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# The Evolutionary History of Dogs in the Americas*

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## Abstract

Dogs were present in the Americas prior to the arrival of European colonists, but the origin and fate of these pre-contact dogs are largely unknown. We sequenced 71 mitochondrial and seven nuclear genomes from ancient North American and Siberian dogs spanning ~9,000 years. Our analysis indicates that American dogs were not domesticated 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. Remarkably, the closest detectable extant lineage to pre-contact American dogs is the canine transmissible venereal tumor, a contagious cancer clone derived from an individual dog that lived up to 8,000 years ago.

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The history of the global dispersal of dogs remains contentious (1). In North America, the earliest confirmed dog remains have been radiocarbon dated to ~9,900 calibrated years before present (cal BP) (Koster, Illinois; (2, 3)), approximately 6,000 years after the earliest unambiguous evidence of humans arriving in North America (4). While 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 introduction of European dogs after the arrival of Europeans, and 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 pre-contact population (8, 9).

We sequenced complete mitochondrial genomes (mitogenomes) from 71 archaeological dog remains collected in North America and Siberia (Fig. 1a; 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 pre-contact dogs (spanning ~9,000 years) formed a monophyletic group within dog haplogroup A (Fig. 1b; Fig. S3; Fig. S6), which we refer to as pre-contact dogs (PCD). This analysis indicated that the most closely related mitochondrial lineage to the PCD clade are ~9,000 year-old dogs from Zhokhov Island in Eastern Siberia (3) (Fig. 1b; Fig. S3; Fig. S6). In addition, molecular clock analyses suggest that all PCD dogs shared a common ancestor ~14,600 years ago (95% high posterior density [HPD]: 16,484-12,965; Fig. 1b; Fig. S6), which diverged from a shared ancestor with the Zhokhov Island dogs ~1,000 years earlier (95% HPD:17,646-13,739; Fig. 1b; Fig. S6). Interestingly, these time frames are broadly coincident with early migrations into the Americas (10–12).

To further investigate the evolutionary history of PCD, we generated low coverage nuclear genome sequences (~0.005-2.0x) from seven pre-contact dogs sampled in six locations in North America spanning ~9,000 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 using single nucleotide polymorphism (SNP) revealed that, like the mitogenome phylogeny, PCD individuals 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 PCD 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 (Fig. S14; Fig. S15) also supported this phylogenetic structure. Combined, our mitochondrial and nuclear results indicate that PCD were not domesticated *in situ* from North American wolves, but were instead introduced by people into the Americas via Beringia from a population that was related to modern Arctic dogs.

Studies of nuclear 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 dogs (9, 14). Our analyses of nuclear data revealed a close relationship between Arctic dogs and PCD which together form 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). Though all three clades are well-supported, the relationships between them are ambiguous. For example, our outgroup f3-statistics analysis (Fig. S13) indicated that the PCD/Arctic clade is basal to the two other Eurasian dog clades. However, when excluding 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 West 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; Fig. S25; (3, 14)), or from a near simultaneous divergence of all three lineages.

Our nuclear data indicates that modern Arctic dogs sampled from both Siberia and North America cluster in a distinct phylogenetic group that forms a sister taxon to PCD (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; Fig. S11; Fig. S13) suggests that PCD are not the direct ancestor of modern American Arctic dogs. It is possible that modern American Arctic dogs are the descendants of dogs brought by the PaleoEskimo (~6,000 years ago) or by the Thule (~1,000 years ago)(19). However, both mitogenomic and low coverage nuclear data from a late Paleo-Eskimo dog from Kodiak Island, Alaska (Uyak: AL3198; Fig. 1a; Table S1) indicate that this dog is more closely related to PCD than to modern American Arctic dogs (Fig. S10; Fig. S4). This 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 PCD. 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).

Interestingly, genomic analyses of canine transmissible venereal tumor (CTVT) genomes 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 still carries the genome of this individual (20). To investigate the relationship between the CTVT founder dog and PCD, we analyzed two CTVT genomes alongside a panel of modern and ancient canid genomes.

