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**Article:**

Ní Leathlobhair, M, Perri, A R, Irving-Pease, E K et al. (47 more authors) (2018) The evolutionary history of dogs in the Americas. *Science*. pp. 81-85. ISSN 0036-8075

<https://doi.org/10.1126/science.aao4776>

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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  
672 **Acknowledgement:** We thank L. Orlando, R. K. Wayne and D. Meltzer for their valuable  
673 comments, B. M. Kemp, M. Masson and J. Chupasko for support and J. Southon (Keck Carbon  
674 Cycle Accelerator Mass Spectrometer, University of California, Irvine) for the radiocarbon date on  
675 the Port au Choix dog. We would like to acknowledge the use of the University of Oxford  
676 Advanced Research Computing (ARC) facility for providing computing time. We thank the Illinois  
677 State Museum, the Illinois State Archaeological Survey, the G. A. Black Laboratory of  
678 Archaeology at Indiana University Bloomington, the Instituto Nacional de Antropologia e Historia  
679 and the Ohio Historical Society for access to material. We thank The Rooms (Museum Division),  
680 Board Executive and Government of Newfoundland and Labrador for permission to access and  
681 sample the Port au Choix material. We are grateful to M. Ptaszynska for useful information and to  
682 S. Zhang for assistance with samples. **Funding:** L.A.F.F. was supported by the Wellcome Trust  
683 (210119/Z/18/Z) and by Wolfson College (University of Oxford). L.A.F.F., J.H, A.L., A. H-B,  
684 O.L., K.M.D. and G.L. were supported either by a European Research Council grant (ERC-2013-  
685 StG-337574-UNDEAD) or Natural Environmental Research Council grants (NE/K005243/1 and  
686 NE/K003259/1), or both. M.N.L. and E.P.M. were supported by the Wellcome Trust  
687 (102942/Z/13/A). A.R.P. was supported by the Max Planck Society. E.K.I.P. was supported by a  
688 Clarendon Fund Scholarship, University of Oxford. M.T.P.G was supported by European Research  
689 Council grant (ERC-2015-CoG-681396 – Extinction Genomics). A.M. was supported by the



690 Muséum national d'Histoire naturelle. K.E.W. and R.S.M were supported by a National Science  
691 Foundation grant (BCS-1540336) and a Wenner-Gren grant. V.G. was supported by a Social  
692 Sciences and Humanities Research Council Insight Grant. V.V.P., E.Y.P., and P.A.N. were  
693 supported by Russian Science Foundation project N16-18-10265-RNF. We thank the staff of the  
694 Danish National High-Throughput Sequencing Centre for assistance in data generation and the  
695 Illinois State Museum Society for funding. **Author contributions:** L.A.F.F, G.L. and E.P.M  
696 conceived the project and designed research; A.P., K.D. and G.L. coordinated the archaeological  
697 analyses and sampling collection efforts with input from R.P.M, C.A., A.B-H and K.E.W.; A.P.,  
698 C.A, J.B, E.G., A.J.H, M-H.S.S., S.J.S, M.E., V.G., J.J, A.K.K, P.A.N, C.P.L, A.M., T.M., K.N.M.,  
699 M.O., E.Y.P, P.S, V.V.I., C.W. and V.V.P provided/collected samples; K.W.E, A.L., J.H., O.L.,  
700 S.B., A.D. E.A.D., J.E., J-M. R., M-H.S.S. conducted the ancient laboratory work with input from  
701 R.P.M., G.L., L.A.F.F, E.W., I.B., and M.T.P.G.; M.M., E.P.M., and A.S. provided/collected CTVT  
702 samples; M.N.L. and Y-M.K. conducted the CTVT analyses with input from E.P.M., K.G., and  
703 L.A.F.F.; M.N.L., L.A.F.F and E.K.I.P conducted the analyses of ancient data with input from S.G.,  
704 A.K., A.B. and E.P.M.; L.A.F.F., G.L., E.P.M., M.N.L. and A.P., wrote the paper with input from  
705 all other authors. **Competing interests:** A.D., J.E, and J-M.R. are employees of Arbor Biosciences  
706 which provided target enrichment kits used in this study. J-M.R. is also a founder of Arbor  
707 Biosciences. **Data and materials availability:** The reads for the ancient data have been deposited  
708 at the European Nucleotide Archive (ENA) with project number PRJEB22026. Reads for new  
709 CTVT genomes were deposited at the European Nucleotide Archive (ENA) with project number  
710 PRJEB22148.

711

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)