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1 **Title: The Evolutionary History of Dogs in the Americas**

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67

68

69 **Abstract (129 words):** Dogs were present in the Americas prior to the arrival of European
70 colonists, but the origin and fate of these pre-contact dogs are largely unknown. We sequenced 71
71 mitochondrial and seven nuclear genomes from ancient North American and Siberian dogs
72 spanning ~9,000 years. Our analysis indicates that American dogs were not domesticated from
73 North American wolves. Instead, American dogs form a monophyletic lineage that likely originated
74 in Siberia and dispersed into the Americas alongside people. After the arrival of Europeans, native
75 American dogs almost completely disappeared, leaving a minimal genetic legacy in modern dog
76 populations. Remarkably, the closest detectable extant lineage to pre-contact American dogs is the
77 canine transmissible venereal tumor, a contagious cancer clone derived from an individual dog that
78 lived up to 8,000 years ago.

79

80 **Main Text (2362 words):** The history of the global dispersal of dogs remains contentious (1). In
81 North America, the earliest confirmed dog remains have been radiocarbon dated to ~9,900
82 calibrated years before present (cal BP) (Koster, Illinois; (2, 3)), approximately 6,000 years after the
83 earliest unambiguous evidence of humans arriving in North America (4). While these early dogs
84 were most likely not domesticated *in situ* (5), the timing of their arrival and their geographic origins
85 are unknown. Studies of the control region of mitochondrial DNA have suggested that the pre-
86 contact American dog population was largely replaced following the introduction of European dogs
87 after the arrival of Europeans, and Eurasian Arctic dogs (e.g., Siberian huskies) during the Alaskan
88 gold rush (5–7). It remains possible, however, that some modern American dogs retain a degree of
89 ancestry from the pre-contact population (8, 9).

90

91 We sequenced complete mitochondrial genomes (mitogenomes) from 71 archaeological dog
92 remains collected in North America and Siberia (Fig. 1a; Table S1) and analyzed these with 145

93 mitogenomes derived from a global dataset of modern and ancient canids (3). A phylogenetic tree
94 constructed from the mitogenomes indicated that all sampled pre-contact dogs (spanning ~9,000
95 years) formed a monophyletic group within dog haplogroup A (Fig. 1b; Fig. S3; Fig. S6), which we
96 refer to as pre-contact dogs (PCD). This analysis indicated that the most closely related
97 mitochondrial lineage to the PCD clade are ~9,000 year-old dogs from Zhokhov Island in Eastern
98 Siberia (3) (Fig. 1b; Fig. S3; Fig. S6). In addition, molecular clock analyses suggest that all PCD
99 dogs shared a common ancestor ~14,600 years ago (95% high posterior density [HPD]: 16,484-
100 12,965; Fig. 1b; Fig. S6), which diverged from a shared ancestor with the Zhokhov Island dogs
101 ~1,000 years earlier (95% HPD:17,646-13,739; Fig. 1b; Fig. S6). Interestingly, these time frames
102 are broadly coincident with early migrations into the Americas (10–12).

104 To further investigate the evolutionary history of PCD, we generated low coverage nuclear genome
105 sequences (~0.005-2.0x) from seven pre-contact dogs sampled in six locations in North America
106 spanning ~9,000 years (Table S1). We analyzed these nuclear data alongside publicly available
107 datasets including 45 modern canid whole genomes sampled from Eurasia and the Americas (Table
108 S2)(13–16). A neighbor-joining tree constructed using single nucleotide polymorphism (SNP)
109 revealed that, like the mitogenome phylogeny, PCD individuals clustered in a distinct monophyletic
110 lineage that is more closely related to dogs than to either Eurasian or North American wolves (Fig.
111 1c). Furthermore, our nuclear genome analysis indicated that the closest-related sister clade to PCD
112 consists of modern Arctic dogs from the Americas (including Alaskan malamutes, Greenland dogs
113 and Alaskan huskies) and Eurasia (Siberian huskies; Fig. 1c). Treemix (3) (Fig. 1d), outgroup f3-
114 statistics (Fig. S13) and D-statistics (Fig. S14; Fig. S15) also supported this phylogenetic structure.
115 Combined, our mitochondrial and nuclear results indicate that PCD were not domesticated *in situ*
116 from North American wolves, but were instead introduced by people into the Americas via Beringia
117 from a population that was related to modern Arctic dogs.

