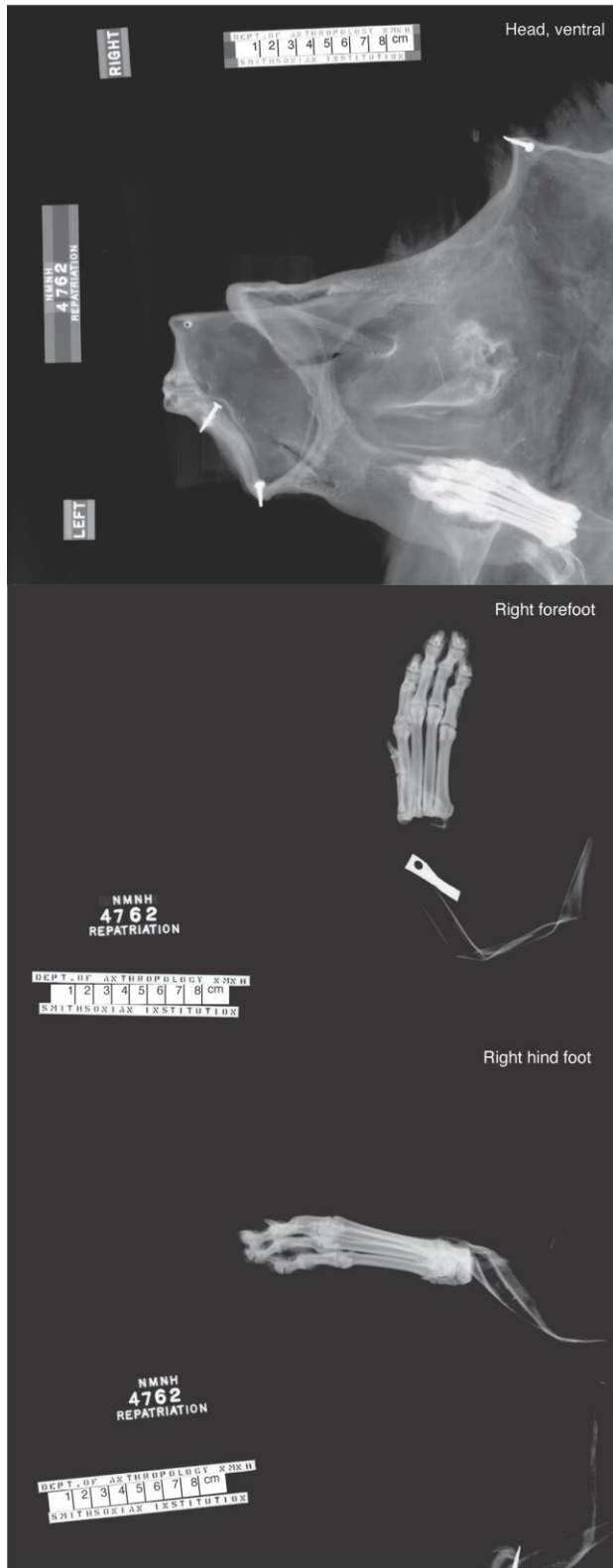


2032
2033
2034

S3. SB Dog Pelt (USNM 3512). *Photograph.*

Fig.

Mutton



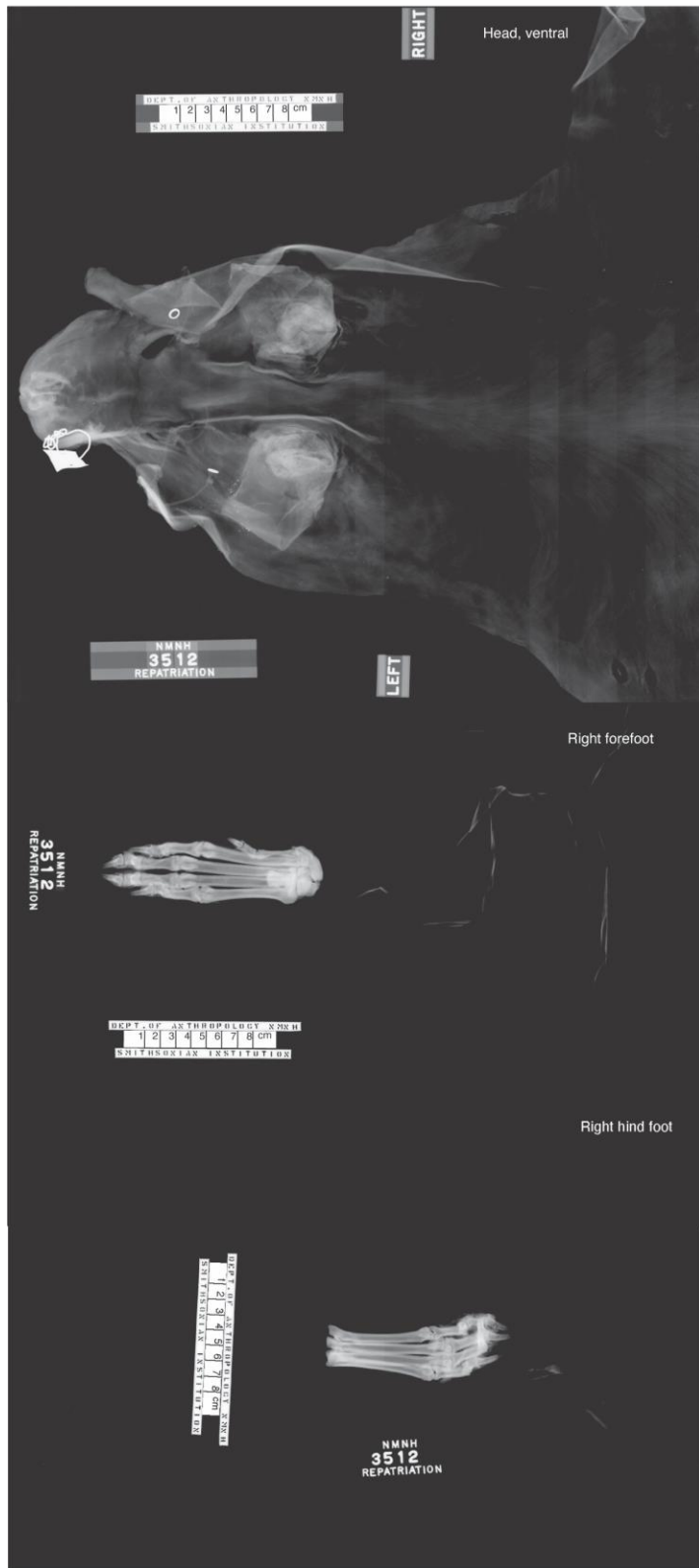
Head, ventral

Right forefoot

Right hind foot

2035
2036
2037
2038

Fig. S4. X-ray of Mutton. *Top - head, ventral. Embedded nails and the left forefoot are visible; middle - right forefoot (front paw) with ID tag, in dorsal position; bottom - right hind foot.*



