

DOMESTICATION

The evolutionary history of dogs in the Americas

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Dogs were present in the Americas before the arrival of European colonists, but the origin and fate of these precontact dogs are largely unknown. We sequenced 71 mitochondrial and 7 nuclear genomes from ancient North American and Siberian dogs from time frames spanning ~9000 years. Our analysis indicates that American dogs were not derived from North American wolves. Instead, American dogs form a monophyletic lineage that likely originated in Siberia and dispersed into the Americas alongside people. After the arrival of Europeans, native American dogs almost completely disappeared, leaving a minimal genetic legacy in modern dog populations. The closest detectable extant lineage to precontact American dogs is the canine transmissible venereal tumor, a contagious cancer clone derived from an individual dog that lived up to 8000 years ago.

The history of the global dispersal of dogs continues to be contentious (1). In North America, the earliest confirmed dog remains (from Koster, IL) have been radiocarbon dated to ~9900 calibrated years before the present (2, 3), ~4500 years after the earliest unambiguous evidence of humans arriving in the Americas (4). Although these early dogs were most likely not domesticated in situ (5), the timing of their arrival and their geographic origins are unknown. Studies of the control region of mitochondrial DNA have suggested that the precontact American dog population was largely replaced following the arrival of European dogs after colonization and the introduction of Eurasian Arctic dogs (e.g., Siberian

huskies) during the Alaskan gold rush (5–7). It remains possible, however, that some modern American dogs retain a degree of ancestry from the precontact population (8, 9).

We sequenced complete mitochondrial genomes (mitogenomes) from 71 archaeological dog remains collected in North America and Siberia (Fig. 1A and table S1) and analyzed these with 145 mitogenomes derived from a global dataset of modern and ancient canids (3). A phylogenetic tree constructed from the mitogenomes indicated that all sampled precontact dogs (PCDs) (from time frames spanning ~9000 years) formed a monophyletic group within dog haplogroup A (Fig. 1B and figs. S3 and S6). This analysis indicated that the mitochondrial lineage

most closely related to the PCD clade is that of the ~9000-year-old population of dogs from Zhokhov Island in Eastern Siberia (3) (Fig. 1B and figs. S3 and S6). In addition, molecular clock analyses suggest that all PCDs share a common ancestor that lived ~14,600 years ago [95% highest posterior density (HPD), 16,484 to 12,965 years ago] (Fig. 1B and fig. S6), which had diverged from an ancestor shared with the Zhokhov Island dogs ~1000 years earlier (95% HPD, 17,646 to 13,739 years ago) (Fig. 1B and fig. S6). These time frames are broadly coincident with early migrations into the Americas (10–12).

To further investigate the evolutionary history of PCDs, we generated low-coverage (~0.005 to 2.0×) nuclear genome sequences from seven PCDs sampled in six locations in North America from time frames spanning ~9000 years (table S1). We analyzed these nuclear data alongside publicly available datasets including 45 modern canid whole genomes sampled from Eurasia and the Americas (table S2) (13–16). A neighbor-joining tree constructed by using single-nucleotide polymorphisms (SNPs) revealed that, like the mitochondrial phylogeny, PCDs clustered in a distinct monophyletic lineage that is more closely related to dogs than to either Eurasian or North American wolves (Fig. 1C). Furthermore, our nuclear genome analysis indicated that the closest-related sister clade to PCDs consists of modern Arctic dogs from the Americas (including Alaskan malamutes, Greenland dogs, and Alaskan huskies) and Eurasia (Siberian huskies) (Fig. 1C). Treemix (3) (Fig. 1D), outgroup f3 statistics (fig. S13), and D statistics (figs. S14 and S15) also supported this phylogenetic structure. Combined, our mitochondrial and nuclear results indicate that PCDs were not domesticated in situ from North American wolves but were instead introduced by people into the Americas via Beringia from a population related to modern Arctic dogs.