In order to accomodate for the fact that CTVT is a cancer, and to limit the impact of somatic mutations, we confined our genotyping analysis to SNPs which mapped to genomic regions that have retained both parental chromosomal copies in CTVT (20), and excluded singleton SNPs exclusively called in CTVT genomes. Remarkably, CTVT clustered with PCD on neighbor-joining trees (Fig. 1c; Fig. S10; Fig. S11), a Bayesian tree (Fig. S12), Treemix (Fig. 1d) and admixture graphs (Fig. S25). This result is further supported by both outgroup f3 (Fig. S13) and D-statistics (Fig. S14; Fig. S15). These findings indicate that the CTVT founder dog is more closely related to PCD than to modern Arctic dogs. Multiple horizontal transfers of mitochondrial genomes from dog hosts to CTVT tumors 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 prior to, or after dogs entered North America, we re-estimated its temporal origin by sequencing the nuclear genomes of two CTVT tumors, 608T and 609T. 608T is a CTVT tumor from the skin of a ten-month-old puppy which was likely engrafted from its mother's vaginal tumor (609T) during birth. We identified mutations with a clock-like mutational process which 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 clock-like somatic mutation in the CTVT lineage (3), we estimated that the CTVT founder dog lived up to 8,225 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 North American endemic canids (coyotes and North American wolves), PCD dogs, modern Arctic dogs, and the CTVT founder dog. Our analyses indicated that, unlike Arctic dogs, PCD dogs share number of derived alleles with coyotes and North American wolves, indicative of admixture (Fig. S16; Fig. S17). The CTVT founder dog also showed some weak evidence of coyote ancestry, but did not appear to possess admixture with North American wolves (Fig. S16; Fig. S17). Because coyotes are restricted to North America, this suggests that CTVT may have originated there. Since we did not ascertain the degree of coyote ancestry in ancient PCD-related dogs in Northern Siberia (such as the Zhokov 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 a deep divergence in Asia and a 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 PCD, although we cannot exclude the possibility that the clone arose in America, then dispersed early into Asia before being reintroduced to America.

The legacy of PCD in modern American dog 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 PCD dogs 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 5,000 modern dogs (including American village dogs) genotyped on a 180K SNP array (9). We found 7-20% PCD ancestry in modern American Arctic dogs using f4 ratios (Alaskan husky, Alaskan malamute and Greenland dogs; Table S10&S11; (3)). This result, however, could reflect ancient population substructure in Arctic dogs rather than genuine admixture (3). Our *f4* ratio analysis did not detect a significant admixture signal from PCD into any modern American dogs of European ancestry (Table S10).

Our ADMIXTURE analysis detected varying degrees of PCD/Arctic ancestry in three individual Carolina dogs (0-33%; Fig. S20). This analysis, however, could not distinguish between PCD and Arctic ancestry, and we cannot rule out that this was result of admixture from modern Arctic dogs and not from PCD (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. S20; Table S10; Fig. 2a), though this analysis may suffer from ascertainment bias.

To further assess the contribution of PCD to modern American dog populations, we also analyzed 590 additional modern dog mitogenomes, including 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 which have not yet been sampled, our results suggest that European dogs almost completely replaced native American dog lineages. This near disappearance of PCD 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 PCD were susceptible.

The first appearance of dogs in the North American archaeological record occurs ~6,000 years after the earliest evidence of human activity (4, 11). In addition, our molecular clock analysis indicates that the PCD lineage appeared ~6,500 years after North American human lineages (Fig. 1b)(10). These discrepancies suggest that dogs may not have arrived into the Americas alongside the first human migration. A recent human genetic study suggests that Northern Native American populations admixed with an East Siberian population ~11,500 years ago(12). 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.

This initial dog population entered North America then dispersed throughout the Americas where it remained isolated for at least 9,000 years. Within the past 1,000 years, however, there have been at least three independent re-introductions of dogs. The first may have consisted of Arctic dogs that arrived with the Thule culture ~1,000 years ago (6). Then, beginning in the 15th century, Europeans brought a second wave of dogs that appear to have almost completely replaced indigenous 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.

## Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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## 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 sequences alignments, genotype files (in plink format), and phylogenetic trees were deposited on Dryad (doi:10.5061/dryad.s1k47j4).