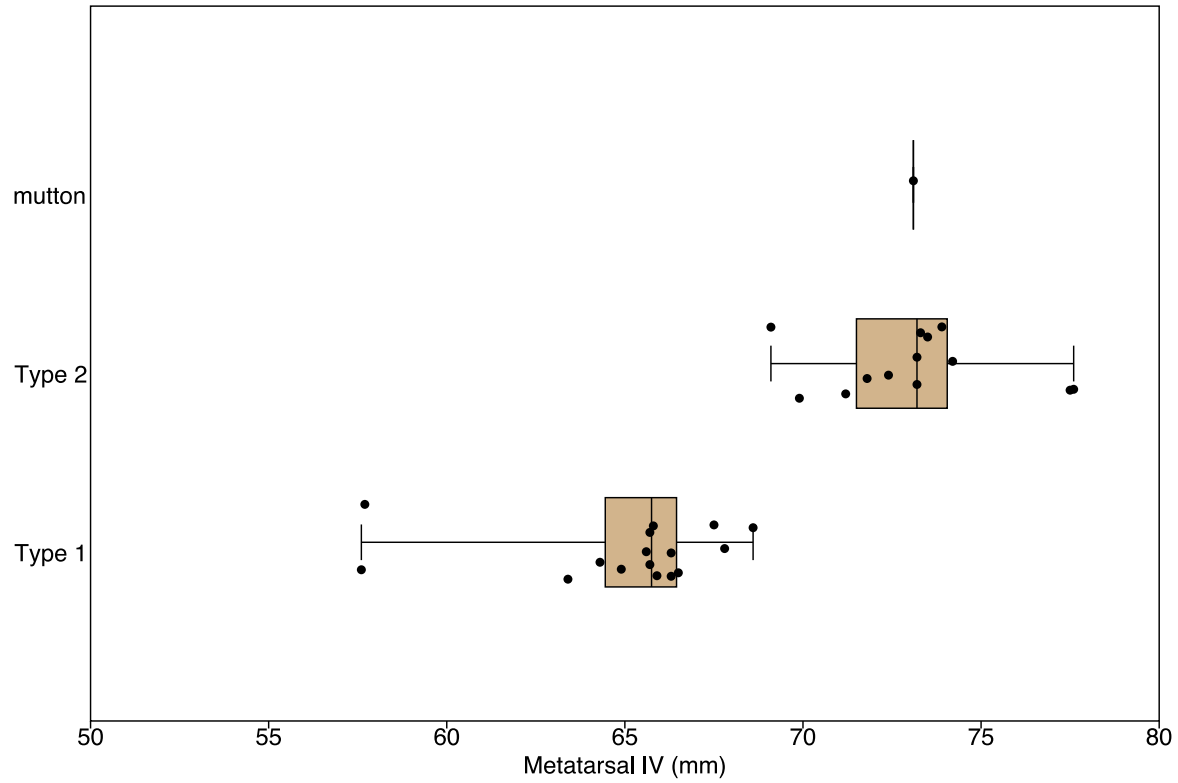
2039
2040 **Fig. S5. X-ray of SB Dog.** *Top – head, ventral. ID tag is visible.; middle – right forefoot (front*
2041 *paw) in dorsal position; bottom – right hind foot.*

2042



2043
2044
2045

Fig. S6. ALAS_015 dog. *Photo courtesy of University of Alaska Museum of the North.*

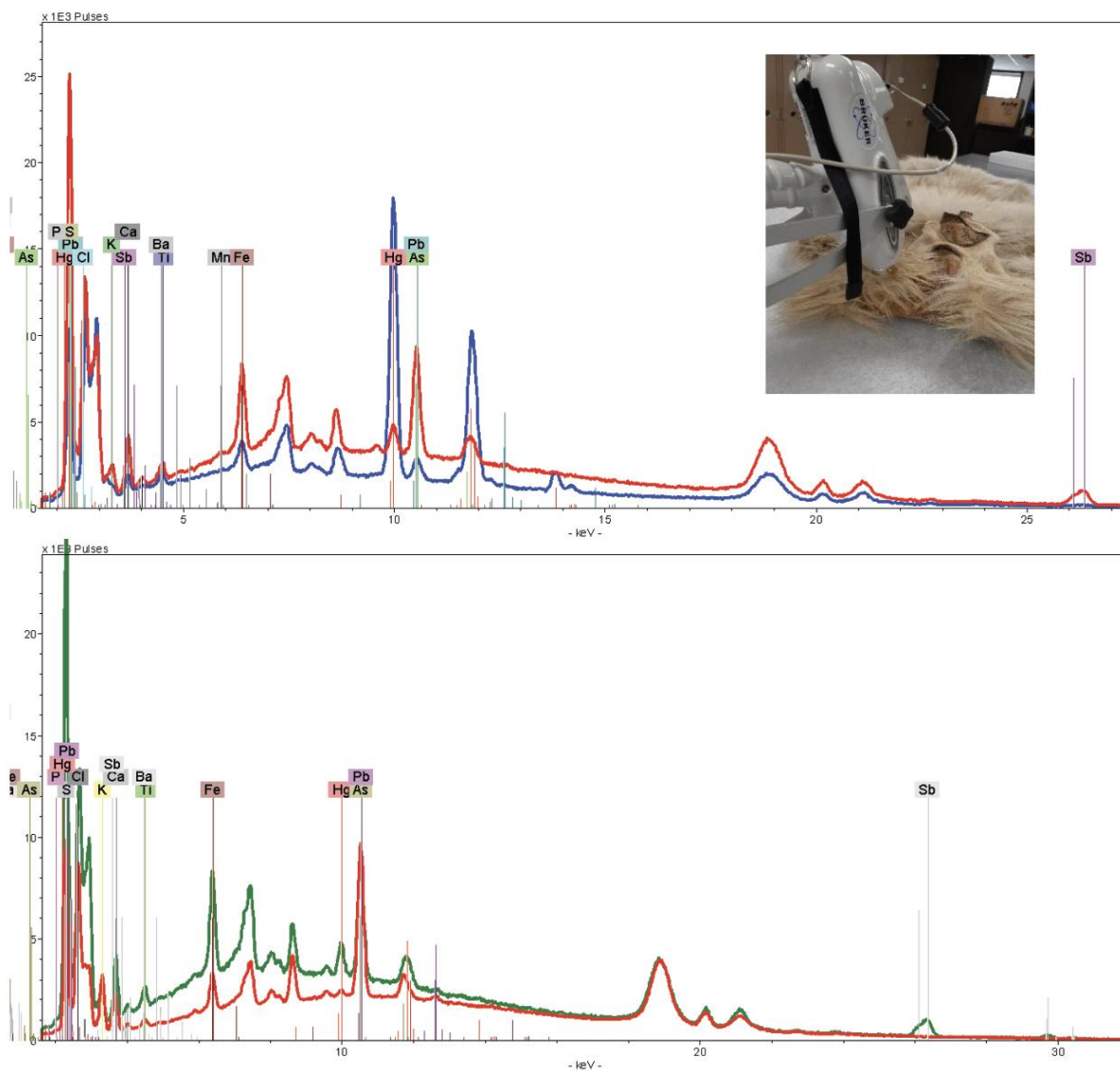


2046

2047 **Fig. S7. Metatarsal IV Measurements of Mutton and archaeological dogs.** *Archaeological*