119 Studies of nuclear data have identified two modern clades of global dogs: an East Asian clade
120 (including dingoes) and a Western Eurasian clade (including European, Indian, and African
121 dogs)(9, 14, 16). These analyses placed modern Arctic dogs with either Western Eurasian (16, 17)
122 or East Asian dogs (9, 14). Our analyses of nuclear data revealed a close relationship between
123 Arctic dogs and PCD which together form a clade (PCD/Arctic) that is basal to both Western
124 Eurasian and East Asian dogs and suggests the existence of a third monophyletic clade of dogs (Fig.
125 1c). Though all three clades are well-supported, the relationships between them are ambiguous. For
126 example, our outgroup f3-statistics analysis (Fig. S13) indicated that the PCD/Arctic clade is basal
127 to the two other Eurasian dog clades. However, when excluding specific East Asian dogs that
128 possess evidence of gene flow from European dogs (Table S7; (14)), East Asian dogs became the
129 most basal clade in a neighbor joining tree, and the PCD/Arctic clade became the sister clade to
130 Western Eurasian dogs (Fig. S11). Conversely, admixture graphs ((3); Fig. S25) and TreeMix (18)
131 (Fig. 1d) suggested that the PCD/Arctic clade is closest to East Asian dogs and West Eurasian dogs
132 are the most basal. Conflicting phylogenies based on nuclear data have been reported on numerous
133 occasions (1, 14, 16), and these inconsistent topologies could result either from substantial post-
134 divergence gene flow among Eurasian dogs (Fig. 1c; Fig. S25; (3, 14)), or from a near simultaneous
135 divergence of all three lineages.

137 Our nuclear data indicates that modern Arctic dogs sampled from both Siberia and North America
138 cluster in a distinct phylogenetic group that forms a sister taxon to PCD (Fig. 1c). This close

139 phylogenetic relationship between modern American Arctic dogs (Alaskan malamutes, Alaskan
140 huskies and Greenland dogs) and modern Eurasian Arctic dogs (Siberian huskies; Fig. 1c; Fig. S11;
141 Fig. S13) suggests that PCD are not the direct ancestor of modern American Arctic dogs. It is
142 possible that modern American Arctic dogs are the descendants of dogs brought by the Paleo-
143 Eskimo (~6,000 years ago) or by the Thule (~1,000 years ago)(19). However, both mitogenomic
144 and low coverage nuclear data from a late Paleo-Eskimo dog from Kodiak Island, Alaska (Uyak:
145 AL3198; Fig. 1a; Table S1) indicate that this dog is more closely related to PCD than to modern
146 American Arctic dogs (Fig. S10; Fig. S4). This suggests that modern American Arctic dogs are not
147 the descendants of Paleo-Eskimo dogs and that Paleo-Eskimos likely acquired local dogs in North
148 America or brought Siberian dogs that were genetically indistinguishable from PCD. Our sampling
149 did not include dogs from sites associated with the Thule culture, so it is plausible that the modern
150 American Arctic dogs included in our analysis, such as Alaskan malamutes and Greenland dogs, are
151 the descendants of dogs introduced by the Thule. Alternatively, the modern American Arctic dogs
152 that we sampled may be the descendants of recently introduced Eurasian Arctic dogs, many of
153 which were introduced during the 19th-century Alaskan gold rush and as sled dog racing stock (6).
154 Regardless, modern American Arctic dog populations have complex histories with potential genetic
155 contributions from both American and Eurasian Arctic dogs (3).

156

157 Interestingly, genomic analyses of canine transmissible venereal tumor (CTVT) genomes indicated
158 a close affinity with modern Arctic dogs (20). CTVT is a contagious cancer clone that manifests as
159 genital tumors and spreads between dogs by the transfer of living cancer cells during mating. This
160 clone first originated from the cells of an individual dog, the “CTVT founder dog”, which lived
161 several thousand years ago, and still carries the genome of this individual (20). To investigate the
162 relationship between the CTVT founder dog and PCD, we analyzed two CTVT genomes alongside
163 a panel of modern and ancient canid genomes.