Studies of nuclear genome data have identified two modern clades of global dogs: an East Asian clade (including dingoes) and a Western Eurasian clade (including European, Indian, and African dogs) (9, 14, 16). These analyses placed modern Arctic dogs with either Western Eurasian (16, 17) or East Asian (9, 14) dogs. Our analyses of nuclear genome data revealed a close relationship between Arctic dogs and PCDs, which together form

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a clade (PCD/Arctic) that is basal to both Western Eurasian and East Asian dogs and suggests the existence of a third monophyletic clade of dogs (Fig. 1C). Although all three clades are well supported, the relationships between them are ambiguous. For example, outgroup f3 statistics analysis (fig. S13) indicated that the PCD/Arctic clade is basal to the two other Eurasian dog clades. However, when we excluded specific East Asian dogs that possess evidence of gene flow from European dogs (table S7) (14), East Asian dogs became the most basal clade in a neighbor-joining tree and the PCD/Arctic clade became the sister clade to Western Eurasian

dogs (fig. S11). Conversely, admixture graphs (3) (fig. S25) and Treemix (18) (Fig. 1D) suggested that the PCD/Arctic clade is closest to East Asian dogs and that Western Eurasian dogs are the most basal. Conflicting phylogenies based on nuclear data have been reported on numerous occasions (1, 14, 16), and these inconsistent topologies could result either from substantial post-divergence gene flow among Eurasian dogs (Fig. 1C and fig. S25) (3, 14) or from nearly simultaneous divergence of all three lineages.

Our nuclear genome data indicate that modern Arctic dogs sampled from both Siberia and North America cluster in a distinct phylogenetic

group that forms a sister taxon to PCDs (Fig. 1C). This close phylogenetic relationship between modern American Arctic dogs (Alaskan malamutes, Alaskan huskies, and Greenland dogs) and modern Eurasian Arctic dogs (Siberian huskies) (Fig. 1C and figs. S11 and S13) suggests that PCDs are not the direct ancestor of modern American Arctic dogs. It is possible that modern American Arctic dogs are the descendants of dogs brought onto the continent by the Paleo-Eskimos (~6000 years ago) or by the Thule (~1000 years ago) (19). However, both mitogenomic and low-coverage nuclear data from a late Paleo-Eskimo dog from Kodiak Island, Alaska (Uyak site sample AL3198) (Fig. 1A