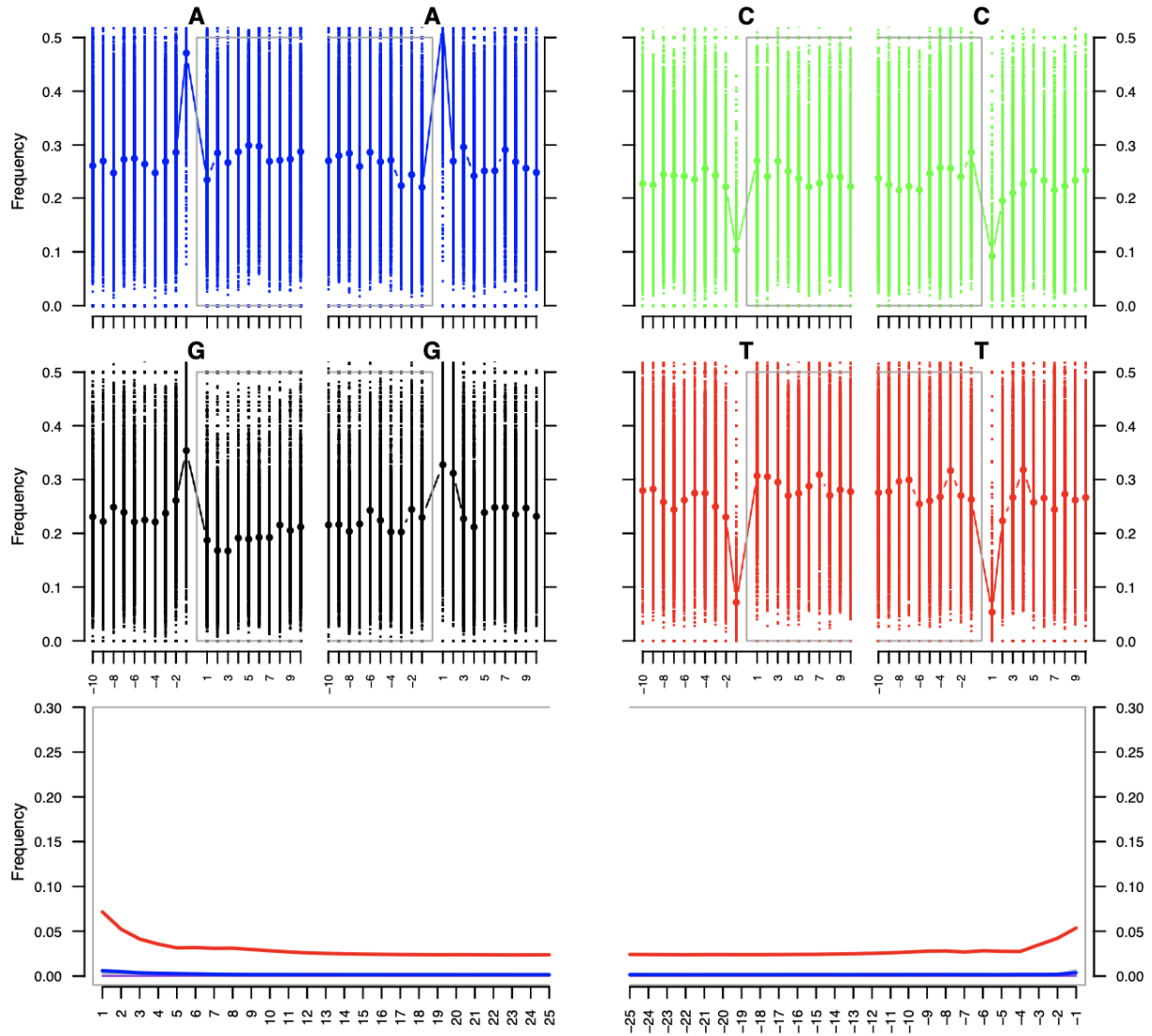
2048 *dog data according to Crockford (94): Type 1 “woolly” dogs (n=16) & Type 2 “Village” dogs*

2049 *(n=13).*



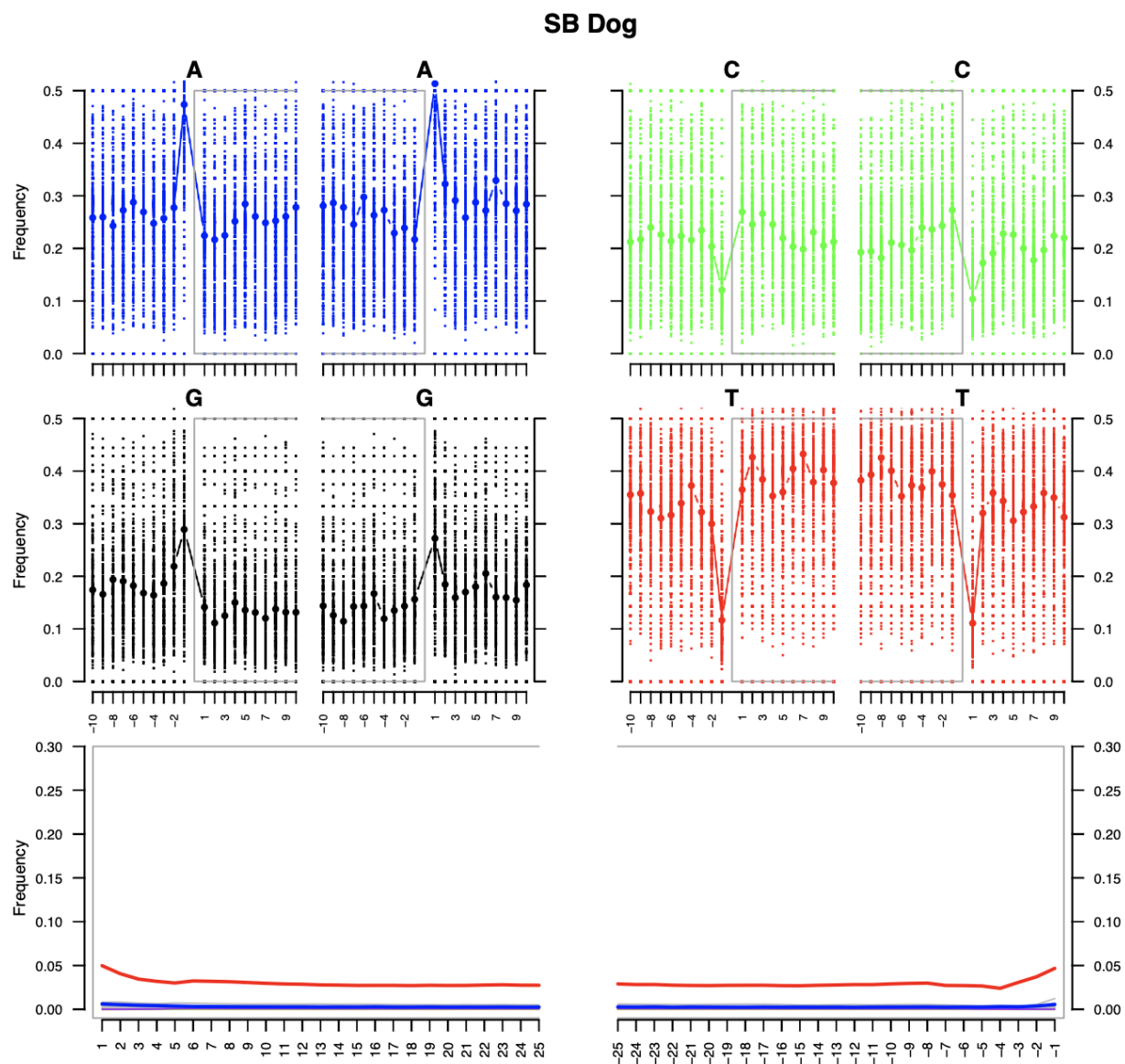
2050
 2051 **Fig. S8. Overlay of XRF spectra of a pelt from Mutton (USNM 4762) and SB Dog (USNM**
 2052 **3512).** (top) Mutton, Location 01_red hair (blue) and 02_white hair (red). (bottom) Location
 2053 02_white hair (green), and SB dog (USNM 3512), location 07_fur head (red).
 2054

Mutton



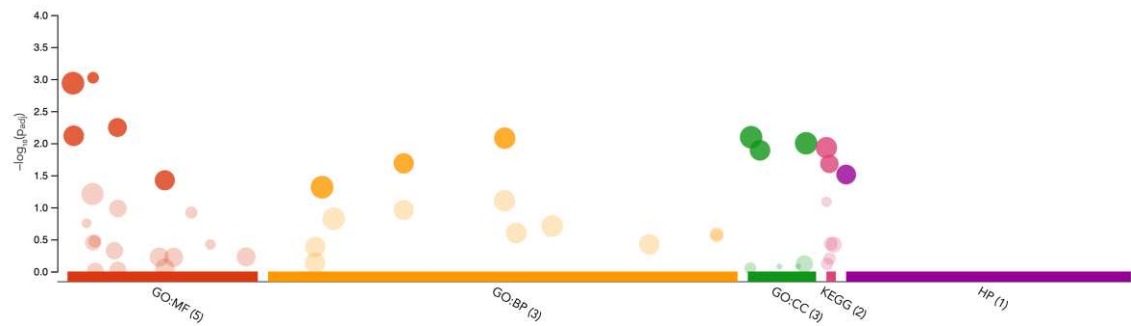
2055
2056
2057
2058

Fig. S9. Mutton MapDamage (88) results. Frequency of A, C, G, T nucleotides and the characteristic 5' and 3' damage patterns seen in the bottom panel.