164

165 In order to accommodate for the fact that CTVT is a cancer, and to limit the impact of somatic
166 mutations, we confined our genotyping analysis to SNPs which mapped to genomic regions that
167 have retained both parental chromosomal copies in CTVT (20), and excluded singleton SNPs
168 exclusively called in CTVT genomes. Remarkably, CTVT clustered with PCD on neighbor-joining
169 trees (Fig. 1c; Fig. S10; Fig. S11), a Bayesian tree (Fig. S12), Treemix (Fig. 1d) and admixture
170 graphs (Fig. S25). This result is further supported by both outgroup f_3 (Fig. S13) and D-statistics
171 (Fig. S14; Fig. S15). These findings indicate that the CTVT founder dog is more closely related to
172 PCD than to modern Arctic dogs. Multiple horizontal transfers of mitochondrial genomes from dog
173 hosts to CTVT tumors has led to the replacement of the founder dog’s mitogenome (21, 22), thus
174 we could not determine the mitochondrial haplogroup of the CTVT founder dog and we limited our
175 analyses to the nuclear genome.

176

177 To assess whether the CTVT founder dog lived prior to, or after dogs entered North America, we
178 re-estimated its temporal origin by sequencing the nuclear genomes of two CTVT tumors, 608T and
179 609T. 608T is a CTVT tumor from the skin of a ten-month-old puppy which was likely engrafted
180 from its mother’s vaginal tumor (609T) during birth. We identified mutations with a clock-like
181 mutational process which were present in 608T, but not detectable in 609T, and used these to derive
182 a lower bound for a somatic mutation rate for CTVT (3). Applying this rate to the total burden of
183 clock-like somatic mutation in the CTVT lineage (3), we estimated that the CTVT founder dog

184 lived up to 8,225 years ago (3). This time frame postdates the initial arrival of dogs into the
185 Americas, raising the possibility that CTVT may have originated in a dog living in North America.
186

187 To further assess this scenario, we quantified the degree of introgression between North American
188 endemic canids (coyotes and North American wolves), PCD dogs, modern Arctic dogs, and the
189 CTVT founder dog. Our analyses indicated that, unlike Arctic dogs, PCD dogs share number of
190 derived alleles with coyotes and North American wolves, indicative of admixture (Fig. S16; Fig.
191 S17). The CTVT founder dog also showed some weak evidence of coyote ancestry, but did not
192 appear to possess admixture with North American wolves (Fig. S16; Fig. S17). Because coyotes are
193 restricted to North America, this suggests that CTVT may have originated there. Since we did not
194 ascertain the degree of coyote ancestry in ancient PCD-related dogs in Northern Siberia (such as the
195 Zhokov Island dogs, Fig 1), however, this analysis does not establish the location in which CTVT
196 originated. Furthermore, studies that used somatic mutations to reconstruct the phylogeography of
197 the CTVT clone indicated a deep divergence in Asia and a recent introduction to the Americas (21).
198 Altogether, these results suggest a scenario in which CTVT originated in Asia from a dog that was
199 closely related to PCD, although we cannot exclude the possibility that the clone arose in America,
200 then dispersed early into Asia before being reintroduced to America.
201

202 The legacy of PCD in modern American dog populations is uncertain. It has been suggested that
203 some North American wolves obtained a mutation leading to black coat color possibly via
204 admixture with early American dogs (23). This allele was not present, however, in either of the two
205 higher coverage ancient PCD dogs in this study (3) or in CTVT (20). Additional ancient genomes
206 are necessary to determine if this allele was present in the PCD population.
207

208 In addition, previous studies have argued that some modern American dog populations possess a
209 genetic signature from indigenous American dogs (8, 9, 24). To test this hypothesis, we analyzed
210 nuclear data obtained from more than 5,000 modern dogs (including American village dogs)
211 genotyped on a 180K SNP array (9). We found 7-20% PCD ancestry in modern American Arctic
212 dogs using f_4 ratios (Alaskan husky, Alaskan malamute and Greenland dogs; Table S10&S11;
213 Supplementary Material). This result, however, could reflect ancient population substructure in
214 Arctic dogs rather than genuine admixture (Supplementary Material). Our f_4 ratio analysis did not
215 detect a significant admixture signal from PCD into any modern American dogs of European
216 ancestry (Table S10).
217

218 Our ADMIXTURE analysis detected varying degrees of PCD/Arctic ancestry in three individual
219 Carolina dogs (0-33%; Fig. S20). This analysis, however, could not distinguish between PCD and
220 Arctic ancestry, and we cannot rule out that this was result of admixture from modern Arctic dogs
221 and not from PCD (3). The majority of modern American dog populations, including 138 village
222 dogs from South America and multiple “native” breeds (e.g., hairless dogs and Catahoulas), possess
223 no detectable traces of PCD ancestry (Fig. S20; Table S10; Fig. 2a), though this analysis may suffer
224 from ascertainment bias.
225