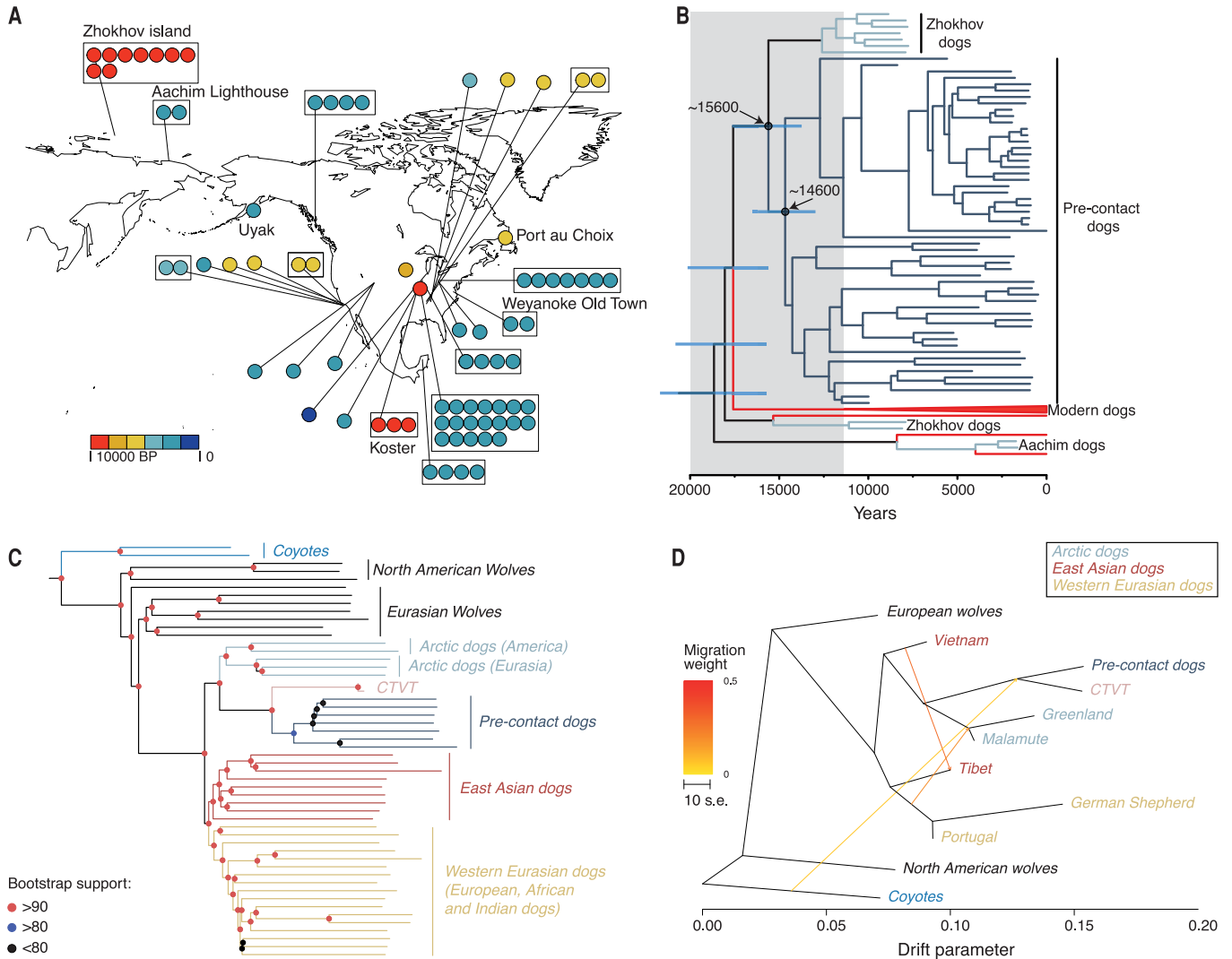
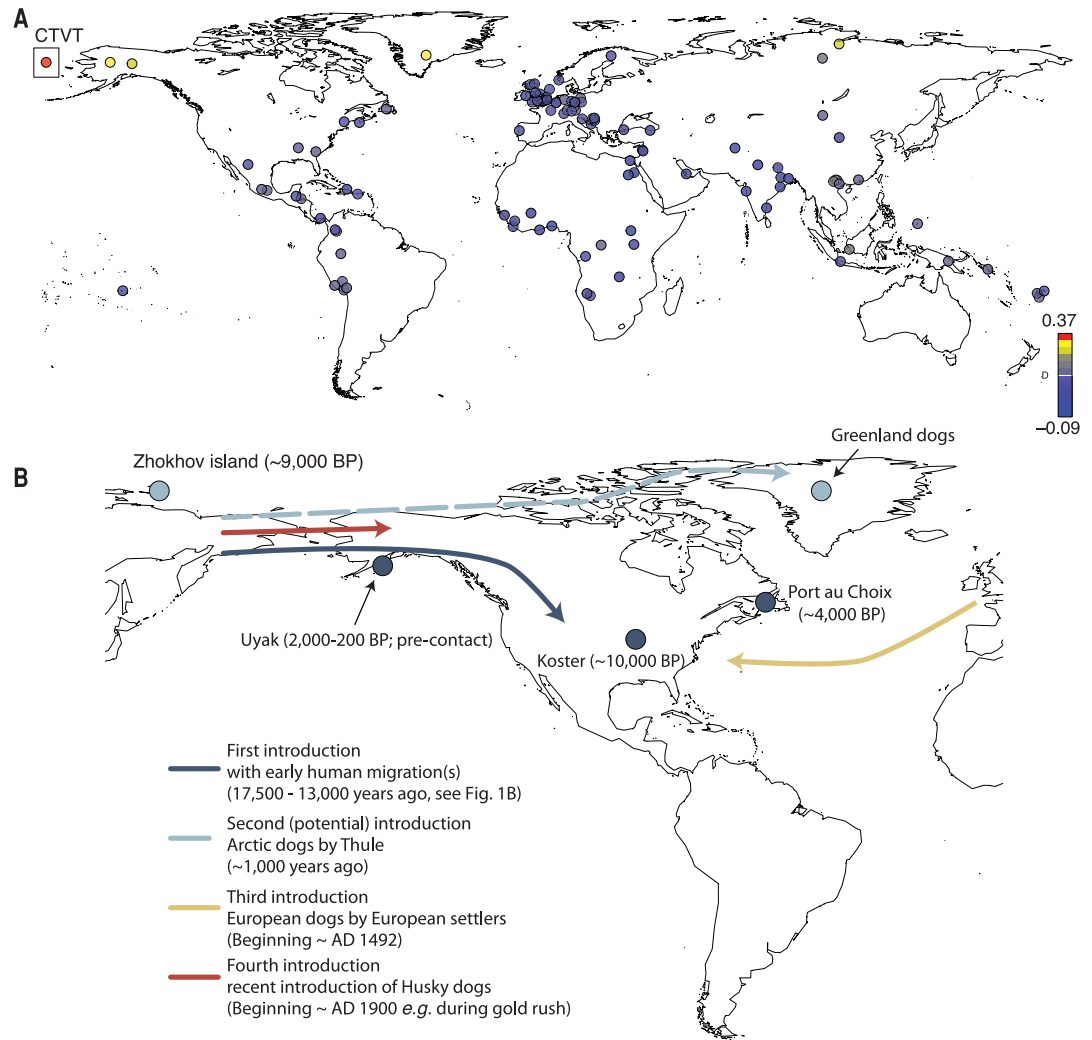