2060
2061
2062
2063

Fig. S10. MapDamage (88) results for SB Dog. Frequency of A, C, G, T nucleotides and the characteristic 5' and 3' damage patterns seen in the bottom panel.



version e109_eg56_p17_1d3191d
 date 5/2/2023, 2:10:16 PM
 organism clfamiliaris

g:Profiler

2064

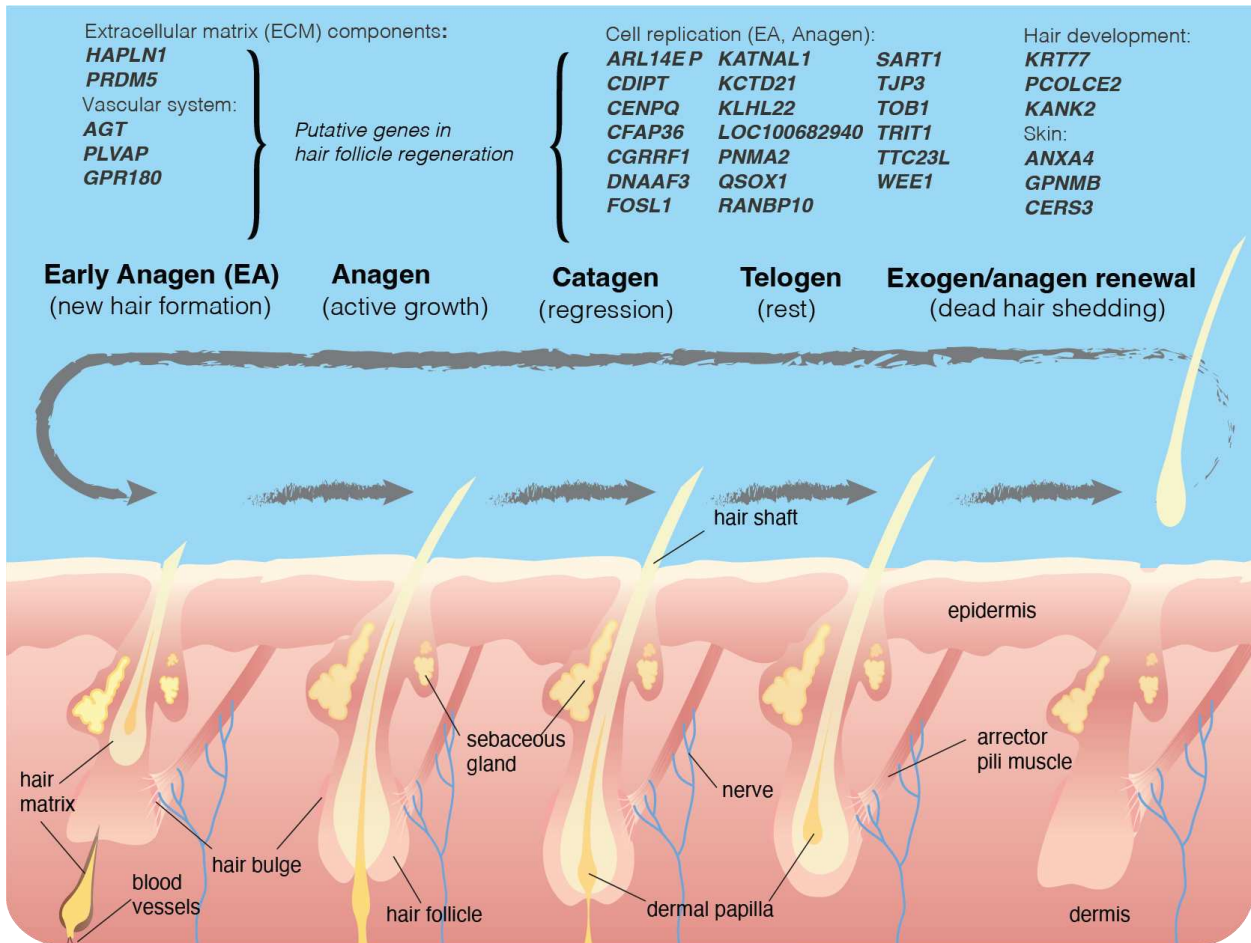
2065

2066

2067

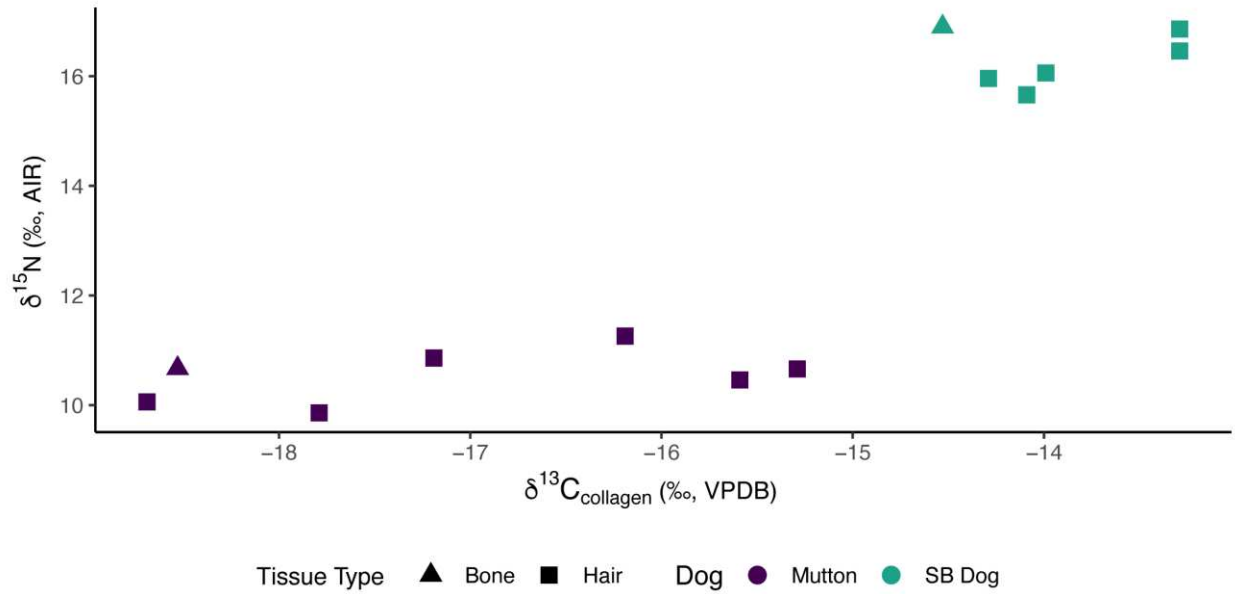
2068

Fig. S11. G:Profiler (108) results after querying 125 enriched genes to the *Canis lupus familiaris* organism. Statistical domain scope includes all known genes, g:SCS (108) significance threshold, and a user threshold of 0.05.