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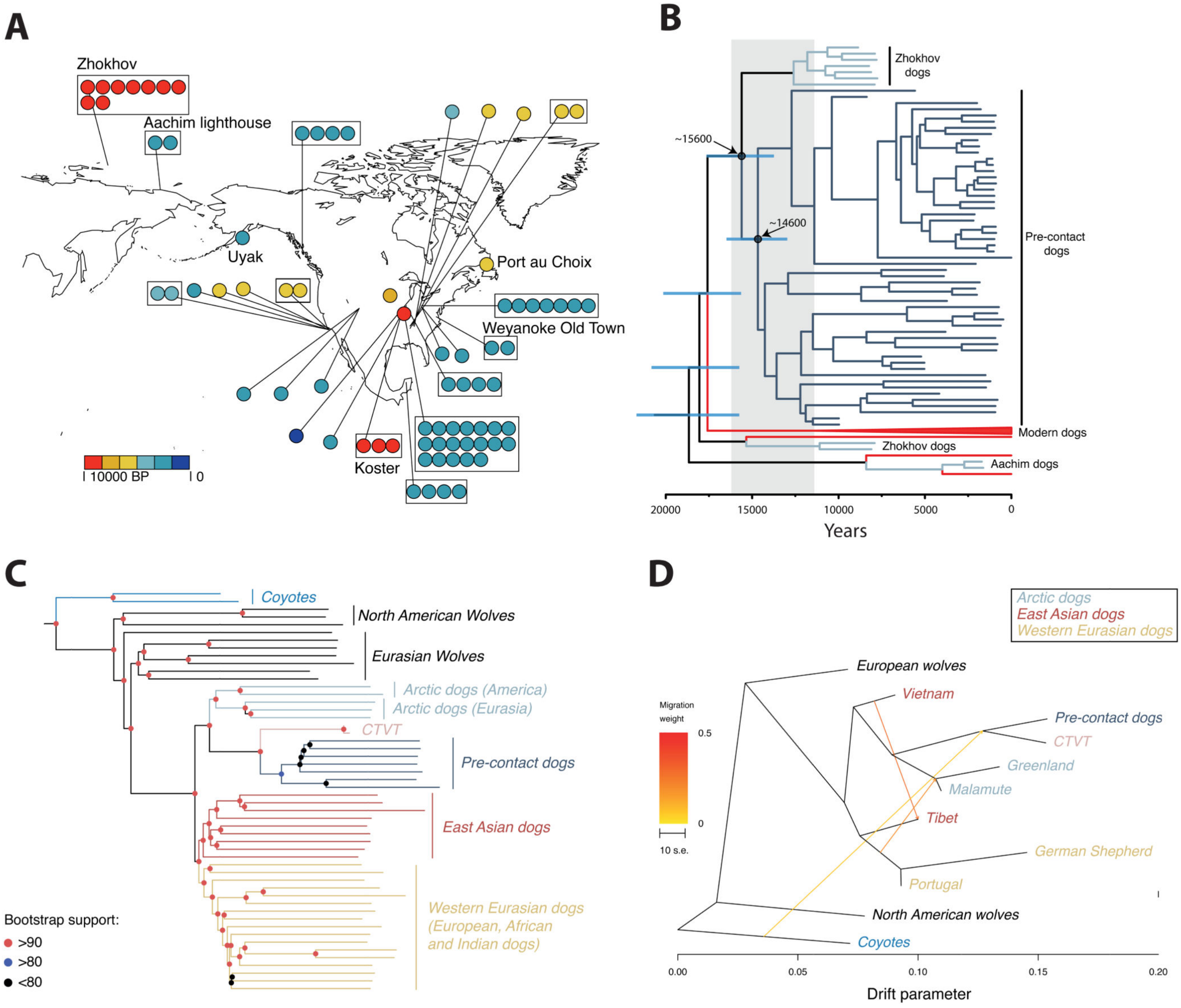

**Figure 1. Sample location and ancestry of pre-contact dogs**

**a**.A map depicting the location and age of the archeological remains analyzed in this study. Each dot represents a single sample, and multiple samples per archeological site are grouped in boxes. Sites mentioned in the text are labelled. **b.** A tip calibrated Bayesian mitochondrial phylogenetic tree of dogs, within haplogroup A. This analysis was conducted with 71 novel ancient mitogenomes together with 145 publicly available mitogenomes from both modern and ancient canids (3) (Fig. S6). Red branches represent modern dogs. Blue horizontal bars on nodes represent 95% High Density Posterior age. The grey shaded area represents the time frame during which people entered the Americas (10–12) **c.** A neighbor-joining tree built with whole genomes (3). **d** An admixture graph constructed with *TreeMix* (based on transversions; (3)) depicting the relationship between PCD (including the Port Du Choix [AL3194] and Weyanoke Old Town [AL3223] samples) and other dog and wolf populations.