Fig. 1. Sample locations and ancestry of PCDs. (A) A map depicting the locations and ages of the archaeological remains analyzed in this study. Each dot represents a single sample, and multiple samples per archaeological site are grouped in boxes. Sites mentioned in the text are labeled. BP, before the present. **(B)** A tip-calibrated Bayesian mitochondrial phylogenetic tree of dogs within haplogroup A. This analysis was conducted with 66 novel ancient mitogenomes (all genomes with at least 10× coverage) together with 145 publicly available mitogenomes from both modern and ancient canids (3) (fig. S6). Red branches represent modern dogs, dark blue represents PCDs, and light blue denotes ancient DNA from Arctic dogs. Blue bars on nodes

represent 95% HPD ages. The gray shaded area represents the time frame during which people likely entered the Americas based on the age of divergence between Native Americans and ancient Beringians (~20,000 years ago) (12) and the flooding of the Bering land bridge (~11,000 years ago) (11). **(C)** A neighbor-joining tree built with whole genomes (3). **(D)** An admixture graph constructed with Treemix (on the basis of transversions) (3, 18) depicting the relationship between PCDs [including the Port au Choix (AL3194) and Weyanoke Old Town (AL3223) samples] and other dog, wolf, and CTVT populations. The scale bar shows 10 times the average standard error (s.e.) of the entries in the sample covariance matrix (18).

Fig. 2. Legacy of PCDs in modern American dogs.

(A) A map showing the locations of dog populations obtained from (9) and their degrees of relatedness (D statistics) to the ~4000-year-old Port au Choix dog (AL3194) [see (3) and fig. S14]. Higher values (in red) represent closer relatedness. The location of the founder CTVT individual, labeled in the plot, is unknown. (B) A map depicting the multiple introductions of dogs into the Americas.



and table S1), indicate that this dog was more closely related to PCDs than to modern American Arctic dogs (figs. S4 and S10). This finding suggests that modern American Arctic dogs are not the descendants of Paleo-Eskimo dogs and that Paleo-Eskimos likely acquired local dogs in North America or brought Siberian dogs that were genetically indistinguishable from PCDs. Our sampling did not include dogs from sites associated with the Thule culture, so it is plausible that the modern American Arctic dogs included in our analysis, such as Alaskan malamutes and Greenland dogs, are the descendants of dogs introduced by the Thule. Alternatively, the modern American Arctic dogs that we sampled may be the descendants of recently introduced Eurasian Arctic dogs, many of which were introduced during the 19th-century Alaskan gold rush and as sled dog racing stock (6).