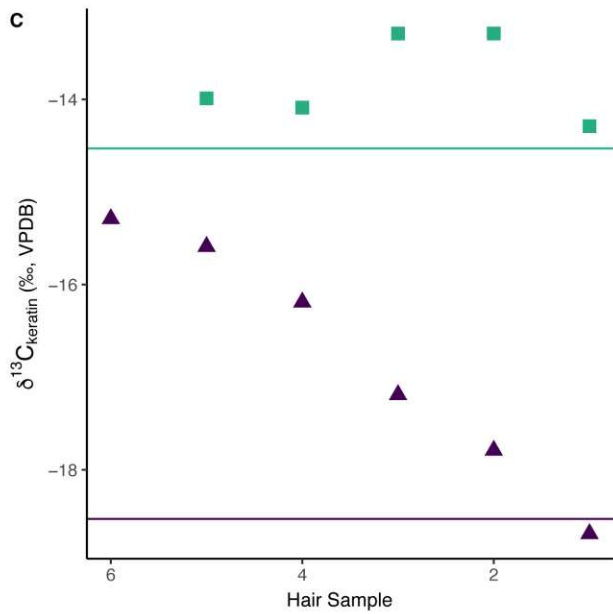
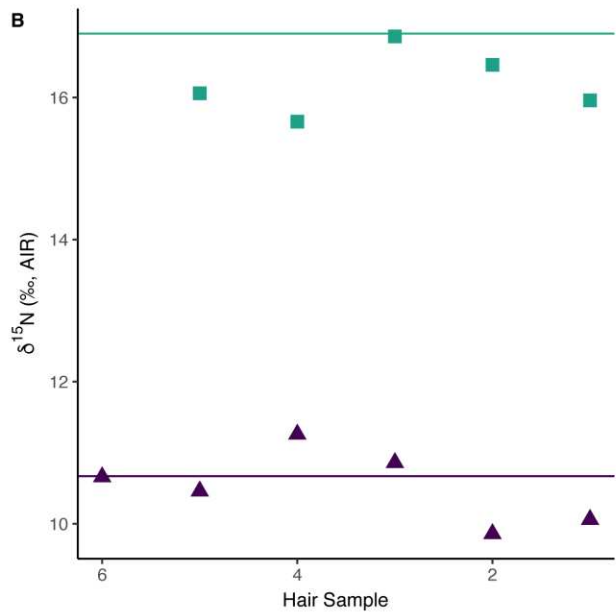
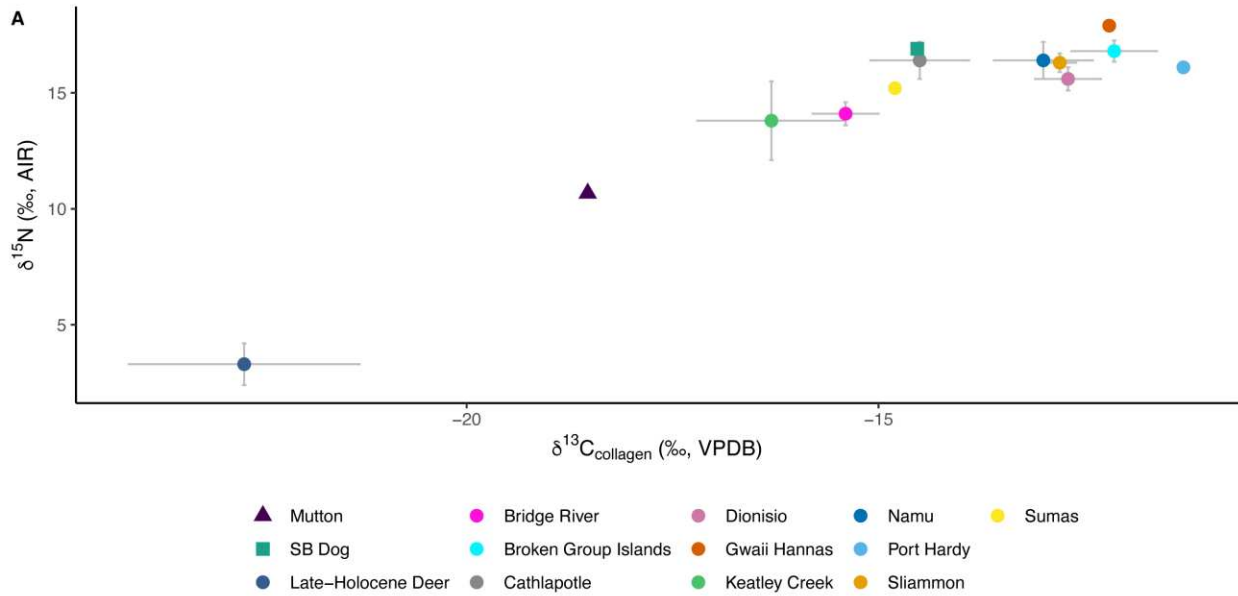
2070
 2071
 2072
 2073
 2074
 2075
 2076
 2077
 2078
 2079

Fig. S12. Proposed model of gene candidates involved in the hair growth cycle of woolly dogs. The hair growth cycle is complex and involves regulation of stem cell quiescence and activation, cell proliferation, differentiation, and apoptosis (122). The hair growth cycle consists of 1) early anagen (EA), where new hair is formed; 2) anagen, the stage of active hair growth; 3) catagen, where the hair stops growing and the hair follicle undergoes apoptosis-driven regression; 4) telogen, the resting phase where the hair follicle is dormant; 5) exogen, where the hair shaft is released. Image modified from the original (created by lebergvector on Freepik).



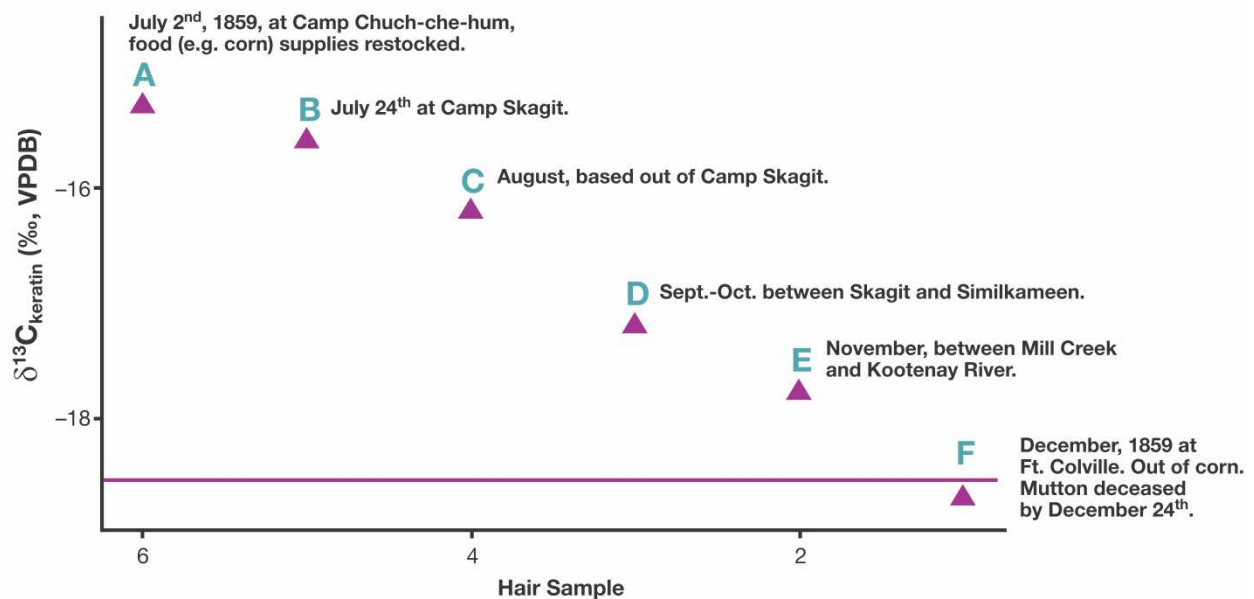
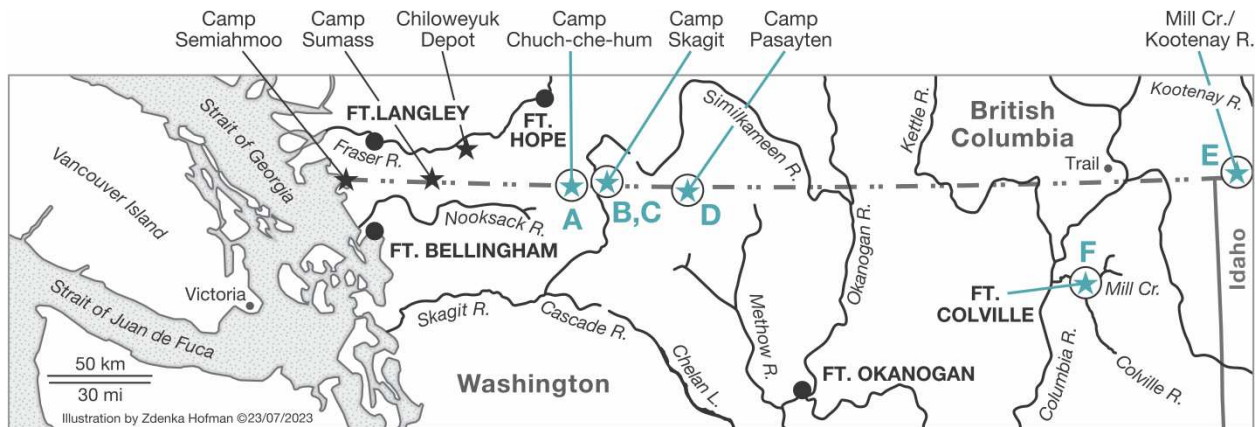
2080
 2081
 2082
 2083
 2084

Fig. S13. Stable isotope values of bone collagen and hair keratin. $\Delta^{13}\text{C}$ and $\delta^{15}\text{N}$ bone collagen stable isotope values and converted $\delta^{15}\text{N}$ hair keratin stable isotope values of Mutton and the SB Dog.