We only used Greenland dogs and Malamute (American Arctic dogs) for this analysis as these are the least admixed with Western Eurasian dogs (3).

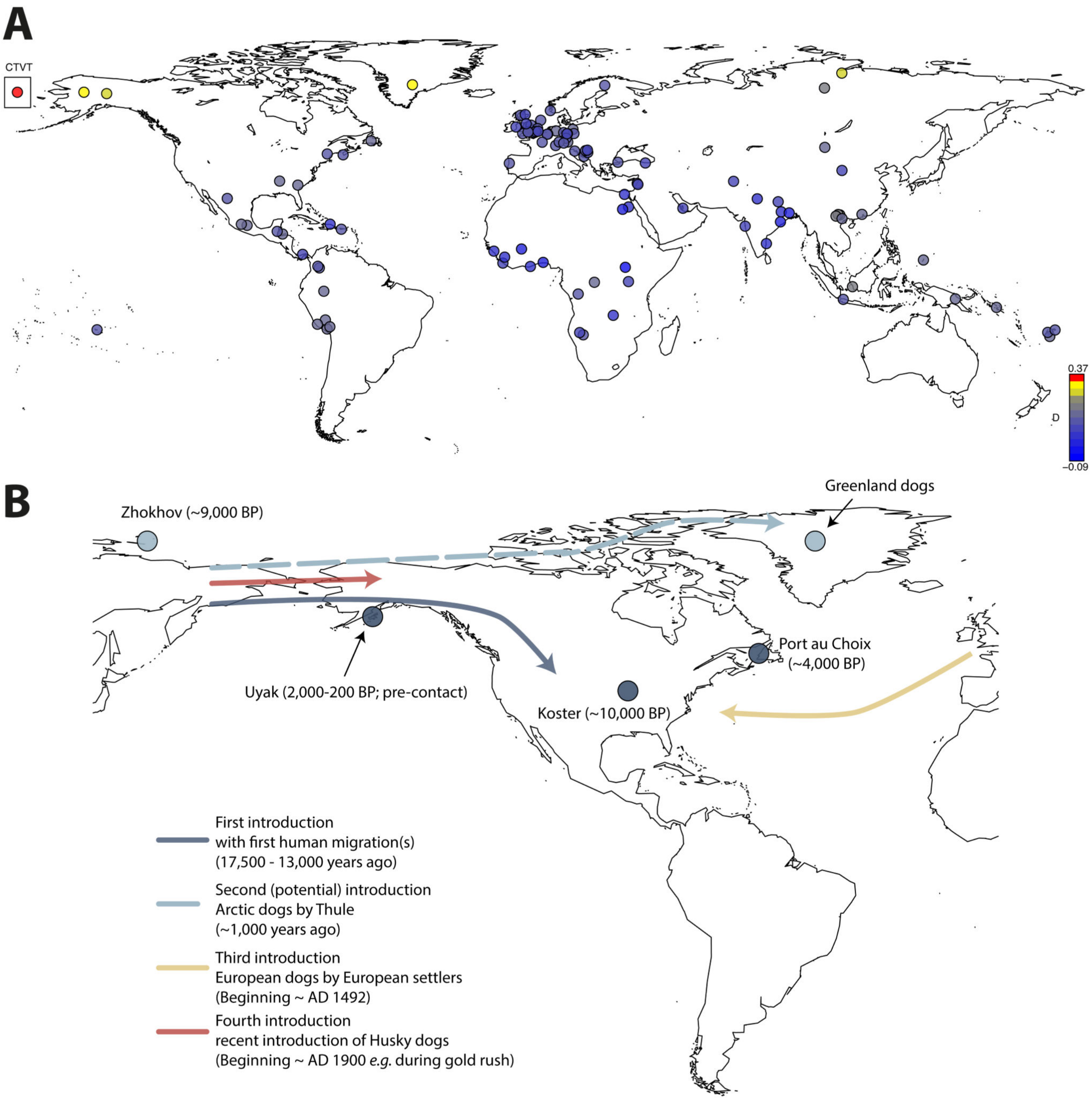

**Figure 2. Legacy of pre-contact dogs in modern american dogs**

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