Previous genomic analyses of the canine transmissible venereal tumor (CTVT) genome indicated a close affinity with modern Arctic dogs (20). CTVT is a contagious cancer clone that manifests as genital tumors and spreads between dogs by the transfer of living cancer cells during mating.

This clone first originated from the cells of an individual dog, the “CTVT founder dog,” which lived several thousand years ago, and the clone still carries the genome of this individual (20). To investigate the relationship between the CTVT founder dog and PCDs, we analyzed two CTVT genomes alongside a panel of modern and ancient canid genomes.

Because CTVT is a cancer, and to limit the impact of somatic mutations, we confined our genotyping analysis to SNPs mapping to genomic regions that have retained both parental chromosomal copies in CTVT (20) and excluded singleton SNPs called exclusively in CTVT genomes and not found in any other canid genome. CTVT clustered with PCDs on neighbor-joining trees (Fig. 1C and figs. S10 and S11), a Bayesian tree (fig. S12), Treemix (Fig. 1D), and admixture graphs (fig. S25). This result is further supported by both outgroup f_3 statistics (fig. S13) and D statistics (figs. S14 and S15). These findings indicate that the CTVT founder dog is more closely related to PCDs than to modern Arctic dogs. Multiple horizontal transfers of mitochondrial genomes from dog hosts to CTVT has led to the

replacement of the founder dog’s mitogenome (21, 22); thus, we could not determine the mitochondrial haplogroup of the CTVT founder dog, and we limited our analyses to the nuclear genome.

To assess whether the CTVT founder dog lived before or after dogs entered North America, we re-estimated its temporal origin by sequencing the nuclear genomes of two CTVTs, 608T and 609T. 608T is a CTVT from the skin of a 10-month-old puppy and was likely engrafted from the mother’s vaginal tumor (609T) during birth. We identified mutations generated by a clocklike mutational process that were present in 608T but not detectable in 609T and used these to derive a lower bound for a somatic mutation rate for CTVT (3). Applying this rate to the total burden of clocklike somatic mutations in the CTVT lineage (3), we estimated that the CTVT founder dog lived up to 8225 years ago (3). This time frame postdates the initial arrival of dogs into the Americas, raising the possibility that CTVT may have originated in a dog living in North America.

To further assess this scenario, we quantified the degree of introgression between canids endemic to North America (coyotes and North

American wolves), PCDs, modern Arctic dogs, and the CTVT founder dog. Our analyses indicated that, unlike Arctic dogs, PCDs share a number of derived alleles with coyotes and North American wolves, indicative of admixture (figs. S16 and S17). The CTVT founder dog also showed some weak evidence of coyote ancestry but did not appear to possess admixture with North American wolves (figs. S16 and S17). Because coyotes are restricted to North America, this finding suggests that CTVT may have originated there. As we did not ascertain the degree of coyote ancestry in ancient PCD-related dogs in Northern Siberia (such as the Zhokhov Island dogs) (Fig. 1), however, this analysis does not establish the location in which CTVT originated. Furthermore, studies that used somatic mutations to reconstruct the phylogeography of the CTVT clone indicated deep divergence in Asia and recent introduction to the Americas (21). Altogether, these results suggest a scenario in which CTVT originated in Asia from a dog that was closely related to PCDs, although we cannot exclude the possibility that the clone arose in America and then dispersed early into Asia before being reintroduced to America.