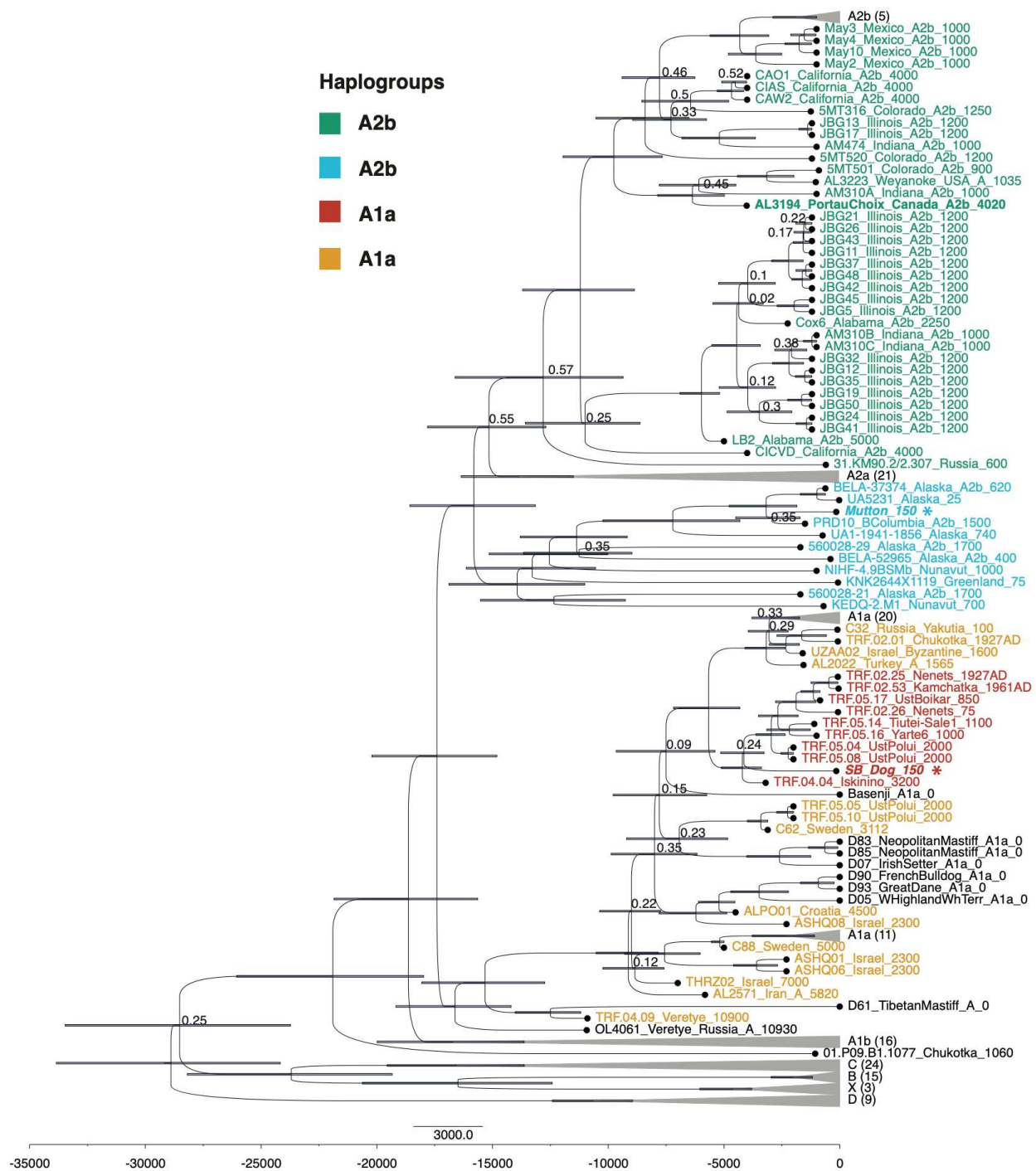


2085
2086
2087
2088
2089
2090
2091
2092
2093
2094

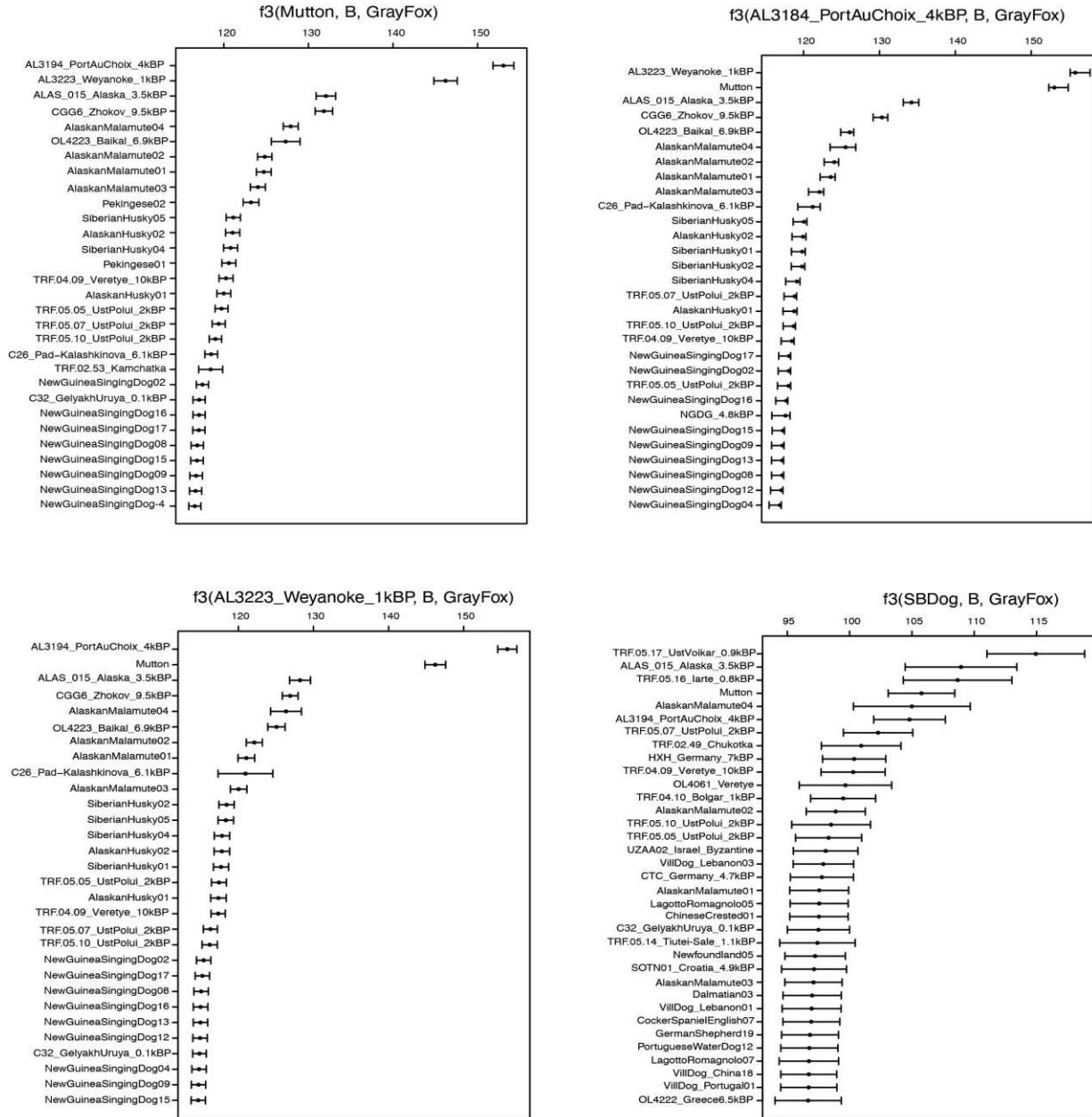
Fig. S14. Stable isotope values of bone collagen and hair keratin. *A)* $\delta^{13}C$ and $\delta^{15}N$ bone collagen values of SB Dog and Mutton, plotted with other archaeological dog and deer from (22). *B)* $\delta^{15}N$ hair keratin values of SB Dog and Mutton (converted to bone values), with bone values as horizontal guidelines. Hair samples are presented with the hair sample representing the oldest time period on the left and the time period right before death on the right. *C)* $\delta^{13}C$ hair keratin values of SB Dog and Mutton, with bone values as horizontal guidelines. Hair samples are presented with the hair sample representing the oldest time period on the left (e.g. hair 6) and the time period right before death on the right (e.g. hair 1).