226 To further assess the contribution of PCD to modern American dog populations, we also analyzed
227 590 additional modern dog mitogenomes, including 169 village and breed dogs that were sampled
228 in North and South America (21). We identified two modern American dogs (a chihuahua and a
229 mixed breed dog from Nicaragua) that carried PCD mitochondrial haplotypes (Fig. S5); consistent

230 with a limited degree of PCD ancestry (<2%) in modern American dogs. We also identified three
231 East Asian dogs that carried a PCD haplotype, possibly as a result of ancient population
232 substructure or recent dog dispersal (Fig. S5; (3)). Although greater degrees of PCD ancestry may
233 remain in American dogs which have not yet been sampled, our results suggest that European dogs
234 almost completely replaced native American dog lineages. This near disappearance of PCD likely
235 resulted from the arrival of Europeans, which led to shifts in cultural preferences and the
236 persecution of indigenous dogs (25). Introduced European dogs may also have brought infectious
237 diseases to which PCD were susceptible.

238
239 The first appearance of dogs in the North American archaeological record occurs ~6,000 years after
240 the earliest evidence of human activity (4, 11). In addition, our molecular clock analysis indicates
241 that the PCD lineage appeared ~6,500 years after North American human lineages (Fig. 1b)(10).
242 These discrepancies suggest that dogs may not have arrived into the Americas alongside the first
243 human migration. A recent human genetic study suggests that Northern Native American
244 populations admixed with an East Siberian population ~11,500 years ago(12). This timing is
245 compatible with both the archaeological record and our PCD divergence time estimate and suggests
246 a scenario in which dogs were brought to the Americas several thousand years after the first people
247 arrived.

248
249 This initial dog population entered North America then dispersed throughout the Americas where it
250 remained isolated for at least 9,000 years. Within the past 1,000 years, however, there have been at
251 least three independent re-introductions of dogs. The first may have consisted of Arctic dogs that
252 arrived with the Thule culture ~1,000 years ago (6). Then, beginning in the 15th century, Europeans
253 brought a second wave of dogs that appear to have almost completely replaced indigenous dogs.
254 Lastly, Siberian huskies were introduced to the American Arctic during the Alaskan gold rush (25).
255 As a result of these more recent introductions, the modern American dog population is largely
256 derived from Eurasian breeds, and the closest known extant vestige of the first American dogs now
257 exists as a worldwide transmissible cancer.

258

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652
653 **Figure 1 Sample location and ancestry of pre-contact dogs a.** A map depicting the location and
654 age of the archeological remains analyzed in this study. Each dot represents a single sample, and
655 multiple samples per archeological site are grouped in boxes. Sites mentioned in the text are
656 labelled. **b.** A tip calibrated Bayesian mitochondrial phylogenetic tree of dogs, within haplogroup
657 A. This analysis was conducted with 71 novel ancient mitogenomes together with 145 publicly
658 available mitogenomes from both modern and ancient canids (3) (Fig. S6). Red branches represent
659 modern dogs. Blue horizontal bars on nodes represent 95% High Density Posterior age. The grey
660 shaded area represents the time frame during which people entered the Americas (10–12) **c.** A
661 neighbor-joining tree built with whole genomes (3). **d** An admixture graph constructed with
662 *TreeMix* (based on transversions; Supplementary Material) depicting the relationship between PCD
663 (including the Port Du Choix [AL3194] and Weyanoke Old Town [AL3223] samples) and other
664 dog and wolf populations. We only used Greenland dogs and Malamute (American Arctic dogs) for
665 this analysis as these are the least admixed with Western Eurasian dogs (3).

666
667 **Figure 2 Legacy of pre-contact dogs in modern american dogs a.** A map showing the locations
668 of dog populations obtained from (9) and their degree of relatedness (D-statistics) with the ~4ky old
669 Port au Choix dog (AL3194; see (3) and Fig. S14). Higher values (in red) represent closer
670 relatedness. **b.** A map depicting the multiple introductions of dogs into the Americas.

671
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712 **Supplementary Materials:**

713 Material and Methods

714 Figs. S1 to S28

715 Tables S3 to S8, and S12 to S16

716 Captions for Tables S1, S2, S9 to S11

717 References 26-187

718

719 **Other Supporting Online Material for this manuscript includes the following:**

720 Tables S1, S2, and S9 to S11 (Excel)