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

In addition, previous studies have argued that some modern American dog populations possess a genetic signature from indigenous American dogs (8, 9, 24). To test this hypothesis, we analyzed nuclear data obtained from more than 5000 modern dogs (including American village dogs) genotyped on a 180,000 SNP array (9). We found 7 to 20% PCD ancestry in modern American Arctic dogs (Alaskan huskies, Alaskan malamutes, and Greenland dogs) by using f_4 ratios (tables S10 and S11) (3). This result, however, may reflect ancient population substructure in Arctic dogs rather than genuine admixture (3). Our f_4 ratio analysis did not detect a significant admixture signal from PCDs in any modern American dogs of European ancestry (table S10).

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

To further assess the contribution of PCDs to modern American dog populations, we also

analyzed 590 additional modern dog mitogenomes, including those from 169 village and breed dogs that were sampled in North and South America (21). We identified two modern American dogs (a chihuahua and a mixed-breed dog from Nicaragua) that carried PCD mitochondrial haplotypes (fig. S5), consistent with a limited degree of PCD ancestry (<2%) in modern American dogs. We also identified three East Asian dogs that carried a PCD haplotype, possibly as a result of ancient population substructure or recent dog dispersal (fig. S5) (3). Although greater degrees of PCD ancestry may remain in American dogs that have not yet been sampled, our results suggest that European dogs almost completely replaced native American dog lineages. This near disappearance of PCDs likely resulted from the arrival of Europeans, which led to shifts in cultural preferences and the persecution of indigenous dogs (25). Introduced European dogs may also have brought infectious diseases to which PCDs were susceptible.

The first appearance of dogs in the North American archaeological record occurred ~4500 years after the earliest evidence of human activity on the continent (4, 11). In addition, our molecular clock analysis indicates that the PCD lineage appeared ~6500 years after North American human lineages (Fig. 1B) (10). These discrepancies suggest that dogs may not have arrived into the Americas alongside the very first human migration but were instead potentially part of a later arrival (12) before the flooding of the Bering land bridge ~11,000 years ago (11). This timing is compatible with both the archaeological record and our PCD divergence time estimate and suggests a scenario in which dogs were brought to the Americas several thousand years after the first people arrived there.

This initial dog population entered North America and then dispersed throughout the Americas, where it remained isolated for at least 9000 years. Within the past 1000 years, however, at least three independent reintroductions of dogs have occurred. The first may have consisted of Arctic dogs that arrived with the Thule culture ~1000 years ago (6). Then, beginning in the 15th century, Europeans brought a second wave of dogs that appear to have almost completely replaced native dogs. Lastly, Siberian huskies were introduced to the American Arctic during the Alaskan gold rush (25). As a result of these more recent introductions, the modern American dog population is largely derived from Eurasian breeds, and the closest known extant vestige of the first American dogs now exists as a worldwide transmissible cancer.

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officer of Embark Veterinary. K.M.D. currently holds honorary professor positions in the departments of archaeology at both the University of Aberdeen and Simon Fraser University. **Data and materials availability:** The reads for the ancient data have been deposited at the European Nucleotide Archive (ENA) with project number PRJEB22026. Reads for new CTVT genomes were deposited at the European Nucleotide Archive (ENA) with project

number PRJEB22148. Mitochondrial sequence alignments, genotype files (in plink format), and phylogenetic trees were deposited in Dryad (26).

SUPPLEMENTARY MATERIALS

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Materials and Methods

Figs. S1 to S27
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Lineage losses for man's best friend

Dogs have been present in North America for at least 9000 years. To better understand how present-day breeds and populations reflect their introduction to the New World, Ní Leathlobhair *et al.* sequenced the mitochondrial and nuclear genomes of ancient dogs (see the Perspective by Goodman and Karlsson). The earliest New World dogs were not domesticated from North American wolves but likely originated from a Siberian ancestor. Furthermore, these lineages date back to a common ancestor that coincides with the first human migrations across Beringia. This lineage appears to have been mostly replaced by dogs introduced by Europeans, with the primary extant lineage remaining as a canine transmissible venereal tumor.

Science, this issue p. 81; see also p. 27

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