2095
 2096 **Fig. S15. Sites and stable isotope values of hair keratin corresponding to the last months of**
 2097 **Mutton's life.** Chart aligning Mutton's six carbon hair values (triangles) and numbers showing
 2098 approximate locations where Mutton and George Gibbs may have been for the last few months
 2099 of Mutton's life. These values are based on the journal entries of Gibbs' and those of the survey
 2100 team. Supplies (including cornmeal and molasses) were picked up at Camp Chuchchehum and
 2101 by Ft. Colville corn supplies had run out. Specific dates were from survey team correspondence
 2102 (162), general dates are from Gibbs' field notes (15), and geographical coordinates of the camps
 2103 and stations are from the United States Northwest Boundary Survey (65).
 2104



2105
 2106 **Fig. S16. Full mtDNA time tree.** Colors are of notable dog haplogroups and correspond to Fig
 2107 2A. Black bars at the nodes represent 95% common ancestor highest posterior density. Node
 2108 posterior support values <60% are labeled. Scale bars indicate years from present. **Bolded** dogs
 2109 are newly generated genomes. **Mutton** and **SB Dog** are bolded and marked with an asterisk*



2111

2112

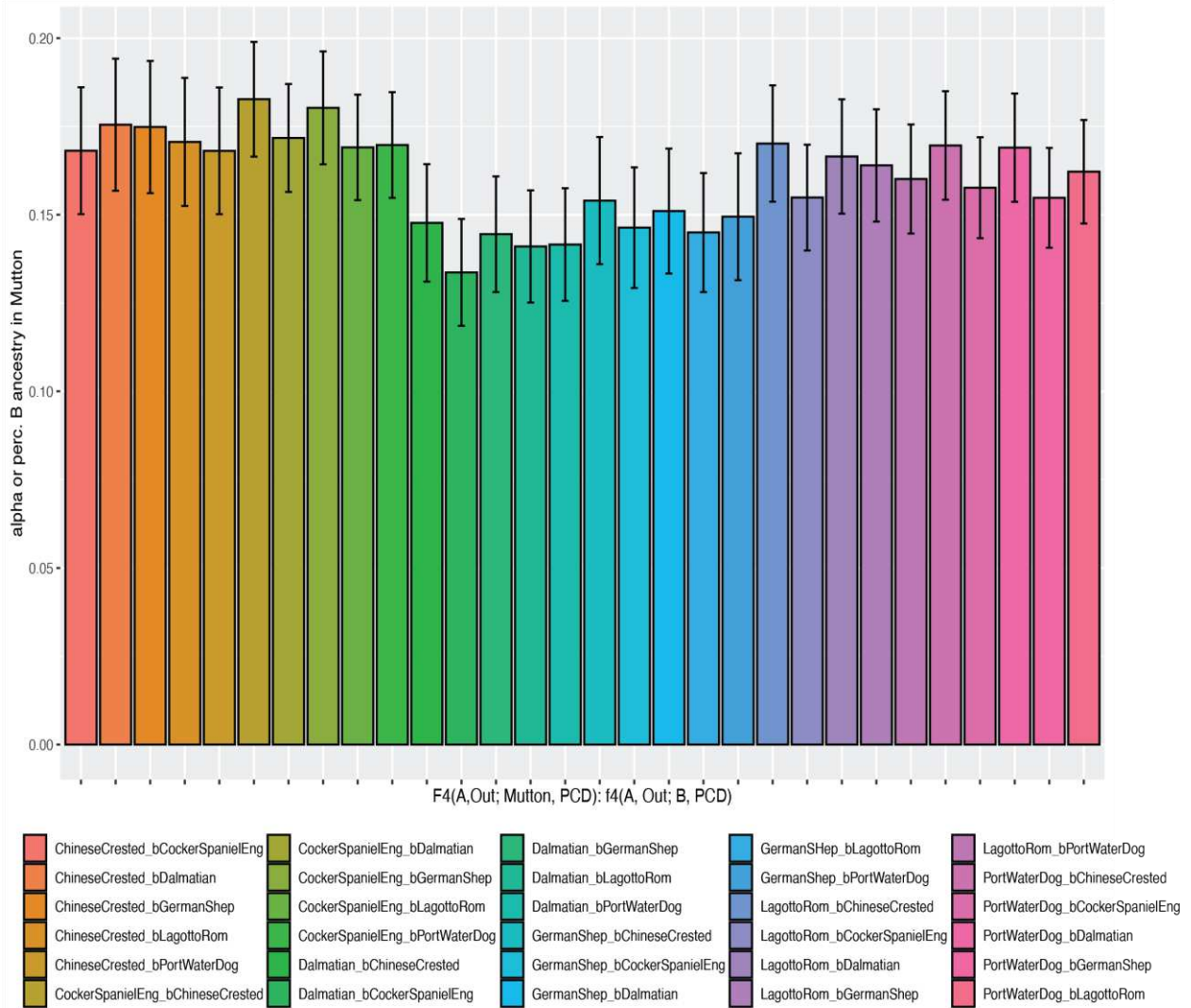
2113

2114

2115

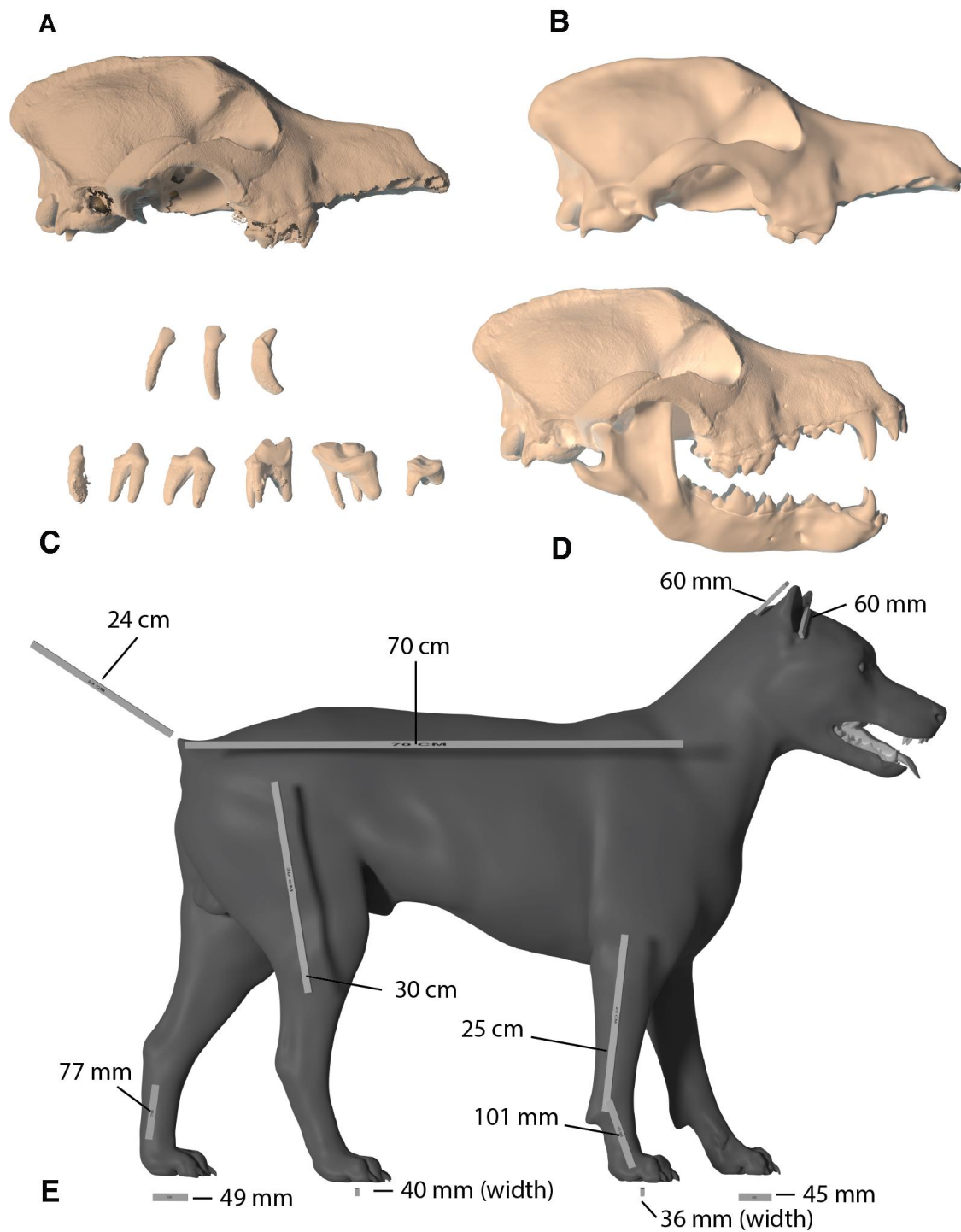
2116

Fig S17. F-3 outgroup statistics of Mutton, ancient PCD dogs, and SB Dog. Clockwise from top left are plots for Mutton, AL3194 (Port au Choix dog), AL3223 (Weyanoke dog), and SB Dog compared to top 30 ancient and modern dogs, with GrayFox as the outgroup population. Whiskers indicate error bars.



2117
 2118
 2119
 2120
 2121
 2122
 2123

Fig. S18. F4-ratio analysis. Bar plots of f_4 -ratio analysis with the following syntax: $f_4(A, Out; Mutton, AL3194 PortauChoix)$: $f_4(A, Out; B, AL3194 PortauChoix)$ where 6 modern dog breeds (Chinese Crested dog, English Cocker Spaniel, Dalmatian, German Shepherd, Lagotto Romagnolo, and Portuguese Water Dog) are in the A and B placement, and AL3194 (Port au Choix dog) represents a proxy for all PCD dogs.



2124
 2125 **Fig. S19 Steps in the forensic reconstruction of Mutton.** A) 3D model of archaeological woolly
 2126 dog cranium from Little Qualicum River site (4, 162) originally analyzed at the University of
 2127 Victoria Zooarchaeology lab. The scan was done by UVic library with permission from Iain
 2128 McKechnie and hosted on Sketchfab (<https://sketchfab.com/3d-models/coast-salish-wool-dog-skull-aa9f839b9fdb84347b5da41c8b76e0263>). B) Simplified and smoothed version of skull scan.
 2129 C) Teeth fitted to the upper and lower mandibles. Fourth Molar is based on "4th cheek tooth (4th
 2130 premolar) dog (upper jaw)" (<https://sketchfab.com/3d-models/4th-cheek-tooth-4th-premolar->
 2131

2132 *dog-upper-jaw-e09fee4434c840a2a6c7a69d70ce70cb*) by *vetanatMunich*
2133 (<https://sketchfab.com/vetanatMunich>) licensed under *CC-BY-NC-ND-4.0*)
2134 (<http://creativecommons.org/licenses/by-nc-nd/4.0/>). *Incisors and molars for* are taken from
2135 (<https://skfb.ly/6TSB6>) by *vetanatMunich* is licensed under *CC Attribution-NonCommercial-*
2136 *NoDerivs* (<http://creativecommons.org/licenses/by-nc-nd/4.0/>). *D) Teeth fitted to mandible,*
2137 *which was taken from* (<https://skfb.ly/o67JH>) by *RISD Nature Lab* is licensed under *Creative*
2138 *Commons Attribution* (<http://creativecommons.org/licenses/by/4.0/>). *E) Hairless model of*
2139 *Mutton with superimposed measurements taken from Mutton 's pelt.*
2140
2141

2142

2143

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.

2144 Note: Whenever hypothesis is offered for possible material identification, this should be
 2145 confirmed with a complementary technique. Other materials are possible. The instrument cannot
 2146 detect organic materials and materials containing only elements lighter than aluminum. Also,
 2147 elements present in very small quantities may escape detection. The argon (Ar) peak from the air
 2148 can be detected when no vacuum pump is used. The rhodium (Rh) peak is due to the instrument
 2149 tube (as well as traces of palladium (Pd) and possibly nickel (Ni), copper (Cu), and zinc (Zn)).

2150

2151

2152

2153

2154

2155

2156

2157

2158
2159

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

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).

2160 Note: Whenever hypothesis is offered for possible material identification, this should be
 2161 confirmed with a complementary technique. Other materials are possible. The instrument cannot
 2162 detect organic materials and materials containing only elements lighter than aluminum. Also,
 2163 elements present in very small quantities may escape detection. The argon (Ar) peak from the air
 2164 can be detected when no vacuum pump is used. The rhodium (Rh) peak is due to the instrument
 2165 tube (as well as traces of palladium (Pd) and possibly nickel (Ni)). On the spectra, only the
 2166 elements related to the samples have been labelled.
 2167
 2168

2169 **DataS1. [Supplementary spreadsheet]**
2170 IDs and metadata of newly generated genomes (NewGenomesMetadata), Extracts data from
2171 Mutton and SB Dog (ExtractsData), estimated error rates in ancient genomes used
2172 (AncientGenomeError), samples and metadata for mtDNA analyses (mtDNAdataset), samples
2173 and metadata for RoHan analysis (RoHanDataset), samples and metadata for dn/dS analysis
2174 (dNdSDataset), samples and metadata for outgroup- f_3 analyses (f3Dataset).

2175
2176 **DataS2. [Supplementary spreadsheet]**
2177 g:Profiler (*108*) results after querying 125 genes. Separate tabs show results within the categories
2178 in GO: Molecular Function (GO_MF), GO: Biological Process (GO_BP), GO: Cellular
2179 Component (GO_CC), KEGG, and Human Phenotype Ontology (HP), gene list with dn/dS
2180 values in Mutton (mutton_dndList), hypergeometric test results for gene enrichment
2181 (res_Hypergeometric), Wilcoxon rank-sum test results for gene enrichment (res_RankSum),
2182 Gene Ontology Resource query results for several hair/skin genes (AmiGO2).

2183
2184 **DataS3. [Supplementary spreadsheet]**
2185 125 gene list annotated manually (Annotations) by DAVID (*110, 111*), (geneList), and results of
2186 querying hair and skin categories in MGI Gene Ontology database
2187 (<https://www.informatics.jax.org/>) (MGI_GO_MP_Databases).

2188
2189 **DataS4. [Supplementary spreadsheet]**
2190 Mutton's genotype of variants associated with hair phenotype in dogs.

2191
2192 **Data S5. [Supplementary spreadsheet]**
2193 Bone collagen and hair keratin $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Mutton, SB Dog, and referenced
2194 comparative dog bone collagen data from previous research in the PNW (22).

2195